Finding pathways to human–elephant coexistence: a risky business

Anna Songhurst, Graham McCulloch and Tim Coulson

Abstract Finding ways for people and wildlife to coexist requires affording both parties access to critical resources and space, but also a behavioural change by both to avoid conflict. We investigated pathway use in a population of free-ranging African elephants *Loxodonta africana* in the Okavango Panhandle, Botswana that share their range with humans in a multi-use, heterogeneous landscape. We used detailed ground surveys to identify and map elephant movement pathways, and mixed-effect models to explore factors influencing elephant numbers and movement behaviour on and around these pathways. We found deviation in pathway use among the elephant population, suggesting behavioural adaptations to avoid human-associated risk: avoiding pathways near settlements, particularly near larger settlements; avoiding pathways close to cultivated land; and adopting a safety-in-numbers strategy when moving through areas of human use. Our findings suggest there is opportunity to capitalize on risk avoidance by elephant populations, to minimize resource-use overlap and reduce conflict between humans and elephants. We discuss a strategy that involves ensuring appropriate protection of elephant pathways in land-use planning, using development-free buffer zones, combined with mitigation techniques along the interface with agricultural lands to increase risk levels and reinforce human–elephant interface boundaries. We recommend further examination of the use of landscape-level mitigation techniques that encourage elephants to use pathways away from human activity and help define spatial boundaries for management of human–elephant conflict in multi-use landscapes.

Keywords Botswana, elephant, human–elephant conflict, land use zones, *Loxodonta africana*, migration corridors, risk avoidance

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Introduction

In many places outside protected areas ecosystem/habitat connectivity across the landscape is characterized by distinct pathways connecting important resources (Blake & Inkamba-Nkulu, 2004; Von Gerhardt et al., 2014). Studies have shown that encroachment of development onto wildlife paths is an important driver of human–wildlife conflict (Guerbois et al., 2012; Songhurst & Coulson, 2014). Although temporal and spatial patterns of crop raiding by wildlife appear to be influenced by a variety of other factors associated with the location of fields in relation to landscape features such as water availability, protected areas and daytime refuges for wildlife (Naughton-Treves, 1998; Linkie et al., 2007; Graham et al., 2010; Guerbois et al., 2012), appropriate land-use planning is advocated as a requirement to protect wildlife pathways and alleviate human–wildlife conflict (Weaver et al., 1996; Osborn & Parker, 2003; Douglas-Hamilton et al., 2005; Fernando et al., 2005; Linnell et al., 2005; Von Gerhardt et al., 2014). Few studies, however, have examined elephant *Loxodonta africana* behaviour at a population level to help justify pathway protection as an important strategy in conflict intervention. If protecting pathways is to be effective in reducing human–wildlife conflict we need a greater understanding of how a population at large is using these critical movement pathways, and the extent to which the movement of wildlife along the pathways is influenced by the presence and activity of people.

How elephants utilize various landscapes is determined by a combination of environmental (e.g. Hanks, 1979; Viljoen & Bothma, 1990; Redfern et al., 2003; Murwira & Skidmore, 2005; Chamaillé-Jammes et al., 2007; Loarie et al., 2009; Young et al., 2009) and social factors (e.g. Moss & Poole, 1983; Stokke, 1999; Wittemyer et al., 2007). Movements also vary temporally according to seasons (Douglas-Hamilton et al., 2005; Young et al., 2009), time of day, the speed of movement and the length of time spent in any one location (Graham et al., 2009). In areas where home ranges overlap with human habitation and infrastructure, animals also have to adapt their behaviour to avoid disturbance by people (Martin et al., 2010). Disturbances to animals may arise as a result of physical impediments to movement (i.e. fences, roads, cultivated land), or human behaviour such as hunting, farming and wildlife conflict mitigation activities. Animals have been found to adapt to risks associated with humans; for example, elephants tend to move under cover of darkness and travel

more quickly in areas close to human habitation (Douglas-Hamilton et al., 2005; Galanti et al., 2006; Graham et al., 2009). Studies have also reported elephants avoiding unprotected areas with high human population density and activity (Parker & Graham, 1989; Happold, 1995; Hoare, 1999; Graham et al., 2009), and moving in high-risk areas such as cultivated fields predominantly at night (Osborn, 1998; Sitati et al., 2003). Carnivores appear to respond in a similar way to the presence of humans (Martin et al., 2010). Guerbois et al. (2012) argued that for improved management of human–elephant conflict, elephants need to associate human landscapes with perceived risk. Risk avoidance is fundamental to the design of various mitigation techniques to alter movement behaviour and deter elephants from individual fields and settlements (Conover, 2002), but it is not clear how such behavioural adaptations can be incorporated into the design of practical conservation management strategies at a landscape level.

Here we examine the fine-scale movement behaviour of a population of free-ranging elephants that share their range with humans in a multi-use heterogeneous landscape, and the extent to which adaptations in the elephants' movement that define risk avoidance behaviour contribute to spatial separation in land use.

Study area

The study was conducted during January 2008–July 2010 on the eastern side of the Okavango Panhandle, where the Okavango River reaches the Okavango Delta in Botswana (Fig. 1). The eastern Panhandle covers 8,732 km² and its northern and southern boundaries are delineated by the Namibian border and the northern buffalo fence, respectively. There are protected areas to the north, south and east of the area, which are utilized by tourism operations.

Mean annual rainfall is 360–500 mm, and the rainy season is generally mid October–March. The mean monthly maximum temperature is 26.1–35.1°C, with July being the coldest month and October the hottest. Deep Kalahari sands are predominant throughout the study area but the area can be divided broadly into dry woodland savanna in the wildlife management areas NG11 & 13 and the Okavango wetland in NG12 (Fig. 1). Elevation is 880–1,110 m (Songhurst, 2012).

The 2011 census recorded 16,306 people living in the eastern Panhandle (CSO, 2011), with 12 villages (population > 500), and additional settlements occurring between villages. Subsistence agriculture is an important livelihood strategy and, depending on rainfall, the planting of crops occurs during November–January and harvesting occurs during April–June. During the crop season many people move to their agricultural lands to guard their fields. The elephant population in the eastern Panhandle is estimated to be

c. 15,000 and is considered trapped by the fences to the north, east and south, and the Okavango River to the west (Songhurst, 2012). It has been observed that elephants use distinctive pathways to move between the Okavango Delta and foraging areas in dry woodland habitat in the study area (Jackson et al., 2008). These pathways are bisected by the main road that services all villages in the eastern Panhandle, which are distributed in a ribbon type development pattern along the edge of the wetland. Elephants damage crops, break fences, damage property and chase, injure and sometimes kill livestock and people. Meanwhile, people are modifying the elephants' habitat through cultivating land and developing new settlements, and they also chase, injure and occasionally kill elephants. Crop damage is the most prevalent cause of human–elephant conflict in the area, but the number of crop raiding incidents (frequency) per month and the amount of damage incurred (intensity) per month vary annually (Songhurst, 2012). During 2008–2010 788 fields were raided and a total of 162 ha of crops, predominantly millet, were damaged by elephants in the eastern Panhandle (Songhurst & Coulson, 2014).

Methods

It is difficult to observe elephants directly in the Panhandle, and therefore we used an indirect method based on examining footprints (Western et al., 1983; Lee & Moss, 1995) to estimate group size and composition, similar to the studies of Chiyo & Cochrane (2005) and Von Gerhardt et al. (2014). Male and female elephant groups were distinguished by the presence or absence of footprints of elephants < 8 years old (footprint length ≤ 30 cm), which has been used successfully by Balasubramanian et al. (1995), Chiyo & Cochrane (2005) and Von Gerhardt et al. (2014). Groups whose footprints were all > 30 cm were categorized as male-only groups (Lee & Moss, 1995; Whitehouse & Hall-Martin, 2000; Moss, 2001).

Ground surveys of the main road (180 km) were conducted on dry mornings (06.00–09.00), bi-monthly over 3 years (2008–2010) to assess recent elephant activity. Transects were driven in different directions each time to avoid bias. We recorded all elephant footprints crossing the transect, counted the number of elephant groups at each intersection between a pathway and the main road, and estimated the number of individuals per group, and their direction of travel. Group size was estimated by counting the number of different footprints present. This was achieved, in a similar way to Chiyo & Cochrane (2005), by following elephant tracks at crossings back along pathways to see how many elephants utilized those paths. Data were collected with the assistance of an experienced local tracker, who identified only fresh footprints and separated groups of elephants per observation. Stander et al. (1997) showed that
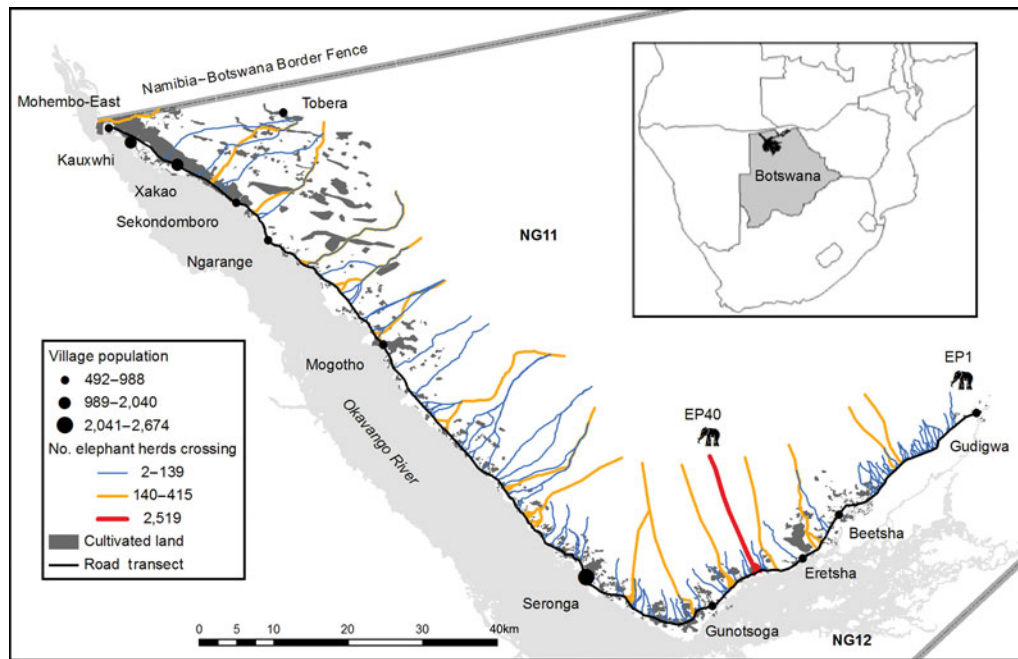
FIG. 1 Location of 12 villages in the study area in the Okavango Panhandle, with the main elephant *Loxodonta africana* pathways shown. Paths are colour coded to show low (blue), medium (orange), and high (red) utilization gradients, based on the number of herds crossing the road over 3 years. Pathways were numbered from east to west (i.e. the path furthest to the east is EP1). The area shaded in black on the inset indicates the location of the Okavango Delta in Botswana.

local trackers, with their indigenous knowledge, were able to identify individuals by spoor with 94% accuracy. All footprints were cleared after counting to avoid double counting in subsequent assessments. Locations of the start and end of footprints on each intersection were recorded using a global positioning system, and elevation and vegetation type were recorded at the location of each footprint.

Although the substrata in the area comprise mostly fine Kalahari sands and alluvial clays, which show clear footprints, the identification of individual elephant tracks is difficult and therefore calculations of numbers of elephants per group are considered to be estimates. Subsequent analyses therefore used two response variables in generalized linear mixed-effect models: the number of herds using pathways, and the number of individuals using pathways.

Aerial orthophotographs (1 : 50,000) and *Google Earth* (Google Inc., Mountain View, USA) were used to digitize well-worn elephant paths between the dry mixed woodland habitat and the Okavango River and Delta, as well as human settlements, fences and cultivated land, using *ArcMap v. 9.3* (ESRI, Redlands, USA). These maps were verified using a combination of methods: ground surveys; comparisons with existing maps based on data from collared elephants (Jackson et al., 2008), management plans (ODMP, 2002), and reports (Albertson, 1998); and consultations with local community members. Only permanent pathways, with floors devoid of vegetation and used regularly by elephants, were selected (Blake & Inkamba-Nkulu, 2004). Regular use

of pathways by elephants was confirmed through visual observation of dung, feeding damage and footprints (Von Gerhardt et al., 2014).

Data on human population numbers in the study area were collated from the Botswana Central Statistics Office (CSO, 2011). Songhurst (2012) showed that fields < 1 km from an elephant pathway are 50% more likely to be raided. A 1 km buffer was therefore calculated and drawn around each pathway, and the area of cultivated land within the buffer was calculated. The minimum distance between each pathway and a settlement or village was measured using the proximity buffer tool in *ArcMap*.

Statistical analysis

All analysis was carried out using *R v. 2.11.1* (R Development Core Team, 2010). The characteristics of path use by herds of elephant (i.e. herd composition, direction of movement, favoured paths) were explored using χ^2 tests, with significance determined at $P < 0.05$. Bi-monthly surveys of elephant pathway road crossings may have resulted in temporal pseudoreplication in the data, causing non-independence in errors and a higher risk of spuriously significant results (Hurlbert, 1990; Crawley, 2007). Generalized linear mixed-effect models are a useful tool for the analysis of such data (Pinheiro & Bates, 2000; Crawley, 2007). Models were fitted to the response variables 'elephants

present on pathway or not' (coded 1 or 0) with binomial errors, 'if elephants present, estimated number of herds per crossing', and 'if elephants present, estimated number of elephants per crossing' with Poisson errors. The models were fitted with two crossed random effects: elephant pathway and month. Continuous explanatory variables included the area of cultivated land within a 1 km buffer of an elephant path, the distance from a path edge to the nearest settlement, and the elevation at the intersection between an elephant path and the main road. Continuous response and explanatory variables were square root transformed to conform better to a normal distribution where appropriate. Significance tests of the fixed effects were limited to two-way interactions, to avoid overfitted models, and model selection was based on the Akaike information criterion (AIC), as suggested by Whittingham et al. (2006). All possible combinations of fixed effects and two-way interactions were explored, and models were compared using Akaike weights. The model with the highest Akaike weight (i.e. the weight of evidence in its favour) was considered to be the best model within the set (Burnham & Anderson, 2002). Interactions were plotted to aid interpreting model predictions. A variance components analysis of the final mixed-effects models was carried out (Pinheiro & Bates, 2000; Crawley, 2007) to estimate the variation explained by the crossed random effects: elephant pathway and month.

Results

During 3 years we identified 106 elephant pathways crossing the main road transect (Fig. 1). A total of 12,836 elephant herd crossings were recorded during March 2008–June 2010, with a mean of $119 \pm SD$ 255 herds crossing per pathway. We recorded significantly more family groups than male-only herds ($\chi^2 = 171.7$, df = 1, $P < 0.001$).

Both male herds and female-led family groups used certain pathways more frequently than others. One pathway (EP40) was utilized significantly more frequently throughout the year than all other pathways combined ($\chi^2 = 8.8$, df = 1, $P < 0.001$; Figs 1 & 2). Analysis was conducted with and without this pathway to assess its effect on results.

More crossings where elephants were travelling away from the river were recorded ($\chi^2 = 84.7$, df = 1, $P < 0.001$). To avoid double counting crossings by the same herd (i.e. counting their going to and coming from the river as two separate groups) only data from groups travelling away from the river (n = 6,757) were used in subsequent analyses.

The generalized linear mixed-effect model of whether elephants used a pathway or not, with the smallest AIC value (AIC = 3,010) and highest model weight ($w_i = 0.34$) retained the main fixed effects elevation (maximum likelihood estimate = $-5.8 \pm SE$ 2.1) and human population (maximum likelihood estimate = $-4.7 \pm SE$ 1.2), and the two-way

interaction between these two effects (maximum likelihood estimate = $0.18 \pm SE$ 0.07; Tables 1 & 2). This model shows there are likely to be elephants present when the human population in the nearest settlement is small, but the probability of elephants occurring when human populations are larger increases at higher elevation. The variance components of the random effects show that 38.8% of explained variation is between elephant paths and 61.2% is between months at each pathway.

The model of the square root of the number of elephant herds (if present) using a pathway, with the smallest AIC value (AIC = 631.1) and highest model weight ($w_i = 0.21$) retained the main fixed effects human population in the nearest settlement (maximum likelihood estimate = $-0.01 \pm SE$ 0.005), area of agriculture within a 1 km buffer of the path (maximum likelihood estimate = $-0.03 \pm SE$ 0.01), and distance to nearest human settlement (maximum likelihood estimate = $-0.003 \pm SE$ 0.003), and the two-way interaction between the latter two effects (maximum likelihood estimate = $0.0008 \pm SE$ 0.0003; Tables 1 & 2). This model shows more herds are likely to cross on pathways near less populated settlements. There are also likely to be fewer herds crossing where there is a larger area of agriculture near a pathway and where pathways are close to human settlements, but the likelihood of more herds crossing when there are larger areas of agriculture increases with increasing distance to human settlements. Variance components show that 67.8% of variation is between pathways and 32.2% is between months at each pathway.

The model of the estimated number of elephants (if present) using a pathway, with the smallest AIC value (AIC = 1662.3) and highest model weight ($w_i = 0.33$) retained the main fixed effects human population in nearest settlement (maximum likelihood estimate = $-0.02 \pm SE$ 0.006), elevation (maximum likelihood estimate = $1.33 \pm SE$ 0.48), area of agriculture within a 1 km buffer of the path (maximum likelihood estimate = $3.49 \pm SE$ 0.99), and distance to nearest human settlement (maximum likelihood estimate = $-0.007 \pm SE$ 0.003), and the two-way interaction between elevation and area of agriculture (maximum likelihood estimate = $-0.11 \pm SE$ 0.03) and distance to nearest settlement and area of agriculture (maximum likelihood estimate = $0.001 \pm SE$ 0.0004; Tables 1 & 2). This model shows that, similar to number of herds, more elephants are more likely to cross on pathways near less populated settlements. There are also likely to be more elephants using a path if it is near larger areas of agriculture and further from settlements. Although it is likely that more elephants will use a path if it is near large areas of agriculture, this likelihood decreases with increasing elevation. Graphs of these interactions show a small amount of curvature, however, indicating that such relationships are unlikely to be biologically important. Variance components show that 53% of variation is between elephant pathways and 47% is between months at each pathway.
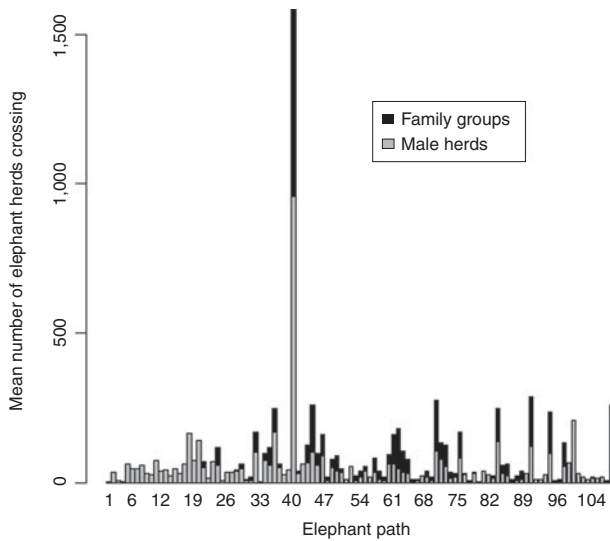
FIG. 2 Number of herds of family groups and male elephants that utilized each elephant pathway in the Okavango Panhandle (Fig. 1) during 2008–2010.

When all the models were fitted to a subset of data where crossings on pathway EP40 were removed, the model estimates for the fixed effects were not significantly affected.

Discussion

By mapping localized elephant pathways and monitoring fine-scale movement behaviour of an elephant population, rather than individual elephants, by means of detailed ground surveys we were able to record varying behavioural strategies adopted by the elephant population that contributed to risk avoidance, including avoiding pathways near human settlements, particularly those close to larger settlements, avoiding pathways close to large cultivated areas of land, and adopting a safety-in-numbers strategy when moving through large areas of cultivated land close to human settlements. Elephants in the eastern Panhandle of the Okavango Delta appear, therefore, to adapt their behaviour in response to associated levels of risk connected with humans, which influences their preferred choice of movement pathways.

Elephants generally avoided highly populated settlements and large areas of cultivated land, indicating a certain amount of risk associated with these areas of high human activity, which is consistent with the findings of other similar studies (Hoare & du Toit, 1999; Douglas-Hamilton et al., 2005; Graham et al., 2009). The number of herds crossing in highly cultivated areas increased with distance from settlements, indicating elephants may be avoiding people. Areas of agricultural land appear to present a lower risk of disturbance than areas near settlements, thereby providing a safer route of passage and hence attracting larger numbers of elephant herds. The variance components analysis showed that

TABLE 1 Fixed effects of the mixed effects model of whether elephants *Loxodonta africana* used a pathway or not, the number of elephant herds (if present) using a pathway, and the number of elephants (if present) using a pathway, with mean estimate ± SE, Z and P.

Fixed effects	Estimate ± SE	Z	P
Elephants used pathway?			
Intercept	147.58 ± 37.73	3.91	$9.16e^{-05}$
Sqrt(Hpopset)	5.78 ± 2.10	−2.75	0.006
Sqrt(Elevation)	4.70 ± 1.20	−3.91	$9.07e^{-5}$
Sqrt(Hpopset):sqrt (Elevation)	0.18 ± 0.07	2.73	0.006
Number of elephant herds			
Intercept	1.57 ± 0.19	8.33	$< 2e^{-16}$
sqrt(Human population in nearest settlement)	−0.02 ± 0.01	−2.57	0.01
Number of elephants			
Intercept	−3.96 ± 1.51	−2.62	0.008
Sqrt(Agric)	3.49 ± 9.89	3.54	0.0004
Sqrt(DSett)	$-6.69e^{-3} ± 3.41e^{-3}$	−1.96	0.05
Sqrt(Hpopset)	$-1.64e^{-2} ± 5.58e^{-3}$	−2.95	0.003
sqrt(Elevation)	$1.33 ± 4.81e^{-1}$	2.76	0.006
Sqrt(Agric) : sqrt(DSett)	$1.23e^{-3} ± 3.25e^{-4}$	3.78	0.0002
Sqrt(Agric) : sqrt (Elevation)	$-1.13e^{-1} ± 3.15e^{-2}$	−3.59	0.0003

the variation between the numbers of herds using various paths was affected more by the path itself (67.8%) than by the month (32.2%), indicating that the location of the path had a larger influence than seasonal variation on the number of herds utilizing a pathway. There were also differences in path use between female and male elephants, with some paths closer to areas of high human activity used only by groups of male elephants, indicating a higher level of risk taking by male-only groups (Sukumar, 1991). We investigated a limited number of possible drivers of elephant movement, and differences in observed path use between the sexes warrant further investigation to determine the impact of other social and environmental factors. We found that path use by elephants was influenced by elevation, but a greater understanding of how resource availability affects the movement of elephants in the Panhandle is also needed.

We found a clear example of elephants aggregating in larger numbers near human activity, which could be a strategy to minimize risk (safety in numbers; Hamilton, 1971). Pathways near cultivated land attracted fewer groups but larger numbers of elephants per group. This could be a result of group size being fluid, with families (or males) gathering into larger groups when entering high-risk areas, or perhaps only larger groups enter high-risk areas. Further investigation is needed to account for such differences but both scenarios suggest a behavioural adaptation to avoid risk.

Larger numbers of elephants per group using paths near cultivated land could also be a result of elephants being attracted to the high nutritional content in crops compared with natural

TABLE 2 Akaike information criteria (AIC) and Akaike model weights (w_i, estimated probabilities of model truth) relating the probability of elephants using a path or not (coded 1 or 0), the likelihood of a larger number of herds ($>$ 0) present at a pathway crossing, and the likelihood of a larger number of elephants ($>$ 0) present at a pathway crossing to combinations of environmental and human habitat modification variables, for the top five models ranked according to AIC model weights.

	Model*	AIC	w_i
Elephants used pathway?			
Main effects	H + E	3014.9	0.04
	A + H + E	3016.5	0.02
	D + H + E	3016.8	0.01
	A + D + H + E	3018.5	0.01
	A + H	3019.7	0.00
2-way interactions	H : E	3010.4	0.34
	H : E + A : E	3012.3	0.14
	H : E + A : H	3012.4	0.13
	H : E + A : D	3012.4	0.13
	H : E + A : E + A : D	3014.2	0.05
Number of elephant herds			
Main effects	H	633.8	0.05
	A + H	635.3	0.03
	D + H	635.6	0.02
	A + D + H	636.5	0.01
	A + H + E	637	0.01
2-way interactions	A : D	631.1	0.21
	A : D + A : E	632.1	0.13
	A : D + A : H	632.1	0.13
	A : D + H : E	632.4	0.11
	A : D + A : E + H : E	633.3	0.07
Number of elephants			
Main effects	A + H	1688.1	$8.6e^{-07}$
	H + D	1688.4	$7.3e^{-07}$
	H	1688.9	$5.6e^{-07}$
	A + H + D	1689.1	$5.1e^{-07}$
	H + D + E	1689.9	$3.5e^{-07}$
2-way interactions	A : D + A : E	1662.3	0.33
	A : D + A : E + H : E	1662.9	0.25
	A : D + A : E + A : H	1664.1	0.14
	A : D + A : E + D : E	1664.3	0.12
	A : D + A : E + D : E + H : E	1664.6	0.12

*A, sqrt(Area of agriculture within 1 km of path); E, sqrt(Elevation); D, sqrt(Distance to nearest settlement); H, sqrt(Human population in nearest settlement)
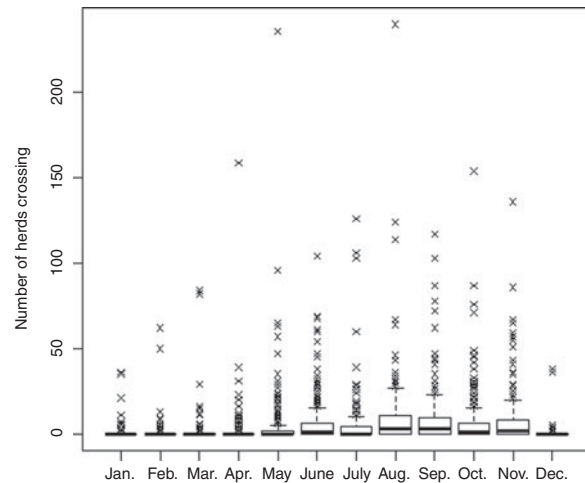

FIG. 3 Total number of elephant herds that crossed the main road in the Okavango Panhandle each month during 2008–2010. The horizontal lines show the median number of elephant herds crossing per month, the whiskers show 1.5 times the interquartile range, and the crosses are outliers.

forage, as surmised in previous studies (Sukumar, 1989; Osborn, 1998; Chiyo et al., 2005). If this were the case, however, we would have expected more elephant groups to have crossed in these areas, not necessarily more elephants per group. The temporal patterns of path use by elephants indicate that significantly more herds used paths closer to cropland after the crop season during May–November (Fig. 3), which indicates that many elephants may be avoiding cultivated areas during the ploughing season, thus adapting their temporal movement

behaviour to avoid increased disturbance from human activity. Apparent seasonal variation in pathway use close to cultivated lands was consistent with our variance components analysis, which showed a higher percentage of variation between whether elephants used a path or not explained by month (61.2%) rather than pathway (38.8%). Not all elephants will be deterred from human disturbance, but there is no clear evidence to suggest that the elephant population is generally attracted to cultivated land in the eastern Panhandle. The likelihood of a field being raided by an elephant increases significantly when the field is within 1 km of a main pathway, suggesting that crop raiding incidents are predominantly opportunistic (Songhurst & Coulson, 2014). Affording elephant pathways protection with a 1 km development-free buffer zone could, therefore, play an important role in reducing crop raiding by elephants.

Our results suggest that elephants have the ability to learn and adapt to varying levels of disturbance from humans, as other animals do in response to varying levels of predation risk (Laundré et al., 2010). Our findings support the suggestion by Guerbois et al. (2012) to incorporate the so-called ecology of fear in the design of mitigation strategies for human–elephant conflict. According to Schoenfeld (1969) any avoidance response may be conditioned or controlled by an appropriate selection of values of three parameters, among others: operant level of the response, stimulus frequency, and stimulus intensity in both positive and negative reinforcement schedules. The various types of avoidance behaviour we observed suggest a response to negative stimulus from human encounters, and therefore risk avoidance by elephants could be conditioned or controlled by increasing or intensifying a negative stimulus

associated with human inhabitation or development zones. Appropriate deterrent techniques, such as the use of capsicum oleoresin (Osborn, 2002; Sitati & Walpole, 2006; Hedges & Gunaryadi, 2010) or bees (King et al., 2011), could intensify the negative stimulus to deter elephants at interfaces between pathways and arable fields. We argue that in combination with appropriate land use zones, such negative stimuli could be effective in alleviating spatial and resource use overlap at a landscape level, reinforcing boundaries around human-inhabited areas and ensuring safe passage for elephants.

Correctly managed buffers or adaptive management zones outside protected areas may be as important as wildlife reserves for the long-term viability of wide-ranging species (Noss et al., 1996). Such strategies require creating zones within a multi-use landscape to minimize negative interactions between people and wildlife (Fernando et al., 2005; Linnell et al., 2005). Knowledge of their risk avoidance behaviour may be used to encourage elephants to use certain pathways when moving through human inhabited areas, and deter them from fields and settlements. Landscape-level management interventions could help define boundaries at the human–wildlife interface, minimizing opportunistic crop raiding by elephants, while protecting critical movement paths and habitat connectivity. We recommend monitoring elephant movements at a population level, as we have done, in further studies of the effectiveness of protecting elephant pathways in reducing human–elephant conflict. Long-term monitoring of path use with and without negative stimuli at the interface between development-free buffer zones and agricultural or settlement zones is necessary to reveal the potential of combining pathway buffers and mitigation techniques as a strategy to avoid human–elephant conflict. Such investigations could inform and motivate appropriate land use planning initiatives, but it will be essential to galvanize the political will among local and national land authorities to implement such measures.

Acknowledgements

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