Linking crop availability, forest elephant visitation and perceptions of human–elephant interactions in villages bordering lvindo National Park, Gabon

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Abstract Feeding by Critically Endangered forest elephants Loxodonta cyclotis in rural plantations is a conservation issue in Gabon, but studies characterizing drivers of spatiotemporal patterns of human-elephant interactions remain sparse, hindering mitigation. In this study, we use GPS tracking data from two elephants to characterize temporal patterns of village visitation, and surveys of 101 local farmers across seven villages to determine local patterns of crop planting and harvesting and of human-elephant interactions. Local farmers' perceptions of elephant visitations and empirical data on such visits were positively correlated with local crop availability. However, considering the two elephants separately revealed that the correlations were driven by just one individual, with the second elephant showing weak links between crop availability and visitation, highlighting the challenges in reliably predicting humanwildlife interactions. The most popular local perceptions of the drivers of elephant visitation were the presence of crops (53% of responses) and logging (39%). The most popular proposed interventions were letting the government find a solution (32%), killing problem elephants (30%) and providing compensation for lost crops (22%). We discuss the potential feasibility and efficacy of the proposed solutions in the context of human-elephant interactions. Future research efforts should focus on collaring elephants in zones with high potential for negative human-elephant interaction and expanding perception surveys to villages with contrasting ecological contexts (e.g. with and without logging in their surrounding forests), as these could influence local perceptions of conflicts and conservation initiatives.

Keywords Crop raiding, forest elephant, Gabon, GPS tracking, human–wildlife conflict, *Loxodonta cyclotis*, perceptions

The supplementary material for this article is available at doi.org/10.1017/S0030605323000704

Received 5 October 2022. Revision requested 14 December 2022. Accepted 19 May 2023. First published online 7 December 2023.

Introduction

uman land-use practices and encroachment into nat-🔲 ural habitat can have harmful effects on wildlife, often forcing animals to modify their travelling routes and foraging behaviour, potentially resulting in negative interactions between people and wildlife. This is particularly true for forest elephants Loxodonta cyclotis, a species categorized as Critically Endangered on the IUCN Red List because of poaching for ivory, habitat degradation and human-elephant conflicts (Gobush et al., 2021). Land-use change appears to be increasing contact events between people and elephants, and negative interactions occur when people and elephants compete over shared resources (e.g. water, trees, fruits and leaves; Kharel, 1997; Buchholtz et al., 2019). Human-elephant interactions are common around villages in Gabon, whose estimated c. 95,000 forest elephants represent over half of the remaining global population (Maisels et al., 2013; Laguardia et al., 2021). Pervasive foraging by forest elephants in crops (often referred to as crop raiding) threatens the food security of local people and increases their antipathy towards conservation efforts (Walker, 2010; Ngama et al., 2016; Terada et al., 2021). Consequently, it is important to characterize the spatial and temporal patterns of elephant activities around villages to design effective management interventions for minimizing negative human-elephant interactions. To do this, we need to understand how factors such as the timing of crop planting influence elephant movement (Nsonsi et al., 2018).

Research suggests that forest elephant movements are strongly predicted by the presence of human settlements and associated activities (Blake et al., 2008; Molina-Vacas et al., 2020), and it is only within such human-disturbed habitat that other environmental conditions start to influence elephant spatial patterns (Wall et al., 2021). However, in Gabon, human pressure and protected areas are not the strongest factors predicting forest elephant abundance, as elephant population densities are high throughout the country (Laguardia et al., 2021). Furthermore, GPS collaring of 96 elephants across Gabon showed that individuals show movement behaviours that cannot be explained by environmental factors alone, and analysing trends in the movements of specific individuals could help identify so-called problem elephants that feed on crops (Beirne et al., 2021).

Oryx, 2024, 58(2), 261–268 © The Author(s), 2023. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605323000704 https://doi.org/10.1017/S0030605323000704 Published online by Cambridge University Press

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Where people and elephants coexist, human activity can influence elephant behaviour in several ways. For example, elephants in locations with high human disturbance levels move in larger groups, move faster, show increased nocturnal activity (Graham et al., 2009; Songhurst et al., 2016) and approach villages for forage (Cook et al., 2015). Damage caused by elephants is of particular conservation interest because where it occurs it is often both frequent and severe (Osborn & Parker, 2003; Prins et al., 2022). In the villages of south-west Gabon, for example, encroachment into villages and crop damage by elephants have remained the major drivers of negative human-wildlife interactions over the last decade and are amongst the main causes of the impoverishment of local people (Fairet, 2012; Hill, 2017; Terada et al., 2021). This situation is reported in public dialogue across rural Gabon, although studies on the exact extent of the damage from crop-foraging elephants and how to identify the individual elephants that engage in it are rare.

An important factor to consider when studying humanelephant interactions is how local people perceive forest elephants and the issues related to them (Tutin et al., 1997; Walker, 2010, 2012; Ngama et al., 2016; Prins et al., 2022). Perceptions represent a form of evidence that deserves a central place in monitoring, evaluating and adapting conservation programmes and policies (Bennett, 2016). Qualitative and quantitative studies based on perceptions are effective, holistic and better suited to certain questions; in particular, knowledge of the perceptions of people regarding human-elephant conflict through local assessments can facilitate understanding of the social impacts of conservation (Bennett, 2016).

Here we use GPS tracking data to characterize spatiotemporal patterns in elephant village visitations, and we use surveys to determine local perceptions of crop seasonality and human-elephant interactions. We integrate data on elephant movements and perception of local farmers to explore the potential drivers of negative human-elephant interactions around villages. We hypothesize that elephants

approach villages more closely and frequently when crop availability is high and that peaks in elephant visitation should coincide with local perceptions of when negative interactions occur. We further hypothesize that local farmers would perceive that food availability in plantations, logging and conservation policies are the key drivers of negative human-elephant interactions.

Study area

We conducted this study in the area bordering the north of Ivindo National Park near the town of Makokou in the Ogooué-Ivindo Province of north-eastern Gabon (Fig. 1). The area exhibits bimodal seasonality, with two dry seasons (December-February and June-August) and two wet seasons (September-November and March-May). Mean annual precipitation is c. 1,700 mm and mean annual temperature is 23.9 °C (Beirne et al., 2019). Ivindo National Park is one of 13 national parks established in Gabon in 2002, and in 2021 it became the second park in Gabon to be recognized as a UNESCO World Heritage Site. The villages in the region are known to experience strong humanelephant conflict, and this figures prominently in rural and urban conversations broadcast in the national media.

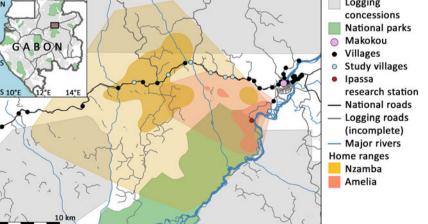
Methods

Satellite collar data

In October 2015, the National Park Authority of Gabon initiated a forest elephant collaring programme across Gabon (Mills et al., 2018; Beirne et al., 2020). Two of the 98 elephants collared thus far have approached village plantations north of Ivindo National Park: Amelia, a female with two juveniles during the time of study, and a male named Nzamba (Fig. 1). We processed the GPS collar data of these two elephants, which recorded their location once

Logging concessions National parks Makokou 0 ABOA Villages . Study villages 0 Ipassa research station National roads Logging roads (incomplete) Major rivers Home ranges Nzamba Amelia

FIG. 1 Home ranges of the two collared study elephants Loxodonta cyclotis, Amelia (female) and Nzamba (male), near the town of Makokou and the locations of the seven study villages north of Ivindo National Park, Gabon. The larger polygons with light shading represent 100% minimum convex polygons and the smaller polygons with dark shading represent 50% kernel density estimates of all geographical locations recorded by the collars. Neither elephant appeared to venture south of the Ivindo river. (Readers of the printed journal are referred to the online article for a colour version of this figure.)



every hour, using the following steps: (1) imported the geographical locations of the two elephants during April 2017-April 2019 (representing 27,228 recorded locations) to ArcMap 10.3 (Esri, Redlands, USA); (2) computed the home ranges of the two elephants, and used the villages within these ranges as focal villages; (3) drew a 500-m buffer around each of the focal villages (the distance within which almost all plantations occurred), using the houses visible from satellite imagery to define the village extent; and (4) intersected the geographical locations with the village polygons (including the 500-m buffer), providing a filtered data set of elephant presence, a hybrid metric representing a combination of the frequency and duration of elephant approaches to villages (e.g. three locations could represent either three separate approaches or one approach lasting 3 h). We also extracted the time of day and month and identified the nearest village to each presence location.

To estimate the home ranges of both elephants, we created a 100% minimum convex polygon of all of their location points. To identify the area where they spent 50% of their time, we created a 50% kernel density estimate (Seaman & Powell, 1996; Mohaymany et al., 2013; Bonnier et al., 2019) using the *adehabitat* package (Calenge, 2006) in *R* 4.2.1 (R Core Team, 2022).

Perceptions surveys

We identified seven villages that were visited by one or both of the elephants during the study period and were accessible by the survey team. In July 2019, we administered a semistructured standardized survey (Hill et al., 2002; Treves et al., 2006; Fairet, 2012) to 101 households (one adult from each) across each of the seven villages to determine: (1) what crops each farmer grows and when; (2) when farmers perceive crop use by elephants to be high; (3) which crops farmers perceive elephants to prefer; (4) what farmers currently do to reduce crop damage; and (5) what farmers perceive as being principal drivers of human-elephant conflict. Our survey contained 53 questions collecting both qualitative and quantitative data of respondent perceptions (Supplementary Material 1). We first conducted a pilot study in the village of Mbes (18 respondents), and subsequently adjusted the survey as necessary by editing questions to ensure clarity. We included the pilot data in the data analysis.

We administered the surveys using a random procedure in all study villages. We first divided the village into two parts separated by the national road (north and south) and flipped a coin to determine where to begin the survey. We then flipped a coin again to determine whether to begin the survey at the eastern or western end of the village. After surveying 25% of households in each of the four sections (e.g. north-west), we moved to the opposite section, and we repeated this process for the remaining two sections. The data from this survey include information on the plantations, their distance from the village, the type of crop, the period of planting, the time of harvest and the crops preferred by elephants (in order of preference). Other questions included whether the presence of elephants was a problem, the level of impact of the problem, the causes of the problem, the financial valuation of losses, the distance from the village to the crops where elephants foraged and any mitigation strategies used.

We categorized and codified the survey transcripts, collapsing similar response categories into broader ones. For example, 'loggers', 'deforestation because of all the noise [from machinery] in the forest' and 'they follow the food because loggers have cut everything [fruit-bearing trees]' were all grouped under the category 'logging'.

Data analysis

To characterize the daily and monthly trends in elephant visitation events, we used the *activity* package (Rowcliffe et al., 2014) in *R*. In both instances we used the number of elephant visitation events as the response variable and month of the year or time of day as explanatory variables. We also characterized temporal patterns in crop availability and perceived patterns in elephant visitation from the survey data using the same technique as described above. For this, we used the number of respondents reporting elephant visitation, crop planting and crop harvest as the response variables and month of the year as the explanatory variable. In all instances we converted time of day or month of the year into radians and then used the default settings of the *fitact()* function to estimate a kernel density distribution for each response term.

We used correlation coefficients to explore how the empirical elephant visitation data and perceptions surveys were linked. In each instance we used monthly elephant visitation data or the perceptions of survey respondents reporting elephant visits each month as the response variable. The significance of the correlation coefficient was determined using the *F*-statistic from linear models in *R*, for which we deemed P < 0.05 as strong evidence of a link between actual/perceived visits and crop availability.

Results

Elephant movements and patterns of village visitation

There was considerable difference between the ranging behaviours of the two focal elephants: Amelia had a 100% minimum convex polygon of 148 km² and a 50% kernel density estimate of 25 km², whereas Nzamba had a 100% minimum convex polygon of 742 km² and a 50% kernel density estimate of 113 km² (Fig. 1). Amelia approached within 500 m

of four study villages, although just one of these (Loaloa) comprised 92% of her village presence. She also spent a lot of time near the Ipassa Research Station within Ivindo National Park. Nzamba also approached within 500 m of four study villages: Loaloa rarely (6% of his presence) and three villages (which were not visited by Amelia) to a relatively similar degree (22, 36 and 36% of his village presence).

Both elephants had bimodal patterns of visitation, with peaks in April and September for Amelia (Fig. 2) and in July and December/January for Nzamba (Fig. 2b). Collared elephants were typically present near villages from dusk to dawn (67% of visitations were during 18.00–06.00), with Amelia being slightly less nocturnal in her time near villages than Nzamba (62% from dusk to dawn vs 72%; Fig. 2).

Perceptions

The survey responses suggested that local farmers perceived a bimodal peak in elephant visitations, with peaks during March-April and September-October (Fig. 3). The most frequent perceptions of farmers regarding the factors driving elephant visits (Fig. 3) were proximity of fields to villages ('crops'; n = 47, 53%), followed by logging activities, primarily the felling of fruiting trees (a primary food source for forest elephants) and increased elephant access to villages via logging roads ('logging'; n = 34, 39%) and local conservation policy as the source of elephant encounters around houses ('policy'; n = 7, 8%). Self-reported crop planting and harvest were also markedly seasonal (Fig. 3). The most widely cultivated crops were manioc (cassava), banana (plantain), peanuts and maize, which were typically planted during August-September (rainy season; Fig. 3). All of these crops were widely perceived as being affected by elephants. Also cultivated in smaller quantities were sugarcane, yams, African pistachios (commonly called cucumbers), pineapples and a variety of vegetables (amaranth, sorrel, aubergine, okra). Of these, sugarcane and yams were widely perceived as being affected by elephants.

Correlations between perceptions and elephant visits

Taking the data from both elephants together suggests that elephant presence near villages (location points and perceived) was generally positively correlated with crop availability (Table 1). There was strong support for corn harvest timing and weak support for peanut harvest timing being correlated with perceived elephant activity, and both of these correlations were negative (peanut and corn harvests generally occur when perceptions of conflict are low). The empirical visitation data showed different patterns: there was strong support for a positive correlation between sugarcane planting and weaker support for a positive correlation between manioc planting and elephant visitation. However, analysis of the two individuals separately reveals a more complex pattern of behaviour: Amelia's visits generally correlate positively with crop availability (with strong support for a positive correlation with banana planting and harvest and manioc corn and yam planting), whereas Nzamba's visits generally, although weakly, correlated negatively with crop availability. The correlation between the timing of the different crop planting and harvest times makes it difficult to determine which crops might be the most important in driving elephant visits; for example, sugarcane planting occurs during banana harvest (Fig. 3).

Solutions

Participants in the survey proposed six distinct solutions to human–elephant conflict in the area (Fig. 4). Over 20 respondents proposed government authorities must find a solution (32%), killing elephants that approach villages (30%) and compensation for their lost crops (22%). Ten respondents proposed building electric fences (10%; this has been implemented as a mitigation strategy since August 2018 in one of the study villages, Simintang), and five respondents proposed a halt to logging (4%). A single person proposed development of animal husbandry initiatives to replace the food and income lost as a result of elephant crop use (1%).

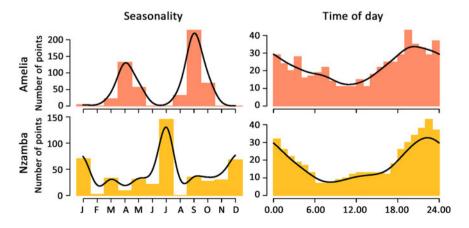


FIG. 2 Overview of location points of the two elephants (Amelia, female; Nzamba, male) within 500 m of study villages in Gabon (Fig. 1) by month and time of day. Lines represent the fitted model of seasonality and time of day from the *activity* package in *R*. Note that for seasonality the scale of the y-axes differs between graphs.

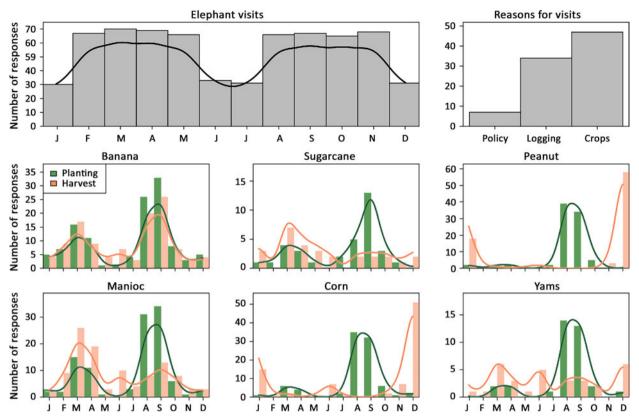


FIG. 3 Perceptions of respondents regarding the monthly elephant visitation patterns and the reasons for their visits (for the latter, see text for details) and of the monthly availability of six crops, by planting and harvest. Note that the scale of the y-axes differ across graphs.

Discussion

This is one of the first studies to empirically link the perceptions of communities experiencing interactions with forest elephants with elephant presence near villages as

TABLE 1 Correlation coefficients between monthly indices of forest elephant *Loxodonta cyclotis* presence around villages in Gabon determined from both local perceptions and from geographical locations \leq 500 m from villages of two collared elephants (Amelia, female; Nzamba, male) and timing of planting and harvest of six crops, as determined from the surveys.

	Perceived	Amelia	Nzamba
Banana planting	0.45	0.68*	-0.29
Banana harvest	0.49	0.64*	-0.40
Sugarcane planting	0.43	0.85*	-0.14
Sugarcane harvest	0.27	0.17	-0.24
Peanut planting	0.31	0.54†	-0.25
Peanut harvest	-0.56^{+}	-0.28	0.29
Manioc planting	0.43	0.66*	-0.28
Manioc harvest	0.49	0.38	-0.37
Corn planting	0.35	0.57*	-0.27
Corn harvest	-0.58*	-0.32	0.28
Yams planting	0.34	0.59*	-0.26
Yams harvest	-0.10	0.06	-0.23

*, strong evidence of relationship (P < 0.05); †, weak evidence of a relationship (0.05 > P < 0.1).

derived from GPS collar data (but see Ngene et al., 2009, and Buchholtz et al., 2020, for savannah elephant examples). We discuss the perceived patterns and drivers of humanelephant interactions from the social surveys, how they link to both the elephant movement data and the proposed solutions put forward by farmers, and implications for conservation in Gabon.

We found that the majority of survey participants perceived that crop availability around villages was the most important factor driving elephant visitations to villages in

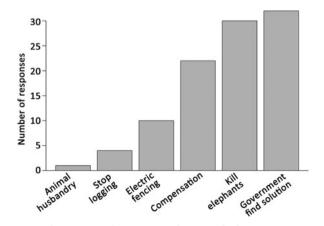


FIG. 4 Solutions to reduce negative human-elephant interactions, as proposed by survey respondents in Gabon.

this study area, and we identified manioc and banana as the most widely planted crops and those in which elephants most commonly foraged, as also reported in other studies (Fairet, 2012; Nse Nkoghe, 2019). However, elephants were also perceived to forage in other crops such as yams and sugar cane. There was a general consensus that elephants fed on crops at specific times of the year (February–May and August–November), although this was also reported at other times (albeit it at a c. 50% lower rate).

The two elephants had markedly different patterns in their interactions with people. The visits of Amelia were positively related to the planting and harvesting of most crops (10 of 12 crops assessed, significant for six of the 12) defined as attractive to elephants by survey participants. The significant connection with banana harvesting and planting and the cultivation of all other crops in August and September implies a compelling attraction to villages during these periods. However, Nzamba's visits were consistently negatively correlated with the planting and harvesting of most crops (10 of 12), and most strongly so for the banana (R = -0.40) and manioc harvest (R = -0.37).

Although there was a general agreement between the empirical elephant visitation data and participant perceptions, the two elephants did not respond to crop availability in the same way: one elephant appeared drawn to periods of high human activity and high resource abundance (the planting and harvesting periods), whereas the other appeared to avoid these periods. Previous research has highlighted that elephants show consistent differences in their movement responses to anthropocentric disturbance and seasonality (Blake et al., 2008; Bastille-Rousseau & Wittemyer, 2019; Beirne et al., 2020; Wall et al., 2021), which is in part because of sex differences in movement behaviour. The same could be true here: the elephant drawn towards the availability of crops is female (Amelia), whereas the male (Nzamba) showed a lower affinity for crops, perhaps because male elephants are more likely to have larger tusks and are targeted more by ivory poachers. Nzamba's village visits were slightly more nocturnal than Amelia's, perhaps indicating greater caution (Gaynor et al., 2018); when following elephants for another project, we have also found him to be fearful of human scent and presence. These differences could also represent different foraging tactics, with Nzamba visiting many villages frequently, less predictably and for shorter durations, whereas Amelia is more predictable in her movements and stays longer in each location because of the lower threat of poaching that she faces and the need to provide for her offspring. The differences observed could also be because of reproductive tactics, with the larger home range of Nzamba reflecting a search for potential mates (Vidya & Sukumar, 2005). Additionally, the use of a 1-h resolution of location fixes, as common in other studies, could mask crop visitation by Nzamba between fixes.

Even at this local scale it is clear that caution must be exercised in generalizing results from individual elephants to broader mechanisms of human-elephant interactions without collaring larger numbers of both sexes. The majority of forest elephant collaring initiatives to date have focused on protected areas, often far from human settlements (Beirne et al., 2020), but forest elephants occur across almost all of Gabon (Laguardia et al., 2021), and 85% of potential forest and savannah elephant habitat across Africa lies outside current protected areas (Wall et al., 2021). Consequently, we recommend that future collaring targets elephants that might specialize in foraging in and around villages outside protected areas. Only then will we be able to determine whether the tactics adopted by the male and female in this study are consistent with other individuals in other locations and what proportion of elephants regularly use crops. During the course of our surveys some participants indicated they could recognize the individual elephants who foraged in their crops. Such local knowledge should be combined with GPS collar data in future initiatives to identify elephants that consistently visit crops.

Understanding how many elephants visit crops and how often they do so is potentially important for assessing the effectiveness of conservation interventions designed to reduce such visitation. This is relevant to the second most frequent proposal by survey participants for reducing elephant visitation (after the proposal that the government finds a solution), to kill elephants that approach villages. Knowledge of numbers visiting and frequency of visitation would allow us to determine whether this proposed solution would be appropriate. If a low number of elephants consistently forage in crops, culling these specific individuals might be a solution to protect local livelihoods without adversely affecting elephant conservation. However, if a high number of elephants visit crops, even infrequently, sustainable culling might be both impossible and ineffective.

The third most frequent proposal was compensation for lost crops. Gabon, like many other countries, lacks standardized assessment guidelines for compensation (Shaffer et al., 2019). If Gabon were to scale up compensation, care would be needed to avoid related problems faced elsewhere (Shaffer et al., 2019). Electric fencing was the next most frequently proposed solution. One of our study villages had a large-scale electric fence, built by the national park agency shortly before our fieldwork. In the years following installation the fence suffered from low maintenance and ultimately stopped working. This resulted in elephants finding ways to circumvent the fence and enter the plantation (Graham et al., 2009; Mutinda et al., 2014; Shaffer et al., 2019), eventually resulting in the death of one person. There have been recent efforts to implement smaller-scale fencing, including in some of our study villages, but their efficacy over time remains unknown.

Only five interviewees proposed a halt to logging as a resolution to human-elephant conflict, despite 34 interviewees stating that logging is a driver of the conflict. Perhaps people perceive the economic benefits of logging to outweigh the costs of human-elephant conflict, perceive stopping logging as politically impossible or perceive it to be too late to mitigate the damage done by logging. For example, large moabi Baillonella toxisperma trees, a species categorized as Vulnerable on the IUCN Red List (White, 1998) because of overexploitation, the fruits of which are eaten by elephants, have disappeared from logged forests near villages. Changes in forest ecology beyond logging were not mentioned by survey respondents but are also occurring: in nearby Lopé National Park there was an 81% decline in tree fruiting during 1986-2018, associated with an 11% decline in forest elephant body condition during 2008-2018 (Bush et al., 2020). The spatial and temporal dynamics of ivory poaching and how elephants respond to this have also undergone change. Studies comparing levels of human-elephant interaction in villages with logged and unlogged surrounding forests need to be conducted to examine the relationship between logging and humanelephant conflict.

Of the seven survey respondents who perceived conservation policy as a driver of human-elephant conflict, four came from a village on the banks of the Ivindo river, close to the town of Makokou. This village is the closest of our study villages to Ivindo National Park headquarters and, of the villages in our study, has the most frequent interaction with park personnel. The section of the National Park close to this village is also contiguous with the forest around other villages along the national highway. It is thus possible that the National Park may not have differing effects on conflict across these villages but rather that local perceptions of the park-human-elephant interaction vary. This would contradict findings from a study in northern Congo that showed perceptions of elephants to be most positive in the village with the strongest conservation presence (Nsonsi et al., 2018). Both human-elephant interactions and solutions to any conflict can have effects on how conservation efforts in general are perceived and thus responded to, and effectively reducing negative human-wildlife interactions remains a key challenge for the conservation not only of forest elephants but of the wider biodiversity of the Congo Basin rainforest.

The purpose of our study was to determine when and where perceptions of negative wildlife interactions correspond with actual visitation events and which factors (e.g. crop availability) might drive these perceptions. We identified that the degree of agreement between perceptions and actual human-wildlife interactions depended on the identity of the elephant and its movement patterns. This could help future studies to determine the behavioural profiles of the elephants responsible for crop damage and to make more effective decisions about crop protection and elephant conservation in Gabon.

Acknowledgements We thank Nicholas School of the Environment of Duke University for financial and logistical support in preparing the study and in administering field surveys in the villages around Makokou; the village chiefs and rural people who encouraged the publication of this study; the Institut de Recherche en Ecologie Tropicale within the Centre National de la Recherche Scientifique et Technologique for permission to conduct research in Gabon; the Agence National des Parcs Nationaux and Duke University for permission to use the elephant collar data; Carole Mbamy for her help with fieldwork; and the Navjot Sodhi Conservation Research Award for their recognition of this work.

Author contributions Study design: all authors; fieldwork: WM; data analysis: WM, CB, GZLF; writing: WM, CB, GZLF, JRP.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards. We obtained authorization to conduct research in Gabon through the Institut de Recherche en Ecologie Tropicale within the Centre National de la Recherche Scientifique et Technologique (N\degree AR0057/18/MESRS/CENAREST/CG/CST/CSAR and N\degree AR004/20/MESRTT/CENAREST/CG/CST/CSAR). We followed the principle of free, prior and informed consent at both the community and individual levels. Communities gave oral prior and informed consent during meetings before we conducted any research; individual respondents gave oral consent in response to a written prior and informed consent statement that we read to them. Respondents understood that we would publish anonymized data and explicitly asked us to name their communities in all research publications.

References

- BASTILLE-ROUSSEAU, G. & WITTEMYER, G. (2019) Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals. *Ecology Letters*, 22, 1417–1427.
- BEIRNE, C., HOUSLAY, T.M., MORKEL, P., CLARK, C.J., FAY, M., OKOUYI, J. et al. (2021) African forest elephant movements depend on time scale and individual behavior. *Scientific Reports*, 11, 12634.
- BEIRNE, C., MEIER, A.C., BRUMAGIN, G., JASPERSE-SJOLANDER, L., LEWIS, M., MASSELOUX, J. et al. (2020) Climatic and resource determinants of forest elephant movements. *Frontiers in Ecology and Evolution*, 8, 96.
- BEIRNE, C., MEIER, A.C., MBELE, A.E., MENIE MENIE, G., FROESE, G., OKOUYI, J. & POULSEN, J.R. (2019) Participatory monitoring reveals village-centered gradients of mammalian defaunation in Central Africa. *Biological Conservation*, 233, 228–238.
- BENNETT, N.J. (2016) Using perceptions as evidence to improve conservation and environmental management: perceptions and conservation. *Conservation Biology*, 30, 582–592.
- BLAKE, S., DEEM, S.L., STRINDBERG, S., MAISELS, F., MOMONT, L., ISIA, I.-B. et al. (2008) Roadless wilderness area determines forest elephant movements in the Congo Basin. *PLOS One*, 3, e3546.
- BONNIER, A., FINNÉ, M. & WEIBERG, E. (2019) Examining land-use through GIS-based kernel density estimation: a re-evaluation of legacy data from the Berbati-Limnes survey. *Journal of Field Archaeology*, 44, 70–83.
- BUCHHOLTZ, E.K., FITZGERALD, L.A., SONGHURST, A., MCCULLOCH, G.P. & STRONZA, A.L. (2020) Experts and elephants: local ecological knowledge predicts landscape use for a species involved in humanwildlife conflict. *Ecology and Society*, 25, 26.

BUCHHOLTZ, E.K., REDMORE, L., FITZGERALD, L.A., STRONZA, A., SONGHURST, A. & MCCULLOCH, G. (2019) Temporal partitioning and overlapping use of a shared natural resource by people and elephants. *Frontiers in Ecology and Evolution*, 7, 117.

BUSH, E.R., WHYTOCK, R.C., BAHAA-EL-DIN, L., BOURGEOIS, S., BUNNEFELD, N., CARDOSO, A.W. et al. (2020) Long-term collapse in fruit availability threatens Central African forest megafauna. *Science*, 370, 1219–1222.

CALENGE, C. (2006) The package '*adehabitat*' for the *R* software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519.

COOK, R.M., HENLEY, M.D. & PARRINI, F. (2015) Elephant movement patterns in relation to human inhabitants in and around the Great Limpopo Transfrontier Park. *Koedoe*, 57, 1–7.

FAIRET, E. M. (2012) Vulnerability to crop-raiding: an interdisciplinary investigation in Loango National Park, Gabon. PhD thesis. Durham University, Durham, UK.

GAYNOR, K.M., HOJNOWSKI, C.E., CARTER, N.H. & BRASHARES, J.S. (2018) The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.

GOBUSH, K.S., EDWARDS, C.T.T., MAISELS, F., WITTEMYER, G., BALFOUR, D. & TAYLOR, R.D. (2021) Loxodonta cyclotis (errata version published in 2021). In *The IUCN Red List of Threatened Species* 2021. dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS. T181007989A204404464.en.

GRAHAM, M.D., DOUGLAS-HAMILTON, I., ADAMS, W.M. & LEE, P.C. (2009) The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12, 445–455.

H1LL, C.M. (2017) Crop raiding. In *The International Encyclopedia of Primatology* (eds M. Bezanson, K.C. MacKinnon, E. Riley,
C.J. Campbell, K.A.I.A. Nekaris, A. Estrada et al.), pp. 1–5. John
Wiley & Sons, Hoboken, USA.

HILL, C.M., OSBORN, F.V. & PLUMPTRE, A.J. (2002) *Human–Wildlife Conflict: Identifying the Problem and Possible Solutions.* Albertine Rift Technical Report Series, Volume 1. Wildlife Conservation Society, New York, USA.

KHAREL, F.R. (1997) Agricultural crop and livestock depredation by wildlife in Langtang National Park, Nepal. *Mountain Research and Development*, 17, 127.

LAGUARDIA, A., BOURGEOIS, S., STRINDBERG, S., GOBUSH, K.S., ABITSI, G., BIKANG BI ATEME, H.G. et al. (2021) Nationwide abundance and distribution of African forest elephants across Gabon using non-invasive SNP genotyping. *Global Ecology and Conservation*, 32, e01894.

MAISELS, F., STRINDBERG, S., BLAKE, S., WITTEMYER, G., HART, J., WILLIAMSON, E.A. et al. (2013) Devastating decline of forest elephants in Central Africa. *PLOS One*, 8, e59469.

MILLS, E.C., POULSEN, J.R., FAY, J.M., MORKEL, P., CLARK, C.J., MEIER, A. et al. (2018) Forest elephant movement and habitat use in a tropical forest–grassland mosaic in Gabon. *PLOS One*, 13, e0199387.

MOHAYMANY, A.S., SHAHRI, M. & MIRBAGHERI, B. (2013) GIS-based method for detecting high-crash-risk road segments using network kernel density estimation. *Geo-spatial Information Science*, 16, 113–119.

MOLINA-VACAS, G., MUNOZ-MAS, R., MARTÍNEZ-CAPEL, F., RODRIGUEZ-TEIJEIRO, J.D. & LE FOHLIC, G. (2020) Movement patterns of forest elephants (*Loxodonta cyclotis* Matschie, 1900) in the Odzala-Kokoua National Park, Republic of Congo. *African Journal of Ecology*, 58, 23–33.

MUTINDA, M., CHENGE, G., GAKUYA, F., OTIENDE, M., OMONDI, P., KASIKI, S. et al. (2014) Detusking fence-breaker elephants as an approach in human–elephant conflict mitigation. *PLOS One*, 9, e91749. NGAMA, S., KORTE, L., BINDELLE, J., VERMEULEN, C. & POULSEN, J.R. (2016) How bees deter elephants: beehive trials with forest elephants (*Loxodonta africana cyclotis*) in Gabon. *PLOS One*, 11, e0155690.

NGENE, S.M., VAN GILS, H., VAN WIEREN, S.E., RASMUSSEN, H., SKIDMORE, A.K., PRINS, H.H.T. et al. (2009) The ranging patterns of elephants in Marsabit protected area, Kenya: the use of satellitelinked GPS collars. *African Journal of Ecology*, 48, 386–400.

NSE NKOGHE, E. (2019) Contribution de l'analyse spatiale à la compréhension du Conflit Homme-Éléphants dans la région de Gamba. MSc thesis. Université Omar Bongo, Libreville, Gabon.

NSONSI, F., HEYMANS, J., DIAMOUANGANA, J., MAVINGA, F.B. & BREUER, T. (2018) Perceived human–elephant conflict and its impact for elephant conservation in northern Congo. *African Journal of Ecology*, 56, 208–215.

OSBORN, F.V. & PARKER, G.E. (2003) Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. *Oryx*, 37, 80–84.

PRINS, H.H.T., LIEFTING, Y. & DE JONG, J.F. (2022) Marginal farmers carry the burden of damage caused by Asian elephants *Elephas maximus* in Bardiya National Park, Nepal. *Oryx*, 56, 73–81.

R CORE TEAM (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. R-project.org [accessed 21 September 2021].

ROWCLIFFE, J.M., KAYS, R., KRANSTAUBER, B., CARBONE, C. & JANSEN, P.A. (2014) Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, 5, 1170–1179.

SEAMAN, D.E. & POWELL, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085.

SHAFFER, L.J., KHADKA, K.K., VAN DEN HOEK, J. & NAITHANI, K.J. (2019) Human–elephant conflict: a review of current management strategies and future directions. *Frontiers in Ecology and Evolution*, 6, 235.

SONGHURST, A., MCCULLOCH, G. & COULSON, T. (2016) Finding pathways to human–elephant coexistence: a risky business. *Oryx*, 50, 713–720.

TERADA, S., YOBO, C.M., MOUSSAVOU, G.-M. & MATSUURA, N. (2021) Human–elephant conflict around Moukalaba-Doudou National Park in Gabon: socioeconomic changes and effects of conservation projects on local tolerance. *Tropical Conservation Science*, 14, 194008292110267.

TREVES, A., WALLACE, R.B., NAUGHTON-TREVES, L. & MORALES, A. (2006) Co-managing human-wildlife conflicts: a review. *Human Dimensions of Wildlife*, 11, 383-396.

TUTIN, C.E.G., WHITE, L.J.T. & MACKANGA-MISSANDZOU, A. (1997) The use by rain forest mammals of natural forest fragments in an equatorial African Savanna. Utilizacion de Fragmentos de Bosque Natural por Mamiferos de Selva Lluviosa en una Sabana Ecuatorial Africana. *Conservation Biology*, 11, 1190–1203.

VIDYA, T.N.C. & SUKUMAR, R. (2005) Social and reproductive behaviour in elephants. *Current Science*, 89, 1200–1207.

WALKER, K.L. (2010) Moving away from prescriptive pachyderm palliatives: toward an integrated assessment of farmer–elephant conflict in Gabon. PhD thesis. University of Michigan, Ann Arbor, USA.

WALKER, K.L. (2012) Labor costs and crop protection from wildlife predation: the case of elephants in Gabon. *Agricultural Economics*, 43, 61–73.

WALL, J., WITTEMYER, G., KLINKENBERG, B., LEMAY, V., BLAKE, S., STRINDBERG, S. et al. (2021) Human footprint and protected areas shape elephant range across Africa. *Current Biology*, 31, 2437–2445.e4.

WHITE, L. (1998) Baillonella toxisperma. In The IUCN Red List of Threatened Species 1998. dx.doi.org/10.2305/IUCN.UK.1998.RLTS. T33039A9752397.en.