Behavioural changes in African elephants in response to wildlife tourism

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Abstract

Eco-tourism and human-wildlife interaction can lead to increases in stress, vigilance and aggression in many species, however, studies investigating wildlife viewing are scarce. We present the first study investigating the impact of wildlife tourism on African elephant, *Loxodonta africana,* behaviour. Over 15 months, we studied the effect of monthly tourist pressure (tourist numbers) on the occurrence of stress-related, vigilance and conspecific-directed aggressive behaviour in 27 individually identified elephants and the effect of up to 3 vehicles on the direction of travel of non-identified herds using five-minute continuous focal observations. We analysed the effect of tourist pressure and vehicle presence using generalised linear mixed models, including habitat type, herd type and size, and season, as well as sex and age for behaviour models, as additional factors. We found no effect of factors on stress-related behaviour, but elephants were more likely to perform vigilance behaviours at waterholes compared to other habitat types. As tourist pressure increased, conspecific-directed aggression in elephants increased and male elephants were more likely to perform conspecific-directed aggression compared to female elephants. Further, we found that elephant herds became increasingly likely to move away with increasing numbers of vehicles present. Results suggest that reserves should monitor elephant behaviour to identify when tourist pressure has potential effects on elephant welfare and train guides to monitor behaviour and adjust minimum distances flexibly to ensure high welfare standards and tourist safety. This study further contributes to a small but growing body of literature on non-consumptive wildlife tourism impacts on wild animals.

Keywords: eco-tourism, conservation, stress, animal welfare, game drive, wildlife-viewing

1. Introduction

Observing wildlife as a non-consumptive tourist attraction for recreational purposes has become increasingly popular (Orams, 2002) and plays a key role in global wildlife conservation (Burger & Gochfeld, 1993; Newsome, Dowling & Moore, 2005). Wildlife viewing, where carried out sustainably, facilitates protection of wildlife habitats, biodiversity and natural ecological processes worldwide (Reynolds & Braithwaite, 2001; Maciejewski & Kerley, 2014). In terms of the management of such protected wildlife habitats, tourist satisfaction is usually the driving goal (Novellie, 1991). Negative impacts on animal welfare caused by wildlife tourism have been reported (Moorhouse *et al.*, 2015). Where negative impacts elicit chronic stress, they can potentially lead to decreased reproduction, increased risk of predation, starvation, susceptibility to diseases, dispersing away from release site (Reynolds & Braithwaite, 2001; Teixeira *et al.*, 2007; Bhattacharjee *et al.*, 2015) and lasting effects on behavioural patterns (McEwen & Wingfield, 2003). Impacts of wildlife tourism on animals are not well understood (Wardle *et al.*, 2018) and the few studies that have assessed viewing impact on animals found increases in fear, alert, aggressive, vigilance and stress behaviour (*Elephas maximus* (Ranaweerage, Ranjeewa & Sugimoto, 2015), *Rhinoceros unicornis* (Lott & McCoy, 1995), *Phoca groenlandica* (Kovacs & Innes, 1990), *Ursus maritimus* males (Dyck & Baydack, 2004), *Sula spp.* (Burger & Gochfeld, 1993)), reduced reproductive fitness (*Pygoscelis adeliae* (Giese, 1996), *Haliaeetus leucocephalus* (Grubb & King, 1991)), increased probability of retreat (*Bison bison*, *Odocoileus hemionus*, *Antilocapra americana* (Taylor & Knight, 2003), *Oreamnos americanus* (Lott, 1992)) and increased physiological stress responses (*Loxodonta africana* (Szott *et al.*, sub.), *Spheniscus magellanicus* (Fowler, 1999)).

Mega-fauna, such as African elephants, *Loxodonta africana,* are among the most popular species for wildlife viewing, particularly for international tourists (Lindsey *et al.*, 2007), yet research assessing the impact of tourist pressure, in form of monthly numbers of tourists, or tourist presence, in form of vehicle presence, on elephant behaviour is scarce. Elephants in unfenced areas have been reported to avoid human roads and settlements by altering their behaviour and movement (Hoare & Du Toit, 1999; Douglas-Hamilton, Krink & Vollrath, 2005; Jackson *et al.*, 2008; Graham *et al.*, 2009; Roever, van Aarde & Leggett, 2013) suggesting active avoidance of human contact by some herds. Only one study has investigated viewing-induced disturbance in elephants (Asian elephants, *Elephas maximus* (Ranaweerage *et al.*, 2015)) in a relatively large population of over 1000 individuals in a fenced national park. Tourist behaviour and vehicle presence increased the likelihood of elephants switching their behaviour from feeding to fear, alert, stress-related or aggressive behaviour. Additionally, increasing tourist pressure has been shown to be related to increased physiological stress levels of individuals in our study population of African elephants (Szott *et al.*, sub.).

The most widely used sustainable method to conserve elephant habitat is to allow wildlife tourism to take place in the form of viewing animals from vehicles, either self-driven or guided (World Tourism Organization, 2014). Tourist demand to view elephants is high (Chase *et al.*, 2016; Arbieu *et al.*, 2017). Human population growth in Africa is rapidly increasing and, by 2050, the population in Africa is predicted to double, with South Africa predicted to increase from an estimated population of 57.7 million people in 2018, to 81.8 million in 2050 (Population Reference Bureau, 2018). Such increases in human populations no only cause habitat loss but also increase possibilities of interactions between elephants and humans (Armbruster & Lande, 1993; Pozo *et al.*, 2017) Given the increasing populations of both humans and elephants in South Africa, it is important to investigate the impact of tourist pressure on elephant welfare. To our knowledge no published research has assessed the impact of tourist pressure or vehicle presence on the behaviour of African elephants.

In elephants physiological stress levels have previously been shown to be affected by season, where low availability of water and key nutrients during the dry season increased elephant stress levels (Foley, Papageorge & Wasser, 2001; Viljoen*et al.*, 2008). In a fenced area, elephants are forced to revisit foraging patches more frequently (Loarie, van Aarde & Pimm, 2009) and overcrowding and the increased frequency of interactions with unrelated individuals are thought to present a consistent social stressor for elephants (Munshi-South *et al.*, 2008). Elephants compete over access to resources, where agonistic interactions have been reported to occur at point resources such as fruiting trees, waterholes (Archie *et al.*, 2006), or mineral rich soil (*pers. obs*.). Further, bulls regularly come into musth, a reproductive state during which testosterone levels are heightened (Hollister-Smith *et al.*, 2007). Even when not in musth, males have been shown to be the more aggressive sex (Ganswindt *et al.*, 2005; Hollister-Smith *et al.*, 2007), often engaging in dominance interactions with each other (Goldenberg *et al.*, 2014) or bullying younger males (Buss & Smith, 1966). Stress-related, vigilance or aggressive behaviour in elephants may therefore be caused by a variety of factors other than tourism.

Our aim was to investigate the effect of wildlife tourism on elephants displaying aggressive, stress-related and vigilance behaviours as well as direction of herd movement in relation to tourists viewing them. Madikwe Game Reserve (Madikwe) in South Africa provided a suitable population to study the effects of tourist pressure on elephant behaviour. The founding population was introduced from various backgrounds, such as culling and poaching, and as the effects of such events can be long-lasting (Bradshaw *et al*., 2005; Gobush, Kerr, & Wasser, 2009; Jachowski, Slotow, & Millspaugh, 2013) these elephants may be particularly sensitive to the presence of vehicles. Additionally, such traumatic experiences are not an exception for elephant populations across Africa (Chase *et al.*, 2016). Given that previous research found effects of wildlife tourism on stress-related, vigilance and aggressive behaviour in viewed animals, we predicted that tourists would be a stressor for elephants and that increasing tourist pressure would increase vigilance to avoid the stressor and, if avoidance was not possible, increased stress-related and aggressive behaviour. Because point resources, season and sex are known to influence stress and aggression in elephants, we included these factors in our analysis as control factors, alongside age and herd type. Lastly, we predicted that elephant herds would be more likely to retreat from tourists observing them from vehicles with increasing numbers of vehicles present.

2. Materials and Methods

Study site and driving regulations

Madikwe Game Reserve (Madikwe) is a reserve managed by a state/private/communal partnership (Fig. 1). The reserve, approximately 680km^2 in size, was fenced and held an estimated 1348±128 elephants (July 2017, P. Nel, *pers. comm.*) that is, 1.9 elephants per km^2, representing one of the highest population densities of elephants in South Africa. Elephants were first introduced to Madikwe in 1992 when 25 orphaned juvenile elephants from Kruger National Park culls (operations where herds of adult individuals were lethally wounded, and youngsters translocated to other reserves as a measure of population control) were introduced. In 1994, entire herds (194 individuals) from Zimbabwe were introduced from a background of severe drought, two bush wars and heavy poaching. In 1998 and 1999, six and two adult bulls (measured by a minimum 3.2 m shoulder height) were introduced from Kruger National Park, respectively.

Figure 1 here

Private vehicles are restricted to a few roads to travel between lodges and gates in Madikwe. Hence, elephant viewing occurs almost exclusively from game drive vehicles (GDs) where they encounter elephants on roads. A GD is a large, open vehicle, driven by a qualified field guide, that seats up to ten people as well as a 'spotter' at the front of the vehicle. No more than three GDs were allowed at an elephant sighting. The researchers' vehicle was not included in this number. All vehicles were obliged to park leaving an unobstructed exit before switching the engine off but were not limited in how close they could approach. Vehicles were not permitted to position themselves between individuals of a herd and had to remain on roads. All guests were briefed on appropriate behaviour. Standing up, loud noise or use of camera flash was not permitted. Eating, drinking and smoking were strictly forbidden during game drives. All these regulations are part of Madikwe's Code of Conduct and no regulations were amended for the purpose of this study.

Data collection

Data were collected from the 18th of April 2016 until the 28th of June 2017. The mean (±SD) number of observation days per month was 14 ±5. The area was sampled by driving random routes as well as communicating with field guides about elephant presence. Thirty-one lodges were spread across the reserve and conducted game drives in the morning from sunrise until approximately 11am, and in the afternoon between approximately 3.30pm until 8pm.

The primary investigator collected all data in the field. For the behaviour analysis, we identified 27 individuals (14 males, 13 females) based on distinguishing features. Herds included in travel direction analyses were not individually identified herds, but those encountered throughout data collection. Upon spotting an elephant, the researcher aimed to keep 30 m distance from the nearest elephant. If the animal was spotted at <30 m distance, the vehicle was slowly reversed to 30 m before the engine was switched off. When animal/s moved parallel to the road without displaying signs of distress (such as vigilance, body posture changes such as 'ears out' threats or moving away whilst repeatedly looking back at the vehicle), the researcher followed at a distance before switching the engine off again. A bull group was defined as such when several bulls were within a 500m radius of each other, whilst a mixed group was defined as such when an adult bull was within 200m of a cow-calf group.

We collected data on a Lenovo TAB 2 A8-50F tablet using the Prim8 app (McDonald & Johnson, 2014). We classed elephants as juvenile or adult based on size (elephantvoices.org, 2018). Adult females had mammary glands and an angled forehead, whilst adult males had a rounded forehead, wider skulls and could be twice the size of adult females. Juveniles were smaller than adult females, moving and foraging independently of their mothers and had tusks of approximately ten centimetres in length. Once a sighting was made from the road, we randomly selected a focal elephant to observe using continuous sampling (Altmann, 1974) for five minutes and noted identity if known, along with additional factors (Table 1).

Table 1 here

We noted the direction of travel of the whole herd by visually comparing herd location at the start and end of the focal observation and inferring direction of travel. If the centre of the herd increased its' distance from the observer or, if present, the closest GD ≥10 m (without simultaneously approaching another GD), we classed it as 'retreat', otherwise we classed it as 'stay'. We only recorded one herd movement observation per encounter, during the first five-minutes after a herd was encountered or after a GD(s) arrived, as a measure of immediate reaction of herd movement to the potential stressor.

Following previously published ethograms (Langbauer, 2000; McComb *et al.*, 2014; elephantvoices.org, 2018), behaviours were categorised (see supplementary material for full ethogram) as stress-related, vigilance or aggressive. Because several aggressive behaviours could be directed at either humans or conspecifics, we made note of the direction of the recipient of the threat, and we included all aggression not explicitly directed at a human in the analysis of conspecific-directed aggression.

Season was defined as wet or dry based on average monthly rainfall measured at four stations within Madikwe by the South African Weather Service. Average total rainfall during the study period was 189.69 mm. Wet season was defined as the period in which 95% of precipitation for the study year fell (Loarie, van Aarde & Pimm, 2009a) and therefore wet season lasted from October 2016-February 2017 and dry season lasted from April 2016-September 2016 and March 2017-June 2017. North West Parks Board provided the total number of tourists visiting Madikwe each month and this number was defined as tourist pressure per month.

Data analysis

Only focal observations where the animal was visible for $\geq$4 mins 30 s were retained for analysis. For the analysis of monthly tourist pressure, we selected observations with only the research vehicle present. This was to avoid the possibly confounding effect of game drive vehicle presence on behaviour. We included individuals that had a minimum of n=2 observations. For herd movement direction analysis, we included observations with game drive vehicles present. Where GDs arrived or left within the five-minute observation but were present for less than 60 s, the observation was excluded from analysis. If GDs were present for more than 60 s, the herd movement was considered to be in response to the number of GDs present for that time. This means that, if one GD was present from the beginning, but a second GD arrived and stayed for over 60 s, herd movement was in response to two GDs present. If a second GD arrived but left in under 60 s, the whole observation was considered in response to one GD.

We analysed data using R v. 3.4.1 (R Core Team, 2000). We scored each behaviour as occurring or not, and elephant herd travel as retreat or stay, forming binary response variables. First, we assessed factors to rule out collinearity using variance of inflation factor analysis (Fox & Monette, 1992), using a cut-off value of 2. We specified three General Linear Mixed Effects Models (package *lme4*, (Bates *et al.*, 2014)) to analyse the effect of tourist pressure on stress-related, vigilance and conspecific-directed aggression:

glmer (formula = Behavioural category ~ Tourist pressure + Herd type + Sex + Habitat type + Season + Herd size + Age + (1|ID), family = binomial, data = Data)

We scaled and centred the tourist pressure and herd size variables and included animal ID as a random effect to control for repeated observations from known elephants. We analysed significance of fixed effects with a type II ANOVA (Langsrud, 2003). Where categorical fixed effects were significant, we assessed differences between the levels using a Tukey post-hoc test in the *multcomp* package (Hothorn, Bretz & Westfall, 2008), checking that 95% confidence intervals did not cross zero.

For the direction of travel dataset, we excluded the open grassland habitat type from analysis as only n=5 observations had one GD present, resulting in poor model fit. The following Generalised Linear Model was used:

glm (formula = Travel ~ Herd type * GD number + Habitat type * GD number + Season * GD number + Herd size, family = binomial, data = Data)

We scaled GD number and herd size. We included an interaction with GD number and herd type as we predicted that different age and sex classes may have been affected differently by GD presence.

Further, we included an interaction between habitat type and GD number, as well as season and GD number, as we predicted that differences in thickness of vegetation and varying constraints during the seasons may have affected individual's reaction to GD presence. To account for non-independence in the data due to potential pseudoreplication, we performed 1000 iterations of bootstrapping, using the package *boot* (Canty & Ripley, 2018) to obtain bootstrapped 95% confidence intervals. We considered fixed effects significant if confidence intervals did not cross zero. We plotted all graphs using the *effects*- (Fox, 2003) and *ggplot2* (Wickham, 2016) packages.

3. Results

A total of 156 observations of known individuals were collected (mean ±SD = 6 ±6 per individual). These observations were from 10 adult males (18 observations as lone males, 8 in bull groups, 3 in mixed groups), 10 adult females (56 observations in cow-calf groups, 37 in mixed groups), 3 juvenile females (8 observations in cow-calf groups, 2 in mixed groups) and 4 juvenile males (16 observations in cow-calf groups, 8 in mixed groups). Removal of individuals with a small sample size did not change the effect of tourist pressure below. We collected travel direction of herds during 479 observations (81 bull groups, 141 cow-calf groups, 100 mixed groups and 157 lone males).

Stress-related behaviour

We found no effects of any variables on stress-related behaviour (Table 2).

Table 2 here

Vigilance behaviour

Vigilance behaviour was significantly more likely to occur at waterholes, compared to all other habitat types (Table 3).

Table 3 here

Conspecific-directed aggression

Increasing tourist pressure was significantly related to increased conspecific-directed aggression (Table 4, Fig.2). Male elephants were significantly more likely to perform conspecific-directed aggression compared to female elephants (Table 4). Although conspecific directed aggression appeared to be affected by habitat type (Table 4), Tukey post-hoc tests between habitat types revealed that the confidence intervals crossed zero.

Table 4 here

Figure 2 here

Herd movement

Increasing numbers of GDs present was related to increased likelihood of elephant herds moving away (Table 5, Fig. 3). None of the other variables affected herd movement (Table 5).

Table 5 here

Figure 3 here

4. Discussion

Our study found that wildlife tourism pressure and game drive vehicle presence influenced the behaviour of African elephants in Madikwe Game Reserve and adds to a small but growing body of literature monitoring the effects of tourist viewing on wildlife (e.g. Dyck & Baydack, 2004). Elephants were more likely to move away from tourists with increasing numbers of GDs present. High tourist pressure was related to increased conspecific-directed aggression. Our results showed effects of habitat type on vigilance behaviour, and sex on conspecific-directed aggressive behaviour. We further present the first report of any behavioural measure of the Madikwe elephant population.

We found a significant interaction between number of GDs and herd type on travel direction. More GDs were related to an increased likelihood of herds moving away from tourists (Fig. 3); this effect was most marked in bull groups compared to mixed groups. This supports the idea that elephants may remove themselves from a tourist stressor as a coping mechanism and is in line with other studies that found flight responses were affected by tourist presence (Lott & McCoy, 1995; Taylor & Knight, 2003). It is interesting that this effect was most pronounced in adult males (bull groups and lone males) compared to largely adult females (cow-calf groups and mixed groups). It is possible that this reflects a difference in willingness to, or the ability to quickly, move away from a resource (Stokke & du Toit, 2002; Woolley *et al.*, 2009). Cow-calf group and mixed groups contain neonates and young calves, smaller individuals that have reduced mobility and higher rates of water turnover. This may constrain the movements of lactating cows, growing juveniles and calves, and may present a trade-off between the perceived risk and the value of a resource from which groups containing adult females and dependent young move away. Unfortunately, we do not have data on proximity to water sources or nutrient content of forage during GD events to investigate this possibility.

We found mixed effects of tourist pressure on individuals' behaviour. Conspecific-directed aggression was more likely during high tourist pressure, supporting a similar effect in sea lions (*Neophoca cinerea*) and Asian elephants (Lovasz, Croft & Banks, 2008; Ranaweerage *et al.*, 2015). Contrary to our expectation, high tourist pressure did not increase vigilance or stress-related behaviour. As vigilance behaviour is known to be affected by spatial position in the herd (Burger & Gochfeld, 1993; Hunter & Skinner, 1998; Beauchamp, 2007), it is possible that this influenced our findings. Unfortunately, we did not have data on spatial position to control for this possibility. The lack of an effect on stress-related behaviour was surprising as we previously found increased physiological stress levels were likely when tourist pressure was high in our study population (Szott *et al.*, sub.). However, in a study of Barbary macaques, faecal glucocorticoid levels were not related to measures of tourist pressure (number, duration, proximity) but were related to aggressive interactions with tourists, whilst a behavioural indicator of anxiety (scratching) was positively related to the maximum number of tourists present (Marechal *et al.*, 2011). Thus, whilst these measures have been found to be useful indicators of physiological stress in many species (Fowler, 1999; Rehnus, Wehrle, & Palme,

2014) it is possible that behavioural expression and physiological response are triggered by different aspects of the stressor (Higham *et al.*, 2009; Mandalaywala *et al.*, 2014; Young *et al.*, 2014).

As predicted, habitat type had an impact on vigilance behaviour and sex impacted on conspecific-directed aggression. Waterholes are a point resource (Archie *et al.*, 2006) where vigilance behaviour was significantly more likely to occur, and male elephants have repeatedly been shown to be the more aggressive sex (Ganswindt *et al.*, 2005).

Prior research has demonstrated the effect of consumptive tourism, such as elephant trophy hunting, on stress levels of non-targeted herds in the population, leading to changes in behaviour that could potentially be fatal for humans (Burke *et al.*, 2008). From our findings, it appears that regulated non-consumptive tourism has the potential to be carried out in a more ethical manner than trophy hunting, with fewer welfare implications (no effect on vigilance or stress-related behaviour) for elephant populations. Although consumptive use generates larger amounts of money within a short amount of time, issues persist such as false hunting quota, corruption, and inequity of distribution of money (Lindsey, Roulet, & Romañach, 2007), in addition to welfare concerns for the wider population.

Practical implications

Studies highlight the contribution that behavioural indicators of welfare can make to the management and success of wild populations (Goldenberg *et al.*, 2017). Our results show that even with regulations in place, where wildlife viewing is carried out exclusively from GDs driven by qualified guides and overall numbers of tourists viewing elephants at any time are restricted, tourism led to changes in behaviour of the viewed elephants. However, the changes in behaviour were relatively limited, possibly because elephants were able to move away from the stressor, and suggest that, with careful management, wildlife tourism can be conducted in a welfare focused manner and hold a promising future for wildlife tourism as a conservation measure.

The Code of Conduct in Madikwe did not stipulate a minimum distance to be kept from elephants. Due to individuals performing more aggressive behaviours during high tourist pressure, and because waterholes are a point resource over which elephants compete, we recommend consideration of the increased chance of conflict with nearby GDs during times of high tourist pressure and at waterholes. Elephants at waterholes could experience frustration and stress, as well as being the target of aggressive behaviour from conspecifics, increasing the possibility that they will display redirected aggressive behaviours (Rajaram, 2006) towards bystanders such as vehicles. At Madikwe, field guides were aware of elephant behaviours signalling aggression (I. Szott, *pers. obs.*), highlighting the value of the ability to interpret behaviour when approaching wild animals. We suggest that a consistent minimum distance from the nearest individual, especially upon first approach, should be introduced to guidelines for wildlife viewing to alleviate the potential for conflict between tourist vehicles and wildlife. This will ensure not only the safety of guests but would also alleviate potential stress caused by increased agonistic interactions which could otherwise lead to elevated physiological or even chronic stress (McEwen & Wingfield, 2003; Pinter-Wollman, Isbell & Hart, 2009; Jachowski *et al.*, 2013). It would further give elephant herds, or indeed other wildlife, more space and may reduce the likelihood of animals moving off, giving tourists longer, more natural viewing experiences.

Due to strict regulations in Madikwe, tourist pressure is based on maximum availability of lodges hosting tourists and GDs are restricted to small numbers in sightings. However, most wildlife viewing, not only of elephants but a broad range of species, is carried out in areas where fewer/ no restrictions apply and is under growing demand worldwide (World Tourism Organization, 2014). Research into non-consumptive wildlife tourism, where no direct interactions between human and non-human animals take place, is scarce but has consistently reported aggressive, stress-related or vigilance-related responses by wildlife (Dyck & Baydack, 2004; Lovasz *et al.*, 2008; Ranaweerage *et al.*, 2015). Consideration of personality traits (Goldenberg *et al.*, 2017) would further inform our understanding of the differential effects of wildlife tourism on wild animals. It is important that future research investigates whether animals in other areas react in a similar manner, showing changes in behaviour. This will allow management decisions to be guided by up-to-date, quantitative and qualitative findings and allow reserves to advertise high animal welfare standards.

Ethical Statement

All data collected were non-invasive and received ethical clearance from Liverpool John Moores University (NK_IS/2016-6) as well as permission from the North West Parks Board. This research adhered to the Association for the Study of Animal Behaviour guidelines for ethical treatment of animals.

Data Accessibility

Prim8 Software can be accessed and downloaded here: http://www.prim8software.com/

R Statistical Software can be accessed and downloaded here: https://www.R-project.org/

Data and code can be accessed here: Link to data on figshare will be made available here upon MS acceptance

Author's Contributions

I.S. carried out data collection, statistical analysis, conceptualized the project and wrote the paper.

N.K. supervised and conceptualized the project and edited several drafts of the paper.

Y.P. co-supervised and conceptualized the project and edited the final draft.

Conflict of Interest

We have no conflict of interest.

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Figure 1.

Map of Madikwe Game Reserve, South Africa, in 2014. Dark grey areas are private concessions, grey areas are private concessions used with lodge permission, and light grey areas are open plains where off-roading was prohibited. Lines are roads, triangles are locations of lodges, and all waterholes (containing water either year-round or during the wet season) are indicated as circles. Map courtesy of P. Hattingh (2014).

Table 1. Factors recorded for five-minute continuous behavioural observations of African elephants, *Loxodonta africana*, carried out in Madikwe Game Reserve, South Africa.

Factor	**Levels**	**Description**
Sex	Female, male	Sex of focal individual
Age	Adult, juvenile	Age of focal individual
Herd type	Lone male, bull group, cow-calf group, mixed group	Type of herd in which focal individual was observed
Herd size	1-100	Number of animals in the herd
Habitat type	Shrub, dense shrub, open grassland, waterhole[a]	Type of habitat the focal individual was observed in
Season	Dry, wet	Season in which observation took place.
Vehicle	0-3	Number of GD vehicles present during the focal observation
Travel direction	Retreat, stay	The direction of movement of the core of an elephant herd in relation to present GD vehicles. If a herd moved parallel to, or towards vehicles, it was classes as stay, if the distance of the core of the herd increased by ≥10 m from vehicles, it was classed as retreat

[a]Shrub= various bushes and trees in observed area but not obscuring observation noticeably; dense shrub= shrub and trees in observed area, growing so densely that observation only possible at close distance and dense enough to cover view of large areas of the body of the focal animal; open grassland= observation area vastly open with only occasional bushes or trees; waterhole= water accumulated either naturally or pumped artificially with enough water for one or more elephants to drink

Table 2: Results of a type II ANOVA on a GLMM for the occurrence of stress-related behaviour in known African elephants, *Loxodonta africana*, in Madikwe Game Reserve, South Africa. Fixed effects' estimates and standard errors (SE) are from the model summary and X^2 values, degrees of freedom (df) and p-values are from a type II ANOVA.

Fixed effect	**Levels**	**Estimate (± SE)**	**X^2**	**df**	***p*-value**
Intercept		-0.581(±1.41)			
Tourist		-0.138(±0.23)	0.378	1	0.539
Herd type (Bull group)	Cow-calf group	-0.871(±1.29)	1.74	3	0.628
	Lone male	-1.418(±1.09)			
	Mixed group	-0.938(±1.3)			
Sex (Female)	Male	-0.235(±0.83)	0.081	1	0.777
Habitat (Dense shrub)	Open grassland	0.067(±1.12)	1.372	3	0.712
	Shrub	-0.168(±0.66)			
	Waterhole	0.425(±0.69)			
Season (Dry)	Wet	-0.106(±0.5)	0.045	1	0.833
Herd size		-0.19(±0.3)	0.406	1	0.524
Age (Adult)	Juvenile	0.199(±0.77)	0.068	1	0.795

Table 3: Results of a type II ANOVA on a GLMM for the occurrence of vigilance behaviour in known African elephants, *Loxodonta africana*, in Madikwe Game Reserve, South Africa. Fixed effects' estimates and standard errors (SE) are from the model summary and X^2 values, degrees of freedom (df) and p-values are from a type II ANOVA. Significant effects in bold, where significance was assigned at $p \leq 0.05$.

Fixed effect	**Levels**	**Estimate (± SE)**	X^2	**df**	***p*-value**
Intercept		-0.238(±1.38)			
Tourist		-0.091(±0.21)	0.199	1	0.656
Herd type (Bull group)	Cow-calf group	-0.880(±1.31)	1.858	3	0.602
	Lone male	-0.002(±1.01)			
	Mixed group	-1.318(±1.31)			
Sex (Female)	Male	-0.258(±0.80)	0.103	1	0.749
Habitat (Dense shrub)	Open grassland	0.654(±0.89)	26.758	3	**<0.001**
	Shrub	0.187(±0.54)			
	Waterhole	2.924(±0.69)			
Season (Dry)	Wet	0.420(±0.44)	0.899	1	0.343
Herd size		0.118(±0.28)	0.184	1	0.668
Age (Adult)	Juvenile	0.627(±0.77)	0.667	1	0.414

Table 4: Results of a type II ANOVA on a GLMM for the occurrence of conspecific-directed aggressive behaviour in known African elephants, *Loxodonta africana*, in Madikwe Game Reserve, South Africa. Fixed effects' estimates and standard errors (SE) are from the model summary and X^2 values, degrees of freedom (df) and p-values are from a type II ANOVA. Significant effects in bold, where significance was assigned at $p \leq 0.05$.

Fixed effect	**Levels**	**Estimate (± SE)**	X^2	**df**	***p*-value**
Intercept		-6.506(±2.19)			
Tourist		0.704(±0.30)	5.439	1	**0.02**
Herd type (Bull group)	Cow-calf group	2.496(±1.83)	2.980	3	0.395
	Lone male	-0.494(±1.61)			
	Mixed group	1.984(±1.76)			
Sex (Female)	Male	2.843(±1.22)	5.409	1	**0.02**
Habitat (Dense shrub)	Open grassland	1.359(±1.72)	7.915	3	**0.048**
	Shrub	1.176(±1.21)			
	Waterhole	2.729(±1.23)			
Season (Dry)	Wet	0.049(±0.61)	0.006	1	0.936
Herd size		0.567(±0.33)	3.050	1	0.081
Age (Adult)	Juvenile	-1.046(±1.14)	0.836	1	0.361

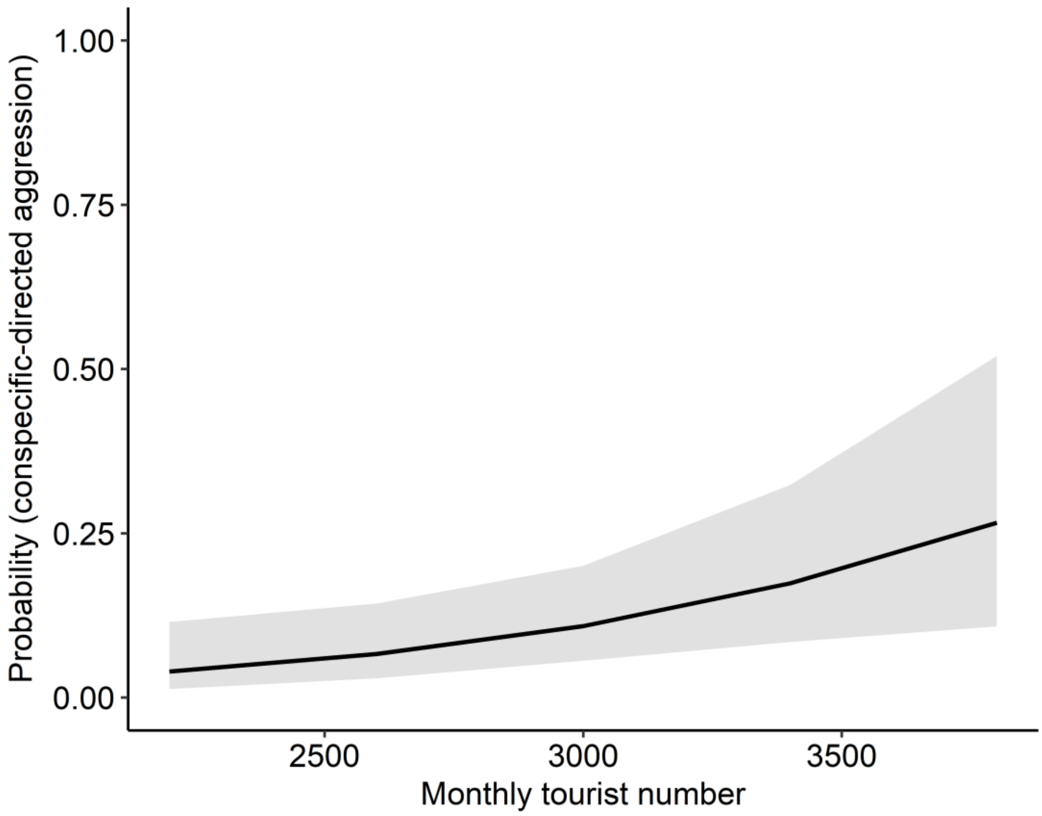

Figure 2.

Predicted mean probability of a Generalized Linear Mixed Model analysing the effect of tourist pressure on the probability of known African elephants, *Loxodonta africana*, in Madikwe Game Reserve displaying conspecific-directed aggressive behaviour. Grey areas represent 95% confidence intervals.

Table 5: Results of a nonparametric bootstrap (1000 iterations) of a GLM for the impact of several fixed effects on the probability of African elephant herds, *Loxodonta africana*, in Madikwe Game Reserve, South Africa, moving away from observers. Fixed effects' estimates and standard errors are from the model summary, and level comparisons and 95% Confidence Intervals are from bootstrapped confidence intervals. Significant effects are shown in bold.

Fixed effect	**Levels**	**Estimate (± SE)**	**Levels (reference level vs. comparison level)**	**95% Confidence Intervals**
Intercept		-0.500(±0.39)		
Herd type (Bull group)	Cow-calf group	0.394(±0.35)	Bull group: Cow-calf group	-0.068 to 0.233
	Lone male	0.215(±0.32)	Bull group: Lone male	-0.095 to 0.169
	Mixed group	0.457(±0.40)	Bull group: Mixed group	-0.069 to 0.269
			Cow-calf group: Lone male	-0.187 to 0.093
			Cow-calf group: Mixed group	-0.112 to 0.159
			Lone male: Mixed group	-0.118 to 0.225
Vehicle		0.540(±0.66)		-0.230 to 0.481
Habitat (Dense shrub)	Shrub	-0.318(±0.27)	Dense shrub: Shrub	-0.221 to 0.060
	Waterhole	-0.340(±0.33)	Dense shrub: Waterhole	-0.241 to 0.086
			Shrub: Waterhole	-0.117 to 0.101
Season (Wet)	Dry	-0.128(±0.21)	Dry: Wet	-0.130 to 0.063
Herd size		0.005(±0.13)		-0.055 to 0.065
Herd type *GD (Bull group *GD)	Cow-calf group *GD	-0.485(±0.47)	Bull group*GD: Cow-calf group*GD	-0.360 to 0.038
	Lone male *GD	-0.283(±0.44)	Bull group*GD: Lone male*GD	-0.304 to 0.079

	Mixed group *GD	-0.515(±0.41)	**Bull group*GD: Mixed group*GD**	**-0.340 to -0.001**
			Cow-calf group*GD: Lone male*GD	-0.111 to 0.236
			Cow-calf group*GD: Mixed group*GD	-0.147 to 0.197
			Lone male*GD: Mixed group*GD	-0.174 to 0.063
Habitat type *GD (Dense shrub *GD)	Shrub *GD	0.034(±0.50)	Dense shrub*GD: Shrub*GD	-0.268 to 0.308
	Waterhole *GD	0.103(±0.52)	Dense shrub*GD: Waterhole*GD	-0.271 to 0.349
			Shrub*GD: Waterhole*GD	-0.092 to 0.138
Season *GD (Dry *GD)	Wet *GD	-0.044(±0.22)	Dry*GD: Wet*GD	-0.108 to 0.118

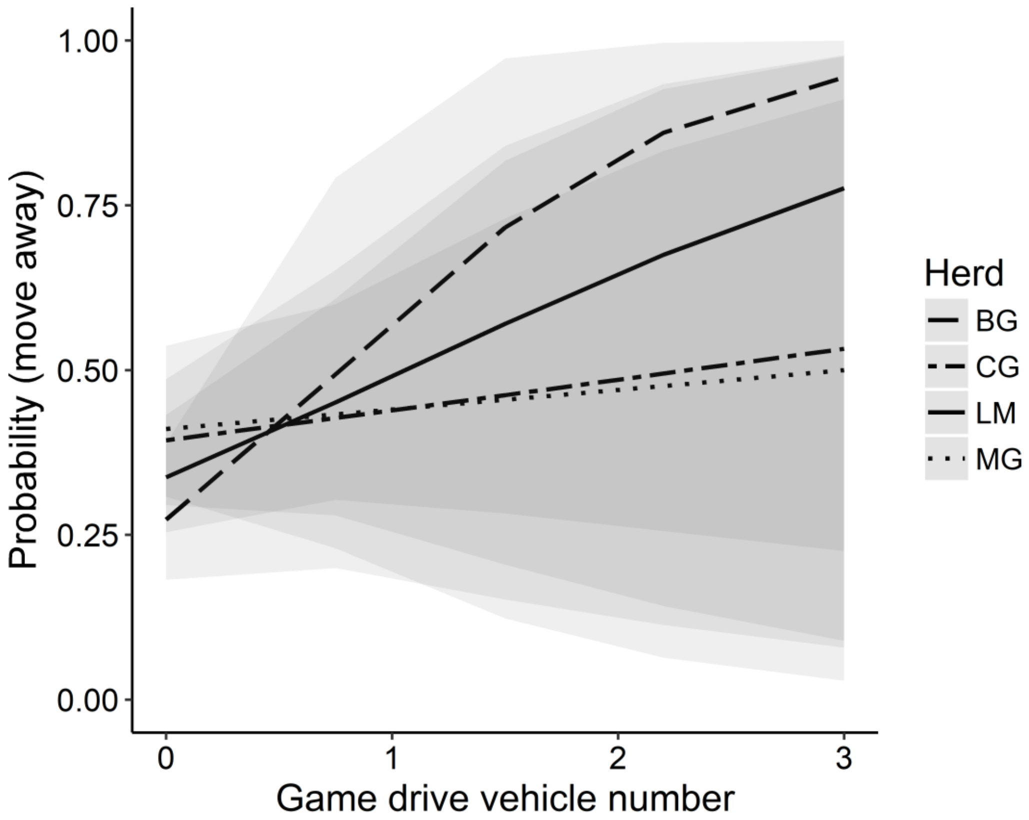

Figure 3.

Predicted mean probability of a Generalized Linear Model analysing the effect of game drive vehicle presence on the probability of African elephant herds, *Loxodonta africana*, in Madikwe Game Reserve moving away from observation points in different herd types. BG: bull group; CG: cow-calf group; LM: lone male; MG: mixed group. Grey areas represent 95% confidence intervals.

Table S1. Full ethogram of all behaviours included in this study of African elephants, *Loxodonta africana*, in Madikwe Game Reserve. Each behaviour was assigned to a specific category for statistical analysis.

Behaviour category	**Behaviour included**	**Description of behaviour**
Stress-related behaviour	Run	Animal is moving fast without feeding and often with the whole herd moving away from a specific stimulus such as a predator
	Trunk to body	Animal is touching own body with trunk. Different from scratching. Can happen during locomotion
	Trunk to face	Animals' trunk is touching its face for very short duration. Can happen during locomotion
	Trunk twirl	Animal is curling its trunk in a swift motion. Can happen during locomotion
Vigilance behaviour	Smell	Animal extends the trunk down or up, with the tip of the trunk curled horizontally. Often the trunk is rotated in several directions to pick up scent. Can happen during locomotion
	Trunk to mouth	Animal puts the tip of its trunk into its own mouth without ingesting any food or water possibly processing chemicals using its vomeronasal organ. Can happen during locomotion
	Vigilance	Animals' head is held high and ears are spread out. Often the head is moved from one side to another such as to listen to the surrounding
Conspecific-directed aggressive behaviour	Charge	Fast walk, often with ears out and head held high, towards a conspecific. Can be accompanied by a trumpet
	Displace given	Focal animal is approaching a conspecific which leaves the currently occupied spot
	Ears flapping	Animal is moving ears in and out resulting in a loud noise when the ears hit the body. Can happen during locomotion
	Ears out	Animal is spreading its ears outwards, away from the body, making it appear larger. Can happen during locomotion
	Head shake	Animal rapidly moves the head in a flowing motion tilting it from the right to the left, resulting in the ears flapping against the body and making a loud sound. Often, this is done whilst turning towards the stimulus at which the head shake is directed
	Pushing object	Animal is pushing an object such as a tree with its body
	Redirected aggression	Animal often will have received aggression by a dominant individual or was the loser of a play or aggressive sparring interaction. Often redirected aggression can be throwing around leaves or sticks or turning rapidly from the dominant individual and push a tree over or uproot a bush
	Slap	Animal is using its trunk or head to strike a conspecific
	Sparring aggressive	Animal is pushing with conspecific head to head often with their trunks entwined and tusks clashing against each other
	Standing tall	Animal is standing with its head held high up and glancing forwards over the trunk
	Trunk swing	Animal is swinging trunk backwards and forwards between the front legs, often whilst exhaling or stepping forward. Can happen during locomotion
	Tusk	Animal is pushing its tusks into conspecifics body. Can happen during locomotion

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