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Reduced older male presence linked to increased rates of aggression to non-conspecific targets in male elephants

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Abstract

Males in many large mammal species spend a considerable portion of their lives in all-male groups segregated from females. In long-lived species, these all-male groups may contain individuals of vastly different ages, providing the possibility that behaviours such as aggression vary with the age demographic of the social environment, as well as an individual's own age. Here, we explore social factors affecting aggression and fear behaviours in non-musth male African elephants (*Loxodonta africana*) aggregating in an all-male area. Adolescent males had greater probabilities of directing aggressive and fearful behaviours to non-elephant targets when alone compared to when with other males. All males, regardless of age, were less aggressive toward non-elephant targets, e.g., vehicles and non-elephant animals, when larger numbers of males from the oldest age cohort were present. Presence of older males did not influence the probability that other males were aggressive to conspecifics or expressed fearful behaviours toward non-elephant targets. Older bulls may police aggression directed toward non-elephant targets, or may lower elephants' perception of their current threat level. Our results suggest male elephants may pose an enhanced threat to humans and livestock when adolescents are socially isolated, and when fewer older bulls are nearby.

Key words: life history, long-lived mammals, male aggression, human-wildlife conflict, risk perception, policing

Introduction

Since male fitness is mainly driven by the number of successful fertilisations (1), aggression in males is typically viewed through the lens of sexual competition, with a focus on direct mate guarding (2), defence of territory and resources to gain access to females (3), or establishment of dominance hierarchies in order to monopolise mating (4). However sexual segregation and bachelor groups occur in many large mammal species (5,6), providing potential for aggressive behaviours by males in the absence of females to directly contend for. Currently, we know comparatively little about the factors that influence aggressive behaviours in all-male groups. This represents an important gap in knowledge as many males spend the majority of their lives in such all-male groups. Additionally, in long-lived species with distinct life history stages (e.g. prolonged adolescent periods with higher investment in learning and development, and lower investment in reproductive activities) the possibility arises that differences in the ages of males in all-male groups may influence the aggressive behaviours that are performed by members (7,8,9,10).

Male African savannah elephants (*Loxodonta africana*) dispersed from their natal herd spend most of their lives sexually segregated from females (11), with males spending 63% of their time in all-male groups, and 18% of their time alone (12). The species is also one of the few non-predatory species whose aggressive behaviours can serve an immediate lethal threat to humans and their livelihoods (13,14), and males are disproportionately involved in human-elephant conflicts compared to females (15). Social disruptions during development in African elephants can lead to negative behavioural outcomes, including abnormal hyper aggression (16). Mature bulls appear to have a role in inhibiting musth (sexually active state in male elephants, characterised by high rates of aggression (17)) in younger males (7,8), suggesting both an individual's life history stage and the social environment can influence aggression in this species. Understanding the patterns of aggression in male elephants, including the nature and targets of this aggression, and how factors such as age and social context within all-male groups can influence these behaviours is therefore of paramount importance owing to its relevance to human safety and well-being.

Here, we quantify the agonistic behaviours of non-musth male African elephants in a male-dominated area under different social contexts. We first examined how social isolation was linked to elephants of different ages' expressing "flight or fight" (fear and aggression behaviours respectively) responses towards non-elephant targets. Whilst directing aggression to a perceived threat may be one reactive response for elephants under stress ("fight" response), they may also respond with more "flight" type fearful anti-predator responses, i.e., running away from the perceived threat (18,19,20). Male elephants form larger groups when in higher risk environments, for example when outside of protected areas (5) We therefore predicted, both due to their lack of previous experience in assessing and responding appropriately to real risk (11,21), as well as a greater genuine vulnerability (e,g, predation risk (22), and dispersal risks in a novel environment (23)), that adolescents would be more likely to perform fear-related behaviours when alone compared to when in the company of other males. In contrast, being alone was not expected to represent as severe a threat for adults, who are more experienced and physically larger (11). We therefore predicted adults males that were socially isolated would express fear and aggression behaviours to non-elephant targets at equal rates to those in the company of other males.

Secondly, we tested if the number of males of different age classes present in the immediate environment was associated with performance of agonistic behaviours (both to conspecifics and non-elephant targets). Specifically, we hypothesised greater number of mature males in the immediate environment would reduce the expression of aggressive and fear behaviours in male elephants.

In a prominent case study of “delinquent” young male elephants in Pilanesberg National Park (South Africa), abnormal aggression and premature musth in young males was corrected once mature bulls were introduced to the population (7,8). This observation is reminiscent to the finding that dominant individuals act as policers of subordinates’ conflicts in primates (24), and that lower adult-young ratios in horse groups leads to greater aggression in young horses due to adult regulation of young horse’s aggression behaviours (10). It is likely that aggression directed to conspecifics differs in function to the aggression directed to non-elephant targets and relates more to dominance hierarchy establishment and access to resources, as opposed to a reactive response to a perceived threat or irritant (25). We predicted there would be increases in aggression to conspecifics with reduced mature male presence, which may indicate disruptions to the linear dominance hierarchy (7,8,26), and/or a potential policing influence of mature males on younger male's conflicts (24,27). Additionally, mature males may also police aggression behaviours to non-elephant targets as a behaviour that is also potentially detrimental to group cohesion (24), and we also predict elephants will direct less aggression to non-elephant targets with increased mature male presence in the environment.

Alternatively, elephants may be more likely to direct aggression to non-elephant targets with decreased mature bull presence as they may perceive themselves to be at greater risk in the absence of experienced individuals in the environment (28). Increases in elephants performing fear behaviours to non-elephant targets with decreased mature bull presence would also support this risk perception hypothesis. In horses, informed (often older) individuals appear to play an important role in transmitting information to group mates regarding safety, for example, naïve horses have reduced fear responses when paired with informed demonstrators (29), and young foals weaned without adults express increased aggression and behavioural and physiological stress (9). An age structured effect on risk assessment has been in shown in female groups of African elephants, for example, where older matriarchs make better assessments about risk, which they communicate to group mates (30). Such findings would highlight the need to investigate the social role of mature individuals in all-male groups, and provide new insights to the importance of older individuals from a wildlife management perspective.

Methods

The study was conducted within, but at the border of Makgadikgadi Pans National Park (MPNP), Botswana, a bull area where 98% of elephant sightings are sexed as male (31). The region adjacent to the site of data collection has the highest reported rate of human-wildlife conflict in Botswana (32), with 71% of residents in Greater Khumaga interviewed stating that elephants threatened their safety (33). We conducted focal sampling of male African elephants aggregating at hotspots of elephant social activity along the Boteti River, which marks the border of the MPNP (Supplementary Figure 1). Data were collected between September 2015 and September 2018 at 5 hotspot locations. Hotspots were areas of river with easy access for elephants and were the terminal points of elephant pathways in the MPNP landscape (34). Hotspot boundaries were defined by natural landmarks in the environment, based on the general area in which elephant aggregations remained during a visit to the river (Supplementary Table S1 for locations, boundaries and approximate area covered).

Data collection

Individual subjects were filmed for the entirety of their stay within social hotspots, starting either as the subject arrived over the bank, or as he entered the hotspot having moved from another stretch of river up or downstream of the hotspot, and terminating when similar boundaries were crossed during departure. Elephants arrived at hotspots alone, or in coordinated all-male group processions (34). However, following arrival, considerable mixing of males occurred from multiple arriving groups and original groupings became indiscriminate from the larger all-male aggregation. Males were categorised into 4 age classes, adolescents, 10-15 years & 16-20 years, and adults, 21-25 & 26+ years, based on body size, shoulder height (35), head size and shape, and tusk girth and splay (36). The age class 26+ years represents an age where males are largely considered sexually and socially mature (37), begin experiencing regular annual musth periods and achieving mating success (17,37). The age class of focal subject to be recorded was randomly preselected, and the first elephant of the assigned age class to arrive at the hotspot since the start of the session was the subject of a focal animal sample (elephants were aged in the field, if the arrival group had multiple individuals from the preselected age class, the focal was selected at random from the choice). Recordings of visits to hotspots were taken from focal individuals only once over the study period. Individuals were identified by distinguishing features such as tears, holes and notches in the ears, tusk morphology, skin wrinkles, tail length and other body abnormalities (38).

Subjects of focal animal samples were filmed using a video cam-corder (JVC quad proof AVCHD) fixed to a tripod, with the subject kept central to the frame, but zoomed out enough to allow for potential interactors to be captured. Video recordings were taken between 08:00 and 18:30 (Supplementary Note S1). The research vehicle was parked at a safe distance (minimum 50m) from points expected to receive elephants (pathway arrival points, popular drinking points, mudholes). Non-musth males in the MPNP are largely relaxed around vehicles, and if the engine was off for the entire focal session, it was common for elephants to not look in the direction of the human observer (Supplementary Note S2 for methods for addressing vehicle presence).

Focals could stay at social hotspots for several hours (average time spent at hotspot for focal elephants seen arriving and leaving via bank = 1h 13min, range= 9min – 7h 5min, SD= 59min), over which time, the males present at aggregations with focals could be highly dynamic. Since individuals arriving in all-male groups tend to arrive within 10 minutes of one another (34), focal follows were subdivided into 10-minute follows (e.g., a focal follow of an elephant staying 40 minutes at the hotspot, would produce four 10-minute focal follows), to which a corresponding social context was assigned (see below), in order to capture the temporally dynamic nature of male aggregations at the hotspots.

In 15 10-minute follows (from 6 individuals), females were also present at the hotspot. Presence of females was rare in this bull area, so it is possible this could impact on aggressive interactions between males. Presence of females did not predict the expression of any behaviours of interest by males in the study (Supplementary Table S2). Nevertheless, to be conservative, the 15 focal samples where females were present were excluded from our analyses. Additionally, 52 focal animal samples (from 10 individuals), were collected on elephants in musth. Due to the established consensus that bulls act differently in musth state, with greater aggression to same-sex conspecifics (17), we excluded musth bull focals from our data set. The supplementary materials (Supplementary Figure S2) provide a comparison of aggressive behaviours of musth compared to non-musth males in this study. Finally, if a subject was out of view for over 2 minutes within a follow, i.e. over 20% of time (N 10-min follows= 201), the 10-minute focal follow was excluded from analysis. For 126 10-minute focal follows the focal elephant was out of view for 00.01 – 01:59 minutes, however, for most cases (N 10-min focal follows =1514) the subject was in view for the full 10 minutes.

Scoring of behaviours

Focal follow videos were scored by one researcher (CA) to standardise scoring of behaviours, with each follow observed for behaviours 3 times. Behaviours of interest (aggression directed to conspecific, aggression to non-elephant target, fear to non-elephant target (Table 1)) were scored as number of events per 10-minute focal follow.

Table 1: Ethogram of behaviours recorded during focal follows and their categorisation for analysis in the current study (39,40).

Behavioural category	Summary

Conspecific aggression	Aggressive behaviours relating to dominance assertion and gaining access to resources, as well as potentially re-directed aggression including “Advancing toward”, “Spreading ears”, “Holding head high”, “Ear folding”, “Head shakes”, amongst other behaviours (Supplementary Note S3 for full list of behaviours and detailed descriptions) directed by the focal subject towards conspecifics.
Aggression directed to non-elephant target	Many of the behaviours employed during aggression to conspecifics are similarly directed at non-elephant targets that are perceived as threats or irritants, including “Advance toward”, “Head high”, “Spreading ears”, “Head shakes”, among others (Supplementary Note S4 for full list of behaviours and detailed descriptions). Targets of non-elephant aggression included other animal species (e.g. ungulates, carnivores, reptiles and birds), vegetation and tourist vehicles, but in most cases the target of the aggressive behaviour was unidentifiable (Supplementary Figure S3 for distribution of targets of aggression by age class).
Fear directed to non-elephant target	Defensive and fearful behaviours, including “Running away”, “Tail raised”, “Jaw tilted upward”, among others (Supplementary Note S5 for full list of behaviours and detailed descriptions), employed by elephants in response to perceived threats. Targets of (or rather, the triggers of) these non-elephant directed fear behaviours included other species (e.g. ungulates, carnivores, reptiles and birds) and tourist vehicles, but in most cases the triggers of these behaviours were unidentifiable (Supplementary Figure S3 for distribution of targets of fear behaviours by age class).

Social Context

During field observations, data were collected on the number of, and ages of, all other elephants present at the hotspot with the subject elephant, such that for every 10-minute focal follow there was a corresponding recording of all ages observed as present with the focal within that time window (Supplementary Figure S4). The social context at the social hotspot was unknown to researcher scoring behaviours from videos and was only matched to corresponding focals subsequent to all videos being coded for behaviours.

Statistical Analyses

For our analyses we ran generalized logistic mixed-effects models (GLMMs) in R. Within each 10-minute focal follow, each of the 3 behaviours of interest (Table 1) were transformed to a binary 1/0 (present/absent) term due to a considerable right skew in the data set (e.g., for aggression directed at non-elephant targets, 1047 10-min focal follows had 0 events, 312 10-min follows had 1 event, and 168 10-min follows had >1 events of aggression (range 2-12 events)). Due to a small sample size for 10-15 year old focals sighted alone (eight 10-min focal follows), we merged age classes of focal elephants into the categories "adult" (21+ years; N=846 10-min focal follows from 147 individuals) and "adolescent" (10-20 years; N=681 10-min focal follows from 134 individuals) to test the effect of social context on the behaviours of subjects.

Firstly, we explored if social isolation was related to elephants' (i) expression of aggressive behaviours to non-elephant targets, and (ii) expression of fear behaviours to non-elephant targets. For these GLMM's, each behaviour (dependent variables) was modelled in relation to season, hotspot location, age category (adult or adolescent), social isolation condition (where 1 represented a subject being alone at a hotspot, and 0 represented other elephants being present with the subject), and the interaction between age category and social isolation condition (whereby reference class of age category was switched to explore the influence of social isolation on the aggression and fear behaviours for adolescent and adult bulls separately). Elephant ID was included as a random effect in both models.

Secondly, we investigated if the number of mature bulls (26+ years) at the hotspot was related to the probability that a subject directed aggressive behaviours at (i) conspecific targets and (ii) non-elephant targets, and (iii) fear behaviours at non-elephant targets. For these models, only males observed with other elephants at the hotspot were included (lone subjects were excluded). We fit GLMMs predicting each behaviour (dependent variable) by focal age category (adult or adolescent), season, hotspot location and number of each age class present during the 10-minute focal follow (i.e. number of each age class 10-15, 16-20, 21-25 and 26+ years were included as separate predicting variables). This allowed us to compare whether the number of other age classes present also influenced behaviours. In cases where the expression of a behaviour was only predicted by number of mature bulls and not the presence of individuals from other age classes, we re-ran this analysis to include interaction terms between focal age category and number of mature bulls, to test if the number of mature bulls in the environment had a different effect on adolescents compared to adults. All non-significant fixed effects from the initial model were excluded in this second interaction model. Elephant ID was again included as a random effect in all models.

In all the above analyses, we also included a fixed effect of whether this type of behaviour had also been performed in the preceding 10-minute follow to control for the potential influence of temporal autocorrelation (Supplementary Note S6). We also included season in all our GLMMs because availability of resources, and potentially body condition, are linked to season (41) which may influence elephants' tolerance in sharing limited resources, or influence linear dominance hierarchies (26) (Supplementary Note S7 for season determination methods). Furthermore, focal observations conducted in the wet season had higher numbers of other elephants present at the hotspot compared to the dry season (Supplementary Figure S4) and we wanted to account for this seasonal difference in aggregation sizes. Lastly, season also represented the best indicator of numbers of other species (potential targets of behaviours) sharing the hotspot resource with elephants, with some 20,000 zebra and wildebeest frequenting the Boteti River over the dry season, but absent in the wet season (42). As a control, hotspot location was also included as a fixed effect in all models, since the 5 hotspot locations differed in factors such as proximity to human-dominated landscapes and tourist presence, which may influence behaviours.

Results

Social isolation significantly predicted the likelihood of adolescents, but not adults, performing both aggression and fear-based behaviours to non-elephant targets, with adolescent males more likely to perform both these behaviours when alone compared to when observed with other elephants (Figure 1; Adjusted odds ratio (aOR) for directing fear behaviours to non-elephant targets when alone compared to with other elephants; adolescents = 2.775, p =0.013; adults= 1.206, p=0.736. aOR for directing aggression behaviours to non-elephant targets when alone compared to with other elephants; adolescents = 2.624, p =0.021; adults= 1.387, p=0.400; Supplementary Tables S3&4 for full outputs of GLMMs including 95% confidence intervals).

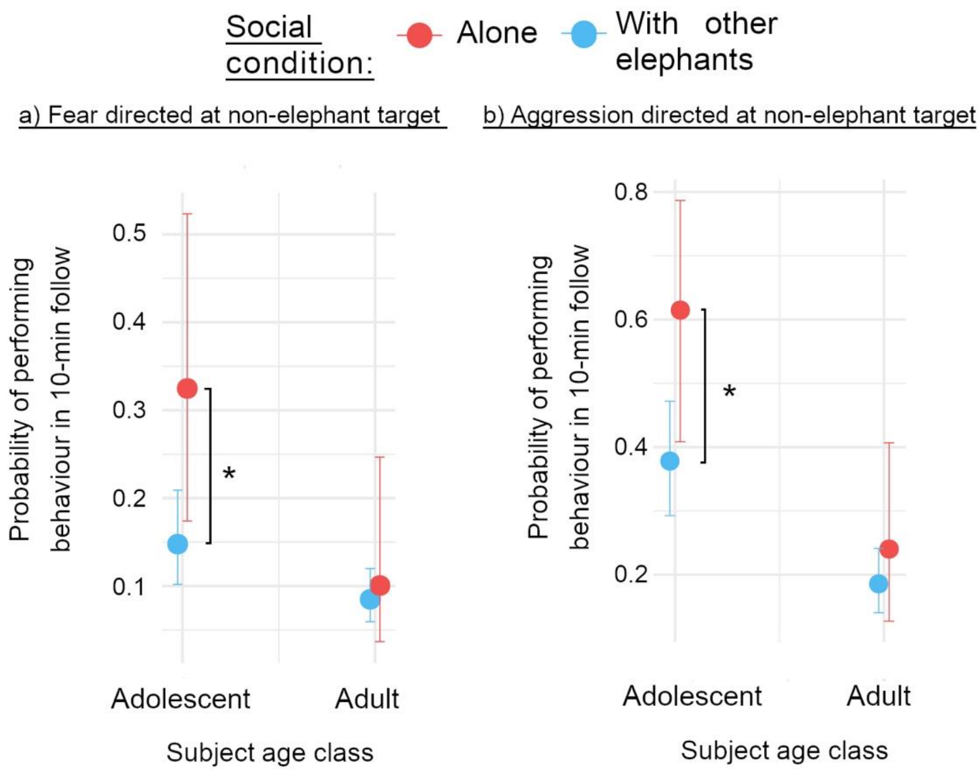

Figure 1: a) Being alone significantly predicted the likelihood of adolescents performing fear behaviours to non-elephant targets, but not adult elephants (Supplementary Table S3 for full output of GLMM). b) Being alone significantly predicted the likelihood of adolescents performing aggression behaviours to non-elephant targets, but not adult elephants (Supplementary Table S4 for full output of GLMM). Significant regression coefficients indicated with (*), 95% confidence intervals indicated.

Excluding subjects alone at hotspots, 10-minute focal follows had on average 2.85 (SD=3.98, Max=22) 10-15 year olds, 4.22 (SD=4.88, Max=28) 16-20 year olds, 2.15 (SD=2.44, Max=21) 21-25 year olds and 1.04 (SD=1.48, Max=10) 26+ year olds present with the focal subject. However, there were differences between adolescent and adult subjects concerning the mean number of other age classes present with them. Adolescent subjects had more 10-15 year olds present with them at hotspots than adult subjects did, and adult subjects had more elephants aged 16-20, 21-25 and 26+ years present with them at hotspots than adolescent subjects did (Supplementary Table S5).

Adults were more likely to direct aggression to conspecifics compared to adolescents (aOR adult compared to adolescent = 1.686, p=0.014). The number of elephants of each age class present at a hotspot did not predict the likelihood of subjects directing aggression to conspecifics (Supplementary Table S6 for output of GLMM).

Adults were less likely to direct fear behaviours to non-elephant targets compared to adolescents (aOR adult compared to adolescent= 0.556, p=0.016). Only the number of 10-15 year olds present at a hotspot predicted the likelihood of subjects directing fear behaviours to non-elephant targets, with elephants directing more fear to non-elephant targets when greater number of 10-15 year olds were present (Regression coefficient: 0.113, p=0.015; Supplementary Figure S5 & Table S7 for output of GLMM).

The number of 26+ year olds present at a hotspot did predict the probability of a subject directing aggression to non-elephant targets. As the numbers of mature bulls present increased, the likelihood of subjects directing aggression to non-elephant targets decreased (Regression coefficient: -0.242, p =0.001; Figure 2). No relationship was found between the likelihood of a subject directing aggression to non-elephant targets and the number of elephants present of all the other age classes (Supplementary Table S8). Adults were less likely to direct aggression to non-elephant targets than adolescents (aOR adult compared to adolescent= 0.378, p <0.001; Supplementary Table S8), but there was no significant interaction between age category of the subject and the number of 26+ year olds present at a hotspot in predicting the likelihood of the subject directing aggression to non-elephant targets (Supplementary Table S9). That is, when greater numbers of mature bulls were present, the probability of males of any age acting aggressively to non-elephant targets decreased.

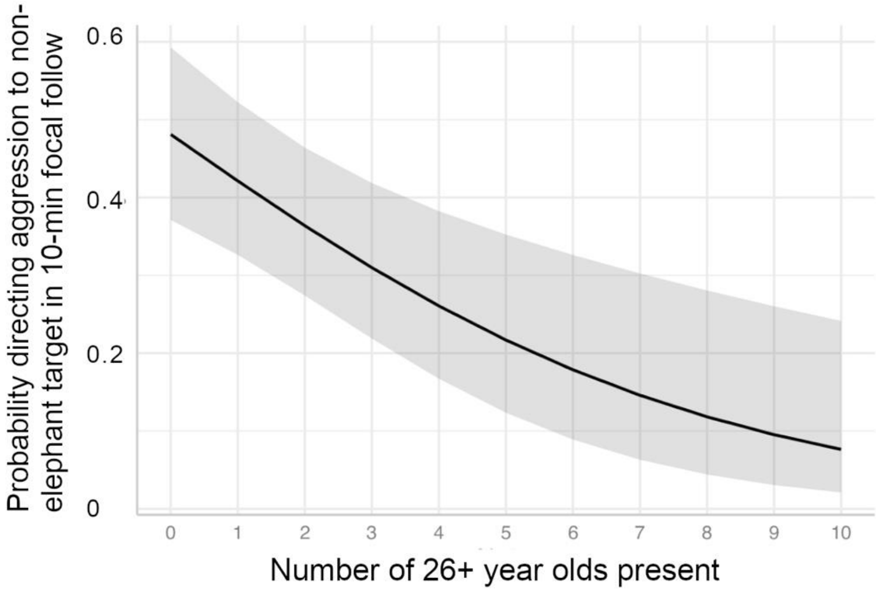

Figure 2: Elephants were less likely to direct aggression to non-elephant targets with greater numbers of 26+ year olds present at social hotspots. Grey area represents 95% confidence intervals based on standard errors (Supplementary Table S8 for output of GLMM).

Season had no influence on probability of an elephant directing aggression to either conspecific targets (Supplementary Table S6) or non-elephant targets (Supplementary Tables S4 & S8), nor on probability of directing fear behaviours to non-elephant targets (Supplementary Tables S3 & S7). Hotspot location did not predict likelihood of behaviours being performed in any of our models, apart from in the main effects model predicting aggression directed to non-elephant targets by numbers of each age class present, whereby aggression was more likely to be performed at hotspot 1 compared to hotspot 4 (Supplementary Tables S4-S9). In all models, performance of behaviours in a 10-min follow were also predicted by whether that type of behaviour had also been performed in the 10-min follow immediately previous, apart from the model predicting fear directed to non-elephant targets by numbers of each age class present (Supplementary Tables S4-S9).

Discussion

When alone, adolescents were more likely to perform aggression and fear behaviours to non-elephant targets compared to when with other males at hotspots, and overall, adolescent male elephants were more likely to direct aggression and fear behaviours to non-elephant targets than adult males. These “fight or flight” type responses to non-elephant targets may be a reflection of the physiological and psychological state of elephants, driven by their perception (both real or perceived) of their current risk and threat level (25, 28). Aside from human threats, adult bulls have no other natural predators (43). Adult elephants may be less fearful in the exposed habitat of the riverbed hotspot environment that they may have frequented multiple times over their lifetime and thus have a greater level of familiarity with (11). Adolescents, on the other hand, are still vulnerable to a real threat of predation from lions (22). Adolescents are also more likely to be recently dispersed from their natal herd and may be more sensitive to perceive the potentially novel, unknown environment as risky (11,23,44,45). Less experienced adolescents may also perceive the social hotspots as dangerous due to close proximity to human settlements, to which they are not yet habituated (the hotspots mark the boundary of a protected area and a human-dominated landscape (31)) (46). Indeed, elephants are very sensitive to human scent (18), and adolescents may additionally be less habituated to tourist presence, hence more likely to perform self-defence type aggression and fear behaviours in the national park (25,47). Animals adjust vigilance rates in response to group size and respond with flexible heightened anti-predator and flight behaviour when they perceive human or predatory threats (48,49). When socially isolated, the real and perceived risks described are likely exacerbated (e.g. individual risk of predation is greater (22)) and younger males may experience a further lowered threshold of risk perception (25,44,49), demonstrated by their increases in fear and aggression behaviours to non-elephant targets. In contrast, the behaviour of adult males did not appear to be influenced by social isolation, suggesting that physically larger, and more socially experienced adults do not experience a change to their real or perceived threat level when alone (45).

In many species that experience an adolescent life history stage, where individuals are not fully socially mature, hormones in the adolescent's physiology can drive exploratory tendencies, novelty seeking and motivation for risk-taking behaviours that could be more likely to put the individual in dangerous situations (50,51). This highlights a potential dilemma of cause and effect in our findings. It may not be possible to discern whether adolescents are more prone to social context influencing their behaviour compared to adults (i.e. their increased sensitivity in performing more agonistic behaviours to non-elephant targets when alone), or alternatively whether adolescents with temporary hormonal and aggressive "surges" separate themselves and choose to be alone, or are excluded from groups owing to their disruptive hyper-aggressive and fearful behaviours. Furthermore, the observed lack of variation in adult agonistic behaviours to non-elephant targets depending on grouping condition may be due to selective disappearance of the individuals that are overly fearful and aggressive when alone (52) (i.e. individuals that express heightened fear and aggression behaviours when alone don't reach adulthood). Whilst a longer-term study would be needed to address the potential of selective disappearance of individuals with a low threshold to coping with risk in adulthood, we believe it is unlikely that the sample of lone elephants represented individuals that were actively excluded from groups, or choosing to be alone. Hotspots were routinely visited by large numbers of elephants, and our method of scoring social context quantified the presence of all elephants at the hotspot, not necessarily reflecting the individuals preferred choice of social companions. Whilst it is possible that individuals excluded from groups or choosing to be alone can fissure from groups out in the larger landscape of the MPNP, the hotspots are a large, shared and popular resource, and elephants have no control over the arrival of conspecifics.

For both adult and adolescent elephants, the probability of performing aggressive behaviours to non-elephant targets was greater when there were fewer older male elephants in the immediate environment. One interpretation of this result could be that elephants perceived themselves to be at higher risk in these cases. Male elephants of all ages prefer to have the oldest males in a population as their nearest neighbours, potentially to reap benefits from their heightened ecological knowledge, which could include knowledge regarding environmental risk assessment (53). Some researchers suggest that due to their heightened experience with age, older males hold a similar role as matriarchs do in female family groups in their importance to the wider bull society (12,30,34,53). In elephant family groups, older matriarchs are better at assessing risks in the environment, which provides survival benefits to their group mates (30). We suggest that, for males too, with fewer older mature males present in environment, males may perceive themselves to be at higher risk, and experience lower levels of certainty about their safety (28), which is expressed though the observed increases in aggression to non-elephant targets. In other words, older males may act as particularly effective partners in social buffering (54), relieving stress and anxiety in group mates. In addition, we also found elephants were more likely to direct fear behaviours to non-elephant targets when greater numbers of 10-15 year olds were present, this may reflect a social contagion and spread of fear behaviours triggered by greater numbers of more skittish, fearful young adolescents being present.

Whilst the increased probability of performing aggressive behaviours to non-elephant targets when in higher-risk social contexts may represent responses to targets actually perceived as threatening by elephants with a heightened sensitivity, this aggression may alternatively or additionally be a form of re-directed or displaced aggression linked to an acute stress response induced by a perceived threatful social condition (39,55). Indeed, aggression to non-elephant targets often appeared not to be a true anti-predator defence because it was directed at non-threatening objects or bystanders (for example bashing of vegetation, charging of birds or smaller ungulates) or had no obvious target (target was unidentifiable, see Supplementary Figure S3). In many social mammals, following a stressful experience, redirecting aggression to third parties of their own species is thought to represent a stress-reducing behavioural outlet (55,56). However, we suggest in such a large and weaponised species, displacing aggression to a conspecific carries too much risk due to potential for escalated conflict, which can potentially turn lethal. African elephants may therefore tend to displace aggression to non-elephant targets. Whilst in the case of the "delinquent" males of Pilanesberg national park, young males were far more isolated from mature bulls than our current study, with total absence of mature bulls in the environment leading to a pre-mature musth in young males (7), we find it interesting to note that there too, in the absence of mature bull influence, elephants directed lethal aggression to rhinos, not conspecifics (8).

Finally, mature bulls may also act as policers of aggressive behaviour directed at non-elephant targets. Reduced presence of mature bulls in the environment may have led to an uninhibited expression of these behaviours (7,24). These aggressive behaviours are potentially highly disruptive to the social groups activities, cohesion and stability (57), as well as run risk of escalating and spreading further in the group as bystanders become affected and themselves anxious (personal observation, 27). For example, the calls of distressed elephants can make elephants act aggressively (58). Mature bulls may have a role in regulating such behaviours that are disruptive to all-male groups (24). Future research should focus on whether mature bulls are actively policing the aggressive behaviours of other males through ongoing punishment (our results might suggest this is not the case, as whilst adults performed more aggression behaviours to conspecifics compared to adolescents, elephants did not increase their aggression to conspecifics with the increased presence of any age class) (24,27,59). Alternatively, it was often observed that approaches of mature bulls to younger elephants evoked submissive responses even in the absence of dominance and aggressive signalling from the older male (although we cannot exclude the possibility that aggressive vocalisations could be being performed by the older male). Older elephants, with their clear dominance owing to greater size (35) and greater potential to inflict harm obvious to younger males, may have a more passive policing influence on other males, i.e, elephants may simply “behave better” when mature bulls are around without receiving particular policing behaviours (60).

Conclusions and practical implications

Understanding elephant aggression is essential for protecting the lives and livelihoods of people that live alongside the species (13,14). Whilst this study was conducted in an area with only moderate tourist presence with humans outside of vehicles absent, the aggressive behaviours observed by elephants have the potential to also be performed in areas with greater human presence, including where people move without the protection of vehicles. Globally, elephants are responsible for a significant proportion of large-mammal caused injury and fatality to humans (61), and previous research has suggested physiologically stressed elephants may be more prone to aggressive encounters with humans (62). Our results suggest wildlife managers should be careful to ensure mature bulls are present in elephant populations, as their increased presence was associated with decreased male elephant aggression to non-elephant targets. Adolescent male elephants that are socially isolated, or all ages that are unable to associate with mature males may have a heightened sensitivity to act aggressively and may serve as a greater threat to humans and livestock.

Ethical Review Statement

This work received approval from the University of Exeter Research Ethics Committee (application ID: eCLESPsy000545 v3.2), and was conducted with permission of the Botswana Department of Wildlife and National Parks, under research permit EWT 8/36/4 XXXVI (57).

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Supplementary Materials

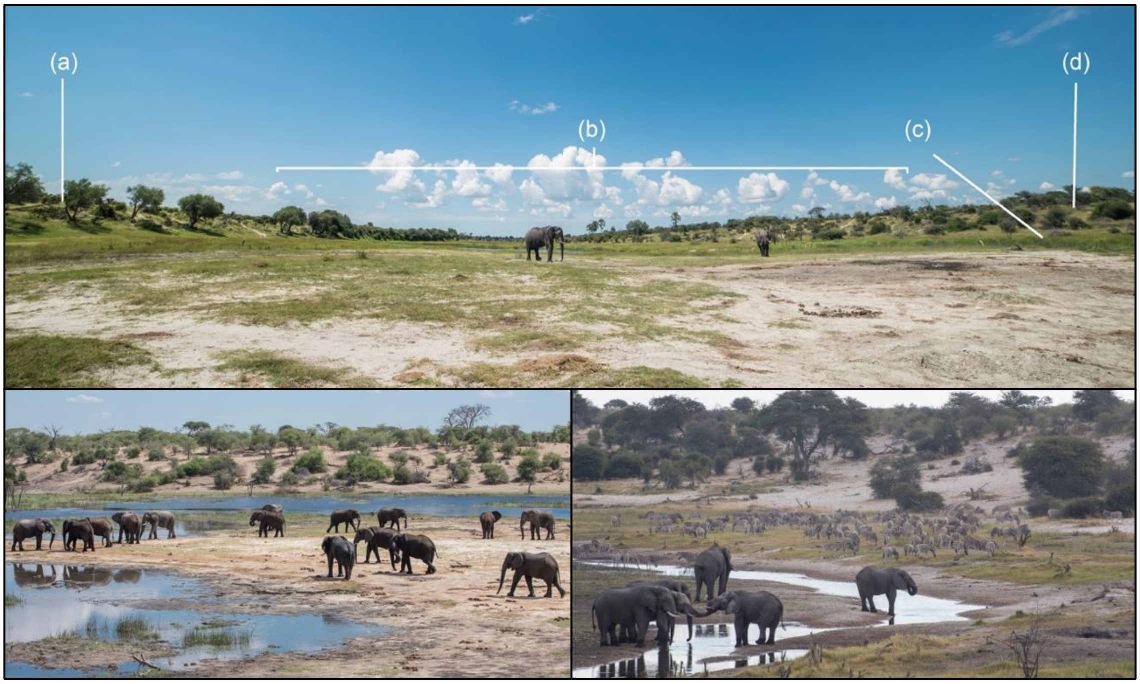


Figure S1: Example images of Boteti River hotspots. A hotspot consisted of the river (c), the surrounding flat, largely vegetation free sand (b), and a slope leading down to the river (a & d), populated with riverine shrub and thorn savannah (Kgathi & Kalikawe, 1993). The majority of elephants arrived at hotspots at predictable points on the bank, having travelled on fixed elephant pathways to reach the river. The Boteti River marks the boundary of the MPNP, whilst most elephants during the study arrived via the bank slope on the national park side (a) (N elephants= 2543, percent total= 65.42%), a minority arrived via the bank slope that leads out towards community owned land (d) (N elephants= 285, percent total= 7.33%). Furthermore, some elephants arrived having walked along the river from up or down stream of the hotspot. These individuals were recorded when they crossed the defined hotspot boundaries (N elephants= 1059, percent total= 27.24%). The water level of the river fluctuated at hotspots throughout the study, as a result of local rainfall and seasonal flood waters of the Okavango Delta system (Vanderpost & Hancock, 2018). Despite the river running dry at various locations during the study’s duration, deep water, enough to fully submerge an adult bull, was always present at all hotspots during the tenure of the study. Other key features of hotspots included dusting and mudhole sites for wallowing, and patches of dry riverbed from which elephants consumed dust/sand (presumably for mineral content (Weir, 2009)). On occasion, elephants were observed eating reeds growing in the river, or the sparse vegetation available on trees on the bank slope (a & d) – however, feeding did not dominate behaviour of elephants at hotspots. Male elephants also utilised hotspots for social purposes, with time spent at hotspots often exceeding the amount of time needed for drinking, mud wallowing and feeding on minerals.

Table S1: Locations and approximate sizes of hotspot locations

Hotspot name	**GPS most northern point**	**GPS most southern point**	**Approx. length (m)**	**Approximate area (km^2)**
Boma	20°28'55.68"S, 24°30'58.63"E	20°29'9.27"S, 24°30'54.68"E	503.14	0.069
Camera trap 6	20°23'45.22"S, 24°31'3.43"E	20°23'59.63"S, 24°31'12.14"E	527.21	0.169
Lion point	20°23'28.69"S, 24°30'43.55"E	20°23'45.22"S, 24°31'3.43"E	763.04	0.195
Island	20°23'17.60"S, 24°30'7.99"E	20°23'25.01"S, 24°30'34.75"E	793.34	0.185
Meno	20°19'19.80"S, 24°18'57.92"E	20°19'15.58"S, 24°19'14.30"E	556.68	0.052

Note S1: Recording sessions at the Boteti River

Individual recording sessions aimed to be a minimum of 4 hours long, and were extended until focal subjects left hotspots. To spread the distribution of subject arrival times across the day, we aimed to begin 1/3 of video sessions between 08:00-10:00, 1/3 between 10:00-12:00, and 1/3 between 12:00-14:00 (i.e. a session beginning at 14:00 would end around 18:00).

Note S2: Addressing Tourist vehicle presence in our study

The MPNP has a low tourist presence compared to other national parks in Botswana (Zyl, 2019), however tourist activity tended to focus on routes along the Boteti River for best wildlife viewing, which was also the site of data collection. Previous research in Madikwe Game Reserve, South Africa, found that elephants increased conspecific aggression as tourist pressure increased (Szott et al., 2019). Whilst importantly, the authors in this study noted that these elephants were founded from a population of cull and poaching survivors, who are highly sensitive to human presence (unlike the population of the MPNP who appear relaxed around appropriately distanced vehicles (50m+) with the engine off (personal observation)), it is recognised from various other studies that tourist presence can have large influences on animals' stress, aggression, vigilance and fear behaviours (Ranaweerage et al., 2015; Zanette & Clinchy, 2020). We therefore conducted supplementary analyses to confirm that tourist vehicle presence did not correlate with key social context factors, to be sure this factor was not likely to explain the significant effects in our models.

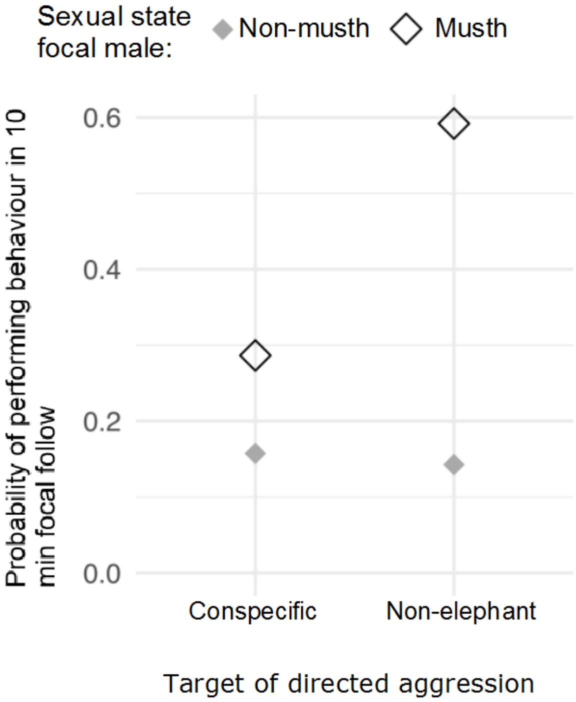
A tourist vehicle entering within 50m of a focal elephant's proximity showed no correlation with the age category of focal elephants, nor with a focal elephants' social isolation condition (phi coefficient = 0.060 for both factors). Wilcoxon rank sum tests were used to determine if focal samples with more elephants present dominated situations where a tourist vehicle did or did not enter within 50m of the focal follow.

There were no differences in number of elephants present between focal follows where a tourist vehicle did or did not enter within 50m of focals (Wilcoxon rank sum test with continuity correction: W=158850, p=0.4513, mean N elephants present with focal in 10-minute follow when vehicle entered within 50m focal= 9.65, vehicle did not enter within 50m focal= 10.50 (excludes lone male focals))

Table S2: Generalized logistic mixed-effects models (GLMMs) predicting likelihood of focal elephants a) directing aggression to conspecific, b) directing aggression to non-elephant target and c) directing fear behaviours to non-elephant targets during a 10-minute focal follow, by presence of females at hotspot with focal. Focal elephant ID included as random effects in all models.

Table S2: Effect of female presence at hotspot on behaviour of focal elephants				
a) Aggression directed by focal to conspecific target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-1.884	0.152 (0.122-0.189)	**<0.001 ***
Females	Absent	*Ref*	*Ref*	
	Present	1.179	3.250 (0.792-13.335)	0.102
b) Aggression directed by focal to non-elephant target				
Intercept		-0.884	0.413 (0.348-0.490)	**<0.001 ***
Females	Absent	*Ref*	*Ref*	
	Present	-0.801	0.449 (0.080-2.510)	0.362
c) Fear directed by focal to non-elephant target				
Intercept		- 2.290	0.104 (0.082-0.133)	**<0.001 ***
Females	Absent	*Ref*	*Ref*	
	Present	1.096	2.993 (0.666-13.452)	0.153

Figure S2: Comparison of probabilities of directing aggression to conspecific and non-elephant targets during a 10-minute focal follow between focal elephants aged 26+ years that were and weren't identified as being in musth at the time of sampling. 52 10-minute focal follows were made of elephants identified to be in musth and were subsequently removed from further analysis.



Note S3: Behaviours recorded as events of "conspecific aggression" directed by focal elephants.

Over the accumulative approximate 273 hours of focal follow observation only 6 events of escalated aggression were observed in the form of "charges" (no observations of parallel walk, ramming, duelling (Poole & Granli, 2011)). Due to this low occurrence, escalated aggression was included together with all social aggression, alongside more subtle dominance and threat displays between males. Elephant behaviours compiled from the work of Poole & Granli (2011) and Estes (1991) as well as our own observations:

Spreading ears: ears spread out perpendicular to body in direction of opponent, from the front view the elephant appears larger

Head high: Head held above shoulders, with chin tucked in

Folding ears: pressing lower portion of ears towards body, leading to a distinct ridge to appear across ear

Standing tall: head held above shoulders, tusks raised, often looking down towards opponent

Throw trunk toward: swinging trunk in direction of opponent

Head jerk: rapid upward movement of the head towards opponent

Head shake: twisting of head to one side, followed by rapid shake/ rotation of head from side to side, with the contact of ears to neck skin causing a load slap. Recorded as threat to conspecific when the performers focus was orientated toward another elephant prior or latter to performing the behaviour

Turn toward: orienting body in the direction of opponent (combined with other aggression behaviours that indicate behavioural context is hostile intent)

Advance toward: purposed walking toward opponent (combined with other aggression behaviours that indicate behavioural context is hostile intent)

Charge: running toward opponent (combined with spread ears and raised head), may stop abruptly (mock charge) or follow through to physical contact with opponent, tusks first (real charge)

Pursuit: aggressively following or chasing an opponent. Often occurs after another agonistic interaction – whereby the victor pursues the defeated elephant

Pushing: physically pushing another elephant off a resource (e.g. mudhole) or out of a desired location (e.g. point where conspecific is drinking), typically with the head

Tusking: more aggressive form of pushing, the tusks are used to poke another elephant off a resource or desired location

It was rare that the behaviours listed above were performed in isolation, many behaviours are often used in combination or routine succession from one another, E.g. elephants may (1) advance toward a conspecific, with (2) head held high and (3) ears spread. In the case where multiple behaviours were recruited in the overall aggressive act, the event was still only recorded as 1 event, for example the example given above would be 1 event.

A new aggressive event was only recorded if between there had been a seizure of previous aggressive behaviours (e.g. advance towards halted, and ears returned to relaxed posture), or there was a drastic change in intensity of the aggressive act. For example, an elephant performing “standing tall” posture in the direction of an opponent, transitioning to a sudden charge would be recorded as 2 events. Most aggressive acts were however short, distinct and easy to quantify as individual events, with elephants quickly returning to a relaxed state following temporary conflict.

Note S4: Behaviours recorded as events of “aggression to non-elephant targets” (towards non-conspecific species, vehicles as well as unknown targets) directed by focal elephants.

Over the accumulative approximate 273 hours of focal follow observation most aggression to non-elephant targets was of a display nature, physical contact with the target was only observed in a few instances of bush-bashing behaviour. The most frequently performed behaviour was the headshake. Distribution of targets of non-elephant directed aggression can be found in Figure S3. Elephant behaviours compiled from the work of Poole & Granli (2011) and Estes (1991) as well as own observations:

Head high: head held above shoulders, with chin tucked in

Spreading ears: ears spread out perpendicular to body in direction of threat or irritant

Folding ears: pressing lower portion of ears towards body, leading to a distinct ridge to appear across ear

Standing tall: head held above shoulders, tusks raised, often looking down towards threat or irritant

Throwing trunk toward: swinging trunk in direction of irritant or threat, may be combined with throwing of objects and debris

Head jerk: rapid upward movement of the head towards threat or irritant

Head shake: twisting of head to one side, followed by rapid shake/ rotation of head from side to side, with the contact of ears to neck skin causing a load slap. Most typical of the recorded aggression directed at “unknown” target, whilst suggested to be a behaviour performed out of elephant experiencing annoyance or irritation over current situation, headshakes were often performed towards no obvious threatening target or irritant

Turn toward: orienting body in the direction of threat or irritant (combined with other aggression behaviours that indicate behavioural context is hostile intent)

Advance toward: purposed walking toward threat or irritant (combined with other aggression behaviours that indicate behavioural context is hostile intent)

Mock charge: running toward threat or irritant, combined with spread ears and raised head, halting abruptly ahead of making physical contact

Pursuit: aggressively following or chasing a threat or irritant

Tusking vegetation/ Bush-bashing: Violent thrashing of vegetation with head and tusks in non-playful context

See Note S3 for details on how individual aggression events recorded, as individual aggression events typically employ a combination of listed behaviours performed together.

Note S5: Behaviours recorded as events of “fear to non-elephant targets” (towards non-conspecific species, vehicles as well as unknown targets) directed by focal elephants.

Distribution of targets of non-elephant directed fear can be found in Figure S3. Elephant behaviours compiled from the work of Poole & Granli (2011) and Estes (1991) as well as own observations:

Flattening ears: ears flattened against the body

Tail raised: holding tail erect, typically to horizontal position, may wrap to one side around the body

Jaw tilted upward: lifted jaw posture, with ears slightly spread, when combined with moving away from threat, elephant may look back over shoulder to threat

Turn away: rapid turning away from perceived threat (combined with other fear behaviours that indicate behavioural context is fearful)

Backing away/ retreat: moving away from perceived threat (combined with other fear behaviours that indicate behavioural context is fearful)

Running away: fleeing from perceived threat with fast pace

As with aggressive behaviours, it was rare that the behaviours listed above were performed in isolation, often many of the behaviours listed were performed in combination or in succession from one another and treated as one event for analysis. A new fearful event was only recorded if there had been a seizure of previous fearful behaviours (e.g. retreat halted, and body returned to relaxed posture), or there was a drastic change in intensity of the fearful behaviour. For example, an elephant backing from a non-elephant threat with ears held flat and head low, transitioning to running away with tail raised would be recorded as 2 events.

We excluded apprehensive behaviours discussed in the literature, such as displacement feeding, displacement grooming, touching face etc. (Poole & Granli, 2011), due to ambiguity in quantifying these behaviours.

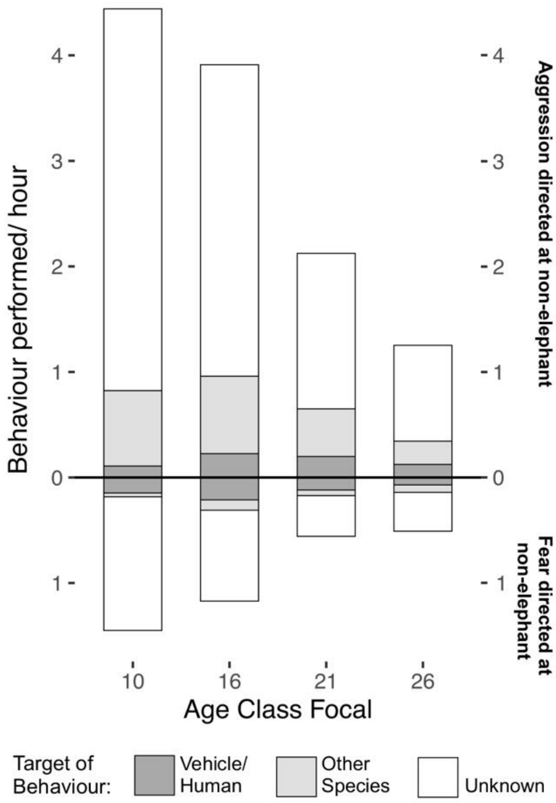


Figure S3: Distribution of targets of aggression and fear behaviours to non-elephant targets by age class (10= 10-15 years, 16= 16-20 years, 21= 21-25 years, 26= 26+ years). Accumulated total number of all observed instances of behaviours, from all focal follows, controlled for by sample time collected for each age class.

Note S6: Addressing temporal autocorrelation in the study.

Lack of temporal independence between 10-minute follows may impact expression of behaviours through autocorrelation, activity fatigue or state-behaviour feedback effects (Sih et al., 2015; Mitchell et al., 2019). To be conservative, for all our models exploring performance of behaviours of interest, we included a fixed effect of whether this aggression behaviour had been performed in the preceding 10-minute follow to control for the influence of temporal autocorrelation.

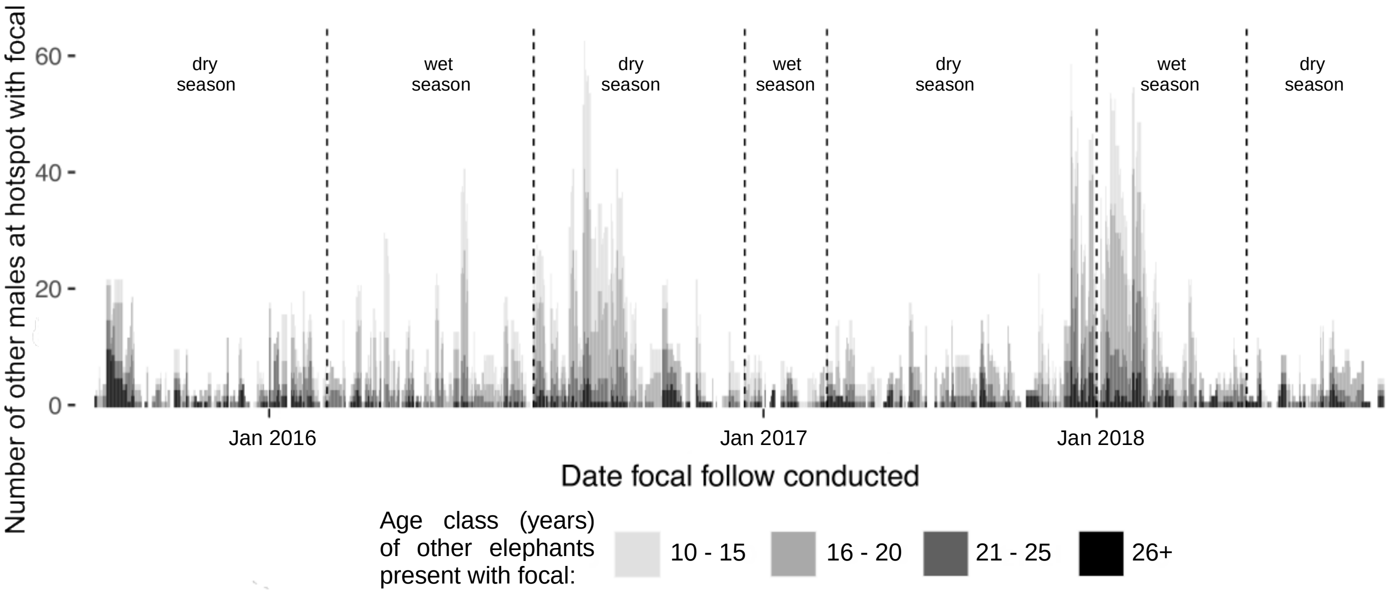


Figure S4: Number of elephants present at hotspots during focal follows (excludes focal), including ages. Dry and wet season periods indicated. More elephants were present at hotspot with focals in the wet season than in the dry season (average number of elephants present at hotspot with focal in dry season= 8.94, wet season= 10.35, Wilcoxon rank sum test with continuity correction: W= 209540, p= 0.038).

Note S7: Determination of Season

Timing of arrival of rains, and volume of rainfall varied from year to year, so season was determined using rainfall records at the Elephants for Africa research camp (GPS coordinates: 20°27'28.42"S, 24°30'56.52"E) over the course of the study (September 2015- September 2018). Onset of the wet season was defined by the first substantial rainfall, over 15 mm, as in previous years this volume tended to mark the beginning of regular rainfall. Onset of the dry season was defined as 14 days after the last rainfall (regardless of volume), this lag was to account for the potential presence of surface water holding away from the Boteti River, and for the period following last rains where vegetation was still of high quality.

Table S3: Output of GLMM – focal age category, season, hotspot location, previously directed fear, social isolation, and interaction between focal age category and social isolation conditions' effect on likelihood of elephant subject directing fear behaviours to non-elephant targets during a 10-min focal follow. Focal ID included as random effect. Reference class of age category switched to obtain effect of social condition on adolescents and adults.

Table S3: Dependent variable: Fear directed at non-elephant target Reference Class - Adolescent				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-1.753	0.173 (0.113-0.264)	**<0.001 ***
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.625	0.535 (0.350-0.819)	**0.004 ***
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	1.021	2.775 (1.236-6.230)	**0.013 ***
Season	Dry	*Ref*	*Ref*	
	Wet	-0.434	0.648 (0.408-1.027)	0.065
Hotspot location	1	*Ref*	*Ref*	
	2	-0.395	0.674 (0.413-1.097)	0.113
	3	-0.353	0.703 (0.224-2.203)	0.545
	4	-0.272	0.762 (0.404-1.436)	0.400
	5	-0.282	0.754 (0.250-3.799)	0.616
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		-0.857	2.357 (1.462-3.799)	**0.004 ***
Social Condition* Age category	Adult*Alone	-0.834	0.434 (0.112-1.676)	0.226
Reference Class – Adult				
Intercept		-2.378	0.093 (0.063-0.136)	**<0.001 ***
Age category	Adolescent	0.625	1.868 (1.221-2.857)	**0.004 ***
	Adult	*Ref*	*Ref*	
	With elephants	*Ref*	*Ref*	

Social Condition	Alone	0.187	1.206 (0.407-3.570)	0.736
Season	Dry	*Ref*	*Ref*	
	Wet	-0.434	0.648 (0.408-1.027)	0.065
Hotspot location	1	*Ref*	*Ref*	
	2	-0.395	0.674 (0.413-1.097)	0.113
	3	-0.353	0.703 (0.224-2.203)	0.545
	4	-0.272	0.762 (0.404-1.436)	0.400
	5	-0.282	0.754 (0.250-3.799)	0.616
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		-0.857	2.357 (1.462-3.799)	**0.004 ***
Social Condition* Age category	Adolescent *Alone	0.834	2.302 (0.597-8.880)	0.226

Table S4: Output of GLMM – focal age category, season, hotspot location, previously directed aggression, social isolation, and interaction between focal age category and social isolation conditions' effect on likelihood of elephant subject directing aggression behaviours to non-elephant targets during a 10-min focal follow. Focal ID included as random effect. Reference class of age category switched to obtain effect of social condition on adolescents and adults.

Table S4: Dependent variable: Aggression directed at non-elephant target Reference Class – Adolescent				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-0.498	0.608 (0.414-0.894)	**0.011 ***
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.982	0.375 (0.265-0.530)	**< 0.001 ***
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	0.965	2.624 (1.157-5.955)	**0.021 ***
Season	Dry	*Ref*	*Ref*	
	Wet	0.122	1.130 (0.777-1.643)	0.523
Hotspot location	1	*Ref*	*Ref*	
	2	-0.194	0.824 (0.550-1.235)	0.348
	3	-0.127	0.880 (0.352-2.202)	0.786
	4	-0.383	0.682 (0.408-1.138)	0.143
	5	0.372	1.450 (0.634-3.316)	0.379
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.627	1.871 (1.405-2.492)	**<0.001 ***
Social Condition* Age category	Adult*Alone	-0.638	0.529 (0.173-1.617)	0.264

Reference Class – Adult				
Intercept		-1.479	0.228 (0.163-0.318)	**<0.001 ***
Age category	Adolescent	0.982	2.669 (1.886-3.776)	**<0.001 ***
	Adult	*Ref*	*Ref*	
Social Condition	With elephants	*Ref*	*Ref*	
	Alone	0.327	1.387 (0.647-2.974)	0.400
Season	Dry	*Ref*	*Ref*	
	Wet	0.122	1.130 (0.777-1.643)	0.523
Hotspot location	1	*Ref*	*Ref*	
	2	-0.194	0.824 (0.550-1.235)	0.348
	3	-0.127	0.880 (0.352-2.202)	0.786
	4	-0.383	0.682 (0.408-1.138)	0.143
	5	0.372	1.450 (0.634-3.316)	0.379
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.627	1.871 (1.405-2.492)	**<0.001 ***
Social Condition* Age category	Adolescent *Alone	0.638	1.892 (0.619-5.787)	0.264

Table S5: Means and standard deviations of the number of each age class present at hotspots with adult and adolescent focal elephants (excludes elephants sighted alone). The mean number of other elephants of each age class present during focal follows significantly differed between adolescent and adult subjects (Wilcoxon rank sum tests with continuity correction; Mean N of 10-15 years males present at hotspot with focal: W= 252610, p<0.001; Mean N of 16-20 years males present at hotspot with focal: W=195972, p<0.001; Mean N of 21-25 years males present at hotspot with focal: W=182296, p<0.001; Mean N of 26+ years males present at hotspot with focal: W=175750, p<0.001).

Age category of subject	**Mean (Standard deviation) number of other age classes of male elephants at hotspot with focal**			
	10-15 years	**16-20 years**	**21-25 years**	**26 + years**
Adolescent (10-20 years)	3.50 (4.47)	4.12 (4.88)	2.00 (2.47)	0.850 (1.43)

Adult (21+ years)	2.29 (3.41)	4.32 (4.87)	2.30 (2.40)	1.21 (1.51)

Table S6: Output of GLMM – focal age category, season, hotspot location, previous aggression directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing aggression to conspecifics. Focal ID included as random effect.

Table S6: Dependent variable: Aggression directed at conspecific				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-2.029	0.131 (0.077-0.224)	**<0.001 ***
Age category	Adolescent	*Ref*	*Ref*	
	Adult	0.522	1.686 (1.113-2.555)	**0.014 ***
Season	Dry	*Ref*	*Ref*	
	Wet	0.048	1.049 (0.667-1.648)	0.836
Hotspot location	1	*Ref*	*Ref*	
	2	-0.341	0.711 (0.428-1.183)	0.190
	3	0.137	1.147 (0.391-3.362)	0.803
	4	-0.513	0.599 (0.310-1.157)	0.127
	5	0.809	2.245 (1.235-2.733)	0.060
Aggression to conspecific target in 10-minute follow previous (control for temporal autocorrelation)		0.608	1.837 (1.235-2.733)	**0.003 ***
Number 10-15 year olds present		0.059	1.061 (0.983-1.146)	0.131
Number 16-20 year olds present		-0.026	0.975 (0.901-1.054)	0.516
Number 21-25 year olds present		0.021	1.021 (0.904-1.153)	0.736
Number 26+ years present		-0.103	0.902 (0.764-1.064)	0.222

Table S7: Output of GLMM – focal age category, season, hotspot location, previous fear directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing fear to non-elephant target. Focal ID included as random effect.

Table S7: Dependent variable: Fear directed at non-elephant target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-1.575	0.207 (0.116-0.369)	**<0.001 ***
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.586	0.556 (0.345-0.897)	**0.016 ***
Season	Dry	*Ref*	*Ref*	
	Wet	-0.303	0.739 (0.436-1.251)	0.260
Hotspot location	1	*Ref*	*Ref*	
	2	-0.406	0.667 (0.370-1.202)	0.178
	3	-0.362	0.696 (0.184-2.639)	0.595
	4	-0.155	0.856 (0.424-1.732)	0.666
	5	0.001	1.001 (0.311-3.221)	0.998
Fear to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.327	1.387 (0.774-2.486)	0.272
Number 10-15 year olds present		0.113	1.120 (1.023-1.226)	**0.015 ***
Number 16-20 year olds present		-0.082	0.922 (0.831-1.022)	0.123
Number 21-25 year olds present		-0.127	0.881 (0.735-1.056)	0.171
Number 26+ years present		0.050	1.051 (0.874-1.265)	0.595

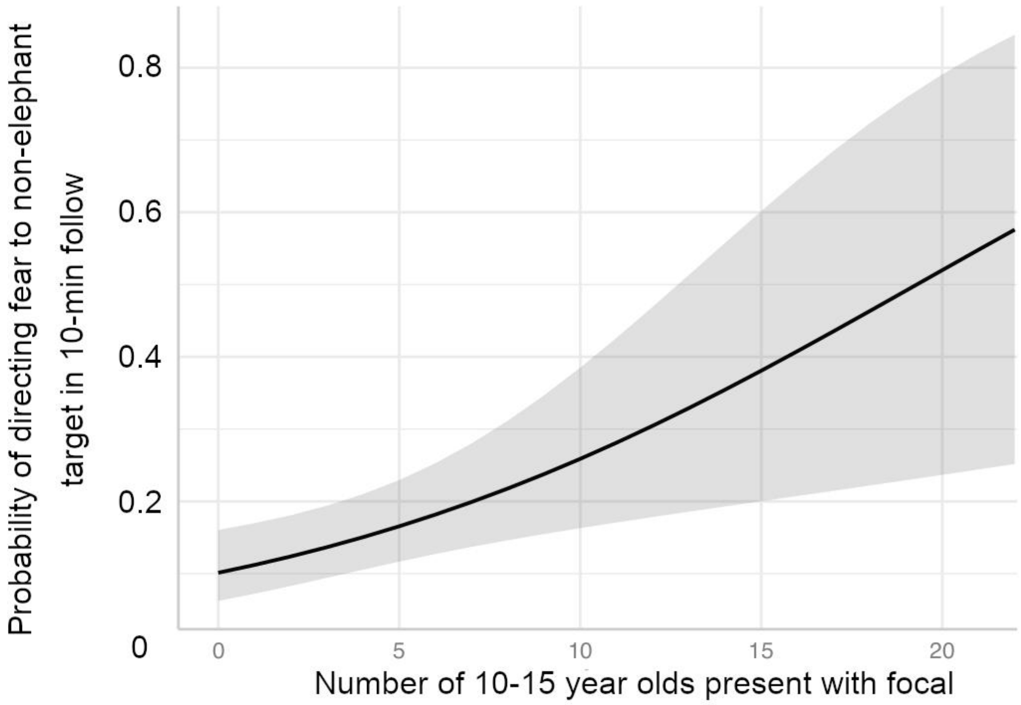


Figure S5: Elephants were more likely to direct fear behaviours to non-elephant targets with greater numbers of 10-15 year olds present with them at hotspots. Grey area represents 95% confidence intervals based on standard errors (Supplementary Table S7 for output of GLMM).

Table S8: Output of GLMM, focal age category, season, hotspot location, previous aggression directed and number of elephants of each class present at hotspot with focals' effect on likelihood of focal subject directing aggression to non-elephant targets. Focal ID included as random effect.

Table S8: Dependent variable: Aggression directed at non-elephant targets.				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-0.142	0.868 (0.542-1.389)	0.554
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.972	0.378 (0.263-0.544)	**<0.001 ***
Season	Dry	*Ref*	*Ref*	
	Wet	-0.000	1.000 (0.671-1.490)	0.999
Hotspot location	1	*Ref*	*Ref*	
	2	-0.401	0.670 (0.431-1.041)	0.075

	3	-0.232	0.793 (0.297-2.116)	0.643
	4	-0.559	0.572 (0.331-2.116)	**0.045 ***
	5	0.016	1.017 (0.422-2.448)	0.971
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.631	1.879 (1.382-2.555)	**<0.001 ***
Number 10-15 year olds present		-0.029	0.971 (0.906-1.041)	0.409
Number 16-20 year olds present		-0.007	0.993 (0.925-1.067)	0.852
Number 21-25 year olds present		-0.081	1.084 (0.970-1.211)	0.154
Number 26+ years present		-0.242	0.785 (0.677-0.911)	**0.001 ***

Table S9: Output of GLMM – hotspot location, previous aggression directed, focal age category and number of 26+ year olds present at hotspot with focals, and interaction between the latter two predictors' effect on likelihood of focal subject directing aggression to a non-elephant target. Focal ID included as random effect.

Table S9: Dependent variable: Aggression directed at non-elephant target				
Predictor		**Coefficient**	**aOR (+95% CI)**	**P value**
Intercept		-0.163	0.850 (0.584-1.237)	0.396
Age category	Adolescent	*Ref*	*Ref*	
	Adult	-0.950	0.387 (0.255-0.585)	**<0.001 ***
Number 26+ years present		-2.080	0.812 (0.685-0.963)	**0.017 ***
Age category* Number 26+ years present		0.035	1.035 (0.816-1.314)	0.775
Aggression to non-elephant target in 10-minute follow previous (control for temporal autocorrelation)		0.639	1.894 (1.393-2.574)	**<0.001 ***
Hotspot location	1	*Ref*	*Ref*	
	2	-0.370	0.691 (0.461-1.035)	0.073
	3	-0.185	0.831 (0.322-2.144)	0.702
	4	-0.503	0.605 (0.356-1.027)	0.063
	5	0.025	1.025 (0.441-2.385)	0.953

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