

Challenges of using behavior to monitor anthropogenic impacts on wildlife: a case study on illegal killing of African elephants

S. Z. Goldenberg^{1,2,3}, I. Douglas-Hamilton^{3,4}, D. Daballen³ & G. Wittemyer^{1,2,3}

¹ Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

² Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA

³ Save the Elephants, Nairobi, Kenya

⁴ Department of Zoology, University of Oxford, Oxford, UK

Keywords

anti-predator behavior; behavioral indicator; anthropogenic impacts; landscape of fear; *Loxodonta africana*; personality; poaching; rapid behavioral assessment.

Correspondence

Shifra Z. Goldenberg, Colorado State University, 1474 Campus Delivery, Fort Collins, CO, 80523, USA.

Tel: (970) 491-2303; Fax: (970) 491-5091

Email: shifra.z.goldenberg@gmail.com

Editor: Iain Gordon

Received 05 March 2016; accepted 14 September 2016

doi:10.1111/acv.12309

Abstract

Monitoring anthropogenic impacts on wildlife can be challenging, particularly when human activities affecting wildlife are cryptic. Using anti-predator behaviors as proxies for perceived pressure is appealing because of the relative ease with which they can be recorded and the presumed relationship between the threat of interest and a predator stimulus. However, behaviors are plastic and affected by factors unrelated to human activity. Consequently, it is critical to assess the relationship between behavioral indicators and their context before interpretation. In this study we used a combination of behavior, movement and demography from a threatened population of African elephants in northern Kenya to determine whether reaction to research vehicles was indicative of poaching pressure. We used mixed-effects models predicting reaction of elephants to observer vehicle approaches in which we treated individuals as random effects and included ecological, anthropogenic, spatial, social and demographic predictor variables. Contrary to our hypothesis, recorded levels of reactive behavior did not increase with poaching levels in either a population-level dataset or a data subset of individuals whose spatial behavior was precisely known via radio-tracking. Rather, primary productivity positively predicted reactive behavior in both datasets. This relationship was heightened by the presence of musth males in the radio-collar dataset. Reactivity was not related to the time since entering the protected areas, but increased among groups that spent less time in the protected areas. Inter-individual differences were apparent, suggesting the importance of inherent differences (e.g. personality) across groups. In our study, elephants plagued by a severe human threat did not react defensively to humans in another context, suggesting nuanced discrimination of threats. Our study demonstrates the caution that should be taken in designing studies that use behavioral indices to represent threat and contributes to a growing body of literature employing behavioral indicators to monitor wildlife populations of conservation concern.

Introduction

Animals modify their behavior to avoid predation while attempting to minimize related fitness costs (Lima & Dill, 1990). Anti-predator responses (e.g. proactive responses like grouping patterns or reactive responses like increased vigilance) have been used to monitor populations and as a proxy for mortality impacts (Caro, 2005; Creel, Schuette & Christianson, 2014). In particular, anti-predator behaviors have been measured as indicators of human activities in harvested or otherwise disturbed populations (Benhaïem *et al.*, 2008; Magige *et al.*, 2009; Reimers *et al.*, 2009;

Kiffner *et al.*, 2014; Tarakini & Crosmarty, 2014). Anti-predator behavior in wildlife may not only serve as a useful metric of threat, but can directly influence fitness via energetic trade-offs (Anthony & Blumstein, 2000; Frid & Dill, 2002; Lone *et al.*, 2015). Flight from suitable habitat and heightened vigilance may reduce access to resources and increase energy expenditure, which in turn contributes to poor body condition and decreased reproductive rates (Frid & Dill, 2002). Thus, wildlife behavior may serve as a proxy for population status or health, where direct fitness metrics are not possible or practical to collect (Bejder *et al.*, 2009).

Flightiness (quantified as flight initiation distance, time to flight or distance of flight) is the most common response recorded by researchers because of its apparent connection to predator stimuli and the relative ease with which it can be measured (Stankowich & Blumstein, 2005; Setsaas *et al.*, 2007; Benhaïem *et al.*, 2008). However, these metrics should be tailored to systems of interest; whether flightiness is effective as an anti-predator metric across evolutionarily disparate taxa should be tested. In addition, relevant variables influencing flightiness may be unavailable or unknown and therefore excluded from analyses (Gill, Norris & Sutherland, 2001; Griffin *et al.*, 2007). For instance, an anti-predator response may result from variables unrelated to the anthropogenic threat of interest like the social nature of the activity, population density, habitat quality relative to alternative sites or the presence of vulnerable young (Cooper, 2009; Moller *et al.*, 2013; Semeniuk *et al.*, 2014). Although these potential pitfalls have been recognized (Gill *et al.*, 2001), few studies using behavior to understand human impacts have also assessed the extent to which non-anthropogenic variables account for anti-predator behaviors or have assessed the applicability of such a general metric.

Despite the complications of interpreting flightiness, it may be of considerable value to wildlife managers. Poaching of wildlife is a pervasive problem (Muth, 1998; Dinerstein *et al.*, 2007; Magige *et al.*, 2009; Wittemyer, Daballen & Douglas-Hamilton, 2011), and direct information about such illegal activity is often difficult to obtain (Knapp *et al.*, 2010; Liberg *et al.*, 2012). Measuring flightiness is markedly easier and less expensive than directly measuring illegal harvest (Caro, 2005). Such behavioral indicators can advance the design and implementation of monitoring programs, enhance security operations (Anthony & Blumstein, 2000) and provide timely warning for wildlife managers (Donadio & Buskirk, 2006; Wildermuth, Anadón & Gerber, 2013).

The African savannah elephants *Loxodonta africana* of the Laikipia/Samburu ecosystem of northern Kenya – a region divided into a variety of land-use patches (Kahindi *et al.*, 2010) – comprise the second largest Kenyan elephant population and one of the largest on the continent to range primarily outside of protected areas (Omondi *et al.*, 2002). The population has been intensively studied since 1997 in a project that records social, movement and demographic parameters of individual elephants in a relatively small protected area within the ecosystem (Wittemyer, 2001). Ivory poaching is a considerable risk to these elephants (Wittemyer, 2011; Wittemyer, Daballen & Douglas-Hamilton, 2013; Wittemyer *et al.*, 2014) and the population range was designated as one of the sites for the Monitoring of Illegal Killing of Elephants (MIKE) program of the Convention on International Trade in Endangered Species (CITES). It has been intensively monitored for illegal killing since 2002 (Kahindi *et al.*, 2010). This coupling of behavioral and demographic data provides an opportunity to investigate the relationship between behavioral monitoring and high effort, demographic-based measures of human impact and to assess the utility of flight metrics in elephants.

Although some studies have examined correlations between flight behavior and demographic parameters (Müller, Eduard Linsenmair & Wikelski, 2004; Griffin *et al.*, 2007), rigorous analyses exploring potential confounding variables that may explain flight behavior are rare (Donadio & Buskirk, 2006; Kiffner *et al.*, 2014). Elephants have been shown to discriminate among threats that are associated with different levels of risk, like between garments belonging to people from different ethnic groups (Bates *et al.*, 2007) and voices belonging to people of different ages and genders (McComb *et al.*, 2014). This sophisticated ability to differentiate threats may extend to elephants' keen spatial understanding (Polansky, Kilian & Wittemyer, 2015; Wittemyer *et al.*, 2016); understanding risk inherent to area use may influence anti-predator behavior. These characteristics specific to elephants may complicate the employment of widely used flight metrics. Nonetheless, if flight behavior reliably reflects poaching levels such metrics would provide a valuable management tool to assess pressures on this wide-ranging species, particularly where monitoring ability is spatially limited relative to the population's range as in this study system. In this study, social, ecological, demographic, spatial and anthropogenic variables are related to elephant response to the approach of humans in vehicles in protected areas (where elephants are accessible for study). This behavioral metric was designed to provide an index of human threat exposure that the wide-ranging study individuals encountered in inaccessible, poorly monitored regions. We test the hypothesis that this behavioral metric collected within a protected area could serve as an index for human pressure in the greater ecosystem by assessing the relationship between elephant reactivity and illegal killing levels, collected independently. We identify the variables offering the greatest predictive insight on behavioral response of elephants to research vehicle approach and discuss the implications for wildlife management.

Materials and methods

Data collection

Research teams led by one of three primary observers collected data in Samburu and Buffalo Springs National Reserves, northern Kenya (Fig. 1), between 2000 and 2014. The reserves are unfenced, border the Ewaso Ngiro River (the only permanent water source in the region) and are situated within a complex human land-use mosaic throughout which elephants range (Omondi *et al.*, 2002). The reserves represent <10% of the monitored elephants' range (Wittemyer *et al.*, 2005a). Elephants are individually identified by ear and tusk idiosyncrasies (Douglas-Hamilton, 1972; Moss, 1996) as a part of an ongoing individual-based monitoring project (Wittemyer, 2001). Elephant ages are known from observed births or estimated using established methods (Moss, 1996). New calves are registered as they occur and individuals are considered dead when their carcasses are found or when repeatedly missing from their group (Wittemyer *et al.*, 2013). Rates and locations of poached carcasses

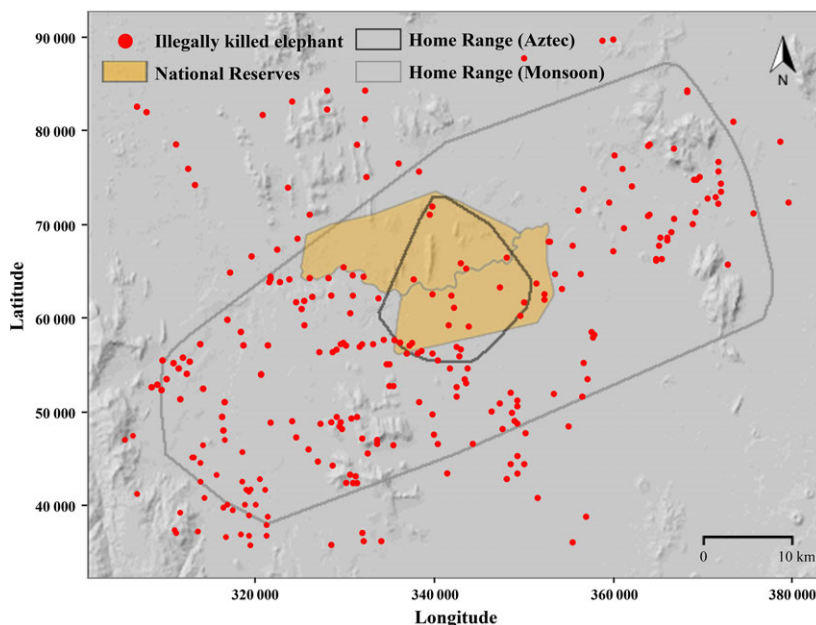


Figure 1 Poaching levels varied by elephant home range. The 95% minimum convex polygon home ranges are presented here for two radio-collared females with different space use strategies that exposed them to different levels of poaching (red dots represent poached elephant locations between 2000 and 2014).

are available from the CITES MIKE program (Kahindi *et al.*, 2010; Wittemyer *et al.*, 2014). Global positioning system (GPS) locations were available for a subset of tracked females ($n = 12$) at 1- to 3-h intervals with 5–20 m spatial accuracy, allowing accurate determination of the time each collared individual spent within or outside protected areas. Collared elephants in this study ranged from an estimated 23 to 48 years old and were associated with core groups ranging in size from 5 to 22 individuals. Observations of tracked families ranged from 5 to 87 (median = 18.5, $SD = 26.5$).

We recorded the behavioral responses of known elephants to the research vehicle, termed *reaction index* (RI), when we approached an elephant group within 20 m consistent with research protocol. The measure is a relative ranking from 1 to 4, where behavior is ranked as 1 = calm with activity uninterrupted, 2 = initially skittish but calm within 10 min, 3 = actively avoiding vehicle and 4 = running from the vehicle. RI is considered a group-level metric, as all group members generally behave similarly in the presence of a research vehicle. In addition to RI, we recorded the date, time, GPS coordinates, aggregation size (an aggregation was defined as a spatially cohesive and behaviorally coordinated group of elephants within a 500 m radius of an observer-estimated center) (Wittemyer, Douglas-Hamilton & Getz, 2005b), individuals present and presence of bulls in musth.

Data analysis

Due to very few observations of RI = 3 or 4, we consolidated RI values = 2, 3 and 4 into a single category representing reactive behavior. Similar to other systems (Kiffner *et al.*, 2014),

for the purpose of analysis we binned these behaviors as RI = 0 (did not react) and RI = 1 (did react). To examine the factors influencing RI, we fitted a set of candidate regression models with RI as the response variable. We conducted analyses on two subsets of the data: (1) from observations including radio-collared females only, and (2) from all available observations for which all breeding females present were recorded (population level). The former allowed us to analyze the effects of time since entering protected areas and home range, which we expected might influence elephant responses to human beings. Therefore, we collated information for the subset of individuals for which radio-tracking data were available, where each female represented a distinct core group (the closest level of bonding in elephant society) (Wittemyer *et al.*, 2005b).

For this radio-tracked subset, we ran generalized linear mixed-effects models with a logit link function in which core group identities were incorporated as random effects. Intercepts were allowed to vary by core group identity, thereby partitioning variance due to independent variables from inherent baseline reactivity levels of core groups and controlling for repeated measures within groups. Population-level models did not incorporate a random effect. Within the regression models, we investigated aggregation-specific covariates including aggregation size (*size*); presence/absence or number of calves present ≤ 3 months of age (based on a developmental threshold (Lee, 1986; Owen-Smith, 1988), present/absent: *calf*, count: *calves*); ratio of mature females to juveniles in the core group (*adult:juvenile*); presence or absence of a bull in musth (defined by urine dribbling, *musth*) (Poole, 1989); number of core group members that died or were wounded within 1 year prior to the date of the

observation (*mortality*); age of matriarch (*age*); time since entering the protected area (where we considered the adjacent Samburu and Buffalo Springs National Reserves a single protected area block, *time*) and proportion of months in the year that we saw the group in the protected area (*months*).

Model covariates explored on study area conditions at the time of the observation were ecosystem primary productivity measured as 10-day composite Normalized Difference Vegetation Index (*NDVI*) for a region comprising the core range use of the study population (960 km²), as described in Wittemyer, Rasmussen & Douglas-Hamilton (2007a); the proportion of illegally killed carcasses in the Laikipia/Samburu ecosystem for the year of the observation [Proportion of Illegally Killed Elephants (*PIKE*)], with higher *PIKE* values occurring in the latter years of the study (Kahindi *et al.*, 2010; Wittemyer *et al.*, 2014); and the *PIKE* value ascertained for each radio-collared female for the year of the observation within the 95% minimum convex polygon area of her home range, constructed from radio-tracking data (Median_{points}: 22 281, Range_{points}: 6891–53 066; *mcp PIKE*) (Fig. 1). We also considered the year of the observation (*year*). We assessed correlations between explanatory variables using Pearson correlations, considering two variables to be strongly correlated when $|r| > 0.6$. Only *year* and *PIKE* met this criterion. We, therefore, excluded *year* from the models because we were especially interested in the effects of poaching pressure on elephant response. All relevant covariates were available for 354 observations for the subset comprised of radio-collared elephants. For the population-level dataset that did not consider core groups independently, 3356 observations of elephant aggregations were available.

We ran models predicting the probability of a reactive response to a research vehicle in R using the *glmmADMB* and the *stats* packages (R Core Team, 2013; Skaug *et al.*, 2014). We standardized covariates prior to running models to aid in model convergence and for ease of interpretation. For each of the two datasets, we determined a set of candidate models including a global model with all uncorrelated independent variables and interactions hypothesized to be of importance (social–seasonal interactions as well as the interaction between matriarch age and young calves) (Moss, 1988; McComb *et al.*, 2011), subsets of the global model and a varying intercept-only null model for the radio-collar subset (Supporting Information Table S1). We compared models using a model selection approach, and used Akaike's information criterion corrected for small samples (*AIC_c*) as the metric for comparison with the *bbmle* package for R (Burnham & Anderson, 2002; Bolker & R Development Core Team, 2014). We present and interpret results from the top ranked model.

Statement on animal subjects

We collected data with permission from the Kenya Wildlife Service, Colorado State University, the Samburu and Isiolo County Councils and Save the Elephants (IACUC 12-3414A).

Results

Radio-collared dataset

The top model for the radio-collared female cohort (global model; Table 1) indicated *NDVI* was a strong positive predictor of elephant reactivity. *RI* during the wet season was heightened in the presence of a bull in musth and diminished with the presence of a young calf and increasing group size (Fig. 2); however, only the coefficients for *NDVI* and *NDVI* × *musth* were significant (i.e. coefficient 95% confidence intervals did not overlap 0). The proportion of months in the year that a core group spent in the protected areas was significantly negatively related to *RI* (Fig. 2). Contrary to our expectations, neither mortality data nor time since entering the protected reserves was correlated with *RI*. *PIKE* was in fact negatively related to *RI*, although this result was not significant in the radio-collar dataset. The standard deviation of random intercepts (3.03e-8) was large relative to the mean (1.48e-14), indicating that inherent differences between groups were important in this system (Table 2).

Population-level dataset

Results from the top model assessing predictors of *RI* for the population-level dataset, again, did not support our

Table 1 Ecological, social, demographic, anthropogenic and spatial variables were related to reaction of African elephants to researchers in Samburu and Buffalo Springs National Reserves, Kenya. The models accounting for ~95% of *AIC_c* weight in both the radio-tracked and population-level datasets are presented^a

Model	<i>AIC_c</i>	Δ <i>AIC_c</i>	ω_i
Radio-collar observations (<i>N</i> _{observations} = 354)			
Size + calf + adult:juvenile	259.40	0	0.57
+ musth + mortality			
+ months + age +			
time + <i>NDVI</i> + <i>PIKE</i>			
+ <i>mcp PIKE</i> + <i>NDVI</i> × size			
+ <i>NDVI</i> × calf + <i>NDVI</i>			
× musth + <i>NDVI</i>			
× adult:juvenile + calf × age			
<i>NDVI</i> + <i>NDVI</i> × size + <i>NDVI</i>	260.94	1.5	0.26
× calf + <i>NDVI</i> × musth +			
<i>NDVI</i> × adult:juvenile			
<i>NDVI</i>	262.36	3.0	0.13
All observations (<i>N</i> _{observations} = 3356)			
Size + calves + musth +	1756.13	0	1.00
<i>NDVI</i> + <i>PIKE</i> + <i>NDVI</i> × size			
+ <i>NDVI</i> × calves + <i>NDVI</i> × musth			

NDVI, Normalized Difference Vegetation Index; *PIKE*, Proportion of Illegally Killed Elephants.

^a Δ *AIC_c* represents the difference in *AIC_c* value between the model and the top-ranked model, and ω_i represents Akaike weight (totaling one across all considered models), where lower *AIC_c* values and higher weight correspond to models with greater explanatory power (see Supporting Information for a full list of candidate models and Methods for definition of model covariates).

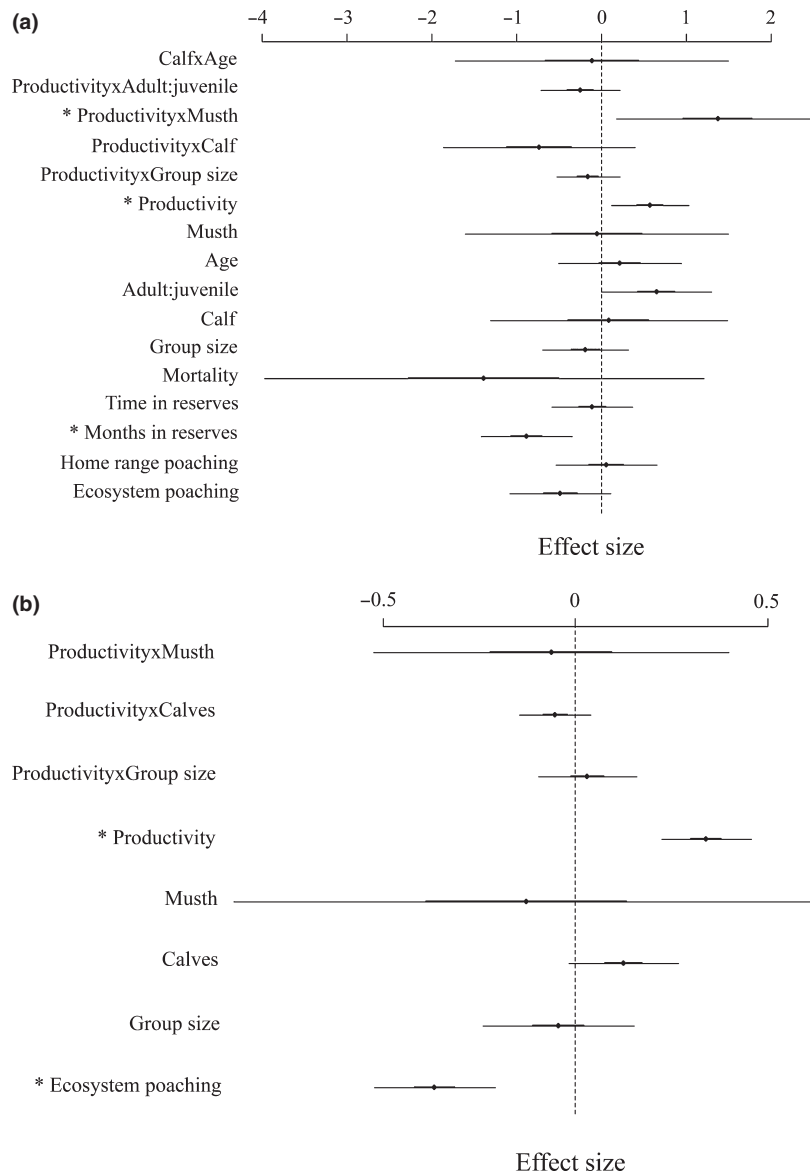


Figure 2 Standardized coefficient values from the top model for radio-collared females (top) and the population level (bottom). Asterisks denote significant coefficients. Thick and thin lines around estimates represent 50% and 95% confidence intervals, respectively.

hypothesis that an increase in illegal killing rates predicted reactivity (Table 1). Rather, *PIKE* was significantly negatively correlated with RI in the top model, and *NDVI* was significantly positively associated with a reaction (Figs 2 and 3). In addition, the number of young calves present was positively correlated with RI (Fig. 2).

Discussion

Reaction indices and illegal killing

Behavioral assessment can be a valuable and low-cost approach to monitor threats to populations; however, behavior can be influenced by multiple factors, complicating

simple interpretation of its meaning (Gill *et al.*, 2001). Our results demonstrated that a high level of poaching did not increase reactivity as recorded for the study population inside the reserves. Contrary to our expectation, *PIKE* was negatively correlated with RI, significantly so in the population-level dataset. In the subset model for which spatial use was controlled, there was no relationship between reactivity and the *PIKE* specific to an elephant’s home range. These results may be a function of the highly nuanced reactions that elephants demonstrate toward humans. Elephant defensive responses to visual, olfactory and auditory human cues recorded in a different Kenyan population captured fine-scale discrimination between ethnic groups and genders associated with different degrees of risk (Bates *et al.*, 2007; McComb

et al., 2014). It is likely that the elephants in this study did not perceive research vehicles as a threat connected to the poaching experienced outside the protected area, given that poaching in our study area is primarily conducted on foot and tourist presence (within vehicles) has been consistently high in the protected area for decades. Elephant experiences with vehicles in the reserves likely range from positive to negative, but are rarely fatal (vehicle collisions have occurred). Consistent lack of association with mortality risk may lead to tolerance of vehicles by elephants, which may be especially heightened in periods when risk from humans on foot is high.

Table 2 Intercept values in mixed-effect models predicting reactive behavior for radio-collared females represent differences among core groups in baseline reactivity levels, where higher intercept values represent elephant groups that were more likely to respond when controlling for explanatory variables

Radio-collared elephant	Intercept value
Aztec	-4.68e-8
Rosemary	-4.42e-8
Resilience	-2.22e-8
Mercury	-1.53e-8
Jerusalem	-1.44e-8
Wendy	-2.81e-10
Annabelle	-2.16e-10
Maua	1.12e-8
Goya	1.61e-8
Bonsai	3.29e-8
Amina	3.56e-8
Monsoon	4.75e-8

Furthermore, levels of poaching pressure are low inside the protected areas relative to the outlying, unprotected areas (Wittemyer *et al.*, 2013). Elephants' keen spatial knowledge (Polansky *et al.*, 2015) likely structured results in our study. Elephants have been shown to move more quickly through high-risk areas and spend more daylight hours in low-risk areas (Graham *et al.*, 2009) as well as to adjust resting patterns and circadian activity patterns relative to risk (Wittemyer *et al.*, 2014, 2016). They react strongly to a person on foot within the reserves. However, such mismatches between threats to wildlife (e.g. person on foot) and the behavioral monitoring stimulus (e.g. vehicle approach) are common, especially in areas where walking on foot is prohibited and dangerous (Frid & Dill, 2002; Caro, 2005; Donadio & Buskirk, 2006; Kiffner *et al.*, 2014). Assessing whether generalized behavioral monitoring stimuli are appropriate proxies for threat is critical; employing such proxies offers a simple and inexpensive monitoring approach, much sought if effective. In particular, monitoring of elephant populations often occurs in spatially restricted areas (e.g. baies in Central African forests) (Turkalo, Wrege & Wittemyer, 2013), where broader ecosystem monitoring is prohibitively difficult to perform.

Differences in reactivity were related to differences in spatial use across groups. Among collared groups, those that spent a greater proportion of the year within the protected areas were calmer. Repeated exposure to vehicles (tourist and researcher) likely allows elephants to more readily recognize that people in vehicles are not a threat and therefore minimize unnecessary flight responses. In contrast, time since entering the reserves by collared individuals had no effect on elephant RI. Taken together these results suggest that longer-

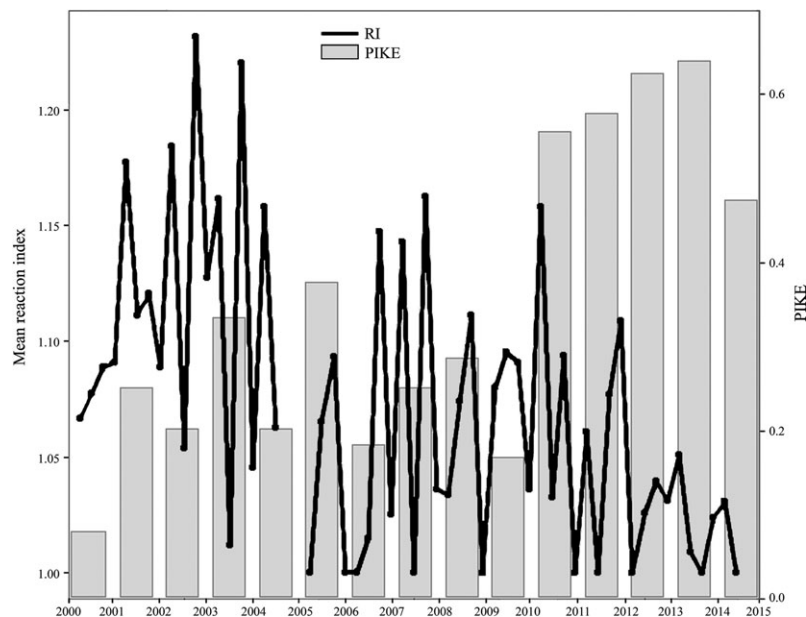


Figure 3 Mean reaction index (RI) and Proportion of Illegally Killed Elephants (PIKE). For this figure the mean of raw RI values was calculated at quarterly intervals. Annual PIKE values are plotted at the midpoint of each year.

term spatial patterns are more predictive of behavior toward human approach in the reserves and that more recent experience is less important. A trend towards lower reactivity during increased poaching could indicate an association between vehicle presence and safety, although active avoidance of vehicles was not uncommon. Our unexpected findings related to elephant behavior and human activity underscore the importance of testing the assumptions of behavioral assessment prior to interpretation of such data (Gill *et al.*, 2001; Bejder *et al.*, 2009). Complexity in the degree to which elephants adjust behavior to exploitation pressure has been observed in other systems as well (Caro, 2005; Kiffner *et al.*, 2014).

Environmental stimuli and inherent group traits

Despite reactivity not being an effective indication of poaching pressure, a number of interesting insights were gleaned through this analysis. For example, elephants were more reactive when NDVI was high in both datasets. Elephants undergo dramatic changes in body condition between the wet and dry seasons (Foley, Papageorge & Wasser, 2001; Rasmussen *et al.*, 2007; Wittemyer *et al.*, 2007a), and greater tolerance of potential threats during the dry season may reflect a physiological state of energy conservation rather than risk assessment (Gill *et al.*, 2001). The study elephants expand their range and travel more during the wet season (Wittemyer *et al.*, 2007b), and reactivity may therefore also relate to changing movement patterns and associated risks on the landscape, although the fine-scale spatial variables did not emerge as important in analyses. In addition, increased forage availability (and related increased physiological condition) during the wet season corresponds to a period of greater social activity, with the largest aggregation sizes (Wittemyer, 2001) and the majority of mating and birthing events (Wittemyer *et al.*, 2007a) occurring during that time. The positive interaction found between NDVI and the presence of a musth bull supports the idea that reproductive events heighten excitement in elephants which in turn influences response to human observers.

While primary productivity and group composition strongly predicted elephant response, model intercepts varied considerably among core groups, indicating that baseline differences in the temperament across groups existed. Social animals may gauge their anti-predator responses by the responses of those around them, which may be especially relevant where more experienced, dominant or bolder individuals are present in the group. In elephant society matriarchs may have disproportionate effects on group behavior (McComb *et al.*, 2001; Foley, Pettoelli & Foley, 2008); observed differences among groups may therefore relate to inherent differences among matriarchs, although the collection of RI as a group metric limited such inference here. Inherent matriarch effects may also interact with environmental covariates. For example, differences in social dominance among individuals are correlated with differential use of the protected areas (Wittemyer *et al.*, 2007b), which itself was a

predictor of group behavior. Lower reactivity could therefore relate to individual traits like dominance, potentially complicating the ability to characterize level of threat within the ecosystem based on individual responses unless their social context is determined.

Implications for personality research

While aspects of this study are specific to elephant behavior, our findings hold implications for the use of behavior to assess human impact in wild populations and extend to other disciplines like personalities (Dall, Houston & McNamara, 2004). Reaction to a human observer is often employed as a measure of shyness–boldness (Réale *et al.*, 2007). Although such metrics may represent inter-individual differences along the shyness–boldness personality continuum, it is also possible that they are more reflective of the subject's recent experiences, reproductive state or ecological conditions. In our case, environmental context was a strong driver of our behavioral metric. Mixed-effects models allow investigation of such behavioral metrics by partitioning the variance due to differences among individuals while controlling for the effects of environmental variables (Dingemanse & Dochtermann, 2013). Individual intercepts can thereby be interpreted as metrics of personality, after controlling for external stimuli that influence the behavioral metric. In this particular study, the behavioral measure was a group-level metric and therefore not easily used for personality measures. However, matriarchs are known to disproportionately affect group behavior, which may be true for group responses to predator stimuli. As such, the variation among core group intercepts reported here potentially reflected personality differences among matriarchs. In this case, elephants with higher intercepts might be considered less bold or more reactive than the rest of the individuals in the sample.

Ensuring the utility of flight response monitoring

In addition to demonstrating the complexities of behavioral assessment, our study highlights the need to extend such research beyond conventionally adopted flight metrics and tailor metrics for greater relevance to the system of interest (Gill *et al.*, 2001; Kiffner *et al.*, 2014). Elephants assess threat using olfactory, auditory and visual cues (Bates *et al.*, 2007; McComb *et al.*, 2014), and cues of researchers are different from those of the people who might present risk to elephants in this system. Behavioral studies should be carefully designed to address potential mismatches between threats to wildlife and anti-predator stimuli. Efforts should also be made to measure other variables that may affect the study species, like availability of alternative habitat, seasonal constraints on activities like breeding or socializing and presence of vulnerable young. Furthermore, behavioral manifestations unrelated to human stimuli may also be informative. For example, we have observed instances in which elephants known to have experienced poaching events responded calmly to research vehicles in the days following the event but were generally skittish toward

other stimuli unrelated to humans. Recognition of such nuances in study systems will be critical for the effective use of behavioral indicators (increasingly being advocated for use in the conservation of species that are difficult to monitor) (Berger-Tal & Saltz, 2016) to characterize population threats and trends. Finally, it is essential for researchers to account for confounding proximate variables that may explain wildlife behavior in studies measuring personality traits or effects of human disturbance. The mixed-effects approach implemented here provides a promising avenue for future work in both fields, where inherent differences among individuals may be separated from environmental variables (Dingemans & Dochtermann, 2013).

Acknowledgments

We thank the Kenyan Office of the President, the Kenya Wildlife Service and the Samburu and Isiolo County governments for permission to work in Samburu and Buffalo Springs National Reserves. Funding was provided by the National Science Foundation Graduate Research Fellowship number DGE-1321845 (S.Z.G.) and Save the Elephants.

References

- Anthony, L.L. & Blumstein, D.T. (2000). Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce Ne. *Biol. Conserv.* **95**, 303–315.
- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Moss, C.J., Poole, J.H. & Byrne, R.W. (2007). Elephants classify human ethnic groups by odor and garment color. *Curr. Biol.* **17**, 1938–1942.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H. & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* **395**, 177–185.
- Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A.J.M., Morellet, N. & Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Anim. Behav.* **76**, 611–618.
- Berger-Tal, O. & Saltz, D. (2016). *Conservation behavior: applying behavioral ecology to wildlife conservation and management*. Cambridge: Cambridge University Press.
- Bolker, B. & R Development Core Team. (2014). *bbmle: Tools for general maximum likelihood estimation*. R Package version 1.0.17.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multi-model inference: a practical information-theoretic approach*. Berlin: Springer.
- Caro, T.M. (2005). Behavioural indicators of exploitation. *Ethol. Ecol. Evol.* **17**, 189–194.
- Cooper, W.E. (2009). Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behav. Ecol. Sociobiol.* **63**, 1765–1771.
- Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.* **25**, 773–784.
- Dall, S.R.X., Houston, A.I. & McNamara, J.M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739.
- Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., *et al.* (2007). The fate of wild tigers. *Bioscience* **57**, 508.
- Dingemans, N.J. & Dochtermann, N.A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54.
- Donadio, E. & Buskirk, S.W. (2006). Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biol. Conserv.* **127**, 139–145.
- Douglas-Hamilton, I. (1972). *The ecology and behaviour of the African elephant: the elephants of Lake Manyara*. PhD thesis, University of Oxford, Oxford, UK.
- Foley, C.A.H., Papageorge, S. & Wasser, S.K. (2001). Noninvasive stress and reproductive measures of social and ecological pressures in free ranging African elephants. *Conserv. Biol.* **15**, 1134–1142.
- Foley, C., Pettorelli, N. & Foley, L. (2008). Severe drought and calf survival in elephants. *Biol. Lett.* **4**, 541–544.
- Frid, A. & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* **6**, 11.
- Gill, J., Norris, K. & Sutherland, W. (2001). Why behavioural responses may not reflect the population consequences of human disturbance. *Biol. Conserv.* **97**, 265–268.
- Graham, M.D., Douglas-Hamilton, I., Adams, W.M. & Lee, P.C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Anim. Conserv.* **12**, 445–455.
- Griffin, S.C., Valois, T., Taper, M.L. & Scott Mills, L. (2007). Effects of tourists on behavior and demography of Olympic marmots. *Conserv. Biol.* **21**, 1070–1081.
- Kahindi, O., Wittemyer, G., King, J., Ihwagi, F., Omondi, P. & Douglas-Hamilton, I. (2010). Employing participatory surveys to monitor the illegal killing of elephants across diverse land uses in Laikipia-Samburu, Kenya. *Afr. J. Ecol.* **48**, 972–983.
- Kiffner, C., Kioko, J., Kissui, B., Painter, C., Serota, M., White, C., *et al.* (2014). Interspecific variation in large mammal responses to human observers along a conservation gradient with variable hunting pressure. *Anim. Conserv.* **17**, 603–612.
- Knapp, E.J., Rentsch, D., Schmitt, J., Lewis, C. & Polasky, S. (2010). A tale of three villages: choosing an effective method for assessing poaching levels in western Serengeti, Tanzania. *Oryx* **44**, 178.
- Lee, P.C. (1986). Early social development among African elephant calves. *Natl. Geogr. Res.* **2**, 388–401.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012). Shoot, shovel and shut up:

- cryptic poaching slows restoration of a large carnivore in Europe. *Proc. Roy. Soc. B. Biol. Sci.* **279**, 910–915.
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Lone, K., Loe, L.E., Meisingset, E.L., Stamnes, I. & Mysterud, A. (2015). An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim. Behav.* **102**, 127–138.
- Magige, F.J., Holmern, T., Stokke, S., Mlingwa, C. & Røskaft, E. (2009). Does illegal hunting affect density and behaviour of African grassland birds? A case study on ostrich (*Struthio camelus*). *Biodivers. Conserv.* **18**, 1361–1373.
- McComb, K., Moss, C., Durant, S.M., Baker, L. & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science* **292**, 491–494.
- McComb, K., Shannon, G., Durant, S.M., Sayialel, K., Slotow, R., Poole, J., *et al.* (2011). Leadership in elephants: the adaptive value of age. *Proc. Roy. Soc. B.* **278**, 3270–3276.
- McComb, K., Shannon, G., Sayialel, K.N. & Moss, C. (2014). Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proc. Natl. Acad. Sci. USA* **111**, 5433–5438.
- Moller, A.P., Grim, T., Ibanez-Alamo, J.D., Marko, G. & Tryjanowski, P. (2013). Change in flight initiation distance between urban and rural habitats following a cold winter. *Behav. Ecol.* **24**, 1211–1217.
- Moss, C.J. (1988). *Elephant memories: thirteen years in the life of an elephant family*. Chicago: University of Chicago Press.
- Moss, C.J. (1996). Getting to know a population. In *Studying elephants*: 58–74. Kangwana, K. (Ed.). Nairobi: African Wildlife Foundation.
- Müllner, A., Eduard Linsenmair, K. & Wikelski, M. (2004). Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biol. Conserv.* **118**, 549–558.
- Muth, R.M. (1998). The persistence of poaching in advanced industrial society: meanings and motivations – an introductory comment. *Soc. Nat. Resour.* **11**, 5–7.
- Omondi, P., Bitok, E., Kahindi, O. & Mayienda, R. (2002). *Total aerial count of elephants in Laikipia/Samburu ecosystem*. Nairobi, Kenya: Kenya Wildlife Service.
- Owen-Smith, R.N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge: Cambridge University Press.
- Polansky, L., Kilian, W. & Wittemyer, G. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *Proc. Biol. Sci.* **282**, 20143042.
- Poole, J.H. (1989). Announcing intent: the aggressive state of musth in African elephants. *Anim. Behav.* **37**, 140–152.
- R Core Team. (2013). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rasmussen, H.B., Okello, J.B.A., Wittemyer, G., Siegismund, H.R., Arctander, P., Vollrath, F., *et al.* (2007). Age- and tactic-related paternity success in male African elephants. *Behav. Ecol.* **19**, 9–15.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T. & Dingemanse, N.J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* **82**, 291–318.
- Reimers, E., Loe, L.E., Eftestøl, S., Colman, J.E. & Dahle, B. (2009). Effects of hunting on response behaviors of wild reindeer. *J. Wildl. Mgmt.* **73**, 844–851.
- Semeniuk, C.A.D., Musiani, M., Birkigt, D.A., Hebblewhite, M., Grindal, S. & Marceau, D.J. (2014). Identifying non-independent anthropogenic risks using a behavioral individual-based model. *Ecol. Complex.* **17**, 67–78.
- Setsaas, T.H., Holmern, T., Mwakalebe, G., Stokke, S. & Røskaft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas? A case study from the Serengeti Ecosystem, Tanzania. *Biol. Conserv.* **136**, 563–570.
- Skaug, H., Fournier, D., Bolker, B., Magnusson, A. & Nielson, A. (2014). *Generalized linear mixed models using AD model builder*. R Package version 0.8.0.
- Stankowich, T. & Blumstein, D.T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proc. Biol. Sci.* **272**, 2627–2634.
- Tarakini, T. & Crosmay, W. (2014). Flight behavioural responses to sport hunting by two African herbivores. *S. Afr. J. Wildl. Res.* **44**, 76–83.
- Turkalo, A.K., Wrege, P.H. & Wittemyer, G. (2013). Long-term monitoring of dzanga bai forest elephants: forest clearing use patterns. *PLoS ONE* **8**, e85154.
- Wildermuth, R.P., Anadón, J.D. & Gerber, L.R. (2013). Monitoring behavior: assessing population status with rapid behavioral assessment. *Conserv. Lett.* **6**, 86–97.
- Wittemyer, G. (2001). The elephant population of Samburu and Buffalo Springs national reserves, Kenya. *Afr. J. Ecol.* **39**, 357–365.
- Wittemyer, G. (2011). Effects of economic downturns on mortality of wild African elephants. *Conserv. Biol.* **25**, 1002–1009.
- Wittemyer, G., Daballen, D., Rasmussen, H., Kahindi, O. & Douglas-Hamilton, I. (2005a). Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. *Afr. J. Ecol.* **43**, 44–47.
- Wittemyer, G., Douglas-Hamilton, I. & Getz, W. (2005b). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.* **69**, 1357–1371.
- Wittemyer, G., Barner Rasmussen, H. & Douglas-Hamilton, I. (2007a). Breeding phenology in relation to NDVI variability in free-ranging African elephant. *Ecography (Cop.)* **30**, 42–50.
- Wittemyer, G., Getz, W.M., Vollrath, F. & Douglas-Hamilton, I. (2007b). Social dominance, seasonal movements, and

- spatial segregation in African elephants: a contribution to conservation behavior. *Behav. Ecol. Sociobiol.* **61**, 1919–1931.
- Wittemyer, G., Daballen, D. & Douglas-Hamilton, I. (2011). Rising ivory prices threaten elephants. *Nature* **476**, 282.
- Wittemyer, G., Daballen, D. & Douglas-Hamilton, I. (2013). Comparative demography of an at-risk African elephant population. *PLoS ONE* **8**, e53726.
- Wittemyer, G., Northrup, J.M., Blanc, J., Douglas-Hamilton, I., Omondi, P. & Burnham, K.P. (2014). Illegal killing for ivory drives global decline in African elephants. *Proc. Natl. Acad. Sci.* **111**, 13117–13121.
- Wittemyer, G., Keating, L.M., Vollrath, F. & Douglas-Hamilton, I. (2016). Graph theory illustrates spatial and temporal features that structure elephant rest locations and reflect risk perception. *Ecography (Cop.)* **39**, 001–008.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. List of candidate models.