



# Elephants rest more when the poaching risk is high and do not recover the lost time within a diel cycle

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## ABSTRACT

Poaching for ivory has caused disturbances in the behaviour of elephants. The nature and magnitude of such disturbance are not yet fully understood. Here, we studied the daily activity cycles of 10 elephants tracked for a minimum of two years each in the Samburu ecosystem in Kenya. The elephants were tracked over a spatial or temporal gradient of poaching risk in their distribution area. Laikipia Samburu landscape is shared with humans and is a mosaic of land ownership and management practices, all of which lead to varied levels of illegal killing. Using movement data of elephants tracked on various dates between 2002 and 2016, we studied the daily activity cycle when they were in their different core areas. Using Generalized Additive Models, we found that elephants moved less around midday in high poaching areas. Despite the adaptive shift in activity times, elephants were moving for fewer hours per day in areas with higher risk, reducing total movement daily in risky areas or times. The elephants lost one hour daily from their usual movement time when they went into high-risk areas, which they did not compensate for despite increased activity at dawn and dusk. The level of illegal killing was the best explanatory variable for altering the activity cycle. We infer that such risk avoidance behaviour culminates in the potential reduction of foraging efforts in a risky area. A deficit in their activity time may have consequences for their social life, reproduction, or overall foraging success, aspects of elephant ecology that are not fully understood yet. We discuss the results in light of the increasing need for more fine-scale temporal analyses of the influence of risk on the diel activity of elephants for sites that achieve both movement data and verified records of causes of elephant deaths.

## 1. Introduction

Predation risk alters the behaviour of large herbivores in space and time, frequently involving shifts in spatial and temporal

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patterns to avoid overlapping with their respective predator (Tambling et al., 2015). Avoiding encounters with a predator may increase the probability of its survival in the short term but may compromise its long-term survival (Wang and Zou, 2017; Cresswell, 2011; Creel and Christianson, 2008). The magnitude of antipredator behavioural responses to direct predation is expected to be stronger under higher risk (Davies et al., 2016; Wang and Zou, 2017). For example, prey species may reduce activity levels during periods and areas of high risk to reduce encounter and detection probability (van Beest et al., 2013; Lima et al., 1999). When the predation risk is low and remains constant, animals achieve and maintain a stable level of antipredator behaviour, but when the risk fluctuates, the animals express strong antipredator behaviour in tandem with the magnitude of the risk (Lima and Bednekoff, 1999; Sih and McCarthy, 2002). Knowledge of the scale-dependent behavioural responses to predation risk is valuable for making inferences on the fitness costs incurred by a prey species (Lima and Dill, 1990).

A global decline in the general movement of terrestrial mammals has been observed and attributed to adaptive changes in animals' behaviour over time as their environment changes (Tucker et al., 2018). The interaction between foraging and predation risk affects animal movement behaviour, as herbivores strive to minimize their possible encounter with predators (McArthur et al., 2014; Lima and Dill, 1990; Cowlshaw, 1997). Predation risk may lead to an overall loss of foraging opportunities as animals adjust their movement behaviour (Eccard and Liesenjohann, 2014). Animals adapt their diel pattern of movement to the magnitude of predation risk (Lima, 2002; Lima and Dill, 1990; Brown et al., 1999; Creel et al., 2014). When animals can detect and respond to the risk at a fine temporal scale, the magnitude of antipredator behavioural response is commensurate with the risk level (Creel and Christianson, 2008; Sih, 2013; Hodges et al., 2014). The studies on the periods of inactivity during the midday hours have continued eliciting interest, and past studies have generally recognized the inactive period as 'resting' (Poche, 1980; Tsalyuk et al., 2019; Kalemera, 1987; du Plessis et al., 2021). Optimal foraging strategies should maximize available opportunities, especially in the core areas (Lima and Dill, 1990). A time-minimizing approach implies that an animal is attempting to minimize its exposure to temperature extremes, predators, or other environmental factors while foraging (Kie et al., 2002). Understanding the magnitude of changes in overall diel activity due to risk is essential to understanding predator-prey interactions, given their implications on foraging, energetics, interactions with conspecifics (e.g. reproduction), and other species.

Elephants (*Loxodonta africana*) are larger than the preferred prey species of sympatric carnivores, e.g. lions (*Panthera leo*), and for this reason, their diel movement behaviour pattern is not affected by these natural predators (Tambling et al., 2015). At the landscape level, home-range selection is driven by macro-scale processes like water and forage, and elephants make broad selections in favour of either based on the magnitude of the prevailing risk (Davis et al., 2023; Bastille-Rousseau and Wittemyer, 2022). Poaching and conflict with humans have become the most significant immediate threat to elephants besides 'predators' of elephants through illegal hunting (Nellemann et al., 2013). Elephants move faster when migrating through risky areas or on crop-raiding bouts (Graham et al., 2009; Douglas-Hamilton et al., 2005). Elephants increase their nocturnal activity when facing the daytime risk of human disturbance or hunting (Gaynor et al., 2018; Ihwagi et al., 2018). Finer scale signals of behavioural responses to risk by elephants are masked when studies focus on large-scale landscape dynamics (Creel et al., 2005; Bastille-Rousseau and Wittemyer, 2022). Activity peaks at dawn, dusk and midnight were reported from early field visual observations on captive elephants (Kuhme, 1962) and later on wild elephants (Wyatt and Eltringham, 1974). These early field-based observations further suggested that elephants are active for approximately 17 h a day (Ruggiero, 1989) and are least focused on foraging in areas experiencing poaching threats (Barnes, 1982; Ruggiero, 1990). The diel movement behaviour of elephants is a reliable indicator of their foraging behaviour (Polansky et al., 2013).

The Laikipia-Samburu landscape, home to an estimated 8500 elephants in northern Kenya, is a complex of land ownership and diverse land management types, with only 3 % under formal protection (Ihwagi et al., 2015). The human-dominated unprotected landscape presents a unique study area as the risk is mainly human-driven instead of the usual ecological scenario. Past studies in the landscape have focused on the behavioural response of elephants to the levels of illegal killing at large spatial and temporal scales encompassing the entire distribution (Douglas-Hamilton et al., 2005; Kioko and Seno, 2011; Wittemyer et al., 2016a; Bastille-Rousseau and Wittemyer, 2022). A few studies on the fine-scale change in the movement behaviour of elephants in the landscape in relation to risk have been accomplished, e.g., the number of resting bouts (Wittemyer et al., 2016a), path tortuosity (Ihwagi et al., 2019) and day-night speeds (Ihwagi et al., 2018). The movement of elephants and nomadic pastoralists in shared landscapes is influenced by the availability of surface water (Butt and Turner, 2012; Tyrrell et al., 2017). The presence of livestock at shared resource points in the ecosystem during the daytime in the hours could potentially influence the activity cycle because of direct competition for shared resources like drinking points and, at times, direct aggression on the elephants by herders.

The timing of elephants' response to increased poaching and fatal conflict risk in the Laikipia-Samburu ecosystem within the hours of a day is less understood. The formally designated Monitoring of Illegally Killed Elephants (MIKE) site has achieved multiple years of detailed fine-scale temporal resolution GPS tracking data across a spatial, temporal gradient of risk concurrent with a field-based body count and verification of the cause of mortality of elephants. Against the backdrop of the already documented behavioural adjustments, this study focused on the magnitude of variation of the timing of the resting phases when elephants are in low- and high-risk areas and quantified the movement time in hours within a diel cycle. We hypothesize that whilst an elephant has a choice to migrate when risk is high, if the risk is widespread or unavoidable, as it was in the Laikipia-Samburu landscape from the year 2010–2012 (Ihwagi et al., 2015), the elephants would adjust the diel behaviour accordingly likely resulting in a loss of active time.

Specifically, we sought to determine the following:

- 1) How the diel cycle of elephants is influenced by risk.
- 2) If there is a difference in the overall movement duration per day when they are within core areas with different levels of illegal killing.

We expected to see increased resting phases for individual elephants during the day, a possible compensation by moving more at night, or even a significant loss of moving hours in a diel cycle as the poaching levels intensified.

## 2. Methods

### 2.1. Study area

We conducted this study in the Laikipia-Samburu ecosystem of northern Kenya, which lies between 0.4° S to 2° N, 36.2° E to 38.3° E and has an area of 34,000 km<sup>2</sup> (Fig. 1). The ecosystem is delineated roughly by the geographical extent of the Ewaso Nyiro River and its tributaries in the lowlands between Mt. Kenya and the Aberdare ranges (Georgiadis, 2011). The ecosystem is semi-arid, with a north-south (low – high) rainfall gradient and associated range of habitats from dry lowlands to wet highlands (Georgiadis, 2011) and extensive plains interrupted by rugged terrain and isolated hills (Wall et al., 2006). Wildlife shares the landscape freely with the predominantly pastoral communities (Ihwagi et al., 2015). At the interface of the private ranches and subsistence farmers, which mark the southern limit of the ecosystem, wildlife fences are constructed to reduce human-elephant conflicts but impede elephant movement.

### 2.2. Monitoring the illegal killing of elephants (MIKE)

Under the MIKE programme, field verification of elephant mortality is an ongoing exercise that involves landowners, herders, conservancy managers and government wildlife rangers (Kahindi et al., 2010). The Proportion of Illegally Killed Elephants (PIKE) is an unbiased estimate of the poaching level (Jachmann, 2013; Douglas-Hamilton et al., 2010). The PIKE is calculated as:

$$PIKE (\%) = \frac{\text{Number of illegally killed elephants}}{\text{Total number of dead elephants recorded}} \times 100$$

We used PIKE to measure the levels of illegal killing in each of the elephants' core areas (see the definition of core area in the GPS tracking section below). To determine the PIKE values, we used 3103 elephant carcasses recorded between the years 2002 and 2016. We calculated the PIKE for each elephant's score areas from the records of mortality accumulated up to the last year it was tracked, and therefore, for each elephant, we have different levels of PIKE. We considered an elephant's core areas as distinctly different in risk level

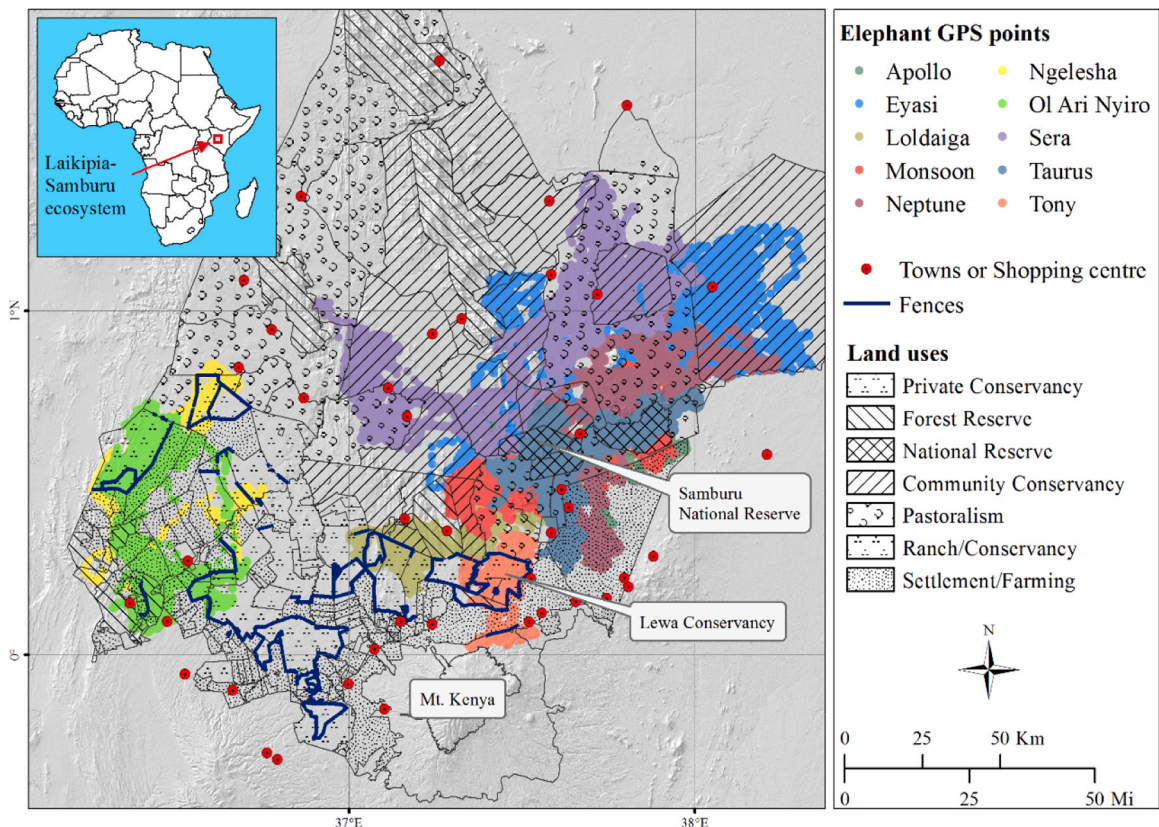


Fig. 1. GPS locations of ten elephants tracked on various dates between 2002 and 2016 in the Laikipia-Samburu ecosystem.

if their PIKE values had a difference of over 10 %. Human-elephant conflicts are incidences where unauthorized personnel, primarily farmers, kill elephants that invade their farms on the spot, or they injure elephants in a way that leads to their eventual deaths when they retreat from the farms. Although PIKE comprises both human-elephant conflict and poaching-related mortality, poaching accounts for more than 95 % of the deaths reported in the landscape from 2002 to 2014 (Ihwagi et al., 2015). The domination of poaching cases in the PIKE compared to conflict-related deaths of elephants makes the reference to PIKE akin to poaching levels.

### 2.3. GPS tracking data

The study required a careful selection of elephants tracked for an extended period encompassing several seasons, low and high poaching times, and wide-ranging traversing low and high PIKE land units. Collar technology has advanced rapidly over time. Most of the elephant collars that were deployed in the earlier years lasted for very short periods; only a few individuals were tracked (a) for over two years, (b) through low and high poaching times or across land units with a significant gradient of risk. We used movement data of ten adult elephants aged between 30 and 50, tracked on various dates from 2002 to 2016. The years 2010–2012 had high levels of illegal killing, with a peak of 73 % annual PIKE in 2012, and all other years had low levels, with a minimum of 28 % PIKE in 2002 (Ihwagi, 2018, Ihwagi et al., 2015). The elephants comprised five females from different families and five bulls. We fitted the elephants with GPS collars sourced from African Wildlife Tracking (AWT) ([www.awt.co.za](http://www.awt.co.za)) and FOLLOWIT ([www.followit.se](http://www.followit.se)), each recording a fix on the hour. Licensed government veterinarians carried out immobilization and collar deployment using standard procedures. We acquired 176,342 GPS points from 10 elephants within the core areas alone, an equivalent of 7347 elephant days (20.1 elephant years' worth of data) (Table 1). We calculated the distance between consecutive hourly GPS points from the collar data. We removed spurious GPS points corresponding to unlikely speeds >7 km/hr, i.e., points 7 km apart (Wall et al., 2013).

We used time density, a recent development for estimating home range, to delineate distinct core areas in the elephant home range's low and high PIKE zones (Wall et al., 2013; Wall et al., 2014). The time-density value estimates the proportion of total tracking time for an elephant in each grid cell of user-defined size based on the 90 % percentile value of the Weibull speed distribution. The time density method estimates the proportionate time spent in each grid out of the total tracking time based on the length of track segments within a grid. We used grid sizes measuring 500 m × 500 m, approximates to double the median hourly distance walked by elephants in the landscape (Wall et al., 2013), into which we aggregated and/or measured the values of the environmental variables. Land use and management types in the Laikipia-Samburu ecosystem are critical determinants of within-site variation in poaching gradient (Ihwagi et al., 2015). From the time-density grid of each elephant, we identified the core areas and spatially linked them to the underlying land management units, e.g., conservancies, national reserves, or ranches. The land units were adopted in full (no clipping) because they are the smallest units used for the compilation of mortality data and subsequent calculation of PIKE.

### 2.4. Environmental variables

In addition to poaching, we explored the effect of other environmental variables that vary within a daily time scale or influence an elephant's short-term movement behaviour, such as water and livestock. We compiled surface water locations acquired from ground mapping and digitized images from Google Earth imagery to create a GIS layer of potential drinking points for wildlife and livestock. The water points included wells, rivers, boreholes, dams, springs and pans. One limitation of the data we used was the inability to quantify the longevity of some of the water points. Our assumption in this regard was that when the rains fell or ceased, the number of water points per unit area increased or decreased respectively at the same rate across the landscape. Thus, the relative abundance at any time would not significantly change. For each grid cell, we calculated the Euclidean distance in meters from its centroid to the nearest potential water point and assigned the value to the grid.

During this study, two total aerial counts of large mammals and livestock were undertaken in 2008 and 2012 (Ihwagi et al., 2015). We obtained counts of all livestock species and calculated their densities in each grid. We considered this a measure of livestock's relative abundance because those were just two snapshots. The same aerial count data included records of all occupied homesteads, i.e., semi-permanent and temporary dwellings. All GIS operations to prepare the tracking and other spatial data were performed using

**Table 1**

The number of hours each of the ten tracked elephants spent in the core areas with low and high PIKE levels. The sex of each elephant is denoted in brackets as 'M' or 'F'.

Elephant	Tracking period	Hours in low PIKE core area	Hours in high PIKE core area	PIKE low PIKE core area	PIKE high PIKE core area
Apollo (M)	Feb 02 - Jan 04	3190	4698	22 %	56 %
Eyasi (F)	Feb 13 - Sep 16	3962	8509	22 %	60 %
Loldaiga (F)	Aug 06 - Jan 09	5389	3546	27 %	57.5 %
Monsoon (F)	Jan 02 - Sep 16	11,825	3301	22.0 %	56.0 %
Neptune (F)	Jan 02 - Mar 07	20,028	8268	22.0 %	56.0 %
Ngelesha (M)	Aug 08 - Feb 12	10,428	338	38.0 %	51.7 %
OI ari Nyiro (M)	Aug 07 - Feb 12	9164	16,359	38.0 %	51.7 %
Sera (M)	Aug 06 - Apr 11	10,787	12,773	38.0 %	87.7 %
Taurus (F)	Jan 11 - Sep 16	26,267	8797	22.0 %	56.0 %
Tony (M)	Jan 11 - Sep 16	8359	354	22.0 %	51.5 %

ArcGIS 10.4 (ESRI, 2014).

## 2.5. Statistical analyses

We analyzed data using R 3.3.0 (R Development Core Team, 2012). We constructed twelve Generalized Additive Model (GAM) regression models (Hastie and Tibshirani, 1986). We chose the GAM because it enables the modelling of elephants' highly nonlinear activity patterns at the hourly scale. To determine if the elephants had significant differences in their overall diel activity patterns between the low and high poaching areas, we started by fitting a GAM model with time (i.e. time-smoother) as the only explanatory variable. To account for variation due to individuals' behavioural plasticity, we controlled each model for elephant identity and generated individual-specific time smoothers. Having a separate smoother for each elephant is also akin to having a random intercept for each elephant and, therefore, accounts for the issue of non-independence in data coming from the same elephant. We plotted individual elephants' smoothers and tested their difference between the -time-smoothened curves from the core area with low and high PIKE values. After testing for differences between each set of smoothers for every elephant, we pooled the data. We plotted a standard set of smoothers for activity between low and high PIKE areas. We fitted the models using Maximum Likelihood estimation (ML). We selected the best model based on Akaike's Information Criterion (AIC) and refitted it using Restricted Maximum Likelihood estimation (REML). The response variable was log-transformed-hourly-speed in km/hr transformed to normalize the data (Zuur et al., 2009). The explanatory variables were PIKE, the density of livestock, NDVI, the distance to water, and the interaction between them. We constructed 11 plausible models based on different combinations of the above variables. The predictor variables were standardized to reduce collinearity (Marquardt, 1980) and improve interpretability (Schielzeth, 2010). The model was implemented using the *mgcv* package.

To obtain the overall resting time per day, we considered still moments as when the displacement between any two consecutive GPS points was less than 25 m (i.e., a speed of less than or equal to  $0.025 \text{ Km h}^{-1}$ ). We considered the distance of 25 m, which accounts for the horizontal position error of the GPS, usually about 10 m, and possibly some minimal movement that elephants may make within a rest location interacting with other family members. Though it is technically possible that an elephant could occasionally walk and loop back to the same point in an hour, our data with thousands of hourly records is enough to render the effect of such occasional loops negligible. We assigned each GPS point a binary value of active (moving)" or not moving" (resting). To calculate the percentage resting time, we aggregated the resting" and moving" records for each hour of the day for the entire period an elephant was tracked separately for each home area. We used the Kolmogorov-Smirnov test to test for the differences between the proportion of hours elephants were not moving in the low and high-risk core areas. We used the median instead of the mean as the preferred measure of central tendency because the data was not normally distributed (Zar, 1999).

Results Testing for the difference in hourly speeds in low and high poaching areas

Time of day was a significant predictor of the diel activity pattern for the ten elephants in their respective core areas with low PIKE ( $F = 2827.7$ ,  $edf = 9.67$ ,  $P < 0.001$ ), and with high PIKE ( $F = 795.3$ ,  $edf = 9.65$ ,  $P < 0.001$ ) poaching levels (Fig. 2). We present the time diel movement smoothed curves for each elephant as supplementary material.

There were significant differences in the daily movement cycle of each elephant between its ranges in low and high poaching levels ( $P < 0.001$ ,  $edf > 9$ ). The elephants took a longer rest during the daytime hours while they were in high-risk areas (Supplementary material). While the individual elephant's time smoother plots showed that the absolute speeds varied amongst individuals, the general change in activity pattern was consistent. Two habitual crop raiders (Ngelesha and Ol ari Nyiro) whose home ranges were adjacent to farms had a markedly higher shift than the others, as they completely became nocturnal, staying in a nearby forest all day and crop raiding all night. The median resting time per day was 5 % (1 h) in low poaching areas and 8 % (2 h) in high poaching areas (Kolmogorov-Smirnov test;  $D = 0.163$ ,  $P < 0.003$ ) (Fig. 3). The elephants moved for 23 h and 22 h when they were within low and

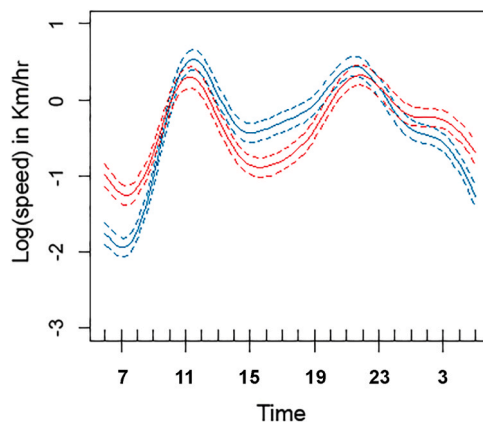


Fig. 2. The time-smoothers of the daily movement pattern, i.e., the average speed (y-axis) at different hours of the day (x-axis) for ten elephants combined when they were in their two home areas. The blue and red curves are for all the days when they were in low and high poaching areas, respectively. The dashed lines correspond to 95 % confidence intervals.

high-risk areas, respectively.

### 2.6. Modelling the hourly variation of speed as a function of poaching risk, livestock and water

The most accurate model was selected using the AIC values featured PIKE and the density of livestock (Table 2).

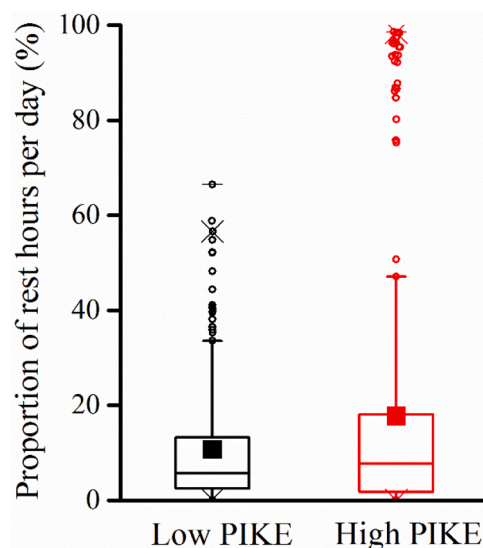
The most accurate model shows reduced movement when PIKE is high (Table 3). The model with livestock alone (besides time smoother) showed reduced movement but at a lesser magnitude (negative coefficient) compared to the model featuring PIKE. The model which included livestock and PIKE, predicted increased movement rates.

## 3. Discussion

Using GPS tracking data of ten elephants (a total of 172342 tracking hours in core areas), we assessed the diel activity cycle of elephants in the human-dominated Laikipia-Samburu ecosystem. The sample size of ten elephants, though relatively small, was an achievement for this study, noting the tight criteria required to test our hypothesis of long-term tracking for each elephant. Despite the small sample size, each of the elephants was tracked for a period of no less than a year. On average, at least two years of monitoring data per elephant were used, excluding time spent outside the core areas. We opine that the large number of GPS points was sufficient to offer reasonable confidence in concluding a potential behavioural change.

The levels of illegal killing of elephants within the Laikipia-Samburu landscape reached an all-time high in all land management units in the years 2010–2012; some land units recorded over 73 % PIKE, up from lows of 28 % in previous years (Ihwagi, 2018). We found that when the poaching levels were high, elephants rested more during the mid-day hours, and in some cases, they ceased moving completely. Each of the elephants studied showed a significant variation in the activity cycle when in areas of low and high risk, though the magnitudes varied. The elephants became more active at dawn than at midday when they were in the land units with a high risk of poaching or human-elephant conflict. The magnitudes of variation were different for each elephant. Understandably, in the human-dominated landscape, human activities peak around midday. Although the diel cycle is a well-documented observation (Wyatt and Eltringham, 1974; Vancuylenberg, 1977), this study adds a fine-scale quantification of the behavioural adjustment to the existing body of knowledge. Understanding the magnitudes of the behavioural changes, especially in the human-dominated landscape, is a step towards a better understanding of the impact of humans on elephant activity. It warrants a comparative study of the behavioural adjustment between elephants in -dominated landscapes and elephants in protected areas, which this study was unable to achieve.

Where the nature of the risk was predictable direct conflict, i.e. human-elephant conflicts around the dense human settlements and cultivation area, the elephants' variation of the diel comprised a near cessation of activity by daytime. Water was not a significant driver of the variation in the activity cycle. Elephants, like other herbivores, drink and rest when the day is hot and often take a rest under the riverine forest. This study was interested in the alteration of that evolutionary and behaviourally adopted activity cycle. We established that the alteration of the movement cycle led to more hours of rest that were not compensated for within the diel activity pattern. Giving up temporal activity within a particular time of day is a short-term antipredator behaviour of animals of different taxa: common voles (*Microtus arvalis*) (Jacob and Brown, 2000), black-backed jackals (*Canis mesomelas*) (Ferguson et al., 1988), grasshoppers (Schmitz et al., 1997) and deer (*Cervus elaphus*) (Godvik et al., 2009). Already, some risk effects have been observed amongst



**Fig. 3.** The box plots detail the proportion of hours that elephants were at rest every 24 h when they were tracked in the core areas with low and high levels of illegal killing, respectively. Elephants move less when they are in high-risk areas. The solid marks and the horizontal lines inside the boxes represent the average and median hourly speeds, respectively.

**Table 2**

Candidate models in the analyses of the relationship between the hourly speed of elephants and the Proportion of Illegal Killing of Elephants (PIKE), livestock density and the proximity to surface water using the Generalized Additive Model (GAM).

Model	Model description	AIC
1	speed ~ PIKE* livestock + time smoothers**	595090.8
2	speed ~ PIKE* water + livestock + time smoothers**	595091.5
3	speed ~ PIKE + water* livestock + time smoothers**	595247.5
4	speed ~ PIKE + water + time smoothers**	595268.5
5	speed ~ PIKE + water + livestock + time smoothers**	595269.5
6	speed ~ PIKE + livestock + time smoothers**	595297.0
7	speed ~ water* livestock + time smoothers**	595376.4
8	speed ~ water + livestock + time smoothers**	595389.9
9	speed ~ water + time smoothers**	595391.1
10	speed ~ livestock + time smoothers**	595394.4

\*\*The smoothers were the same for each model; s(Time, by = ("Sera")) + s(Time, by = ("Monsoon")) + s(Time, by = ("Apollo")) + s(Time, by = ("Eyasi")) + s(Time, by = ("Loldaiga")) + s(Time, by = ("Neptume")) + s(Time, by = ("Ngelesha")) + s(Time, by = ("Taurus")) + s(Time, by = ("Tony")) + s(Time, by = ("Ol ari Nyiro")).

\* Denotes interactive effects between the two variables

**Table 3**

The standardized coefficients of the best Generalized Additive Model of the speed of elephants are a function of the level of illegal killing and livestock density. The level of illegal killing had the greatest negative influence on the elephant movement.

	Estimate	L.C.I	U.C.I
(Intercept)	-1.687	-2.53568	-0.83832
PIKE	-2.044	-2.40464	-1.68336
livestock	-0.045	-0.05284	-0.03716
PIKE*livestock	0.075	0.06128	0.08872

elephants under poaching risk; notably, a shift towards more nocturnal activity (Ihwagi et al., 2018), walking faster when walking through risky migratory corridors, i.e., streaking (Douglas-Hamilton et al., 2005, Graham et al., 2009). We quantify that the elephants studied did not just shift activity to a different window of the day as earlier understood, but they indeed lost some activity time.

When the risk is highly predictable within the hours of a day, a prey animal adjusts the foraging period accordingly (Lima and Dill, 1990). We observed that the daytime section of their activity cycle of two elephants, Ngelesha and Ol ari Nyiro, entailed a complete cessation of movement activity when they were in the core area with the highest risk and neighbour farms. These two elephants are -known as habitual crop raiders; they went into the farms only when it was dark and retreated into a nearby patch (Lariak Forest) by dawn. The settlement areas are hotspots for human-elephant conflicts (Ihwagi et al., 2015; Douglas-Hamilton et al., 2010). In the case of these two elephants, the immediate risk was conflict from the farming community. The complete cessation of movement during the day is attributed to a lack of anywhere to move to. Unlike in the pastoral lands where pastoralists have a tolerance for wildlife in general, the subsistence farmers have zero tolerance, and the elephants have seemingly learnt the timing of human activity during the daylight hours. The behaviour of these two elephants is consistent with a recent finding that elephants hide during the daytime at specific preferred locations (nodes) outside protected areas to minimize their risk exposure (Wittemyer et al., 2016b). The inclusion of the two elephants with a risk well known to be primarily from conflict is in a PIKE-based study justified in line with the generally accepted norm that PIKE is a reliable and widely used metric, and it is derived from poaching and conflict cases.

Most predator-prey interactions comprise behavioural adjustments by the prey to avoid encountering a predator, and the prey must maintain a baseline level of apprehension (Brown et al., 1999). For an actively searching predator, the shell-game concept predicts that the prey should move more when the predation risk is higher (Laundre, 2010). The elephants studied moved less in high poaching or livestock areas. Still, a combined effect of these resulted in more movement. Apparently, livestock had a small but significant negative effect on the variation in the diel pattern, indicating that livestock alone, and relatedly the pastoralists, are not a major threat to elephants. The elephants in the landscape have learned to co-exist with humans and adapted to the predictable cycle of human activity. The poaching risk throws elephants off balance in terms of their behaviour. Due to their large mass and associated high energy costs, elephants cannot sustain high movement rates for long (Wall et al., 2006). The change in the behaviour of predators and prey to each other should encourage the stability of the predator-prey system (Brown et al., 1999), an outcome that cannot be guaranteed while the predator is a man. The risk allocation hypothesis postulates that animals feeding under temporal variation in risk of predation face a problem in the allocation of antipredator behaviour across different states of risk (Lima and Bednekoff, 1999). This study illustrates that elephants' response to risk is a learnt form of behaviour out of past experiences (past years' poaching levels) in specific zones of their home ranges. Elephants exposed to the long-term effects of poaching suffer from prolonged, up to six years, high levels of stress hormones, which impacts their reproductive physiology (Gobush et al., 2008). We suggest that a study linking the levels of stress hormones and resting behaviour would be a valuable additional information to the existing body of knowledge.

Elephants move less freely in risky landscapes and cannot adapt their behaviour sufficiently or timely enough to evade illegal

hunters. Failure to move freely has negative implications for the foraging success of animals (Brown et al., 1999; Brown and Kotler, 2004). The spatial and temporal variation of predation risk, critical components in modelling animal responses and effect on foraging success (Brown and Kotler, 2004), is bound to vary when the predator is a human being. For an animal to learn and predict risk from humans, substantial exposure to the risk would be required. The elephants of the Laikipia-Samburu landscape, living in a human-dominated landscape, have been in constant human presence throughout their life. Behavioural responses at short-temporal scales are more related to the consequences of fine-scale effects that influence their foraging behaviour than the general environmental variation (Owen-Smith et al., 2010). This study links the alteration of the hourly activity cycle to the risk of routinely encountering livestock (or the associated humans) in the landscape. The alteration of the activity cycle and overall reduction of activity time may affect the foraging success of the elephants. Livestock and elephants share watering points, and many of such watering sites are the locations of conflict recorded in the landscape. It is plausible that elephants would increase their behavioural adaptation when the presence of livestock compounds onto the levels of illegal killing.

We speculate that being more active at dawn is an apparent effort towards compensation for the minimal activity anticipated later during the daytime hours. Still, it was not sufficient to compensate for the loss. Increased rest time, beyond what is evolutionarily adopted due to physiological needs, in the early afternoon minimizes their risk exposure, especially from pastoralists. Profound behavioural change results in a reduced ability to forage when resources are limited (Ruggiero, 1990). The ratio of attacks by a predator, rather than an absolute number of attacks, influences the allocation of antipredator behaviour (Lima and Bednekoff, 1999). A loss of one hour of activity time per day implies that despite the elephant's efforts to adjust their daily activity pattern, increased risk leaves them with a time deficit from their usual active time. We speculate this might be a loss of foraging time in a resource-limited landscape, especially during the daytime. This reduction of movement is in line with the recently confirmed decline in mammals' global movement (Tucker et al., 2018).

Disentangling the role of conflicts separate from poaching requires a much larger sample size of individuals studied, with home ranges predominant to zones of either cause of death. Acquiring a substantial number of individually verified causes of death to generalize the cause of death in each elephant's distribution area is a challenge. The main challenge in data acquisition is that detailed site-level records of MIKE monitoring are hard to come by because elephant range-states submit only site-level total number of dead elephants and the associated Proportion of Illegally Killed Elephants (PIKE) (<https://cites.org/eng/node/17051>). The detailed knowledge and distinction of the nature of risk is a plus and a basis for a potentially more exhaustive study comparing or contrasting the responses of elephants to the diverse nature of threats. Such a detailed teasing out of actual threat would be achieved if range states availed the individually verified carcass reports. This study provides a first insight into potential fine-scale behavioural responses of elephants to poaching, which is much needed as we strive to understand the evolution of animal behaviour under risk.

Understanding the temporal scales of the responses of elephants, a megaherbivore, to risk (Owen-Smith, 1988) provides insights into the least understood aspects of their behavioural ecology. On a large temporal scale, the migratory movement of the elephants is attributed to the prolonged levels of poaching (Thouless, 1993). Understanding the behavioural response to poaching risk at a fine scale depends on the availability of both movement data at a commensurately short time scale and the availability of both movement data at a commensurately short time scale and a corresponding detailed risk map. Courtesy of GPS tracking and detailed within-site field verification of causes of mortality, this study confirms that elephants respond to poaching on a near real-time basis by adjusting their hourly movement in a risky landscape. We recommend a comparative study of diel activity patterns of elephants in unprotected and protected areas with less human disturbance analyses of responses to categorized nature of risk where individual carcass records are available and a multiple ecosystem collaboration by tracking groups where data meets the criteria. Enhancement of GPS tracking data with camera trap data would help overcome the costs associated with acquiring fine-scale movement.

#### Author contributions

Conceived and designed the experiments: FI AS GB AT ID. Performed the experiments: FI AS GB TW AT ID. Analyzed the data: FI GB AS. Contributed reagents/materials/analysis tools: FI AS TW AT ID. Wrote the paper: FI AS GB TW AT ID.

#### CRediT authorship contribution statement

**Albertus Toxopeus:** Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Iain Douglas-Hamilton:** Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation. **Festus W. Ihwagi:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andrew Skidmore:** Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Guillaume Bastille-Rosseau:** Visualization, Validation, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Tiejun Wang:** Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



## Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02911](https://doi.org/10.1016/j.gecco.2024.e02911).

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