



Research Article

Poaching Lowers Elephant Path Tortuosity: Implications for Conservation

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ABSTRACT Poaching is the most immediate threat to African elephants (*Loxodonta africana*). Several continental-wide surges in poaching have occurred since the latter half of the twentieth century, and the latest surge occurred from 2007 to 2012. The behavioral responses of elephants to poaching risk has not been studied widely because of a lack of high-resolution movement data collected simultaneously with verified causes of mortality. We managed to collate 2 such datasets from 2004 to 2013. We studied the spatial-temporal changes in movement behavior of 11 elephants in their core areas. Past studies have focused on elephant movement along corridors. We tested for the effect of poaching risk on their path straightness (i.e., tortuosity) while controlling for other environmental and human activities in the landscape using a set of generalized linear mixed models. To test for temporal variation of tortuosity, we used a time-series linear model. Elephants turned less frequently while they were in poaching locations and at times with a high level of poaching activity, even though their speed did not change. The variation of tortuosity is a good indicator of differences in poaching risk as perceived by the elephants, which could complement patrol-based anti-poaching efforts by wildlife managers, especially in remote, inaccessible landscapes. © 2019 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society

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Animals that live in landscapes that have been recently altered by humans exhibit sub-optimal movement behavior as they seek to evade predators (Fahrig 2007). The path tortuosity of an animal is a measure of how direct a path is from a certain point to the intended destination, and in open landscapes with no physical obstacles or barriers, it is

inversely proportional to the efficiency of the orientation mechanism involved, unless major obstacles abound (Benhamou 2004). The nature of survival strategies influences the path tortuosity of animals that live in heterogeneous landscapes, but it is affected by intrinsic and extrinsic factors (Schooley and Wiens 2004, Prevedello et al. 2010, Sih 2013). An animal should exhibit its maximum effort towards avoiding predators during high-risk times (Lima and Bednekoff 1999). If animals can reliably detect and make efforts to avoid exposure to the risk, movement tortuosity should be inversely proportional to the magnitude of risk in space and time to reduce the animals' exposure (Hodges et al. 2014). Maneuverability while escaping risk is also influenced by body size, with smaller, faster animals being able to turn more sharply, and

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larger ones moving in straighter paths (i.e., with lower tortuosity; Hodges et al. 2014). How risk influences the tortuosity of animals is poorly understood because most studies have been conducted in laboratories or using mathematical models, rather than in complex natural habitats (Domenici et al. 2011*b*). It has been hypothesized that if large animals can perceive danger and make efforts to avoid it, the rate of tortuosity should decrease in risky habitats to minimize their exposure to risk (Domenici et al. 2011*a*, Hodges et al. 2014).

An animal's ability to assess and influence the risk of encountering predators by changing its behavior affects its decision-making (Sih 1987). Behavioral plasticity is essential for an animal to be able to respond to fast changes in the environment brought about by rapid human activities (Sih 2013). The landscape of fear is an individual animal's perception of fear, a concept that is not geographically dependent (Laundré et al. 2010). The mean rate of change of an animal's foraging tenacity is the best measure of its landscape of fear; the higher the difference in risk, the higher the mean difference in foraging tenacity should be (Laundré 2010, Bleicher 2017). The path tortuosity of a herbivore when foraging is commensurate with the heterogeneity and spatial distribution of its preferred forage items (Etzenhouser et al. 1998). The animal's past experiences in the landscape, including encounters with predators, influence its current landscape of fear (Bleicher 2017) and, in turn, how it forages. There are, therefore, links between an animal's path tortuosity, its foraging tenacity, and the current and historical exposures to risk. There is a widespread need for scientists, conservationists and wildlife managers to better understand the variation in animals' behavioral responses to habitats that are undergoing rapid changes due to human activities like habitat loss and illegal harvesting (Sih 2013).

Besides the loss of habitat, the most immediate threat to African elephants (*Loxodonta africana*) is poaching and other deadly conflicts with humans (Nellemann et al. 2013, Wittemyer et al. 2014). Hunting by humans is a form of predation risk (Frid and Dill 2002, Shannon et al. 2014). The poacher-elephant system has already offered numerous insights into how prey can respond to the risk of encountering humans. For instance, by increasing speed when traversing unsafe areas, switching from the day to night-time travel, and avoiding settlements during the daytime (Douglas-Hamilton et al. 2005, Graham et al. 2009, Wittemyer et al. 2017, Ihwagi et al. 2018). These studies focused on the alteration of speed when elephants venture out of their (presumably safer) core areas. Elephants increase their speed in migratory corridors to traverse unsafe areas quickly, a behavior called streaking (Douglas-Hamilton et al. 2005). In a landscape dominated by humans, in which different core areas for elephants lie in distinct land management units that have different levels of poaching, we would expect elephants to change their short-term movement behavior as they forage in full vigilance. Change in behavior is an aspect that movement speed alone would probably not capture.

Poaching has long-term effects on the population of elephants affected, and this is evident from the sustained high levels of stress hormones detected for as long as 6 years after a poaching surge (Gobush et al. 2008). Elephants switch to moving more at night than in the day in times and places with high levels of illegal killing (Ihwagi et al. 2018); however, little is known about what factors influence the fine-scale variation in behavior in relation to poaching risk. The hourly adjustment of movement behavior in relation to risk is poorly understood because few studies have access to a multi-year high-resolution movement dataset and a concurrent dataset of causes of elephant mortality verified in the field. Our study has compiled and made use of such datasets. Although poaching causes a decline in many populations of African elephants (Nellemann et al. 2013, Wittemyer et al. 2014, Chase et al. 2016), it is still unclear how elephants adjust their movement in response to poaching risk on short time-scales. Several studies have reported on elephant movement behavior along their migration corridors (Douglas-Hamilton et al. 2005, Galanti et al. 2006, Mpanduji et al. 2009, Jachowski et al. 2013, Roeber et al. 2013). The home ranges of migratory elephants comprise core areas linked with narrow corridors through which they migrate at faster speeds than usual (Douglas-Hamilton et al. 2005). Elephants walking through safe or risky areas, however, can have the same average speed between path segments but show a varied tortuosity in each area because the risks influence the animals' rates of turning along the way (Angilletta et al. 2008). Speed, therefore, has limited applicability to understanding the effect of the risk landscape on animal movement.

Between 2007 and 2012, the levels of poaching increased gradually, affecting all African elephant populations (Wittemyer et al. 2014, Chase et al. 2016). The population of the Laikipia-Samburu ecosystem, which lies under different conservation statuses, is the most intensely monitored in Africa regarding the causes of elephant mortality. A participatory network verifies each report of a dead elephant (Kahindi et al. 2010). During the 2007 to 2012 poaching surge, the levels of poaching in the ecosystem increased in tandem with the continental trend, and even some of the previously safe land units, like private ranches, were affected by the surge (Douglas-Hamilton et al. 2010, Ihwagi et al. 2015). Our study goal was to evaluate elephants' behavioral adaptation to the increasing levels of illegal killing in their core foraging areas using path tortuosity as the main study parameter. We predicted that the tortuosity of elephants would be lower in places and times when there were high levels of illegal killing. Using movement and mortality data collected before and during the period when poaching levels rose so markedly, we investigated how the tortuosity of elephants varied with poaching levels spatially and temporally.

STUDY AREA

We conducted this study from 2002–2013 in the Laikipia-Samburu ecosystem, Kenya, which covers an area bounded by 0.2°S to 1.5°N, and 36.2°E to 38°E (Fig. 1). The

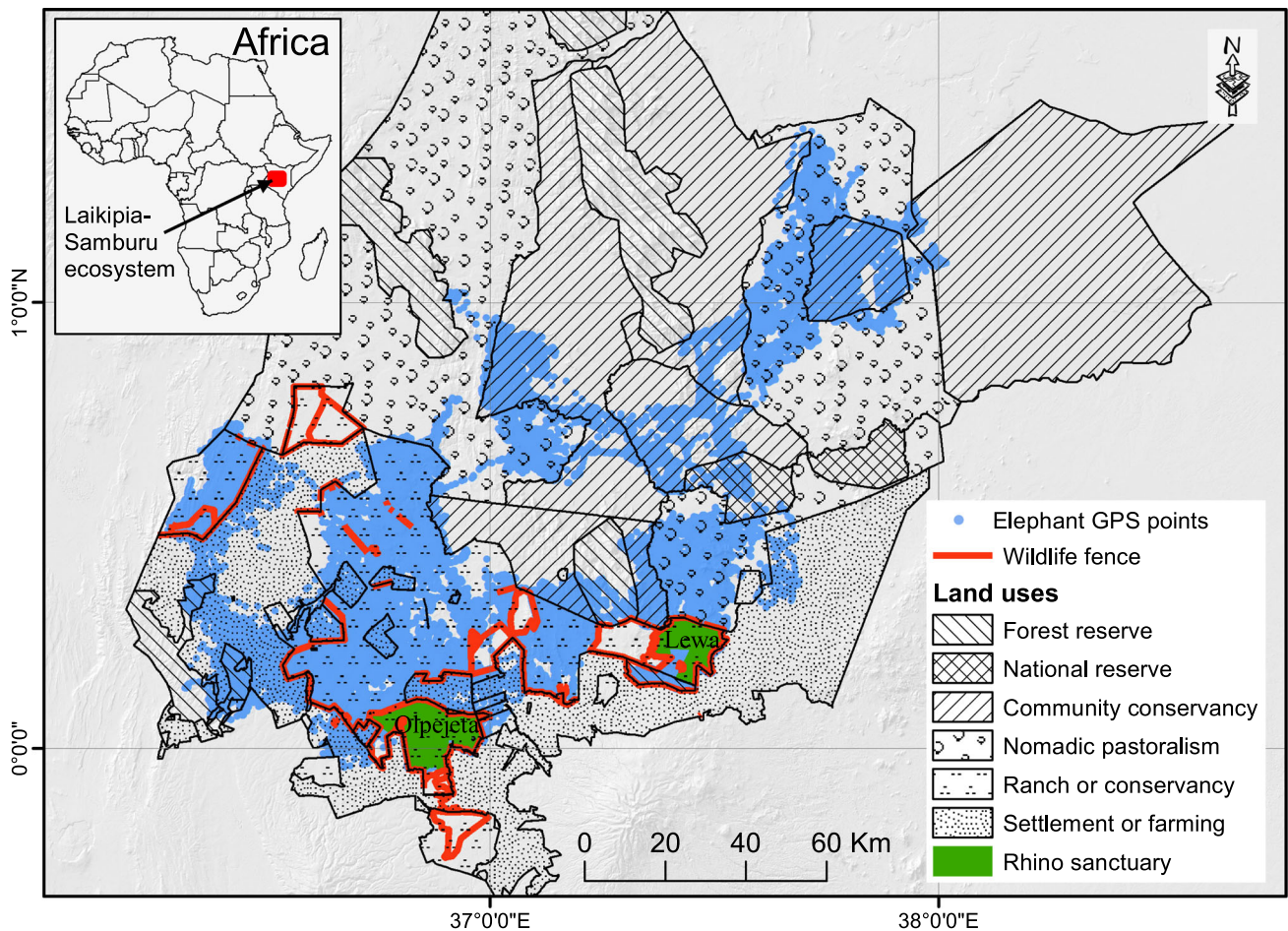


Figure 1. Map of Laikipia-Samburu ecosystem showing the coverage of global positioning system (GPS) fixes for 11 African elephants tracked between 2004 and 2013, and the ecosystem's complexity with regard to land use types.

ecosystem is delineated by the extent of the Ewaso Nyiro River and its tributaries, encompassing roughly 33,000 km² (Thouless 1995). It has a north-south rainfall gradient, with a marked decline in rainfall towards the north (Georgiadis 2011). The rainfall pattern in the ecosystem is highly variable and bimodal, with peaks in April and November and a yearly range of <400 mm in the north to a maximum of 600 mm in the south (Barkham and Rainy 1976, Ihwagi et al. 2012). The onset of the rains in April and November marks the beginning of short and long rainy seasons, respectively. The terrain in the northern part of the landscape comprises expansive plains interrupted by rugged terrain and isolated hills. In the northern part of the landscape, the surface geology is characterized by complex rocks that consist of horn-blend gneisses and schists, and banded biotite gneisses (Krhoda et al. 2015). The southern part of the landscape is marked by tertiary and more recent flows of olivine basalt giving rise to a plateau of poorly structured and excessively drained volcanic soils.

The vegetation of the Laikipia-Samburu ecosystem is dominated by wooded grassland with an underlying large cover of perennial and annual grasses and thorny acacia (*Acacia* spp.) scrubland (Pratt et al. 1966, Barkham and Rainy 1976). The major river in the landscape, the Ewaso, supports a riverine forest dominated by river acacia (*Acacia*

elatior) and fever tree (*Vachellia xanthophloea*), which attracts large numbers of animals in the dry months (Ihwagi et al. 2010). The diverse plant community supports an equally diverse fauna. In addition to elephants, the ecosystem is home to other large mammals that include reticulated giraffe (*Girrafa camelopardalis*), plains zebra (*Equus quagga*), Grevy's zebra (*Equus grevyi*), Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), defassa waterbuck (*Kobus ellipsiprymnus defassa*), and common waterbuck (*Kobus ellipsiprymnus*; Ihwagi et al. 2010). Other animal species found in the landscape but in relatively fewer numbers include beisa oryx (*Oryx beisa*), eland (*Taurotragus oryx*), and gerenuk (*Litocranius walleri*).

The landscape is a complex mosaic of land use types owned by individuals, government, or communities, and elephants walk freely through most of the land units. There is a significant variation in levels of poaching within different land units, with higher poaching levels being associated with communal grazing areas (Ihwagi et al. 2015).

METHODS

Monitoring Illegal Killing of Elephants (MIKE)

Under the auspices of the MIKE program of the Convention on International Trade in Endangered Species (CITES),

causes of elephant mortality were verified in the field by a participatory community network of landowners, herders, conservancy managers, and government wildlife rangers (Kahindi et al. 2010). We analyzed data collected from 2002 to 2013. The proportion of illegally killed elephants (PIKE) has been adopted as an unbiased estimator of the levels of poaching (Douglas-Hamilton et al. 2010, Jachmann 2013). The formula for calculating PIKE is:

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

The number of illegally killed elephants comprises those that died from poaching and those that died from human-elephant conflicts. The PIKE is a reliable metric for comparing levels of illegal killing even between sites with different sampling efforts per unit area (Douglas-Hamilton et al. 2010, Jachmann 2013). Despite PIKE comprising both human-elephant conflict incidents and poaching ones, in the Laikipia-Samburu MIKE site, poaching accounts for the highest numbers of illegally killed elephants, with over 91% of illegally killed elephants in the MIKE site in any of the years studied (Ihwagi et al. 2015). Because the number of poached carcasses represents the majority of all illegally killed elephants, the estimates of PIKE in the ecosystem are almost synonymous with the actual poaching levels, and we can thus make direct reference to poaching levels in many instances.

We calculated PIKE values for each core area by averaging the PIKE of the land units used by the elephants. To determine the PIKE value associated with an elephant's home range, we included all mortality records for the time before and during its global positioning system (GPS) tracking period because elephants have a long-term spatial memory (Gobush et al. 2008, Polansky et al. 2015) and we assumed they were still responding to past experiences encountered before we put collars on them.

GPS Tracking and Calculation of Path Tortuosity

We collected hourly GPS positions of 11 mature elephants (7 females aged 30–40 yr, and 4 males aged >30 yr). The males were solitary, but each of the females represented a

separate family of ≥ 10 elephants. With the help of government veterinarians, we fitted the elephants with GPS collars sourced from African Wildlife Tracking (Pretoria, South Africa) and FOLLOWIT (Lindesberg, Sweden); each recorded 1 fix/hour. We abbreviated sex as F for a female, M for a male and assigned a number for ease of reference (e.g., F1 for female 1). The full identities and sex of elephants tracked were Loldaiga (F1), Wangari (F2), Ngelesha (M1), Ol ari Nyiro (M2), Sera (F3), Genghis (M3), Mpala (M4), Mutara (M5), Olpejeta (M6), Tia Maria (F4), and Drachmae (F5), but hereafter we refer to each of them using the number in parentheses. The elephants exhibited more directed movements on a fine temporal scale (1 hr) compared to larger temporal scales (Street et al. 2018), which made use of hourly GPS fixes useful in inferring behavioral change. Five of the elephants; F1, F2, F3, M1, and M2 were wide-ranging (migratory) and used multiple, distant land units, making them ideal candidates to test spatial trends, whereas the other 6 were residents of distinct land units in different parts of the ecosystem and thus were ideal candidates for testing temporal trends within each elephant's home. We filtered out GPS points that corresponded to unlikely speeds of >7 km/hour (Hutchinson et al. 2003, Hutchinson et al. 2006).

We used a fixed-kernel home range estimator to identify core areas, which we delineated as those areas within 50% contour lines (Worton 1987, 1989). We tracked the elephants on different dates between September 2004 and December 2013 (Table 1). For each hourly GPS fix, we calculated the tortuosity as $\log(L/R^2)$, where L is the hourly segment length and R is the net displacement (Whittington et al. 2004). We used the current and previous 2 GPS points to calculate tortuosity at any point as follows: assuming hourly measurements, the net displacement at 1100 hours would be the straight-line distance between the elephant's location at 0900 hours and 1100 hours. Tortuosity measures have an exponential distribution. A straight line (i.e., a line with the lowest tortuosity) has a value of zero or negative. The magnitude of the negative value depends on the actual ratios of the 2 successive, unidirectional line segments whose simple addition equals the displacement. The longer the immediate step length compared to the previous one on

Table 1. The dates of tracking for each of the 6 male (M) and 5 female (F) elephants in Laikipia-Samburu ecosystem, Kenya, and the number of hours they spent in their respective core areas.

Elephant identity (sex and number)	Dates tracked	Hours in core area 1	Hours in core area 2
F1	Aug 2006–Jan 2009	3,383	3,597
F2	Sep 2004–Jul 2006	10,649	1,511
M1	Aug 2008–Feb 2012	2,874	1,524
M2	Aug 2007–Feb 2012	7,241	14,327
F3	Aug 2006–Apr 2011	11,078	12,773
M3	May 2004–Jun 2012	41,943	NA ^a
M4	Feb 2007–Dec 2011	39,134	NA
M5	Feb 2009–Jun 2013	13,095	NA
M6	Sep 2006–Feb 2009	17,022	NA
F4	Feb 2008–Aug 2012	31,715	NA
F5	Feb 2008–Dec 2013	37,353	NA

^a Indicates the elephant had only 1 core area (was not migratory).

a straight line, the more negative the tortuosity value. A high tortuosity is achieved when an elephant makes an acute angle resulting in very short displacement, and the tortuosity approximates a value of 2. Should the elephant turn and walk back through the previous location, the net displacement would be less than that step length line segment, and the tortuosity would thus be negative, as expected for such a highly tortuous path. This explains why the use of actual displacement alone is not as good a parameter for elephant movement as calculating tortuosity. Theoretically, should the elephant walk back to its precise previous location, this would yield a displacement of zero, and the calculation for tortuosity would yield an error; however, in our analyses, such an occurrence is extremely rare, and could be flagged, manually checked, and corrected. We adhered to the guidelines for the care of elephants by employing the services of a government veterinarian from the Kenya Wildlife Service to immobilize the elephants for fitting their collars. The elephants had multiple core areas, although the migration from one core to another was not in any regular cycle that could be linked to the seasons.

Collating other Environmental Variables

To disentangle the role of poaching risk from other environmental factors affecting the tortuosity of elephants, we modeled their tortuosity as a function of the poaching levels, land cover, type of terrain, distance from water points, livestock density, and the presence of permanent and temporary human dwellings in the landscape. We adopted a grid size of 500 m × 500 m for environmental variables, which aligns conveniently to the Universal Transverse Mercator grid and is also the same size as the grid adopted for measures of tortuosity. We performed a sensitivity analyses of tortuosity to the changes in grid sizes by calculating the variability of mean tortuosity values within progressively increasing size of grids (50 m, 100 m, 150 m, 200 m, 300 m, 400 m, 500 m, 750 m, and 1,000 m) using GPS data for the wide-ranging elephants (i.e., those with multiple core areas; Fig. S1, available online in Supporting Information). We found that tortuosity is resistant to the changes in grid sizes. Land cover influences the permeability of habitat to animals (Saunders et al. 1993, Goad et al. 2014, Cooney et al. 2015). We used land cover data provided by the Food and Agriculture Organization to assign the dominant cover type in each grid square (Food and Nations 2015). The 14 land cover types were rain-fed herbaceous crop, scattered (in natural vegetation or other) rain-fed herbaceous crop (field density 20–40% of polygon area), isolated (in natural vegetation or other) rain-fed herbaceous crop (field density 10–20% polygon area), closed trees, open trees (65–40% crown cover), very open trees (40–15% crown cover), closed to open woody vegetation (thicket), open shrubs (45–40% crown cover), open low shrubs (65–40% crown cover), open to closed herbaceous vegetation, shrub savannah, tree- and shrub savannah, open to closed herbaceous vegetation on temporarily flooded areas, and natural waterbodies.

Human settlements negatively affect the distribution of elephants and, in most instances, tend to occupy prime resource areas for the elephants, thereby inadvertently setting the stage for competition (Verlinden 1997). The landscape is dominated by temporary shelters for nomadic pastoralists (bomas, which were vacated seasonally), and by permanent settlements around the few, scattered towns. We calculated Euclidean distance to each category of settlement. We hypothesized that the bomas and permanent settlements would affect elephants differently because of the contrasting occupations of residents, and thus categorized them as separate features. We classified the 2 settlement types (2 features) and calculated for each the distances from each grid's centroid to the nearest feature.

The availability of surface-water influences elephant distribution because they need to drink at least once a day (Buss 1961, Western 1975). Elephants turn less when they are farther away from a source of water (Duffy et al. 2011). We calculated the distance from each grid's centroid to the nearest known water point. Elephants avoid climbing hills, with a gradient of 30 degrees being prohibitive (Wall et al. 2006), so we assumed that even at a distance away from the base of a continuous ridge or escarpment, elephants would align their movement to circumvent it. We defined the base of the hills as the level with a gradient of >30 degrees on a 30-m digital elevation model. We calculated the distance from each grid's center to the base of the nearest hill or escarpment.

Elephants and livestock in the ecosystem overlap in space and time and share critical resources like water and forage (Raizman et al. 2013). From the results of 2 total-count aerial censuses conducted in 2008 and 2012, we combined the numbers of all livestock species (i.e., cattle, sheep, goats, donkeys, and camels) for each census year, and calculated their average density per square kilometer in each grid. The aerial census dataset also included locations of occupied bomas. The pastoral communities shift their bomas over time and build new ones. The shift, however, is often only over a short distance and within the same land management unit that we adopted for calculating PIKE; it does not therefore affect our analyses. Wildlife fences create edge effects and modify elephant movement behavior directly by coercing them onto a unidirectional path (Newmark 2008, Vanak et al. 2010, Nams 2014). We excluded all GPS tracking data points that fell within a distance of 2 km of any wildlife fence from our analyses.

Statistical Analysis

We analyzed data using R 3.3.0 (R Development Core Team 2012). The calculation of tortuosity included a log transformation that corrected for non-normality. To test for spatial variation of the tortuosity of the 5 migratory elephants (F1, F2, F3, M1, and M2) in relation to the level of illegal killing and other covariates, we used 28 generalized linear mixed models grouped into 3 categories: physical environmental factors, human activity related factors, and plausible combinations of these in a model

Table 2. Candidate models of factors affecting tortuosity of 5 migratory elephants (F1, F2, F3, M1, and M2) that inhabited different land management units in the Laikipia-Samburu ecosystem, Kenya, 2004–2013. All models included sex and elephant identification as a random factor in addition to the listed covariates.

Model	Variables
Scenario 1	Only physical environment affects path tortuosity Water Hills Land cover
Scenario 2	Only human activity affects path tortuosity PIKE ^a + livestock density × distance from boma + distance from town PIKE × distance from town + livestock density PIKE + livestock density + distance from boma PIKE + distance from town PIKE × distance from town + distance from boma PIKE + livestock density × distance from boma PIKE + livestock density Livestock density Livestock density + distance from hill Livestock density + distance from boma Livestock density + distance from town + distance from boma Livestock density × distance from town Livestock density × distance from boma Distance from town + distance from boma PIKE + sex
Scenario 3	Both human and physical environmental factors affect tortuosity PIKE + livestock density × distance from town + distance from water + distance from hills + distance from boma PIKE + livestock density + land cover type PIKE + livestock density + distance from town + distance from water PIKE × livestock density + distance from town + distance from water + land cover type PIKE + land cover type Distance from town + distance from water + distance from hills PIKE + livestock density + distance from hills PIKE + distance from hills Livestock density + land cover type Distance from town + distance from water + distance from hills + land cover type

^a Proportion of illegally killed elephants.

Table 3. The ranking for different top-ranked models predicting tortuosity of elephant movement paths in the Laikipia-Samburu ecosystem, Kenya, 2004–2013.

Model ^a	K^b	AIC_c^c	ΔAIC_c^d	Lik^e	w_i^f	LL^g	Cum. wt ^h
(PIKE × town) + boma + sex	9	6,520.89	0.00	1.00	0.32	−3,251.43	0.32
(PIKE × livestock) + town + water + land cover + sex	25	6,521.10	0.21	0.90	0.29	−3,235.42	0.61
PIKE + (livestock × boma) + town + sex	10	6,522.19	1.30	0.52	0.17	−3,251.07	0.78
PIKE + (livestock × town) + water + hills + boma + sex	12	6,522.65	1.76	0.41	0.13	−3,249.29	0.92

^a PIKE is the proportion of illegally killed elephants; boma is the distance to temporary settlements of nomadic pastoralists; water refers to the distance to nearest water point; and hills represents the distance to the base of the nearest hill, town refers to the distance to the nearest town, land cover refers to the physical material at the surface of the earth, livestock refers to the average density of livestock species per square kilometer counted from air in 2008 and 2018.

^b Number of parameters.

^c Second-order Akaike's Information Criterion.

^d The difference in AIC_c between the current and the most appropriate model.

^e Model likelihood.

^f AIC_c weight.

^g log likelihood.

^h Cumulative weight of the models.

selection framework (Table 2). We performed a quasi-experiment that controlled for individual elephant, sex, and spatial autocorrelation of points. We scaled all covariates to enable direct comparison of the coefficients in the model summary. To account for spatial autocorrelation, we included an exponential correlation function based on the coordinates of the centers of each grid cell. The autocorrelation term also included control for repeated measures from individual elephants. We included the elephant's identity in the model as a random effect. Some of the models included interactions between some variables, where plausible. We selected the best model as the one with the lowest second-order Akaike's Information Criterion (AIC_c) value within the model selection framework (Burnham and Anderson 2002). We implemented the mixed effects regression models using the function `lme` within the package `nlme`.

To examine temporal changes in tortuosity and poaching, we used data from the 2 elephants (M2 and M4) that inhabited 2 regions: land units that experienced a gradual increase in levels of illegal killing (i.e., private ranches) and poaching-free sanctuaries. The other 4 were residents of 2 poaching-free rhino (white rhino [*Ceratotherium simum*] and black rhino [*Diceros bicornis*]) sanctuaries, Lewa and Ol Pejeta conservancies, at distant locations from each other. We modeled tortuosity as a function of time and land use type (i.e., poaching-free sanctuary or private ranches) with elephant identity as a random effect, using a linear mixed-effect model. The modeling of change on tortuosity over time focused only on the 2 elephants where there was a temporal trend in tortuosity. We tested statistical significance at $\alpha = 0.05$.

Data Availability

The site summaries of elephant mortality data are publicly available on the CITES website (www.cites.org). The GPS coordinates of elephant positions are not publicized because they are an endangered species. Exposing their

Table 4. The standardized coefficients for the top-ranked model of tortuosity of elephant movement paths in the Laikipia-Samburu ecosystem, Kenya, 2004–2013, as a function of the proportion of illegally killed elephants (PIKE) and other human and environmental variables.

	Estimate	Lower 95% CI	Upper 95% CI	SE
(Intercept)	-6.705	-7.451	-5.958	0.381
PIKE	-1.049	-1.113	-0.984	0.033
Distance from town (km)	0.057	0.009	0.105	0.025
Distance from bomas (km)	-0.136	-0.187	-0.085	0.026
Sex-male	1.599	-0.319	3.516	0.602
PIKE × distance from town	0.012	-0.032	0.057	0.023

locations may be counterproductive to ongoing anti-poaching efforts.

RESULTS

All models that included PIKE ranked above all other models. We chose the top-ranked model, which comprised of PIKE, distance from town, distance from boma, and sex, because of its parsimony (Table 3). The significant factors in the best model included PIKE and distance from settlements (towns and bomas; Table 4). The interaction between level of illegal killing and town was not significant even though it was included in the top model ($P = 0.548$), and the coefficients for the distance from settlements were very small despite being statistically significant. The tortuosity of elephants reduced by a factor of 0.4, i.e., $\exp(\text{Estimate})$, for every 1% increase in the proportion of illegal killing. For every increase in 500 m of distance from towns and bomas, the median tortuosity values increased by a factor of 1.1 and decreased by 0.9, respectively. The second-ranked model included PIKE, the density of livestock, distance from town, distance from water, land cover, and sex and had a similar AIC_c value, despite having more parameters.

The tortuosity of the 2 elephants (M3 and M4) that inhabited private ranches, where PIKE increased gradually throughout the study period, were lower and decreased more over time compared to the tortuosity of those that inhabited poaching-free rhino sanctuaries (Fig. 2A). The level of illegal killing over time was inversely related to the change in tortuosity for the 2 elephants in private ranches (Fig. 2B). The coefficients of the model showed a strong influence of PIKE levels for the elephants in private ranches (Fig. 2C).

DISCUSSION

Environmental factors influenced the tortuosity of all the elephants we studied, and, in addition, human factors influenced those elephants that were outside the (highly secured, low human density) rhino sanctuaries. The models with the highest support from the data featured PIKE as the most important variable. The distance from town is a proxy for human population density, likely disturbances, and the positive relationship between tortuosity and distance from

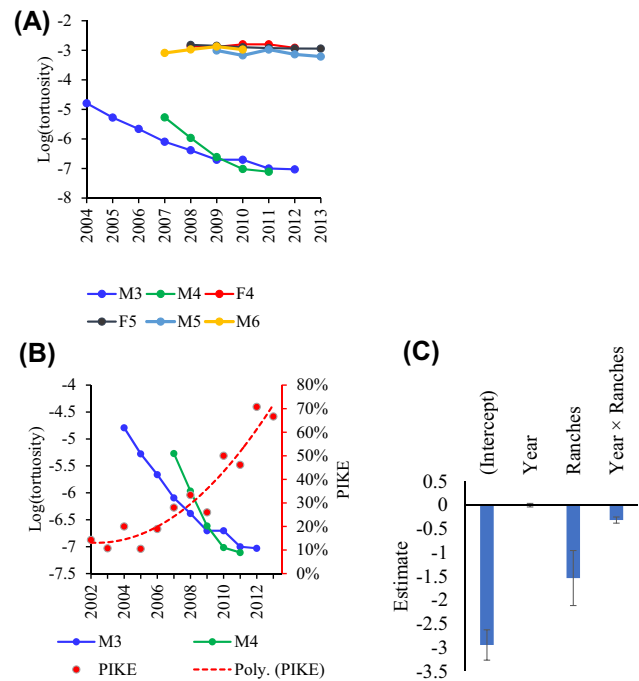


Figure 2. A) The mean annual tortuosity values of 6 male and 5 female elephants tracked in the Laikipia-Samburu ecosystem, Kenya, at different dates between 2004 and 2013. Four elephants, i.e. F4, F5, M5, and M6 that inhabited poaching-free sanctuaries showed a constant mean annual tortuosity throughout the period. M3 and M4 inhabited the Laikipia Ranches, where poaching levels increased gradually, and their tortuosity decreased over time as the yearly proportion of illegally killed elephants (PIKE) increased. B) The yearly mean tortuosity of M3 and M4, decreased over time as the yearly proportion of illegally killed elephants (PIKE) increased. A second order polynomial (Poly) best represented the trendline of PIKE and for this dataset we plotted data collected from 2002 for the purpose of presenting the historical trend. C) The coefficients of the linear mixed-effects model of change in tortuosity of elephants as a function of (regional) poaching levels over time. Ranches represents a contiguous set of land units managed primarily for large-scale cattle production but also hosts wildlife.

town indicated that elephants walk with reduced tortuosity as they come near towns. On the contrary, we found that elephants walked with higher tortuosity when they were near the dwellings of nomadic people (bomas). The latter was not surprising because elephants have traditionally co-existed with the nomadic pastoralists (Gadd 2005, Kideghesho 2008), and bomas are thus not perceived as a risk by elephants. These temporal dwellings of nomads in northern Kenya are often located close to key resource areas like water and forage (Berger 2003), resources that elephants also seek (Ngene et al. 2009, Bohrer et al. 2014).

Temporally, the variation in tortuosity corresponded to the annual variation of PIKE in the affected land use types, and the inclusion of poaching-free land units was a perfect control case. Our results support earlier observations that habitat quality alone is not sufficient to explain elephant movement behavior (Boettiger et al. 2011) because human activities also affect it (Lima 1987). This study identifies the level of illegal killing as the best predictor of tortuosity of elephant movements in their crucial foraging areas.

Many studies have emphasised the importance of speed in describing elephant movement behavior within diverse contexts (Douglas-Hamilton et al. 2005, Hutchinson

et al. 2006, Graham et al. 2009, Chamaille-Jammes et al. 2013, Jachowski et al. 2013). Elephants use a direct movement strategy in which they maintain straighter paths rather than increase speed to reach an intended foraging spot (Duffy et al. 2011). Because of the high energy requirements of large animals, a change of direction is more favorable than a change of speed when navigating through a complex landscape or risk area (Wall et al. 2006, Angilletta et al. 2008). Unlike smaller species, where the trade-off between speed and tortuosity is more important (Angilletta et al. 2008), elephants with their large mass and high energy requirements have minimal flexibility with regards to increasing their speed (Wall et al. 2006). They thus choose to walk straighter paths than to increase speed. The constant risk model postulates that vigilance is minimal in a visually obstructive environment, where scanning takes time and is too costly to the animal (Lima 1987). Logically, for animals with low visual acuity such as elephants (Rensch and Altevogt 1955), active vigilance would entail frequent turns and as a result higher tortuosity. The elephants, however, exhibited lower tortuosity in risky areas, implying they exercised low vigilance, in line with the constant risk model.

Future studies characterizing the movement behavior of elephants in risky habitats should therefore incorporate tortuosity because it is more informative than speed alone. We propose that relative change of tortuosity is a useful variable for assessing elephants' landscape of fear in their crucial foraging areas; with regard to poaching it has a steep gradient that speed alone does not illustrate. The absolute values of tortuosity, however, depend on the temporal scale of the data and for a comparative study, the resolutions should be the same (Street et al. 2018).

A recent study explored the variation of tortuosity of elephant movement within corridors and core areas (Jachowski et al. 2013), but neither the variation of tortuosity between core areas nor its relationship with poaching risk was explored. We found that elephants turn more when in their respective low-risk areas. This finding is consistent with past observations that when elephants are foraging, they turn less often (instead of increasing speed) to reach their intended point faster; this strategy saves energy (Duffy et al. 2011). Our results indicate that a high level of illegal killing and other risk factors make a habitat less favorable and lead elephants to walk straighter paths through it. The presence of both males and females in our group of elephants residing in poaching-free rhino sanctuaries was a good control dataset to illustrate that tortuosity of both sexes changed primarily according to the risk from poaching and not because of other environmental factors or sex-related differences. We nonetheless found that the change in tortuosity was influenced by the level of risk and that although sex as a key variable did not have a significant effect in the top model, male elephants had a marginally higher tortuosity than females.

Lower path tortuosity of herbivores in heterogeneous habitats implies lower foraging efficiency because it corresponds to lower searching effort (Doerr and Doerr

2004). The foraging of elephants involves variation in their daily displacement in relation to resource availability (Polansky et al. 2013). A risk-induced reduction in tortuosity in the prime foraging areas thus implies a change to optimal foraging strategy. The foraging success of elephants in core areas in risky environments may have been compromised by the need to keep moving, instead of actively searching and exploiting food resources thoroughly. A study with a higher temporal resolution of data is warranted to better understand the effect of reduced tortuosity on evolutionarily adapted foraging strategy. In the locations and times with higher poaching risk, the elephants probably maximized their foraging at specific safe spots, which may not necessarily be the richest in forage quality.

The major limitation to establishing a relationship between elephant movement tortuosity and poaching levels has been the lack of sufficient records of individually verified causes of elephant mortality recorded concurrently with movement data. Our study was able to collate such data and show that a change in elephant tortuosity values in circumstances other than migration or physical obstacles can be used as an indicator of the stress induced by poaching. We have shown that poaching affects their natural pace and movement behavior.

The human population density, poverty levels, and livestock densities around MIKE sites are strongly correlated with poaching levels (CITES 2012). As the human population increases, the encroachment on elephant home ranges is expected to increase, and elephant movement behavior will be more affected. In our study, however, despite featuring in the top model, the variables measuring distance from human dwellings had very low coefficients. Also, there was no significant interaction between PIKE and human settlements. This lack of interaction suggests that the influence of settlements is not necessarily through poaching, but possibly elephants simply avoiding encounters with humans. Another possible explanation is that elephants, intelligent as they are, do not associate risk with the mere presence of human dwellings. Instead, the elephants respond to specific human activities, and one response is to avoid real-time encounters (Graham et al. 2009). Elephants are intelligent enough to distinguish levels of threat and they can even distinguish pastoralists from other persons by odor and clothing color (Bates et al. 2008). An animal's behavioral response to a known risk depends on their assessment of the risk magnitude (Sih 2013).

MANAGEMENT IMPLICATIONS

Elephants in landscapes with high levels of illegal killing move with reduced path tortuosity. Changes in path tortuosity can serve as a useful proxy for changes in levels of illegal killing at the site level and the success of different models of conservation in contiguous land units with different conservation statuses. A reduction in path tortuosity implies reduced searching intensity per unit area, which might have negative implications in the foraging success of elephants in risky landscapes where food resources are limited.

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