# LIVING IN A RISKY LANDSCAPE:
# ELEPHANT MOVEMENT IN RESPONSE TO POACHING

Festus Wanderi Ihwagi

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# LIVING IN A RISKY LANDSCAPE:
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DISSERTATION

to obtain
the degree of doctor at the University of Twente,
on the authority of the rector magnificus,
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on account of the decision of the graduation committee,
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by
Festus Wanderi Ihwagi
born on 21 May 1977
in Nyeri, Kenya

This thesis has been approved by

**Prof.dr. A.K. Skidmore**, supervisor
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To my wife; Margaret Ngima, son; Ben-Gurion Ihwagi and Daughter;
Nataniah Nyokabi.

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# Chapter 1

# Introduction

## 1.1 Background

Global decline of biodiversity has been attributed to illegal hunting (Milner-Gulland and Leader-Williams, 1992, Harris *et al.*, 2009, Vié *et al.*, 2009, Nellemann *et al.*, 2013). Trophy hunting has been practised for centuries by the inhabitants who share landscapes with wildlife across the globe either for local use or sale (Selous, 1881, Lyell, 1910, Stigand, 1913, Woodhouse, 1976, Youth, 2005). The communities often overexploit the resources to meet the market demands (Selous, 1881, Lyell, 1910, Martin, 1990, Bodmer *et al.*, 1994, Rao *et al.*, 2011). Many rangelands are affected by the threat of illegal hunting, be it for meat or non-meat trophies (Lindsey *et al.*, 2015).

Landscape modification and its fragmentation are threats to global biodiversity (Fischer and Lindenmayer, 2007), and have affected many taxonomic groups (Gardner *et al.*, 2007). The demand for land for both settlement and agriculture has led to massive fragmentation of land on which wildlife used to roam freely (Kamugisha *et al.*, 1997, Ogutu *et al.*, 2009, Akin *et al.*, 2012, Ogutu *et al.*, 2014). Changes in land use have left many species' home ranges either completely cut off or restricted to inviable geographical extents (Turner, 1994, Kinnaird and O'Brien, 2012, Ogutu *et al.*, 2014). The change of the use of land parcels in an uncoordinated manner leads to mosaics of land use types which restricts or cuts off some animals' home ranges. Restriction of the home ranges of large herbivores leads to over-utilisation of available forage resources and subsequent land degradation (Vesey-FitzGerald and al., 1968, Croze, 1972, Ruess and Halter, 1990). The effects of diversity-dependent ecosystem feedbacks are cumulative and have become more pronounced over time (Reich *et al.*, 2012). There are numerous efforts by individuals, communities, institutes and governments to rehabilitate degraded land or restore endangered species across the world. Special attention has been given to the endangered species whose trophies have high commercial value in the legal and illegal markets. Elephant ivory is one such trophy whose demand has led to an escalation of poaching to unsustainable levels (Nellemann *et al.*, 2013).

### *Historical hunting of the African elephants, the associated decline of populations and its illegalization*

For centuries, elephant ivory has been an object of desire for many ancient and modern kingdoms and societies whose carving is a part of their cultures (Soper, 1965, Woodhouse, 1976). From late 19th century through to the first half of the 20th century, ivory merchants from around the world, especially the Portuguese, routinely visited Africa on hunting expeditions (Selous, 1881, Neumann, 1898, Lyell, 1924, Kay, 1961). The long distance ivory trade was supported by indingineous rulers, colonial chiefs and game wardens who provided porters to carry ivory through the vast, remote wild lands to the seaports (Buxton, 1902, Bell, 1923, Holman, 1967a, Holman, 1978, Douglas-Hamilton, 1980b). Unquantified volumes of ivory were shipped from all over Africa; from the then Portuguese East Africa (Ward, 1953), Belgian-Congo (Offermann, 1951), West Africa (Allison, 1943) and South Africa to various sea ports.

Formal reports of the decline and changes in the distribution of various populations of elephants driven by over-hunting began appearing in the literature as early as 1903 and continued through to the middle of 20th century (Bryden, 1903, Hubbard, 1928, Curry-Lindahl, 1954). In the early 20th century, the respective colonial governments in various African countries outlawed unlicensed hunting, and the practice of illegal hunting acquired the name poaching. Despite the ban on illegal hunting, i.e. poaching, some countries have legally regulated domestic and touristic hunting, but these activities have also been blamed for the decline of some populations (Caro *et al.*, 1998). Elephants that had extra-large tusks that would touch the ground while the elephant was in a standing position, i.e., the “great tuskers”, were the prime targets for poachers (Hubbard, 1928, Brooks and Buss, 1962, Irwin, 1964). Between 1900 and 1960, the colonial governments were unable to stop poaching and the associated trade in wildlife trophies as the poachers progressively formed organized gangs (Stone, 1972). As a result of the selective hunting of the great tuskers; both legal via hunting expeditions and poaching, a reduction in the average weight of tusk on mature elephants was reported in the 1960s (Brooks and

Buss, 1962, Jachmann *et al.*, 1995). Widespread selective hunting of the great tuskers has severely altered the gene pool of the major populations of elephants resulting in a reduction of the frequency of occurrence of mature elephants with tusks (Whitehouse and Harley, 2001, Whitehouse, 2002).

In the latter half of 20th century, poaching levels escalated to unsustainable levels across the elephant range states to magnitudes described as 'massacres' (Holman, 1967b). The first continental assessment of the status of elephant populations was conducted in 1979, and it described distinct phases that include a period of uncontrolled hunting from 1850 to 1900, introduction of game laws from 1900 to 1949, crowding into protected areas from 1950 to 1970, and period of excessive poaching in the 1970s (Douglas-Hamilton, 1979). Massive declines were confirmed through total aerial counts. At this time, there were an estimated 44,000 elephants in Kenya down from 67,000 in 1973 (Douglas-Hamilton, 1979). The population of South Luanga, a key population in Zambia in Southern Africa, declined by 40% between 1973 and 1979 where only 16,280 elephants remained (Douglas-Hamilton *et al.*, 1979).

In the 1980s, concerted efforts by some governments to stop poaching and ivory trade were made across many range states (Douglas-Hamilton, 1984a). Few populations of elephants begun stabilizing, especially in Botswana, but there was no full recovery yet to the numbers recorded in the early 1970s (Douglas-Hamilton, 1984b). The 1980s and 1990s were marked with aggressive campaigns by various governments to shut ivory markets. Kenya, in particular, made a gesture of its commitment to ending the trade by burning several tons of ivory in 1988.

### *The current conservation status of African elephants: 2000-2018*

A 2005 assessment of the status of 51 populations of elephants in Africa revealed that the Southern African elephants were recovering, but populations in East and Central Africa remained stagnant (Blanc *et al.*, 2005). It was confirmed that the population in West Africa decreased by

65% since the 1970s, largely due to poaching (Bouche, 2002, Bouche *et al.*, 2010). Between 2008 and 2012, another surge of illegal killing was witnessed throughout the African elephant range states leading further declines of already depleted populations by a further 40% (Wittemyer *et al.*, 2014, Chase *et al.*, 2016). Site-specific assessments revealed even much higher declines; 65% for forest elephants in Central Africa (Maisels *et al.*, 2013), 60% of Selous population in Tanzania (Chase *et al.*, 2016).

### *Monitoring of the Illegal Killing of Elephants (MIKE) programme*

Alarm was raised over the inadequacy of the international community to monitor and control poaching as there lacked a unified scientific approach across range states (Payne *et al.*, 1999). In response to this, the global community through the Convention on International Trade in Endangered Species (CITES) established the Monitoring of the Illegal Killing of Elephants (MIKE) programme under its *Resolution Conf. 10.10* (CITES. Secretariat, 1999). Some 57 sites were designated for MIKE monitoring in Africa, encompassing key populations. The objectives of MIKE programme include (i) to measure and record levels and trends of illegal hunting and trade (ii), to assess to what extents observed trends are related to the resumption of ivory trade, and (iii), to establish a comparative information base for management purposes. To enable direct comparison of the records from different sites noting that the efforts varied greatly, the Proportion of Illegally Killed Elephants (PIKE) was described and adopted by CITES Secretariat as a standard measure of the severity of poaching at a given space or time (Douglas-Hamilton *et al.*, 2010, Jachmann, 2013).

The first detailed site level analysis of MIKE data was done in 2008-2009, (Douglas-Hamilton *et al.*, 2010, Kahindi *et al.*, 2010), followed by a continental analysis soon after (Burn *et al.*, 2011) and these analyses identified a surge in poaching levels. The Laikipia-Samburu MIKE site is home to an estimated 7500 elephants. The MIKE site includes private, community and government land and through a successful participatory network, the site has the most comprehensive and consistent records in Africa (Douglas-Hamilton *et al.*, 2010, Kahindi *et al.*, 2010).

### *Elephant movement in relation poaching risk and the presence humans in the landscape*

African elephants respond to the spatial heterogeneity of vegetation at large spatial scales in the range of 457 - 734 m (Murwira and Skidmore, 2005). Attention has been given to the movement behaviour of elephants at various spatial and temporal scales in relation to poaching risk and the presence of human beings in shared landscapes. At the large temporal scales, major shifts in the usual seasonal migration, or distributions have been attributed to the poaching surges that elephant populations underwent (Western, 1989, Thouless, 1993, Thouless, 1995). At shorter time scales, the speed of travel has been the most relied on metric of assessing elephant behaviour in many studies, all with consistent results that elephants increase their speed when traveling through risky areas (Barnes, 1982, Douglas-Hamilton *et al.*, 2005, Blake *et al.*, 2008, Graham *et al.*, 2009, Wittemyer *et al.*, 2016).

In landscapes dominated by humans, the home range of elephants comprises distinct home ranges connected by tenuous migratory corridors though areas with high human destines of human population, along which elephants walk at faster speeds and often at night (Douglas-Hamilton *et al.*, 2005, Ngene *et al.*, 2010). Besides poaching, loss of habitat through infrastructural developments and change of land use is the most significant threats to elephants in the long term (Nellemann *et al.*, 2013). The habitats of African elephants have decreased from 26% to 15% of the continent's land area between 1995 and 2007 mainly due to the expansion of human settlements (Said *et al.*, 1995, Blanc *et al.*, 2007). The construction of highways across many landscapes has cut off elephant home ranges, and when elephants cross those highways, they move faster (Blake *et al.*, 2008).

### *Knowledge gap about the elephants' perception and reaction to threats*

Field biologists have observed elephants making repeated visits and spending time around the dying members and carcasses of the recently dead family members, an insight that elephants are cognisant of loss of life locations where they have suffered attacks (Douglas-Hamilton *et al.*, 2006). Besides such observations, the mean rate of change of an animals usual activity pattern is the best measure of its perception of risk in its environment (Laundre, 2010, Bleicher, 2017). The movement of a herbivore when it is foraging is commensurate with the heterogeneity and spatial distribution of its key resources (Etzenhouser *et al.*, 1998). However, the past and present experiences in the landscape in relation to encounters with predators influence animals' behaviour (Bleicher, 2017). Stress hormones persist in the wild elephants for extended periods of up to six years since the last time a population experienced poaching-related disturbances (Gobush *et al.*, 2008). Understanding how elephants alter their movement behaviour at fine temporal scale under the threat of poaching has not been possible because very few studies have achieved concurrent datasets of long-term GPS tracking and detailed individually verified records of causes of mortality. Regarding the fine-scale movement of elephants in landscapes with a near complete overlap with humans, there are very few MIKE sites that are entirely within human-dominated landscapes to enable a detailed study. We sought to understand how elephants adapt to the risk of poaching and presence of humans in the most complex MIKE site.

Using a long-term GPS tracking data, this thesis seeks to explore the elephants' movement in relation to spatial and temporal changes in levels of PIKE. Exploratory data analyses (EDA) is an established tradition in statistics that offers a computational and conceptual framework to foster hypothesis development (Tukey, 1977, Behrens, 1997).

## 1.2 Research objectives

The main objective of this study is to understand the site-level correlates of poaching and the elephant's movement in relation to the risk of illegal killing. Specific objectives are:

1) To determine the conservation efficacy of land under different ownership and land use types based on the distribution of live

elephants and the spatial and temporal changes in the levels of illegal killing in Laikipia-Samburu ecosystem, Kenya.

2) To determine how elephants adjust their movement in response to the poaching at short time scales:
    a) hourly
    b) night and day (12 hours), and
    c) daily (24 hours) activity cycle

## 1.3 Study area

The study was conducted in the Laikipia-Samburu ecosystem of northern Kenya from the year 2002 to 2016 (Fig. 1.1). The ecosystem lies within 0.4°S to 2°N, 36°E to 38.5°E, an area of approximately 34,000 km$^2$. It is delineated by the geographical extent of the Ewaso Nyiro River and its tributaries, in the low lands 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 solitary hills (Wall *et al.*, 2006). Wildlife shares the landscape freely with the predominantly pastoral communities (Georgiadis, 2011). 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 by restricting their movements to the wildlife-friendly private ranches and conservancies.

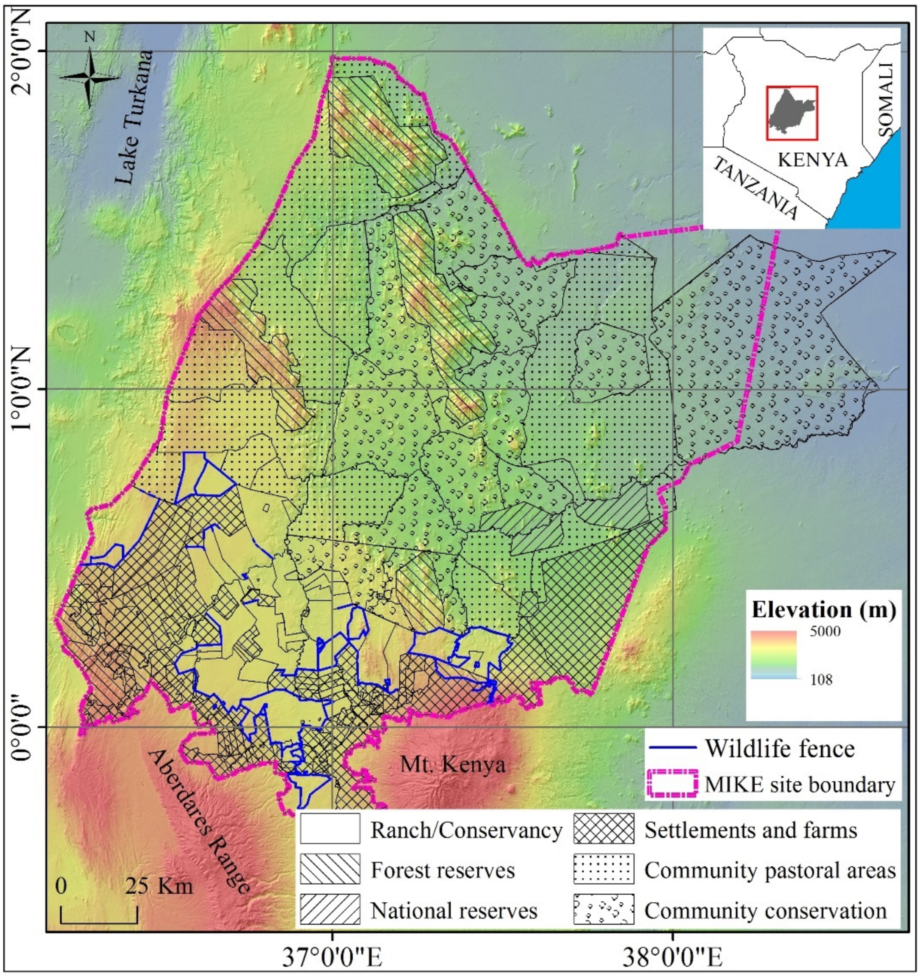

**Figure 1.1** The Location of Laikipia-Samburu ecosystem at the National level (inset) and the regional level (main map). The landscape has a sharp elevation gradient, and the land is subdivided into numerous parcels under six interspersed major land uses. The land uses in the map are as they were in the years 2002 to 2012 when the bulk of data was collected.

## 1.4 Outline of the thesis

This thesis consists of six chapters; a general introduction, four core chapters and a synthesis. Each of the core chapters is based on a distinct article that has been submitted or is already published in a journal.

Chapter 1 provides an overview of the history of poaching, the effect of poaching on population trends and the efforts to monitor and control poaching in Africa.

Chapter 2 presents a background of the complexity of the study site in terms of land ownership and land uses, which influence the conservation statuses of different parcels of land. Using the distribution of live elephants, and spatial-temporal trends of illegal killing the chapter explores the efficacy of different land management units in protecting elephants.

Chapter 3 explores the hourly variation of elephant movement behaviour of elephants in their respective core areas. It explores the variation of path tortuosity of elephants in places and times of high and low poaching levels.

Chapter 4 explores the night-day variation of movement rates. It explores a new method; the night-day speed ratio, to detect variation in behaviour within day and night when the elephant is on low and when it moves into high poaching areas.

Chapter 5 explores the overall activity cycle of elephants within a 24-hour period when they are in low and high poaching areas.

Chapter 6 is a synthesis of the implications of behavioural adaptations of the elephants to poaching risk on their ecology.

# Chapter 2

# Using poaching levels and elephant distribution to assess the conservation efficacy of private, communal and government land in Northern Kenya[*]

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[*] This chapter is based on: Ihwagi, F. W., Wang, T., Wittemyer, G., Skidmore, A. K., Toxopeus, A. G., Ngene, S., King, J., Worden, J., Omondi, P. & Douglas-Hamilton, I. 2015. Using Poaching Levels and Elephant Distribution to Assess the Conservation Efficacy of Private, Communal and Government Land in Northern Kenya. PLoS ONE 10:e0139079.

## Abstract

Efforts to curb elephant poaching have focused on reducing demand, confiscating ivory and boosting security patrols in the elephant range. Where land is under multiple uses and ownership types, determining the local poaching dynamics is important for identifying successful conservation models. Using 2,403 verified elephant, *Loxodonta africana*, mortality records collected from 2002 to 2012 and the results of total-aerial counts of elephants conducted in 2002, 2008 and 2012 for the Laikipia-Samburu ecosystem of northern Kenya, we sought to determine the influence of land ownership and use on diurnal elephant distribution and on poaching levels. We show that the annual proportions of illegally killed (i.e., poached) elephants increased over the 11 years of the study, peaking at 70% of all recorded deaths in 2012. The type of land use was more strongly related to levels of poaching than was the type of ownership. Private ranches, comprising only 13% of land area, hosted almost half of the elephant population and had significantly lower levels of poaching than other land use types except for the officially designated national reserves (covering only 1.6% of elephant range in the ecosystem). Communal grazing lands hosted significantly fewer elephants than expected, but community areas set aside for wildlife demonstrated significantly higher numbers of elephants and lowered illegal killing levels relative to non-designated community lands. While private lands had lower illegal killing levels than community conservancies, the success of the latter relative to other community-held lands shows the importance of this model of land use for conservation. This work highlights the relationship between illegal killing and various land ownership and use models, which can help focus anti-poaching activities.

## 2.1 Introduction

Land ownership has a substantial effect on the potential use of an area for wildlife conservation (Newmark and Hough, 2000, Fitzsimons and Wescott, 2007, Petrzelka and Marquart-Pyatt, 2011), while land use also typically influences the distribution and abundance of herbivores (Blom *et al.*, 2005, Georgiadis *et al.*, 2007, Ogutu *et al.*, 2009, Ogutu *et al.*, 2014). In turn, animal distribution and abundance can determine the location and intensity of illegal hunting activities (Waltert *et al.*, 2009, Maingi *et al.*, 2012). Land under an official conservation status is traditionally associated with higher protection and abundance of wildlife and is recognized as critical for the conservation of species (Hedges *et al.*, 2005, Pia *et al.*, 2013). Nevertheless, the relationship between wildlife protection and the different ownership and land use models outside the government-protected areas has not been widely studied.

Over-hunting of wild animals is a primary driver of species decline (Peres, 1990, Wiederholt *et al.*, 2010). It has been designated as one of the 'evil quartet' drivers of extinction (Diamond, 1984). Through the Monitoring of Illegal Killing of Elephants (MIKE) programme of the Convention on International Trade in Endangered Species (CITES), the cause of elephant deaths is collected in selected sites across the elephant range to assess changes in illegal killing pressure over time. The monitoring data compiled under the MIKE programme across the range states provide useful information on the status of populations that have been synthesized into site, national, or continental level appraisals (Burn *et al.*, 2011, Milliken *et al.*, 2012, Nellemann *et al.*, 2013, Wittemyer *et al.*, 2014). During the years 2011 and 2012, an all-time high in the poaching rate and ivory trade level was recorded across the entire African elephant range (Nellemann *et al.*, 2013, Wittemyer *et al.*, 2014). An increase in the levels of poaching in Kenya had already been reported earlier on in the year 2009 (Douglas-Hamilton, 2009). In addition to being important for assessing global trends, MIKE data provides a potential unique opportunity to investigate the fine-scale spatial patterns of illegal killing at the site level, which has not been fully exploited.

Due to the covert nature of poaching and the ivory trade, it is difficult to gather information on these aspects as well as the key drivers. This is compounded by the unequal conservation efforts across expansive landscapes with varied types of land ownership and land use (Kahindi *et al.*, 2010). Detailed site-level studies of elephant poaching can provide the opportunity to identify factors that contribute to rising or falling poaching levels. In Kenya, land ownership is private, communal or public (Simon, 1979, Bekure *et al.*, 1990), and focused wildlife management is represented across all ownership types. Areas under distinct land use encompass varied habitat types and their large geographical extent exceeds the spatial scale at which elephants respond to habitat heterogeneity (Murwira and Skidmore, 2005). The Laikipia-Samburu ecosystem is one of the few designated MIKE monitoring sites with a variety of land uses and ownership categories. It is home to Kenya's second largest elephant population, estimated at approximately 6,500 elephants (Thouless *et al.*, 2008), and has been the focus of the most comprehensive carcass monitoring (yielding the largest dataset) of all MIKE sites (Douglas-Hamilton *et al.*, 2010). A combination of community-based information gathering, research, and security patrols has generated a detailed dataset on elephant mortality (Kahindi *et al.*, 2010).

Kenya's national elephant management and conservation strategy underscores the need to identify land use types that are compatible with conservation (Omondi and Ngene, 2012). Wildlife populations in the protected and unprotected areas of Kenya declined sharply from the 1980s to 2009 (Western *et al.*, 2009). The general decline in migratory herbivores in Kenya is attributed partly to the loss of dispersal areas (Ottichilo *et al.*, 2000). Despite the overall decline in wildlife numbers at the national level, the Laikipia- Samburu ecosystem has had stable or increasing numbers of some species including elephants (Didier *et al.*, 2009). The largest proportion of Kenya's wildlife is found on private and communally owned land, as reflected in the Laikipia-Samburu ecosystem (Western *et al.*, 2009). The combination of land ownership and land use types in Laikipia Samburu ecosystem offers an opportunity to investigate the influence of different covariates on poaching at the site level. This study investigated the relationships between the level of illegal killing, elephant distribution, land ownership and land uses over a period of eleven years in northern Kenya.

## 2.2 Materials and Methods

Kenya Wildlife Service, the custodian of wildlife resources in Kenya, played an integral part in this study, which was thus exempt from requiring a permit.

### *2.2.1 Study area*

The study was conducted in the Laikipia-Samburu ecosystem of northern Kenya. The ecosystem is defined by the geographic extents of the Ewaso Nyiro river and the historical elephant migration range (Georgiadis, 2011). The ecosystem lies within 0.4°S to 2°N, 36.2°E to 38.3°E, and encompasses an area of 33,817 km$^2$. A wide range of habitats are linked with the elevation and climatic gradients that characterize the region: from cool, wet highlands in the south to hot, dry lowlands in the north (Georgiadis, 2011). Rugged mountains interrupt the otherwise gently undulating open landscape, which elephants would generally avoid (Wall *et al.*, 2006). The confirmed Laikipia-Samburu elephant range encompasses six major land use types: community conservancies, private ranches, communal pastoral areas, state-protected forest reserves, settlements mainly under sedentary subsistence production, and the national reserves (Fig. 2.1).

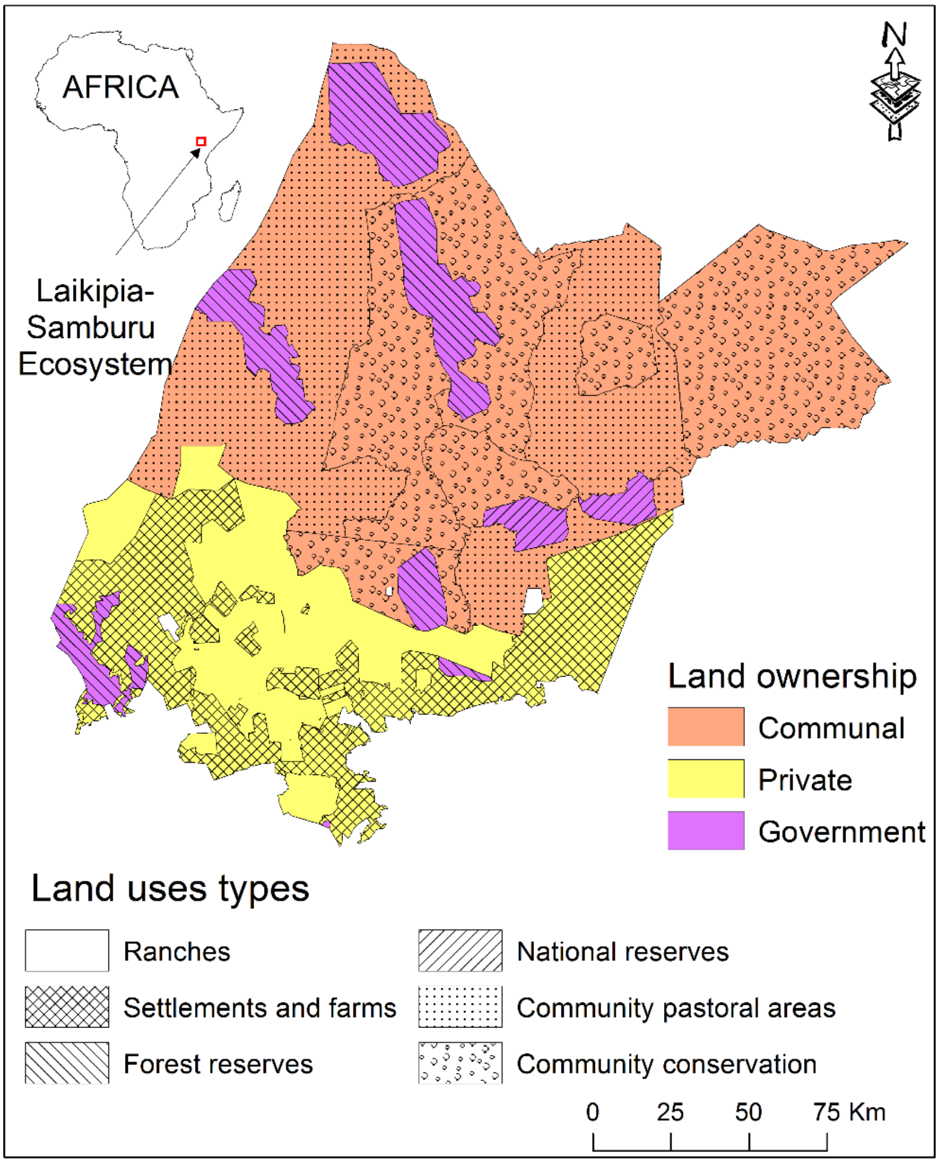

**Figure 2.1** Land ownership (private, communal or government) and types of use (managed to enhance wildlife or not) in the Laikipia-Samburu ecosystem. Ranches, community conservancies and national reserves have active wildlife protection measures in place.

The private, government and community lands comprise 30%, 11% and 59% of the landscape, respectively. The area of land under each different land use type ranges from 533 km$^2$ to 11,457 km$^2$ (Fig. 2.2).

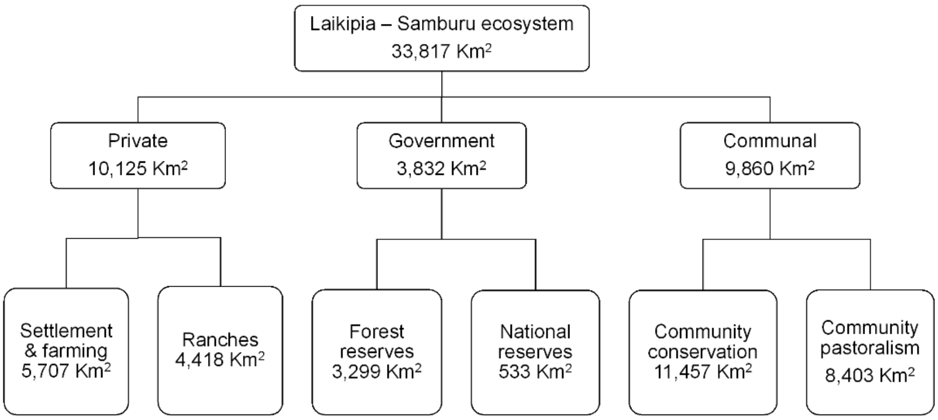

**Figure 2.2** Land ownership, the corresponding land use types and approximate sizes of each category in the Laikipia-Samburu ecosystem.

Non-conserved communal land is occupied by nomadic pastoral communities, and inhabited by both livestock and wildlife, but it lacks any systematic security patrolling. There are also communities that actively manage their land for wildlife protection (i.e., community conservancies), and have trained (and in some cases armed) rangers to patrol the conservancies. The government land comprises national reserves managed for wildlife conservation, and forest reserves, which are national heritage sites but with no active management for wildlife. There are three national reserves in the ecosystem, Samburu, Buffalo Springs and Shaba. These are located in the centre of the ecosystem but are relatively small (533 km$^2$ in total), representing only 1.5% of land under the confirmed elephant range. The national reserves are managed by local government authorities, which employ armed rangers to safeguard wildlife. Unauthorized access to national reserves is prohibited, although there are concessions for communal use and access by surrounding and/or nomadic communities is common but regulated. The forest reserves are managed by the national government, and they often coincide with mountain ranges. Unlike the national reserves, the communities living around forests have uncontrolled access to them. They use the forests as additional grazing land. The southern limit of the Laikipia-Samburu ecosystem is primarily private land (i.e., settlements and ranches). In the settlements, the land is highly subdivided into plots of less than ten hectares. A few of these plots are not yet permanently occupied but are instead utilized as extra grazing areas by neighbours. Over 50 private ranch properties, ranging from approximately 10 hectares to 35,000 hectares, are managed for commercial cattle production, with owners generally allowing wildlife access on their properties. Some of the ranches have tourism establishments and activities. They have establishments such as hotels, lodges and campsites, etc., whereas activities include day-trippers/day safaris and tour operator visits.

### *2.2.2 Total aerial count of elephants*

To assess elephant distribution, population status and trends, total aerial counts were conducted in June 2002 (dry season), November 2008 (wet season) and November 2012 (wet season) using standard total aerial counting techniques (Douglas-Hamilton, 1996, Craig, 2004). High-wing Cessna aircraft (10 in 2002, 10 in 2008 and 13 in 2012) were used in each of the week-long counting exercises. The interval between the flight lines was set at one or two kilometres, depending on visibility, to ensure all the ground was scanned and all the elephants were counted. The waypoints and corresponding elephant counts were assigned to land ownership, and land uses for further analyses. The average densities of elephants were estimated from the three counts yielding a relative abundance across the wet and dry seasons.

### *2.2.3 Collecting elephant mortality data*

Information on incidences of elephant mortality was gathered through a network of nomadic herders, researchers, community conservancy scouts, private ranch managers, and Kenya Wildlife Service rangers (Kahindi *et al.*, 2010). The information from herders and ranch managers was verified by a field visit to the carcass by a Kenya Wildlife Service ranger, a trained community scout, or a researcher. A standard data sheet devised by the MIKE Technical Advisory Group was completed for each carcass, including the estimated date of death, GPS coordinates and the cause of death (CITES. Secretariat, 1999). Four causes of death were recognized, i.e., poached, human-elephant conflict, problem animal control (killed by authorized personnel in defence of life or property), and natural mortality.

Where it was not possible to identify the cause of death with certainty, the cause of death was listed as ‘unknown’. A total of 2,403 dead elephants were recorded from 2002 to 2012 (Table 2.1).

**Table 2.1** The number of elephant carcasses recorded from 2002 to 2012, their cause of mortality, and the average number of live elephants recorded within different land use types in the Laikipia-Samburu ecosystem.

| Land use | Area (km$^2$) | Live elephants | Causes of elephant mortality | | | | |
|---|---|---|---|---|---|---|---|
| | | | HEC* | Natural | PAC | Poached | Unknown |
| Settlement & farming | 5,707 | 73 | 14 (12%) | 29 (25%) | 27 (23%) | 30 (26%) | 16 (14%) |
| Ranches | 4,418 | 2652 | 43 (7%) | 235 (37%) | 39 (6%) | 220 (34%) | 103 (16%) |
| Forest reserves | 3,299 | 407 | 55 (14%) | 95 (25%) | 13 (3%) | 154 (40%) | 64 (17%) |
| National reserves | 533 | 602 | 2 (1%) | 80 (56%) | 2 (1%) | 41 (28%) | 19 (13%) |
| Community conservation | 11,457 | 1872 | 82 (10%) | 259 (33%) | 8 (1%) | 308 (39%) | 139 (17%) |
| Community pastoralism | 8,403 | 785 | 41 (13%) | 84 (26%) | 6 (2%) | 125 (38%) | 70 (21%) |

*HEC refers to elephant mortality resulting from human-elephant conflict incidences. PAC refers to problem animal control, i.e., elephant mortality as a result of the killing of problematic elephants by authorised personnel. The proportionate cause of mortality within each land use type is indicated in brackets. The live elephants refer to the average number recorded within land under each type of use in the years 2002, 2008 and 2012.

Search efforts by herders and patrol officers on ranches and in pastoral areas were not recorded. The search effort was generally expected to vary between the different land use types, but constant within each land use type over time. Likewise, the financial and human resources deployed by land managers were not available. Preliminary analyses of the effectiveness of the data collection protocol were performed using data for the first three years, 2001 to 2003, and showed that the numbers of carcasses due to various causes did not vary considerably between the different participants in the data collection network (Kahindi *et al.*, 2010). The Proportion of Illegally Killed Elephants (PIKE) has been validated as a reliable measure of the severity of illegal killing in monitoring sites, irrespective of the availability of effort information (Douglas-Hamilton *et al.*, 2010, Kahindi *et al.*, 2010, Jachmann, 2013). The PIKE is calculated as:

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

PIKE values exceeding 54% have been identified as indicative of declining populations (Nellemann *et al.*, 2013, Wittemyer *et al.*, 2014). The ratio of dead to all the counted live and dead elephants, i.e., the carcass ratio, provides insight into population trends (Douglas-Hamilton and Burrill, 1991, Kahindi *et al.*, 2010), and was examined alongside the carcass monitoring data. This study used the ground-based carcass count together with the aerial live-elephant count to determine the carcass ratio.

### *2.2.4 Statistical analyses*

The observed distribution of elephants per land use category was compared to the expected distribution using a Chi-square test. The expected distribution was derived from a null or random distribution assumption (the study area's average elephant density multiplied by the area of land use zone). Spatial and temporal variation in the level of poaching over the 11-year study period were analysed using a logistic regression generalized linear model (GLM) (binomial family with a logit function and implemented with the "lme4" package in R) (R Development Core Team, 2012a). The response variable was the number of elephant carcasses found as a binary outcome of two main causes of deaths, i.e., illegally killed or not illegally killed. The probability of illegal killing of elephants was modelled using a bivariate covariate for each of the land ownership types (private, communal or government). Land use type, either managed for wildlife or not, was also assigned a bivariate covariate. Elephant density was factored in the model as a continuous variable. Time was factored in as "year of death". The land use type officially designated for wildlife conservation (national reserves) was used as the reference covariate. Models with different combinations of covariates and their interactions were fitted and compared using the second-order Akaike Information Criterion (AICc) (Burnham and Anderson, 2002).

Some of the community conservancies were established more recently than others. Their development differs in terms of staff recruitment and conservation budgets, but there were no comparable management records available for all the conservancies to enable us to perform a systematic analysis of these factors. The fully operational conservancies as of 2005 were ascribed a conservancy status in the analysis. Those not fully established were lumped together with the unmanaged communal grazing areas.

Upon breaking down the dataset into individual land use types by year, there were wide variations in sample sizes. Consequently, the annual PIKE values across the individual land use and ownership types were not normally distributed. Due to these irregularities, non -parametric tests were applied to assess differences in PIKE across land use types. The differences in PIKE levels were compared among the land uses under the same ownership category using the Kruskal-Wallis test. The differences in PIKE across the six land use types were tested using pairwise Mann-Whitney tests. Pearson's product-moment correlation coefficient ($r$) was used to assess the correlation between the study area's carcass ratios and PIKE within the land use types. Pearson's $r$ was also used to test for the relationship between the number of live elephants and the number killed illegally, as well as the number of deaths from natural causes. Linear regression was used to test the significance of the trend in PIKE level from 2002 to 2012. All tests of statistical significance were conducted at $\alpha = 0.05$.

## 2.3 Results

### *2.3.1 Distribution of elephants in relation to land ownership and land uses*

A total of 5,447 elephants were counted in 2002, 7,415 in 2008 and 6,365 in 2012 (Fig. 2.3).

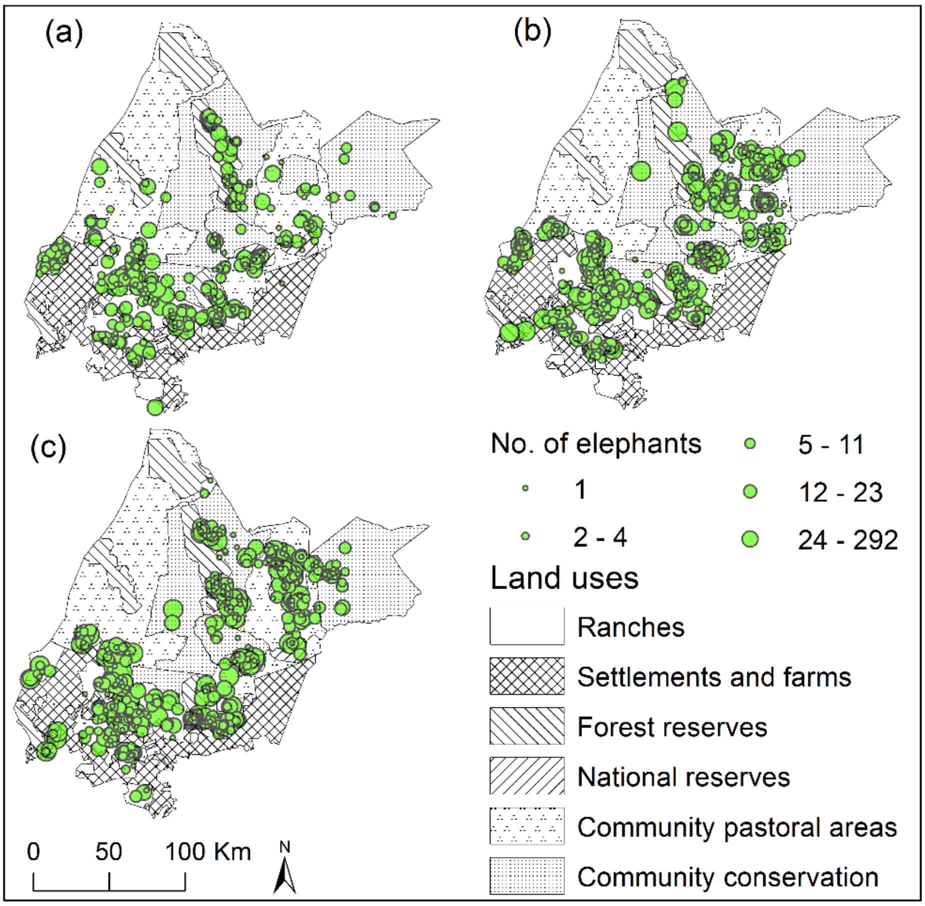

**Figure 2.3** The distribution of elephants in the Laikipia-Samburu ecosystem derived from total aerial counts in (a) 2002 (n = 5,447), (b) 2008 (n = 7,415), and (c) 2012 (n = 6,365). Elephants were found in large numbers within private ranches and the national reserves.

There were significant differences between the observed and expected numbers (based on land area) of live elephants across the three land ownership types ($\chi^2 = 776.6$, $P < 0.001$) and also within the six land uses ($\chi^2 = 301.7$, $P < 0.001$). The site's average elephant density was 0.314 elephants per square kilometre. The private ranches and national reserves were higher than the average at 0.537 and 0.993 elephants per square kilometre, respectively. There was a close match between the observed and expected number of elephants within the community conservancy areas (conservancies comprise 33.9% of the elephant range and hosted 29.3% of the elephants). The communal land under pastoralism, comprising 24.8%

of the elephant range, hosted half of the expected number of animals at only 12.3% of the elephant population.

### *2.3.2 PIKE on land under different ownership and uses*

The overall PIKE increased significantly over the 11 years of the study ($R^2 = 0.8$, n = 10, $P < 0.05$) (Fig. 2.4). The private ranches, settlements and national reserves had the lowest levels of average annual PIKE for the entire study period at 21%, 24% and 26% respectively. On the other hand, community conservation areas, forest reserves, and community pastoral areas had higher levels of average annual PIKE at 37%, 38% and 39% respectively. Annual PIKE increased in each land use category except for the national reserves and settlement areas (Fig. 2.5).

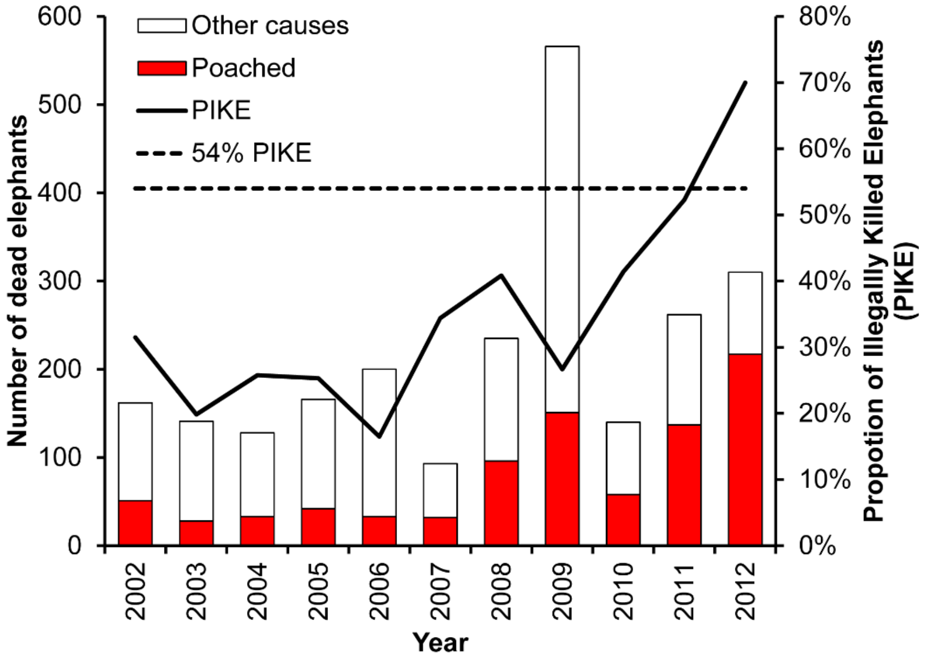

**Figure 2.4** The numbers of elephants that died from poaching and other causes from 2002 - 2012. The dotted line indicates the level of poaching (i.e., 54% PIKE) beyond which populations cannot compensate via births and decline is imminent.

The PIKE levels did not differ significantly between the three different ownership types if land use within each type was not accounted for (Kruskal-Wallis $\chi^2 = 5.248$, $P = 0.073$). There were significantly lower levels of PIKE in areas managed for wildlife on government land (i.e. national reserves had a lower PIKE than forest reserves) (Mann-Whitney test: $U$ = 19.682, $Z$ = 2.405, $P$ = 0.016), as well as lower levels in conservancies relative to pastoral areas within community land (Mann-Whitney test: $U$ = -16.182, $P$ = 0.048). However, there was no difference in PIKE found between private ranches and settlements (Mann-Whitney test: $U$ = 0.409, $Z$ = 0.05, $P$ = 0.96) (Fig. 2.6).

A set of eleven generalized linear models with different combinations of covariates were constructed (Table 2.2). The top two models were selected using the second-order AICc. The coefficients of the top model are shown in Table 2.4 The top model featuring only land use, its ownership type and time factor (i.e., year of observation) explain 38% of the variation seen in the level of illegal killing of elephants in the Laikipia-Samburu ecosystem (Table 2.3).

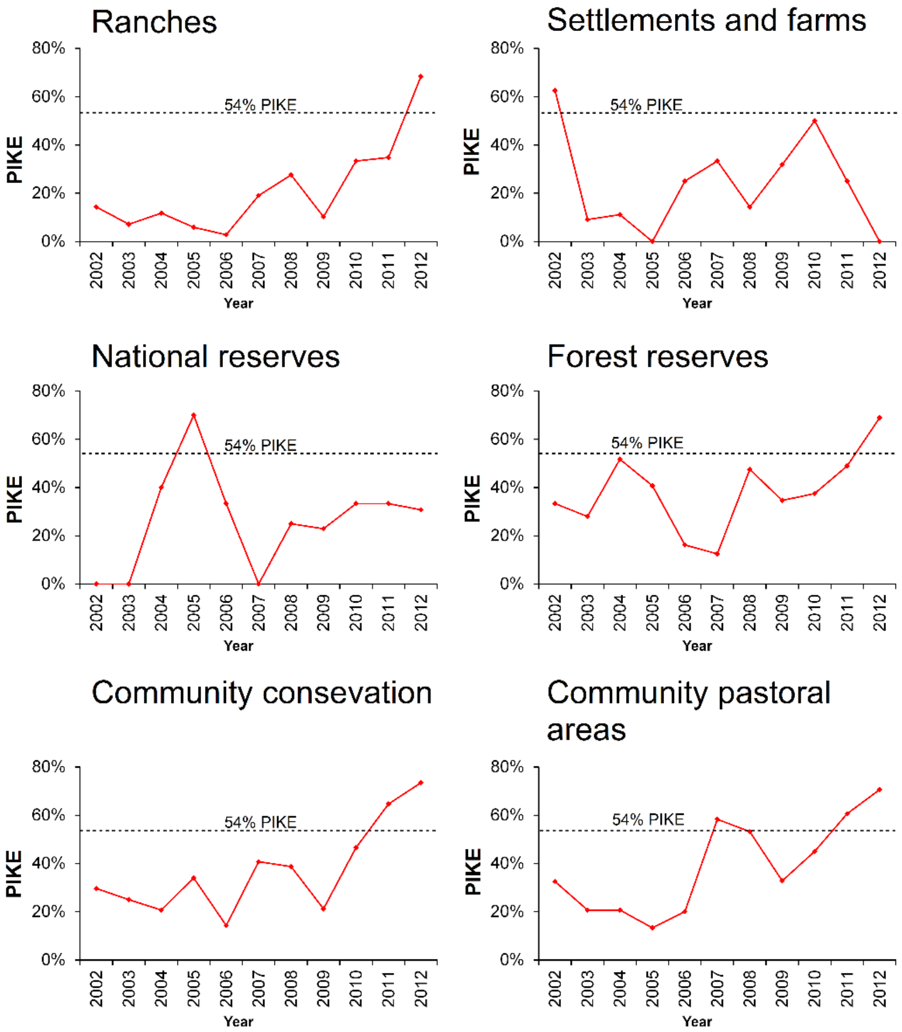

**Figure 2.5** Trends in the level of the Proportion of Illegally Killed Elephants (PIKE) across the different types of land use for 2002 - 2012. An increase in PIKE from 2010 - 2012 was recorded in most of the land use types.

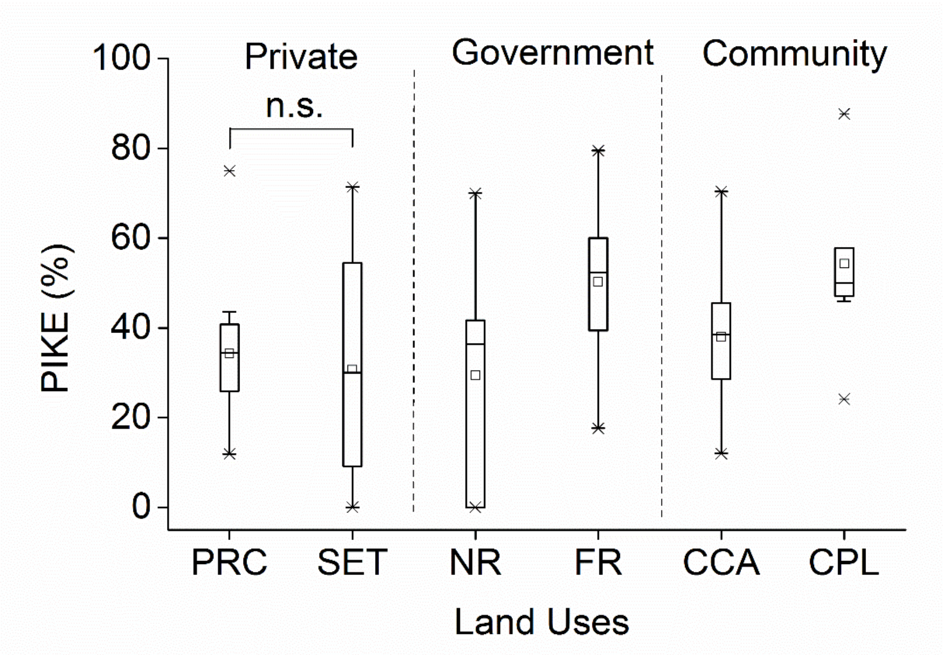

**Figure 2.6** Trends in the Proportion of Illegally Killed Elephants (PIKE) across the different types of land use for 2002-2012. An increase in PIKE from 2010 - 2012 was recorded in most of the land use types.

**Table 2.2** Candidate models in the analyses of the relationship between the probability of illegal killing of elephants ($P_{illegal}$), land ownership, land use and elephant densities.

| Model | Model description |
|---|---|
| 1 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{private}) + \beta_3(\text{community}) + \beta_4(\text{WF}) + \beta_5(\text{private*WF})$ |
| 2 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{density})+ \beta_3(\text{private}) + \beta_4(\text{community}) + \beta_5(\text{WF})+ \beta6(\text{private*WF})$ |
| 3 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})$ |
| 4 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})+ \beta_3(\text{density}) + \beta_4(\text{community})$ |
| 5 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})+ \beta_3(\text{density}) + \beta_4(\text{private})+ \beta_5(\text{community})$ |
| 6 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})+ \beta_3(\text{private}) + \beta_4(\text{community})$ |
| 7 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})+ \beta_3(\text{density})$ |
| 8 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{WF})+ \beta_3(\text{density}) + \beta_4(\text{private})$ |
| 9 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{year}) + \beta_2(\text{density})$ |
| 10 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{private}) + \beta_2(\text{community}) + \beta_3(\text{WF}) + \beta_4(\text{private*WF})$ |
| 11 | $P_{\text{illegal}} = \beta_0 + \beta_1(\text{density}) + \beta_2(\text{private}) + \beta_3(\text{community}) + \beta_4(\text{WF})+ \beta_5(\text{private*WF})$ |

‘WF’ denotes wildlife-friendly land regardless of ownership. The asterisk between covariates shows the only interactive effects of ownership and use that were found to be significant predictors of illegal killing.

**Table 2.3** Selection statistics for the top two models of the analyses of relationships between the probability of illegal killing of elephants, land ownership, land uses and elephant density.

| Model | AICca | Δib | Wic |
|---|---|---|---|
| -290.15 + 0.15 (year) -0.71(private) + 0.24 (community) -0.89(WF) +1.16 (Private*WF) | 465.7 | 0.00 | 0.76 |
| -289.81 + 0.15(year) +0.18(density) - 0.67(private) + 0.29(community) - 0.94(private*WF) | 468.0 | 2.28 | 0.24 |

The coefficient for each variable is presented alongside each variable. 'WF' denotes wildlife-friendly land regardless of ownership. * denotes interactive effects. aAICc: Second-order Akaike Information Criterion; bΔi: delta AIC values; Wic: Akaike weights.

**Table 2.4** The coefficients of the covariates of the top model and their statistical significance.

| | Estimates | Standard error | *Z* | *P* |
|---|---|---|---|---|
| Intercept | -290.147 | 33.727 | -8.603 | < 0.001 |
| Year | 0.145 | 0.017 | 8.604 | < 0.001 |
| Private land | -0.714 | 0.243 | -2.934 | 0.003 |
| Communal land | 0.243 | 0.124 | 1.966 | 0.049 |
| Managed for wildlife | -0.886 | 0.119 | -7.472 | < 0.001 |
| Private*managed for wildlife | 1.159 | 0.266 | 4.364 | < 0.001 |

* denotes interactive effects

**Table 2.5** The deviance explained by various covariates of the top model for the probability of illegal killing of elephants in the Laikipia-Samburu ecosystem. Land use and time factor explain 38% of the variation in illegal killing.

| | Deviance | Residual deviance | Deviance explained |
|---|---|---|---|
| NULL | 392.03 | | |
| Year | 80.52 | 311.51 | 20.54% |
| Private land | 8.56 | 302.95 | 22.72% |
| Communal land | 0.42 | 302.54 | 22.83% |
| Wildlife-friendly use | 39.06 | 263.48 | 32.79% |
| Private*Wildlife friendly use | 19.98 | 243.51 | 37.88% |

* denotes interactive effects

From the aerial survey results, we found that the study area had an average carcass ratio of 3.5. The numbers of carcasses from natural mortality in the different land use categories were significantly correlated with the numbers of live elephants (Pearson's $r = 0.951$, $P = 0.004$). In contrast, the numbers of carcasses from poaching were not correlated with the number of live elephants (Pearson's r = 0.205, $P = 0.696$). The average carcass ratios in the entire study area for the three census years were significantly correlated with the corresponding proportions of poached carcasses (Pearson's $r = 0.997$, $P = 0.003$), but not with the proportion of natural mortalities (Pearson's $r = -0.906$, $P = 0.094$).

## 2.4 Discussion

### 2.4.1 Elephant distribution, land ownership and land use

The lands managed by private ranches and community conservancies are manifestly important for conservation because they have a much higher number of elephants on them than we had expected to find. Elephants move from the private ranches to the settlement areas under cover of darkness, especially during the crop-growing seasons (Graham *et al.*, 2009); this behaviour may lead to their occupancy of the settlements being under-represented by aerial counts, which are conducted during daylight hours. This nocturnal behaviour has been reported in the southern part of the Laikipia-Samburu ecosystem where private ranches border dense and permanent settlements (Graham *et al.*, 2009). Unlike in the settlements and ranches interface, the diurnal movement of elephants between pastoral community land and the protected areas is minimal (Raizman *et al.*, 2013).

We found the community conservancies are important for the conservation of elephants because they have significantly higher elephant densities relative to the unprotected pastoral areas. The community lands are also important for connectivity in the greater ecosystem (Douglas-Hamilton and Vollrath, 2005). However, wildlife access to prime grazing areas of communal land is, at times, affected by conflicts amongst pastoral tribes seeking control of such areas. A key consequence of establishing conservancies has been the peaceful resolution of disputes and promotion of harmonious co-existence (Greiner, 2012), which has benefited both wildlife and people. In the Samburu-Laikipia ecosystem, armed conflicts were leading to incursions into the prime wildlife habitats, including the national reserves. These were causing the wildlife to disperse elsewhere. The occupation of protected areas by illegally armed nomadic pastoralists during bouts of tribal conflict, for example in Shaba National Reserve in the year 2010, further hinders the security patrol efforts and puts elephants and other wildlife at greater risk of poaching.

### *2.4.2 Temporal trend in poaching*

Analysing the site level dynamics of poaching in landscapes under varied ownership and uses can inform management on where to focus anti-poaching activities. The increase in poaching over time in the Laikipia-Samburu ecosystem was consistent with the internationally observed trend of a general increase in the illegal killing of elephants across the African elephant range (Nellemann *et al.*, 2013). It likely reflects the increasing black market price of ivory in the region and the increasing trafficking of illegal ivory through Kenya during this period (Wittemyer *et al.*, 2014). The temporal change in levels of poaching also interact with land use categories (see discussion below). In the year 2010, the private ranches that had previously sustained relatively low levels of poaching experienced more poaching as well.

In 2009, there was a severe drought that led to the death of an unusually high number of elephants (Wittemyer *et al.*, 2013). The number of carcasses recorded in the drought year reached an all-time high of 566, compared to an average of 160 carcasses per year in the preceding years. In this drought year, 286 deaths were confirmed to have been from natural mortality. The drought-related natural deaths led to a marked reduction of PIKE for the year. Nevertheless, the absolute numbers of poached elephants increased from 96 in 2008 to 151 in 2009. Since we were unable to control for security patrol efforts, we cannot infer poaching trends from the absolute numbers of carcasses (Kahindi *et al.*, 2010, Jachmann, 2013). However, other approaches relying on intensive monitoring of individual elephants captured an increase in poaching rates in 2009 (Wittemyer *et al.*, 2014).

Poached elephant carcasses found in the national reserves were mainly of elephants shot outside the reserves, but which succumbed in the reserves as they sought refuge (Wittemyer *et al.*, 2013). A number of injured elephants were also seen in the national reserves and treated for gunshot wounds. Consistent with the observed increase in poaching levels throughout Africa, the proportion of poached elephants in forest reserves rose steadily from the year 2010 to an all-time high of 76% in 2012; this was higher than in any other land use type. The unhindered access to the forest reserves may make it easier for the poachers to operate.

The private ranches hosted approximately 42% of elephants in the ecosystem and had a low level of PIKE relative to all the land uses until the poaching surge in 2010-2012. In 2012, the PIKE went up to 77%. An average of 58 dead elephants (from various causes) was recorded each year on private ranch land. Though we did not analyse PIKE within individual ranches due to small sample sizes, we observed that the surge in poaching overwhelmed a few of the ranches (Laikipia Ranch, ADC Mutara and Ngorare ranches) that suffered unauthorized incursions by pastoralists. The leading causes of mortality in the settlements were problem animal control and human-elephant conflict. To understand why PIKE levels were not different between the two management levels on private lands (i.e., ranches and settlements), we need to have finer scale metrics including individual land owner's investments towards elephant protection, which however are not available. However, we suspect that there is a minimal disparity in the level of security investments and other infrastructural developments across the privately-owned lands. The community pastoral areas had the highest overall levels of poaching during the entire study period (average annual PIKE = 49.8%), but the PIKE in these areas also increased in 2010-2012 in line with the trend seen in the other land use types. Likewise, the community conservancies had lower levels of poaching until the year 2010 when PIKE started increasing. Overall, it is apparent that there was a major change in illegal killing activity during 2011 and 2012 when even better-protected areas experienced markedly higher levels of poaching.

Variation in carcass ratio can be attributed to sampling effects as well as demographic drivers of immigration, emigration, births and deaths (Douglas-Hamilton and Burrill, 1991). The positive correlation between PIKE and carcass ratio is an indication that the variation in carcass ratio can, at least in part, be attributed to poaching. The 14.2% decline in elephant numbers in the years 2008-2012 (from 7,415 to 6,365) can most likely be attributed to the drought and to poaching, rather than migration as the counts were conducted at exactly the same time of the year (season) and the dispersal areas were limited. A lack of correlation between PIKE and local elephant densities shows that the activity of poachers was not influenced by the local elephant densities. The conservation efforts in various land use units are the most likely determinants of where and when poachers strike since we have shown that land use and time explains 38% of the variation seen in the illegal killing of elephants in this study. Encouraging and promoting landowners to adopt land use types that recognize the importance of protecting wildlife would thus substantially reduce poaching levels. The rest of the variation in poaching levels could be explained by other factors related to human activities or variation in law enforcement which we had no data for, and also possibly by natural resource distribution which was beyond the scope of this study.

### *2.4.3 Poaching, land use and land ownership*

Non-protected elephant habitats are important to the conservation of elephants (Nellemann *et al.*, 2013), but are often the areas under most threat (Gardner *et al.*, 2007, Caro and Sherman, 2011). In the Samburu-Laikipia ecosystem, which is largely unprotected, we found poaching levels were not simply a function of elephant density (the primary correlate of natural mortality in the system). This differs from a parallel analysis conducted in a protected area, where poachers were selecting sites based on elephant population density (Maingi *et al.*, 2012). Rather, here our results show that land use has a strong influence on the level of poaching in the Laikipia-Samburu system, but this relationship cannot be predicted by ownership type alone. Instead, we found that specific types of land use within ownership categories were more clearly related to levels of poaching.

Land outside the protected areas is pivotal for elephant conservation in the Laikipia-Samburu ecosystem because it accounts for 98.5% of the elephant range. The unprotected land under private ranching and community conservation had the highest densities of elephants, indicating their importance for elephant conservation in the ecosystem. Significantly higher densities of elephants in the community conservancies than in the community pastoral areas indicate the success of this model of conservation: management of wildlife alongside communal grazing. Despite lower densities of live elephants and higher ratios of illegally killed carcasses, the unprotected community pastoral land is important for connecting the formally protected areas and the wildlife-friendly private ranches and conservancies in the greater ecosystem (Douglas-Hamilton *et al.*, 2005).

### *2.4.3 Conclusions and Recommendations*

Levels of poaching in the Laikipia-Samburu ecosystem are heterogeneous in space and time and strongly related to land use type (more than to ownership model). The most successful models of conservation (land uses), based on elephant density and levels of illegal killing, were private ranching and community conservation. This study suggests that how local interventions to reduce elephant poaching can be more effective if they are focused on the most affected areas, and not necessarily on where elephant densities are highest (although both are important).

Our results indicate that the promotion of ecotourism and related facility development in communal areas has translated into better protection for elephants. In addition, ecotourism is recognized as a key contributor to the economy of the private ranches (Gadd, 2005, Woodroffe and Alan Rabinowitz, 2005). In the pastoral community land and forest reserves, where poaching incidences were remarkably high, enhancing security patrols is an important measure. The community land has the highest potential for elephant conservation. Enhancing incentives for wildlife conservation in these pastoral communities could be beneficial to wildlife conservation in the ecosystem. Financial investments in anti-poaching and elephant protection should prioritize the newly established conservancies to accelerate their growth towards self-sustainability. A further study on the drivers (specific human activities and environmental factors) of poaching which transcends land use delineations is recommended.

# Chapter 3

# Poaching risk lowers elephant's path tortuosity with potential consequences on their foraging success*

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* This chapter is based on: Ihwagi F.W., Skidmore, A.K., Wang, T., Guillaume-Bastille, R., Toxopeus, A. and Douglas-Hamilton I. Submitted to the Journal of Wildlife Management

## Abstract

Poaching is the most significant immediate threat to African elephants besides habitat loss. A continental-wide surge in poaching levels occurred between the years 2009 and 2012. We studied how elephants responded to poaching risk in an intensively monitored site. Using GPS tracking data of 11 elephants tracked between the years 2004 and 2016, and over 2000 field verified mortality records, we studied the hourly movement behaviour of elephants in relation to varied levels of poaching in spatially and temporally. We tested for the effect of poaching risk on the path straightness, i.e., tortuosity, while controlling for other environmental and human activities using a set of Generalized Least Square models. To test for temporal variation of tortuosity, we used a time-series linear model on movement data of elephants tracked for multiple years through the poaching crisis period. We found that elephants walked in with lower tortuosity, i.e., turn less frequently, while they are in places and times with poaching levels. Past studies have not picked this aspect of elephant behaviour because they relied on speed alone besides focusing on movement behaviour within corridors alone. We illustrate that speed alone is insufficient to understand elephant's movement behaviour at the hourly intervals when elephants are within core foraging areas. Our results illustrate that monitoring changes in tortuosity of elephants within core areas is a reliable indicator of rising poaching levels (or potentially other short-term human-induced disturbances) within the elephants' home range. Tortuosity values of tracked elephants could be a useful metric of the success of local anti-poaching efforts in complex human-dominated landscapes as perceived by elephants, and it is possibly the best metric of the elephants' landscape of fear developed by ecologists so far.

## 3.1 Introduction

Animals that live in landscapes that have been recently altered by humans exhibit sub-optimal movement behaviour as they seek to evade predators (Fahrig, 2007). The path tortuosity of an animal is a measure of how wiggled or direct a path is from a point to a destination (Benhamou, 2004). The nature of animals' survival strategies influences their path tortuosity in heterogeneous landscapes, but it is affected by both 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 minimise exposure to the risk, movement tortuosity should be proportional to the magnitude of risk in space and time as this would reduce the animals exposure (Hodges *et al.*, 2014). Manoeuvrability while escaping risk is influenced by body size, with smaller, faster animals being able to manage sharper turns, while larger ones move in straighter paths, i.e., with lower tortuosity (Hodges *et al.*, 2014). The role of risk in shaping the tortuosity of animals is poorly understood as most studies are conducted in laboratories or using mathematical models rather than in the complex natural terrestrial habitats (Domenici *et al.*, 2011b). If large animals can perceive mortality risk and make efforts to avoid it, the rate of turning along their paths, i.e. their tortuosity, should decrease in risky habitats to minimise their exposure to risk (Domenici *et al.*, 2011a, Hodges *et al.*, 2014).

An animal's ability to assess and behaviourally control the chances of encountering predator influences how it makes its decisions (Sih, 1987). Behavioural plasticity is essential for an animal to be able to respond to the 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 animals foraging tenacity is the best measure of its landscape of fear; the higher the difference in risk, the higher should be the mean difference in foraging tenacity (Laundre, 2010, Bleicher, 2017). The path tortuosity of a herbivore when it is foraging is commensurate with the heterogeneity and spatial distribution of its preferred forage items (Etzenhouser *et al.*, 1998). However, the past experiences in the landscape about encounters with predators influence animals current landscape of fear (Bleicher, 2017), and in turn how they forage. There is, therefore, a linkage between path tortuosity of an animal, its foraging tenacity and the exposure to risk. There is a need to understand the variation in behavioural responses of animals in the habitats that are undergoing rapid changes (Sih, 2013).

Besides the loss of habitat, the immediate threat to African elephants is poaching and 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 already has numerous insights regarding how elephants can respond to the risk of encountering humans. For instance, increasing speed when in unsafe areas to avoid settlements by daytime hours (Douglas-Hamilton *et al.*, 2005, Graham *et al.*, 2009, Graham *et al.*, 2010, Wittemyer *et al.*, 2017). Past studies focused on alteration of speed when the elephants venture out of their presumably safer core areas. They reported that elephants increase their speed within migratory corridors to traverse unsafe areas quickly; a behaviour termed as streaking (Douglas-Hamilton *et al.*, 2005). However, we observe that the high energy costs associated with their large mass (Wall *et al.*, 2006), must affect the sustainability of such high speeds in the long term while they are actively foraging in their core areas. In a human-dominated landscape where different core areas of elephants lie within distinct land management units that have different levels of poaching, it should be expected that elephants would alter their short-term movement behaviour as they forage in full vigilance, an aspect that movement speed alone may not capture.

Poaching has a long-term effect on the affected population of elephants and this is evident from sustained high levels of stress hormones for as long as six years since exposure to poaching related disturbances (Gobush *et al.*, 2008). Elephants switch to moving more in the night than during the day in times and places with high levels of illegal killing as (see Chapter 4) (Ihwagi *et al.*, 2018). The general knowledge of the drivers of the fine-scale variation in behaviour in relation to poaching risk is least understood. The hourly adjustment of movement behaviour in relation to risk is less understood because few studies have achieved both a multi-year high-resolution movement dataset and a concurrent dataset of field-verified causes of elephant mortality which this study achieves.

Although poaching is known to cause the decline of 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 at short time-scales. Past studies have focused on the elephant movement behaviour within their migration corridors (Douglas-Hamilton *et al.*, 2005, Galanti *et al.*, 2006a, Mpanduji *et al.*, 2009, Jachowski *et al.*, 2013, Roever *et al.*, 2013). The home ranges of migratory elephants comprise of core areas linked with narrow migratory corridors through which they walk at faster speeds than usual (Douglas-Hamilton *et al.*, 2005). An animal walking through safe and risky areas can have the same average speed between the segments of its path, but different tortuosity in each of the areas because the risk influences its rate of turning along the way (Angilletta *et al.*, 2008). Since for large animals the speed has severe limitation, we sought to use tortuosity rather than speed to model elephant movement, and we did this with locations recoreded at hourly intervals.

Between the years 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 elephants in Samburu-Laikipia ecosystem is the most intensively monitored in Africa with regard to causes of elephant mortality where a participatory network of land owners and herders verifies each reported case (Kahindi *et al.*, 2010). 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 (Douglas-Hamilton *et al.*, 2010, Ihwagi *et al.*, 2015). Our goal in this study was to evaluate elephants' behavioural adaptation to increasing levels of illegal killing in their core foraging areas. We hypothesised that the tortuosity of elephants would be lower in places and times when the levels of illegal killing were high. Using movement and mortality data collected when poaching levels rose remarkably, we sought to answer the following questions:

1. Is there a difference in (a) speed, and (b) the tortuosity of migratory elephants between their core areas?
2. What is the relationship between tortuosity of elephants and poaching levels (a) spatially and (b) temporally?

## 3.2 Methods

### *3.2.1 Study area*

This study was conducted in the Laikipia-Samburu ecosystem of Kenya from the year 2002 and 2016. The ecosystem is bounded by coordinates 0.2°S to 1.5°N, and 36.2°E to 38°E. The ecosystem is delineated by the extent of Ewaso Nyiro River and its tributaries, encompassing approximately 33,000 km$^2$ (Thouless 1995). It has a north-south gradient of rainfall with a marked decline in rainfall towards the north and relatedly, a range of habitats (Georgiadis 2011). The rainfall is highly variable and bimodal with peaks in May and November and a yearly range from less than 400 mm in the north to a maximum of 600 mm in the south (Barkham and Rainy, 1976, Ihwagi *et al.*, 2012). The terrain comprises expansive plains interrupted by rugged terrain and isolated hills. The landscape is a mosaic of land use types owned by individuals, government or communities (Fig. 3.1). There is a significant variation of levels of poaching within different land units; with higher poaching levels being associated with the communal grazing areas (Ihwagi *et al.*, 2015) (see Chapter 2).

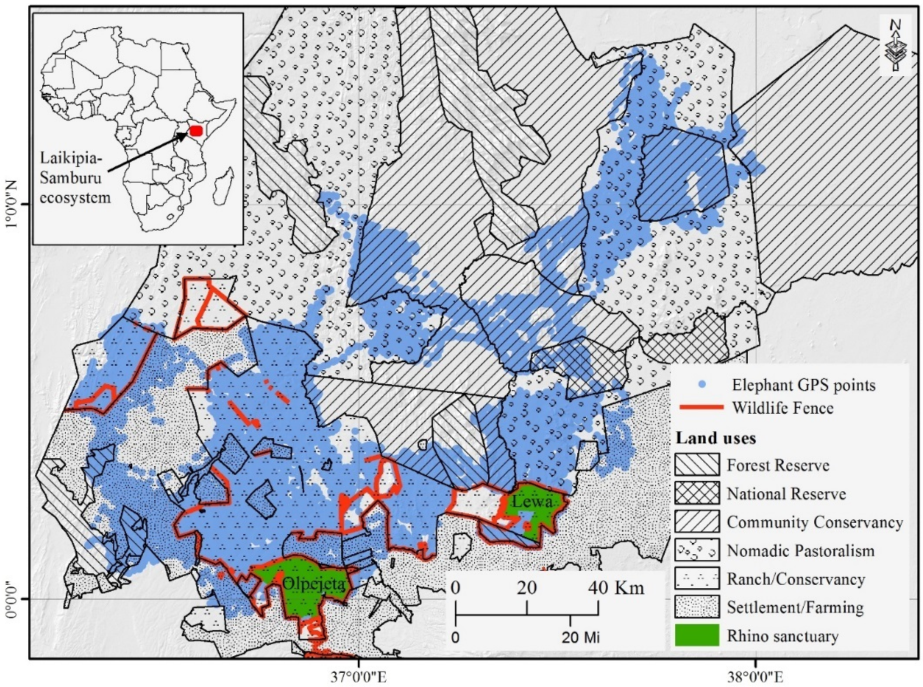


**Figure 3.1** Map of Laikipia-Samburu ecosystem, also showing the extent of the GPS tracking data of 11 elephants tracked between 2004 and 2013, the land use types and the location of wildlife fences.

### 3.2.2 *Monitoring Illegal Killing of Elephants (MIKE)*

Under the auspices of the MIKE programme of the Convention on International Trade in Endangered Species (CITES), field verification of cause of elephant mortality was done in a participatory community network of landowners, herders, conservancy managers and government wildlife rangers (Kahindi *et al.*, 2010). We analysed data collected from 2004 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 as follows:

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

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

The elephants that had multiple core areas visited either of them severally with no discernible relationship to seasonality. We calculated PIKE values for each core area by averaging the PIKE of the land units utilised by the elephants (see section 3.2.3 fore description of core areas). To determine the PIKE value associated to an elephant's core area, we included all mortality records for all the time before and during its GPS tracking period because elephants have long-term memory and we believe that they were still responding to past experiences encountered before we collared them.

### 3.2.3 GPS tracking, description of the core areas, and calculation of path tortuosity

We collected hourly GPS positions of 11 elephants as part of an ongoing field monitoring research project. With the help of government veterinarians, we fitted elephants with GPS collars sourced from African Wildlife Tracking (AWT) (www.awt.co.za) and FOLLOWIT (www.followit.se), each recording one fix per hour. Elephants exhibit more directed movements at fine temporal scale (one hour) compared to larger temporal scales (Street *et al.*, 2018), which makes use of hourly GPS fix useful in inferring behavioural change. Five of the elephants were wide-ranging (migratory) and the other six were residents of distinct land units in different parts of the ecosystem. We filtered out GPS points that corresponded to unlikely speeds of more than seven kilometres per hour (Hutchinson *et al.*, 2003, Hutchinson *et al.*, 2006).

We used fixed kernel home range estimator to identify core areas which we delineated as those areas within 50% contour lines (Worton, 1987, Worton, 1989). After identifying the location of core areas, we adopted the entire land units that contained the core area, because PIKE, our most important variable was calculated based on full land units. The elephants were tracked at varied dates between September 2004 and December 2013 (Table 3.1). Some of the elephants are named after the land units or locations where they were first collared at, and to distinguish reference to a land unit from an elephant by similar name we italicize the names of elephants in the text. 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 from the current GPS location for the past two hours at any one time (Whittington *et al.*, 2004). The log transformation is necessary for correcting the skewed distribution, which is common with animal GPS tracking data.

**Table 3.1** The dates when each of 11 elephants were tracked and the number of hours that each of them spent in their respective core areas.

| Elephant | Dates tracked | Hours in core area 1 | Hours in core area 2 |
|---|---|---|---|
| *Loldaiga* (F) | Aug 06 - Jan 09 | 3383 | 3597 |
| *Wangari* (F) | Sep 04 - Jul 06 | 10649 | 1511 |
| *Ngelesha* (M) | Aug 08 - Feb 12 | 2874 | 1524 |
| *Ol ari Nyiro* (M) | Aug 07 - Feb 12 | 7241 | 14327 |
| *Sera* (F) | Aug 06 - Apr 11 | 11078 | 12773 |
| *Genghis* (M) | May 04 - June 12 | 41943 | NA |
| *Mpala* (M) | Feb 07 to Dec 11 | 39134 | NA |
| *Mutara* (M) | Feb 09 - June 13 | 13095 | NA |
| *Olpejeta* (M) | Sep 06 - Feb 09 | 17022 | NA |
| *Tia Maria* (F) | Feb 08 - Aug12 | 31715 | NA |
| *Drachmae* (F) | Feb 08 - Dec 13 | 37353 | NA |

### 3.2.4 Collating other environmental variables

To disentangle the role of other environmental factors in the tortuosity of elephants, we also included land cover, terrain, water, livestock density, and the distance from human dwellings in the model. We adopted a grid size of 500 m × 500 m for environmental variables, which aligns conveniently to the Universal Transverse Mercator (UTM grid) and is also the same size as the grid adopted for measures of tortuosity (see section 3.2.5). 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 Food and Agriculture Organization (FAO) to assign the dominant cover type in each grid square (Food and Nations, 2015). Human settlements affect the distribution of elephants negatively, and in most instances, these tend to occupy prime resource areas inadvertently setting the stage for competition (Verlinden, 1997). We calculated the distances of each grid's centroid to the nearest town, and to the nearest temporally settlements locally referred to as '*bomas*'. The availability of surface-water influences elephants distribution as they need to drink at least once a day (Buss, 1961, Western, 1975). Elephants turn less when they are further away from the source of water (Duffy *et al.*, 2011). We calculated the distance from each grid's centroid to the nearest known water points. Elephants avoid climbing hills exceeding a gradient of 30 degrees (Wall *et al.*, 2006). We assumed that even at a distance away from the base of a continuous ridge or escarpment, elephants would align their movement so as to circumvent it thus there was need to include distance from the bases of hills. We defined the base of the hills as the level with a gradient of more than 30 degrees on a 30M Digital Elevation Model (DEM) and we calculated the distance from each grid's centre to the base of nearest hill or escarpment.

Elephants and livestock in the ecosystem overlap in space and time and they share critical resources like water and forage (Raizman *et al.*, 2013). From the results of two total-count aerial censuses conducted in the years 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 kilometre in each grid. The aerial census dataset included locations of occupied *bomas*. The pastoral communities also shift their *bomas* over time and build new ones. However, the shift is only for a short distance away from the old one within the same land management unit that we adopted for calculation of PIKE and thus does not affect the analyses. Wildlife fences create edge effects and modify elephant movement behaviour directly by coercing a unidirectional path (Newmark, 2008, Vanak *et al.*, 2010, Nams, 2014). We excluded all GPS tracking data points that fell within a distance of 2000 m from any wildlife fence from the analyses.

### *3.2.5 Determining the sensitivity of tortuosity measurements to the size of grid squares*

The movement of African elephants in response to the spatial heterogeneity of habitat is well captured within spatial sampling scales ranging from 457 to 734 m (Murwira and Skidmore, 2005). The spatial scale of looping by elephants during the day is approximately 1 km (Dai *et al.*, 2007). From these existing literature, a grid size anywhere between 457 and 1000 m would have sufficed for modelling tortuosity values in a landscape. However, as a precaution, noting that our study area was unique with regard to different conservation statuses of the land and the presence of human beings, we performed sensitivity analyses of tortuosity measures to grid sizes. We calculated means and variances of tortuosity within square grids measuring 50 m, 100 m, 150 m, 200 m, 300 m, 400 m, 500 m, 750 m and 1000 m. Tortuosity values were not sensitive to grid sizes as no trend was observed consistently for all elephants (Fig 3.2). We adopted 500 m × 500 m grids; a grid size which; (i) approximates to double the median hourly distance (Wall *et al.*, 2013) and (ii), is within the range of previously established optimal spatial scales (Dai *et al.*, 2007). The turning angles of elephants are not auto-correlated temporally at sampling intervals above 20 minutes (Dai *et al.*, 2007). Our sampling frequency of one-hour interval was therefore above the established range of temporal autocorrelation.

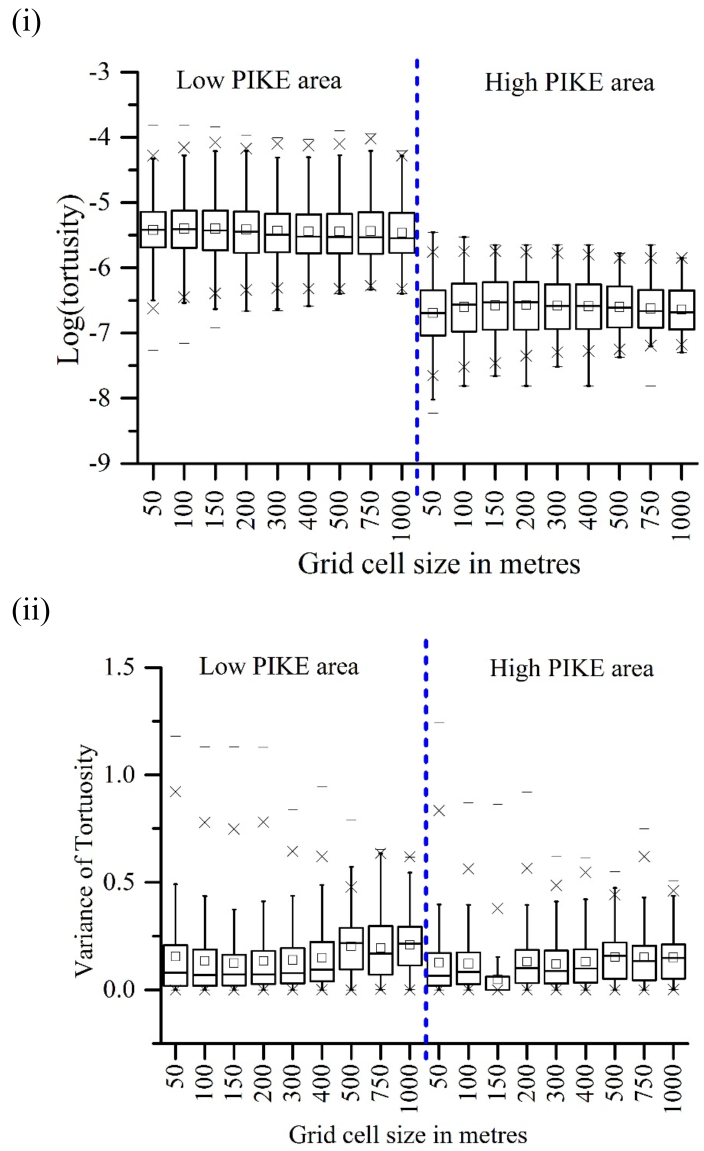


**Figure 3.2** (a) Sensitivity analyses of mean and variances of tortuosity to grid sizes for *Loldaiga*. The mean tortuosity and the variances of each elephant were calculated for data aggregated into grid squares of various sizes when the elephant was in core areas with low and with higher levels of the Proportion of Illegally Killed Elephants (PIKE).

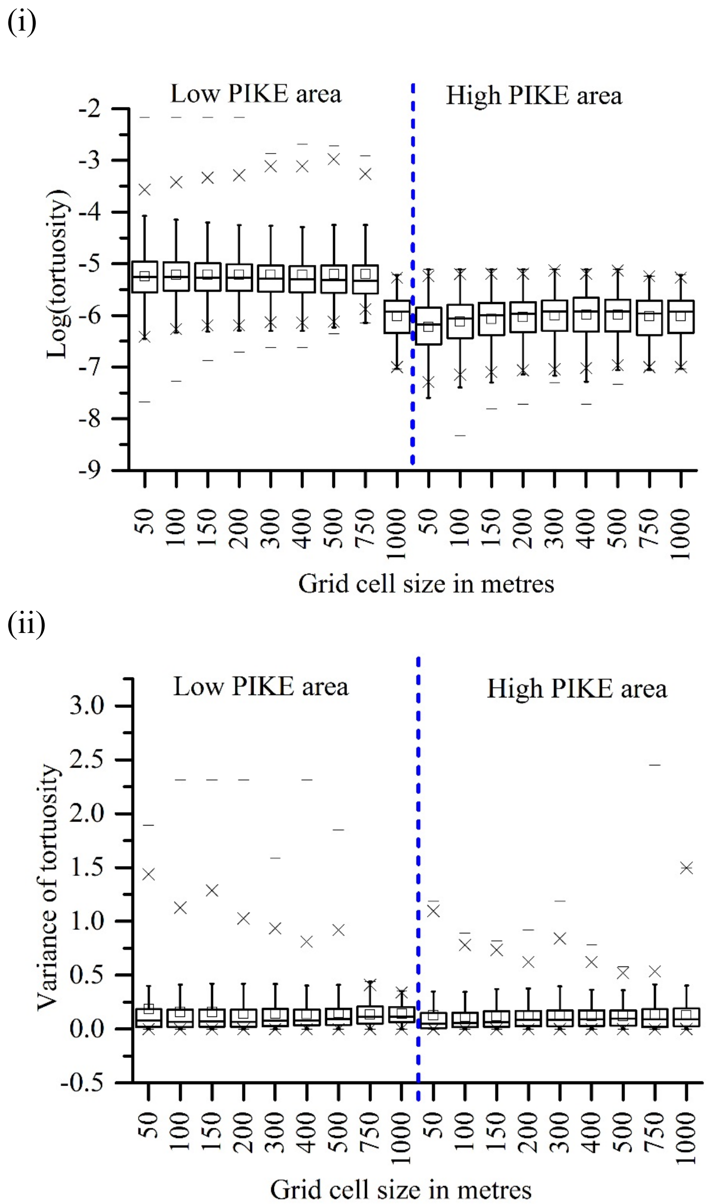
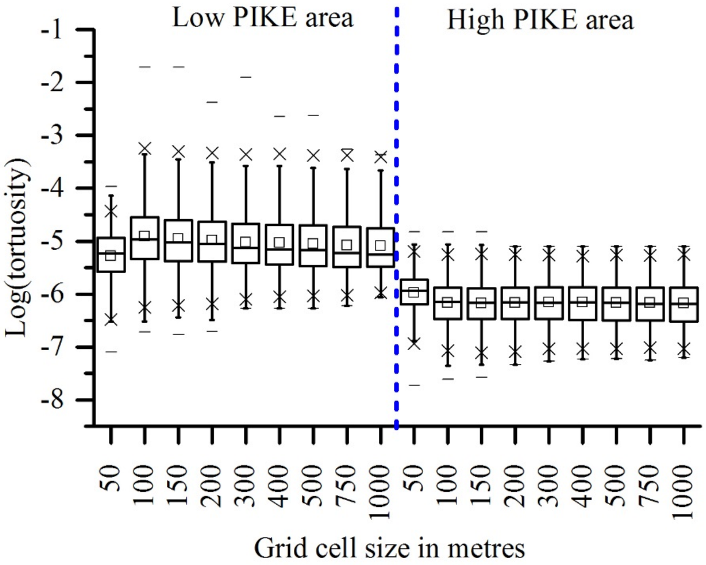


**Figure 3.2** (b) Sensitivity analyses of mean and variance of tortuosity to grid sizes for *Ngelesha*. The mean tortuosity and the variances of each elephant were calculated for data aggregated into grid squares of various sizes when the elephant was in core areas with low and with higher levels of the Proportion of Illegally Killed Elephants (PIKE).

(i)



(ii)

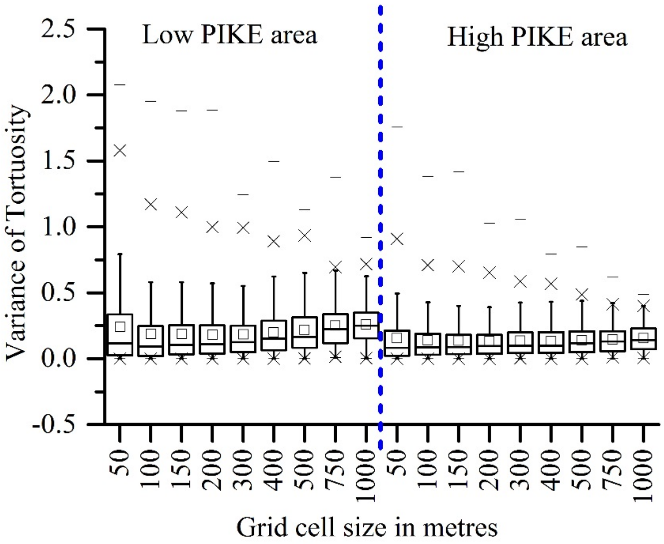
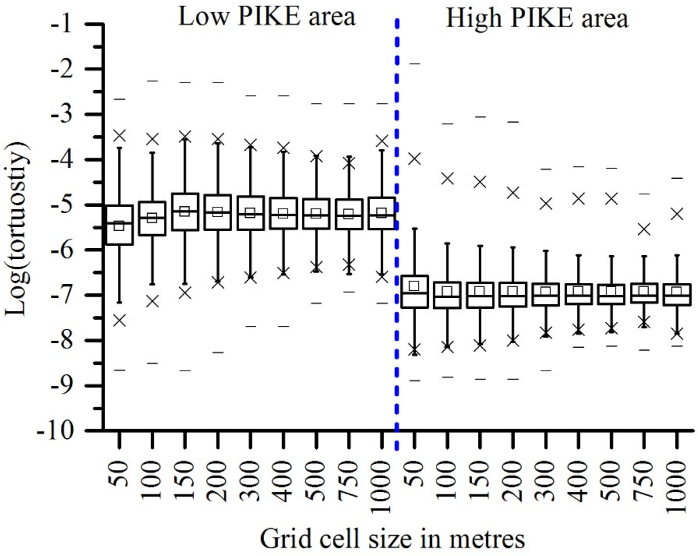


**Figure 3.2** (c) Sensitivity analyses of mean and variance of tortuosity to grid sizes for *Ol ari Nyiro*. The mean tortuosity and the variances of each elephant were calculated for data aggregated into grid squares of various sizes when the elephant was in core areas with low and with higher levels of the Proportion of Illegally Killed Elephants (PIKE).

(i)



(ii)

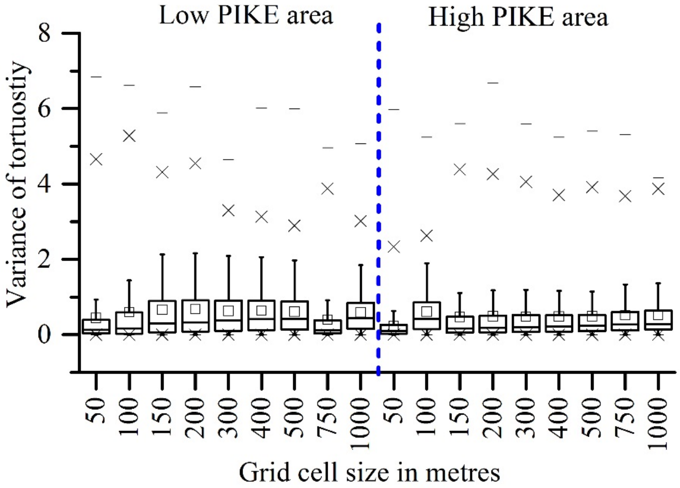


**Figure 3.2** (d) Sensitivity analyses of mean and variance of tortuosity to grid sizes for Sera. The mean tortuosity and the variances of each elephant were calculated for data aggregated into grid squares of various sizes when the elephant was in core areas with low and with higher levels of the Proportion of Illegally Killed Elephants (PIKE).

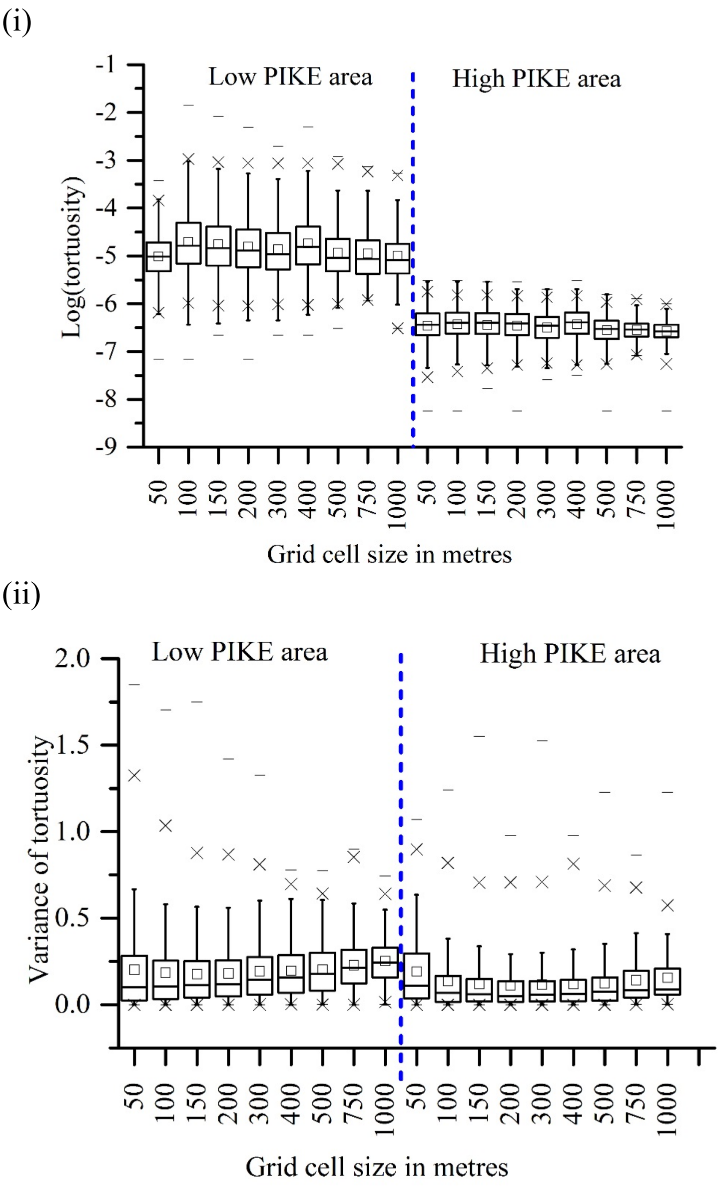


**Figure 3.2** (e) Sensitivity analyses of mean and variance of tortuosity to grid sizes for *Wangari*. The mean tortuosity and the variances of each elephant were calculated for data aggregated into grid squares of various sizes when the elephant was in core areas with low and with higher levels of the Proportion of Illegally Killed Elephants (PIKE).

### *3.2.6 Statistical analysis*

We analysed data using R 3.3.0 (R Development Core Team, 2012b). Using *t*-test, we tested for the difference in hourly tortuosity for each of the migratory elephant between its two core areas. To test for the difference in speed of elephants between their respective two core areas, we used Mann-Whitney *U* test. To test for spatial variation of the tortuosity in relation to PIKE and other covariates, we used 29 Generalized Least Square (GLS) regression models grouped into natural environmental factors, human activity related factors and plausible combinations of these in a model selection framework (Table 3.2). We performed a quasi-experiment that controlled for individual elephant and spatial autocorrelation of points. The GLS regression model was favoured because it allows inclusion of spatial autocorrelation term (Dormann *et al.*, 2007). We scaled all covariates by z-scoring 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 centres of each grid cell. The autocorrelation term also included a control for individual elephants repeated measures. We formulated 29 GLS models with various combinations of covariates representing a *priori* hypotheses of covariates that possibly explain tortuosity. Some of the models included interactions between some variables where plausible. We selected the best model using the second order Akaike's Information Criterion (AICc) in the model selection framework (Burnham and Anderson, 2002). We implemented the regression models using the package 'nlme'.

To examine temporal changes in tortuosity and poaching, we used data from two elephants that inhabited land units that experienced a gradual increase in levels of illegal killing, i.e., private ranches. The other four were residents of two poaching free sanctuaries, Lewa and Ol Pejeta, at distant locations from each other. We created a time-series dataset and modelled tortuosity as a function of time using linear regression, accounting for temporal autocorrelation.

**Table 3.2** Combinations of variables in Generalised Least Square (GLS) candidate models of factors affecting tortuosity of five migratory elephants that inhabited different land management units within Laikipia-Samburu ecosystem.

| Model | Variables |
|---|---|
| Scenario 1 | Only physical environment affects path tortuosity |
| 1 | water |
| 2 | hills |
| 3 | land cover |
| Scenario 2 | Only human activity affects path tortuosity |
| 4 | PIKE*livestock + towns + bomas |
| 5 | PIKE + livestock*bomas + towns |
| 6 | PIKE*towns + livestock |
| 7 | PIKE + livestock + bomas |
| 8 | PIKE + towns |
| 9 | PIKE*towns + bomas |
| 10 | PIKE + livestock*bomas |
| 11 | PIKE + livestock |
| 12 | livestock |
| 13 | livestock + hills |
| 14 | livestock + towns + bomas |
| 15 | livestock*towns |
| 16 | livestock*bomas |
| 17 | towns + bomas |
| 18 | towns |
| 19 | PIKE |
| Scenario 3 | Both human and physical environmental factors affect tortuosity |
| 22 | PIKE + livestock*towns + water + hills + bomas |
| 21 | PIKE + livestock + land cover |
| 22 | PIKE + livestock + towns + water |
| 23 | PIKE*livestock + towns + water + land cover |
| 24 | PIKE + land cover |
| 25 | towns + water + hills |
| 26 | PIKE + livestock + hills |
| 27 | PIKE + hills |
| 28 | livestock + land cover |
| 29 | towns + water + hills + land cover |

## 3.3 Results

There was a significant reduction in tortuosity of elephants when they moved into the core areas with higher levels of illegal killing; *Loldaiga* (*t*-test: $t = 84.929$, $df = 5059$, $P = 000$), *Wangari* (*t*-test: $t = 83.342$, $df = 8660$, $P = 0.000$), *Sera* (*t*-test: $t = 69.666$, $df = 2469$, $P = 0.000$), *Ol ari Nyiro* (*t*-test: $t = 39.374$, $df = 1115$, $P = 0.000$); and *Ngelesha* (*t*-test: $t = 16.876$, $df = 437$, $P = 0.003$). Although there were differences in the tortuosity of each elephant between its core area with low and that those with higher poaching levels, there was no difference in the speeds for any of them between the respective core areas (Mann-Whitney U test: $P \geq 0.005$) (Fig. 3.3).

The best GLS model predicting tortuosity featured PIKE and land cover. The competing model featured PIKE land cover and livestock (Table 3.3). The tortuosity of elephants was low when they were in the land units with higher poaching levels. Amongst the covariates related to human activities, PIKE had the greatest influence on the tortuosity of each elephant, only second to land cover type (Table 3.4).

**Table 3.3** Performance of the two best models predicting path tortuosity of five elephants occupying different land units in the Laikipia Samburu ecosystem.

| Model | K | AICc | Delta_AICc | AICcWt |
|---|---|---|---|---|
| PIKE + land cover | 19 | 6786.05 | 0.00 | 0.66 |
| PIKE + livestock + land cover | 20 | 6787.42 | 1.36 | 0.33 |

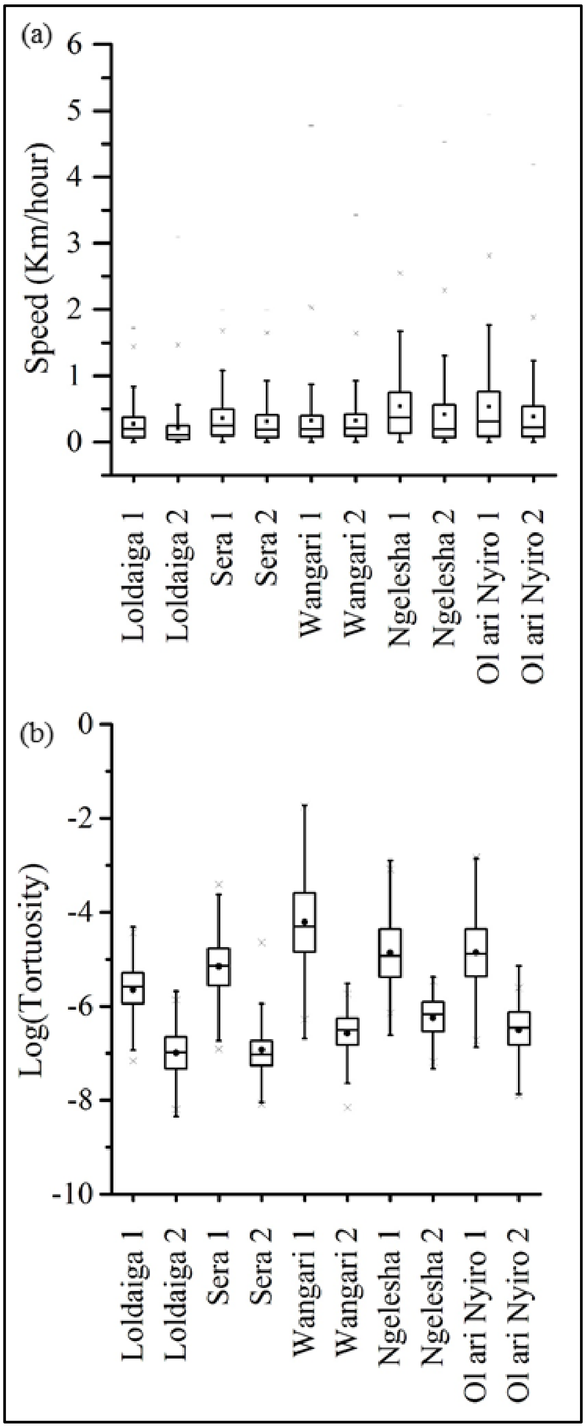


**Figure 3.3** The hourly (a) speed and (b) tortuosity of five migratory elephants within each of their two main core areas, suffixed as "1" and "2". Core areas numbered "2" were in the land units with higher levels of illegal killing. The speed of each elephant was not different between its core areas, but the tortuosity was significantly different. This result illustrates that speed alone is not a reliable metric of elephants' behavioural response to risk at fine spatial and temporal scales, as elephants can exhibit similar speeds in different environments, but with varied tortuosity.

**Table 3.4** The parameters of the best model of the tortuosity of elephants, which featured the Proportion of Illegally Killed Elephants (PIKE) and land cover type.

| | Value | L.C.I. | U.C.I |
|---|---|---|---|
| (Intercept) | -5.178 | -5.335 | -5.016 |
| PIKE | -0.540 | -0.614 | -0.465 |
| Land cover | -0.908 | -1.114 | -0.702 |

The decline in tortuosity for both elephants over time was significant ($F_{2, 41945}$, = 2186, $P < 0.001$ for *Genghis*) and ($F_{2, 39136}$, = 29500, $P < 0.001$ for *Mpala*). The time series decomposition graphs showed a decline in the tortuosity of *Genghis* over time (Figure 3.4), and the fitted regression line showed that the trend was a significant decline of tortuosity over time (Figure 3.5). The coefficients of the regression model for the line "*tslm(formula = genghismonthlyts[,20] ~t +t2)*" were significant (Table 3.5).

**Table 3.5** The output statistics for the regression line of the linear time series data of the male elephant; *Genghis*.

| | Estimate | Std. Error | *t* | *P* |
|---|---|---|---|---|
| (Intercept) | 1.62e+05 | 2.51e+03 | 64.54 | <0.001 |
| t | -1.61e+02 | 2.50e+00 | -64.44 | <0.001 |
| t2 | 3.99e-02 | 6.22e-04 | -64.34 | <0.001 |

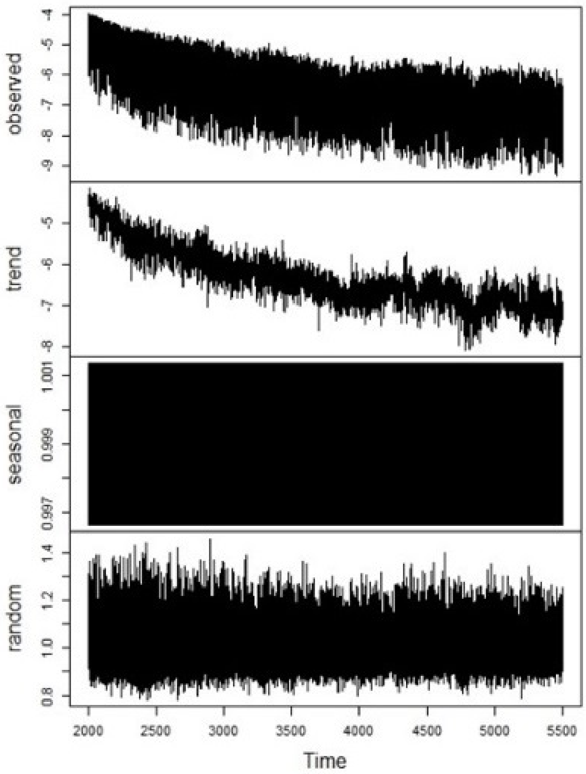


**Figure 3.4** Decomposition of time series data for *Genghis* (male) showing the raw data (observed), trend, seasonal and random effects. The elephant was tracked from May 2004 to June 2012.

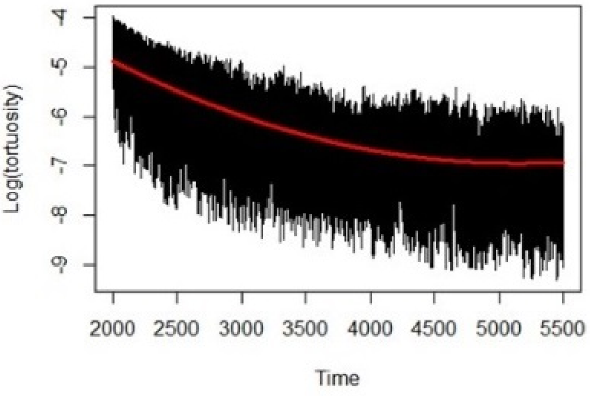


**Figure 3.5** The time series data for *Genghis* (male) and the regression model of the trend. The elephant was tracked from May 2004 to June 2012.

The time series decomposition graphs showed a decline in the tortuosity of *Mpala* over time (Figure 3.6), and the fitted regression line showed that the trend was a significant decline of tortuosity (Figure 3.7). The coefficients of the regression model for the line "*tslm(formula = mpalamonthlyts[,20] ~t +t2)*" were significant (Table 3.6).

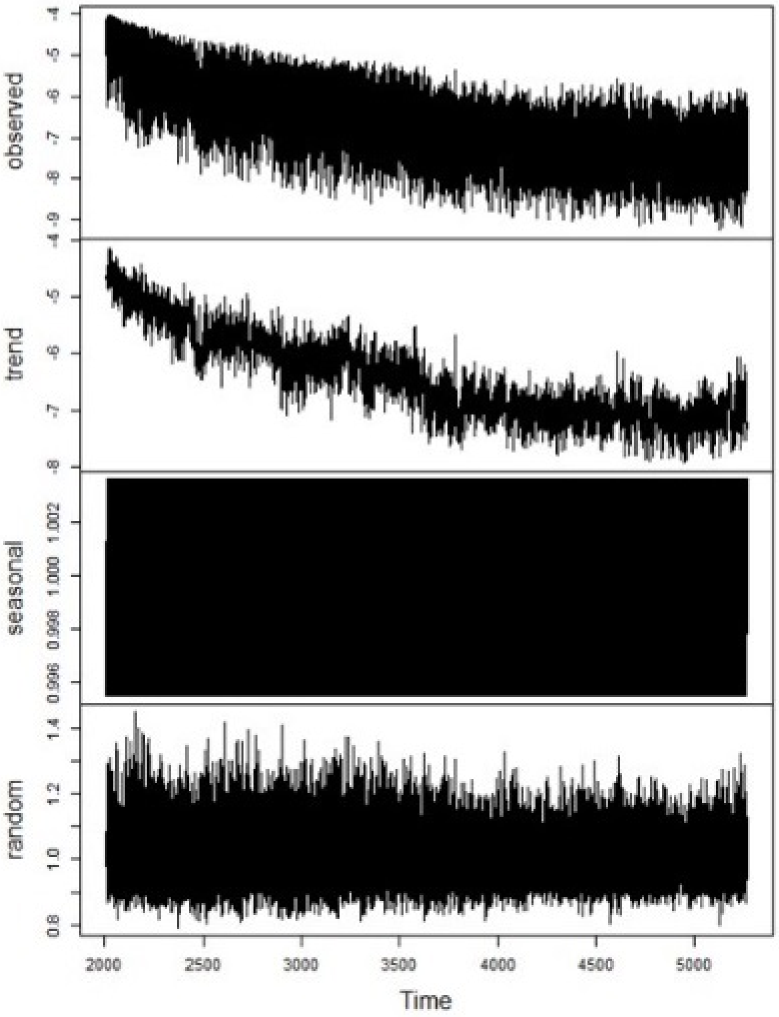


**Figure 3.6** Decomposition of time series data for *Mpala* (male) showing the raw data (observed), trend, seasonal and random effects. The elephant was tracked from February 2007 to December 2011.

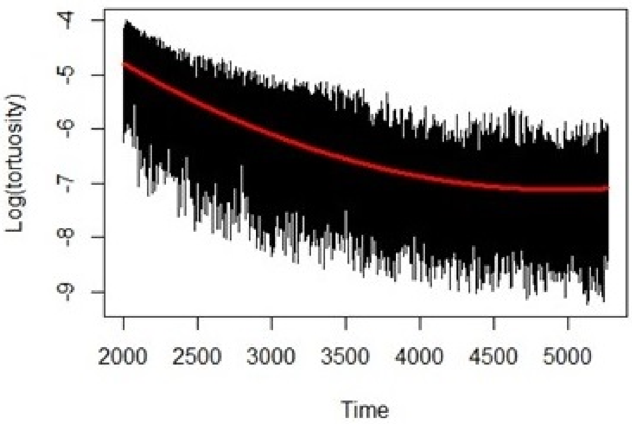


**Figure 3.7** The time series data for *Mpala* (male) and the regression model of the trend. The elephant was tracked from May 2004 to June 2012.

**Table 3.6** The output statistics for the regression line of the linear time series data of the male elephant; *Mpala*.

| | Estimate | Std. Error | *t* | *p* |
|---|---|---|---|---|
| (Intercept) | 7.16e+05 | 9.68e+03 | 73.97 | <0.001 |
| t | -7.13e+02 | 9.64e+00 | -73.92 | <0.001 |
| t2 | 1.77e-01 | 2.40e-03 | 73.86 | <0.001 |

The tortuosity of the two elephants, *Mpala* and *Genghis*, that inhabited private ranches, where PIKE increased significantly throughout the study period, were lower and decreased further over time, while the tortuosity of those that inhabited poaching free conservancies that double as rhino sanctuaries was higher and remained unchanged over time (Fig. 3.8).

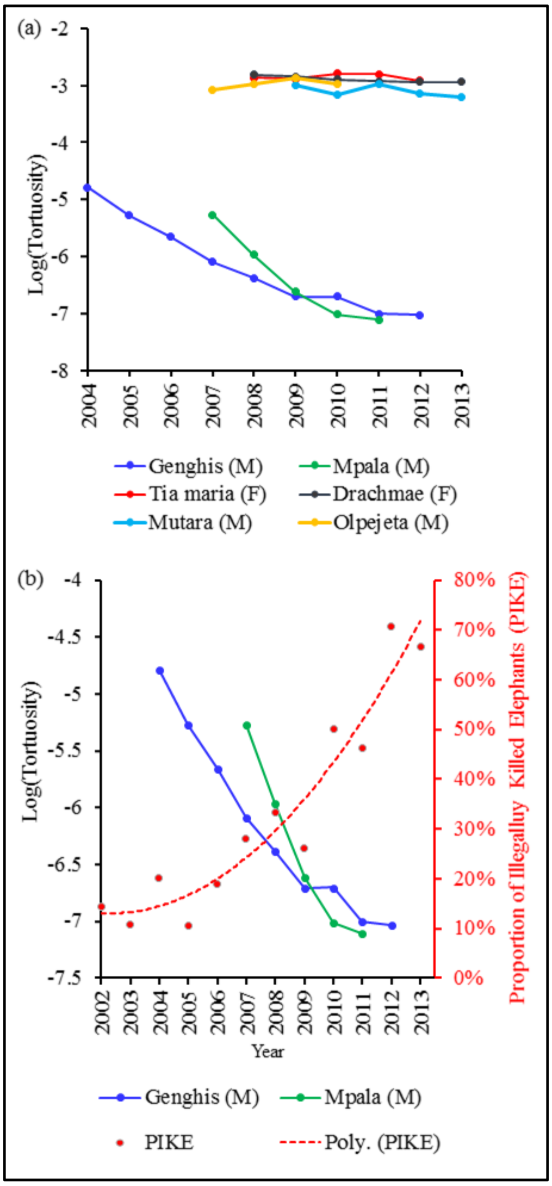


**Figure 3.8** (a) The tortuosity values of elephants tracked in Laikipia-Samburu ecosystem at different dates between 2004 and 2013. Four elephants, i.e., *Drachmae*, *Tia Maria*, *Mutara* and *Ol Pejeta*, inhabited poaching free sanctuaries, and their tortuosity remained unchanged. *Genghis* and *Mpala* inhabited Laikipia Private Ranches, where poaching levels increased gradually, and their tortuosity decreased commensurately. (b) The inverse relationship between yearly mean tortuosity of two elephants and the yearly Proportion of Illegally Killed Elephants (PIKE) in the private ranches. The trend lines of *Genghis* and *Mpala* were derived from time series regression models. The PIKE trend is derived from raw MIKE data.

## 3.4 Discussion

Both human and environmental factors, i.e., poaching and land cover, affected the tortuosity of the elephants. The models with the highest explained variance featured PIKE as the most important variable, though other variables, especially habitat type and livestock density, were also important. Temporally, the variation in tortuosity corresponded to the annual variation of PIKE in the affected land units. The inclusion of poaching free land units was a vital control case and this enable us to illustrate that tortuosity does not change over time where there was no change of PIKE. Our results support earlier observations that habitat quality alone is not sufficient to explain elephants movement behaviour (Boettiger *et al.*, 2011), but human activities affect it too (Lima, 1987). This study identifies the level of illegal killing as the human related predictor of tortuosity of elephants in their key foraging areas.

Many studies have emphasised the importance of speed in describing elephant movement behaviour 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, Bohrer *et al.*, 2014). We illustrate that the tortuosity of an elephant's path is a better metric for modelling fine-scale movement behaviour within core areas than speed. 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). Due to the high energy requirements by large animals, a change of direction is more favourable than a change of speed when navigating through a complex or risky landscape (Wall *et al.*, 2006, Angilletta *et al.*, 2008). Unlike in smaller species where the trade-off between speed and tortuosity is primal (Angilletta *et al.*, 2008), elephants, owing to their large mass and associated high energy costs have minimal flexibility with regards to speed (Wall *et al.*, 2006). They resort to walking straighter paths than increasing their 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, like the elephants (Rensch and Altevogt, 1955), active vigilance would entail frequent turns and as a result higher tortuosity. However, the elephants exhibited lower tortuosity in risky areas implying they practised low vigilance in line with the constant risk model. Future studies characterising movement of elephants in risky habitats should incorporate tortuosity as 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 as it has a steep gradient with regards to poaching levels, which speed does not detect. The absolute values of tortuosity are however dependent on the temporal scale of the data, and for a comparative study, the resolutions should, therefore, be 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 has been explored. We found that elephants turn more when in low poaching areas. This finding is consistent with past observations that and in a bid to save energy, when elephants are foraging they turn less instead of increasing speed to reach an intended point faster (Duffy *et al.*, 2011). Our result indicates that high level of illegal killing makes a habitat less favourable and leads elephants to walk straighter paths.

Lower path tortuosity of a herbivore in heterogeneous habitats implies lower foraging efficiency as it corresponds to lower searching effort (Doerr and Doerr, 2004). The foraging success of elephants entails variation of daily displacement in relation to resource availability (Polansky *et al.*, 2013). A risk-induced reduction in tortuosity in the prime foraging areas implies an alteration of the elephants' optimal foraging strategy. Foraging success of elephants in core areas may have been compromised as a result of a quest to keep moving than search more for food more thoroughly when in a risky environment. A study with a higher temporal resolution of data is warranted to understand the effect of reduced tortuosity on the elephants' foraging success.

The major hindrance to the establishment of a relationship between elephant movement tortuosity and poaching levels has been lack of sufficient records of individually verified causes of elephant mortality recorded concurrently with movement data. This study has filled this information gap, and a change in tortuosity values in the circumstances other than migration or around physical obstacles should be an indicator of stress induced by poaching, which impacts the elephant's natural pace.

The human population density, poverty levels and livestock densities around MIKE sites are strong correlates of poaching levels (CITES, 2012). As the human population increases, it should be expected that the encroachment on elephant’s home ranges will increase, and elephant’s movement behaviour will be affected more. However, in this study, the distance from human dwellings did not feature in the two top models. A possible explanation is that elephants, as intelligent as they are, do not associate risk with the mere presence of the dwellings of humans. Instead, the elephants respond to specific, human activities. Elephants are intelligent enough to distinguish threat level, and they can even distinguish (often friendly) pastoralists from other persons by odour and clothing colour (Bates *et al.*, 2008). An animals behavioural response to a known risk depends on their discrimination of the magnitude of the risk (Sih, 2013).

The result of this study has two potentially useful applications in the management and conservation of elephants. (i) Tortuosity is a useful indicator of changes in poaching levels or other short-term human-induced disturbances in the elephants’ home range as perceived by marked elephants, i.e., can be used as a variable for describing their landscape of fear. (ii) The changes in mean tortuosity can serve as a useful means of evaluating the success of anti-poaching efforts of different actors across a landscape within different conservation statuses or over time using elephant movement behaviour as the proxy.

# Chapter 4

# Night-day speed ratio of elephants as an indicator of poaching levels[*]

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[*] This chapter is based on: Ihwagi, F.W., Thouless, C., Wang, T., Skidmore, A.K., Omondi, P. & Douglas-Hamilton, I. (2018) Night-day speed ratio of elephants as an indicator of poaching levels. *Ecological Indicators*, **84**, 38-44.

## Abstract

Poaching has escalated in recent years and is becoming the greatest immediate threat to elephants' survival. There is an urgent need to develop innovative and cost-effective methods for monitoring changes in elephant poaching levels remotely to complement the existing traditional field-based ground surveys. Since elephants are known to respond to anthropogenic risks by alterations in their speed of travel, we quantified this alteration as a ratio of nighttime speed to the daytime speed (night-day speed ratio) and examined its relationship with poaching levels. Our hypothesis here is that poaching is a clear daytime risk, and thus an increase in nighttime movement rates over those seen during the day will support this hypothesis. Using elephant GPS tracking and mortality data collected in the Laikipia-Samburu ecosystem of northern Kenya between 2002 and 2012, we calculated the mean night-day speed ratio for collared elephants that utilised any of 13 contiguous land units, each under different ownership and management status, and related this ratio to the corresponding poaching levels before and during a poaching surge. Our study shows that the mean night-day speed ratio of both male and female elephants did not vary significantly by month, ruling out possible seasonal effect. However, both male and female elephants moved more at night than during the day where and when poaching levels were high. The relationship between poaching levels and night-day speed ratios was stronger for females than for males. We concluded that the variation in the night-day speed ratio of elephants might be used as an effective indicator for changes poaching levels on a near real-time basis. We recommend its adoption as a complimentary anti-poaching tool, where GPS tracking data is already available because it would increase the geographical range for monitoring of poaching levels. The significant alteration in movement behaviour by elephants in response to poaching also has potential implications for their foraging strategy, reproduction and ultimate survival, all of which are not yet fully understood.

## 4.1 Introduction

Killing for ivory has been a leading cause of the decline in the number of African elephants (*Loxodonta africana* Blumenbach, 1797) (Wittemyer *et al.*, 2014). In the 1970s, a poaching surge led to widespread concern about the future of many elephant populations in Africa (Eltringham and Malpas, 1976, Douglas-Hamilton, 1980a, Eltringham and Malpas, 1980, Douglas-Hamilton, 1988). Another poaching surge occurred across the African continent between 2010 and 2012, during which the rate of illegal killing of elephants exceeded the natural sustainability level (Wittemyer *et al.*, 2014).

The Monitoring of Illegal Killing of Elephants (MIKE) programme, a programme of the Convention of the International Trade in Endangered Species (CITES), provides a framework for collecting information on elephant mortality based on a standardised protocol (MIKE, 2001). Designated intensive MIKE monitoring sites encompass only 40% of the African elephants' range (Nellemann *et al.*, 2013). During the latest surge of poaching that peaked in the year 2011, an estimated 40,000 elephants were killed in these sites (indication potentially 100,000 elephants across their African range) leading to a catastrophic decline in key populations before poaching levels stabilised in the year 2013 (Wittemyer *et al.*, 2014). A standard measure of the level of poaching in the MIKE sites, the Proportion of Illegally Killed Elephants (PIKE), has been adopted by the Secretariat of CITES (Kahindi *et al.*, 2010, Jachmann, 2013). An elephant population with a PIKE value of over 54% has a high probability of declining, as there are insufficient births to compensate for the number of deaths (Wittemyer *et al.*, 2014). Poaching levels in Africa have been on the decline since the year 2011, but in some sites, the levels are still above the naturally sustainable level of 54% PIKE (https://cites.org/sites/default/files/eng/prog/MIKE/MIKE_report_released_WWD_3Mar2017.pdf: accessed 21 March 2017). Since elephant poaching remains rampant, there is an urgent need to develop innovative near real-time but cost-effective methods for monitoring poaching beyond the traditional ground-based time-consuming patrols, which are often restricted to designated sites (O'Donoghue and Rutz, 2016).

A male elephant recently collared in Tana River, a different ecosystem in South Eastern Kenya near the highly insecure Somali border, became more nocturnal as he approached and moved into less secure areas (Douglas-Hamilton pers. comm. 2016). This led us to consider whether variation in movement rates between day and night times by elephants in risky areas is a general phenomenon and we sought to analyse existing data. Exploratory data analyses (EDA) is an established tradition in statistics that offers a computational and conceptual framework to foster hypothesis development (Tukey, 1977, Behrens, 1997). EDA encompasses the understanding of patterns in existing data. Elephants are intelligent social beings able to perceive a loss of the life of conspecifics and react to the presence of potentially threatening human beings (Douglas-Hamilton *et al.*, 2006, Bates *et al.*, 2008, Hart *et al.*, 2008). Elephants avoid encroaching human settlements that present a risk of conflict and human-related mortality during the day (Galanti *et al.*, 2006b, Graham *et al.*, 2009, Boettiger *et al.*, 2011). In fragmented ecosystems, elephants have distinct home ranges connected by travel corridors along which they move faster in response to prevailing danger (Douglas-Hamilton *et al.*, 2005). They also increase their speed when crossing busy roads (Blake *et al.*, 2008). Since most encounters with humans, including poachers, occur in the daytime and elephants are intelligent, it would make sense for them to become more nocturnal when they are under threat as has been observed in studies on elephant movement behaviour at the interface between farming and ranching communities (Graham *et al.*, 2009).

In ecology, some species threatened by predation are known to respond in a graded way that corresponds to the degree, magnitude and temporal scale of the threat posed (Helfman, 1989, Levin, 1992, Kitchen *et al.*, 2000, Creel *et al.*, 2005, Fischhoff *et al.*, 2007, Sanchez-Mercado *et al.*, 2008, Chittka *et al.*, 2009). Experiments regarding the day-night behaviour of coyotes (*Canis latrans* Say, 1823), showed that their diurnal activity increased after exploitation by humans ceased. Plains zebras (*Equus burchelli* Gray, 1924) have been observed to walk faster at night time in areas where they risked predation by lions (*Panthera leo* Linnaeus, 1758). Poaching is the greatest immediate threat to elephants' survival

(Nellemann *et al.*, 2013). Understanding how elephants alter their movement behaviour during the day and night under the threat of poaching is a step towards understanding how they adapt to the short-term threat. Since elephants are known to respond to anthropogenic risks by alterations in their speed of travel (Douglas-Hamilton *et al.*, 2005, Blake *et al.*, 2008, Graham *et al.*, 2009), we examined the relationship between day-night movement rates and mortality risks due to poaching. Our hypothesis here is that the day-night movement rates are a predictor of poaching threat. To test this hypothesis, we sought to determine the following:

(1) Are there significant differences in the mean night-day speed ratio of elephants over time (within the months and between the low and high poaching periods)?
(2) Is there a significant relationship between the night-day speed ratio of elephants and prevailing poaching levels?

## 4.2 Materials and methods

### *4.2.1 Study area*

To test our hypothesis, we needed a study site with sufficient elephant GPS tracking data, as well as ground-verified elephant mortality records for the same period. The Laikipia-Samburu ecosystem in northern Kenya meets these criteria as it is home to a long-term elephant tracking programme (Wittemyer *et al.*, 2005a). As a designated MIKE site, the ecosystem has a consistent dataset detailing causes of elephant mortality (Kahindi *et al.*, 2010). The ecosystem encompasses different land units, which encounter varying levels of poaching (Ihwagi *et al.*, 2015), thus presenting an ideal poaching gradient for testing the hypothesis.

The Laikipia-Samburu ecosystem lies within the coordinates 0° and 2°N, and 36.2°E and 38.3°E (Fig. 4.1). The area experiences highly variable bimodal rainfall with peaks in May and November and yearly totals ranging from below 400 mm towards the north to a maximum of 600mm in the south (Barkham and Rainy, 1976, Ihwagi *et al.*, 2012). There were an estimated 6000 elephants in the ecosystem during the study period

(Thouless *et al.*, 2008, Ihwagi *et al.*, 2015). Reports of elephant mortality from different small land holdings are aggregated into larger contiguous land units in order to collate enough sample sizes to reliably calculate the Proportion of Illegally Killed Elephants (Douglas-Hamilton *et al.*, 2010).

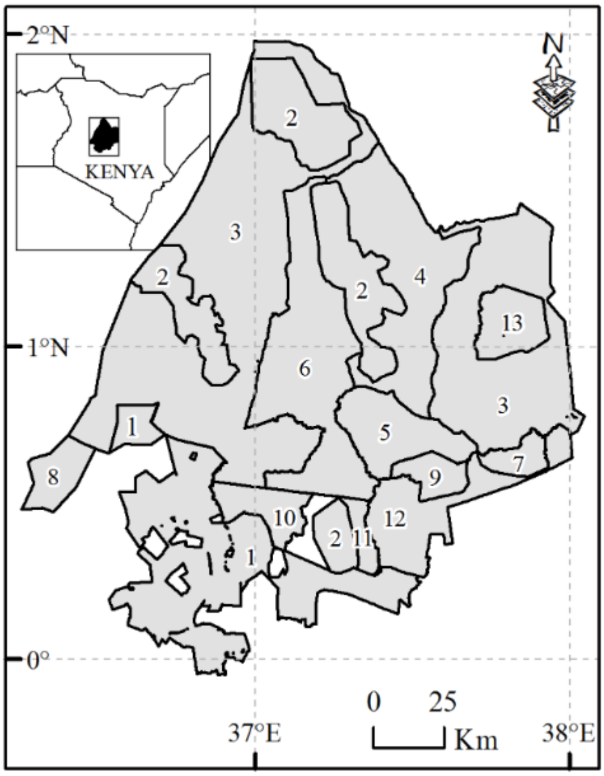

**Figure 3.1** Location of the Laikipia-Samburu ecosystem in northern Kenya. The land units used for site aggregation of mortality data were assigned generalised names in this study. These are: (1) Laikipia Private Ranches, (2) Forest Reserves, (3) Waso-Baragoi, (4) Wamba East-Namunyak, (5) West Gate-Kalama, (6) Kipsing-Meibae, (7) Shaba National Reserve, (8) Laikipia Nature Conservancy, (9) Samburu and Buffalo Springs National Reserves, (10) Naibunga, (11) Lekuruki-Ilngwezi, (12) Isiolo West, and (13) Sera.

### *4.2.2 GPS tracking data and calculation of night-day speed ratio*

Unlike male African elephants, who are usually solitary, female African elephants live in matrilineal families that can have as many as 36 members (Wittemyer, 2001, Wittemyer *et al.*, 2005b). Only one individual elephant was tracked per family unit. The collars used were sourced from either

African Wildlife Tracking (AWT) from South Africa (www.awt.co.za), Savannah Tracking (http://www.savannahtracking.com/), or FOLLOWIT (www.followit.se) from Sweden. The collars comprised the following models: Lotek 1000, Lotek 2000, TVP Simplex, AWT GSM, AWT SAT, AWT GSM, Savannah Tracking, Argos and TVP Sat. The different types of GPS collars are comparable in their performance regarding the acquisition of locations, though their lifespan may vary (Pastorini *et al.*, 2015). The choice of the type of collar is thus influenced by their technical specifications, the environment they are deployed in and their cost. The collars were programmed to record and transmit their location every hour.

The elephants were tracked for varying lengths of time ranging from a few months to over three years per individual. The tracking data were filtered for erroneous points due to occasional GPS errors using a biologically defined upper movement limit of 7 km/h (Wall *et al.*, 2013). The data were projected on the Universal Transverse Mercator (UTM) WGS-84 reference system. Elephants exhibit non-usual movement patterns at the edge of their range, either aggregating at fences (Vanak *et al.*, 2010) or crossing roads fast (Blake *et al.*, 2008). In order to focus on responses to possible poaching risk rather than other clear anthropogenic risks, we excluded the areas 2.5 km from roads or fences. The Animal Movement Ecology Tools (ArcMET) (Wall *et al.*, 2014) for ArcGIS 10.2.1 (ESRI, 2014) were used to calculate the hourly speeds between the successive GPS points.

The study area lies on the equator, and as such, there is no variation in day length throughout the year. The GPS locations for night and day were separated by the cutoff times 6:00 AM and 6:00 PM local time (GMT+3). The night-day speed ratio of the elephants in each land unit was calculated as the mean hourly night time speed divided by the mean hourly daytime speed for the entire period an elephant was in each land unit before and/or during the poaching surge. An added advantage of aggregating data into a longer tracking period is that it gives time for a reasonable sample size of dead elephants to be recorded since PIKE is a measure of the proportionate cause of death (Douglas-Hamilton *et al.*, 2010). The value “1” for the night-day speed ratio of the elephants thus corresponds to equal mean night and mean day speeds. As the elephants move more at night, the night-day speed ratio increases and vice versa. In the year 2009, a severe drought affected the ecosystem (Wittemyer *et al.*, 2013). The year 2009 was therefore omitted from the analyses because the elephants were most likely responding to the unusual drought-related environmental stress, which would potentially mask the effect of poaching, our primary concern. The period between 2010 and 2012 was characterised by high poaching levels in the ecosystem (Ihwagi *et al.*, 2015). Therefore, we defined two broad study periods based on the prevailing poaching levels; before (2002 to 2008) and during (2010 to 2012) the poaching crisis. The average night-day speed ratio of all elephants tracked within each land unit before and during the poaching crisis increased (Fig. 4.2).

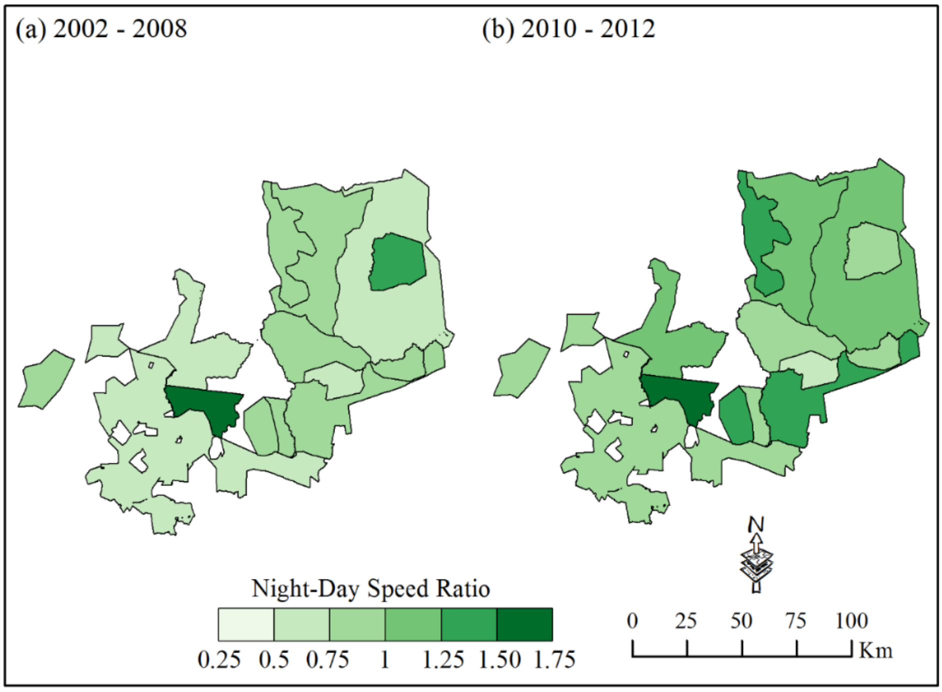

**Figure 4.2** The mean night-day speed ratio of all elephants tracked in the different land units in Laikipia-Samburu ecosystem from (a) 2002 to 2008 and (b) 2010 to 2012.

### *4.2.3 Collecting mortality data and calculation of the Proportion of Illegally Killed Elephants (PIKE)*

A participatory approach involving the key government agency (Kenya Wildlife Service), pastoral herders, researchers, community conservancy managers and ranchers has been established to gather information on the elephant mortality in the area (Kahindi *et al.*, 2010). Particulars of each dead elephant encountered including the estimated date of death, GPS coordinates, local area name, and cause of death (if ascertainable) were collected, as per the standard protocol developed by the Technical Advisory Group (TAG) of the MIKE programme *(CITES. Secretariat, 1999)*. Four categories of death were recognised, i.e. illegal killing, problem animal control by authorised personnel in defence of either life or property, and natural mortality. Where it was not possible to identify the cause of death with certainty, the cause of death was marked as ‘unknown.' The Proportion of Illegally Killed Elephants (PIKE) out of all mortality cases has been adopted by CITES as a measure of the severity of poaching at a given space or time (Douglas-Hamilton *et al.*, 2010, Jachmann, 2013, Nellemann *et al.*, 2013). It has been established that there are significant differences in PIKE values between various land units in the ecosystem (Ihwagi *et al.*, 2015).

A total of 1156 elephant carcases was reported and verified between 2002 and 2012 (Table 4.1). Fig. 4.3 shows the locations of carcasses and whether the elephants were illegally killed or otherwise. Approximately 15% of the carcasses that had an erroneously transcribed GPS were assigned to a land unit based on the name of the local area. The mean PIKE value for each land unit during both the pre-poaching period (2002-2008) and the poaching surge period (2010-2012), was calculated (Figs. 4a and 4b).

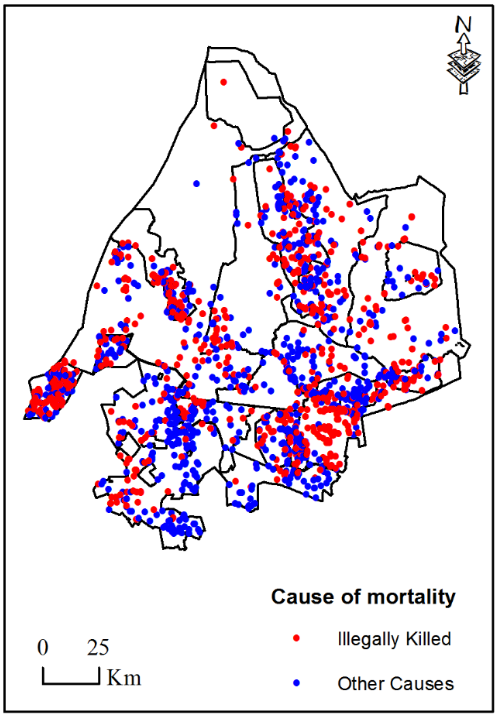

**Figure 4.3** The distribution of elephant carcases recorded from 2002 to 2012 (excluding the year 2009) in the Laikipia - Samburu ecosystem and the main causes of death of the elephants. The year 2009 had a severe drought and natural mortality was unusually high, more than the twice annual sample size from previous years, making it an outlier year.

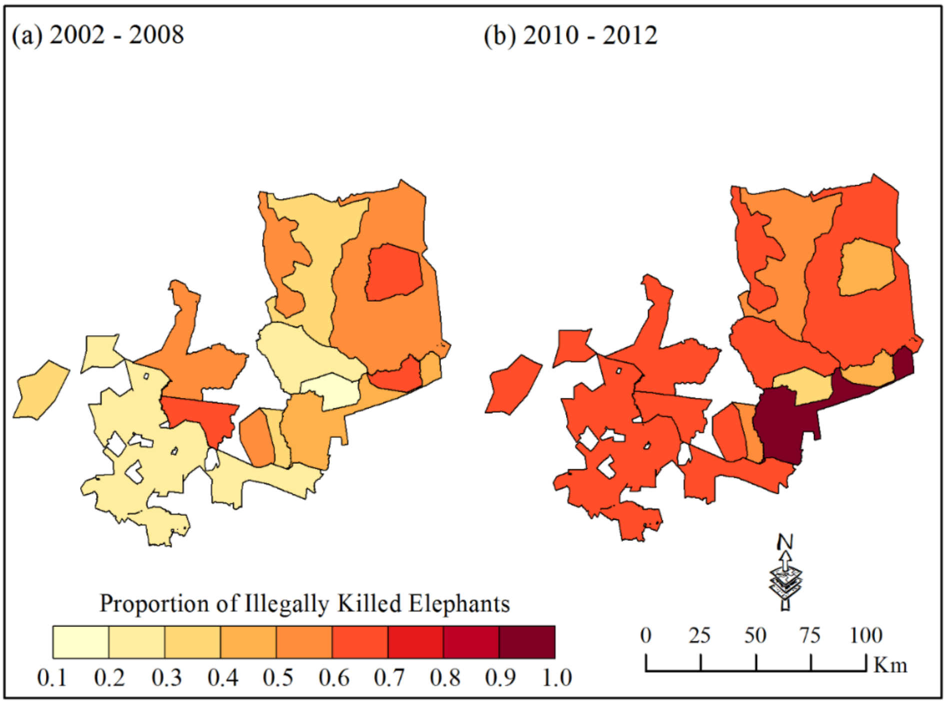

**Figure 4.4** The mean annual Proportion of Illegally Killed Elephants (PIKE) in the different land units within the Laikipia-Samburu ecosystem (a) before the poaching surge (2002 to 2008) and (b) during the poaching surge (2010 to 2012).

### *4.2.4 Elephant utilization units for testing spatial differences in the night-day speed ratio*

To be able to compare the variation in night-day speed ratio of the elephants with the PIKE data for the land units defined by Douglas-Hamilton *et. al*. (2010), movement data of 32 elephants (15 males and 17 females) tracked for at least one year, and which visited more than one land unit were used. We stipulated the minimum tracking period of one-year, because an elephant might by then have walked throughout its full potential range, driven by seasonal variations in resource availability (i.e., through wet and dry seasons). Because elephants utilised multiple land units, this ensured that the areas encompassed a gradient in poaching risk, which was our primary interest. For each elephant, we calculated its average night-day ratio in each land unit, separating the elephants into two groups: those tracked before and those tracked during the poaching surge. the decision was arrived at because there were no monthly (seasonal) differences, but there were differences between the longer periods "before" and "during" the poaching surge.

**Table 4.1** The number of dead elephants from various causes and the Proportion of Illegally Killed Elephants (PIKE) in various land units.

| Time period | Land unit name | No. of dead elephants | PIKE |
|---|---|---|---|
| 2002 - 2008 | Baragoi – Waso | 192 | 49.0% |
| 2002 - 2008 | Forest Reserve | 194 | 53.6% |
| 2002 - 2008 | Koija Community Ranches | 32 | 62.5% |
| 2002 - 2008 | Laikipia Nature Conservancy | 107 | 52.3% |
| 2002 - 2008 | Laikipia Private Ranches | 186 | 19.9% |
| 2002 - 2008 | Lekuruki & Il-Ngwezi | 46 | 32.6% |
| 2002 - 2008 | Nakuprat, Nasuulu & Leparua | 56 | 48.2% |
| 2002 - 2008 | Samburu-Buffalo Springs NRs | 26 | 11.5% |
| 2002 - 2008 | Sera | 26 | 80.8% |
| 2002 - 2008 | Shaba National Reserve | 27 | 51.9% |
| 2002 - 2008 | Wamba East- Namunyak | 91 | 35.2% |
| 2002 - 2008 | Westgate - Kalama | 27 | 25.9% |
| 2010 - 2012 | Baragoi-Waso | 117 | 54.7% |
| 2010 - 2012 | Forest Reserve | 108 | 64.8% |
| 2010 - 2012 | Kipsing-Meibae Conservancies | 64 | 50.0% |
| 2010 - 2012 | Laikipia Nature Conservancy | 73 | 52.1% |
| 2010 - 2012 | Laikipia Private Ranches | 274 | 47.8% |
| 2010 - 2012 | Nakuprat, Nasuulu & Leparua | 132 | 76.5% |
| 2010 - 2012 | Samburu-Buffalo Springs National Reservs | 74 | 20.5% |
| 2010 - 2012 | Sera | 13 | 30.8% |
| 2010 - 2012 | Westgate-Kalama Conservancies | 45 | 28.9% |

### 4.2.5 Statistical analyses

Statistical analyses were performed using R (R Development Core Team, 2012a). All tests were carried at a significance level of 0.05. To test if there were significant monthly (seasonal) variations in the night day speed ratio of elephants over the entire study period, we used ANOVA and only performed this test using data from 2002 to 2008 (pre-poaching crisis) for all available data (60 elephants). For this test, it did not matter how many months an elephant had been tracked for. We used the Student's Two-Sample *t*-Test to determine whether there were significant differences in the night-day speed ratio of elephants in low poaching areas (PIKE < 54%) and high poaching areas (PIKE ≥ 54%).

Some elephants had more data (sampling rates) than others, and it was important to determine if including elephant identity (ID) as a random factor in a model was warranted. Two linear mixed effect models implemented with package "lme4" were created; one with all covariates (average travel speed, area name, sex, the Proportion of Illegally Killed Elephants (PIKE) and the real elephant ID and another model with a constant elephant ID (Galwey, 2007). A value of "1" was allocated for each elephant ID, but to achieve a grouping level necessary to execute the model, one elephant ID was entered as "0.999"; a value very close to "1" thus with no likelihood of being significantly different from "1". The response variable in both models was the ratio of night-day time speed of each elephant for all the period it moved in a given land unit before and/or during the poaching surge. PIKE was factored in the model as a continuous variable ranging from 0% to 100%. The two models were compared using ANOVA to check for the one with lowest AIC and BIC. Since it was not necessary to include ID as a random factor (see results section), we proceeded to model the variation in the night-day speed ratio of elephants with PIKE, speed and sex using a linear model. Models with different combinations of covariates and their interactions were fitted and compared using the second-order Akaike's Information Criterion (AICc) (Burnham and Anderson, 2002).

## 4.3 Results

### 4.3.1 Variation in the night-day speed ratio of elephants within months and between low and high poaching periods

Twenty-eight females and 32 males were tracked for a cumulative total of 72 and 118 months respectively. There was no significant monthly variation of the mean day-night speed ratio of either female ($F_{11,60} = 1.06$, $P = 0.41$) or male ($F_{11,107} = 1.72$, $P = 0.09$) elephants tracked within the same time period with respect to the onset of poaching surge. We compiled a total of 79 elephant utilization units, i.e., summaries of an individual elephant into all land units it visited during the entire study period; 31 for male elephants (18 before and 13 during poaching surge) and 48 for female elephants (33 before and 18 during the poaching surge). We tested for the normality of the data for males and females separately using Shapiro-Wilk's test. The data for females was normally distributed (Shapiro-Wilk test: $W = 0.953$, $P = 0.051$), but that of males was not normally distributed (Shapiro-Wilk test: $W = 0.896$, $P = 0.006$). Using Mann-Whitney test for the male elephants, and an independent samples paired t-test for the female elephants, we tested for the differences in night day speed ratio for the male elephants between the period 2002 to 2008 (before poaching surge) and the period 2010 to 2012 (during poaching surge). There was a significant difference in the night-day speed ratio of elephants for the males (Males: Mann-Whitney test: $U = 169$, $P = 0.039$, n = 32) and the females (t-test: $t = 3.286$, $P = 0.003$, n = 48) (Fig. 4.5).

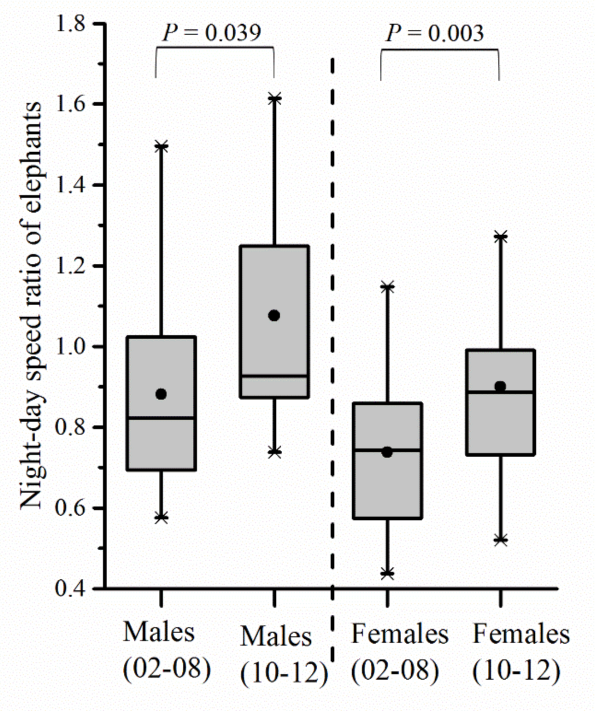

**Figure 4.5** Box plots show the average night-day speed ratio of male and female elephants in the Laikipia-Samburu ecosystem before (the years 2002 to 2008) and during (2010 to 2012) the poaching surge. There was a significant increase in the night-day speed ratio of both male and female elephants.

### *4.3.2 Modelling the variation in night-day seed ratio of elephants with PIKE, speed and sex*

Two linear mixed effects models one with a full set of covariates and elephant ID and another with constant ID were compared using ANOVA (Table 4.2.). The model with constant elephant ID had lower AIC and BIC values (Table 4.3). This showed that there was no significant contribution by the elephant ID when factored as a random effect in a model.

**Table 4.2** The structure of two linear mixed effects models constructed for the purpose of testing for the relevance of treating elephant identity as a random effect covariate in modelling the variation of the night-day speed ratio (NDR) of elephants. One model has real elephant identify while the other one has constant elephant identity. The constant identity used was "1", but one entry was assigned "0.99" to offer the required grouping level for executing the model.

| Model | Model description |
|---|---|
| 1 | lmer(NDR ~ PIKE + sex + speed + (1 \| real elephant ID), data) |
| 2 | lmer(NDR ~ PIKE + sex + speed + (1 \| constant elephant ID), data) |

**Table 4.3** The comparison between a model with and one without elephant ID as a random effect using ANOVA. The model with no random effect (Model 2) had marginally lower AIC and BIC values.

| Model | Df | AIC | BIC | logLik | Deviance | Chisq | Df | Pr(> Chisq) |
|---|---|---|---|---|---|---|---|---|
| lmer1 | 6 | -54.872 | -40.655 | 33.436 | -66.872 | | | |
| lmer2 | 6 | -54.868 | -40.652 | 33.434 | -66.868 | 0 | 0 | 1 |

A set of multiple linear regression models with different combinations of covariates were constructed (Table 4.4).

**Table 4.4** Candidate models in the analyses of the relationship between the night-day speed ratio (NDR) of elephants, the Proportion of Illegally Killed Elephants (PIKE), sex and the mean travel speed in a linear model. The asterisk between covariates shows their interactive effects.

| Model | Model description |
|---|---|
| 1 | NDR= $\beta_0 + \beta_1$(PIKE)+ $\beta_2$(sex)+ $\beta_3$(speed) |
| 2 | NDR= $\beta_0 + \beta_1$(PIKE)+ $\beta_2$(sex*speed) |
| 3 | NDR= $\beta_0 + \beta_1$(PIKE)+ $\beta_2$(speed) |
| 4 | NDR= $\beta_0 + \beta_1$(sex) + $\beta_2$ (speed) |
| 5 | NDR= $\beta_0 + \beta_1$(speed) |
| 6 | NDR= $\beta_0 + \beta_1$(PIKE) |
| 7 | NDR= $\beta_0 + \beta_1$(PIKE)+ $\beta_2$(sex) |

The top two models with were identified by weighting the second-order AIC (AICc) (Table 4.5). The top model featured PIKE and sex. Evidence ratio between models 'PIKE + sex' and 'PIKE + sex + speed' was 3.13, implying that the two models were different and the first model is thus considered most plausible alone (Table 4.6). Using ANOVA, we tested for the significance of the results of the top model featuring “PIKE “and “Sex”. The top model was statistically significant in explaining the variation in the night-day speed ratio of elephants ($F = 47.92$, $R^2 = 0.558$, $P < 0.001$, $DF = 76$).

**Table 4.5** Selection statistics of the top two models for the analyses of relationships between the night-day speed ratio (NDR) of elephants, the Proportion of Illegally Killed Elephants (PIKE), sex, land unit and mean travel speed. AICc denotes the second order Akaike’s Information criterion. ΔAICc denotes Delta AICc which is the difference between the model’s AICc and the lowest of all the AICc values. AICcWt denotes Akaike weights.

| Model | AICc | ΔAICc | AICcWt |
|---|---|---|---|
| PIKE+sex | -79.25 | 0.00 | 0.69 |
| PIKE+sex+speed | -76.97 | 2.28 | 0.22 |

**Table 4.6** The coefficients of the covariates of the top model of night-day speed ratio of elephants as a function of the Proportion of Illegally Killed Elephants (PIKE) and their statistical significance. The model was statistically significant in explaining the variation in the night-day speed ratio of elephants ($F = 47.92$, $R^2 = 0.558$, $P < 0.001$, $DF = 76$).

| | Estimate | Std. Error | *t* value | *p* |
|---|---|---|---|---|
| Intercept | 0.4165 | 0.0849 | 4.907 | 0.000 |
| PIKE | 0.0078 | 0.0009 | 8.555 | 0.000 |
| Sex | 0.1332 | 0.0400 | 3.328 | 0.000 |

## 4.4 Discussion

The night-day speed ratio of elephants increases significantly with the increase in poaching levels, which suggests that elephant movement behaviour could be used as a reliable indicator of changes in the level of poaching risk. As changes in poaching levels cannot be determined instantly from field-verified carcass records, this result offers a potential indicator for changes poaching levels in near real-time using GPS tracking data. For example, elephants in the Sera Conservancy, which experienced declining poaching levels even as the levels in the rest of the ecosystem increased, exhibited a proportionately lower night-day speed ratio. This isolated case of a decrease in poaching levels against the general trend in the ecosystem has been attributed to improved conservation efforts by local communities (Ihwagi *et al.*, 2015), and thus forms a constructive test case for the hypothesis.

The results from GPS tracking data and intensive field monitoring of causes of elephant mortalities are congruent with historical visual field-based observations and notes to the effect that elephants in low poaching environments are more active during the day than at night (Wyatt and Eltringham, 1974, Douglas-Hamilton, 1998a). This study offers an innovative approach that quantifies the change in elephant movement rates between night time and daytime using GPS tracking technology, as an indicator of poaching levels. The increased nighttime activity of elephants encountering heightened poaching levels suggests that poaching activities in the study area occur mainly during the day. The night-day speed ratio of elephants can potentially be applied in many ecosystems, where it is a measure of change in movement rates from a previously observed pattern. In this study, we were not able to establish a baseline activity pattern, i.e., night-day ratio under zero poaching risk, because poaching was prevalent in all land units. We recommend the establishment of a baseline night-day ratio of activity in different environments and seasons (in other elephant populations further from the equator, more seasonal variation may exist).

The lack of seasonal variation in night-day speed ratio of elephants in an environment with seasonal rainfall fluctuations (and presumably changes in forage availability) suggests that their diel movement behaviour is in response to a variable of much shorter timescale, like poaching. This view is corroborated by past findings that seasonal variation in the availability of a natural resource is not expected to result in diurnal movement behaviour of an animal (Godvik *et al.*, 2009). Nevertheless, there might be a need to factor the role of seasonality in, when inferring the level of poaching using night-day speed ratios of elephants inhabiting ecosystems with clearly defined seasons, or with extreme diurnal variation in weather elements such as temperature, as can be expected farther away from the equator. A key challenge in replicating this study in other sites is access to the detailed site level data on mortality locations within sites. The numbers of dead elephants found for each MIKE site are on the website of CITES; https://fusiontables.google.com/DataSource?docid=1juiqNCOUwqperYcoq_uCWaZ5lEs8t09hfRry_I37#rows:id=4 (Accessed on 24th November 2016). The details of elephant carcases within sites are owned by the range States that provided them. We worked with the only dataset that we could access with permission from the Government of Kenya, which is coincidentally the most comprehensive of all reporting sites across Africa. We recommend testing of this new indicator of poaching in places where individual-elephant mortality records can be accessed with permission from the respective governments.

### *Implications and conclusions*

The significant alteration of movement behaviour by elephants in response to poaching risk has potential implications for their foraging strategy, their reproduction, and their ultimate survival, all of which are not yet fully understood. The risk of predation often leads prey species to make use of less good foraging locations (Hamel and Côté, 2007). Reproduction and survival of mammals depend on the cumulative effects of movement behaviour (Powell and Mitchell, 2012). Besides the potential reduction in foraging efficiency, foraging under the cover of darkness might expose elephant calves to predation from lions, which are primarily nocturnal.

We illustrated that GPS tracking data could be used as an anti-poaching tool. The night-day speed ratio can potentially be applied to elephants in diverse ecosystems because it is a relative measure of change in movement behaviour based on a previously observed movement pattern. An advantage is that the tracking dataset across the African elephant range is rapidly increasing (Douglas-Hamilton, 1998b, Douglas-Hamilton *et al.*, 2005, Blake *et al.*, 2008, Wall *et al.*, 2013). This presents an ideal opportunity to assess elephant movement behaviour under risk of poaching using remote sensing data. Application of the night-day speed ratio as a standard metric would enable utilisation of the existing tracking datasets across the elephant range as a poaching monitoring tool, especially outside designated MIKE sites. The approach proposed in this study is not a replacement for the MIKE program, but a complementary method that can aid wildlife managers and researchers in filling knowledge gaps on risk levels across the elephant range.

# Chapter 5

# Elephants lose foraging time as they avoid poaching risk on a daily basis[*]

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[*] This chapter is based on: Ihwagi F.W., Skidmore, A.K., Guillaume-Bastille, R., Wang, T., Toxopeus, A and Douglas-Hamilton I. Submitted to the *International Journal of Geographical Information Systems*

## Abstract

Poaching for ivory has caused disturbances on the normal movement of elephants but nature and magnitude of such disturbances are not yet fully understood. The behavioural adaptation of elephants to risk at the fine temporal scale, as well as the cost of such behavioural adaptation on the foraging efficiency has not been accomplished. Using GPS tracking data of ten elephants monitored for multiple years each between 2002 and 2016, we studied the daily activity patterns of wide ranging elephants, i.e., the cycle of movement speeds sampled at the hourly frequency when they were in the areas with low and with high levels of poaching. Generalized Additive Models revealed that elephants adjusted their peak-times of activity, and ultimately move less within a 24-hour period when they are in areas with high poaching levels. The most notable activity shifts were between dawn and midday hours; elephants moved less at dawn when they were in low poaching areas but remained more active during the day, and vice versa. We conclude that although elephants remain more active at dawn, this does not compensate for the time lost during the day when they hide from poachers or avoid conflicts with other humans. The risk avoidance culminates in the reduction of activity time within a 24-hour cycle. 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.

## 5.1 Introduction

The variation of the risk of predation in space and time alters the behaviour of large herbivores commensurately, as they strive to avoid overlap with the predators (Tambling *et al.*, 2015). Avoiding encountering a predator may increase the probability of its survival in the short-term, but may compromise its long-term survival (Creel and Christianson, 2008, Cresswell, 2011, Wang and Zou, 2017). 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 level during the period of high risk to reduce encounter and detection probability (Lima *et al.*, 1999, van Beest *et al.*, 2013). The risk allocation hypothesis postulates that animals should display their greatest antipredator behaviour in high-risk situations that are brief and infrequent (Lima and Bednekoff, 1999, Sih and McCarthy, 2002). Knowledge of the scale-dependent behavioural responses to predation risk is valuable for making inference on the costs of fitness that are incurred by a prey species (Lima and Dill, 1990).

Elephants are larger than the preferred prey species of sympatric carnivores, e.g. lions, and for this reason, their diel movement behaviour pattern is not affected by these natural predators (Tambling et al. 2015). When the risk of predation is always present at a low level, strong responses are not expected, but if the risk fluctuates, prey species exhibit strong behavioural adjustments (Creel and Christianson, 2008, Sheriff *et al.*, 2011, Hiltunen and Laakso, 2013). Human beings are the most important predators of elephants by way of illegal hunting, a practice that is the most significant immediate threat to elephants beside the albeit longer-term habitat loss (Nellemann *et al.*, 2013). Elephants perceive the risk of encountering humans and actively adjust their movement to avoid it (Graham *et al.*, 2009, Ihwagi *et al.*, 2018). When migratory elephants move along the (often unsafe) corridor areas they walk at faster speeds and resume normal speeds upon completion of the migratory stretch (Douglas-Hamilton *et al.*, 2005). Elephants can distinguish human beings by the colour cloth, odour, ethnicity, gender and age (Bates *et al.*, 2008, McComb *et al.*, 2014). Such observations suggest that elephants have a high situational awareness of threats.

Efforts by an animal to balance foraging needs and to avoid predation risk affects their behaviour (Lima and Dill, 1990, Cowlishaw, 1997, McArthur *et al.*, 2014). A global decline in the general movement of terrestrial mammals was recently confirmed and attributed to general behavioural changes of animals over time, and to the exclusion of species with long-ranging movements from their former foraging areas that have been taken over by human beings (Tucker *et al.*, 2018). Predation risk leads to an overall loss of foraging opportunities as animals adjust their raging behaviour (Eccard and Liesenjohann, 2014). Besides the interaction between predation risk and foraging behaviour, habitat quality by itself influences a large herbivore's time budget (Bjørneraas *et al.*, 2012). While it is well known that animals adjust their diel pattern of movement to the magnitude of predation risk (Lima and Dill, 1990, Brown *et al.*, 1999, Lima, 2002, Creel *et al.*, 2014), it is far less known whether these changes lead to an overall reduction or increase in movement. Such changes in overall movement pattern could be valuable in our understanding of predator-prey interactions and their implications on different aspects of their ecology.

Observations on the daily activity of elephants, while following captive elephants on foot (Kuhme, 1962), and later on wild elephants (Wyatt and Eltringham, 1974), identified peaks of activity at dawn, dusk and midnight. These early field-based observations further suggested that elephants are active for approximately 17 hours in a day (Ruggiero, 1989) and that they are most vigilant in areas where they are experiencing poaching threats (Barnes, 1982, Ruggiero, 1990). Elephants adjust their speed related to the availability of surface water in water-deficient ecosystems; where they have to make regular daily trips to the drinking points (Simon *et al.*, 2007, Chamaille-Jammes *et al.*, 2013). Nomadic pastoralism is the primary economic activity of communities living in semi-arid landscapes, and their movement is influenced by the availability of surface water (Butt and Turner, 2012, Tyrrell *et al.*, 2017). It is therefore plausible and is part of our hypotheses that besides illegal killing the presence of livestock at shared resource points during the daytime hours could potentially influence elephants' activity cycle. Despite extensive knowledge of how elephants respond when faced with the risk and uncertainty of resource availability at large spatial and temporal scales, the timing of their response to increased poaching risk within specific hours of a day is less understood.

In the backdrop of the already documented behavioural adjustments at short time scales, the focus of this study is on the variation of the timing of these daily movements when elephants are in low and high-risk areas, an aspect that has not received much attention. There is a big knowledge gap about the fine-scale behavioural responses of elephants because few studies have achieved detailed multiple years of fine-temporal resolution movement data gathered concurrently with a field-based body count and verification of the causes of mortality of elephants. Variation in the timing of activity to avoid risk may have short-term benefits by minimising encounters with predators, and potentially, longer-term impacts on the fitness of elephants. In this study, we sought to answer the following questions:

(i) How do elephants change the consecutive hourly speeds in a day, i.e. activity cycle when they move to different parts of their home range?
(ii) What covariates contribute to alteration of their daily activity cycle?
(iii) What is the effect of the alteration of activity cycle on the overall movement of elephants throughout the day; when they are within zones that have different levels of illegal killing.

## 5.2 Methods

### *5.2.1 Study Area*

We conducted this study in the Laikipia-Samburu ecosystem of northern Kenya. It lies within 0.4°S to 2°N, 36.2°E to 38.3°E, an area of 34,000 km$^2$ (Fig. 5.1). The ecosystem is delineated by the geographical extent of the Ewaso Nyiro River and its tributaries, in the low lands between Mt. Kenya and the Aberdare ranges (Georgiadis, 2011). It 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 rugged terrain and solitary 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.

### *5.2.2 Monitoring the Illegal Killing of Elephants (MIKE)*

Under the Monitoring of the Illegal Killing of Elephants (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 and comparable metric for the estimate of the poaching levels (Douglas-Hamilton *et al.*, 2010, Jachmann, 2013). PIKE is calculated as:

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

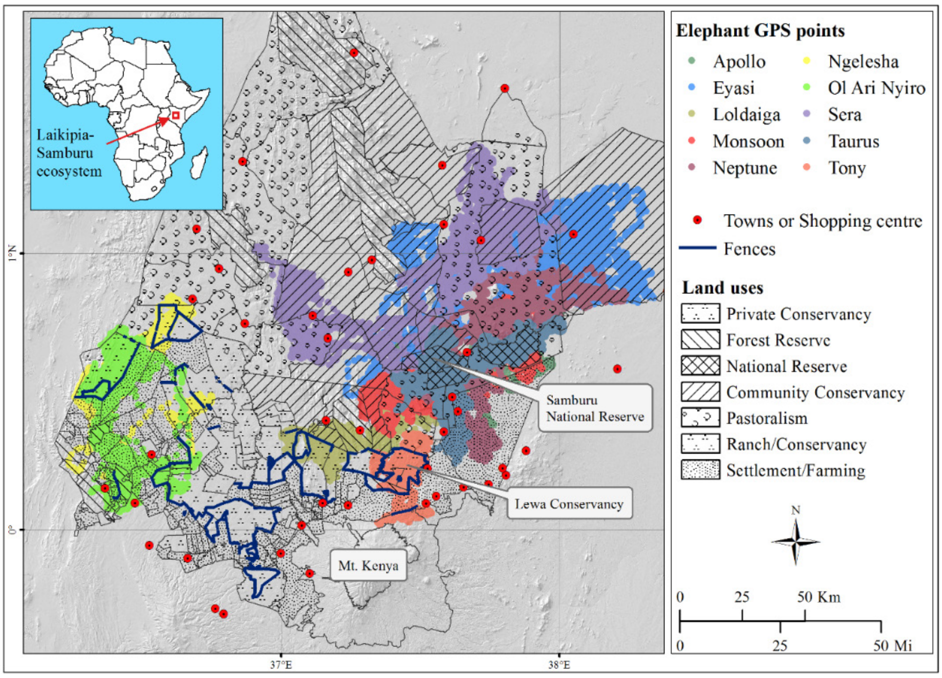

**Figure 5.1** The Laikipia-Samburu ecosystem. Ten elephants were tracked at various dates between the year 2002 and 2016. The ecosystem is shared by humans and wildlife, and it has multiple land uses.

We used PIKE as the measure of the levels of illegal killing in each of the elephants' core areas. To determine the PIKE value, we used 3103 carcasses of elephants recorded between the year 2002 and 2016 throughout the study to calculate PIKE values. We calculated the PIKE for each elephant's core areas from the records of mortality accumulated up to the last year it was tracked, and thus for each elephant, we have different levels of PIKE. Human-elephant conflicts are incidences where unauthorised personnel, mostly 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. Despite PIKE comprising of both human-elephant conflict incidences and poaching ones, the conflict-related mortality accounts for less than 10% of the illegal killing cases (Ihwagi *et al.*, 2015), making reference to PIKE in the study area synonymous with the actual poaching levels.

### 5.2.3 Tracking elephants using GPS collars

We used movement data of 10 elephants tracked at various dates from the year 2002 to 2016. The elephants comprised of eight females from different families and four bulls, fitted with GPS collars sourced from African Wildlife Tracking (AWT) (www.awt.co.za) and FOLLOWIT (www.followit.se), each recording a fix on the hour. Immobilization and collar deployment was carried out by licensed government veterinarians using standard procedures. We acquired over 176,342 GPS points from 10 elephants at an hourly interval, an equivalent of 6585 elephant days (Table 5.1). For each hourly GPS points, we calculated the speed in kmhr$^{-1}$. We removed spurious GPS points that corresponded to unlikely speeds of over than 7 km$^{-1}$ (Wall *et al.*, 2013).

We used time-density, a recently developed tool for estimating home range, to delineate each elephants hotspots, i.e. where they spent most of the time (Wall *et al.*, 2013). Time-density in a grid is an estimate of the proportion of total tracking time for an elephant in each grid cell of user-defined size. The method estimates the proportionate time spent in each grid out of the total tracking time, based on the lengths of track segments within in a grid. We used grid sizes measuring 500 m × 500 m, a size that approximates to double the median hourly distance walked by elephants (Wall *et al.*, 2013), into which we aggregated and or measured the values of the environmental variables. From the time-density grid of each elephant, we identified the hotspots at the extreme ends of the home range and adopted the encompassed land management units, e.g. conservancies, national reserves or ranches. The land units were adopted in full because they are the smallest units used for compilation of mortality data and subsequent calculation of PIKE. We refer to these land units as the core areas. Land use and management types in the Laikipia-Samburu ecosystem are key determinants of within-site variation in poaching levels (see Chapter 2) (Ihwagi *et al.*, 2015).

**Table 5.1** The dates when each elephant was tracked, the number of hours that each of them spent in their respective core areas and the PIKE calculated for each elephant's core area.

| Elephant | Tracking period | Hours in core area 1 | Hours in core area 2 | PIKE core area 1 | PIKE core area 2 |
|---|---|---|---|---|---|
| *Apollo* (♂) | Feb 02 - Jan 04 | 3190 | 4698 | 22% | 56% |
| *Eyasi* (♀) | Feb 13 - Sep 16 | 3962 | 8509 | 22% | 60% |
| *Loldaiga* (♀) | Aug 06 - Jan 09 | 5389 | 3546 | 27% | 57.5% |
| *Monsoon* (♀) | Jan 02 - Sep 16 | 11825 | 3301 | 22.0% | 56.0% |
| *Neptune* (♀) | Jan 02 - Mar 07 | 20028 | 8268 | 22.0% | 56.0% |
| *Ngelesha* (♂) | Aug 08 - Feb 12 | 10428 | 338 | 38.0% | 51.7% |
| Ol'Nyiro (♂) | Aug 07 - Feb 12 | 9164 | 16359 | 38.0% | 51.7% |
| *Sera* (♀) | Aug 06 - Apr 11 | 10787 | 12773 | 38.0% | 87.7% |
| *Taurus* (♀) | Jan 11 - Sep 16 | 26267 | 8797 | 22.0% | 56.0% |
| *Tony* (♂) | Jan 11 - Sep 16 | 8359 | 354 | 22.0% | 51.5% |

### 5.2.4 Environmental variables

In addition to poaching, we explored the effect of other environmental variables that vary within a daily time scale or have an influence on an elephant's short-term movement behaviour; water and livestock. We compiled the locations of surface water acquired from both ground mapping and digitised 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 fall or cease, the number of water points per unit area increase or decrease respectively at relatively the same rate across the landscape, and thus the relative abundance at any one time would not be significantly changed. For each grid cell, we calculated the shortest 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 elephants and livestock were undertaken, in the years 2008 and 2012 (Ihwagi *et al.*, 2015). We obtained counts of all livestock species and calculated their densities in each of the grids. We considered this as a measure of relative abundance of livestock because those were just two snapshots in time. The same aerial count data included records of all occupied homesteads, i.e., semi-permanent and temporally dwellings. All GIS operations to prepare the tracking and other spatial data were performed using ArcGIS 10.4 (ESRI, 2014).

### *5.2.5 Statistical analyses*

We analysed data using R 3.3.0 (R Development Core Team, 2012b). We constructed twelve Generalized Additive Model (GAM) regression models (Hastie and Tibshirani, 1986). We chose the GAM because it enables modelling of the highly nonlinear activity pattern of elephants 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 in 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. In addition to the smoother for all elephants combined, we plotted individual elephant's smoothers and tested for their statistical significance between both home ranges. The models were fitted 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 explanatory variables were PIKE, the density of livestock, NDVI, the distance to water, and interaction between them. We constructed a set of 11 plausible models based on different combination of the above variables. The predictor variables were standardised to reduce their collinearity (Marquardt 1980) and improve interpretability (Schielzeth, 2010). The model was implemented using the *mgcv* package in R (R Development Core Team, 2006).

To obtain the overall resting time (inactive time) per day, we considered the resting moments as when the displacement between any two consecutive GPS points was less than 25m (i.e., a speed of less than or equal to 0.025 Kmhr$^{-1}$). We considered the distance of 25 meters ideal enough to take into account of the horizontal position error of the GPS, usually about 10m, and possibly some minimal movement that elephants may make within a resting location interacting with other family/herd members. Though it is technically possible that an elephant could occasionally walk and loop back to the same point in an hours' time, 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" or "not active" (resting). To calculate the percentage of resting time, we aggregated the "resting" and "active" records for each hour of the day for the entire period an elephant was tracked, separately for each core area. We used Kolmogorov-Smirnov test to test for the differences. We used median instead of mean as the preferred measure of central tendency because the data were skewed (Zar, 1999).

## 5.3 Results

### *5.3.1 Testing for the difference in hourly speeds in low and high poaching areas*

The time of day was a significant predictor of the daily activity pattern for the ten elephants in their respective core areas which comprised a wave with peaks at sunrise and sunset, and reduced activity at midday (Fig. 5.2), and the lines for each elephant were nonlinear ($P < 0.001$, e$df > 9$) (Table 5.2). The individual elephant's time-smoothened plots showed that the absolute speeds varied amongst individuals, but the shift of behaviour followed the same pattern. The activity cycles for all elephants data combined for each of the areas were also nonlinear; low PIKE area ($F = 2827.7$, $edf = 9.67$, $P < 0.001$), and high PIKE area ($F = 795.3$, $edf = 9.65$, $P < 0.001$) (Fig. 5.3). Two elephants that were well known from ground patrols as habitual crop raiders, *Ngelesha* and *Ol ari Nyiro*, whose one home ranges were adjacent to farms had a markedly higher behavioural shift than the others, as they rested all day in a forest and ventured into the farms all night; staying in forests all day and crop raiding all night.

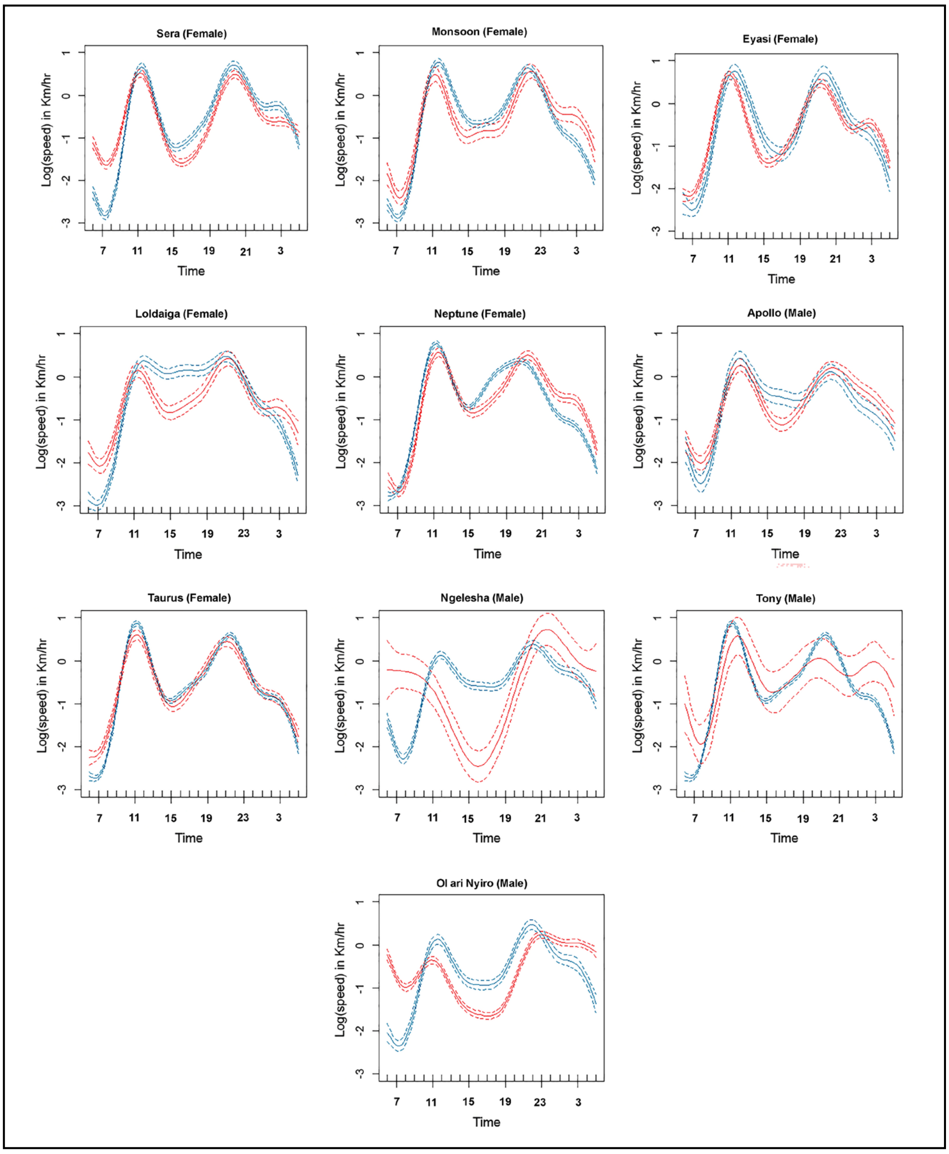

**Figure 5.2** The time-smoothers of the daily movement pattern, i.e., the average speed at different hours of the day for ten elephants combined; when they were in their two home areas. The blue and red curves are for all the days when they were in low and in high poaching areas respectively. The routine of daily movement was different between the two areas of their home ranges and using a Generalized Additive Model we established that the level of illegal killing best explained that shift in activity cycle.

**Table 5.2** The statistics of the time-smoothened average hourly movement speed within a day for each of the elephant. The structure of the Generalized Additive Models (GAM) models was "s(Time):as.numeric(MovDataID = = 'Elephant name')".

| Elephant name | Estimated degrees of freedom (*edf*) | *Ref.df* | *F* | *p* |
|---|---|---|---|---|
| *Sera* | 9.973 | 10 | 476.8 | <0.001 |
| *Monsoon* | 9.958 | 9.999 | 440.8 | <0.001 |
| *Apollo* | 8.851 | 8.993 | 126.1 | <0.001 |
| *Eyasi* | 9.939 | 8.999 | 277.1 | <0.001 |
| *Loldaiga* | 9.962 | 9.994 | 237.8 | <0.001 |
| *Neptune* | 9.971 | 10 | 820.6 | <0.001 |
| *Ngelesha* | 9.901 | 9.997 | 152.4 | <0.001 |
| *Taurus* | 9.981 | 10 | 971.8 | <0.001 |
| *Tony* | 9.938 | 9.999 | 356.6 | <0.001 |
| *Ol ari Nyiro* | 9.93 | 9.999 | 244.6 | <0.001 |

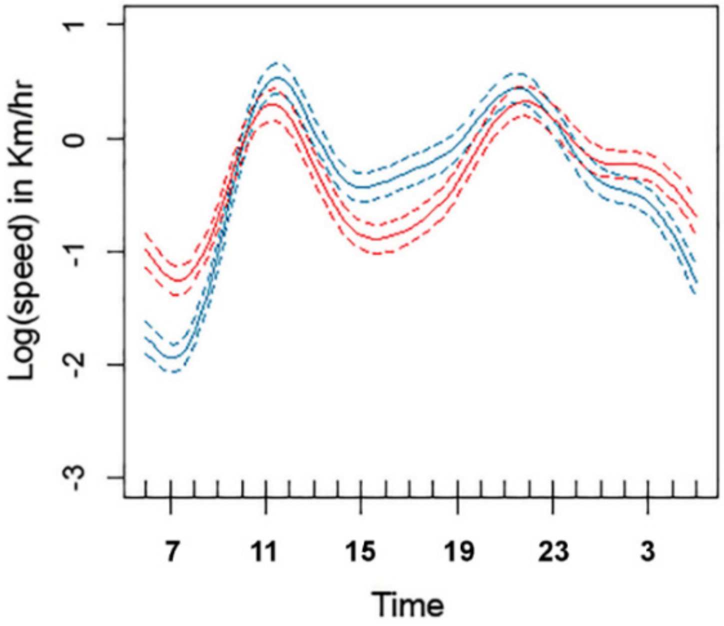

**Figure 5.3** The time-smoothened plots of the hourly movement pattern, i.e., the average speed at different hours of the day for ten elephants combined modelled using Generalized Additive Model (GAM) when they were in they were in low (blue) and high (red) poaching areas. The local time is GMT+3.

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

A set of 10 generalised additive models with different combinations of covariates were constructed, with time-smoothing factors specified for each of the ten elephants (Table 5.3). The best GAM models, i.e., one with lowest AIC, featured PIKE and livestock as the most important covariates, and the former having a greater influence (Table 5.4). The coefficient for PIKE had a negative sign, indicating reduced movement during when PIKE is high. The presence of livestock also contributed to reduced movement but at a lesser magnitude compared to PIKE.

**Table 5.3** Candidate models in the analyses of the relationship between the daily activity cycles (sampled as hourly speed) of elephants and the Proportion of Illegal Killing of Elephants (PIKE), livestock density and the proximity to surface water using Generalised 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 |

* Denotes interactive effects between the two variables

**The smothers were the of same format in 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 = ("*Neptune*")) + s(Time, by = ("*Ngelesha*")) + s(Time, by = ("*Taurus*")) + s(Time, by = ("*Tony*")) + s(Time, by = ("*Ol ari Nyiro*")).

**Table 5.4** The standardised coefficients of the best Generalized Additive Model (GAM) of the activity cycles (hourly speed) of elephants as a function of the level of illegal killing and livestock density. The level of illegal killing had the greatest negative influence on 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 |

### *5.3.3 Resting behaviour of elephants*

Elephants rested for longer times when they were in the higher poaching areas (Fig. 5.4). The median inactive time per day was 5% (1.0 hours) in low poaching areas and 8% (2.0 hours) in high poaching areas (Kolmogorov-Smirnov test; $D = 0.163$, $P < 0.003$). In absolute measures, the elephants were active for 23 and 22 hours when they were within low and high-risk areas, respectively. The extremely high outliers approaching 100% rest indicate that at times they remained inactive for full days in those areas, and the higher risk areas have notably higher-magnitude outliers.

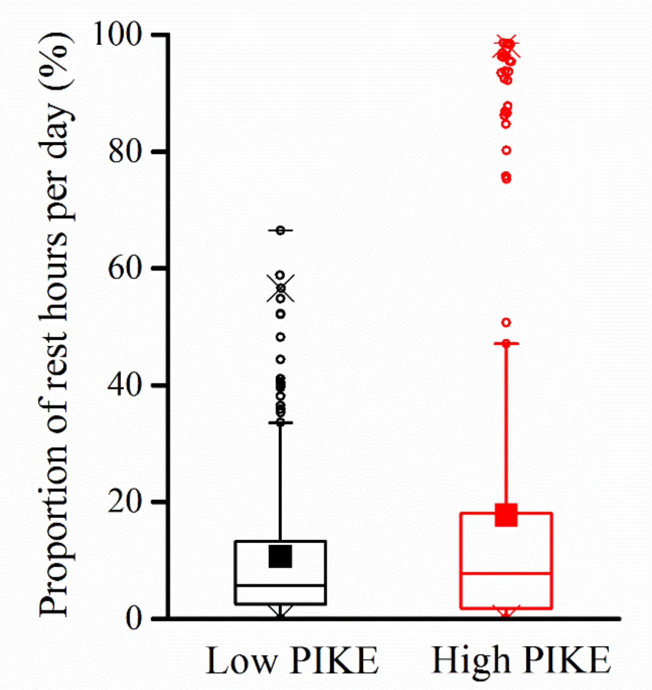

**Figure 5.4** The box plots show the proportion of hours that elephants were at rest within a day in the core areas with low and high levels of illegal killing. The solid marks and the horizontal lines inside the boxes represent the average hourly speeds and the median hourly speed respectively.

## 5.4 Discussion

We found that when elephants move into the areas with higher poaching levels, they change their daily cycle of movement related activity. They become more active at dawn than at midday when they are in the land units with a high risk of poaching or human-elephant conflict. A daily movement cycle comprising a mid-day rest and activity peaks at dawn and dusk amongst elephants is well-known and was first noted from visual field observations (Wyatt and Eltringham, 1974, Vancuylenberg, 1977). In this study, we focused on the alteration of that cycle by the elephants due to risk, especially poaching. Giving up temporal activity within a particular time of day is a short-term antipredator behaviour of animals of different taxa, e.g., common voles (Jacob and Brown, 2000), black-backed jackals (Ferguson *et al.*, 1988), grasshoppers (Schmitz *et al.*, 1997), and deer (Godvik *et al.*, 2009). Already, adjustment of activity due to poaching risk has been observed amongst elephants and these include a shift towards more nocturnal activity (Ihwagi *et al.*, 2018), walking faster when walking though risky migratory corridors, i.e., streaking (Douglas-Hamilton *et al.*, 2005, Graham *et al.*, 2009). We found that elephants are active for 23 hours in a day when they are in areas with lower levels of illegal killing, and 22 hours when they are in areas with higher levels of illegal killing.

When risk is highly predictable within the hours of a day, a prey animal adjusts 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 their high risk core area that also neighbours farms. These two elephants are well known habitual crop raiders; they went into the farms only when dark and retreated into a nearby forest by dawn. The settlement areas are hotspots for human-elephant conflicts (Douglas-Hamilton *et al.*, 2010, Ihwagi *et al.*, 2015). Unlike in the pastoral lands where pastoralists have a high tolerance for wildlife in general, the subsistence farmers have zero tolerance, and the elephants have seemingly learnt the timing of human activity and avoid direct encounters. The behaviour of these two elephants is consistent with a recent finding that elephants hide during the daytime at specific preferred locations when they are outside protected areas to minimise their exposure to risk (Wittemyer *et al.*, 2016).

Most predator-prey interactions comprise of 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 predation is higher (Laundre, 2010). However, the elephants exhibited the opposite of that prediction; they moved less when in high poaching areas. The reduction in movement, while they were in high poaching areas, might be attributed to their high mass which restricts their ability to move faster and sustain the same for long. Instead, they adjust their peak-activity times. The change in the behaviour of predator and prey to each other should encourage stability of the predator-prey system (Brown *et al.*, 1999), an outcome that cannot be guaranteed while the predator is a man, a more intelligent being whose activities elephants cannot predict or respond to in full. Elephants move less freely in risky landscapes, and they cannot adapt their behaviour sufficiently or timely enough to evade illegal hunters. The risk allocation hypothesis postulates that animals feeding under temporal variation in risk of predation faces 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 and conflict levels) in specific zones of their home ranges.

Failure to move freely in space and time 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, key 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. Behavioural responses at short-temporal scales are more related to the consequences of fine-scale effects that influence their foraging behaviour, than to the heterogeneity of the natural environment (Owen-Smith *et al.*, 2010). This study links the alteration of the hourly cycle of activity to the risk of routinely encountering livestock (or the associated humans) in the landscape and to the historical risk. The alteration of activity cycle and overall reduction of activity time may affect the foraging success of the elephants.

When the elephants were in areas with low PIKE, they were more active during the midday hours than when they were in areas with high PIKE. On the other hand, elephants were more active at dawn when they were in core areas with higher poaching levels, but their midday movement was less. We speculate that being more active at dawn is an apparent compensation for the minimal activity anticipated latter during the daytime hours. Less activity in the early afternoon minimises their exposure to risk. Profound behavioural change results in a reduced ability to forage when resources are limited (Ruggiero, 1990). The ratio of attack by a predator, rather than an absolute number of attacks influences the allocation of antipredator behaviour (Lima and Bednekoff, 1999). Relatedly, in this study, the ratio of illegally killed elephants out of all deaths influenced the cycle of activity of elephants. Humans acted as the predators of elephants. A loss of one hour of potential foraging time per day implies that despite the elephant's efforts to adjust their daily activity patterns, poaching leaves them with a deficit in their time budgets. Only cessation of poaching can make them resume regular time budget. This reduction of movement is in line with the recently confirmed decline of the global movement of mammals (Tucker *et al.*, 2018).

Understanding temporal scales of the responses of elephants, a megaherbivore species (Owen-Smith, 1988), to poaching risks provides insights on the least understood aspects of their behavioural ecology. On a large temporal scale, the migratory movement of the elephants has been attributed to the prolonged levels of poaching (Thouless, 1993). Understandably, the behavioural response to poaching risk at a fine scale is dependent on the availability of both movement data at commensurately short time scale as well as a detailed risk map of within-site variation in causes of mortality. Courtesy of fine-scale movement data and detailed within-site field verification of causes of mortality, this study confirms that elephants respond to present and past risk in near real-time basis by adjusting their activity peaks.

# Chapter 6

# Synthesis: Movement of elephants in relation to the spatial-temporal variation of levels of illegal killing in a human-dominated landscape

## 6.1 Introduction

The conservation and management of elephants in the human-dominated landscapes requires an understanding of the specific threats related to human activities and how elephants adapt to them. The way elephants adapt can be deduced from an analysis of their movement at different temporal scales. In human-dominated landscapes, where land parcels are managed independently of each other, maintaining space for elephants entails incorporation of wildlife conservation and ecotourism alongside the mainstream core economic activities of the landowners. Where land use is incompatible with wildlife conservation, e.g. agricultural zones, pro-active efforts to mitigate potentially fatal conflict with humans should be promoted. A comparative assessment of the conservation status and the response of elephants by way of measurable terms is paramount in identifying the best model of conservation. Elephants inhabit wide geographical space, and the vastness of their home ranges make it expensive to cover every part through the traditional, routine ground monitoring patrols. There is therefore a need to develop complementary practical technological tools to infer the risk status remotely.

Attention has invariably been drawn to the impact of over-exploitation on population sizes for many species (Clark, 1973, Fa *et al.*, 1995, Caro *et al.*, 1998, Hutchings, 2000). However, less effort has been given to the direct effect of the disturbances on the animals' behaviour and the existing studies have given more attention on movement in the corridors and dispersal areas (Douglas-Hamilton *et al.*, 2005, Graham *et al.*, 2009, Kioko and Seno, 2011). Understandably, few studies have achieved multiple year datasets of movement and individually verified records of the causes of elephant mortality which are paramount to modelling behaviour changes. The demand for land to settle people and/or to expand agriculture has led to fragmentation of the once continuous wildlife habitats leading to landscape fragmentation. The movement rates of land-dwelling mammals have been significantly affected by the loss of ecosystem connectivity (Tucker *et al.*, 2018). This thesis presents a new indicator of poaching levels derived from GPS tracking data, new insights on the elephant's behaviour change in relation to the prevailing and past levels of illegal killing at fine spatial and temporal scales.

## 6.2 Site level correlates of poaching: the role of land use and land ownership

Scientific studies and formal government reports on levels of poaching of elephants present summaries for entire sites each year leaving out details of the within-site spatial variations if any. The systematic monitoring in Africa is conducted in 57 designated sites referred to as Monitoring of Illegally Killed Elephants (MIKE) sites. Many of the MIKE sites are formally protected as national parks, national reserves or forest reserves (https://cites.org/eng/prog/mike/places Accessed 22/04/2018), implying homogeneity regarding management types encompassed. For the few sites that are heterogeneous with regards to land uses types or conservation statuses, there is a need to conduct within site analyses to understand the local drivers. However, this has not been possible because the custody and release of individual records for such detailed assessment of the causes of death are at the discretion of the governments of respective range states (Craig, 2004). Furthermore, these locational data are safeguarded from public access because elephants are endangered (www.iucnredlist.org Accessed 22/04/2018). Due to the homogeneity of management types within most of the MIKE sites, there has not been a continental-wide motivation to analyse the within-site variation in levels of poaching. In the Laikipia-Samburu MIKE site, the most intensively monitored site, only 3% of the confirmed elephant range is formally protected; Samburu, Shaba and Buffalo Springs National Reserves (Ihwagi *et al.*, 2015). The rest of the landscape is human dominated and comprises a mosaic of land ownership and uses types (Georgiadis, 2011) which served as natural laboratory ideal for detailed analyses of elephant behaviour.

The site level dynamics of illegal killing can be best understood through a monitoring program in which incidences are verified in the field, recorded and aggregated at the finest achievable, meaningful spatial-temporal resolution. Due to the heterogeneity of the landscape with regards to management types, it is expected that levels of illegal killing would vary greatly across the landscape, but the government alone is not able to quantify these. Intensive verification of the causes or elephant mortality is possible through an all-inclusive participatory network of land owners and managers (Kahindi *et al.*, 2010). However, in such a multiple stakeholder led exercise, the effort varies greatly and this was a challenge for comparison of levels of illegal killing until a basic metric referred to as the Proportion of Illegally Killed Elephants (PIKE) was described and adopted (Douglas-Hamilton *et al.*, 2010, Jachmann, 2013). When land units are considered as distinct units for the purpose of within-site analyses, the relatively fewer carcasses collected in each of them per unit of time necessities a considerable length of time for a reasonable trend to be established. This study capitalised on the long-term monitoring spanning over 12 years to model spatial and temporal variation of poaching rates within a MIKE monitoring site. High prevalence of live elephants, coupled with low local levels of poaching is assumed to imply successful conservation model in the respective land unit.

After an assessment of the various combinations of land ownership and use types in relation to the abundance of live and dead elephants, we found that land use type is the strongest covariate of elephant distribution and the levels of illegal killing (Ihwagi *et al.*, 2015). The nature of land ownership in the wild predicts its long term use (Arora *et al.*, 2015). Maintaining and improving the connectivity of elephant landscapes in non-formally protected habitats requires prioritized land use planning (Alkemade *et al.*, 2009, Nellemann *et al.*, 2013). A series of human development scenarios predict that infrastructural developments and human pressures will have major impacts on the habitats and ranges of African elephants by the year 2050 (Alkemade *et al.*, 2009). A major conservation initiative in the 21st century has been to establish a community-based conservation model, in which the communities either set aside some land for wildlife or manage land actively in a manner that takes into account the needs and welfare of wildlife (Hackel, 1999, Igoe and Brockington, 1999, Hulme and Murphree, 2001, Brockington, 2007). A gradual adoption of community conservation model since the year 2005 under the umbrella of Northern Rangelands Trust in the Laikipia-Samburu ecosystem is providing the much-needed space and protection for the elephants and other wildlife species that coexist with the communities (www.nrt-kenya.org Accessed on 24/04/2018). We noted that the oldest community conservancy, Sera, had a sustained decline in the levels of illegal killing, when the rest of the landscape was under the effect of the poaching surge from 2010 to 2012. In tandem with the increased protection of elephants, the numbers of live elephants that remained in Sera Conservancy were higher than other non-managed community lands. The alteration of elephant behaviour in Sera was the reverse of other land units implying that elephants perceived the safety around them. In this study, we found a linkage between the probability of illegal killing, i.e., poaching and conflict, and, the land use types.

## 6.3 Fine-scale movement in relation to levels of poaching

Most studies concerning the drivers of elephant movement have focussed on the influence of the spatial and temporal distribution of key natural resources, i.e., water and forage. The existing attempts at deciphering the role of risk in shaping elephant movement have focused on wide spatial scales, i.e., within and beyond migratory corridors (Douglas-Hamilton *et al.*, 2005, Pittiglio *et al.*, 2012). The studies concur that elephants walk fast when they are within corridors but make assumption that the movement returns to normal status simply because the speed normalises soon after arriving in a core area. This study illustrates that speed alone is useful but is insufficient at fine temporal scale. The linkage between poaching levels and fine-scale movement has not been achieved and is the basis of this thesis. In landscapes that are heterogeneous regarding the management practices, the levels of illegal killing are likely to correspond to the management type and in turn influence elephant movement commensurately. This study quantified the elephant movement at hourly, night-day (i.e., 12-hour intervals), and overall 24-hour cycles in their core areas. We define risk as the probability of death in an elephant's landscape comprises the historical experiences of poaching in different parts where elephants have repeatedly lost family members, as well as the real-time risk associated with direct encounters with human beings, e.g. crop raiding related conflicts.

### *6.3.1 Hourly movement: path tortuosity*

Elephants have the ability to emigrate long distances if and when the levels of the illegal killing rise in one part of their home range, but if all the landscape is affected they have nowhere to emigrate to, they have to survive *in situ*. For many decades, the walking speed of elephants has been used as a metric of behavioural adaptation to avoid risk. However, there is a limit on how fast they can walk or how long they can sustain a high-speed walk in the core areas where they have to live and forage. Movement is a marker of the animals' response to the probability of predation in a landscape (Laundré *et al.*, 2010). Despite the inherent limitations in their flexibility to flee fast, we anticipated that elephants would exhibit other anti-predatory behaviour adaptation besides absolute speed. Elephants have a long lasting memory of the locations of prolonged conflicts with humans as well as poaching incidences, and, the associated stress-related hormones remain in them for up to six years (Gobush *et al.*, 2008). In the high-risk locations, the elephants are faced with a conundrum of a need to forage constantly and remain alert to prevailing danger. The anti-predator behavioural adaptations of an animal are commensurate with the risk status of the places they inhabit. The change of path tortuosity happened as soon as they arrived in another core area (Fig. 6.1). That immediate change of behaviour indicates that the cause of that behavioural shift is a covariate with a sharp contrast between the specific land units, and which the elephants are able to perceive. An assessment of temporal variation of tortuosity for the elephants that were tracked during the years when poaching increased steadily revealed a similar trend, an inverse relationship between tortuosity and levels of illegal killing.

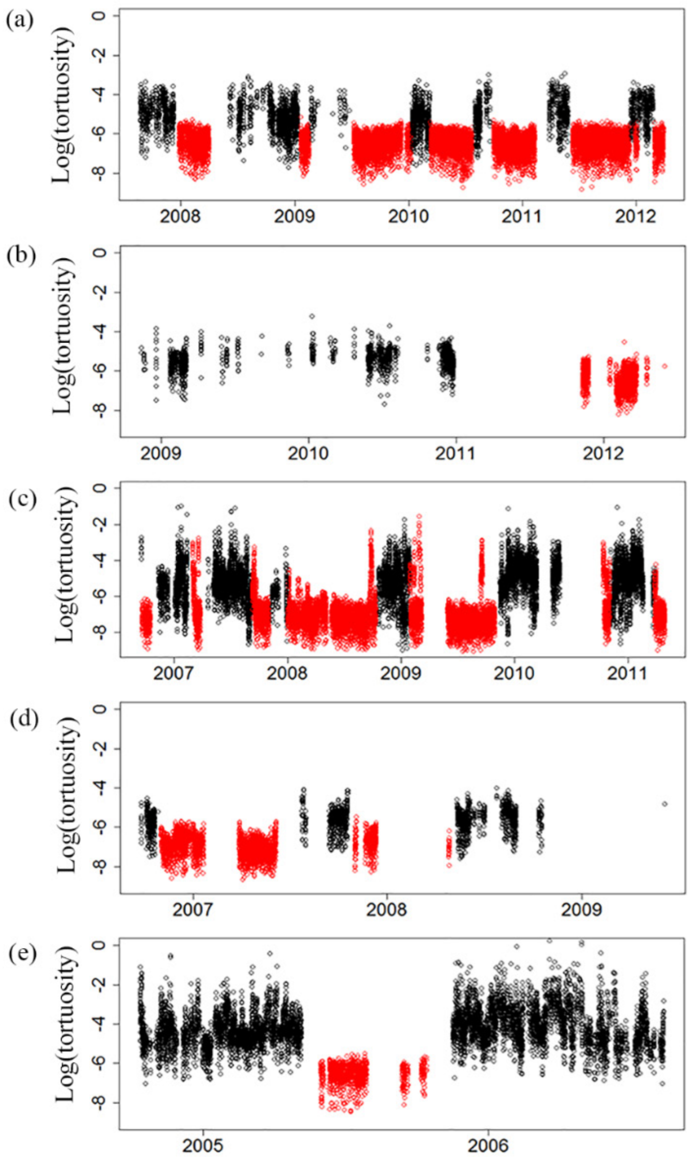

**Figure 6.1** The hourly tortuosity of five elephants tracked within the Laikipia-Samburu ecosystem at various dates between the year 2004 and 2012. The elephant identities are; (a) *Ol ari Nyiro* (Male), (b) *Ngelesha* (Male), (c) *Sera* (Female), (d) *Loldaiga* (Female), and (e) *Wangari* (Female). The black and red coloured points correspond to the time an elephant was in core areas with low and high poaching respectively. The gaps in data are from the times elephant were outside the core areas, i.e., in transit or in the dispersal areas.

Walking is a high energy intensive exercise for the elephants due to their large mass (Wall *et al.*, 2006), and the high speed is thus severely limited.

There is, however, no theoretical limit on turning angles from calculated on the locations on the hourly basis unless physical barriers exist on the landscape. The tortuosity values are ratios of last step length and overall displacement from last but one position. The ratios can remain unchanged even as the absolute speed changes as long as the track segments, and turning angles are of proportionately similar magnitudes. A change in tortuosity alongside a change in speed is likely in circumstances where the elephant charges at a source of a direct threat, such as a human being at close range or lions lurking near their calves, but such high speed is not sustainable for long enough to be picked up at hourly sampling frequency. Such incidences of high speed last short lengths of time below what a GPS would capture adequately at one-hour sampling interval. Lack of a sustained variation of speed is expected for the large animals whose large mass puts a limit on their mobility, unlike smaller animals that can adjust both speed and tortuosity more easily (Angilletta *et al.*, 2008). There is, therefore, no expectation of a clear relationship between tortuosity and speed for elephants due to the constraint in speed.

The concept of area-restricted search illustrates that a herbivore responds by slowing its movement and remaining longer in the vicinity of the most recently located food item (Fauchald and Tveraa, 2003). Intensive search requires an animal to make high turning rates, i.e., walk with higher path tortuosity (Knell and Codling, 2012). In this regard, when the elephants keep moving along straighter lines due to poaching risk within their core forging areas, their ability to search more is likely to be compromised. Individuals face a trade-off between thoroughness and searching efficiency (Doerr and Doerr, 2004). Moving by way of straighter paths, therefore, implies lower foraging efficiency for the elephants.

### *6.3.2 Day and night movement: speed ratio*

At the day and night temporal scales, the analyses of movement speeds has been accomplished in many studies in relation to the presence and activities of humans in shared landscapes, but no direct linkage to the levels of illegal killing has been established. Animals move at different spatial and temporal scales for different purposes (Wiens, 1989). In any given day, a lot of distinct movement-related activities, e.g., foraging, trips to drink water and pursuit of mates take place and each bout of such activity could easily last several hours, and thus not effectively captured by tortuosity measures above. The study explored movement rates at a coarser time-scale using the average speeds. When the risk includes real-time encounters with the threat, it is plausible that a temporal separation is inevitable as prey avoids predator (Laundre, 2010, van Velzen and Gaedke, 2017), and in this regard, we hypothesised that elephants would move less in time periods when risk is high. In this case of elephants in Laikipia-Samburu ecosystem, the threat is the presence of human beings and their activities like herding livestock or guarding crops, activities that vary by day and night (Evans and Adams, 2018). Attention has already been given to the speed of elephants along corridors, and existing literature shows that migration takes place primarily at night (Thouless, 1995, Berger, 2004, Douglas-Hamilton *et al.*, 2005). If elephants were to increase their nighttime movement within the core areas as well, it would be an indication that they are avoiding a form of risk during day-time hours. This study confirmed this is the case; elephants moved more at night than during the daytime hours when they were in the areas and times when levels of illegal killing were high, an apparent attempt at temporal separation from humans.

Past studies on the movement of elephants in relation to humans took place on the interface between farms and elephant habitats where human population density is high (Graham *et al.*, 2009, Graham *et al.*, 2010). This study extended to the remote areas in the northern part of the ecosystem with low human densities and no farms at all. That the elephants moved more during the night time than during daytime even when in far-flung areas with low human presence indicates that the change in behaviour is not only due to real-time encounters, but most likely a historical threat that they perceive. The modelling approach confirmed that the covariate that strongly influenced this alteration of behaviour was the level of illegal killing; PIKE. There were not enough records of the exact time of day that poaching happened noting that it's a criminal activity. Nevertheless, it is plausible that poaching incidences most likely happen during daytime hours as poachers are less likely risk operating at night using flashlights which would draw the attention to them. Hacking off both tusks from a carcass lying on its side is a precision task that is less likely to be accomplished in the dark. The exact time when poaching incidences happen is an aspect that warrants further investigation, especially with the continually improving design of collars that can detect and record gunshots in near real-time. Such precise data on timing of poaching can likewise be analysed in relation to local land use types and the other real-time human activities. The study commenced by confirming a link between land use, the distribution of live elephants and the levels of illegal killing. After analysing elephant movement behaviour, it was noted the that the night-speed ratio within the oldest community conservancy, Sera, decreased over time commensurate with a decrease in poaching levels, the opposite of the trend in the surrounding areas.

### *6.3.3 Daily movement pattern sampled hourly*

As elephants make efforts to avoid encounters with humans and minimise exposure to historical risk in the landscape, it is not clear how successful they are at achieving their usual activity time per day, which would have a bearing on foraging success. If the overall effect of adaptation to risk resulted in reduced foraging time, it would imply that their behaviour is not enough to sustain both their energy intake and to avoid risk at the same time, which is a net loss for them. African elephants have a daily activity cycle that comprises a resting phase during the mid-day hours which is largely attributed to hot temperatures at the time of the day (Wyatt and Eltringham, 1974). We studied alteration of this activity cycle for elephants in the same ecological zone (Pratt *et al.*, 1966), and as such no major spatial variation in temperature which allowed us to test the effect of risk at small spatial-temporal scales with better confidence. The similar patterns of change of behaviour by different elephants between their respective core areas in different parts of the ecosystem indicate that the elephants must be responding to a factor that has a sharp spatial gradient and no seasonality. The research in this thesis established that the elephants are striving to avoid risk, but this costs them valuable activity time that they don’t recover by the end of the day.

### 6.3.4 *The value of long-term monitoring in developing a suite of movement metrics*

The research in this thesis offered three metrics, i.e., tortuosity, the night-day speed ratio and alteration of daily activity cycle and each offered a different insight on elephant movement in response to the risk of illegal killing. An augmentation of the three measures offers an important first step in developing a suite of empirically measurable parameters that would guide ecologists in analysing GPS tracking data of elephants. While tortuosity and night-day speed ratio can be calculated on a daily basis, the alteration of daily activity cycle would be estimated at large spatial and temporal scales. For elephants that utilize different land units with varying levels of risk or conservation statuses, the alteration of daily activity cycle should be assessed concurrently for each land unit as elephants keep moving back and forth. For the elephants whose home ranges are restricted into a homogenous risk-landscape, the alteration of daily activity cycle should be quantified on temporal scales that are commensurate with the frequency at which the risk is recalculated, which is often annually.

Studying animal behaviour in natural habitats requires ample time in the order of seasons or years is necessary before a trend in behaviour can be reliably described. Most studies on animal movement have been conducted on small animals in the field or in manmade laboratory setups where risk is manipulated and the real-time responses recorded (Angilletta *et al.*, 2008, Dvorkin *et al.*, 2010, Dewhirst *et al.*, 2016). Such laboratory-controlled manipulation of behaviour is not possible for large mammals due to the large spatial-temporal scales in which they respond to the environmental heterogeneity. Long-term field-based monitoring offers means for understanding the effects of long-term exposure to risk in particular locations, at scales that are commensurate with the scales of the threats.

## 6.4 Implications of behavioural change on the ecology of elephants, and future work

Land use type emerged as a major covariate of levels of illegal killing and in turn the levels of illegal killing influence behaviour of elephants. The effects of biodiversity loss and or change of behaviour are cumulative and escalate through time (Reich *et al.*, 2012). The alteration of movement behaviour throughout the ecological time scale, i.e., the lifetime of an individual is likely to manifest in their offspring. When elephants continually strive to adapt to risk within the ecological time scale, their offspring are bound to adopt a behaviour pattern learned from their accompanying adults. Contemporary evolution of behaviour in the past few years has been observed in all biomes and these suggest that animals adaptations are dynamic (Carroll *et al.*, 2007). The change of habitats caused by human activities provides an opportunity for studying the behavioural ecology of affected species (Savill *et al.*, 2010). Taking advantage of tragic situations, like the poaching crisis in the case of this thesis research, offers an understanding of behavioural adaptations in crises and contribute knowledge that is a basis for the development of tools aimed at predicting future scenarios (Schroeder *et al.*, 2007, Caro and Sherman, 2011).

Describing the evolution of behaviour starts with paying attention to the variation among individuals in a population (Gordon, 2011). Should the surges of high poaching recur and remain for extended periods, a shift in behaviour amongst the elephants is most likely to be learnt by generations of elephants that have restricted home ranges where they remain under threat all the time. The loss of habitat connectivity is a threat to the free movement of such migratory elephants, implying that over time, the elephants would have to live in less than optimal space. Though elephants have few natural enemies and they can easily see and ward off predators from their calves by day, the direct effect of a shift to nocturnal activity is predisposing the calves to the often-nocturnal carnivores. In an arid environment, i.e., with scarce of surface water and forage, the elephants would need to forage much longer for daily sustenance. For elephants to be deprived of foraging time in such an environment is double jeopardy, and the risk is reduced body condition for extra longer times time of the year. A loss of one hour of active time for an animal in a resource deficient landscape may have consequences that are not well understood. Patch density influences the movement patterns and foraging efficiency of large herbivores (de Knegt *et al.*, 2007). When the risk of illegal killing alters the movement behaviour of elephants in the core areas, presumably the higher-density patches, the consequences on their foraging success are not fully known. Understanding how elephants maximise utilisation of forage patches in risky landscape warrants further studies with finer scale data, specifically at less than hourly sampling frequency.

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# Summary

The illegal killing of elephants, i.e. poaching and human-elephant related mortality, is the greatest immediate threats to elephants. They have led to declining of many populations of elephants in Africa. The Monitoring of Illegal Killing of Elephants (MIKE) program of the Convention on International Trade in Endangered Species (CITES) was set up in the year 2002 as a framework of monitoring trends in illegal killing in 57 African sites. MIKE program seeks to establish the relationships between the levels of illegal killing of elephants and various possible explanatory variables within and beyond the monitoring sites. The effort in implementing MIKE program vary from site to site, and to make the results comparable; a metric referred to as the Proportion of Illegally Killed Elephants (PIKE) out of all recorded deaths in a site has been adopted as the standard measure of severity of illegal killing.

Loss of habitat due to the expansion of agriculture and infrastructural developments are the largest long-term threats to elephants. The migratory corridors of elephants and other wildlife in many landscapes have been cut off. The majority of wildlife resides outside formally protected areas on private and community lands. In the landscapes shared by wildlife and humans, competition for resources influences the spatial-temporal distributions of wildlife. Efforts to win the goodwill of private and community landowners regarding hosting of wildlife on their lands are ongoing in many sites across the elephant range. Despite the numerous studies on the nature of risk faced by elephants, fewer studies have focused on the behavioural adaptations of elephants living in those risky landscapes.

This thesis sought to understand the site level drivers of illegal killing and how elephants adapt to the threat in Africa's most intensively monitored site, the Laikipia-Samburu MIKE in northern Kenya. Using field verified records of causes of elephant mortality, the distribution of live elephants, and, the cadastral attributes of land parcels in the ecosystem, the thesis established that land use type is the most important correlate of levels of illegal killing and not its ownership. The study analyses the movement of elephants at hourly, day and night, and overall 24 hr activity cycle in relation to the spatial and temporal variation of the levels of illegal killing. Past studies have given a lot of attention to movement behaviour along corridors. The research in this thesis focusses on movement within core areas. At the hourly time interval, the research showed that elephants walk with lower tortuosity when they are in core areas with higher levels of illegal killing, i.e., higher risk. The study found that elephants move more at night when they are in core areas with higher risk, than when they are in safer core areas. Based on this finding, the research presents a new metric for inferring the levels of risk, i.e., night-day sped ratio. When elephants move from a core area to another one with a different level of risk, they alter their daily activity pattern to include a longer resting phase during the mid-day hours, and this is even more pronounced in core areas closest to permanent human settlements. The study found that as a result of the alteration of activity cycle within 24-hour periods, elephants loose approximately one hour of activity time.

The results have the potential use as a remote means of assessing the spatial and temporal variation of risk by analysing elephant movement behaviour remotely thus complimenting patrol based anti-poaching efforts. The study provides new insight into the ecology of elephants living in fear. The confirmed increase of night-time movement potentially predisposes calves to the savannah predators, who are more active at night.

# Samenvatting

Het illegaal doden van olifanten, zoals door stroperij of in conflicten tussen mensen en olifanten, is een van de grootste bedreiging in het voortbestaan van olifanten. Dit heeft geleid tot een achteruitgang van veel olifant populaties in Afrika. Het Monitoren van het Illegaal Doden van Olifanten programma (MIKE: Monitoring of Illegal Killing of Elephants) is een door CITES programma opgezet in 2002 als framework voor het monitoren van patronen in illegaal doden van olifanten. MIKE probeert de link te leggen tussen de mate van illegaal doden van olifanten en diverse potentiele verklarende factoren binnen en rondom 57 locaties in Afrika. De hoeveelheid energie die gestoken wordt in de implementatie van MIKE varieert van locatie tot locatie. De ratio tussen illegaal gedode olifanten en de totale olifant sterfte is universeel aangenomen als een standaardmaat voor het niveau van illegale olifant dodingen (PIKE: Proportion of Illegally Killed Elephants).

Het verlies van habitat ten gevolge van een toename van landbouw en infrastructuur wordt gezien als een van de belangrijkste lange termijn bedreigingen voor olifanten. De migratie routes van olifanten en andere dieren worden hierdoor in veel gebieden afgesneden. Het merendeel van het wild in Afrikaanse leeft buiten officiële beschermde gebieden; op gemeenschappelijk land en privé gebieden. Dit leidt tot een concurrentie voor voedsel en water. Deze concurrentie bepaalt de variatie in ruimte en tijd van dichtheden van het wild in het landschap. In veel van de gebieden waar mensen en olifanten samenleven zijn er projecten die zich richten op de verdraagzaamheid van de lokale eigenaren en beheerders van het landschap ten aanzien van olifanten. Ondanks het bestaan van vele studies die kijken naar de risico's waaraan olifanten in het wild bloot staan, zijn er nauwelijks studies te vinden die gekeken hebben naar aanpassingen in het gedrag van olifanten in voor hun gevaarlijke landschappen.

Dit proefschrift tracht te begrijpen wat de factoren zijn die een verklaring geven voor de mate waarin, op een specifieke locatie, illegaal doden van olifanten plaats vindt. De studie is uitgevoerd voor de meest intensief bestudeerde site, het Laikipia-Samburu ecosysteem in Noord Kenia. Op basis van geverifieerde informatie van gedode olifanten, de verspreiding van levende olifanten en de kadastrale gegevens van percelen in de regio concludeert dit proefschrift dat landgebruik de belangrijkste verklarende factor is voor de mate waarin olifanten gedood worden. Eigenaarschap van het perceel is hieraan ondergeschikt. Deze studie analyseert de verplaatsingen van olifanten per uur, overdag en 's nachts en kijkt naar de algehele activiteit op een 24 uurs basis in relatie tot de temporele en ruimtelijke verdeling van historische olifant sterfte. Eerdere studies hebben voornamelijk gekeken naar het gedrag van olifanten in migratieroutes tussen de kerngebieden. In deze studie hebben we specifiek gekeken naar het gedrag binnen de kerngebieden. Op een niveau van uur tot uur bekeken blijken olifanten in risicovolle gebieden doelgerichter rond te lopen (Ze wisselen minder vaak van looprichting). Tevens blijkt dat olifanten 's nachts actiever te zijn in kerngebieden met verhoogd PIKE dan in veiligere kerngebieden. Gebaseerd op deze laatste uitkomsten presenteert dit proefschrift een statistiek om het sterfterisico van olifanten af te leiden: De ratio tussen dag en nacht loopsnelheid. Als olifanten van het ene kerngebied naar een kerngebied met een ander PIKE niveau verplaatsen veranderen ze hun dag activiteit en nemen ze langere rust pauzes in de middag. Als gevolg van deze veranderingen in activiteit verliezen olifanten tot een uur actieve tijd per dag.

In conclusie, dit proefschrift toont aan dat olifant verplaatsingsinformatie gebruikt kan worden om de variatie in ruimte en tijd van gevaar voor olifanten uit af te leiden. Toepassing van een dergelijke remote sensing methode kan gebruikt worden om anti-stroperij activiteiten te ondersteunen. De studie toon een nieuw inzicht in de ecologie van olifanten in gevaarlijke gebieden. De gevonden toenamen in nacht-activiteit leidt tot een groter predatie-risico voor de jongen, aangezien savanne predatoren voornamelijk 's nachts jagen. Daarnaast kan de verschuiving in activiteitpatronen een negatieve invloed hebben op het browse gedrag van de olifanten.

# Biography

Festus Wanderi Ihwagi was born on 21st May 1977 in Nyeri, Kenya. He attended Chieni Primary School, and later, Hiriga Secondary School. In 2001, he obtained Bachelor of Science degree in Botany and Zoology from the University of Nairobi, Kenya. In 2002, he interned at the Ornithology Department of the National Museums of Kenya and was attached to The Peregrine Fund project seeking to unravel the cause of a crash of Asian vultures. In 2003, he pursued a postgraduate certificate course on Biodiversity Conservation in Desert Ecosystems at Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, Israel. From January 2004 to Mid-2005, he worked as a researcher at *Mpala* Research Centre in Laikipia, Kenya, tasked to unravel the cause of the population decline of lelwel hartebeest (*Alcelaphus buselahus*).

In June 2005, he commenced his full-time employment at Save the Elephants, as a research scientist and head of GIS unit. In 2006, he trained on Advanced Analysis in ArcGIS at the Environmental Research Institute (ESRI) Campus, Redlands, USA. In 2008 and 2009, he managed on a multiple species collaborative tracking project funded by the JRS Biodiversity Foundation behalf of Save the Elephants. Under the auspices of Save the Elephants, he obtained a Master of Science degree in Biology of Conservation from the University of Nairobi, Kenya in 2008. Between 2013 and 2016, under the auspices of Save the Elephants, Stop Ivory, he contributed in developing the protocol for inventorying national elephant ivory and rhino horn stock piles. Thereafter, he oversaw the auditing of stock piles for various African countries as stipulated by the Convention on International Trade in Endangered Species (CITES).

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# D I P L O M A

## *For specialised PhD training*

The Netherlands Research School for the
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## *Festus Wanderi Ihwagi*

born on 21 May 1977 in Nyeri, Kenya

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| On behalf of the SENSE board | the SENSE Director of Education |
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The SENSE Research School declares that **Festus Wanderi Ihwagi** has successfully fulfilled all requirements of the Educational PhD Programme of SENSE with a work load of 39.9 EC, including the following activities:

## SENSE PhD Courses

- Research in context activity: ‘Organising and serving as Chief Technical Person for two national elephant censuses in Tsavo (2014) and in Samburu (2017) ‘
- Environmental research in context (2018)

## Other PhD and Advanced MSc Courses

- Species distribution modelling, ITC, University of Twente (2014)
- Geostatistics, ITC, University of Twente (2015)
- Advanced geostatistics, ITC, University of Twente (2015)
- Animal movement analyses, University of Amsterdam (2017)

## Communication

- Winner of the University of Twente Media Award 2017

## Management and Didactic Skills Training

- Supervising two MSc students at the Faculty of Geoinformation and Earth Observation, University of Twente, with thesis entitled ‘Effects of drought on the relationships between herbivores and vegetation types in the Laikipia - Samburu ecosystem’ (2016) and ‘The impact of drought on the association between surface water and herbivore distribution in the Laikipia - Samburu ecosystem’ (2016)
- The chief technical lead of two aerial total counts of elephants, Kenya Wildlife Services (2014 and 2017)
- Teaching PhDs on Basics of GPS tracking, Oxford University (2015)
- Chief trainer and technical lead of the National Elephant Ivory and Rhino Horn inventory, Ministry of Environment and Forestry, Kenya (2015)

## Oral Presentations

- *Elephant distribution in a complex landscape*. The First National Elephant Conference, 6 February 2015, Nairobi, Kenya
- *Elephants in a risky landscape.* Student Conference on Conservation Science, 20-30 March 2018, Cambridge, United Kingdom

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