The influence of hunting activity on African elephant (*Loxodonta africana*) movements

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Declaration

I declare that this thesis is my own, unaided work. It is being submitted for the completion of the Degree of Masters on Science (Environmental Sciences) in the University of the Witwatersrand, Johannesburg. It is original work, and has not been submitted for any degree or examination in any other University or Institution.

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Abstract

African elephants (*Loxodonta africana*) are still being poached and hunted and this could potentially affect their movement. As a keystone species, crucial to maintaining ecosystem function and therefore food webs, it is important to understand the effects hunting may have on their movements. This study was undertaken in the Associated Private Nature Reserves adjacent to the Kruger National Park, where elephants are hunted. I looked at changes in daily displacement distance and distance from hunting and natural mortality events to determine if elephants were affected by hunting events, up to what distance, and to determine whether elephants reacted in the same way to hunting and natural mortality events. I found that elephants are only affected by hunting events when within 1 km of the event, which is consistent with the literature. When considering natural mortality events, they actually diverted movements towards the event location, which is also consistent with literature. These results, however, are based on a very small sample size. In addition, the time of day of the events was not recorded by the wardens of the reserve, and this provided a further limitation for the data analysis and interpretation.

Keywords:

Associated Private Nature Reserves; Kruger National Park; *Loxodonta africana*; movement behaviour; natural mortality; trophy hunting

Chapter 1

Research aim

The aim of this study is to analyse the impacts of hunting as a possible anthropogenic driver of the movements of African elephants in the Associates Private Nature Reserves adjacent to the Kruger National Park, and to contrast these movements with those associated with natural mortality events.

The motivation and need for the study

During the 1970s and 1980s African elephants (*Loxodonta africana*) were hunted almost to extinction for their ivory, which lead to increased conservation efforts to prevent further decline of elephant populations (Kangwana 1996). In order to properly conserve and manage elephant populations it is important to understand their behaviour (e.g. movement) and space use in relation to hunting (Kangwana 1996). Movement and space use of an animal can be affected and altered by the presence of hunters (Kilpatric and Lima 1999; Hodges *et al.* 2000; Stankowich 2008). There has been some research done on the effect of hunting on space use of ungulates (Kilpatric and Lima 1999; Stankowich 2008) as well as other animals such as raccoons (Hodges *et al.* 2000). Burke (2005) looked at elephant movement and stress due to hunting in the Pilansberg National Park and found that elephants fled from hunting events when in close proximity to the events yet showed no reaction when further away. Burke (2005) also found that within two days the stress levels and the movement of the elephants had returned to normal (pre hunting event conditions). However, ungulates in different areas react differently to increased hunting pressure (Stankowich 2008) and there have been no previous studies that have looked at the effect of hunting on elephant movements in the Associated Private Nature Reserves (APNR) which are connected to the Kruger National Park (KNP).

The study of animal movement provides knowledge as to how animals respond to the environment and how they are influencing it (Poole 1996; Whyte 1996; Nathan 2008; Nathan *et al.* 2008). Elephants in particular, influence the environment in which they are found by altering or maintaining vegetation with cascading effects on animal community structures and by acting as agents of seed dispersal (Poole 1996). Therefore elephants are considered as “keystone” species, crucial to maintaining food webs and ecosystem function, in the environments in which they are found (Poole 1996; Cumming *et al.* 1997; Skarpe *et al.* 2004; Rutina *et al.* 2005; Makhabu *et al.* 2006; Pringle 2008; Duffy *et al.* 2011; Valeix *et al.* 2011). However, at high densities, as is seen in game reserves (Harris *et al.* 2008), elephants might have negative effects on the ecosystem and this can lead to decreased biodiversity (Duffy *et al*. 2011).

Elephant movements can be influenced by environmental conditions, such as vegetation availability and anthropogenic activity (poaching and increased human population growth) among others (Poole 1996, Duffy *et al.* 2011). Anthropogenic activity such as recreational game viewing or increased encounters with humans due to increased human populations can cause habituation and escalate conflict, respectively, both of which increase elephant vulnerability to hunting (Boyle and Samson 1985, Poole 1996). The presence of hunters can cause behavioural changes as seen in studies on North American ungulates such as on white-tailed deer (*Odocoileus virginianus*) in the Groton Long Point and Mumford Cove area, Groton, Connecticut, (Kilpatrick and Lima 1999) and on elk (*Cervus elaphus nelson*) in the White River area in north-western Colorado (Conner *et al.* 2001). These two studies showed that hunting activity caused these ungulates to expand their ranges past the hunted area and move to areas with better cover or to areas where hunting did not occur, respectively. In light of what is known about the environmental impacts of elephants it is important to understand how hunting affects the space use by elephants as the decision on where to go might have important cascading effects on other aspects of the ecosystem.

The Associated Private Nature Reserves (APNR), adjacent to the KNP, allow year round trophy hunting provided the hunters have approved permits and follow all the regulations set by the permit (Department of Environmental Affairs 2013). The National Norms and Standards for the Management of Elephants in South Africa also set rules regarding the hunting of elephants. These rules are that (1) no elephants may be hunted within 24 months of being introduced into a new area, (2) only solitary males and damage causing females may be hunted, (3) when in proximity of females no elephant may be hunted, (4) a registered professional hunter must supervise each hunt and be present for the full duration of said hunt, (5) compliance with the Threatened or Protected Species Regulations is required for any hunt to take place (Department of Environmental Affairs and Tourism 2008).

My study will focus on the affects of hunting on elephant movement. While research has been done on the effect of hunting on animal's movement it has focused mostly on North American ungulates and most analyses on the effects of hunting in Africa has focused on the loss of biodiversity and species numbers and not on the movements (Muchaal and Ngandjui 1999; Laurance *et al.* 2005; Selier *et al.* 2014). The North American ungulate studies focus on species that are exposed to seasonal hunting, which only occurs for a short period of time a year. In some cases these ungulates change their behaviour before the hunting season even begins (Root *et al.*1988); hence it may not provide an accurate description or prediction of how elephants might react to hunting that occurs year round. In addition, Stankowich (2008) has pointed out that not all animal populations or individuals respond in the same manner to hunting. Knowledge of how elephants respond to hunting is becoming increasingly important due to the greater population sizes of elephants within protected areas (Harris *et al*. 2008, Duffy *et al.* 2011). Free roaming elephants are also experiencing more encounters with the larger human population leading to increased conflict (Poole 1996). Another reason why it is important to understand the effects of hunting on elephants is because hunting has been seen to effect elephant stress levels (Burke 2005).

Research Objectives

Objective 1: To determine at what distances an elephant is affected by a hunting event by examining changes in daily displacement distance (DDD) and distance from a hunting event (DFHE) subsequent to the hunt.

In particular we knew of three elephants that were within 1 km of a hunted individual in 2013 and hence I separated the objective into the following sub-objectives:

1.1. To determine if the 2013 elephants, reported to be within 1 km of the event, were affected by it, by comparing their DDD and DFHE before the event, on the day of the event and after the event.

1.2. If an effect is found, to determine if similar patterns are always observed when elephants are within 1 km from a hunting event, by examining other instances of elephants within 1 km from an event from the historical data set prior to2013

1.3. If an effect is found within 1 km, to determine whether there is also an effect when the elephants are further than 1 km from an event.

Objective 2: To determine whether natural mortality events and hunting events have similar effects on elephant movements

Literature review

Study animal

Elephants are the largest extant terrestrial mammals, with males (bulls) weighing between 5500 – 6000 kg and females (cows) weighing between 2500 – 2800 kg (Shrader *et al.* 2012) but can weigh up to 3500 kg (Stuart and Stuart 2007). They also have a long lifespan and are believed to be highly intelligent (Poole 1996). African elephants (*Loxodonta africana*) used to roam freely across the entire African continent, however, they are now confined to fenced protected areas in Africa (Skinner and Chimimba 2005; Poole 1996). There are two known subspecies of African elephant, the savanna elephant (*Loxodonta africana africana*), which mainly occurs in sub-Saharan Africa, and the forest elephant (*Loxodonta africana cyclotis*), which occurs in Central and western equatorial/rain forests of Africa (Short 1983; White *et al.* 1993; Gessner *et al.* 2014), which is smaller than the savanna elephant. These two subspecies are known to form hybrids in areas where they encounter each other, where forests and savannas merge (Poole 1996).

Elephant social structure is a fluid one where males and females live separately (Poole 1996).Young males leave their family groups around when they are 10 - 16 years of age and they then either remain solitary or join other adult males (Owen-Smith 1992). Females, however, form family groups which can range in size from 2 to 30 and consist of closely related females i.e. grandmothers, mothers and daughters (Poole 1996; Stuart and Stuart 2007). Within the family groups an experienced female will appoint herself to lead. This female is known as a matriarch and the survival of the family depends on her knowledge of where quality resources are and the age of this female, as older matriarchs dominate younger matriarchs to ensure that their families have access to the best resources (Poole 1996; Stuart and Stuart 2007). Bulls go through a period of heightened aggression and sexual activity known as musth, and when this occurs for the first time it marks the change of males from juveniles to adults (Owen-Smith 1992; Poole 1996). During musth males seek out oestrus cows to mate with and this also leads to conflict between males and can even lead to death of bulls (Owen-Smith 1992; Poole 1996).

African elephants are mixed feeders and are thought to select areas based on forage availability and proximity to water sources (Shrader *et al*. 2012) for which they can travel long distances (Grainger *et al.* 2005). There is also evidence that bulls and cows have different nutritional needs, show different habitat use and hence have different forage behaviour (de Knegt *et al*. 2010). The size and location of the home ranges used by elephants can change depending on the time of year i.e. dry or wet season (Poole 1996; Shannon *et al.* 2006). During the wet season, when resources are abundant and water is not a limiting resource, elephants may travel long distances as their movements are not limited by resource abundance and water (Poole 1996, Duffy *et al.* 2011). However, during the dry season, when resources are scarce, elephants can travel long distances in search of water or remain close to rivers and perennial water sources (Poole 1996, Duffy *et al.* 2011). Chamaillé-Jammes *et al.* (2013) also found that elephants change their speed during the dry season when surface-water resources are constrained, which suggested that the elephants are trying to save time taken to get to water resources.

Movement behaviour

The study of animal movement has recently experienced an increased interest because it has become obvious that proper management of animals requires knowledge of their movements (Nathan 2008) as the knowledge of animal movements can give researchers an idea of how animals respond to their environment (Whyte 1996). Animal movement can be viewed as the change in an animal’s location over time, this means that animal movements occur and change at various spatial and temporal scales in response to observed or anticipated changes in environmental conditions (Fryxell *et al.* 2008; Nathan 2008; Nathan *et al.* 2008;

Van Moorter *et al.* 2015). Small scale movements often refer to daily movements such as moving from one feeding station to another (foraging movement) in response to food depletion at the current station or fleeing from a predator, whereas the large scale movement can either be ranging (dispersal) or migration movement (Dingle and Drake 2007; Nathan *et al.* 2008). These small and large scale movements determine the space use of an animal (Van Moorter *et al.* 2015), which in turn defines the home range of an animal (Moorcroft and Barnett 2008), as they can show the areas that the animals use frequently and the resources that the animals deem necessary for survival.

According to Nathan *et al.* (2008) the motivation of an animal to move from an area is governed by four components; the internal state of the animal, the navigational capacity (orientation ability) of the animal, the motion capacity of the animal (ability to move in different ways) and the external environment (Figure 1). The internal factors that influence animal movements include; body size, sex, reproductive state (e.g. musth or lactation) and age (de Knegt *et al.* 2010; Shrader *et al.* 2012). The external, environmental factors that affect animal movements are both biotic and abiotic in nature (Nathan *et al.* 2008) and include resource availability i.e. food, mates, shelter and water (Dingle and Drake 2007; de Knegt *et al.* 2010), predation (Nathan *et al.* 2008, Duffy *et al.* 2011) and anthropogenic features or activity (Harris *et al.* 2008; Mpanduji *et al.* 2008). The relationship between the above four factors provide insight as to how and why movement occurs (Wittemyer *et al.* 2008). For example; pregnant females (pregnancy = internal factor) will search for high quality forage and water (external factors); elephant bulls in musth (musth = internal factor) will travel, often long distances, in search of mates (mates = external factor).

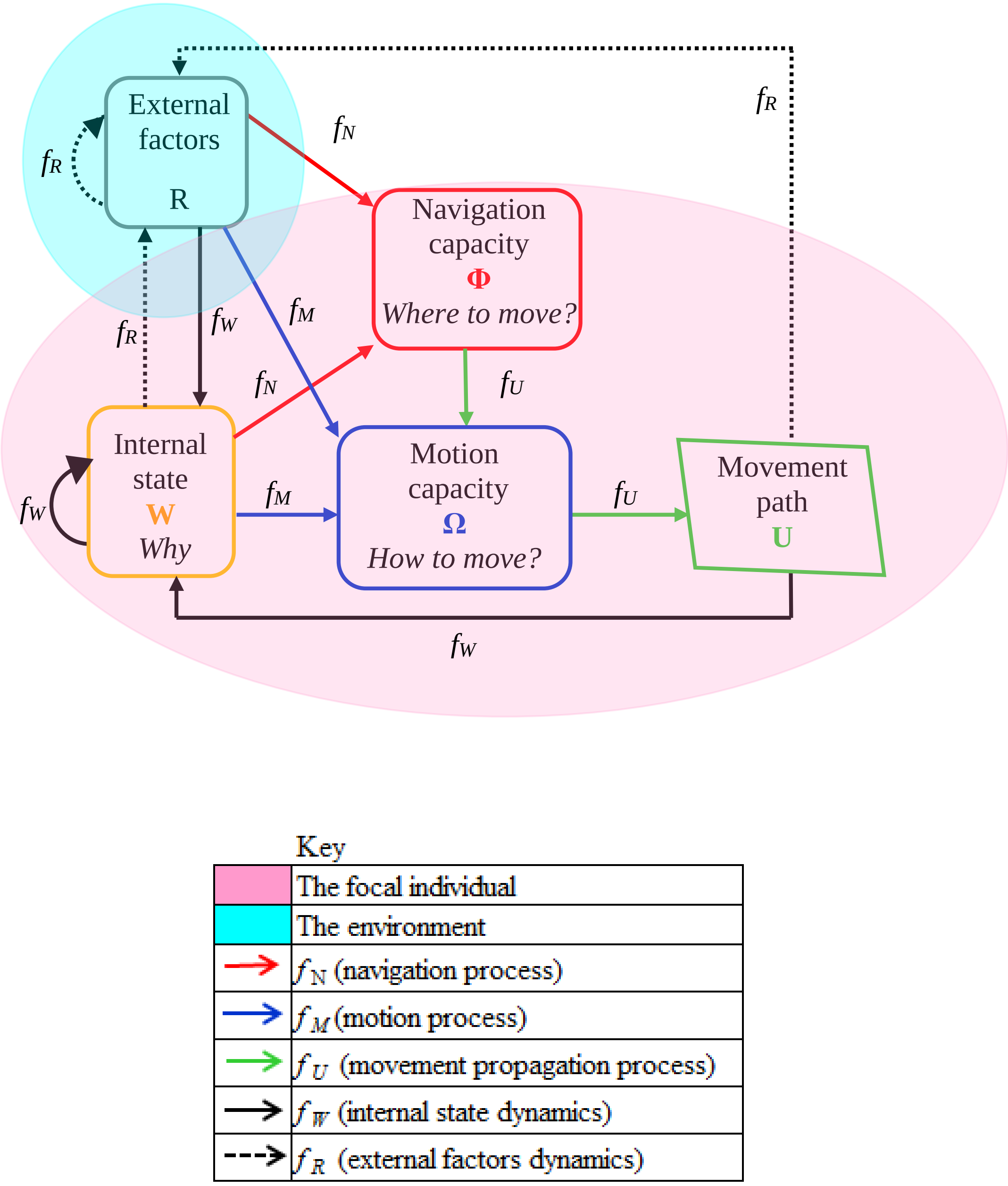


Figure 1: The framework of movement ecology, illustrating the basic components related to the focal individual, the external factors affecting movement and the processes that indicate the relationships between the components and the directional effect of the processes (arrows). (Adapted from Nathan *et al.* 2008).

The internal and external factors found to be most influential to elephant movement behaviour are; forage resources, which have different influences depending on the type, availability and distribution, body size, water (de Knegt *et al.* 2010), sex (Duffy *et al.* 2011), anthropogenic feature (such as fences, human settlements; Loarie *et al.*2009) and anthropogenic activity. The effects of these factors on elephant movement will be discussed below.

It is important to remember that resources vary both spatially and temporally (i.e. seasonally; Senft *et al.*1987; Loarie *et al.*2009). This is especially important when considering that selection of resources is a hierarchical, scale dependent process (Senft *et al.* 1987). This means that animals select resources from landscape scale to home range to vegetation types and finally to specific resource selection (de Knegt *et al.* 2010). For example: elephants establish home ranges within a heterogeneous landscape, they then select for specific vegetation types that have good quality forage and within this area they select for specific woody plant species (de Knegt *et al.* 2010; Shrader *et al.* 2012). However, it is also thought that herbivores make "bottom-up decisions" where they choose specific bites from specific vegetation types and all these small scale choices eventually influence landscape level use of space (Shipley 2007). Based on this, it can be assumed that forage quality is an important determinant of area selection and therefore of movement (Harris *et al.* 2008; Shrader *et al.* 2012) as the higher quality of the bite the more energy is gained (Shipley 2007). In theory all herbivores should select for good quality forage. For example: elephants prefer foraging sites with high quality forage (high greenness), close to water to optimise foraging and movement efficiency (de Knegt *et al*. 2010; Shrader *et al.*2012). However, larger herbivores require a larger intake and can be less selective in their choice of forage site and eat large quantities of lower quality forage than small herbivores, if need be, as they have longer retention time and increased gut capacity (Shannon *et al.* 2010; Shrader *et al.* 2012).

Water resources also play an important role due to the fact that elephants require water every two days, on average, and therefore their distance from the nearest water source is an important determinant of their movement behaviour (de Knegt *et al*. 2010). Water resources are also important when it comes to seasonal changes as African savannas experience a dry and wet season (Cordon *et al.* 2006). During the wet season when there is more water available in surface pool and rivers elephants can move greater distances as there is a greater chance of finding water (Harris *et al.* 2008; Loarie *et al.* 2009). However, during the dry season when water resources are more scarce elephants are found closer to permanent water sources and therefore travel shorter distances as these are the areas with better resources such as water, good quality forage and shade (Harris *et al.* 2008; Loarie *et al.* 2009).

Although African elephants do not show sexual dimorphism in vegetation selection (Shannon *et al.* 2010), they do exhibit it in social structure (Poole 1996); in browsing patterns (Stokke and du Toit 2002) and also in their preferred terrain (de Knegt *et al.* 2010) and in their movement (Duffy *et al*. 2011). Cows have been found to prefer gentle terrain (i.e. less mountainous areas) more than males (de Knegt *et al.* 2010). Duffy *et al.* (2011) found that speed of movement of females is slower than that of bulls, due to social and nutritional demands of a group, yet when the two sexes are together speed of movement of females' increases to move at the average speed of the bulls. This provides evidence that cows alter their behaviour in the presence of males (Duffy *et al*. 2011).

Anthropogenic features also play an important role in the movement behaviour of many ungulates, for example ungulates' movements in African savannas are constrained by fences, especially electrified fences and changing of natural behavioural patterns due to the introduction of artificial water points (Loarie *et al*. 2009). Artificial water holes also increase the negative effects of elephants on the environment because artificial water points can allow for utilization of area previously inaccessible (Loarie *et al*. 2009). Fences affect animal movement in three ways: by decreasing movement distances and lengths and home range sizes, and by facilitating increased encounters with the fences and "bunching up" at the fence

(Loarie *et al.* 2009). This is of particular consequence to elephants because electrified fences cause negative memories, which are retained by elephants as they have extensive, long-term spatial and temporal memories and the ability to learn (de Knegt *et al.*2010). As consequence they will avoid the area close to fences in future (Vanak *et al.* 2010), thereby increasing their negative environmental effects elsewhere.

If elephants have been shown to avoid areas close to fences after having negative experiences in these areas, how would hunting affect them? This is where my study comes in, focusing on one particular aspect of anthropogenic influences (hunting effects) on short term elephant movement response. To date no study has focused explicitly on short term elephant movements related to hunting in the APNR.

The influence of hunting on space use, movement and behaviour

Hunting has been around for centuries and there is evidence of it in many ancient cave paintings, such as the Lascaux Cave paintings in France, which are 15 000 years old and show hunting art (Anonymous 2008; Anonymous 2012).

The presence of hunters can cause a few behavioural changes in animals, including core ranges shift to other areas within the home range where hunting pressure is low (white-tailed deer, Kilpatric and Lima 1999); movement to more covered areas (refugia) inaccessible to hunters (white-tailed deer, Kilgo *et al.* 1998; willow ptarmigan, *Lagopus lagopus*, Broseth and Pedersen 2000; elk, Conner *et al.* 2001; roe deer, *Capreolus capreolus*, Padie *et al*. 2015); increased wariness (review on ungulate flight responses, Stankowich 2008), which increases energy expenditure which can decrease physical condition (impala, *Aepycerus melampus*, Setsaas *et al*. 2007). Behavioural and space use can change depending on the nature of the predation risk presented to an animal (Tolon *et al*. 2009), with responses to human-predation risk being stronger than responses to natural predation-risk, for example in elk (Proffitt *et al.*

2009; Ciuti *et al.* 2012). Hunting events can also cause lasting changes in movement patterns (mainly due to cultural transmission) even if those patterns have been consistent for many years (Grant *et al.* 2008). In the case of elephants, Poole (1996) found that poaching often changed migratory patterns, caused decrease of elephant ranges and aggregation of females against the perceived threat.

The influence of natural mortality events on movement and behaviour

In contrast to the flight response seen by elephants and ungulates in reaction to hunting events (Kilgo *et al.* 1998; Kilpatric and Lima 1999; Conner *et al.* 2001; Burke 2005; Setsaas *et al*. 2007; Stankowich 2008), elephants seem to linger or even return to areas where natural mortality events have taken place (Douglas-Hamilton *et al.* 2006). Showing interest in the body of dead conspecifics is rare and usually fleeting in mammals (McComb *et al*. 2006) yet some species such as chimpanzees *Pan troglodytes* (Goodall 1986) and dolphins *Tursiops aduncus* (Dudzinski *et al.*2003), have been reported to show an intense interest in dead conspecifics. In particular, elephants seem to show the most intense response and interest to sick or dead conspecifics among animals, to the point of suggesting this illustrates that elephants' show compassion much like humans (Douglas-Hamilton *et al.* 2006). This response by elephants comes in the form of attempting to assist sick or dying conspecifics by pushing them back to their feet (Payne 2003; Douglas-Hamilton *et al.* 2006) or remaining in the area after a conspecific has died and touching the body or remains with their feet or trunks (Douglas-Hamilton and Douglas-Hamilton 1975; Payne 2003). These observations lead McComb *et al.* (2006) to perform an experiment to test whether elephants are specifically reacting to the remains of conspecifics and not simply to novel stimuli in the environment. When elephants were presented with remains of dead conspecifics and other species, they were more interested in the skulls and ivory of the dead elephants than the remains of other organisms. This was irrespective of whether the elephant remains were from relatives or not.

The greatest interest was in the ivory of the deceased individual rather than the skeleton, possibly, due to elephants touching the tusks of other elephants with their trunks during social interactions when alive (McComb *et al.* 2006).

However, other behaviours have also been observed (Payne 2003), such as fear responses highlighted by trumpeting noises and flapping of ears; change of their movement behaviours by either hastening towards the dead or by departing hastily from it, due to fear response. Therefore natural mortalities can cause elephants to slow down, speed up or change direction to examine the remains of elephants that have died within their home ranges.

Predictions

Predictions regarding objective 1:

1.1. I expect elephants that were recorded as been seen in proximity to the hunted individual to show increased daily displacement distance (DDD) and distance from the hunting event (DFHE) after the hunt.

1.2. I therefore expect all elephants that according to the historical data set were within 1 km, to show an increased DDD and DFHE after a hunt.

1.3. However I expect elephants not to show an increase in DDD and DFHE when they were further than 1 km from a hunting event.

Predictions regarding objective 2:

2. I expect elephants to respond differently to natural mortalities than to hunting events, as I expect elephants to move towards areas where natural mortalities have occurred.

<u>Chapter 2</u>

Methods and Materials

Study area

The study area consists of four private reserves situated in the Limpopo Province of South Africa that share open borders with the Kruger National Park (KNP) on the east. These four reserves are Balule, Klaserie, Timbavati and Umbabat (Figure 2), which belong to the Associated Private Nature Reserves (APNR) where the trophy hunting occurs, at an average of 17 reported hunting events per year. The KNP is divided into two halves, which differ in climatic conditions, by the Olifants River, (Venter *et al.* 2003; Braak 2006; Cordon *et al.* 2006). The northern half is classified as “arid bushveld” as it only receives 300 – 500 mm of rainfall a year and the southern half is the “lowveld bushveld”, which gets 500 – 700 mm of rain a year (Venter *et al.* 2003; Cordon *et al.* 2006). The KNP is then further subdivided into a western half where granitic soils are found which support broad leaf species (mopane) and an eastern half where basaltic soils are found which support fine leafed species (*Acacia* species; Braak 2006; Cordon *et al*. 2006). The APNR is to the west of KNP below the Olifants River and have similar conditions to the south western portion of the KNP.

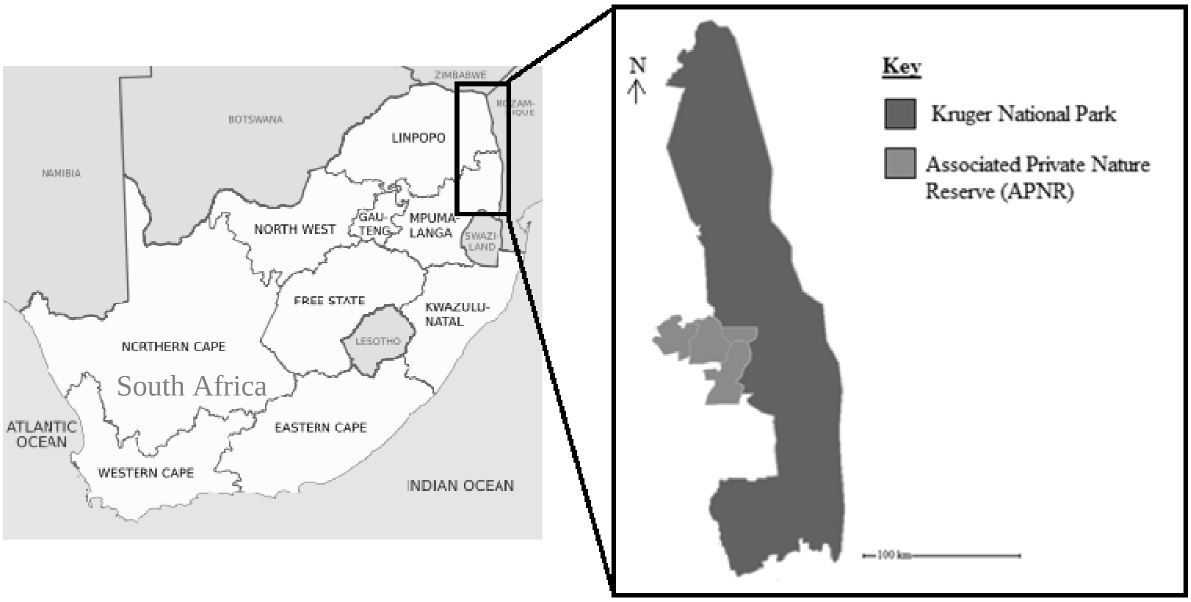


Figure 2: The study site of Kruger National Park (KNP) and the Associated Private Nature Reserves (APNR).

Data used for analysis

The elephant and hunting locations are stored in a database and were sent to me as data points in an Excel spreadsheet by the "Save the Elephants – South Africa" now called "Elephants Alive" (www.elephantsalive.org). I was given data for 5 collared elephants (prime bulls) which were reported to be seen, by the wardens, in close proximity to a hunted individual during two hunting events in 2013. Four of these bulls were present for both hunting events and one was present for only one event, giving a total of nine possible reactions to hunting events to consider in my analysis for the 2013 elephants (objective 1.1). Upon closer examination of the distance from the hunting event, based on the GPS coordinates of the event and GPS location of the elephant, only 3 events had a collared individual within 1 km of the hunted individual.

The remainder of the data (used for objective 1.2 and 1.3) consists of the GPS (Global Positioning System) locations, speed, distance and direction travelled by 19 collared elephants in the APNR, which were recorded hourly or four hourly over six years (1 January 2006 – 31

December 2011). Another data set includes GPS locations of mortality events and the type of mortality (i.e. anthropogenic and natural), collected by the wardens of the reserves. Whilst the data provided has the dates when the hunting events took place, it does not have the time of the day at which these events occurred. All elephants are known individually and named and these names will be used to refer to them in the results and discussion sections.

Nine prime bulls, five adult bulls, and five elephant cows, assumed to be families due to the fact that females travel in families (Poole 1996), had been collared with GPS collars and make up the 19 elephants used in the study as the historical data. I grouped them into the above mentioned age/sex categories according to Henley (2013). I also only used hunting and natural mortality events that had a collared animal within 10 km from the event. Elephants have been reported to hear up to 10 km in distance (Langbauer *et al.* 1991; Larom *et al.* 1997; McComb *et al.*2003; Payne *et al.* 2003). The data were used to test if there was a reaction from elephants within 1 km of a hunting event (objective 1.2), to compare the reactions of these elephants to those that were further than 1 km from a hunting event (objective 1.3) and to compare the effect of natural and hunting mortalities (objective 2). Only prime bulls had locations closer than 1 km to a hunting event, whereas at distances larger than 1 km I had data for prime bulls, adult bulls and adult cows. For the natural mortalities I only had data for prime bulls within 1 km of the event. As adult bulls and adult cows were never reported within 1 km of a natural mortality, they were left out of the natural mortality vs. hunting event analysis because no direct comparisons could be made.

Hunting events for which the exact location was not known, where the cause of death was unknown or it was euthanasia, were not used in the analysis. I also did not include events where the photographs taken before death and the photographs taken after death (post-mortem) did not show the same elephants or the day of the event was just estimated based on photographic time stamps. I also removed natural mortality events where the deaths were caused by the railway line.

Data analysis

GPS locations for the elephants and the hunting and natural mortality events were converted in to Universal transverse Mercator coordinate system (utm) (Dutch 2003). For each elephant within 10 km from a hunting or natural mortality event I calculated the average daily displacement distance (DDD) during the six day period before the day of the hunt (to get a baseline 'pre-event' average daily distance), for the day of the hunt and for a two day period following it. Only two days were chosen for the after hunt period as bull elephants movements are believed to stabilise the day after a hunting event (Burke 2005) and hence if any effect is to be found, it should be found on the day of the event or the following day. For the elephants closer than 1 km I extended the after period to four days to see if the elephants returned to the area of the hunt, which has it appeared they did not (Figure 4).

I calculated the distance from the hunting event (DFHE) or the distance from natural event (DFNE) using the theorem of Pythagoras. The equation is as follows:

Distance (km) = $\sqrt{[(Lat1 - Lat2)^2 + (Long1 - Long2)^2]}/1000$

Where Lat1= northing of the elephant location

Lat2 = northing of hunting location

Long1 = easting of the elephant location

Long2 = easting of the hunting location

For each event that had an elephant within 10 km, I calculated the distance for morning and evening of the day before, morning and evening of the day of the event and morning and evening of the day after the event. The locations closest to 06:00 were used as the morning locations and the locations closest to 18:00 as the evening location.

For objective 1.1 and 1.2, comparing DDD and DFHE of elephants known to be close to a hunting event, because of the limited sample size, I simply plotted changes in the DDD and DFHE over time. For the 2013 elephants I had the hourly locations for two elephants which were in close proximity to the same hunting event while one had four hourly locations (objective 1.1), like the elephants in the historical dataset (objective 1.2). I calculated the hourly displacement rate (HDR) for the elephants that had hourly location. The HDR calculation was performed as follows; I subtracted the DFHE for consecutive points from each other then I used this as a distance travelled in 1 hour which gave the HDR in $km.h^{-1}$. I then calculated the average HDR for 24 hours before the spike in DFHE occurred and the average HDR for a 24 hour period after the DFHE began to decrease after the maximum DFHE.

For objective 1.3, comparing the response of elephants within 1 km to elephants further than 1 km, I compared changes in DDD before, during and after the event for these two sets of elephants. I first considered elephant locations within 1 and 5 km from an event, and if no response was found within this distance, then I did not expect the category of further than 1 km to the whole 10 km buffer. All results are reported as mean followed by standard error (±).

Because of the limited sample size at distances < 1 km (only 2 elephants), I compared the difference between mean DDD for the 6 days before the event and DDD on the day of the event and difference between DDD on the day of the event and mean DDD for the two days following the event graphically for elephants < 1 km and elephants > 1 km, and used Kruskal-Wallis non-parametric statistical test to compare among different age/sex categories further than 1 km. The same was done for the DFHE.

For objective 2, comparing hunting to natural mortality events, I graphically compared the DDD and DFHE of elephants known to be within 1 km from a hunting event to the DDD and DFHE of elephants within 1 km from a natural mortality event, due to the limited sample size that prevented any statistical comparison.

Results

A total of 22 elephants were used in the analysis. These belonged to 3 different sex/age categories. Three elephants were prime bulls that had been reported to be within 1 km of a hunting event in 2013, two twice and one once. According to the data provided two of these elephants were in proximity of the same event. The remainder, 19 elephants, were associated with the historical mortality events, some more than once. From the historical dataset there were a total of 53 mortality events, 43 of which were hunting and 10 natural mortality events. Prime bulls were within 1 km of a hunting event only twice. They were further than 1 km but within 5 km for a hunting event and a natural mortality event, in 20 and 3 instances respectively. Adult bulls were never closer than 1 km from any mortality event, but they were between 1 and 5 km from an event 12 times for hunting events and 3 times for natural events. Adult cows were never within 1 km of a hunting or natural mortality event; they were between 1 and 5 km 9 times for hunting events, and 4 times for natural mortality events.

1.1 DDD and DFHE for 2013 elephants in close proximity to a hunting event

Two of the three elephants within 1 km of the hunted individual appear to show a reaction to the hunting event as there is an increase in the DFHE of these elephants on the day of the hunt (Figure 3). Gower and Proud showed the largest increase in DFHE in the 12 hours from the morning to the evening of the event (Gower, 8.87 km; Proud, 7.07 km). Intwandamela however, only showed an increase of 1.12 km in 12 hours (Figure 3).

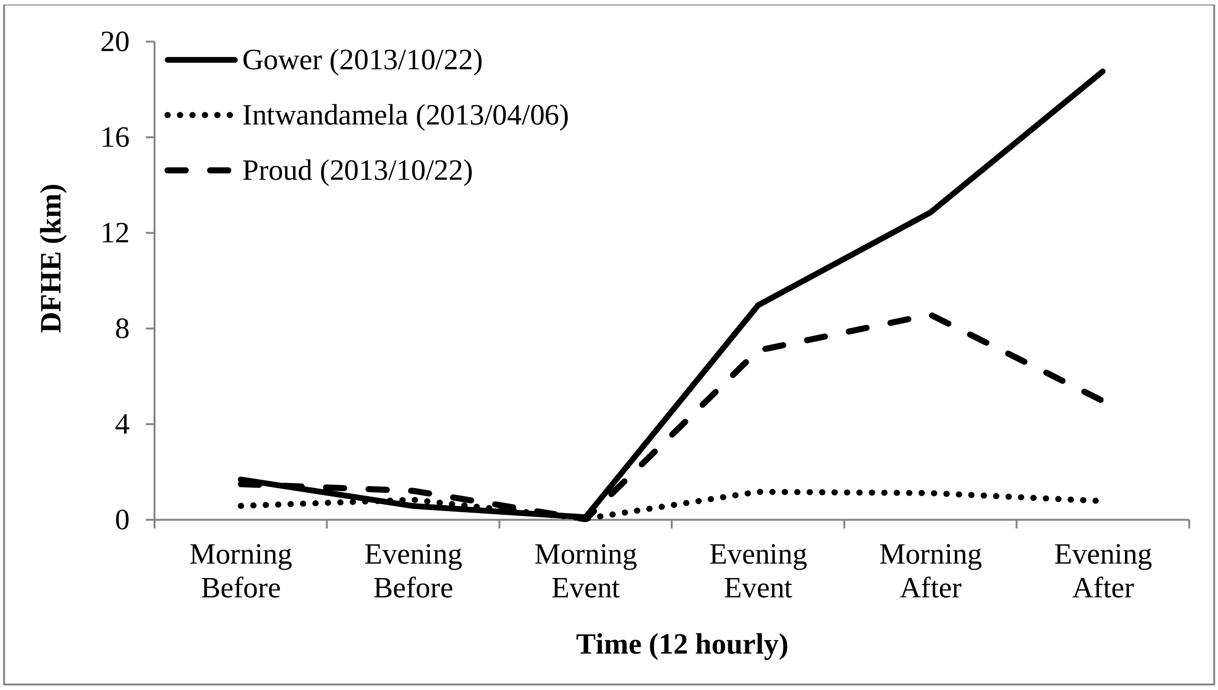


Figure 3: Distance from the hunting event (DFHE) for the 2013 prime bulls' at 12 hour intervals for the day before the event, the day of the event and the day after the event. Gower, event 2013/10/22; Proud, event 2013/10/22; and Intwandamela, event 2013/04/06.

Since I had hourly locations for these animals, a closer examination of hourly changes in DFHE for Gower and Proud (who were in the vicinity of the same hunting event) show that the increase of DFHE did not occur gradually but there was a sudden increase in the DFHE within one hour, from 0.11 km to 4.71 km for Gower and from 0.66 km to 3.38 km for Proud (Figure 4). What is interesting is that this increase occurred at different times, Gower at 06:43 (Figure 4a); Proud at 14:33 (Figure 4b). I extended the after period to four days to see if the elephants returned to the area of the hunt, which it appeared they did not (Figure 4).

As a consequence of these observed sudden increases the average HDR for Gower before 06:43 (0.14 $km.h^{-1}$) was 4.46 $km.h^{-1}$ slower than the first hour after the sudden increase (4.61 $km.h^{-1}$). From that time, the HDR stayed higher than the pre-event HDR until the elephant was 7.08 km from the event location; thereafter the average HDR decreased again (0.36 $km.h^{-1}$). The average HDR for Proud before the sudden increase in DFHE at 14:33 (0.16 $km.h^{-1}$) was 2.55 $km.h^{-1}$ slower than the HDR travelled in the first hour after the sudden increase (2.71 $km.h^{-1}$). Similarly to Gower the HDR stayed higher than the pre-event HDR until Proud was 7.09 km away from the hunting location, and after this the average HDR decreased (0.28 $km.h^{-1}$).

When considering the DDD for the above 3 elephants I expected them to have highest DDD on the day of the event and that the DDD after the event would be greater than that of the period before. I expected this as the period before was assumed to be hunt and stress free, whereas the elephants would still be affected by the hunting event after it had occurred. However, only Gower showed the expected results as he was the only elephant that had the longest DDD on the day of the event (14.83 km) and the lowest for the period before (6.54 km; Figure5). Proud also showed the largest DDD on the day of the event (11.62 km), as expected, but had the lowest DDD for the period after the hunting event (5.06 km; Figure5). Intwandamela, on the other hand, in agreement with the previous results, did not show much difference in the DDD (2.5 km on the day of the event vs. 3.47 km the period before; Figure 5).

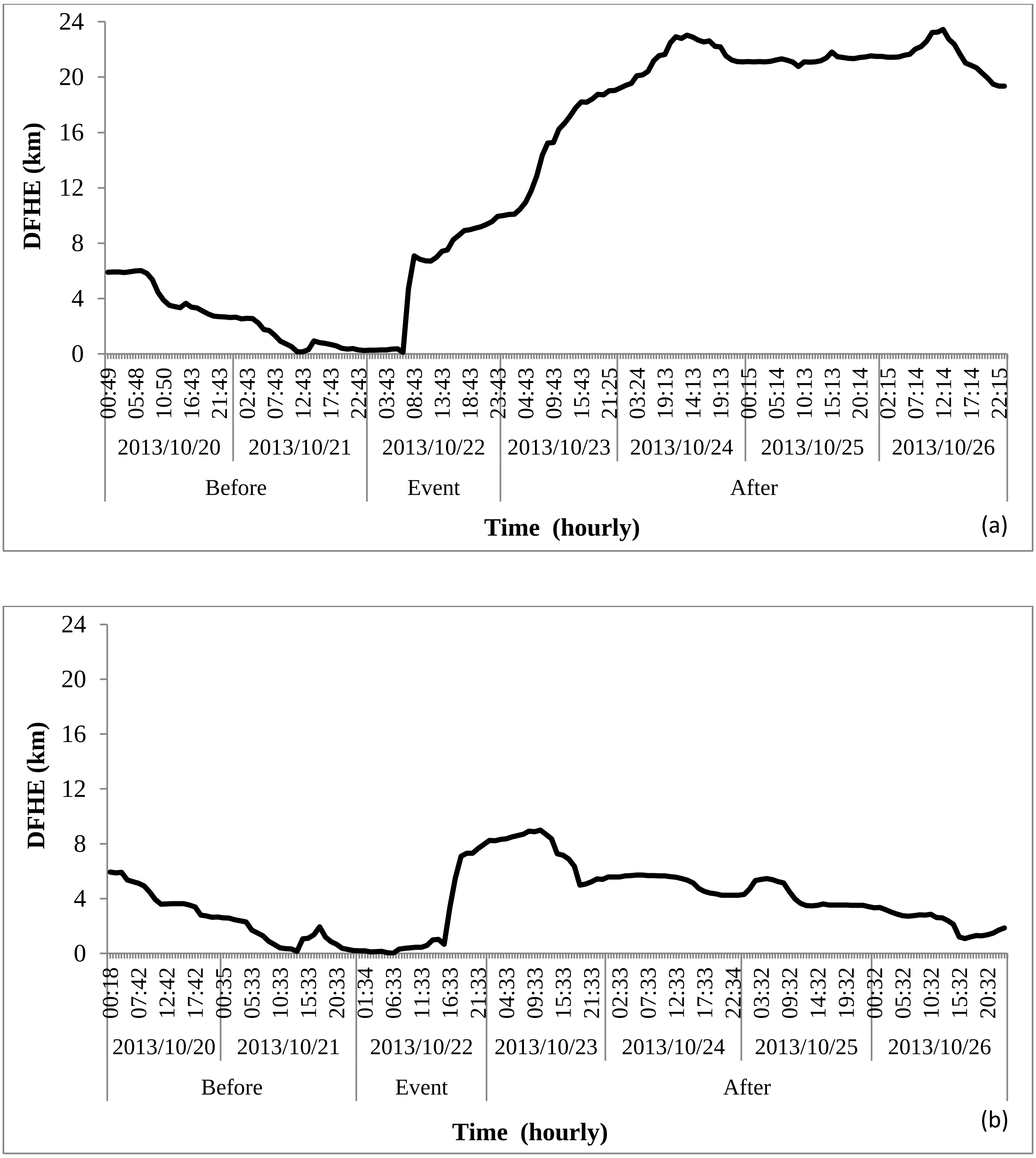


Figure 4: Distance from the event for elephants within 1 km of a hunting event, days before the event and four days after the event (a) Gower movement from 22/10/2013, and (b) Proud movements 22/10/2013.

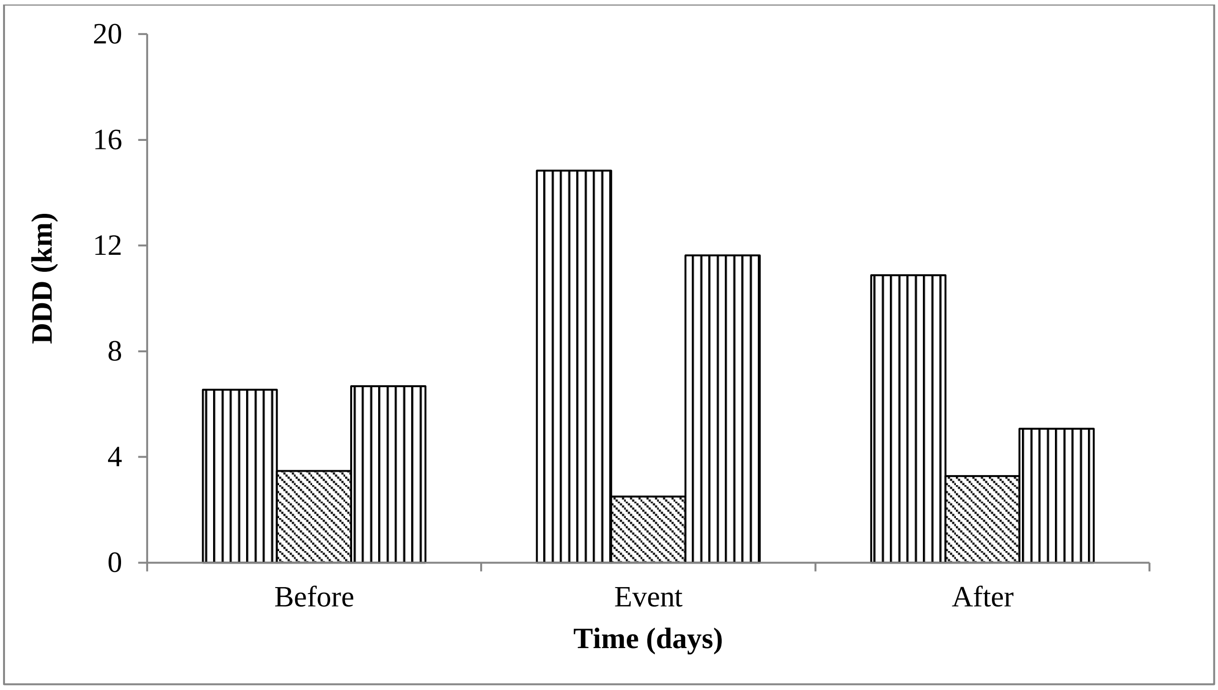


Figure 5: Daily displacement distance (DDD) for the three 2013 prime bulls for the period before the event (Before), the day of the event (Event) and for the period after the event (After) Gower, event 2013/10/22; Proud, event 2013/10/22, and Intwandamela, event 2013/04/06. Vertical stripes = 2013/10/22 and diagonal stripes = 2013/04/06.

1.2 DDD and DFHE for elephants within 1 km of a hunting event between 1 January 2006 and 31 December 2011 (historical data).

For this analysis only prime bulls were considered as they were the only age/sex category that was within 1 km from a hunting event. The historical dataset has two events for prime bulls within 1 km of the hunting event all involving the same collared elephant (Proud). For both events the elephant showed a large increase in the DFHE, from the evening of the event to the morning after the event (from 0.53 km to 4.09 km for event 2010/07/19 and from 1.25 km to 13.75 km for event 2011/06/24; Figure 6).

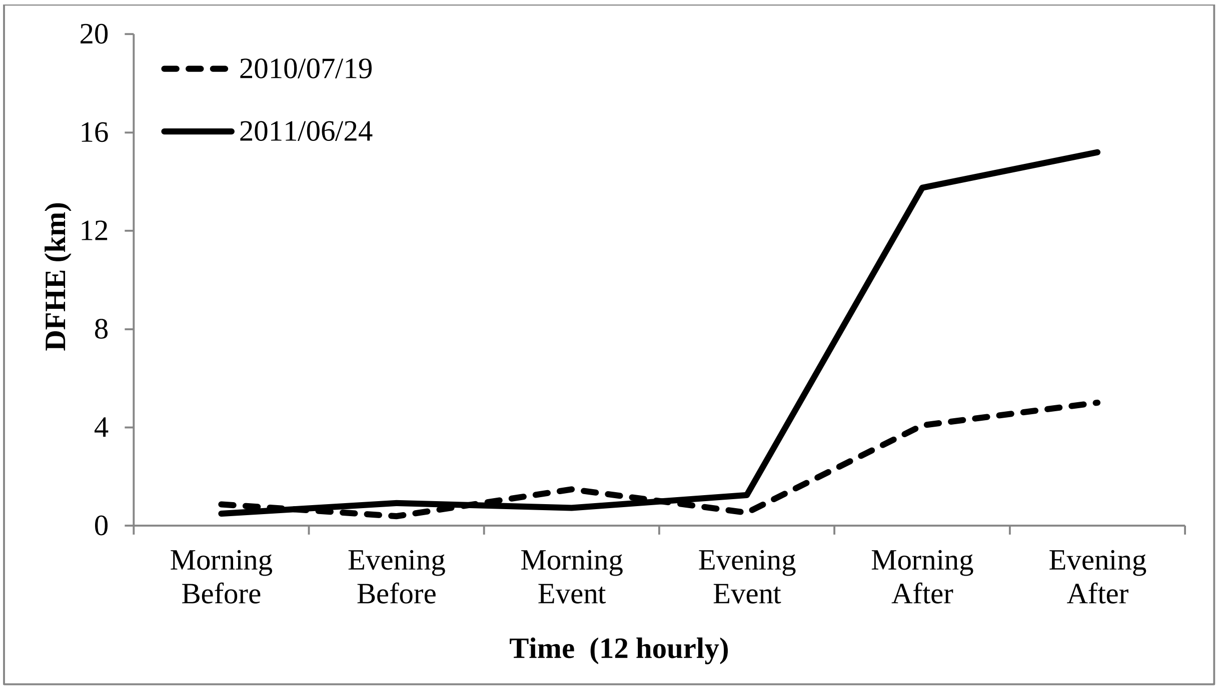
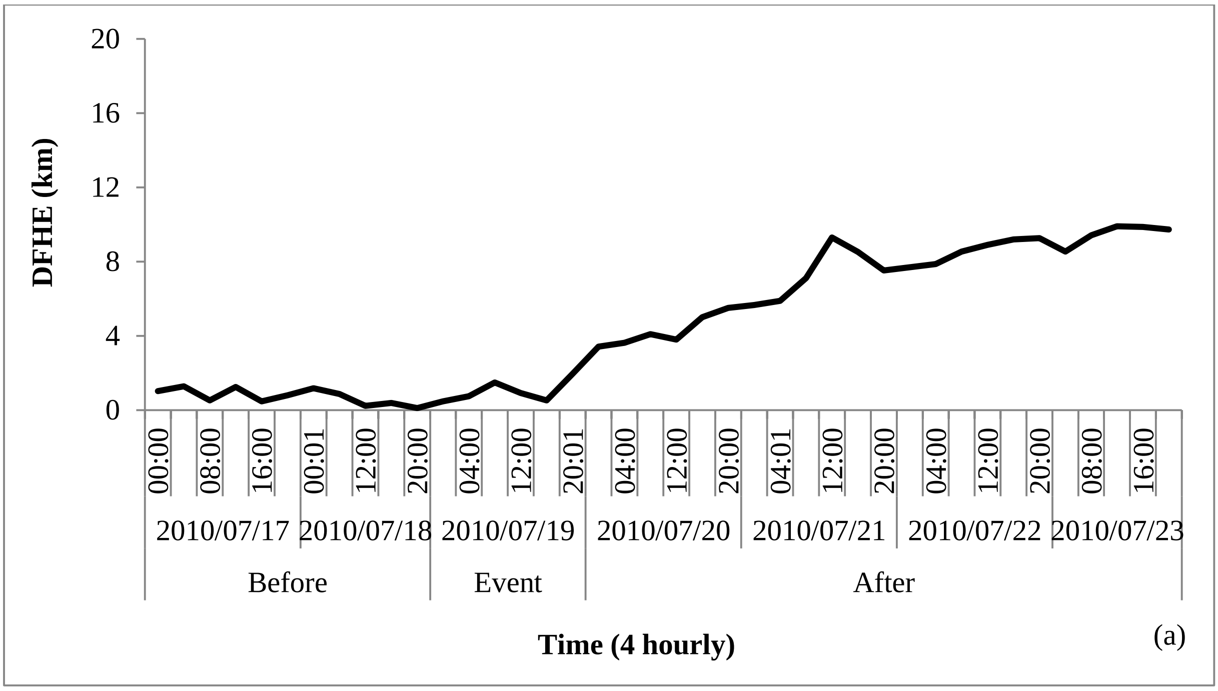


Figure 6: Distance from the hunting event (DFHE) at 12 hour intervals for the day before the event, the day of the event and the day after the event for the prime bull Proud for event on 2010/07/19 and 2011/06/24 during the study period (1 January 2006 – 31 December 2011).

In both instances the elephant remained further than 1 km from the event location for at least 4 days following the hunt (Figure 7) consistent with the 2013 prime bull results. Following the hunting event on 2010/07/19, the elephant showed a sudden movement from the hunting location during the afternoon on the day after the hunting event (from 0.53 km at 16:02 to 4.09 km at 08:00; Figure 7a). After the event, however, the elephants' distance continually increased reaching a peak distance away 2 days after the event (12:00: 9.30 km; Figure 7a).

Similarly following the 2011/06/24 hunting event, the elephant showed an increase in DFHE in the evening on the day of the event and reached a peak DFHE the afternoon after the event (from 0.35 km at 21:00 to 15.20 km at 17:00; Figure 7b) and remained further than 10 km for the hunting event location for at least 4 days afterwards.



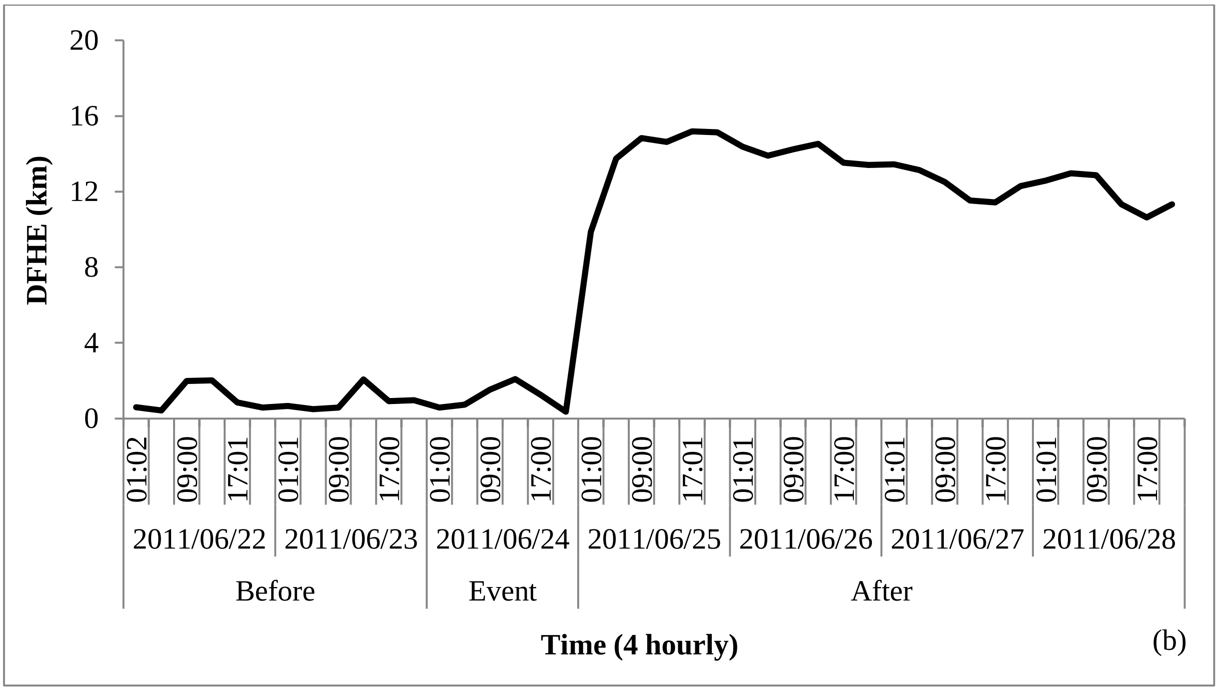


Figure 7: Distance from the event for the elephant within 1 km of a hunting event showing two days before the event and four days after the event (a) Proud: event 2010/07/19 (b) Proud: event 2011/06/24.

The DDD of the elephant within 1 km of the historical hunting events (2010/07/19; 2011/06/24) does follow the predicted pattern of the DDD on the day of the event being greatest (6.21 km and 14.80 km, respectively), followed by the DDD after the event (5.48 km and 7.53 km, respectively), and the smallest DDD seen before the hunting event (4.14 km and 4.28 km, respectively; Figure 8).

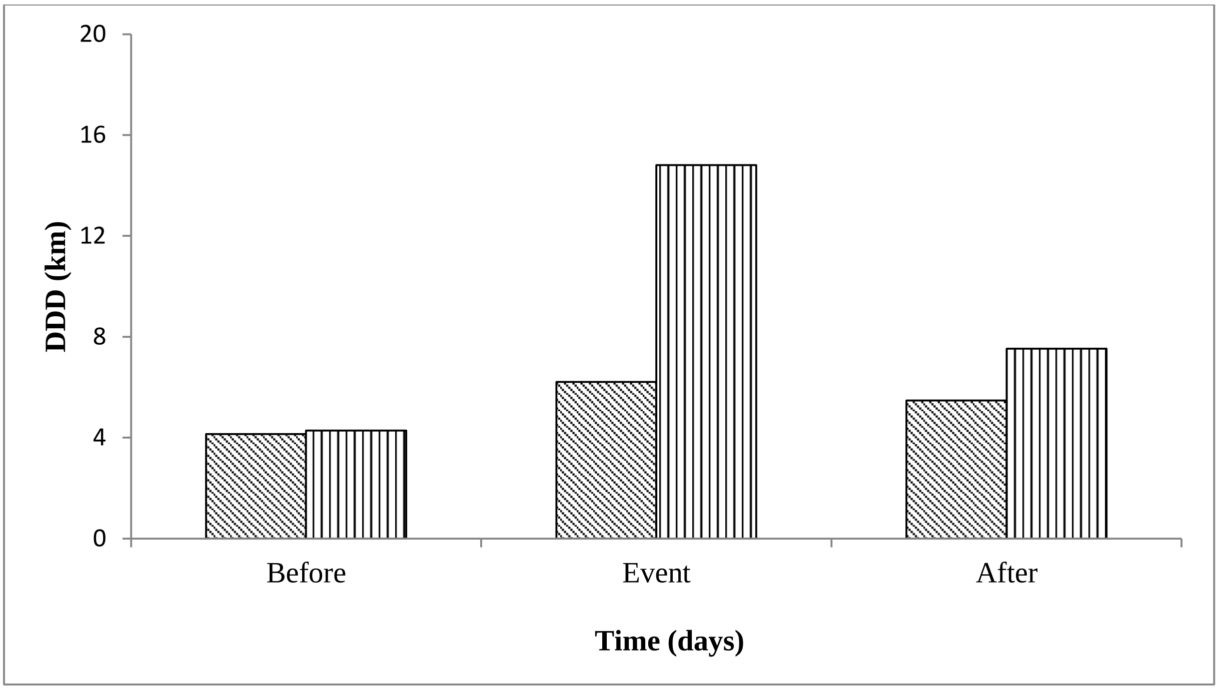


Figure 8: Daily displacement distance (DDD) for the historical elephant data for the period before the event (Before), the day of the event (Event) and for the period after the event (After). Diagonal stripes = 2010/07/19 and vertical stripes = 2011/06/24.

1.3 DDD and DFHE for elephants further than 1 km from a hunting event between 1 January 2006 and 31 December 2011 (historical data)

As expected, elephants showed different responses when within 1 km compared to further than 1 km away from a hunting event, with elephants within 1 km having greater changes in DFHE between the evening of and the morning after the event than those further than 1 km from the hunting event (Figure 9). In addition, the movements of the adult cows/family groups further than 1 km from a hunting event were smaller than those of the adult bulls with regard to the change in DFHE between the evening of and the morning after the event (0.16 km, and 0.82 km, respectively; Table 1).

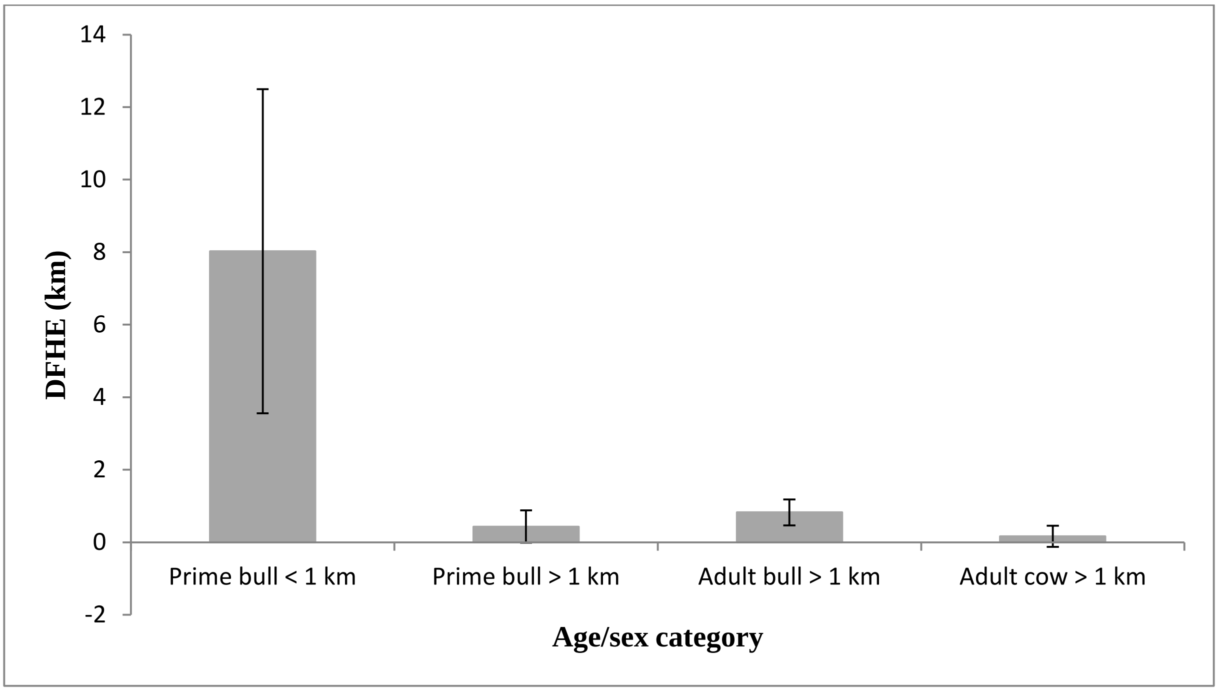


Figure 9: Changes in distance from hunting event (DFHE) between the evening of and the morning after the event comparing the age/sex categories (prime bulls < 1 km; prime bull > 1 km; adult bull > 1 km and adult cow > 1 km).

Table 1: Kruskal-Wallis statistical test results for the comparison of the three age/sex categories (prime bull, adult bull and adult cow) further than 1 km from the hunting event with regard to the DFHE on the evening of the event and morning after the hunting event. Statistical significant difference indicated by *.

Kruskal-Wallis results					
DFHE comparison	Sex/age category comparison	Chi- squared Critical value	degrees of freedom (df)	p-value	significance
Hunting >1 km vs. >1 km	Prime bull vs. Adult cow	7.2453	3	0.06448	-
	Adult bull vs. Adult cow	9.6464	3	0.02182	*

Prime bull vs. Adult bull	1.7631	3	0.62300	-

The difference in DDD between the day of the event and the period before for the elephants within 1 km of a hunting event are larger than for those elephants further than 1 km from the hunting event (Figure 10). When comparing the difference in the DDD between the day of the event and the period before and the difference in the DDD between the day of the event and the period after no difference in the DDD was found for any of the age/sex categories further than 1 km from the hunting event (Table 2).

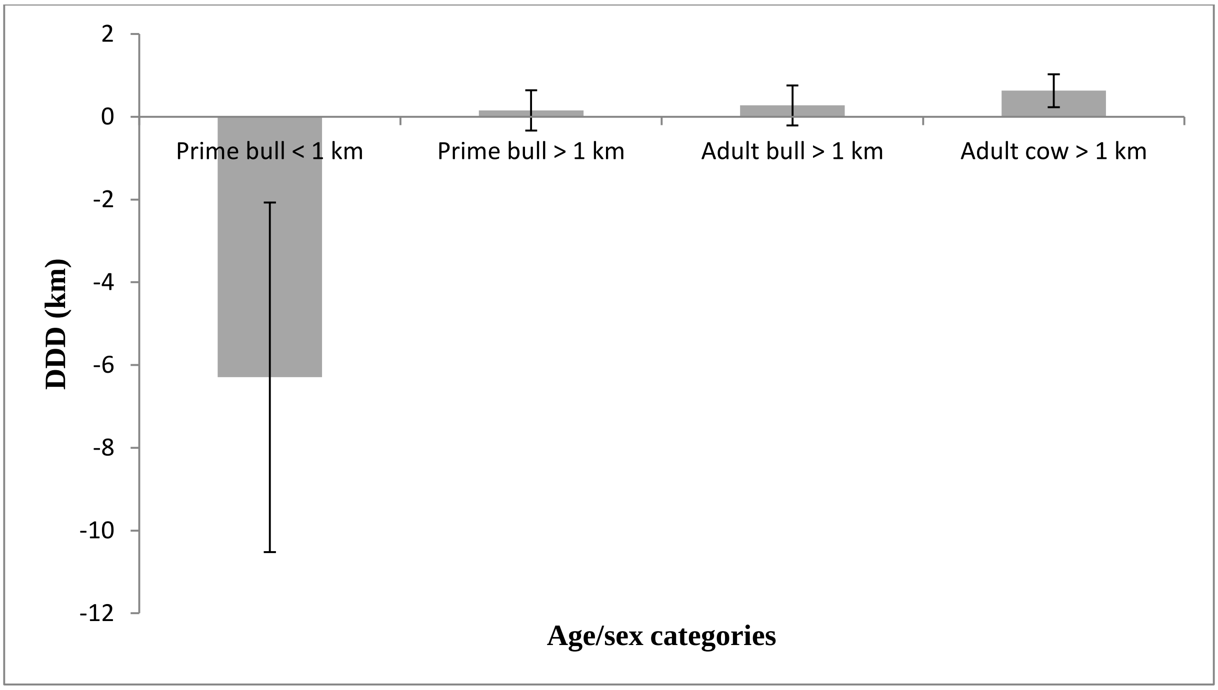


Figure 10: Difference in daily displacement distance (DDD) between the day of the event and the period before the event comparing the age/sex categories (prime bulls < 1 km; prime bull > 1 km; adult bull > 1 km and adult cow > 1 km). Negative scale = DDD on the day of the event; and positive scale = DDD for the period before the event.

Table 2: Kruskal-Wallis statistical test results for the comparison on the elephants (prime bull, adult bull and adult cow) further than 1 km from a hunting event with regard to the difference in DDD before and after a hunting event. Statistical significant difference indicated by *.

Kruskal-Wallis results						
Comparison		Sex/age category	Chi- squared Critical value	degrees of freedom (df)	p-value	significance
Δ before (DDD)	Hunting >1 km vs. > 1 km	Prime bull vs. Adult bull	0.0015	1	0.9690	-
		Prime bull vs. Adult cow	0.3756	1	0.5400	-
		Adult bull vs. Adult cow	0.8535	1	0.3556	-
Δ after (DDD)	Hunting <1 km vs. > 1 km	Prime bull vs. Adult bull	0.0015	1	0.9690	-
		Prime bull vs. Adult cow	0.0800	1	0.7773	-
		Adult bull vs. Adult cow	0.1818	1	0.6698	-

Objective 2: Comparing the DDD and DFE between hunting events and natural mortality events.

Due to the fact that there is no effect of hunting on elephant movements further than 1 km from a hunting event only hunting and natural mortality events within 1 km were used in the natural mortality versus hunting event comparison.

The response of the prime bull that was within 1 km of the natural event on the day of the natural event seems to indicate that the elephant comes to investigate the natural mortality event and then leaves the area, as he is far from the event location before the event, travels to the event and then travels further away the following day (from 8.30 km away before, to 0.24 km away on the day, to 9.51 km away after; Figure 11). The prime bull within 1 km of the natural mortality event, therefore, showed a different response to those elephants within 1 km of the hunting events (Figure 11).

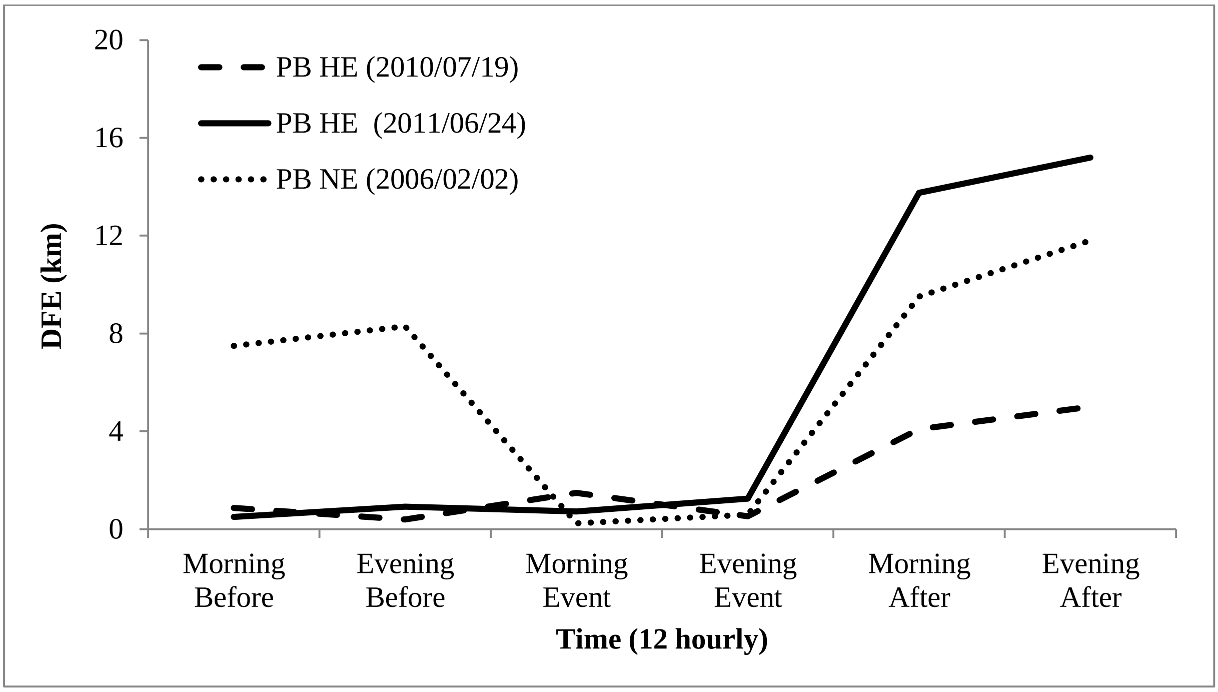


Figure 11: Distance from the event (DFE) for the prime bull, Proud, (hunting event; HE) and prime bull (natural event; NE) during the study period (1 January 2006 – 31 December 2011) plotted against the time in 12 hour intervals taken from 06:00 (Morning) and 18:00 (Evening) periods for the day before the event, the day of the event and the day after the event.

In contrast to the predicted pattern of DDD for a hunting event, the predicted pattern for the DDD for a natural mortality event is that the lowest DDD should be found on the day of the event. The prime bull within 1 km of the natural mortality event shows this predicted pattern (DDD of 10.80 km on the day compared to 15.48 km before and 21.45 km after).

Discussion

As elephants are such important ecosystem engineers it is important to know their reactions to environmental changes and anthropogenic interferences and interactions (Poole 1996; Burke 2005). This is especially important considering the elephant and rhinoceros poaching that is occurring in the Kruger National Park and in countries north of South Africa of late (Tilney 2014).

My results show that much like ungulates, elephants show a flight response when anthropogenic activities such as hunting occur (Conner *et al.* 2001; Burke 2005), which is a fundamentally necessary response as it ensures survival (Stankowich 2008). However, my results also show that elephants must be within 1 km of a hunt to show a flight response, as this was true for both the 2013 elephants and the historical data for elephants prior to 2013. These findings are consistent with those by Burke (2005) who found that elephants that were not present with a hunted individual did not show any reaction to the event, not even females within 2 km of the hunt. Three possible explanations for the apparent lack of response by elephants to hunting events when further than 1 km are; firstly elephants could have become habituated to non-consumptive anthropogenic activities such as game viewing (Kiffner *et al.* 2014) and not view this activity as a threat and therefore would not flee from the hunting vehicle; secondly the elephants could have become habituated to the hunting vehicles as hunting events occur year round in the Associated Private Nature Reserves and this could lead to the elephants judging themselves to be at a safe distance from a hunting event unless they are with the hunted individual or thirdly the lack of response could be due to the weak social bonds between males in pairs or groups and females (Burke 2005). However, Burke (2005) also found that whilst movement behaviour was not affected when elephants were not present with hunted individuals, both elephants present at hunting events and those further away had elevated “stress hormone metabolite concentrations” for 4 days and 1 day following the hunt, respectively.

Prime bulls were the age/sex category affected by hunting events, which are the only elephants found in proximity to hunted individuals. This is consistent with the literature as most often elephants with the largest tusks are targeted for trophy hunting or poaching (Selier *et al.* 2014). This is also consistent with the norms and standards of game hunting in South Africa stating that only individuals that are not in close proximity to females and herds may be killed (Department of Environmental Affairs and Tourism 2008).

When elephants, like other animals, are threatened they have to weigh up to the costs of fleeing with the costs of staying. If animals have to leave an area with high quality resources and their forage is interrupted this can have large costs on their survival such as loss of energy and necessary nutrients, however, staying in the area can lead to death (Stankowich 2008). Therefore, an animal should learn to flee only if there is immediate danger and not when deeming to be at a safe distance (>1 km in the case of elephants and hunting). Elephants in particular have very defined and long term memory which they use to find areas of good resources and also remember, for example, where fences are in order to avoid those areas (Loarie *et al.* 2009; de Knegt *et al.* 2010; Vanak *et al*. 2010)

When I looked at the 2013 data three elephants were within 1 km of the hunting event and two showed an increase in DFHE. Yet, these increases happened at different times for two elephants supposedly in the vicinity of the same event. This difference could be due to one of the elephants showing freeze behaviour (inactivity or decreased activity of animal usually due to a shock or fear; Fanselow 1986; Eilam *et al.*1999) and only moving from the area later once the initial shock had subsided. This response would be consistent with what is seen in elephants listening to calls of conspecifics, stopping to analyse what their response should be before moving away from or towards the call (Langbauer *et al.* 1989). Fanselow (1986) also found that rodents sometimes show a freeze response to an electric shock before fleeing from the stimulus. However, it is also important to consider that the elephant that showed the delayed response was also present when two of the historical hunting events had occurred and this may also have defined his reaction as he could have deemed himself safe from the hunting event and therefore not have left the area right away. Another possible reason for the different movement response observed could have been that another hunting event occurred later and was simply not recorded.

I also found that the HDR for the 2013 elephants increased rapidly when the DFHE increased and started to slow when the elephants were 7 km or more form the event location, suggesting that these elephants could deem themselves to be at a safe distance from a hunting event when they are 7 km or more away.

One elephant (Intwandamela) would appear to be the exception to the rule that elephants will show a response to a hunting event whenever they are within 1 km as he is within 1 km of the hunting event but appears to not show a response. The apparent lack of response to the hunting event could be caused by the fact that his position is only recorded every four hours and therefore more fine scale movement may be missed.

Elephants further than 1 km from a hunting event do not show a response to the hunting event, but I detected a difference in DDD between males and females. The fact that the DDD for females was smaller than that of the males is most likely due to the fact that males and females show sexual dimorphism in movement and social structures and females also are part of family groups and have to compensate for calf movement (Poole 1996). This could also be due to the fact that hunting events usually take place further away from females than males since males are supposed to be hunted at a sufficient distance from the females or breeding herds (Department of Environmental Affairs and Tourism 2008).

The elephants show different reactions to hunting events and natural mortality events, which is to be expected. The elephant within 1 km of the natural mortality event appears to approach the remains of the deceased elephant which is consistent with the findings of Douglas-Hamilton *et al.* (2006), McComb *et al.* (2006) and Owen-Smith *et al.* (2010). Elephants respond to the sound of the gun shot and the calls of fear that conspecifics in the vicinity of the hunting event make (McComb *et al.* 2000; Soltis *et al.* 2014), whereas when there is a natural mortality event the call would be different (distress) and so the elephants would show a different reaction as it has been found that elephants can distinguish between different calls and their meaning (McComb *et al.* 2000; Soltis *et al.* 2014). As I was not physically in the field when the hunting events occurred I assumed that the elephants make distress calls when in proximity to a hunted individual but it is possible that no calls were made and therefore could explain the lack of response discussed.

Limitation of the study

The results obtained for this paper, while consistent with the literature, may not be accurate as the sample size was very small (hence potentially just showing the response of an individual rather than that of elephants in general) and the exact times of the hunting events were not given. I had originally planned to only use elephants that had hourly GPS locations for a three year period, so as to be able to calculate the hourly movement/displacement rates and the elephants' perceived safe distances. However, when I received the data, the sample size was even more limited than I had been told and hence I also included elephants that had 4 hourly movement rates, which meant that I could no longer analyse the hourly movement/displacement rates. This expansion, however, did not increase the sample size much more and I had to expand the time period to six years.

The elephants' perceived safe distance analysis, could anyway not be done as I did not have the exact time of the hunting event from which to start analysing changes in movement rates. However, as I was able to use the 2013 elephants that were known to be in the vicinity of the hunting event and had hourly GPS locations and I was able to make some predictions as to the hourly movement/displacement rates and safe distances based on those instances. The four hourly GPS locations for the historical dataset also means that some fine scale movement may have been missed, which could have provided more insight into the effects of hunting on elephant movement, above all if coupled with a time for the hunt. Not knowing the exact time of the hunting event means that I cannot conclusively say the movements were caused by the hunting event.

I had also planned to compare the effects of hunting on all the age/sex categories, however, females were never closer than 3 km from the hunting event and adult bulls were never within 1 km of the hunting event. The sample size for the natural mortality events was only one, but a main limitation of the data is that the dates of natural mortality events are an estimate; the actual dates could have been different and therefore I might have missed some elephants moving towards the mortality location as I would have been looking at the wrong dates.

In future I suggest that the management of the APNR should record the GPS locations of their collared elephants hourly and that the exact times of events should also be recorded as this will give a better idea as to the reactions of the elephants to hunting. I think these are important considerations since if the information is accurately collected and analysed it could potentially even be used to identify patterns which could help indicate when poaching events may have occurred. In conclusion, I am aware that the dataset I had to work with was limited, and crucial information like time of hunt were missing and therefore that limited the type of analysis I could do. However, it is the first attempt at investigating the effect hunting in the

APNR adjacent to the Kruger National Park might have on the elephants that use the area, and it seems to confirm that a clear behavioural response is only seen within 1 km from a hunt. However, since Burke (2005) found that elephant stress levels can stay elevated for up to four days for those elephants within 1 km of a hunting event and up to one day for those further than 1 km, behavioural changes are possibly not the best indication of elephant distress at being exposed to hunting.

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