PHYSIOLOGICAL AND ECOLOGICAL EFFECTS OF FENCING ELEPHANTS IN MONTANE FORESTS, KENYA

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PHYSIOLOGICAL AND ECOLOGICAL EFFECTS OF FENCING ELEPHANTS IN MONTANE FORESTS, KENYA

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DECLARATION

I hereby declare that the work has been completed by myself and no portion of the work contained within this Thesis has been submitted in support of any application for any other degree or qualification on this, or any other university or institution of learning.

Jacqueline Anne Morrison, 2019

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Abstract

Worldwide, wildlife populations are declining at an unprecedented rate, anthropogenic influences including habitat-loss, poaching, and over-exploitation are driving many species to extinction. A rapidly increasing human population and subsequent conversion of land use, has intensified a competition of resources between humans and wildlife. Human elephant conflict (HEC) is a prominent concern and whilst many attempts have been made to mitigate conflict, many are unsuccessful, as such, Kenya embarked on the necessary strategy of fencing its montane forests to separate elephants from people. Whilst fencing successfully reduced conflict, the physiological and ecological effects of confining elephants in forests is unknown.

This thesis is the first study examining the impact of fencing elephants in montane forests, on both the ecological impact on the integrity of the forest habitat, and the impact of isolation on the demographic structure, and physiology of the elephant population. The outcomes of this study will be used to inform the future management of elephant populations in forest habitats throughout their range. Chapters of this thesis address the following outcomes; (1) the impact of confining African elephants (*Loxodanta africana*) on the extent and quality of a forest habitat and (2) to provide a density estimate of elephants in a montane forest by employing the Random Encounter Model (REM) with camera traps. Additionally (3), it also assesses the impact of restricting dispersal on the demographic structure of elephant populations compared to free-roaming populations, and (4) examines the physiological effect of confinement on elephants.

To provide an assessment of the impact of confinement on the forest habitat, changes in the forest canopy were mapped by applying the Breaks For Additive Season and Trend (BFAST) model using a time-series of MODIS satellite data on the 2 fenced forest habitats of varying sizes. Change maps produced from the BFAST model on MODIS time-series data revealed that 13% of the Aberdare National Park had undergone a change in vegetation, with 0.9% loss to the forest. Similarly, the Shimba Hills National Reserve underwent significant change over the 12-year period, averaging a 9% change in the area per year with both positive 'greening' events and forest degradation. Density estimates calculated from the REM yielded results averaging 0.49 elephants/ km^2 which falls in line with expected estimates in protected areas. Demographic results determined that the age class frequencies for the Aberdare Conservation Area (ACA) were significantly different to parity (x^2 = 147.24, df = 2, p-value < 0.001), showing a skewed age distribution towards adults and sub-adults and a lower proportion of juveniles. Comparison of the age class frequencies in the ACA to 3 populations from published data of known status (stable, and rapidly increasing) revealed that the ACA population were significantly different to both stable populations (x^2 = 495.05, p-value < 0.001; x^2 = 215.98, p-value < 0.001), and the rapidly increasing population (x^2 = 329.1, p-value < 0.001). The number of dependents to adult females was significantly lower compared to the control populations (x2 = 9.0872, df = 3, p-value = 0.02815). Endocrine analysis of adrenal activity found significant differences in FGM concentrations between the confined ACA population, a free-roaming savannah population, and a population from a montane forest that utilises a wildlife corridor to the lowland savannah (R_2 =0.2331, F = 35.1, df= (2), 231, p-value < 0.001). At 3.73 ng/g (95%CI, 3.35-4.16), the confined ACA population is 91% higher than the Lewa Wildlife Conservancy (LWC) population with a wildlife corridor (1.95 ng/g, 95% CI, 1.72-2.21) and 68% higher than the Samburu National Reserve (SNR) population (2.22 ng/g, 95% CI, 1.98-2.59). No significant differences in FGMs were observed between the two free-roaming (LWC and SNR) populations. The greatest difference in FGM concentrations were observed in the sub-adult age class, with the ACA averaging 4.13 ng/gm (95% CI, 3.58-4.76) compared to 1.87 ng/g (95% CI, 1.59-2.1) in the LWC, and 2.74 ng/g, (95% CI, 2.28-3.30) in the SNR.

Whilst the ACA exhibited only small-scale degradation, and the current density of elephants falls within the expected densities for protected areas. Significant differences were observed in the demographic structure and physiological condition of the isolated elephant population. The age-distribution was skewed towards the adult age classes, and concentrations of adrenal hormones were elevated. As such, these could have negative implications on population growth rates, and the subsequent viability of the population.

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Chapter 1

Introduction

1.1 Overview

An expanding human population with a demand for resources, has led to an increase in competition between people and wildlife. When people and wildlife share the same landscape and utilise the same resources, there is a cost to both, and conflict between people and wildlife can occur. Human-wildlife conflict (HWC) is a prominent issue across the world, and is observed in a variety of species from primates (Dickman and Dickman, 2012), to carnivores (Habib et al., 2015). To protect both people and wildlife, fencing has become an increasingly popular strategy to mitigate HWC (Haywood and Kearley, 2008; Packer et al., 2013), the use of fencing however, has contributed to an increase in the fragmented wildlife populations.

There is a body of evidence highlighting the negative effects of isolation on the genetics of wildlife populations (Shaffer, 1981; Frankham et al., 2017), however, there is a paucity of information on the impact of isolation on the demographic structure, and physiology of fragmented populations. Dispersal of individuals plays a fundamental role in population regulation, mate-finding, inbreeding-avoidance, and the acquisition of resources (Caughley, 1976; Chamaillé-Jammes et al., 2007). The confinement of wide-ranging species, could have unintended impacts on population growth, via demographic processes that are reflected in life-history traits (Gaillard et al., 2000; Eberhardt, 2002). Moreover, confinement could induce a physiological stress response caused by an inability to disperse seasonally to acquire nutritional resources (Lendrum et al., 2014), or in the search for mates (Whitehouse and Kerley, 2002). Long term over-activation of the adrenal system has been linked to a number of pathological dysfunctions, and decreased fertility (Mason and Veasey, 2010), presenting concerns for population growth rates, and the viability of a population. Furthermore, confining wildlife, and consequently having static populations within an area, can have negative ramifications for the habitat. The feeding ecology of some species can cause large-scale destruction to vegetation, and has the capacity to permanently modify the habitat (Pringle, 2008).

1.2 African elephant

Despite numbers in the 100,000s and being the subject of substantial conservation efforts, the African elephant (*Loxodanta africana*) is a difficult challenge for conservation management, and has been classified as "*Vulnerable*" on the IUCN Red list since 2007

(Blanc et al., 2010). Although some argue there should be two separate species (Roca et al., 2001; Rohland et al., 2010), the African elephant is divided into two distinct classifications due to morphological differences, habitat preferences, and genetics. The savanna elephant (*Loxodanta Africana*), and the forest elephant (*Loxodanta cyclotis*). Whilst having a large geographical range spanning 37 countries, they have become nationally extinct in a large part of their range, including Burundi, The Gambia, Mauritania and Swaziland where they have now been reintroduced (Blanc, 2010). In the 1940's, the continental population was approximately 3-5 million, yet it experienced several declines (Thouless et al., 2016), particularly during 1970 and 1989 when over half of the continents elephants were killed, predominantly to supply the international ivory trade (Douglas-Hamilton, 1989), today, they have an estimated global population size of 472,000 (IUCN, 2013). Although there is an increasing population trend due to increasing densities at a local scale, their management is a complex issue pertaining to considerable differences in global populations. They are vulnerable to extinction in some regions, yet considered too abundant in others (Whyte et al., 2003; Blake and Hedges, 2004; Stephenson, 2004). Within these sub-regions, historical influences and a growing demand for ivory, have contributed to the large variation in population numbers (Blanc et al., 2010). Despite a stabilisation in poaching levels across the continent following the increasing trends since 2006 and significant improvements in the number of illegal killings in East Africa, the 2015 Conventional on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Monitoring the Illegal Killing of Elephants (MIKE) programme, reported that poaching still exceeds the natural growth rate and is likely driving elephant populations to decline (CITES, 2016).

Although elephants still occupy a large range spanning approximately 2.4 – 3.4 million km^2, many populations, particularly those inhabiting forest environments remain relatively understudied (Chase et al., 2016). It is the responsibility of each nation with elephants within their range, to survey and count elephant numbers, yet with large variations in surveying frequency, coverage and quality, this provides a limitation in setting management priorities at a continent scale (Chase et al., 2016). These challenges, combined with their diminished range resulting from habitat loss and fragmentation due to an expanding human population, and subsequent increases in human-elephant conflict, remain a considerable threat to their survival (Blanc, 2010).

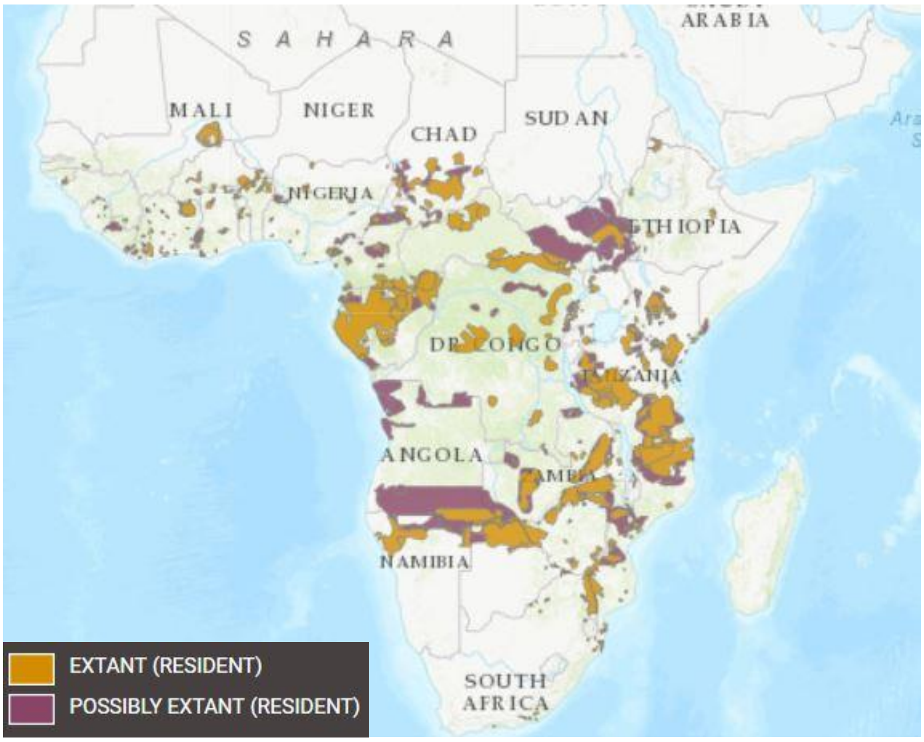

Figure 1.1 Geographic range of the African elephant (reproduced from the IUCN Red List of threatened species, 2008)

1.3 Human Elephant Conflict

Colonial and post-colonial conservation policies in Kenya fared well for elephants with the provision of protected areas, designed to promote a considerable tourist industry (Kabiri, 2010). However, most of these National Parks were too small to sustain populations, and their survival relied on utilising land outside of these protected areas (Evans & Adams, 2018). As a migratory species that follow seasonal rainfall patterns, associated vegetation cycles and have large home ranges spanning circa 3,700km2 (Bohrer et al., 2014), yet in extreme conditions during periods of nutritional stress, they are adapted to traveling distances as large as 24,000 km2 in search of resources (Leggett, 2008). With a rapidly expanding human population, and an increased demand for resources, there have been large-scale changes in land-use, whereby land surrounding protected areas that has historically formed migration routes, has been converted to agricultural land. When elephants leave protected conservation areas and come into contact with people, there are negative associations between the two (Barnes, 1996; Hoare, 1999; O'Connell-Rodwell et al., 2000; Osborn and Parker, 2003; Sitati et al., 2005). With the greatest volume of cerebral cortex of all terrestrial animals (McComb et al., 2000) they are highly intelligent, and have an extensive spatial-temporal and social memory (Hart et al, 2008). They quickly learn the areas that pose the least threat to them and provide the largest source of opportunity with nutritious unguarded farmland (Evans & Adams, 2018).

Conflict with elephants can have a severe impact on local communities, elephants frequently crop-raid neighboring farms destroying entire fields of crops, causing wide-scale damage and substantial economic loss (Graham, 2010). Damage to livestock, property and human injury or death, can lead to retaliation killings of problem elephants, not just from the local population, but also from Government management schemes aiming to control crop-raiding elephants, and to limit damage to the local communities (Mutinda *et al.,* 2014; Evans & Adams, 2016). Because crop-raiding behavior is difficult to predict due to its spatio-temporal nature (Graham et al., 2010), and communication from those affected can be poor, Government response can be perceived to be unsatisfactory and ineffective to the community (Graham et al., 2012; Hoare, 2012). Although elephants do not cause the most damage overall, they are considered the most dangerous to people, are less tolerated, and therefore receive more attention than many other species (Sitati et al., 2003).

By the early 1980's, crop-raiding elephants were a politically prominent issue, and animosity towards the elephants, and people that managed them intensified (Jenkins and Hamilton, 1982; Evans and Adams, 2016). In the early twentieth-century, the Laikipia region in Central Kenya, had the highest incidences of human-elephant conflict throughout East Africa, and elephants were considered the largest, widest ranging and most destructive species (Jenkins and Hamilton, 1982; Graham et al., 2010; Evans and Adams, 2016). During a 3 year period (1990-1993), 130 elephants were killed in Kenya as a result of conflict, and during this same period, 108 people were killed by elephants (Kiiru 1995). Although it is not a new problem, conflict with humans has escalated throughout the elephants entire range, threatening the survival of the species outside of protected habitats. HEC present a concern for elephant management strategies (O'Connell-Rodwell et al., 2000; Sitati et al., 2005). A 2008 assessment by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Blanc, 2010), listed conflict as a major threat to sustaining elephant populations.

Human elephant conflict is a cause for contention, and is perhaps considered the most political, and emotive form of human wildlife conflict (Lee and Graham, 2006). Elephants evoke cultural contradictions. They are considered, not only a nuisance and danger to the local community, but are an underlying cause of land conversion to protected areas, negatively impacting the human population by resulting in a competition for resources. On the other hand, internationally they are an iconic species that are admired and considered a conservation priority (Lorimer, 2010; Barua, 2013). The importance from both perspectives, puts pressure on African countries to reduce human elephant conflict within their range (Evans and Adams, 2016). A number of HEC mitigation methods have been implemented at a local level by farmers, including barrier methods such as constructed fences, ditches and walls, to active deterrents including chilli fences, beehive fencing, lighting fires, and noise generation by banging tins and drums (Hoare 2001; Osborn and Parker 2003). Whilst these have been reported to reduce crop raiding to some extent, they have been largely ineffective on a greater scale, elephants are simply diverted from the deterrents, and crop-raid in other areas, shifting conflict elsewhere (Hoare, 2012; Osipova et al., 2018). The long-term suitability of mitigation methods is also questionable, with indications showing habituation, and elephants returning to crop-raid even in the presence of deterrents (O'Connell-Rodwell et al., 2000). With the failure of many mitigation methods, Governments from a number of countries implemented compensation schemes. Their focus was to reimburse individuals that had been affected by crop and property damage, however these were short-lived, due to verification issues, problems with corruption, and difficulties with administration (Bell 1984; Hoare 1999; Hoare 2001; Sitati & Walpole, 2005).

1.4 Wildlife Fences: impact on wildlife populations

Across Africa, Australia, Europe and Southeast Asia, a staggering 70% of land has been converted for human activity, resulting in a loss of geographical range for many mammalian species (Ceballos and Ehrlich, 2002). In an attempt to conserve biodiversity, many protected areas (PA's) were established across African nations, encompassing 13% of land surface (Newmark, 2008). However, their isolation and the edge effects of human encroachment continued to threaten wildlife populations (Estes et al., 2006; Newmark, 2008). To mitigate these, an increasingly popular, and necessary strategy, is to erect fences that separate wildlife from the surrounding human population. The historical use of fences is two-fold, to separate areas that are rich in resources from any threats, and to exclude entry to those prohibited. In conservation, they are to protect biodiversity from threatening processes including anthropogenic activity, and to protect the human population from conflict with wildlife (Haywood and Kearley, 2008). Within conservation, their use is seen by some as recognition that the human population is failing to coexist with wildlife, and they have become a contentious issue (Haywood & Kerley, 2008; Massey et al., 2014). Whilst fencing in conservation has been implemented on a global scale, differences in their management exist, from Government ownership of wildlife assets in Australia, to ownership led by the private sector predominantly within South Africa (Slotow, 2012). In East Africa, fencing of wildlife was predominantly used by private game reserves (Slotow, 2012) until the more recent implementation of fencing National Parks and Reserves by the Kenya Wildlife Service (KWS) in 2009. Worldwide, the reasons for implementing fencing has varied from protecting reintroduced populations of the Arabian oryx in Saudia Arabia (Treydte et al., 2001), to prohibiting the movement of Iberian lynx in Spain (Sergio et al., 2005). Positive results have been demonstrated in a number of situations, including the preservation of habitats from rabbits and dingos, and the successful management of lion populations (Lunney & Leary, 1988: Packer *et al.,* 2013). Conversely however, it has been argued that the fences themselves can become a threat, either by blocking animals off from essential resources, causing injury from poor fence design, attributing to genetic isolation thereby resulting in a decrease in fitness within wildlife populations, and restricting evolutionary potential (Caughley, 1994).

Confining elephant populations could have a large, and unintended impact on population density and or growth rates (Loarie et al., 2009). Density dependence, which is the negative-feedback mechanism that promotes the continuation of wildlife populations by regulating growth rates in response to density, assists in keeping populations near equilibrium (Sinclair, 2003). Changes within populations can be affected locally, by immigration/migration processes and in response to mortality/fecundity (Chamaillé-Jammes et al., 2007). Additionally, in the absence of predators, populations may expand and then be affected by an exchange between population density and environmental stochasticity (Sinclair, 2003). Although the factors regulating elephant populations remain undecided, evidence suggests that mean annual rainfall (Fritz et al., 2002), vegetation availability (Caughley, 1976), and an interaction between density and spatio-temporal resource availability, play an important role (Chamaillé-Jammes et al., 2008). It has been suggested that for large ranging species, particularly elephants, dispersal is an efficient strategy to moderate density and resource variability (Clobert et al., 2001). The implementation of fencing, curtails migration and dispersal. Over long time periods, this can negatively affect a populations ability to respond to stochastic events, and to climate change (Graham et al., 2009), potentially causing a protected area to exceed its ecological carrying capacity (Clobert et al., 2001). The impact of confinement on population density could be two-sided. A recent assessment on long term data (~50 years) on the effects of fencing on mammalian diversity conducted in the Aberdare National Park, Kenya, revealed that prior to the completion of the fence around the Salient area in the West of the park, wildlife populations were significantly declining (Massey et al., 2014). After completion of the first part of the fence in 1991, there was a significant increase in mammal populations, however, this trend was short-lived, and in the following years continuing declines in population numbers were observed (Massey *et al.,* 2014). Similarly, Chase and Griffin (2009) found that 7 years after the completion of a fence, there was a significant decrease in the Caprivi Strip elephant population in Namibia, due to the fence blocking returning migrating elephants. In contrast, in the Shimba Hills Forest Reserve, Kenya, there was a rapid increase in elephant numbers since the completion of a fence (Knickerbocker & Waithaka, 2005). It even resulted in the translocation of 150 elephants to Tsavo East National Park 6 years later (Pinter-Wollman et al., 2009).

Whilst many authors acknowledge that using electric fencing is the most effective method of reducing conflict (Thouless & Sakwa, 1995; O'Connell-Rodwell et al., 2000; Packer et al.,. 2013), there is a significant gap in the literature about the long term effects (Loarie *et al.,* 2009; Mutinda *et al.,* 2014; Evans and Adams, 2016). Although they may be successful in mitigating conflict, reducing harvesting, and limiting the disturbance of habitats. A thorough understanding of the threats to an area should be determined before deciding to implement fencing (Haywood and Kerley, 2009). Their effectiveness may only lead to short term solutions (Okello and D'Amour, 2008), not only shifting human-wildlife conflict elsewhere (Osipova et al., 2018), but also having negative impacts on the ecosystem (Haywood and Kerley, 2009).

1.5 Impact of confinement on habitats

Spatial and temporal heterogeneity of landscapes is a primary factor in the distribution and abundance of herbivorous species (Pittiglio *et al.,* 2014). Many species, including elephants, have evolved effective life-history strategies by moving seasonally between geographic locations to exploit the heterogeneous environments which differ in terms of graze and browse quality (Wittemyer et al., 2008; Bohrer et al., 2014). Savannah environments, which harbour large populations of elephant, are dynamic ecosystems experiencing temporal fluctuations in productivity, biomass, and grazing animals (Hoffman et al., 2009), which can result in various forms of degradation to the land (Dregne, 2002; Miehe et al., 2010). These areas are characterised by high spatial and temporal variances in rainfall and are considered to be in non-equilibrium, thus suggesting that degradation as a result of grazing is low, because grazing pressure during times of drought is reduced by the limited biomass available (Behnke and Scoones, 1993; Illius and O'Connor, 1999; Sullivan and Rohde, 2002; Wehrden et al., 2012). Stochastic variation is controlled by abiotic factors such as precipitation and temperature, which is the dominating factor in controlling plant biomass (Dorji *et al.,* 2010). Annual herbivore population dynamics are therefore driven by the effects of rainfall, and subsequent availability of forage (Vetter, 2005), and elephant abundance and distribution is directly correlated to the availability of browse (Murwira *et al.,* 2010). During the dry season, elephants migrate large distances, to assemble in areas that have a permanent water supplies, such as in the montane forest regions, during the wet season, they then disperse to the lower land savannas (Rasmussen et al., 2006; Wittemyer et al., 2008; Bohrer et al., 2014). These natural migratory patterns can assist in the regeneration of landscapes due to the temporal nature of resource use (Skarpe *et al.,* 2004).

In recent years, ecologists have become increasing interested in the capacity of some species to significantly modify the environment, permanently altering the habitat and resources available to other species (Pringle, 2008). Elephants have been documented to cause both large and small scale disturbances to the land, including elephant trails/roads through migration routes, digging wells to reach water under the surface, and smoothing rock surfaces and tree stumps whilst rubbing up against them to scratch (Haynes, 2012). When elephants are confined and population sizes exceed the natural carrying capacity of an area, they can have detrimental effects to the ecosystem due to their feeding behaviours (Loarie et al., 2009), with negative ramifications for other species (Buechner & Dawkins, 1961; Laws, 1970; Caughley, 1976). Should elephants be confined in habitats that are in equilibrium, biotic feedbacks between them and their resources control plant biomass, a high density population and subsequent over-grazing, could result in largescale degradation of habitats (Vetter, 2005).

Adult elephants can consume 150kg of vegetation each day, moreover, in the process, they can cause excessive damage due to their inefficient feeding methods (Sikes, 1971). Elephants have altered vegetation communities by bark-stripping, uprooting trees and opening up vegetation by trampling plants during feeding, additionally, their preferential seasonal feeding can cause irreversible damage to trees and bushes (Haynes, 2012). Although the long-term impact of confining elephants in forest ecosystems is little understood. In the Shimba Hills National Reserve, Kenya, which has been fenced since 1999, there is evidence of severe, detrimental impact with evidence of deforestation (Knickerbocker & Waithaka, 2016). A critical question is whether fenced montane forests are able to support healthy elephant populations over the long-term whilst maintaining the integrity of the habitat. The importance of a healthy habitat for elephant population persistence has been illustrated in a study by Wittemyer et al., (2007), who demonstrated a positive correlation between habitat quality measured using the Normalised Differential Vegetation Index (NDVI) and the reproductive success measured as female fecundity.

1.6 Impact of confinement on elephant physiology

Fencing is a popular and often necessary management strategy, however a gap in the literature remains, examining their potential impact on the physiology of confined animal populations. Installation of the perimeter fence, and subsequent restriction of movement of the elephant population has led to a fragmented habitat and prohibited seasonal migratory behaviours. Elephants migrate to the lowland savannahs in the wet-season for the high quality browse (Ngene et al., 2010; Bohrer et al., 2014) following the productive response of vegetation to rainfall (Loarie et al., 1998; Rasmussen et al., 2006; Wittemyer et al., 2008; Bohrer et al., 2014). Consequently, confinement within the montane forest may contribute to physiological and psychological stress attributed to preventing natural migratory behaviours and limiting the availability of quality forage, also potentially resulting in nutritional stress. Additionally, restricting the dispersal of adult males could cause an increase in competition for mates as males compete for access to females within the fenced area (Whitehouse and Kerley, 2002), further eliciting a physiological stress response. Monitoring the impact of management techniques or environmental disturbances using physiological biomarkers, offers benefits over employing traditional demographic studies alone. Physiological effects can be detected early on at the individual level, without the delay of measuring the influences of environmental change at the population level, which in long-living species including elephants, could take generations to be detected (Wikelski and Cooke, 2006).

Studies in the literature examining physiological stress in elephants, are primarily focused, but not limited to; translocation (Millspaugh et al., 2007; Viljoen et al., 2008; Pinter-Wollman et al., 2009; Jachowski et al., 2012; Wong et al., 2016), captive elephant welfare (Mason & Veasey, 2010; Kumar et al., 2014), effects of poaching (Gobush et al., 2008), and reproductive behaviours (Ganswindt et al., 2003). It has been suggested that for elephants, environmental (resource availability), behavioural (courtship or mating), and psychological (culling or translocation) stimuli could trigger stress (Viljoen et al., 2008).

Stress is the reaction to a real, or perceived threat to the physiological or psychological wellbeing of an individual. It is the adaptive response that facilitates an individual with the ability to cope with a changing environment or change of status, and in the presence of short-term stressors is key to survival (McEwen & Wingfield, 2002; Jachowski *et al.,* 2012). The stress response is controlled by the central feedback system, the hypothalamic-pituitary adrenal (HPA) axis, and is initiated via the release of hormones including catecholamines and corticotrophin-releasing hormone (CRH) secreted by the hypothalamus that balance the expenditure of energy, and (Sheriff et al., 2011). The pituitary gland releases adrenocorticotrophic hormone (ACTH) as the result of a stressor, and within minutes, the adrenal glands respond by secreting glucocorticoids, steroid hormones responsible for regulating metabolism, appetite, enhancing cardiovascular activity, and supressing non-survival activities including mating (Sapolsky et al., 2000; Tsigos and Chrousos, 2002). This prepares energy reserves within the body for a number of hours in preparation for ‘fight or flight’ (Sapolsky et al., 2000; Mason & Veasey, 2010; Jachowski *et al.,* 2012) (Figure 1.2). At the end of the stressor, the negative feedback loop to receptors within the brain, cease the production of CRH and ACTH, returning the HPA axis to regular function (Sapolsky et al., 2000). The release of glucocorticoids and the subsequent stress recovery rate, is highly variable between individuals as it is influenced by past experience, type, duration and intensity of the stressor (Romero, 2004). Inherently, the short-term production of stress hormones can enable an individual to balance their energy expenditure and promote survival (Romero et al., 2007; Mason & Veasey, 2010; Jachowski *et al.,* 2012). However, chronic over-activation of the endocrine system can have negative welfare implications and include a number of pathological dysfunctions including decreased growth rates and body condition, suppression of the immune system leading to increased parasite loads, poor wound healing and a reduced response to pathogens and premature death (Munck et al., 1984; Mason & Veasey, 2010). Furthermore, declines in reproductive output as a direct result of reduced fertility, low libido and reduced conception rates have been reported in a number of studies (Liptrap, 1993; Dobson & Smith, 2000; Romero, 2004; Fernando, 2006; Dickens et al., 2010; Mason & Veasey, 2010). With the negative effects associated with stress, combined with the life-history traits of long gestation periods and long generation intervals in elephants, there could be profound consequences for the long-term population stability of an already vulnerable species (Wittemyer et al., 2007).

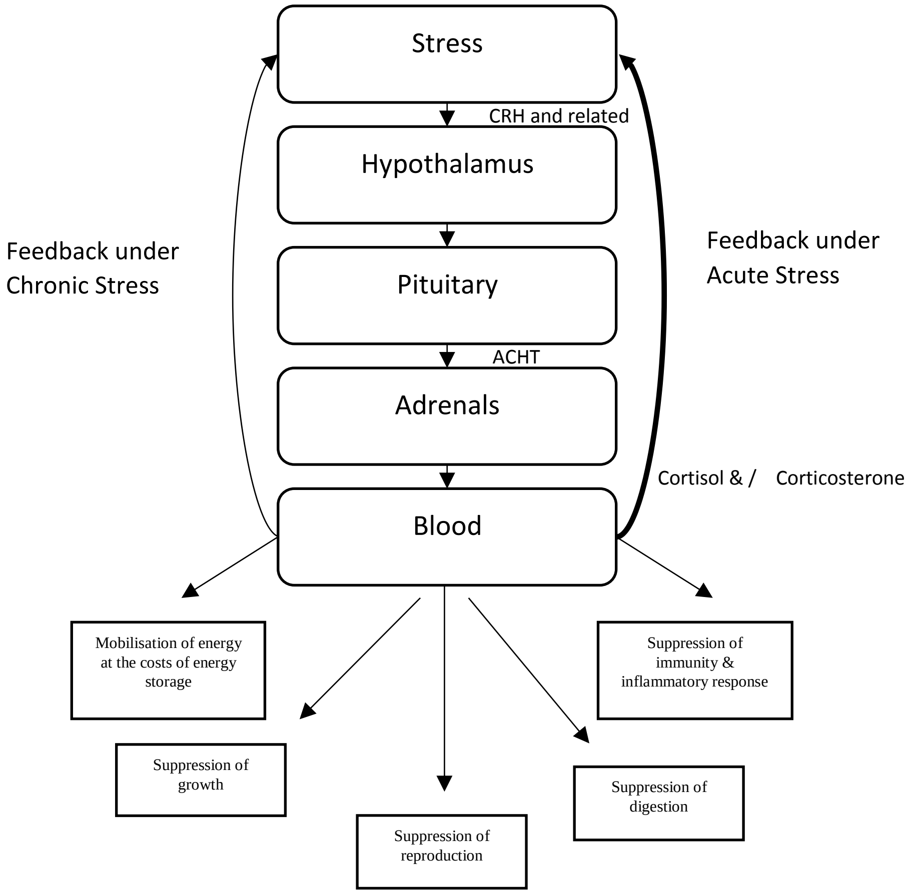

Figure 1.2 The negative feedback response to acute and chronic stressors and their impact on physiology (reproduced from Boonstra et al, 1998)

Although there are several endocrine reactions involved in the stress response, the primary hormones produced in the adrenal-cortex are the glucocorticoids, which are elevated during periods of stress (Mostl & Palme, 2002). Previously, hormone concentrations were determined using blood, which provided an instantaneous analysis of the level of hormones circulating at that exact time (Touma and Palme, 2005). However, in wildlife research this method provided limitations, including the difficulty in obtaining access to animals as it requires capture, and in certain species sedation, but also, the animals reaction to handling can in itself cause stress, compromising the validity of the assessment (Millspaugh & Washburn, 2004; Touma and Palme, 2005). The development of faecal endocrinology techniques measuring concentrations of glucocorticoid metabolites from faeces has become popular with conservation biologists due to their ability to measure long-term stress in a variety of mammalian species, including elephants, in a non-invasive manner (Wasser et al., 2000; Touma & Palme, 2005; Foley et al., 2001; Ganswindt et al., 2003; Viljoen et al., 2008). Moreover, due to their transition time through the through the gastrointestinal tract, they demonstrate an average concentration of glucocorticoids secreted by the adrenal glands over a period of time that is determined via gastrointestinal transit (Touma & Palme, 2005). An important consideration when measuring glucocorticoids from faeces, is that metabolisation of hormones differ between species and therefore requires validation via either physiological (ACTH injection), or biological (natural stressor) methods (Wasser et al., 2000; Watson et al., 2013). Furthermore, biochemical validation of the enzyme immunosorbent assay (EIA) must be performed, to ensure that the assay monitors only the metabolites of interest, with minimal cross reaction of other steroid hormone metabolites (Palme, 2005; Goymann, 2012).

1.7 Thesis aims

To mitigate human-elephant-conflict (HEC) and to protect the forest, Kenya Wildlife Service (KWS) implemented the necessary strategy of fencing the Aberdare Conservation Area, a montane forest in Kenya.

The primary aims of this thesis are to;

- Measure the impact of a confined elephant population on the extent, and quality, of the forest habitat (**Chapter Three**)

- Calculate current density of elephants in the confined montane forest (**Chapter Four)**

- Assess the demographic structure of the confined population in comparison to free-roaming populations (**Chapter Five**)

- Examine the physiological condition of elephants in the confined population compared to free-roaming populations using non-invasive biochemical markers (**Chapter Six)**

1.8 Thesis outline

To quantify the ecological impact of a static elephant population on the integrity of the forest habitat, remote sensing techniques were applied in chapter 3. Study sites include the primary study site, the Aberdare National Park, and a smaller forest, the Shimba Hills National Reserve which has been fenced for a longer period of time. The two study sites were selected in order to assess whether changes to the vegetation structure differed in protected areas of differing sizes, and over a longer-period of time since the confinement of the elephant populations. Satellite data from the MODIS sensor (Product MOD13Q1), were downloaded for the years 2000 to 2016, totalling 386 scenes for each location.

Understanding the long term impact of isolation on the growth potential and viability of the population, requires continuous monitoring of population numbers, and information on the demographic structure. Chapter 4 employs the Random Encounter Model (REM) method using camera traps to estimate elephant density in the confined Aberdare Conservation Area population. A total of 71 individual camera stations were deployed between June and August over the years 2015-2017, resulting in a total survey effort of 1,234 days. Demographic data including the age and sex (when possible) of elephants, were recorded from a total of 815 elephants across the primary study site (Aberdare Conservation Area), and three free-ranging populations. A rapid demographic assessment (RDA) compares the confined elephant population to the free-roaming populations, and against populations of known growth status from published data, providing a reference to the current status of the confined population. Data acquired from these two chapters (4 and 5), is also to be utilised in the continuous, long-term monitoring the population.

Further to chapters 4 and 5 on assessing the future viability of isolated populations. Chapter 6, addresses the paucity of information on the physiological impact of confinement, non-invasive measures of ‘stress’ using endocrinology techniques were employed. A total of 438 fresh faecal samples from elephants were collected over a 3 year period from the primary study site (Aberdare Conservation Area), and from two free-roaming populations (Samburu National Reserve, and Lewa Wildlife Conservancy) to provide a comparative analysis. During exportation, 204 samples were damaged, and subsequently removed from the study. Faecal Glucocorticoid Metabolites (FGM) were extracted, and concentrations measured using an enzyme immunoassay (EIA).

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Chapter 2

Study populations

2.1 Study Locations

Between June 2016 and August 2018, data were collected from five elephant populations in Kenya, East Africa (Figure 2.1).

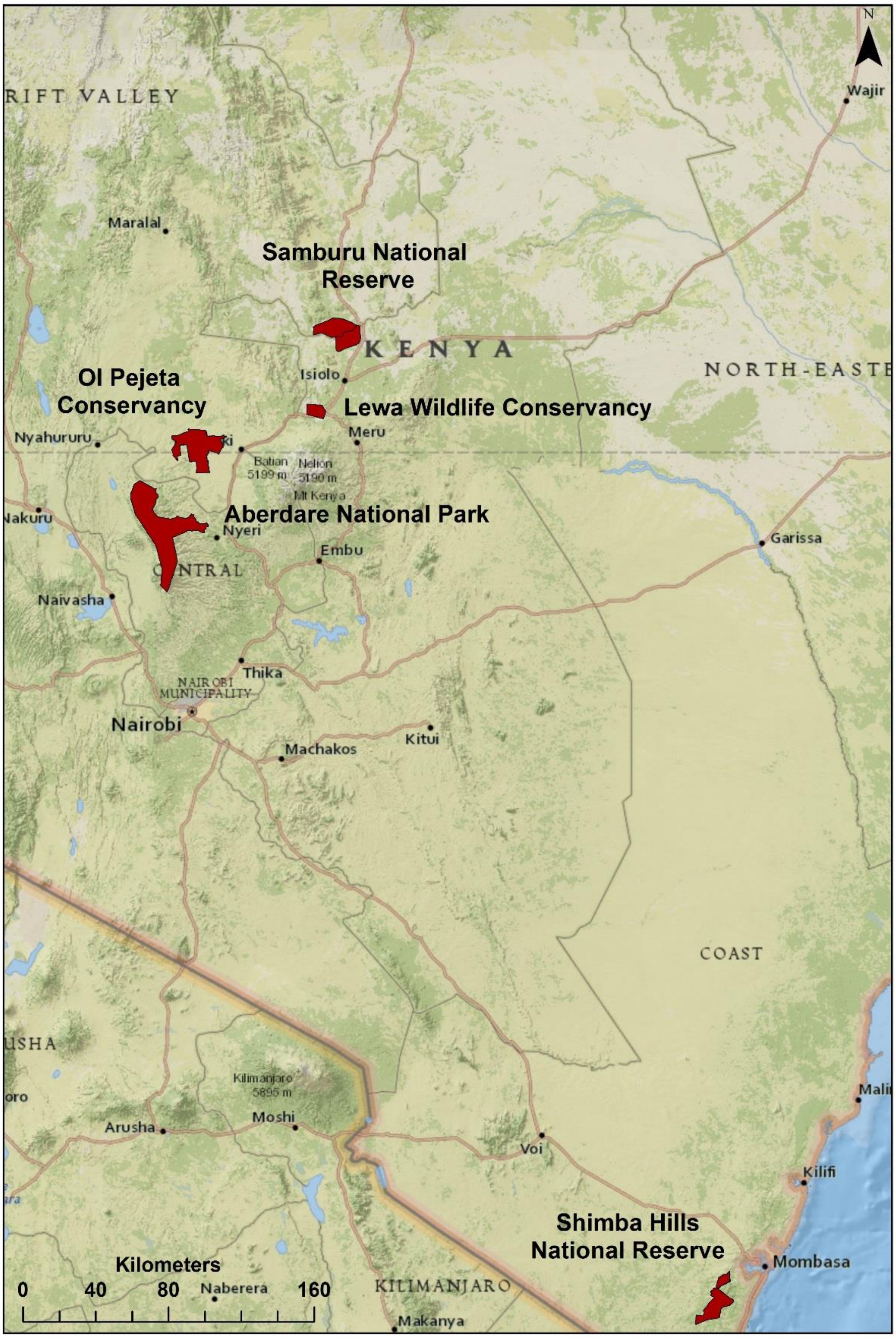

Figure 2.1 Map showing the location of each study population in Kenya

2.2 Aberdare Conservation Area

2.2.1 Overview

The Aberdare Conservation Area (ACA) (36°43’ E 0°25’ S) is located in the Central Province of Kenya on the Equator (Figure 2.1). It lies Southwest of Mount Kenya and forms the Eastern rim of the Great Rift Valley, stretching from the towns of Nyahururu in the North, to Limuru in the South. The Aberdare Conservation Area (ACA) is comprised of the 767km2 Aberdare National Park (ANP), and the surrounding Aberdare Forest Reserves, covering a total area of 1,748 km^2. This montane area became isolated during glacial maxima and the recurrent expansions and contractions of the forest. Constituting part of the Albertine Rift (Demos et al., 2014), the area was identified as a biodiverse hotspot, globally having the second highest concentration of mammalian richness (Ceballos et al., 2005) and is part of the Eastern Afromontane hotspot that became refuges for a wide variety of taxa (Demos et al., 2014).

The Aberdare National Park, along with Mount Kenya, Mau Complex, Cherangani Hills and Mount Elgon, are known as the five “Water Towers” of Kenya, providing essential ecosystem services including water catchment, the production of electricity generated by hydropower, and supporting agricultural irrigation schemes (Lambrechts et al., 2003; Baker & Miller, 2013). However, a rapidly increasing human population, with an estimated population size of 47,633,652 (United Nations, 2016) has increased demands for agricultural land, subsequently encroaching the National Parks, and threatening their integrity. To protect the Afromontane forests, Kenya embarked on a strategy of fencing. In 1989, construction of the world’s largest electric wildlife fence began, it was commissioned in nine phases and completed in 2009 (Figure 2.3).

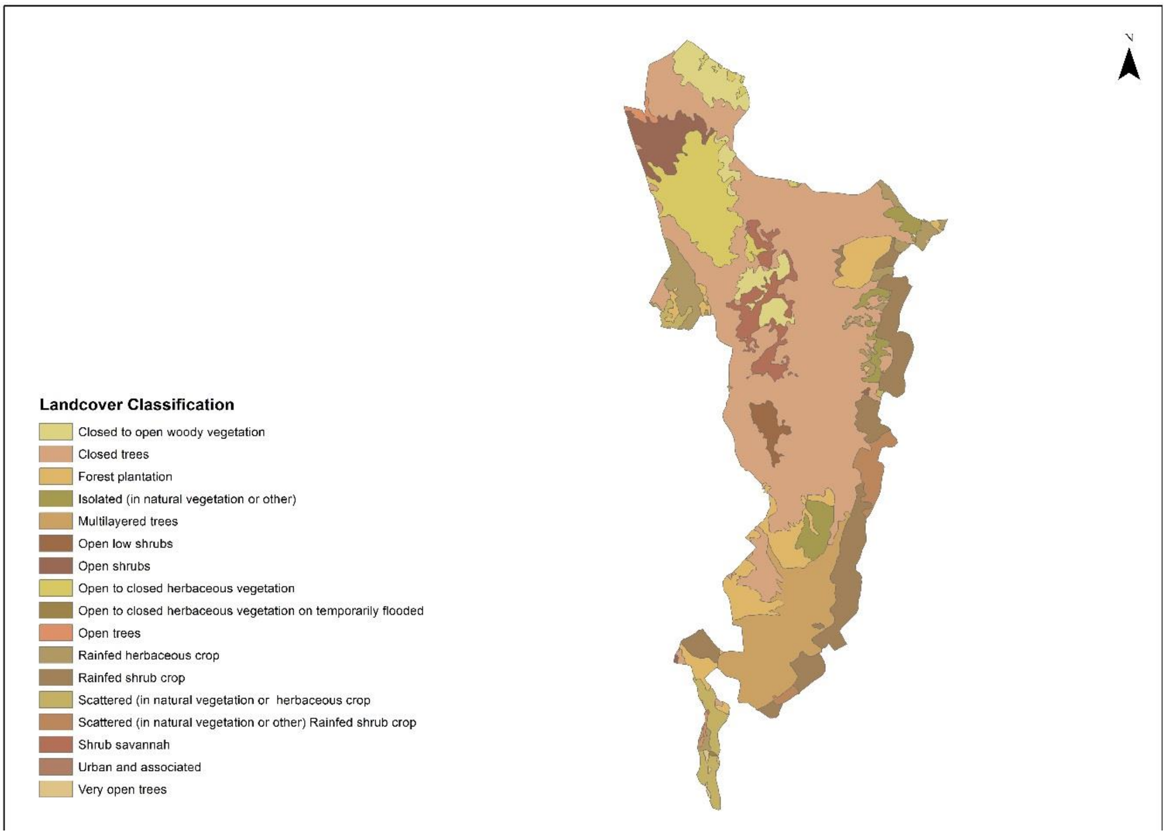

Figure 2.2 Vegetation map of the Aberdare Conservation Area (Africover, 2000)

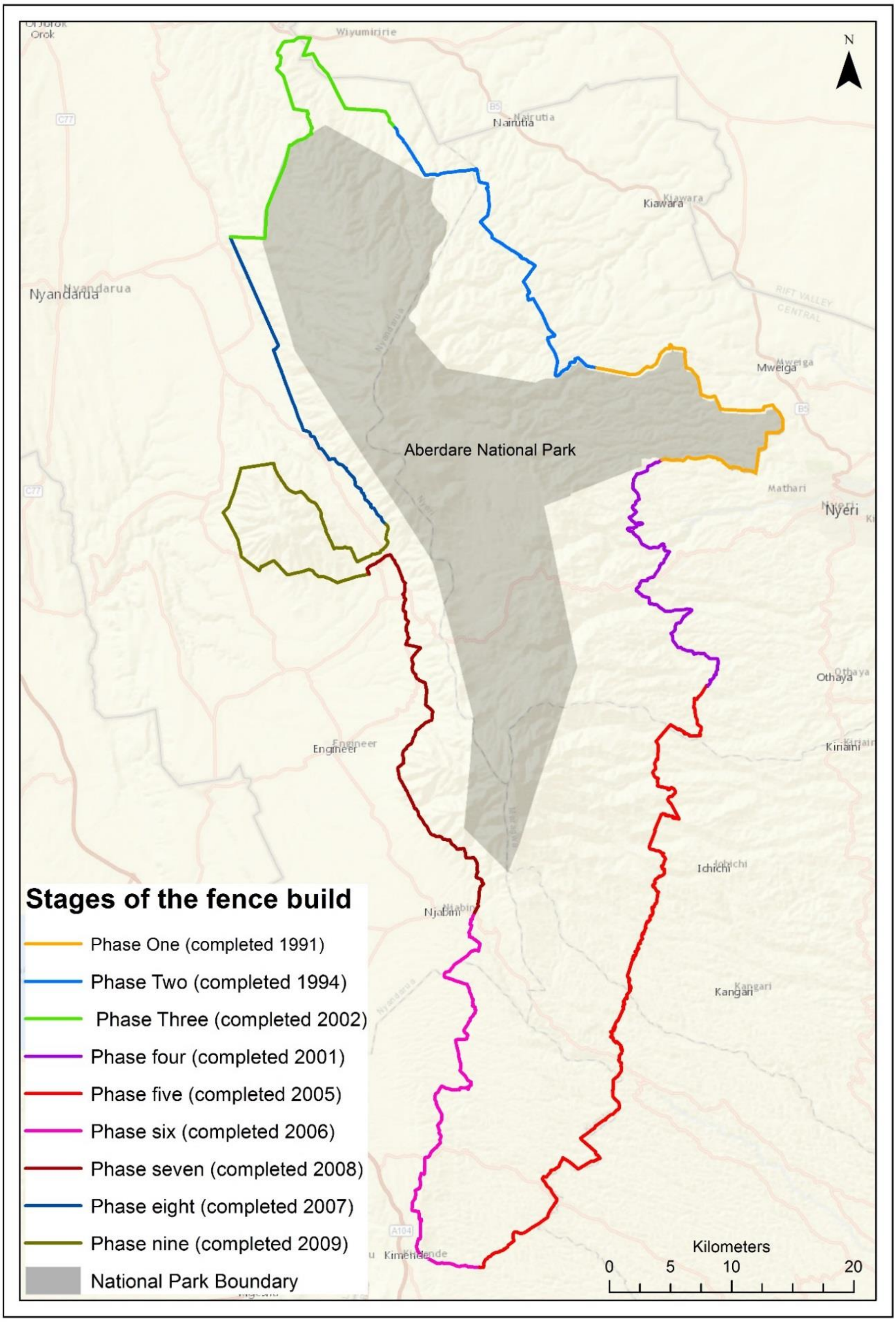

Figure 2.3 Map showing the location, phases, and completion date of the fence surrounding the perimeter of the Aberdare Conservation Area, Kenya

2.2.2 Climate

The region experiences two periods of rainfall per annum, with the long rains occurring from March until late May, and the short rains between October and December. The high altitudes (~ 1800m to ~ 4000 m) mean that there is cloud cover throughout the majority of the year, giving a uniform climate with temperatures averaging 17° C and an average rainfall of 1600mm per annum.

2.2.3 Habitat

There are a wide variety of habitats within the Aberdare Conservation Area, with four main vegetation types (Table 2.1). Common tree species include Camphor (*Ocotea usambarensis*), Cedar (*Juniperus procera*), Podo (*Podocarpus latifolius*), and Hagenia (*Hagenia abyssinica*).

Table 2.1 Description of the main vegetation zones and respective species within the fenced boundary of the Aberdare National Park (reproduced from Rhino ark, 2016)

Vegetation Zone	Altitude (m)	Characteristic Species
Montane forest		
- Moist forest	1900 -2500	- *Cassipourea malosana*, *Ekebergia capensis*, *Teclea nobilis*, *Calodendrum capense*, *Podocarpus latifolius, Nuxia congesta*
	2100 – 2500	- *Ocotea usambarensis, Macaranga kilimandscharica, Neoboutonia macrocalyx, Tabernaemontana stapfiana, Prunus Africana*
- Dry forest	1800 – 2400	- *Juniperus procera, Calodendrum capense, Teclea simplicifolia*
	2300 – 3300	- *Juniperus procera*, *Olea europaea* (*africana*), *Podocarpus*

		falcatus, *Nuxia congesta*
Bamboo	2400 - 3300	- *Arundinaria alpina* with scattered trees, including *Podocarpus latifolius* and *Nuxia congesta*
Hagenia-Hypersicum	2950 - 3500	- *Hagenia abyssinica*, *Hypericum revolutum*, *Rapanae melanophloeos*
Ericaceous	2900 - 3560	- *Erica excelsa*, *Erica trimera*, *Erica arborea*, *Cliffortia nitidula*, *Helichrysum nandense*, *Stroebe kilimandscharica*

2.3 Ol Pejeta Conservancy

2.3.1 Overview

Ol Pejeta Conservancy (OPC) (36°55’ E 00°02’ N) is located on a plateau in the Laikipia District, Central Kenya, with Mount Kenya to the East and the Aberdare Conservation Area (ACA) to the West (Figure 2.1). The 360 km^2 wildlife conservancy was a former, colonial cattle ranch until 1988 when the “Sweet Waters” Game Reserve was established, predominantly as a sanctuary for black rhino. In 2003, the cattle ranch and game reserve were purchased by Fauna and flora international to become Ol Pejeta, a conservancy home to a variety of wildlife, including elephant (*Loxodanta Africa*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), lion (*Panthera leo*), and various ungulates. To reduce human-wildlife conflict the area has an electric perimeter fence, however, the Northern boundary has provisioned wildlife corridors to enable the passage of migratory species, including elephants to move seasonally between the conservancy and the greater Laikipia, and Samburu ecosystems. This area forms one of the control population sites by measuring the physiological condition, including faecal stress hormones, and body condition scores of the free-ranging elephants that seasonally utilise the region.

2.3.2 Climate

There are two periods of annual rainfall, with the long rains occurring from March until late May, and the short rains between October and December. The average annual rainfall is approximately between 600mm to 800mm. The high altitude (~ 1600 m) means that the climate is cooler than expected for an area lying on the equator, with average daily temperatures ranging in the mid-twenties.

2.3.3 Habitat

The conservancy has five main habitat types; grasslands, which are dominated by three main species; *Themeda trianra, Penisetum,* and *Penisetum mezianum.* Open bushland which covers over half of the area and is characterised by the Acacia *(Acaciadrepanolobium*) which elephants browse. Dense bush land where the *Eucleadivinorum* is predominantly found, riverine habitat, dominated by another Acacia species (*Acaciaxanthophloea*), and an area of marsh land that is dominated by *Cyperus*.

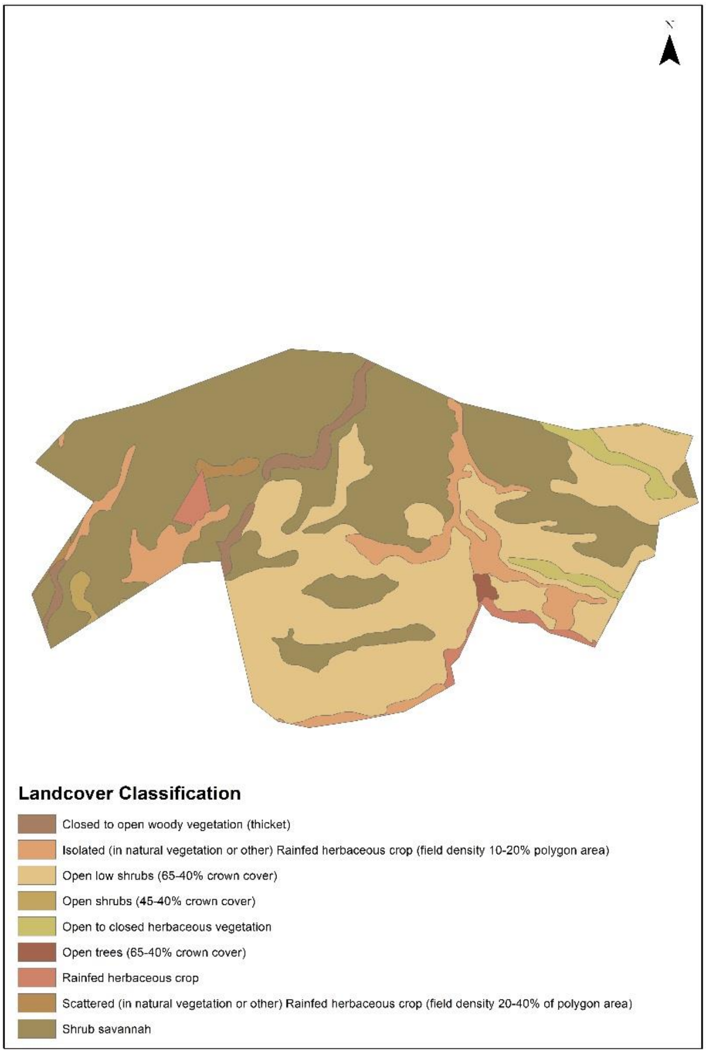

Figure 2.4 Vegetation map of the Ol Pejeta Conservancy (Africover, 2000)

2.4 Lewa Wildlife Conservancy

2.4.1 Overview

Lewa Wildlife Conservancy (LWC) is a 250 km^2 conservancy located in the Isiolo District, approximately 20 km South of Isiolo town, and North of Mount Kenya (Figure 2.1). For over 50 years it was managed as a private cattle ranch and in 1953, the Ngare Sergoi Rhino Sanctuary in the West of the area was established to conserve a declining black rhino population in Kenya. In 1995, the rhino sanctuary was expanded to include the Ngare Ndare forest, forming the Lewa Wildlife Conservancy. As part of the conservation and management strategy for the black rhino (2007-2011), the fence between Lewa and the neighbouring Borana conservancy was removed. Although a perimeter fence surrounds the area to reduce human-wildlife conflict, gaps remain in certain areas allowing the passage of migrating elephants to the surrounding areas and North of Kenya. In addition, the Mount Kenya Elephant Corridor (MKEC) which connects a 14 km traditional migration route, enabling elephants to seasonally migrate between Mount Kenya and the Ngare Ndare forest, to Samburu County in the North via Lewa Wildlife Conservancy. The area forms one of the control population sites by measuring the physiological condition, including faecal stress hormones, and body condition scores of elephants. Due to the corridor connecting the Mount Kenya National Park and Ngare Ndare forest, this population enables a direct comparison to the Aberdare Conservation Area, as the habitat in Mount Kenya National Park is also a montane forest with similar characteristics to the Aberdare National Park, however the elephants utilising Mount Kenya and the Ngare Ndare forest are not prohibited from seasonal migrations.

2.4.2 Climate

As with the Laikipia District, Lewa Wildlife Conservancy experiences two distinct rainfall patterns per annum, however the average annual volume of rainfall is approximately 300-350 mm per annum. With an altitude of ~ 1600 m above sea level, daytime temperatures can range between approximately 10^{o}C and in excess of 30^{o}C.

2.4.3 Habitat

There are four main habitat types in the conservancy; grass plains which are dominated by the *Pennisetum*, *Penisetum stramineum,* and *Penisetum mezianum* species of grass and *Acacia drepanolobium* and *Acacia seyal* for the trees. The hills and slopes habitat is characterised by predominant tree cover of the Acacia species including *Acacia brevispica*, *Acacia mellifera*, *Acacia nilotica*, *Acacia seyal,* and *Acacia tortilis.* The Ngare Ndare Forest is densely covered with *Juniperus procera-Olea Africana, Dodonea* and *Rhus* tree species. The riverine habitat encompasses areas that have elephant exclusion zones and is dominated by the tree species *Acacia xanthophloea.*

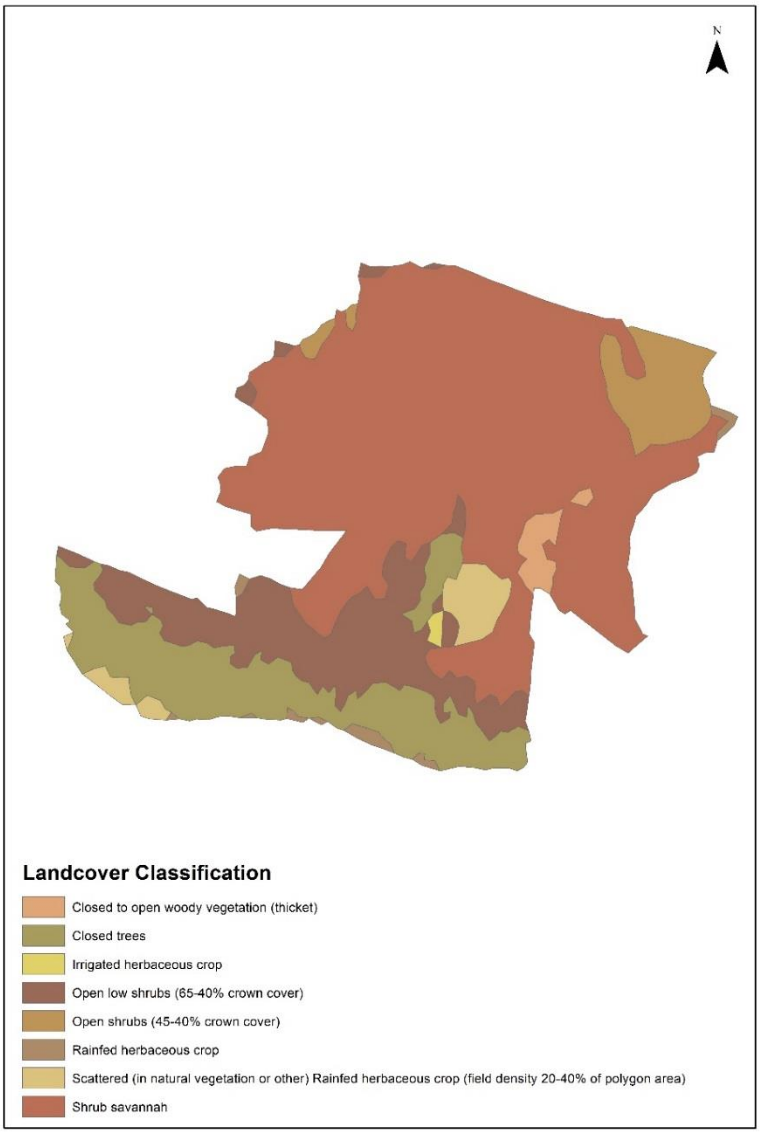

Figure 2.5 Vegetation map of the Lewa Wildlife Conservancy (Africover, 2000)

2.5 Samburu National Reserve & Kalama Conservancy

2.5.1 Overview

Samburu National Reserve (SNR) covers an area of 165 km^2 located in the Samburu District of the Rift Valley Province (0'30' N, 37’30' E) (Figure 2.1). To the south it is bordered by the Ewaso Nyiro river which separates it from the Buffalo Springs National Reserve (131 km^2), and the Kalama community conservancy (461 km^2) borders to the North, there are no fences around these reserves and they are a critical migratory corridor for elephants moving between the northern and southern conservation areas. The area forms one of the control population sites by measuring the physiological condition, including faecal stress hormones, and body condition scores of elephants.

2.5.2 Climate

The area is classified as arid and semi-arid and evapotranspiration is greater than the moisture available. Similar to the Laikipia and Isiolo regions, the area experiences two rainfall seasons occurring from March until late May, and between October and December, with mean annual rainfall of 354mm per annum. With altitudes ranging between 800 m to 1230 m above sea level, daily temperatures vary between 18^{o}C and 30^{o}C and the days can be very hot whilst the nights can be cool.

2.5.3 Habitat

The area has three habitat types; semi-arid bushland consisting of Acacia desert-scrub and Acuciu short-grass types. Thorn-bushland and thicket, and the riverine strip with a mixture of vegetation communities.

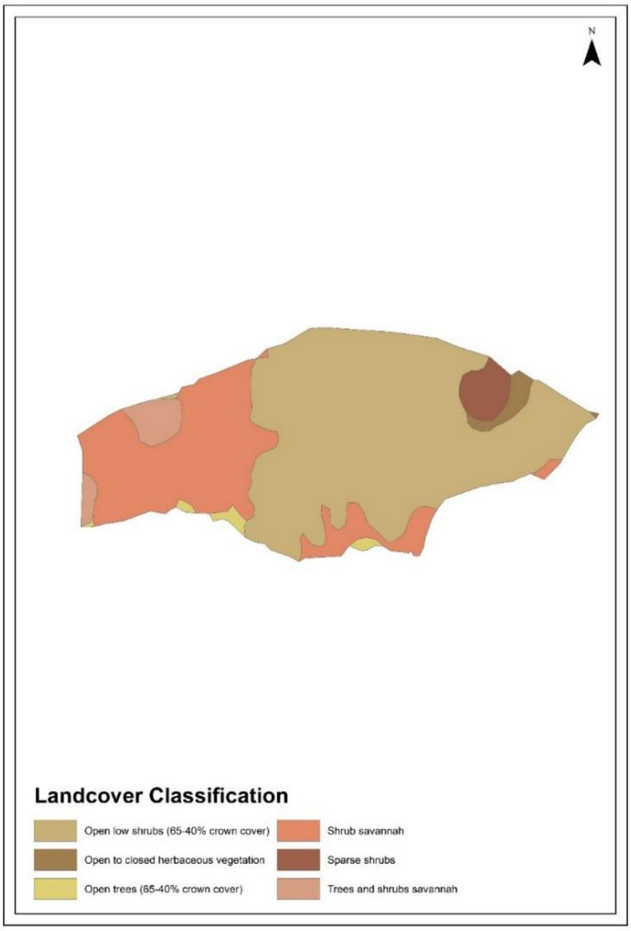

Figure 2.6 Vegetation map of the Samburu National Reserve (Africover, 2000)

2.6 Shimba Hills National Reserve

2.6.1 Overview

Shimba Hills National Reserve (SHNR) (04^{o}15’26’ S, 39^{o}23’16 E) is 253 km^{2} forest reserve located in the Kwale District, in the Coastal Province, approximately 33 km South-West of Mombasa (Figure 2.1). This costal forest forms part of the “Eastern Arc and East African Coastal Forests Biodiversity Hotspot”, one of the world’s 25 biodiverse hotspots (Myers et al., 2000). In 1903 the forested area was appointed a National forest, with the surrounding grasslands incorporated in 1924, and additional extensions in subsequent years brining the Reserve to its current size in 1968. In 1999, a perimeter fence was installed to protect the Reserve, however, this meant that it then contained an estimated 600+ elephants, three times the recommended carrying capacity for an area of its size of approximately 200 individuals (Knickerbocker and Waikika, 2016). As a result of an overpopulation of elephants, 150 individuals were translocated from the area to Tsavo East National Park (Pinter-Woolman et al., 2009).

2.6.2 Climate

The region experiences two rainfall patterns each year, the highest volume of rain occurs between April and July, with shorter rains arriving in October and lasting until November with an average of 1,213 mm per annum. With an altitude of 348m above sea level, the temperature averages at 25°C.

2.6.3 Habitat

The area has five main vegetation types; Forest, Forest/Scrub, Grasslands, Scrub/Grassland, Plantations, and has 1396 indigenous species recorded. The largest families represented are Leguminosae, Gramineae, and Rubiaceae, with *Cyperus*, *Ficus*, and *Ipomoea* being the largest genera (Luke, 2005).

Figure 2.7 Vegetation map of the Shimba Hills National Reserve (Africover, 2000)

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Chapter 3

Detecting vegetation change in response to confining elephants in forests using MODIS time-series

3.1 Introduction

The East African montane forests, rich in biodiversity and providers of vital ecosystem services to the human population, are under intense pressure (Gichuki, 1999; Orodho, 2006; Baker and Miller, 2013). Over 31% of the Earths' surface is covered by forests, and maintaining the integrity of forest ecosystems is a global conservation concern (Sexton et al., 2015). Although there is no consensus on the impact of climate change on lowland productivity (Thornton et al., 2007; Sangeda and Malole, 2014), analysis suggests that some areas have become drier, noticeably reducing the length of the growing season (Sangeda and Malole, 2014). The combination of rising temperatures and altered rainfall patterns, are major factors in food insecurity (Sandstom and Juhola, 2017; Nian et al., 2014; Christensen et al., 2007). Subsequently, with increasing human populations and a decline in productivity in the rangelands, pressure on the East African montane ecosystems is expected to increase.

Montane forests and highland areas account for 15.2% of Kenya's total area (Gichuki, 1999). Five of these, namely the Aberdare National Park (ANP), Mount Kenya, Mau Complex, Cherangani Hills and Mount Elgon, are known as the "Water Towers", they are an important water resource for the country (Baker and Miller, 2013) accounting for 75% of the renewable surface water (UNEP, 2012). Two of these "Water Towers" (Aberdare mountain range and Mount Kenya) produce 55% of Kenya's electricity, which is generated by hydropower, and support major irrigation schemes required by the agricultural sector that contributes to a quarter of the country's GDP (Rhino Ark, 2011). The degradation of Kenya's forests and subsequent impact on climate change, could not only severely affect agricultural production (Hansen and Indeje, 2004; Rarieya and Fortun, 2010), but also have negative ramifications for the human population.

The Kenyan montane forests are refuges that became isolated during glacial maxima and recurrent expansions and contractions of the forest (Demos et al., 2014). This history has produced centers of endemism and biodiversity hotspots which incorporate an extensive range of habitats promoting a unique biodiversity for East Africa. They support a number of threatened mammal species such as the critically endangered mountain bongo (*Ragelaphus eurycerus*), and are an internationally recognised Important Bird Areas. Although not a montane forest, or forming the "water towers" of Kenya, the Shimba Hills forest in the Southern coastal zone is a significant regional water catchment that is also monitored by various state agencies in charge of water towers. It contains three threatened and two restricted-range bird species and is home to the country's only population of sable antelope (*Hippotragus niger*) (Kenya Wildlife Service, 2012).

The areas surrounding Kenya's forests have experienced large-scale changes in land-use change as a result of a rapidly expanding human population, which has also led to an increasing competition for resources between people and wildlife. Human-elephant conflict (HEC) has become a major conservation concern (Graham et al., 2010) with increasing cases of property damage, crop raiding and human death and injury (Knickerbocker and Waithaka, 2016). In response to HEC, and to protect the forests from the pressures of illegal activities, including logging, poaching and illegal kilns to supply the charcoal trade, Kenya has embarked on an strategy of using electric fencing enclosing the montane regions and other forests containing elephant populations. Although fencing some of the "Water Towers" and Shimba Hills National Reserve is already well underway, the impact of confined elephants on forest health, and the ramifications on other taxa that rely on these areas as dry season refugia, is unknown.

Under the threat of degradation by anthropogenic and biogenic pressures, and the little understood impact of fencing it is becoming increasingly common to separate people and wildlife. There's an obvious need to assess the impact of fencing on the integrity of forest ecosystems and to monitor the long term health of forests to guide management strategies to preserve both species, and habitats. Previous techniques assessing the impact of mega-herbivores on ecosystems have been limited to the collection of ground data assessing tree damage (Penzhorn et al., 1974; Barratt and Hall-Martin, 1991; Stuart-Hill, 1992). A major drawback with this approach is that it is limited to only those areas that are relatively easily accessible and can only be conducted on a relatively small scale. Consequently, montane regions have remained relatively understudied as they are commonly found in largely inaccessible areas, with challenging terrain and limited road access (Verbesselt et al., 2012; DeVries et al., 2015).

With increasing habitat fragmentation from fencing and land use change, ecologists have become increasingly interested in the capacity of some species to permanently alter their habitat and modify the environment (Kerley and Landman, 2006; Pringle, 2008). Elephants have been documented to reduce the cover of woodland (Ben-Shahar, 1996) and cause large- and small-scale disturbances to the land. Bark-stripping, uprooting trees, and opening up vegetation by trampling plant communities whilst foraging, combined with their preferential seasonal feeding, can cause irreversible damage to trees and bushes (Haynes, 2012). In addition, they dig wells to reach water under the surface, and smooth rock surfaces and tree stumps whilst rubbing up against them to scratch (Penzhorn et al., 1974; Haynes, 2012; Douglas-Hamilton and Douglas Hamilton, 1975). In instances where there have been significant impacts, wildlife corridors and translocations of elephants have been used as a measure to limit and reverse such damage. In 2005, for example, as a response to elephant overpopulation, negative impacts on the vegetation (Knickerbocker and Waithaka, 2016), and to reduce HEC, 150 elephants were translocated from the Shimba Hills forest to Tsavo East National Park (Pinter-Wollman et al., 2009).

Over the last decade, there has been an increase in the use of remote sensing approaches for monitoring deforestation over large areas, due to the opening of the Landsat archive in 2008 (Woodcock et al., 2008; Wulder et al., 2012; Hansen et al., 2013). The use of Earth observation (EO) data with challenging terrain is undoubtedly faster and more cost effective than approaches employing field data only (Broich et al., 2011).

Mapping changes in forest cover with remotely sensed imagery has most frequently been carried out using a bi-temporal change detection approach, whereby multiple images are selected from key points in time and land cover change maps are produced using a supervised classification technique (e.g. Maximum Likelihood, Random Forests) (Coppin et al., 2004; Yin et al., 2014). However, DeVries et al., (2015) highlighted the potential problem of cloud contamination using this method, particularly when working in the tropics or in montane regions (Ju and Roy, 2008; Mitchard et al., 2012). When using only a limited number of images during temporal comparisons, subtle disturbances and vegetation regrowth processes might be missed due to large temporal gaps in the period between start and end dates. This can be problematic when detailed vegetation dynamics are required to guide habitat management decision-making (Zhu and Woodcock, 2012). To avoid errors in change detection, it is also vital to select scenes that are from the same phenological period as seasonal variability within the forest can result in confusion between forest and non-forest pixels (DeVries et al., 2015; Coppin et al., 2004). The sparse Landsat archive in large parts of East Africa further complicates the ability to choose appropriate imagery at this scale and for this region. As a result, LiDAR (Light Detection and Ranging) data is increasingly being used to map gaps in the forest canopy and to identify degradation (Asner et al., 2013; Mitchell et al., 2017). However, persistent cloud cover, steep topography, limited temporal datasets and the high associated economic costs especially in developing areas means that LiDAR can be unsuitable for detecting change over time, particularly in montane forests (Mitchar et al., 2012).

To increase the sensitivity of detecting discrete changes in montane forest ecosystems, it is, therefore, advantageous to employ more robust approaches of dense time series analysis that can also consider seasonality (Zhu and Woodcock, 2012; Kennedy et al., 2012; Verbesselt et al., 2010; Lambert et al., 2013; DeVries et al., 2014). The recent development of a range of algorithms including LandTrendR (Kennedy et al., 2010) for the Landsat archive and Breaks For Additive Season and Trend (BFAST) (Verbesselt et al., 2012) for Landsat and MODIS datasets, has enabled near real time monitoring in the health and dynamics of ecosystems worldwide (Kennedy et al., 2014). BFAST has previously been applied in a montane forest in Ethiopia and successfully identified small-scale forest disturbances (DeVries et al., 2015). It has been proven to be robust in determining both discrete and abrupt changes in forest cover in a variety of habitats (Lambert et al., 2013; Dutrieux et al., 2015; Hutchinson et al., 2015), even in regions with high cloud contamination such as the Kenyan montane forests. Landsat data with a relatively fine spatial resolution (30m-pixels), spanning more than four decades, could be ideal for studying forest disturbances using LandTrendR or BFAST. However, significant gaps in the archive exist over East Africa for the mid- 1990s and early 2000s (Appendix A1). A trade-off in the spatial dimension, as well as the depth of the historical records, is to use imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) at a very fine temporal (16-day) but coarser spatial (250m pixel) resolution, to detect forest disturbances in this region (Hutchinson et al., 2015; Hansen et al., 2008; De Souza et al., 2009).

Within this context, our aim was to detect vegetation change and assess forest condition in two fenced forests of Kenya. Both climatic and non-climatic drivers of change were considered, along with the impact of fencing elephants in forests, which has never been examined using remote sensing before. We employ BFAST on the Enhanced Vegetation Index (EVI) derived from MODIS time-series data in combination with TAMSAT monthly rainfall estimates and the MODIS burned area product to identify the direction and magnitude of change in the forest canopy. We also map the potential drivers of change, in combination with ground truth data, to assess the suitability of using medium-resolution satellite imagery providing near real-time information on the dynamics of Afromontane forests characterised by gradual change.

3.2 Materials and Methods

3.2.1. Study site – Aberdare National Park, Kenya

The Aberdare National Park (ANP) covers an area of 766 km^2 in the Central Province of Kenya. It lies southwest of Mount Kenya forming the Eastern rim of the Great Rift Valley (Figure 1). The altitude in the park varies from ~ 1800m to ~ 4000 m. This high altitude means that the area experiences cloud cover throughout the majority of the year. It has a uniform climate, with temperatures averaging 17° C. It is characterised by high annual rainfall, as high as 3000 mm in south-eastern areas. There are two 'wet' seasons, with the long rains starting in March and lasting until late May, and the short rains arriving in October and ending in December. In 1989, the construction of the world's largest, electric 'wildlife' fence surrounding the perimeter began. It was commissioned in eight phases and was completed in 2009. The area now contains a confined elephant population with a recent survey estimating ~4000 elephants (pers.com. Kenya Wildlife Service, 2017).

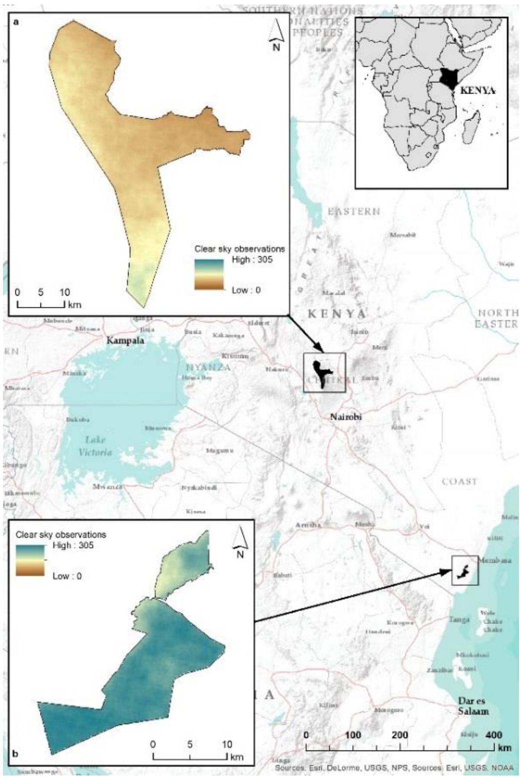


Figure 3.1 Location of the study areas within Kenya and clear sky observations of Modis MOD13Q1 for **(a)** Aberdare National Park and **(b)** Shimba Hills National Reserve

3.2.2. Study site – Shimba Hills National Reserve, Kenya

Shimba Hills National Reserve (SHNR) is a smaller forest reserve covering 253 km^2 located in the Kwale District in the Coastal Province of Kenya (Figure 1). The altitude within this Reserve is much lower than the ANP, averaging at just 348m above sea level, meaning that the cloud cover across the area is significantly lower. With a climate averaging 25°C, the area receives less than half of the annual volume of rain as the ANP, averaging just 1,213 mm per annum. This coastal region experiences two 'rainy' seasons. The highest volume of rain occurs between April and July, with shorter rains arriving in October and lasting until November. The perimeter has been fenced since 1999, with the current estimated elephant population in the reserve of >600 individuals. It is suggested that the elephant population is three times the recommended carrying capacity of circa 200 individuals (Knickerbocker and Waithaka, 2016).

3.3. Satellite-based data

3.3.1. MODIS EVI

The response variable used to detect vegetation change was the MODIS Enhanced Vegetation Index (EVI), a measurement of photosynthetic activity in vegetation at a location, ranging from 0 (indicating no vegetation) to 1 (dense vegetation):

$$EVI = G\frac{NIR - Red}{NIR + C1Red - C2Blue + L}$$

where, G is the gain factor, NIR is the Near Infra-red band, C1 and C2 are the coefficients of the aerosol resistance term, and L is the canopy background. Whilst the Normalized Difference Vegetation Index (NDVI) (Tucker, 1979) is commonly used (DeVries et al., 2015; Dutrieux et al., 2015), as in a number of other forest studies, we chose the EVI, (Matsushita et al., 2007; Brando et al., 2010; Phompila et al., 2015) due to its improved performance in areas of high biomass as a result of a de-coupling of canopy background signals and a reduction in atmospheric influences (Huete et al., 2002). We used the MODIS EVI product MOD13Q1 at 250m spatial and a 16 day temporal resolution downloaded from the United States Geological Survey (USGS; Table 1).

Table 3.1 Datasets used for the change detection

Dataset	Parameter	Spatial Resolution	Temporal Resolution	Source	Number of Scenes per study site
MODIS MOD13Q1	EVI	250m	16 Day	https://espa.cr.usgs.gov	386
TAMSAT	Rainfall	4km	Monthly	https://www.tamsat.org.uk	132
MODIS MCD451A	Fire	500m	Monthly	https://earthexplorer.usgs.gov/	132

All available scenes, totalling 386, average of 23 per year were acquired for each site spanning the period of February 2000 to December 2015 to produce 15 year annual profiles. The MOD13Q1 is provided as a surface reflectance product and masked for water, clouds, heavy aerosols, and cloud shadows. We applied another mask to the data in R (R Core Team, 2014) which employs the quality assessment layer, thus addressing pixel reliability. We only kept those pixels in the time-series analysis that were confidently ranked as of ‘good quality’ in the product information guide.

3.3.2. TAMSAT rainfall

Monthly rainfall was also incorporated in the analysis to evaluate the effect of rainfall on the variation of the EVI values (Table 1). We employed the Tropical Applications of Meteorology Using Satellite and Ground-Based Observations (TAMSAT) monthly data with a 4km spatial resolution (Maidment et al., 2017; Tarnavsky et al., 2014; Maidment et al., 2014). The TAMSAT method calibrates the algorithm using rain gauge observations combined with contemporaneous cold-cloud duration (DDC) to infer rainfall estimates and anomalies (Tarnavsky et al., 2014). We derived anomalies in rainfall patterns based on differences between the observed and expected volume of rainfall for each study site by running the BFAST algorithm on the monthly rainfall estimates data to allow a visual representation.

3.3.3. MODIS burned area

To identify vegetation disturbance as a result of fire, the MODIS monthly MCD451A burned area product at 500m spatial resolution was used to assess the timing and extent of burnt areas within the study sites (Table 1). The algorithm locates rapid changes by analysing the daily surface reflectance changes to identify recent fires. We downloaded data from the USGS archives and kept only the ‘use with confidence’ pixels (as labelled in the quality assessment layer provided with the dataset).

3.4. BFAST method

To detect breakpoints in the MODIS EVI time series, we employed the BFAST approach (Verbesselt et al., 2012) using the ‘bfastSpatial’ package (Lambert et al., 2013; Verbesselt et al., 2010; Verbesselt et al., 2011). Annual vegetation phenology follows a somewhat predictable cycle, with “greening” during the wet season and “browning” throughout the dry. Both seasonality and environmental factors including precipitation and temperature can cause variation in EVI values, particularly in non-forest areas, such as shrubland. The BFAST method breaks-down the time series into trend, season and residual components (Verbesselt et al., 2012). Fitting a seasonal trend accounts for these temporal fluctuations. Despite our focus being on detecting change in areas of primary forest, it was not possible to exclude non-forest pixels due to the absence of detailed land cover maps throughout the study period (Chamber et al., 2011).

There are three stages in classifying change in the time-series using BFAST: (1) fitting a model based on pixel values from a stable history period; (2) testing observations in a time period following the history period in order to detect any deviations from the model; and (3) calculating the magnitude of change by examining the median residuals between the observed and expected value.

3.4.1. BFAST parameters

Model for the additive seasonal trend: The “harmonic” model, used by Verbesselt et al., (2010) to detect forest change, was considered to be the most suitable for phenological change detection of natural vegetation:

$$y_t = \alpha + \gamma \, sin\left(\frac{2\pi t}{f} + \delta\right) + \varepsilon_t$$

where, y_t and t are the response variable and time, f is the temporal frequency, α is the intercept, y and δ are the amplitude and phase of the harmonic component and ε_t is the residual (noise component) (DeVries et al., 2015).

The factor h: The h value was fixed at 0.1 in order for at least one complete phenological cycle between two break-points.

Stable history period: for the Aberdare National Park this was defined as the period between 2000 and 2004. Throughout this period, over 60% of the area remained un-fenced and the elephant population was able to follow former migration routes to the lowlands during the wet season. It was assumed that the pixels within the forest were relatively stable. For Shimba Hills National Reserve, we used a shorter stable history period from 2000 to 2002 as we were informed by Kenya Wildlife Service (KWS) that the northern part of the park within the Mwalunganje elephant sanctuary experienced large areas of degradation as a result of elephant damage after this period. A minimum of two years of stable history period was used as it is recommended that at least two years is required to accurately monitor change when employing the MODIS 16-day product (Verbesselt et al., 2012).

Sequential monitoring: We used a sequential approach and limited the monitoring period to one-year consecutive periods in order to track gradual, incremental changes over time, as highlighted in previous BFAST applications (DeVries et al., 2015). Using a sequential method reduces the large number of observations post change detection and limits the impact this can have on the results of the change magnitude (DeVries et al., 2014; DeVries et al., 2015; Dutrieux et al., 2015).

3.5 BFAST validation

In order to assess the ability of a MODIS-based BFAST approach to detect disturbances in Afromontane forests caused by different drivers (e.g. anthropogenic, climatic, elephant damage), we randomly selected 495 forest and non-forest pixels across both study sites: 227 in the ANP and 268 in SHNR, separated into two strata (change detected and no change detected). Some studies use finer resolution SPOT, RapidEye, or Landsat data (DeVries et al., 2015). However, due to the large temporal gaps in the Landsat archive (Appendix 1) over East Africa, and the failure of the scan-line corrector (SLC) on Landsat 7, we used the EVI profiles from the time-series using the BFAST monitor function within the 'bfastspatial package'. We performed a visual interpretation comparable to TimeSync (Cohen et al., 2010), at the pixel level, of an agreement or disagreement of a breakpoint or non-breakpoint pixel based on the validity of the model fitted and the trend of the EVI values for each pixel. Commission errors were recorded if there was disagreement when the model had incorrectly classified a breakpoint as a result of excessive noise within the data, or an unsuitable model fitted based on the stable history period. Omission errors were reported if the model did not correctly identify a breakpoint.

To further assess BFAST's ability to identify changes, and in the absence of very high-resolution (VHR) data, we carried out field visits and collected geolocated photographs from locations within our study areas were BFAST was able to identify disturbances. Ideally, it would have been preferable to use VHR imagery, e.g. aerial photos. However, these were not available for our study areas and VHR Google Earth imagery (e.g. Worldview 2) only cover the period from 2013 onwards.

3.6 Results

3.6.1 Aberdare National Park

The change maps produced using BFAST on the MODIS EVI data for the Aberdare National Park are shown in Figure 2, together with the year of change and years of burn data based on the MCD45A MODIS data.

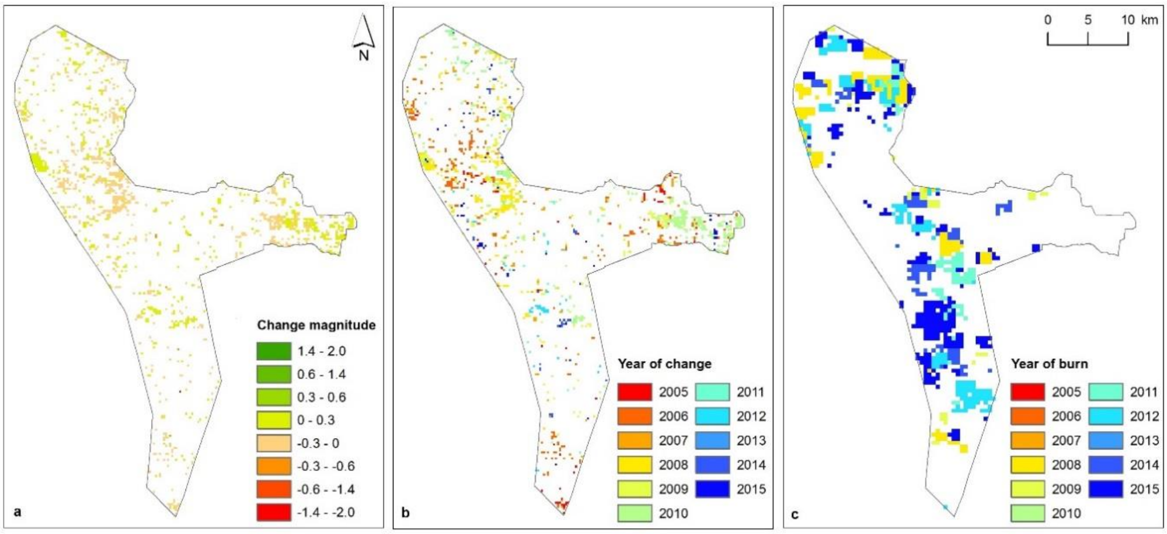
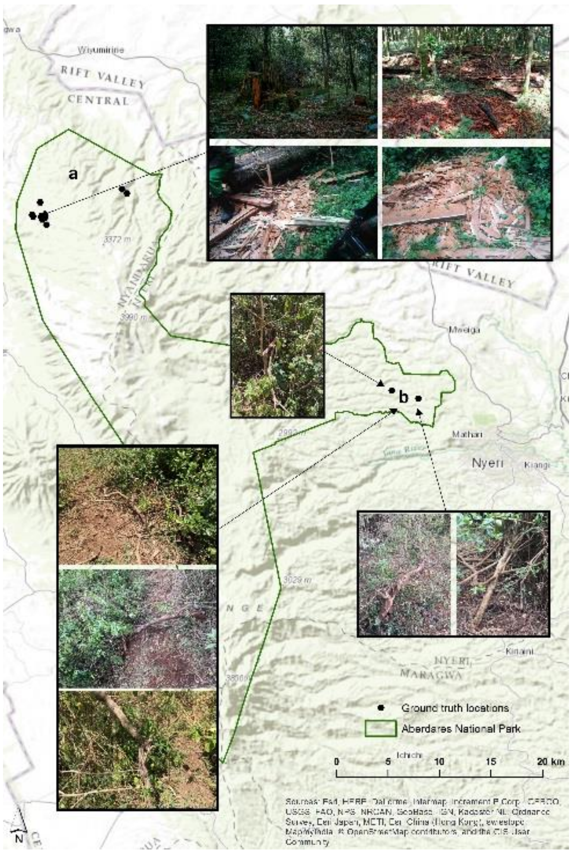


Figure 3.2 Change maps for the Aberdare National Park from 2005 – 2015 showing **(a)** the magnitude of change in the enhanced vegetation index (EVI); **(b)** the year the breakpoint was detected; **(c)** areas of fire detected by the Modis MCD451A product

Throughout the monitoring period, the ANP experienced 102.9 km^2 of change in the vegetation cover as a result of climatic and non-climatic drivers. This represents approximately 13% of the Park. However, only 8 km^2 are negative change in the EVI values therefore only 0.9% of loss to the parks vegetation occurred over the 11 year monitoring period, this corresponds to an annual rate of 0.09%. The direction of change indicates areas of negative change followed by regrowth. Ground truth visits suggest that certain areas of the Park are more susceptible to human influences. In northern parts of the Park, we found evidence of both recent and old logging sites, and charcoal kilns. In central and eastern areas of the park, we found no evidence of tree stumps that had been "clean cut", which is indicative of anthropogenic disturbance, only vegetation damaged by elephants was found (Fig. 3.3).

Whilst data from the MODIS burned area product correlated well with some of the disturbances, there is a large number of disturbances identified by BFAST in locations that are not affected by fire according to the MODIS product (Fig.3.2). Areas of disturbance that are not correlated with rainfall anomalies, anthropogenic disturbance, or fire, are potentially the result of damage caused by elephants, as found during ground truth visits (Fig. 3). The most substantial disturbance in vegetation dynamics was 66.4 km^2 between the years of 2005 and 2009, which was predominantly a negative trend (Fig. 3.4).



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3.3 Photos taken during ground truth data collection in 2016 of the Aberdare National Park showing **(a)** signs on human disturbance in the North and **(b)** elephant damage in the Eastern areas

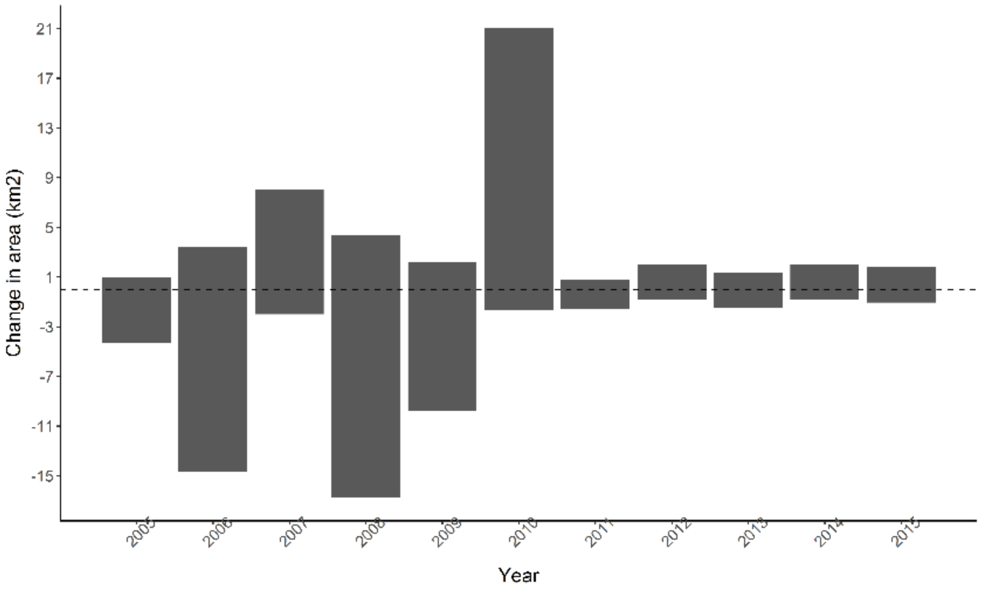


Figure 3.4 Amount of change in km^{2}in the Aberdare National Park

The temporal profiles of MODIS EVI, rainfall anomalies and monthly rainfall estimates from TAMSAT are presented in Figure 5. Negative anomalies in rainfall were experienced in 2007; however, only 2 Km^2 ha of negative change in EVI occurred that year. In 2008, the year succeeding the negative trend in rainfall, small negative changes in the EVI values, with a magnitude of up to 0.2, where found. Overall, negative anomalies in rainfall in the TAMSAT time series dominated the year 2009. Some 98.1 Km^2 of the park showed a decrease in EVI, with breakpoints at discrete magnitudes of 0.1-0.3. However, 0.4 Km^2 showed negative breakpoint magnitudes of 0.6-1.4, suggesting a small-scale, abrupt change, such as forest clearing. After a year of negative rainfall anomalies, the following year, 2010, reported higher-than-normal rains throughout the year, which coincided with 21 Km^2 of the park undergoing positive changes in EVI.

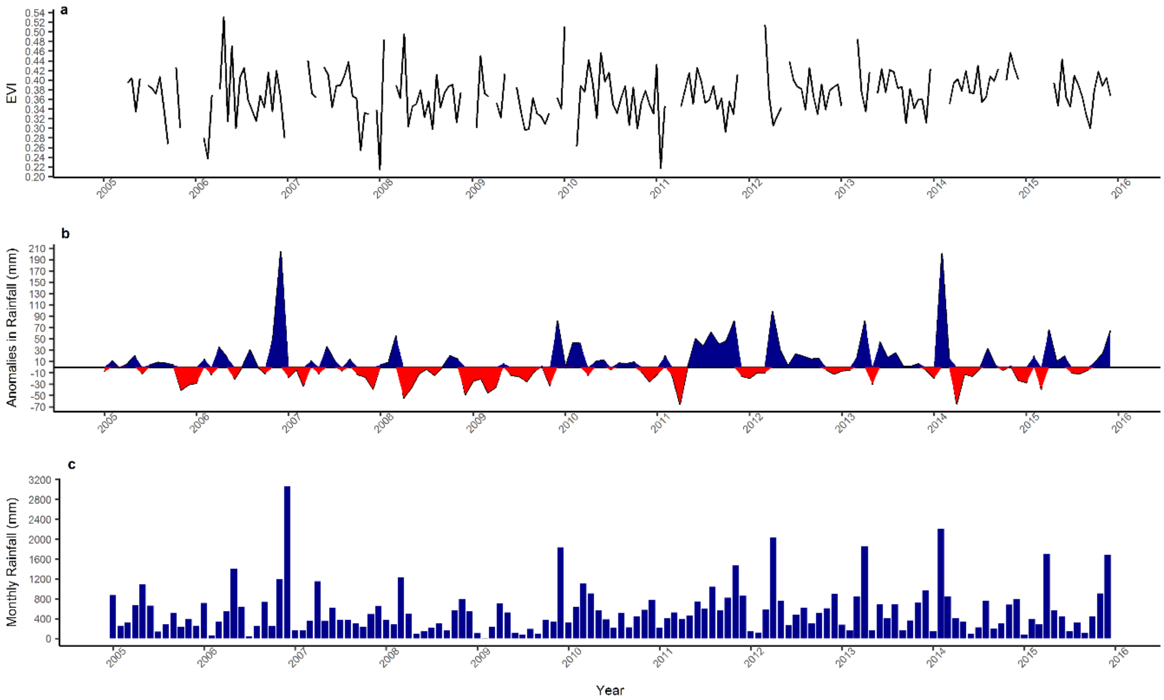


Figure 3.5 Temporal profiles for the Aberdare National Park showing **(a)** EVI from MODIS spatially averaged over the study area; **(b)** Anomalies in rainfall computed from monthly TAMSAT data; **(c)** Monthly rainfall estimates from TAMSAT data

3.6.2 Shimba Hills National Reserve

The change maps produced for Shimba Hills National Reserve are shown in figure 6. Over 306.8 km^2 were found to have undergone significant change over the 12-year period, averaging a 9% of change in the reserve’s area per year. As in the case of the Aberdare National Park, this change is bi-directional with disturbance detected followed by regrowth identified as subsequent breakpoints in the following years. The majority of change occurred between the years 2003 and 2004. Removing these ‘outlier’ years from the analysis reduces the annual rate of change to 1.6%. Overall, approximately 11% of the reserve underwent an improvement with a significant greening of 54% between 2003 and 2004 (Fig. 3.7).

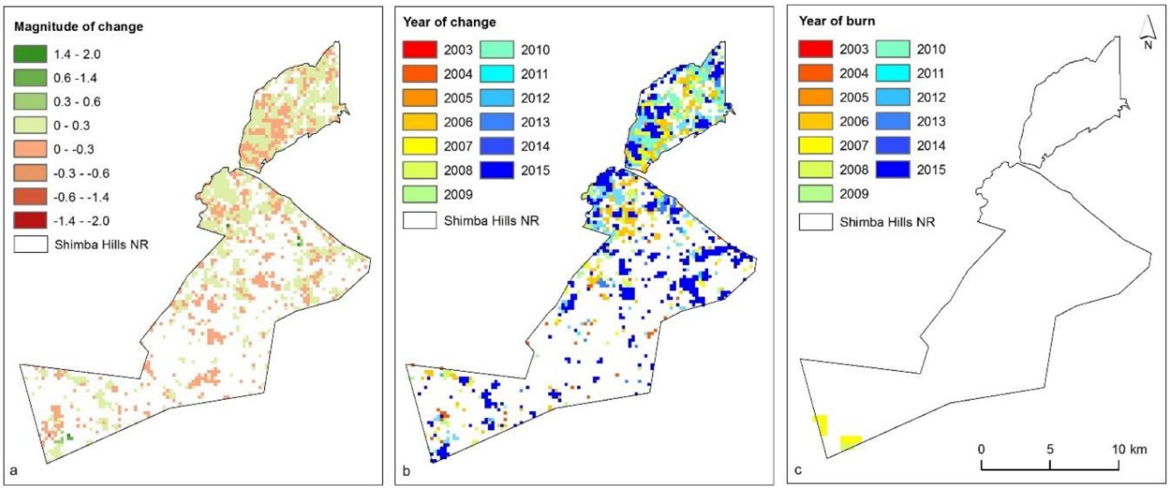


Figure 3.6 Change maps for Shimba Hills National Reserve from 2003 – 2015 showing **(a)** the magnitude of change in the enhanced vegetation index (EVI); **(b)** the year the breakpoint was detected; **(c)** areas of fire detected by the Modis MCD451A product

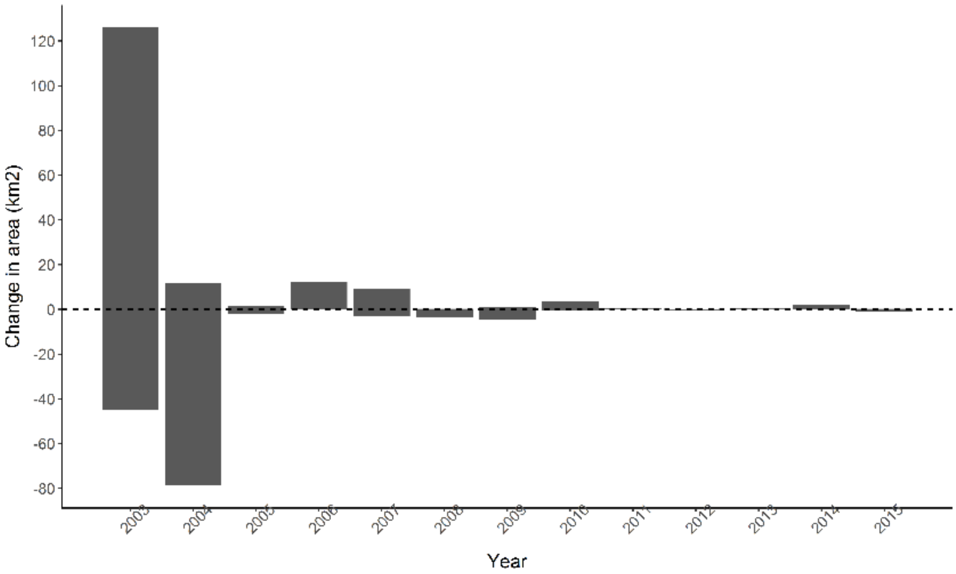
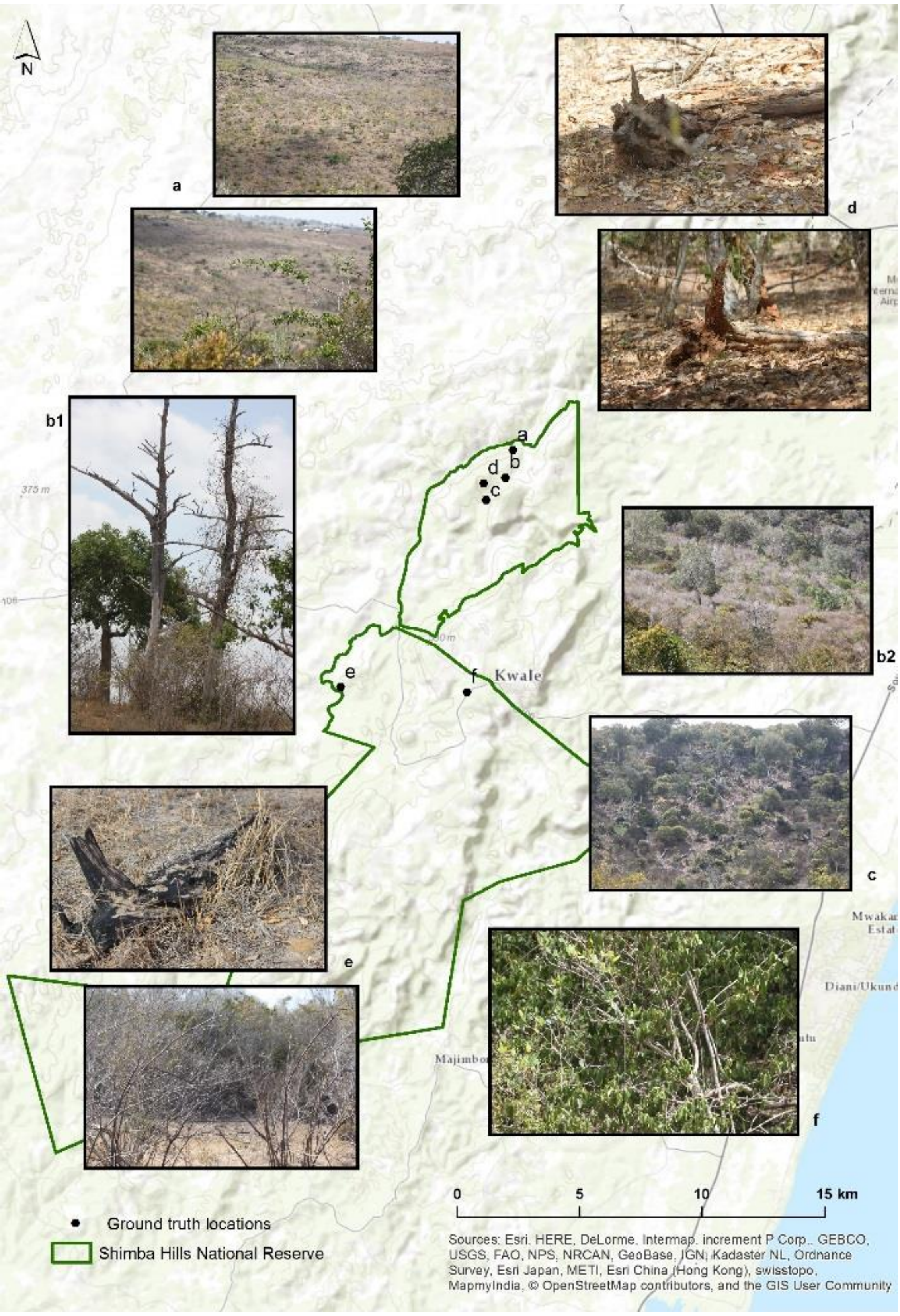


Figure 3.7 Amount of change in km^2 in Shimba Hills National Reserve

Significant gaps in the MODIS burned area data over the SHNR (fig. 6c) meant that the product could not accurately detect burnt areas. We verified this during our ground truth data collection, as we were able to locate a number of areas with clear evidence of fire that the MODIS product had not been able to identify (Fig. 8).



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 3.8 Photos taken during ground truth data collection in 2017 of Shimba Hills National Reserve showing **(a)** previous areas of forest that have now been opened up **(b1)** evidence of bark stripping by elephants **(b2)** evidence of regrowth **(c)** trees trampled by elephants **(d)** uprooting of trees by elephants **(e)** areas of fire damage **(f)** regrowth of shrub in previous areas of forest

The application of BFAST on the TAMSAT data found no statistically significant breaks in the rainfall anomalies throughout the study period. Figure 9 provides a visualization of the temporal profiles of EVI from MODIS, rainfall anomalies and monthly rainfall from TAMSAT. Small changes in the EVI values in 2004 and from 2006 to 2008 may be a response to the climatic driver of the amount of rainfall. The negative rainfall anomalies observed in 2004 might explain the large amount of the Reserve's significant negative change according to BFAST: 31% of the entire reserve. In contrast, in 2006, an increase in precipitation resulted in 1200 ha of greening. The year 2003 experienced negative anomalies in rainfall. In "traditional" models, this would have been seen as a driver for significant browning. However, 50% of the Reserve actually manifested higher EVI values at magnitudes of 0.3 (Figure 6a).

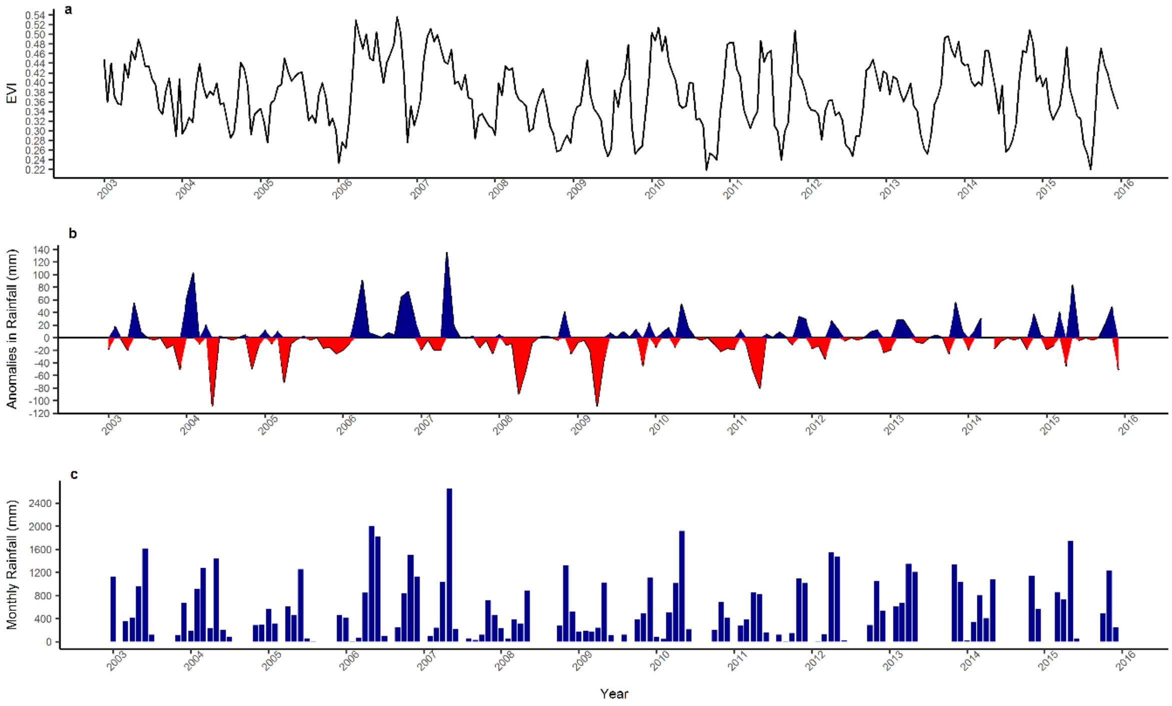


Figure 3.9 Temporal profiles for Shimba Hills National Reserve showing **(a)** EVI from MODIS spatially averaged over the study area; **(b)** Anomalies in rainfall computed from monthly TAMSAT data; **(c)** Monthly rainfall estimates from TAMSAT data

3.6.3 Accuracy assessment

Validation results with accuracy and error rates for the ANP and the SHNR are shown in Tables 2 and Table 3, respectively. Our disturbance maps achieved an overall accuracy (OA) of 72% for the ANP and 79% for the SHNR. On average, the more recent years for both sites resulted in higher OA rates due to a more stable model being fitted as well as the increased number of data points. The years that the model performed worse were 2006 for the SHNR (57% OA) and 2011 for the ANP (52% OA). Except for these two cases, overall error rates for both study sites were ≤ 0.3.

Table 3.2 Accuracy assessment results for the Aberdare National Park

Year	Accuracy	Error Rate	Commission error	Omission error
2005	0.66	0.3	0.46	0
2006	0.66	0.3	0.40	0.20
2007	0.66	0.3	0.45	0.10
2008	0.73	0.3	0.40	0
2009	0.76	0.2	0.35	0
2010	0.64	0.4	0.47	0
2011	0.52	0.5	0.70	0
2012	0.87	0.1	0.20	0
2013	0.79	0.2	0.30	0
2014	0.86	0.1	0.21	0
2015	0.77	0.2	0.35	0
Overall (05-15)	0.72	0.3	0.4	0.03

Table 3.3 Accuracy assessment results for Shimba Hills National Reserve

Year	Accuracy	Error Rate	Commission error	Omission error
2003	0.69	0.3	0.44	0
2004	0.77	0.2	0.33	0
2005	0.73	0.3	0.43	0
2006	0.57	0.4	0.50	0.25
2007	0.92	0.1	0.13	0
2008	0.75	0.3	0.17	0.33
2009	0.94	0.1	0	0.10
2010	0.94	0.1	0.25	0
2011	0.77	0.2	0.42	0
2012	0.76	0.2	0.40	0.9
2013	0.89	0.1	0.25	0
2014	0.92	0.1	0.14	0
2015	0.68	0.2	0.33	0
Overall (05-15)	0.79	0.2	0.29	0.06

3.7 Discussion

Disturbances of the forest canopy occur on a spatial-temporal scale at various gradients from subtle damage to trees, through to forest clearings. The magnitude of the detected change is related to the type of transformation of the habitat. Previous studies within Afromontane forests in Ethiopia classified two types of disturbance: pixels with negative breakpoints of less than -0.2 in EVI were classed as deforestation, whilst pixels with breakpoints between -0.2 and zero as degradation (DeVries et al., 2015; DeVries et al., 2014). Whilst detecting gradual degradation is particularly challenging due to the slow reduction in forest canopy (Chamber et al., 2011; Deshayes et al., 2006), the sequential monitoring approach that we employed using one-year non-overlapping periods of monitoring, enabled the detection of small-scale, subtle changes in the forest with areas of degradation and future regeneration in both study sites.

Annual rates of forest vegetation change in both of our study sites differed from estimates of forest loss of approximately 0.38% (Getahun et al., 2013) and 0.4% (DeVries et al., 2015) within two montane forest regions in Ethiopia. The Aberdare National Park is experiencing lower rates of degradation (0.09% per annum); however, both Ethiopian studies reported forest loss as a result of changes in land-use driven by agriculture. The lower rates of forest loss in the ANP may be attributed to the installation of the fence, which has minimised human-related conversion of land use. Reductions in the forest vegetation cover are predominantly linked to non-anthropogenic drivers and cause gradual degradation rather than large-scale clearings or deforestation. Our ground truth data suggest that certain areas are more susceptible to the influences of logging and charcoal kilns. These activities are possibly related to the proximity to the fence boundary. An aerial survey of the Park in 2002, found that, despite the presence of the fence, there was evidence of human-related habitat degradation and that more than 80% of this anthropogenic activity occurred within a 2.5 to 3km buffer around the boundary (Lambrechts, 2003).

Throughout the monitoring period, disturbances to the SHNR represented on average 9% per annum. Surprisingly, however, the direction of change was predominantly positive with an increase in vegetation activity representing approximately 11% of the area (Fig. 7). This unexpected greening of the forest, which occurred mainly during 2003 (the first year of monitoring), could relate to the large-scale degradation of the area as a result of elephant damage prior to the availability of the MODIS imagery in 2000 (Kenya Wildlife Service, pers.comm., 2016). In any case, this greening was related with the regrowth of secondary forest, and was observed during the collection of ground truth data (Fig.9). Greening from 2006 onwards, may be attributed to the removal of 150 elephants, which were translocated from the Reserve to Tsavo East National Park in 2005, allowing vegetation to recover and limiting further damage (Pinter-Wollman et al., 2009).

Our visual interpretation of the temporal profiles of MODIS EVI, rainfall anomalies and monthly rainfall estimates from TAMSAT, suggest that precipitation may not be a reliable predictor of forest change within our study areas. It has previously been recommended to treat the relationship between EVI and rainfall with caution as heterogeneities in patterns of EVI in the forest may be difficult to explain as a response of variations in climate (Maeda et al., 2014). Using precipitation levels and rainfall anomalies alone has its limitations on assessing the impact of rainfall on forest greenness, as it does not incorporate other variables, such as evaporative demand (Dutrieux et al., 2015; Trenberth et al., 2013). Other studies also found rainfall extremes showed no influence on EVI anomalies (Maeda et al., 2014). We aimed to examine the influence of rainfall patterns on forest phenology. Unexpectedly, negative anomalies in rainfall did not always coincide with a reduction in EVI values in the same year, as in the case of the ANP for the year 2007. Negative changes in the vegetation were limited to only 2 km^2 of the SHNR for that year. The following year, however, small declines in photosynthetic activity in just over 2 km^2 were observed, suggesting a possible lag in the impact of reduced rainfall on vegetation. This has also been reported previously using data collected from 10 rain gauge stations in Kenya, but with smaller time lags of up to three months (Eklundh, 1998).

Within the SHNR in 2003, 50% of the area experienced an increase in EVI at magnitudes of 0.3. In contrast to traditional ecosystem models, whereby there is a reduction in forest “greenness” or EVI values, as a consequence of water-stress (Tian et al., 1998; Botta et al., 2002). Our results support previous evidence from studies conducted in the Amazon rainforest that witnessed widespread greening during the dry season (Huete et al., 2006; Saleska et al., 2007), inferring that our study site could be influenced by more complex relationships between water availability, sun radiation and heterogeneity in EVI patterns.

Ground truth data within areas that were identified by BFAST as having undergone some degree of disturbance were collected from both sites. The data highlighted the ability of BFAST, when applied on coarse resolution imagery, to detect disturbance from fire, anthropogenic clearances, and elephant damage. It enabled us to identify progressive degradation and subsequent regrowth of the vegetation, which would likely have been missed using bi-temporal methods (Kennedy et al., 2014). Extensive cloud cover which is typical of montane forest regions, exasperates the problem of using the extensively employed bi-temporal approach. Interestingly, whilst collecting ground truth data, we identified large areas of damage as a direct result of elephants trampling and uprooting trees, particularly within the Mwaluganje elephant sanctuary in the north of the SHNR (Fig. 9). This supports previous reports of elephants creating large clearings in the forest since fencing the area (Knickerbocker and Waithaka, 2016), and to our knowledge, provides the first evidence of the ability of using remote sensing methods to measure damage influenced by mega-herbivores.

A lack of available high resolution imagery meant that typical validation methods employed in other studies was difficult (DeVries et al., 2015; Dutrieux et al., 2015).However, their integrity is based on a robust, statistical model that has been applied successfully in a number of applications and, as with other studies experiencing similar data constraints, we provided a workaround (Schneibel et al., 2017). Accuracy of the disturbance maps are consistent with other studies. Both field sites attained higher accuracies in recent years due to a more stable model being fitted, owing to an increasing number of data points. A number of studies mapping change from time-series data have reported higher omission than commission errors (Yin et al., 2014; Dutrieux et al., 2015; Schroeder et al., 2014). Commission errors for both study sites were higher than omission errors (Tables 2; Table 3). This is in agreement with other studies (Griffiths et al., 2012; Healey et al., 2017). A paucity of Landsat data meant that we had to employ the coarser resolution MODIS data for the validation exercise, which makes it difficult to identify subtle changes in the canopy (e.g. small size of the clearings) (Hansen and Loveland, 2012). This resulted in considerably higher commission errors for a number of years compared to those reported in other studies. Another reason for our higher commission errors could be the choice of harmonic order in the BFAST model (k=3), which translates to a more sensitive approach in the identification of breaks, subsequently increasing the number of false positives. However, as pointed out by Dutrieux et al., (2015), as the areas of no-change are much larger than those where disturbance was detected, selecting a lower harmonic order increases the omission errors. Given the difficulty in identifying subtle changes using coarse resolution imagery, we opted for the more sensitive approach i.e. the higher k.

A limitation to our study was that we were unable to acquire a temporal profile prior to the start of the construction of the fence in 1989 due to the significant gaps in the Landsat archive over East Africa at the start of our study (Appendix 1). This meant that we had to resort to using MODIS data, which are available from the year 2000. During the period between 1989 and 2000, 78 km of fencing had already been completed on the eastern parts of the ANP. Whilst it is anticipated that elephant damage to the Park should not have occurred due to the majority of migration routes being open, it is possible that the partial confinement might already have impacted the vegetation negatively. Therefore, the stable history period we had to use, may not be entirely “stable”. As such, a decreasing trend may have been fitted to the model resulting in an over estimation of positive breakpoints, which could have caused our higher commission errors. Overall, the model performed more efficiently in the SHNR compared to the ANP. This is potentially due to the higher number of clear-sky observations per pixel in the SHNR (Fig. 1), resulting in fewer gaps in the data. As established in a similar study in an Afromontane forest in Ethiopia, the presence of unmasked clouds or cloud shadows can result in a greatly reduced EVI value for that pixel. Whilst an occasional outlier should not lead to the detection of a false breakpoint (thanks to the calculation of the moving sum of squares, MOSUM), continuous cloud cover, which is characteristic of our study sites and other tropical montane regions, can present a considerable challenge, and indeed lead to the false identification of disturbance (DeVries et al., 2015).

3.8 Conclusion

The Aberdare National Park and Shimba Hills National Reserve, in Kenya, were selected to examine the impact of confinement of mega-herbivores using remote sensing techniques. Fencing has evidently protected the forests from large-scale human disturbance by limiting land-use conversion in both sites, which have experienced significantly lower rates of forest loss than forests that are un-fenced in other studies. Analysis found that our study sites primarily exhibit small-scale, subtle changes in forest canopy, possibly as a result of elephant damage and areas of human activity, including charcoal kilns and logging, which were observed during ground-truth validation. The direct impact of rainfall was difficult to measure, as rainfall anomalies did not always coincide with changes in EVI values. The SHNR experienced much larger areas of change than the ANP, possibly suggesting that smaller, fenced areas are more susceptible to changes in the forest as a result of confining mega herbivores.

Results indicate that employing the sequential monitoring technique within the BFAST method on MODIS (MOD13Q1) time-series presents an opportunity to use remote sensing in environments whereby traditional monitoring approaches are not possible. Providing near real-time information on the ecological impact of confining animal populations, and detecting small-scale human disturbance, can help to inform successful management strategies for the conservation of species and the preservation of habitats.

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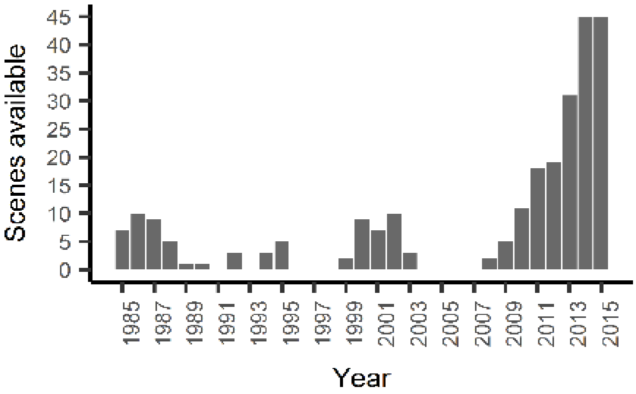

Appendix 3.1. Landsat 5 and Landsat 7 scenes available for the study areas at the time of data analysis

Chapter 4

Using camera traps to estimate density of elephants in forest habitats

4.1 Introduction

Reliable estimates of population numbers are fundamental for the effective conservation of wildlife (Zero et al., 2013). In the absence of reliable information on changes in population sizes it is impossible to assess conservation status, identify key threats, or assess interventions within an active management framework (Varman and Sukumar, 1995; Manzo et al., 2011). Density estimates are particularly challenging for species with clumped spatial distributions, which necessitates monitoring at the landscape scale (Jones, 2011). The difficulty is often compounded by the limited resources inherent in many conservation programmes (James et al., 1999; Ferraro and Pattanayak, 2006).

Whilst direct counts are preferable, they are often impractical for cryptic species or in challenging environments, and have the added problem of typically being resource intensive (Bist, 2003; Stephens et al., 2006). Moreover, when applied, direct counts often under or over-estimate density as they either fail to address issues of detectability or do not have sufficient encounters to accurately model the variation in detectability (Caughley et al., 1976; Kissling and O'Garton, 2006). Estimates involving direct counts are also particularly difficult for wide-ranging species as spatio-temporal variance in resources results in patchy distributions and population clumping (Powell et al., 1997; McLoughlin et al., 2000; Herfindal et al., 2005). In these instances, sampling design must account for the uneven distribution of the population to avoid over-inflated (Rinehart et al., 2014), or underestimated density estimates (Blackburn & Gaston, 1996).

Forest habitats, with poor visibility due to dense undergrowth, closed canopies, and topographic features, present a particular challenge for monitoring (Varman and Sukumar, 1995; Barnes et al., 1997; Tobler et al., 2008). In these environments, or when the target species is a cryptic species, indices derived from indirect surveys are the only feasible option available. Indirect methods, such as dung or nest counts give a relative measure of abundance derived from encounter rates, however genetic studies comparing a variety of these indirect methods, demonstrated substantial errors due to significant undercounting (Zhan et al., 2006; Arrendal et al., 2007) or over-counting (Guschanski et al., 2009) of individuals, and should be treated with caution (Fay, 1991). With the adherent issues of precision and error associated with abundance indices (MacKenzie & Kendall, 2002; Narain et al., 2005), dung and nest count methods can be combined with estimates of production and decay rate to calculate actual density estimates (Hedges, 2012). This has been employed for a variety of species including gorillas (Takenoshita & Yamagiwa, 2008; Guschanski et al., 2009), deer (Marques et al., 2001), elephant (Fay, 1991; Hedges, 2012), orangutans (Johnson et al., 2005), and rabbits (Wood, 1988), yet the reliability of these models is heavily dependent on the estimates of production and decay rates (Hedges, 2012). Inaccuracies can arise due to large variations in the decay rates of dung/nests, and/or when using decay rates calculated from other areas (Nchanjii & Plumptre, 2001). For dung decay, climatic variables which are in part dependent on habitat and altitude, as well as variation in factors such as diet and decay agents like dung beetle abundance, all contribute to varying rates of decay (Nchanjii & Plumptre, 2001; Hedges, 2012). Accurate calibration of multiple production and degradation rates is required to achieve reliable estimates (Nchanjii & Plumptre, 2001; Walsh and White, 2005; Kuehl et al., 2007). Consequently, these indirect methods can be labour intensive, time-consuming, and expensive, particularly if frequent monitoring is required over large spatial scales and heterogeneous areas (Hibby and Lovell 1991; Plumtre and Harris, 1995; Zero et al., 2013).

Methods based on camera trapping have the potential to overcome the problems associated with direct counts and indirect surveys. They have become popular, non-invasive and low-cost alternatives for monitoring species that are not easily observable (Carbone et al., 2001; Cutler and Swann, 1999; Lyra-Jorge et al., 2008 Manzo et al., 2012; Rowcliffe and Carbone 2008). Camera trapping surveys have been previously utilised for studies of abundance, species richness (Tobler et al., 2008) and species occupancy (Linkie et al., 2007), but density estimates traditionally required a capture mark recapture (CMR) approach (Karanth et al. 2006), and more recently, spatially explicit capture mark recapture (SECR) (Wallace et al., 2003; O'Brian and Kinnaird, 2011; Kane et al., 2015). Whilst CMR models are commonly employed, a limitation is that individual recognition is required to be able to 'mark' individuals in the population. In many surveys, marked individuals represent only a portion of the sampled population (Carbone et al., 2001). Frequently, individual identification is not possible (Manzo et al., 2012; Caravaggi et al., 2016), or, identification errors are not addressed (Oliveira-Santos et al., 2010; Caravaggi et al., 2016). In more recent SECR models, populations have been estimated when only a subset of the population can be uniquely identified (Chandler & Royle, 2013; Rich et al., 2014), but this requires large sample sizes, with frequent 'recaptures' of identified individuals to achieve precision (Caravaggi et al., 2016).

The development of new camera trapping methods including the random encounter model (REM) (Rowcliffe et al., 2008; Rowcliffe et al., 2011) and distance sampling (Howe et al., 2017), enable densities to be estimated when individuals cannot be identified. The REM estimates density by modelling random encounters between cameras and subject animals (Rowcliffe et al., 2008); it is based on 'Brownian motion' models describing the rates of collision between gas molecules, and adapted by biologists to describe frequency of contact between animals and cameras (for review see Hutchinson and Waser, 2007). A number of studies have cross-validated estimates calculated from the REM with complete census data, CMR models, and distance sampling (Rowcliffe et al., 2008; Zero et al., 2013; Anile et al., 2014) with convincing results. Following recommendations from a simulation (Rowcliffe et al., 2008), previous field-based applications using the REM have deployed high densities of camera traps and/or used extensive surveying durations (60 days – 6 months) (Manzo et al., 2012; Hero et al., 2013; Anile et al., 2014; Cusack et al., 2015; Caravaggi et al., 2016). This presents financial and time limitations to monitoring; the initial cost of the cameras themselves can be prohibitive (Zero et al., 2013), and long survey duration times, large volumes of batteries, camera maintenance and the potential loss of equipment cause further resource constraints for intensive camera trap studies (Ferraro and Pattanayak, 2006).

Population monitoring for vulnerable species is not limited to a local level, there is often a requirement to report across the entire species range, involving multi-institutional collaborations between Government and conservation agencies. In the case of the African elephant (*Loxodanta africana*), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) oversees the 'Monitoring the illegal killing of elephants' (MIKE) programme, which requires reliable monitoring across the species' range in the face of the persistent and increasing threats from poaching, habitat loss and human-wildlife conflict (Knickerbocker and Waithaka, 2005; Graham *et al.,* 2010; Blanc, 2008). Across the continent montane forests harbour significant populations of forest elephants (*Loxodanta cyclotis*) but also savannah elephants (*Loxodanta africana*) as they provide dry season refugia (Bohrer, 2014), and East Africa alone has in excess of 65,500km^2 of montane forests (WWF, 2019). However, these populations are under threat, not only from habitat loss, but also because of their susceptibility to poaching as the environment is particularly challenging to monitor and provide effective security (Maisels et al., 2013). There is a significant need for a multi-country, high quality census of elephants in forest habitats

(Blake et al., 2007; Chase et al., 2016). However, because of the limitations of the indirect methods outlined above (Fay, 1991; Nchanjii & Plumptre, 2001; Zhan et al., 2006; Arrendal et al., 2007; Guschanski et al., 2009) and the high costs associated with genetic surveys in large populations (Miller et al., 2005; Lukacs et al., 2007), a new approach is needed.

Here, we examine the suitability of using camera traps to estimate the population density of a population of savannah elephants confined within a montane forest in Kenya. Given the limitations of non-invasive methods, particularly in montane environments, the intention is to provide managers and scientists with a robust method that will enable conservation organisations with limited budgets and access to equipment, to continuously monitor elephant populations in these challenging habitats. We employed the REM (Rowcliffe et al., 2008) to estimate the density of the African elephant in the Aberdare Conservation Area (ACA), where habitat, topography, and altitude make other methods unfeasible, or unreliable. Whilst camera traps have been used to document elephant presence (Datta et al., 2008; Gray and Phan, 2011), population dynamics (Varma et al., 2006), and habitat utilisation (Green et al., 2018), to our knowledge, no population density studies have been conducted using camera trapping surveys.

4.2 Materials and Methods

4.2.1 Study Site

The study area is located in the Central Province of Kenya, lying southwest of Mount Kenya and forming the eastern rim of the Great Rift Valley. The Aberdare Conservation Area (ACA), comprised of the Aberdare National Park (ANP) and the surrounding Aberdare Forest Reserve, covers an area of 1,748 km^2. In 2009, the world's largest electric wildlife fence was completed around the perimeter of the ACA, subsequently curtailing seasonal migration of the elephant population from the montane forest to the lowland savannah. Altitude within the ACA varies from ~ 1885 m to ~ 4000 m. The climate is characterised by high annual rainfall of approximately 1600 mm per annum (WildClim, 2018), and mean daytime temperatures range between 16 ^{0}C in July to 21.8 ^{0}C in February (Massey et al., 2014). There are two 'wet' seasons, with the long rains starting in March and lasting until late May, and the short rains arriving in October and ending in December. The major vegetation types can be grouped into three distinct zones: the montane forests that are found at lower elevations (1900-2400 m), the bamboo zone in the middle (2400 -3000m) and the moorlands which are dominated by *Hypericum* and ericaceous species in the highest ranges (2900^{+}m) (Massey et al., 2014).

The montane forests of Kenya are refuges that became isolated during the glacial maxima and experienced recurrent expansions and contractions of the forest area (Demos et al., 2014). The ACA incorporates a wide range of habitats and significant biodiversity including approximately 270 bird, and 50+ mammal species including elephants (*Loxodanta Africana*), leopard (*Panthera pardus*), black rhinoceros (*Diceros bicornis*), and the critically endangered mountain bongo (*Ragelaphus eurycerus*) (Butynski, 1999).

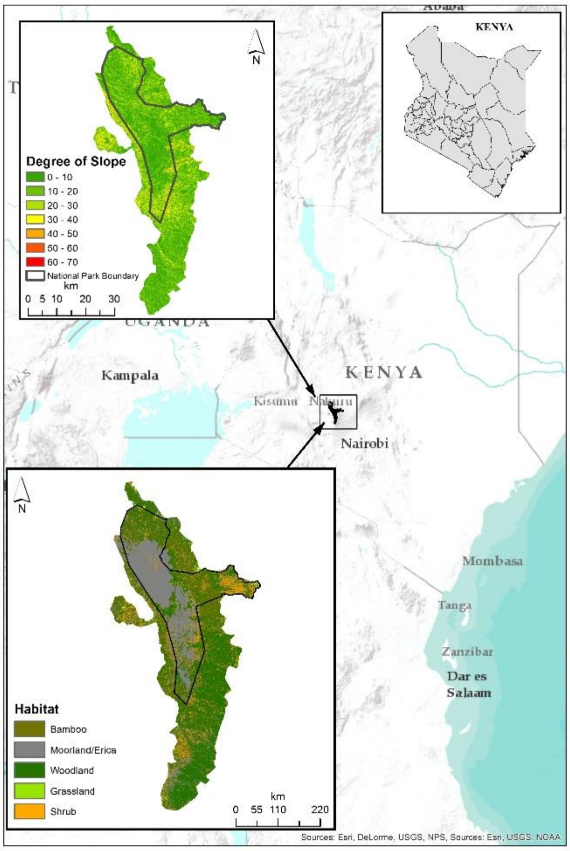

Figure 4.1 Location of the Aberdare Conservation Area showing the degree of slope derived from a digital elevation model (*top*) and a classification of the land-cover produced from a supervised classification (*bottom*)

4.2.2 Camera Trap Placement and Settings

Bushnell™, 14-megapixel 'Natureview' camera traps with 32GB SD cards were deployed between June and August for the years 2015 -2017, giving a total survey effort of 1,234 days (29,616 hours), using 71 individual camera trap locations. To stratify the site and enable weighted placement of camera traps for sampling, we classified Landsat 8 satellite images from the U.S. Geological Survey (https://earthexplorer.usgs.gov). Classification of vegetation types were collated from ground truth data collected from the study area with GPS points recorded as a reference. We performed a supervised classification of the study site (Figure 4.1) using a random forest model with a confusion matrix accuracy for the overall model in excess of 75%; this was undertaken within the '*RStoolbox'* package in R (R Core Team, 2017). The area was stratified into four vegetation types based on clusters from the supervised classification; woodland (closed canopy forest and *Hagenia)*; moorlands; bamboo; and shrub; (Figure 4.1). Random camera placement is recommended for the REM to avoid a potential inflation or deflation of encounter rates in respect to the movement of animals (Rowcliffe et al., 2008). However, some areas of the ACA are largely inaccessible and so suitable areas for camera stations were selected within *ArcMap v. 10.3.1* using the stratified habitat map, a digital elevation model, and road accessibility. Randomly selected points within each stratum were highlighted as potential trapping sites and downloaded into GPS for positioning in the field. Additional data from camera traps as part of an on-going camera trap survey in the Aberdare National Park were utilised in this study. Camera trap data used from the on-going study were deployed in randomly selected grids in the Northern, and Central areas of the study site (Figure 4.2). Although random placement is an assumption of the model, total randomisation in the placement of cameras would likely result in zero detections as elephants typically traverse roads and game-trails, and avoid steep slopes, which are typical in the montane environment (Gadd, 2002; Wall et al., 2006; Pan, 2009). Following Zero et al., (2013), actual trapping sites were selected close to the GPS coordinates if we considered there to be a reasonable chance of detecting elephants if they were present. To avoid violating random placement assumptions (Rowcliffe et al., 2008), and ensure that areas that may be used preferentially, or deliberately avoided, were sampled in proportion to their occurrence in the study landscape (Rowcliffe et al., 2012), cameras were placed in each of the vegetation zones in relation to their proportion of the area. The Eastern area of the Aberdare National Park ('Salient') has a high density of wildlife, including elephants. To reduce sampling bias which would artifitially inflate the density of elephants, the sampling effort (camera numbers, and duration of time) of this area was sampled in proportion to the remaining area of the ACA (Appendix 4.1). We were unable to place cameras in the southern area of the Forest Reserve managed by the Kenya Forest Service (KFS) due to extensive tree felling and extensive conversion to traditional agricultural land.

Cameras were placed on trees between 0.5 to 2.5 meters high and set to take images 24 h per day, taking 3 consecutive photos with a 2 second delay, recording the time and date. Once the cameras were placed, final GPS locations were recorded and downloaded onto the site map in *ArcMap 10.3.1.*

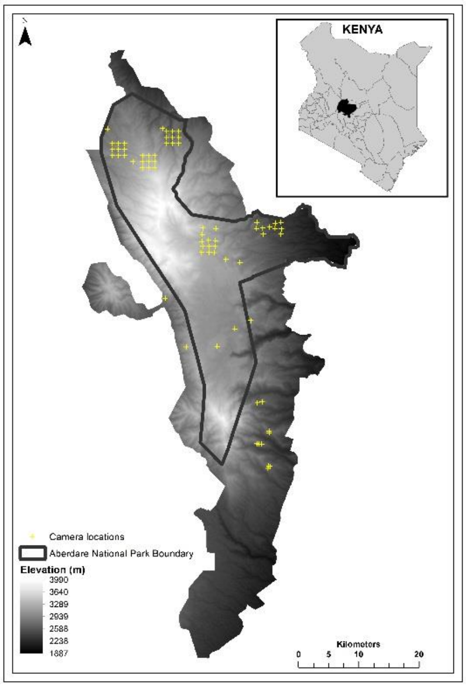

Figure 4.2 Location of camera traps and the digital elevation of the study site

4.2.3 Random Encounter Model

The random encounter model is a method that obtains density estimates from camera trap encounter rates without the need for individual recognition (Rowcliffe et al., 2008) according to the following equation;

$$D = \frac{y}{t}\,\frac{\pi}{vr\,(2+\theta)}$$

Whereby *y* is the number of independent images/events, *t* is the total survey effort, *V* is the average speed of animal movement per day, and *r* and $\boldsymbol{\theta}$ are the camera detection zone (radius and angle). Despite elephants being herd animals, we decided not to calculate the REM density based on group encounter events as it would be difficult to obtain unbiased, independent estimates of group size (Rowcliffe et al., 2008; Zero et al., 2013). Dense vegetation, presents difficulties in observing all individuals, and elephant herd dynamics are heavily influenced by the availability of resources (Fishlock and Lee, 2013). Attempting to count the average herd size of elephants at easily visible locations, such as water points, would likely result in an over-estimation of group size (Varman et al., 1995). Individual elephants were counted from the group images, events were deemed independent when a herd had left the vision of the camera traps and it was clear that a single herd had moved through the field of view (Thomas et al., 2010; Zero et al., 2013; Cusack et al., 2015).

To quantify the *V* variable (animal speed range per day), we used telemetry data based over a 5-month period from elephants in the nearby Mount Kenya Forest Ecosystem (Kenya Wildlife Service, 2019). Daily movement was based on sampling frequencies of one GPS fix every 59 minutes over a 24-hour period. Although short-interval fixes are preferable to reduce potential issues of under-estimation of distance travelled (Rowcliffe et al., 2012), we were limited to the data set-up from existing monitoring. Mean daily range was calculated at 6.5km (min 1.9km, max 15km) (Appendix 4.2). Calibration of the camera trap detection zone is imperative in order to acquire reliable detection parameters from the cameras (Rowcliffe et al., 2011; Manzo et al., 2012). The detection zone parameters of the cameras (*r* and $\boldsymbol{\theta}$) were measured in ex-situ field trials using captive elephants at Chester Zoo. Cameras were set up around the enclosure, and the detection zone was estimated by recording when the camera was first triggered from an approaching elephant in relation to permanent features in the landscape, whereby distance from the camera trap was measured using a rangefinder. To estimate the camera angle ($\boldsymbol{\theta}$), perpendicular approaches to each side of the sensor (left and right) were recorded at the first trigger, and a bearing to the location was taken using a compass placed at the camera location (Cusack et al., 2015). Average values recorded from each trial were used to determine the detection arc, yielding a detection distance (*r*) of 12.9 m, and an angle of 0.89 radians ($\boldsymbol{\theta}$). We computed REM density estimates using the *'remBoot'* package in R (RCoreDevelopment, 2017). Confidence intervals of elephant density for each of the strata were calculated using non-parametric bootstrapping, re-sampling camera encounter rates (*y/t*) with replacement 10,000 times (Rowcliffe et al., 2008; Manzo et al., 2012; Rowcliffe et al., 2011; Zero et al., 2013).

4.2.4 Digital Elevation Model (DEM)

The Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) for the area was downloaded from the U.S. Geological Survey (https://earthexplorer.usgs.gov). The 3D surface volume for the entire study area, and each of the habitat types derived from the supervised classification (Figure 1) was calculated in *ArcMap v. 10.3.1* to determine the total habitat available.

4.3 Results

4.3.1 Camera Trapping Rates

Over the study area, we obtained a total of 51 elephant images captured over 1234 days trap days between the months of June and August 2015-2017. The mean trapping rate was 0.03 photographs per day (SD= 0.09), with elephants being captured in 14 of the 71 camera stations (Figure 4.3).

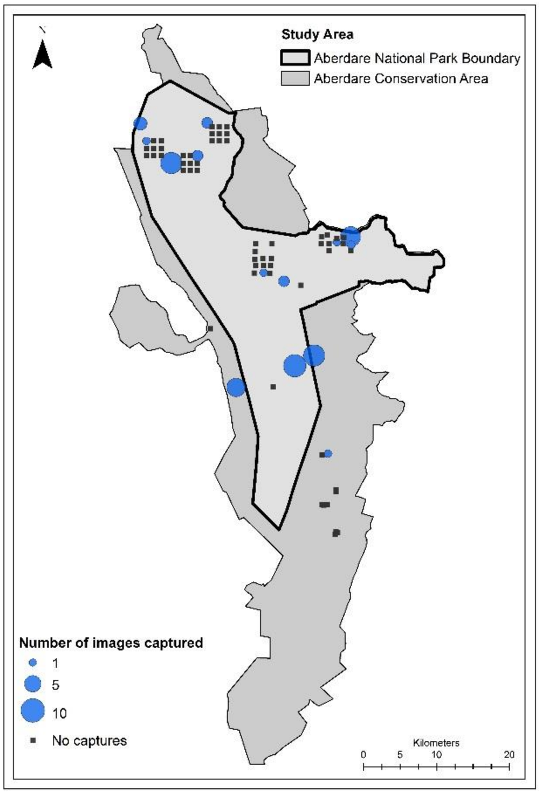

Figure 4.3 Total number of images captured over the study periods in each of the camera trap stations

Trapping rate (per 100 days) was not influenced by habitat type ($X^2 = 2.7222$, df = 3, p-value >0.05), with an average trapping rate of 1.5 (SD=4.0) images in bamboo habitat; 1.8 (SD=3.6) in the moorlands; 2.4 (SD=6.2) in the woodland vegetation; and 12.6 (SD=24.4) images per 100 days in the shrub habitat (Table 4.1).

Table 4.1 Summary of the trapping rates (per 100 days) for each of the 14 camera stations that captured elephants

Camera Trap ID	Habitat Type	Trapping rate
2	Bamboo	15.4
6	Shrub	10
16	Bamboo	10
18	Moorlands	10
28	Woodland	6.1
29	Shrub	20.5
30	Woodland	18.8
33	Moorlands	4.1
43	Woodland	10
53	Woodland	24.2
55	Shrub	70
56	Moorlands	9.1
60	Bamboo	10
63	Bamboo	3.0

4.3.2 Random Encounter Model Elephant Spatial Distribution

Results of the Random Encounter Model show that elephant densities vary between habitat types (Figure 4.4). Density was highest (1.16 elephants / km^2 (CI 95%, 0.07 – 2.68) in the areas of shrub, followed by the woodland zones at 0.33 / km^2 (CI 95%, 0.02 – 0.76), bamboo zone at 0.29 / km^2 (CI 95%, 0.03 – 0.70), then the moorland zone at 0.17 km^2 (CI 95%, 0.0 - 0.37). The total estimated number of elephants within the Aberdare Conservation Area, calculated from the individual densities per habitat type, and weighted by the total representation of vegetation class from the Digital Elevation Model and supervised classification (Table 4.2), is ~661 individuals.

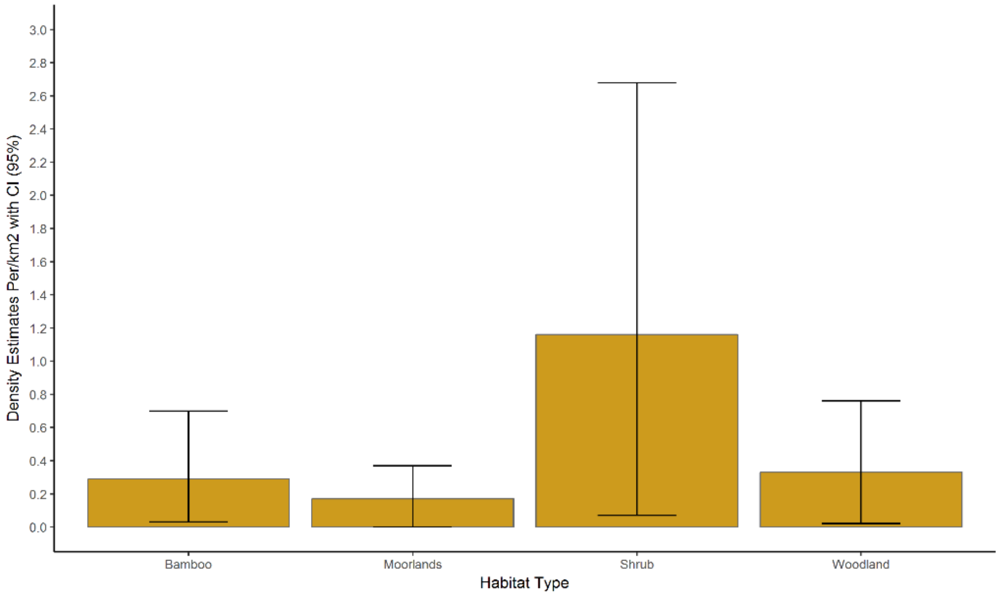

Figure 4.4 Density Estimates with 95% confidence intervals per habitat type

Table 4.2 Summary of the total area (Km^2) of each of the habitats and resulting density estimates derived from the Random Encounter Mode

Habitat Type	Total Area from DEM (km^2)	REM Density /km^2 (CI 95%)	Number of elephants in total area of habitat
Bamboo	404.4	0.29 (0.03 – 0.70)	117
Woodland	783	0.33 (0.02 – 0.76)	258
Shrub	179.4	1.16 (0.07 – 2.68)	208
Moorlands	456	0.17 (0.0 - 0.37)	78
Total Overall	**1823**	**Averaged Density - 0.49**	**661**

4.4 Discussion

The reliable monitoring of Threatened populations is critical, however, many approaches can be problematic, labour intensive, and have high associated costs, which puts a severe strain on conservation budgets and resources (Plumtre and Harris, 1995; Zero et al., 2013; Newey et al., 2015). Although Globally the African elephant has an increasing population trend, their management is a complex issue arising from significant poaching pressure, and regional variations in population status; vulnerable to extinction in some areas, yet considered too abundant in others (Whyte et al., 2003; Blake and Hedges, 2004; Stephenson, 2004). Robust monitoring is therefore essential for the protection and management of elephant populations, and a requirement for each range state under the CITES, MIKE programme (KWS, 2012). In this context, the number of elephants poached is recorded, and actual population numbers rather than abundance is required. Our objective was to evaluate a recently developed camera trap method, which potentially offers improvements over indirect survey methods such as dung surveys, to obtain the population density of elephants in a montane forest with a wide range of biotic and abiotic variates.

There are few studies on savannah elephant (*Loxodanta Africana*) densities within forest habitats. The majority of studies were conducted in the 1990's, predominantly using dung-count surveys (Fay, 1991; Ben-Shahar, 1996; Hall et al., 1997). Density estimates varied greatly, ranging from 0.006 /km^2 (Fay, 1991), to 15.58 /km^2 (Ben-Shahar, 1996). Recent studies focusing on forest habitats, are limited to those on forest elephants (*Loxodanta cyclotis*) which reveal lower densities than savannah elephants, mean densities calculated were between 0.05 /km^2 and 0.66 /km^2 (Blake et al., 2007). However, the forest elephant remains relatively understudied and little is known about their behavioural ecology, therefore direct comparisons on density estimates should be used with caution. A recent continental-scale analysis of the savannah elephant however, calculated density estimates across a variety of habitats and determined that elephants within protected areas, had densities of approximately 0.41 elephants/km^2 (de Boer et al., 2013), this is close to our average estimate across all habitats of 0.49 using the REM in the Aberdare Conservation Area. In further support that our estimate falls in line with continental surveys, the Great Elephant Census (GEC) of 2014, calculated densities averaging 0.30/km^2 (Chase et al., 2016).

Whilst other methods such as CMR are available to calculate density using camera trapping surveys, calculating population numbers of wide-ranging species at low densities has proved to be challenging (Thompson, 2004; Karanth et al., 2006; Marucco et al., 2009). Although using spatial models over earlier CMR models accounts for differences in detection probabilities relative to camera trap placement (Royle and Young, 2008; Borchers, 2012), they require large numbers of 'captured' and 'recaptured' individuals (Sollman et al., 2012). We suspected this would be difficult to achieve at our study site, and a pilot study determined that we were unable to achieve a sufficient number of recaptures of 'marked' individuals.

Previous applications of the REM have deployed various numbers of camera traps, which are often hundreds (Manzo et al., 2012; Zero et al., 2013; Cusack et al., 2015), however, other studies have used just 18 cameras and produced density estimates closely corresponding to those derived using SECR (Anile et al., 2014). Large-scale, high-density camera deployment might not always be necessary if the landscape is homogenous. Obtaining accurate density estimates with increased precision, is attributed to encounter rates and the variance in these rates between individual camera stations (Rowcliffe et al., 2008). Our encounter rate of 71 elephants is comparable with other studies (Manzo et al., 2012; Zero et al., 2013; Anile et al., 2014; Cusack et al., 2015), yet the confidence intervals generated by non-parametric-bootstrapping-with replacement are relatively large, particularly in the 'shrub' habitat (Manzo et al., 2012; Zero et al., 2013; Anile et al., 2014; Cusack et al., 2015). Variance in our data could be explained by the lack of encounters at a number of camera stations, possibly attributed to the clumped distribution of elephants. As with other wide-ranging species, elephants rely on spatially and temporally clustered resources, moving seasonally to areas where those resources are available (Witttemyer et al., 2007; Birkett et al., 2012; Bohrer et al., 2014). Avoiding placing cameras in areas they are frequently observed, would undoubtedly underestimate the population density and violate the assumption of animals moving independently of camera placement (Rowcliffe et al., 2008). When estimating the density of hares (*Lepus europaeus*; *Lepus timidus hibernicus*) using the REM, Caravaggi et al (2014) also found large variations in density estimates between sampled squares (1.9– 11.6 hares per km^2). Variance in encounter rates during population surveys can be a common issue, and is not limited to methods using camera traps (Jathanna et al., 2006).

For increased precision, there is a recommendation to use a minimum of 20 camera trap placements when variance in capture rates is small, or 40 when variance is large, and it is optimal to achieve 10 but preferably 20 captures over the survey period (Rowcliffe et al., 2008). Our survey design using 71 camera stations, with a capture total of 71 images of elephants, suggests that although achieving recommended captures rates may be a challenge, particularly in heterogeneous habitats, our results have met the recommended guidelines for precision. Although there may be difficulties in achieving the recommended number of captures to maintain a low variance between traps when using limited resources, particularly in heterogeneous environments. The REM approach still has merit when time and equipment may be restricted by reducing the duration of time the cameras are in place and moving existing cameras to additional locations (Manzo et al., 2012). This would increase the maximum spatial distribution, potentially increasing precision via a larger sample size, and reducing variance in encounter rates between individual camera locations (Manzo et al., 2012; Zero et al., 2013; Cusack et al., 2015).

Stratifying the study area and accounting for heterogeneities in habitat utilisation is likely to provide improved density estimates. This has been shown in northern raccoons (Prange et al., 2004), Eurasian lynx (Herfindal et al., 2005), American black bears (Powell et al., 1997), and brown bears (McLoughlin et al., 2000). The elephants in our study area are exhibiting a 'clumped' distribution by favouring/avoiding certain characteristics within the habitat. Previous studies have examined this behaviour in elephants in relation to vegetation dynamics (Murwira et al., 2005; Bohrer et al., 2014), access to water sources (De leeuw et al., 2001; Leggett, 2006[a]; Leggett, 2006[b;] Loarie et al., 2009), and the proximity to humans (Ngene et al., 2010). Differences in the density estimates obtained across the various vegetation types (Table 4.2; Figure 4.3) highlight the importance of a stratified sampling design in heterogeneous habitats. Calculating an average density across the entire area without stratifying the study site and deploying cameras weighted to resulting vegetation classes, would likely obscure the spatial variation in elephant distribution, and produce biased estimates for the total population size.

4.5 Conclusion

We have demonstrated the suitability of using camera traps to monitor population densities of large ranging species in challenging habitats where traditional approaches may not be feasible. When access to camera traps are limited, and the distribution of animals is sparse over a wide range, the REM can produce estimates that correspond with expected densities for the study species within protected areas. Stratifying the habitat, particularly for wide-ranging species that exhibit 'clumped' distributions such as elephants, or in heterogeneous landscapes, offers the opportunity of obtaining realistic population numbers, accounting for the spatial distribution of animals within study sites. Whilst confidence intervals are relatively high in some vegetation types due to the variation in encounter rates between individual camera stations. An opportunity to increase the sampling size by relocating camera traps after a period of time, provides a solution to increase precision in density estimates, and offers conservation organisations a trade-off between precision, and time constraints.

Unlike other camera trapping methods such as SECR, the REM presents an opportunity for the continuous monitoring of a species based on the availability of existing equipment and the utilisation of open-source analysis software (REMboot in R). Monitoring over large spatial scales can be conducted by park rangers and scientists, without employing additional staff or purchasing large numbers of equipment, with the added benefit of being able to monitor multiple species at the same time, and acquire density estimates in a relatively short period (Zero et al., 2013).

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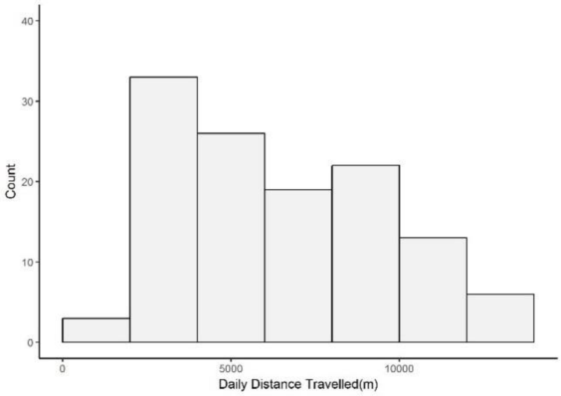
Appendix 4.1 Proportional sampling effort of the 'Salient' and all other areas

Area	Proportion of the study area (%)	Sampling effort (days)	Percentage of actual sampling effort
The salient	9.7	140	11.3
All other areas	90.3	1094	88.6

Appendix 4.2 Summary of the average daily distance moved, calculated from GPS collar data over a 5 month period

Min	1899 m
Mean	6471 m
Std. dev	3216 m
Max	15002 m



Appendix 4.3 Independent variables used to calculate elephant density for the Random Encounter Model

Parameter	Value
Total Images (y)	71
Camera days (t)	1,234
Daily movement (V, km/day)	6.5 ± 2.7
Detection distance (r, km)	0.0129
Detection arc ($\boldsymbol{\theta}$)	0.89 radians

Chapter 5

Demographic structure of a confined elephant population

5.1 Introduction

Wildlife populations across the globe are declining at an unprecedented rate (Aguirre et al., 2008; Nelson et al., 2013), in order to identify the underlying causes of decline and to initiate remedial interventions it is vital to monitor and evaluate the demographic status of animal populations (Freeman et al., 2007; Kendal et al., 2009). Population viability analysis (PVA) modelling of life-history traits is the most effective method to assess the viability of populations (Shaffer, 1990), however, for many populations this is not possible due to a lack of longitudinal data as PVA models require multigenerational life history traits (Jones et al., 2018). In the absence of population specific life history traits, the examination of a population's demographic structure, can be compared to that of a reference population of known status (Kioko et al., 2013; Jones et al., 2018) to assess population trajectories.

Anthropogenic induced factors including habitat-loss, poaching, and over-exploitation are drivers to extinction in a number of species (Gibbons et al., 2000; Nelson et al., 2013; Ceballos et al., 2015), this is particularly the case for the African elephant (*Loxodonta africana).* Despite elephants occupying a wide range approximately 2.4 – 3.4 million km^2 (IUCN, 2013), their modern-day distribution is strongly linked to the historical ivory trade (Douglas Hamilton, 1980; Milner Gulland, 1993). Promisingly, continent-wide poaching levels have recently stabilised following increasing trends since 2006, and improvements in illegal killings across East Africa have been observed. However, levels of poaching still exceed the natural growth rate, and consequently elephant populations are in decline (Blanc, 2007).

A rapidly expanding human population has led to large-scale changes in land-use and the fragmentation of elephant populations (Archie et al., 2007; Blanc et al., 2007; Nyaligu & Parks 2013; Gara et al., 2017). A wide-ranging species that utilises the spatial-temporal variation in seasonal vegetation, elephants move extensively to secure resources (Douglas-Hamilton et al., 2005), which has brought them into increasing conflict with humans (Blanc, 2008; Graham *et al.,* 2010). Agricultural farms and community infrastructure lie within traditional migration routes. Competition for resources between humans and elephants has negative consequences for both, with crop raiding and damage to infrastructure resulting in retaliation killings of elephants (Barnes, 1996; Hoare, 1999; O'Connell-Rodwell et al., 2000; Osborn and Parker, 2003). East Africa, particularly Kenya, has some of the highest incidences of human-elephant conflict (HEC) on the Continent (Jenkins and Hamilton, 1982; Graham et al., 2010; Evans and Adams, 2016). Within the Laikipia District of Kenya, conflict with humans began when elephants migrated from the northern Isiolo and Samburu regions in search of resources in the 1950’s (Thouless, 1993), by the 1970’s human elephant conflict (HEC) had become a prominent issue in the region and a serious impediment to the conservation process (Barnes, 1996; Hoare, 1999; O’Connell-Rodwell et al., 2000; Osborn and Parker, 2003; Sitati et al., 2005; Evans and Adams, 2016). In particular the seasonal movement of elephants from the drier lowland savannah to the wetter montane forests in the region have brought elephants into conflict with small-scale farmers who have settled around the forests. Methods to mitigate HEC such as chili farming have reported limited long-term success (O’Connell-Rodwell et al., 2000; Osipova et al., 2018), and as such, Kenya embarked on the necessary strategy of fencing its montane forests to separate elephants and people. Although successful in reducing conflict, isolating populations which require extensive movement to secure adequate resources could have negative consequences on the viability of these populations (Loarie et al., 2009).

Population size and demographic structure are key components of the growth potential of a population (Foley and Faust, 2010). Demographic processes such as survival, recruitment, inter-calving intervals and mortality rates are frequently examined to assess population health (Jones et al., 2018), and it is this rationale in which conservation status and extinction risk are measured (Foley and Faust, 2010). Whilst elephant populations have demonstrated a resilience to a variety of environmental conditions (Hoffman, 1993; Whitehouse and Hall-Martin, 2000; Foley and Faust, 2010; Jones et al., 2018) it is imperative that the demographic processes relating to population persistence are understood for the implementation of effective conservation management, with limited disruption (Foley and Faust, 2010).

Confinement and the curtailment of migration can impact elephant population viability due to a number of factors. Elephants are highly social, with closely related females living in natal groups and males leaving at the onset of puberty at approximately 12-20 years of age (Hollister-Smith et al., 2007). In wide ranging species, this dispersal helps to regulate population density by reducing competition for available forage, which is considered an important factor in minimising inbreeding (Caughley, 1976; Clobert et al., 2001; Chamaillé-Jammes et al., 2007). In the confined environment with limited forage, this is only exacerbated by the negative impact of confined elephants on the degradation of habitats (Cowling and Kerley, 2002; Guildemond and van Aarde, 2008; Morrison et al., 2018) potentially limiting the long term suitability of an area for sustaining elephant populations by density-dependent regulation (Chamaillé-Jammes et al., 2007). With no recruitment of individuals to the population, there may be an increased competition for mates. Previous studies on fenced elephant populations have witnessed significantly skewed adult sex-ratios pertaining to increased aggression between bulls as a result of inhibited dispersal and increased density (Whitehouse and Kerley, 2002). Confinement can moderate population growth by both ecological and social processes which is reflected in life-history traits. As population numbers reach maximum levels for the ecological carrying capacity of an area, population regulation maintains an equilibrium via changes in demographic processes (Sinclair, 2003), firstly by increasing in juvenile mortality rates, followed by the age of first reproduction, decreases in reproductive rates and finally by increased adult mortality (Gaillard et al., 2000; Eberhardt, 2002; Bonefant et al., 2009).

Long term studies examining life-history traits of a population including survival, recruitment, mortality and inter-calving intervals, provide excellent information on population persistence of individual populations (Jones et al., 2018). Extensive population studies are limited to populations that have long-term datasets, including Amboseli, Addo, Tarangire, and Samburu (Moss, 2001; Gough and Kerley, 2006; Foley and Faust, 2009; Wittemyer et al., 2013). However, the longevity of elephants, with long periods of sexual immaturity and slow reproduction rates, presents a constraint, both logistically and financially (Whitehouse and Hall-Martin, 2000; Moss, 2001) as a complete life-history study could take in excess of 60 years (Moss, 2001). Furthermore, some habitats inhabited by elephants, such as forests, have the additional challenge of dense vegetation and limited accessibility which results in difficulties in detection and they remain largely understudied (Varman and Sukumar, 1995; Barnes et al., 1997; Tobler et al., 2008; Maisels et al., 2013; Chase et al., 2016).

In the absence of long-term data, the rapid demographic assessment (RDA) that records the age structure and sex ratio of a population, can provide an insightful understanding of a population at a given time. It can be used to compare the same population over various points in time, or assessed against other populations that can be used as a reference (Kioko et al., 2013; Jones et al., 2018). Although it has been suggested that short-term studies on demography can be misleading (Whitehouse and Hall-Martin, 2000), it could be argued that simple assessments of population structures of either poorly known species, or understudied populations, can still aid in conservation management (Tella et al., 2013), providing important information on a populations current situation and future potential, particularly in comparison to extensively studied populations. Variances in the response to environmental change, including survival and reproduction are observed not only between the sexes, but also by the age of individuals in the population, as such the population dynamics of large herbivores are driven strongly by age structure (Gaillard et al., 2000). In environments that are reaching ecological carrying capacity whereby elephants are under nutritional stress, there will be higher proportions of juvenile females as they are less costly than males in terms of parental investment (Gough and Kerley, 2005). Populations affected by poaching or the introduction of new individuals, have younger age structures and a larger portion of females (Foley and Faust, 2010; Mackey et al., 2006), whereas stable populations have an even distribution of age structure, and rapidly declining populations have larger numbers of adults/older individuals (Lebreton et al., 1992). Using a comparative approach to identify the impact of confinement by monitoring the age and sex structure of a population to create a demographic profile, can assess the viability of a population by identifying reproductive potential (Lebreton et al., 1992; Rughetti, 2016).

Here I present the demographic structure of an elephant population in a montane forest in Kenya, whereby the population has been confined since 2009. A comparison in the age and sex structure of the confined population, to the demographic structures of free-roaming populations and additionally, to populations in the literature that are suggested to be 1) rapidly growing and 2) stable, to make inferences on population status, and the impact of confinement on the viability of the population

5.2. Materials and Methods

5.2.1 Study sites

Demographic data were collected from four elephant populations in Kenya. One population was the confined elephants in the recently fenced Aberdare Conservation Area

(ACA), a montane forest located in the Central Province of Kenya, with the remaining three were free-roaming populations in the Laikipia and Samburu regions. Two comparative populations (Ol Pejeta Conservancy and Samburu National Reserve) are savanna ecosystems, and one population, the Lewa Wildlife Conservancy, forms part of the ecosystem of the Mount Kenya montane forest that is connected by a 14km long wildlife corridor, enabling traditional seasonal migrations of elephants between Mount Kenya and the Ngare Ndare forest, to Samburu County in Northern Kenya, hereafter this area is referred to as the Mount Kenya Ecosystem (MKE). For detailed information on each of the study sites please refer to Chapter 2.

5.2.2 Data Collection

Data were collected between 2016 and 2018 by one observer to ensure consistency throughout the sampling period. Surveys were conducted either by vehicle, or by observations at water points. Due to the difficulty in observing elephants in the dense forest habitat of the Aberdare National Park (ANP), together with direct observations, images from camera traps were used for the Aberdare National Park and the Mount Kenya ecosystem whereby camera traps in the wildlife corridor were being used for another study. When an elephant was encountered, the number of individuals within that group (defined as the number within a 100m radius showing integrated behaviours (Chiyo et al., 2014), was recorded. I additionally assigned a quality score determining the confidence that all individuals were sighted and recorded, ranging from (1) indicating open vegetation and all individuals clearly sighted, (2) suggested that whilst vegetation was predominantly open, there were areas which could obscure the identification of individuals, and a score of (3) was recorded if the group was observed in dense vegetation and it was unlikely that all individuals were observed. For analysis, any groups assigned a quality score of 3 were omitted from the data. Individuals were classified into one of four broad age groups (< 1 year, 1-8, 9-17, 18+) based on well-established morphological criteria including body shape & size, and tusk appearance (Moss, 1996) that are used by the Convention on International Trade in Endangered Species Monitoring the Illegal Killing of Elephants (MIKE) programme (Appendix 6.1). Whilst other demographic studies have used finer age classes (Moss, 2001; Gough and Kerley, 2006; Foley and Faust, 2010; Jones et al., 2018), a coarser scale was used due to the dense vegetation and restricted viewing opportunities in the Aberdare National

Park and in order to reduce observer error (Chelliah et al., 2013). Where possible, adult and sub-adult elephants were sexed according to features such as body size (adults), shape of the head, tusk shape/size, and external genitalia (Moss, 1996). Juveniles were not individually sexed due to difficulties in accurately determining the sex of elephants under 10 years of age (Jones et al., 2018). Uniquely identifying characteristics of individuals within the observed groups were recorded such as ear notches, damage to tusks, and scars, and re-sightings of these groups were omitted from the data in order to avoid double-sampling (Moss, 2001).

5.2.3 Published data

In order to assess the demographic status of the fenced Aberdare National Park population, comparisons were made to three elephant populations from a published study (Jones et al., 2018). The Tanzanian elephant populations in Ruaha-Rungwa, and Katavi-Rukwa, were considered to be stable between the years 2006-2009, whereas the Tarangire National Park was considered to be rapidly growing during that same period.

5.2.4 Data analysis

The Kruskal-Wallis test was used to test for differences in group size of female herds between the confined population and the free-roaming populations. To examine differences between the age structure of our enclosed population compared to the stable, and increasing populations, Chi-square goodness of fit tests were performed, and the standardised residuals between the observed (ACA population) and expected (comparative populations) frequencies were calculated (Jones et al., 2018).

$$SR = (O - E)/\sqrt{E}$$

Operational sex ratios, defined as the number of adult breeding males available to breeding females (adult and sub-adults), were calculated for each of the populations. The ratio of dependent individuals (juveniles and calves) to adult and sub-adult females was assessed at the group-level for the sampled populations of Ol Pejeta Conservancy (OPC), Samburu National Reserve (SNR), and the Mount Kenya Ecosystem (MKE), using Kruskal-

Wallis test to compare differences and post-hoc Man-Whitney U tests corrected using the 'false discovery rate' method. Comparisons to the populations of Ruaha-Rungwa, Katavi-Rukwa, and Tarangire from the published data could only be performed at a population level due to missing data at the group level. All analysis were undertaken in R version 3.4.3 (R Core Team, 2018).

5.3 Results

A total number of 815 elephants were observed across the study sites. Average group size and the number of dependent juveniles to adult females were calculated from female-only groups in the ANP (*n*=38), Ol Pejeta Conservancy (*n*=10), Mount Kenya Ecosystem (*n*=18), and Samburu National Reserve (*n*=18).

Table 5.1. Summary of the number of elephants of observed in the study by location, age class, and sex if known

Location	Adults	Sub-Adults	Juveniles	Female Adults	Female Sub-Adults	Male Adults	Male Sub-Adults
ANP	256	93	70	107	16	98	40
OPC	46	22	54	33	9	13	13
SNR	35	36	50	29	18	6	18
MKE	61	62	30	27	17	32	41

The structure of the ACA population that has been completely confined for 7 years at the beginning of this study, consists of 2% calves less than 1 year old, 14% juveniles between the ages of 1-8 years, 29% females of breeding age, and 23% adult breeding males. The remainder of the population is represented by sub-adult males, and sub-adult or adults whose sex could not be accurately determined. In OPC 44% of the population is comprised of juveniles, 18% sub-adults, and 38% adults. Within the SNR, juveniles account for 41% of the population, respectively, sub-adults and adults represent 30% and 29% of the total population. The MKE population has a demographic structure consisting of 20% juveniles, 40% sub-adults, and 40% adults.

5.3.1 Group Size

No statistically significant differences were found in the group size between the fenced population and any of the free-ranging populations (x^2 = 5.8391, df = 3, p-value = 0.1197). Group size in the fenced ANP population ranged from 3 to 19 individuals with a median of 7 (Figures 5.2 and 5.3). The OPC had a median group size of 9 and a range of 4 to 21 individuals, similar to that of the SNR with a median group size of 8 and ranging between 4 and 20. Group size in the MKE had a median of 5 and ranged between 3 and 15.

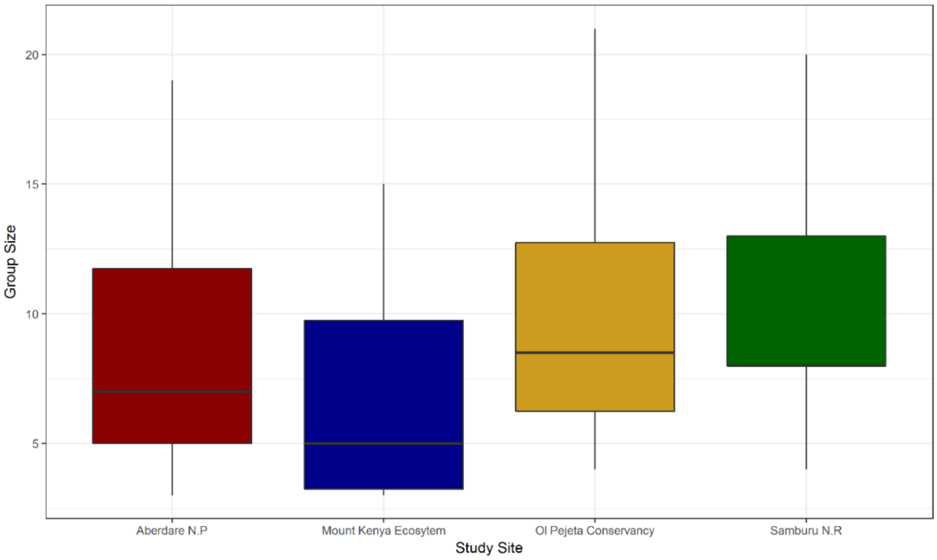


Figure 5.1 Median group size and the ranges of the top and bottom 25% for female herds in the sampled elephant populations

5.3.2 Comparison to known status of populations from published data

Ratios of breeding males to breeding females differed significantly from a theoretical equal distribution in both of the stable populations of Ruaha-Rungwa (χ^2 = 43.46, df = 1, p-value > 0.001) and Katavi-Rukwa (χ^2 = 60.246, df = 1, p-value > 0.001), and also in the rapidly increasing population of Tarangire (χ^2 = 63.439, df = 1, p-value > 0.001). Each of the populations had a higher proportion of breeding females with operational sex ratios of 0.26 (Ruaha-Rungwa), 0.27 (Katavi-Rukwa), and 0.23 (Tarangire) (Figure 5.2).

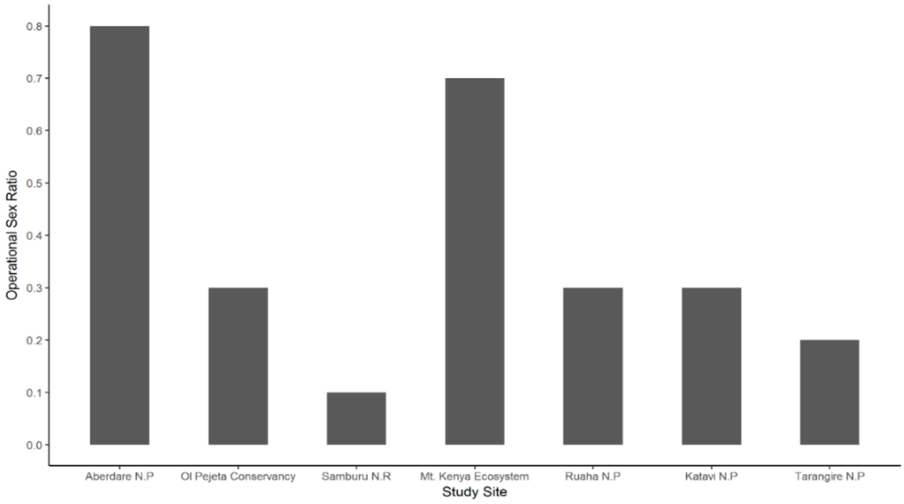


Figure 5.2 Operational sex ratio of all elephant populations

5.3.3 Age structure

Population pyramids representing age structure (Figure 5.3), show that the Aberdare Conservation Area has a highly skewed age distribution, with 83% of its population consisting of adults and sub-adults, and only a small proportion of juveniles (17%). Similarly, the population in the Mount Kenya Ecosystem, is comprised of 80% adults and sub-adults, and 20% juveniles. Age structures of the Ol Pejeta Conservancy, and SNR populations show an increase in the proportions of juveniles, with 76% of the OPC population being adults and sub-adults, and 24% juveniles. The Samburu National Reserve has the highest proportion of the younger age-classes, with juveniles forming 30% of the total population, and adults and sub-adults constituting 70%. Results comparing the number of dependents to adult females at the group level, demonstrate significant differences (χ^2 = 9.0872, df = 3, p-value = < 0.05). The fenced ACA population has the lowest ratio (0.6) of dependent juveniles to adult females, followed by the MKE at 0.8, SNR with 1.0 juvenile to each adult female, and the OPC population had the highest ratio at 1.3 (Figure 5.4).

The rapidly increasing population of Tarangire has a higher proportion of juveniles (58%) compared to adults and sub-adults (42%) in the population. Similarly, Ruaha-Rungwa, which is considered stable, has an equal proportion (50%) of adults and sub-adults to juveniles (50%). Katavi-Rukwa, that is also considered stable, has a higher proportion of adults and sub-adults (79%) in the population compared to juveniles, which constitute 21%.

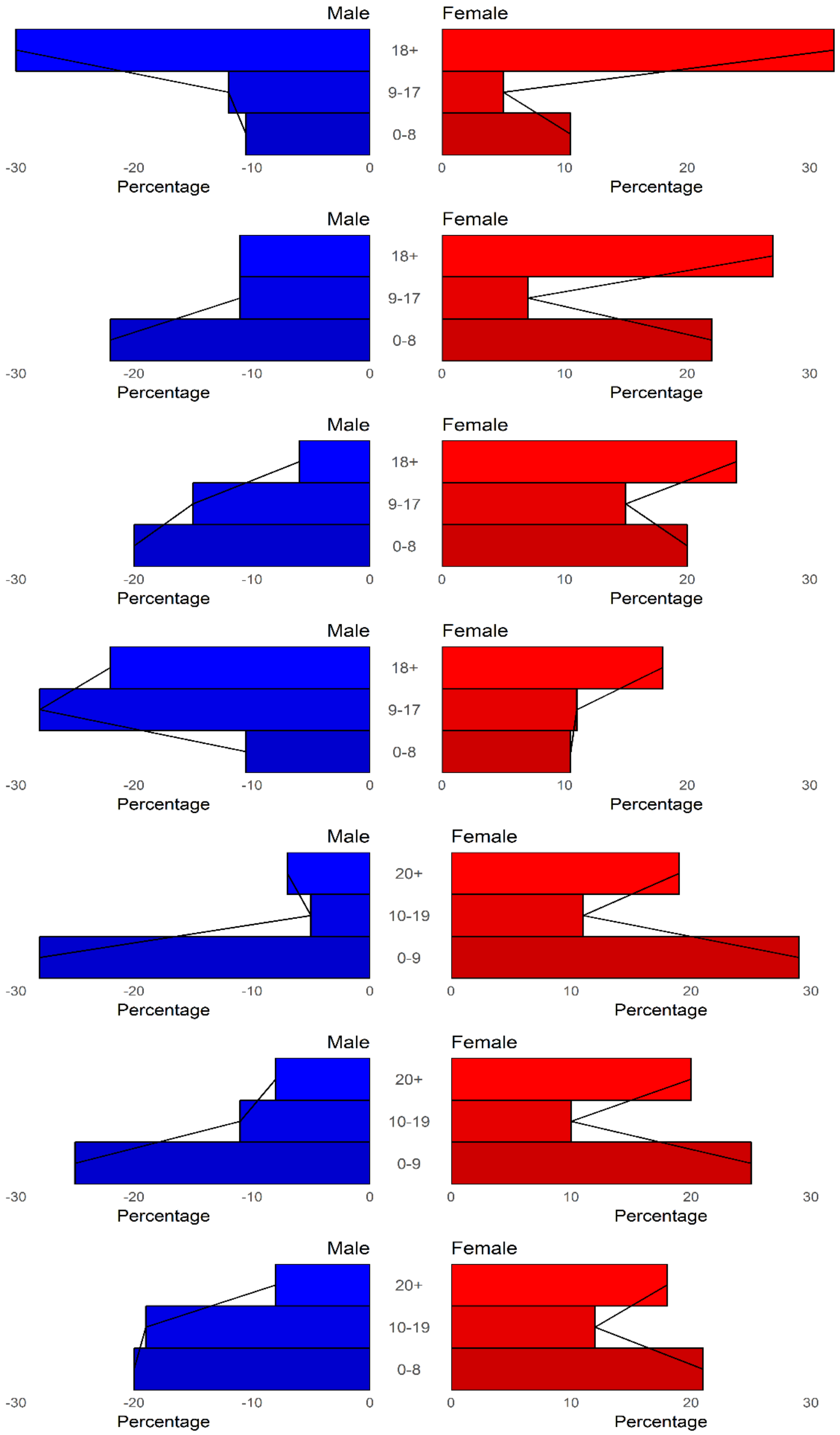


Figure 5.3 Population pyramids showing the age and sex structure of (top-bottom); Aberdare Conservation Area, Ol Pejeta Conservancy, Samburu National Reserve, Mount Kenya Ecosystem, Ruaha-Rungwa, Katavi-Rukwa, and Tarangire populations. Elephants under 9 years old were not sexed in the top four populations, therefore equal distribution was assumed

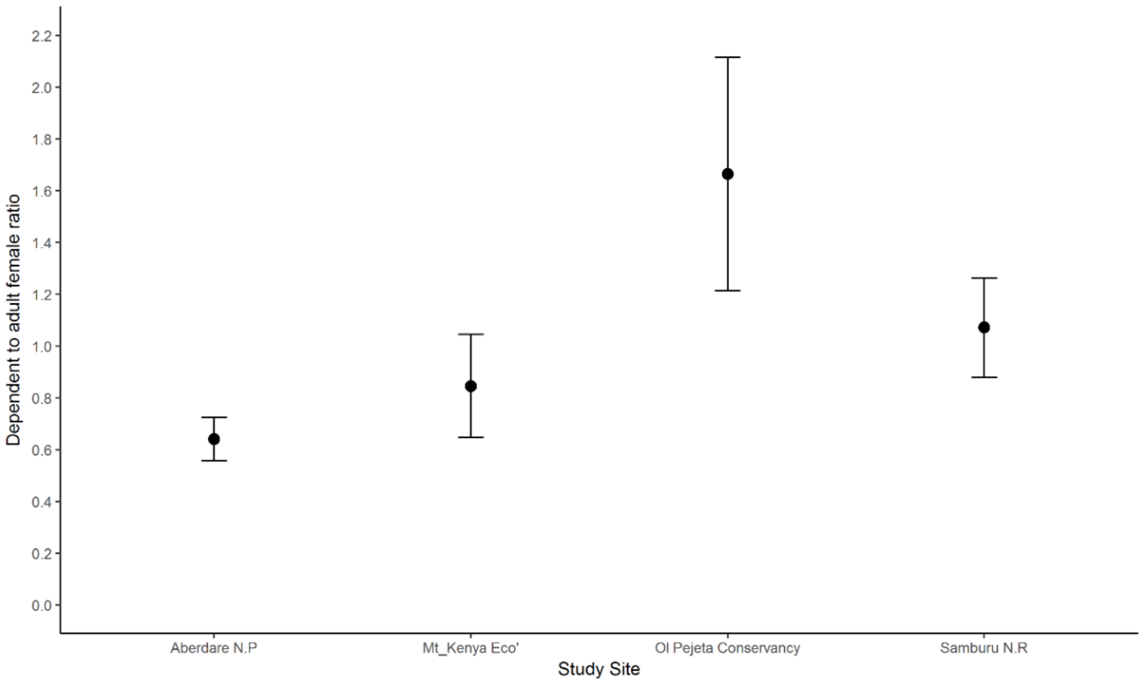


Figure 5.4 Mean (and 95% confidence intervals) ratio of dependent juveniles to adult breeding females at the group level in each of the study sites

5.3.4 Comparison of age-class frequencies to populations from published data

Comparison of the age class frequencies comparing the confined ACA to the published data from populations in Tanzania, determined that the ANP has a significantly different age structure to both of the two stable populations (Ruaha-Rungwa, Katavi-Rukwa), and also to the rapidly increasing population of Tarangire National Park. This was consistent when comparing the entire population, for males only, and for females only (Table 5.2).

Table 5.2 Comparison of the age structures of the Aberdare National Park population and the Ruaha-Rungwa, Katavi-Rukwa, and Tarangire populations from published data

Population	Status	Sex of the population	χ^2	P-Value
Ruaha-Rungwa	Stable	All	495.05	<0.001
		Females	204.17	<0.001
		Males	204.17	<0.001
Katavi-Rukwa	Stable	All	215.98	<0.001
		Females	93.961	<0.001
		Males	205.35	<0.001
Tarangire	Rapidly Increasing	All	329.1	<0.001
		Females	130.14	<0.001
		Males	370.15	<0.001

The standardised residuals comparing the Aberdare Conservation Area to the Ruaha-Rungwa, Katavi-Rukwa, and Tarangire populations show a uniform trend. High positive standardised residuals can be observed in the adult age class, lower positive residuals in the sub-adult class, and high negative residuals in the juvenile class (Figure 5.7). Results indicate that the fenced ACA population has an age structure that is disproportionately high in adults, and low in juveniles in comparison. This is also observed in the number of dependents to breeding females, with higher ratios of dependents observed in the populations from published data. However, in the absence of data at the group level, statistical analysis were unable to be performed on the dependents to breeding females data (Figure 5.6).

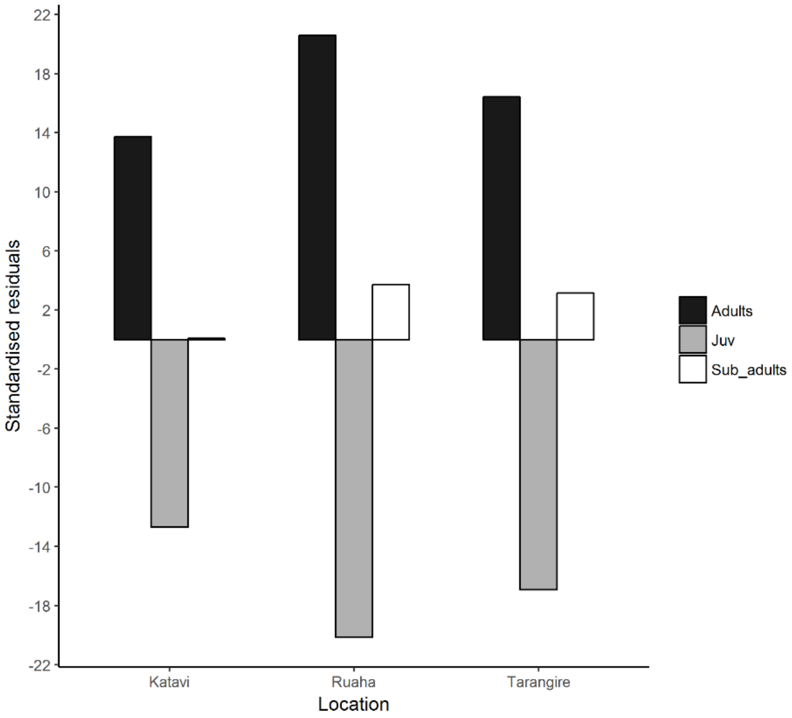


Figure 5.5 Standardised residuals from the chi-square tests comparing the age class frequencies of the confined Aberdare National Park population to the Ruaha-Rungwa, Katavi-Rukwa, and Tarangire populations from published data

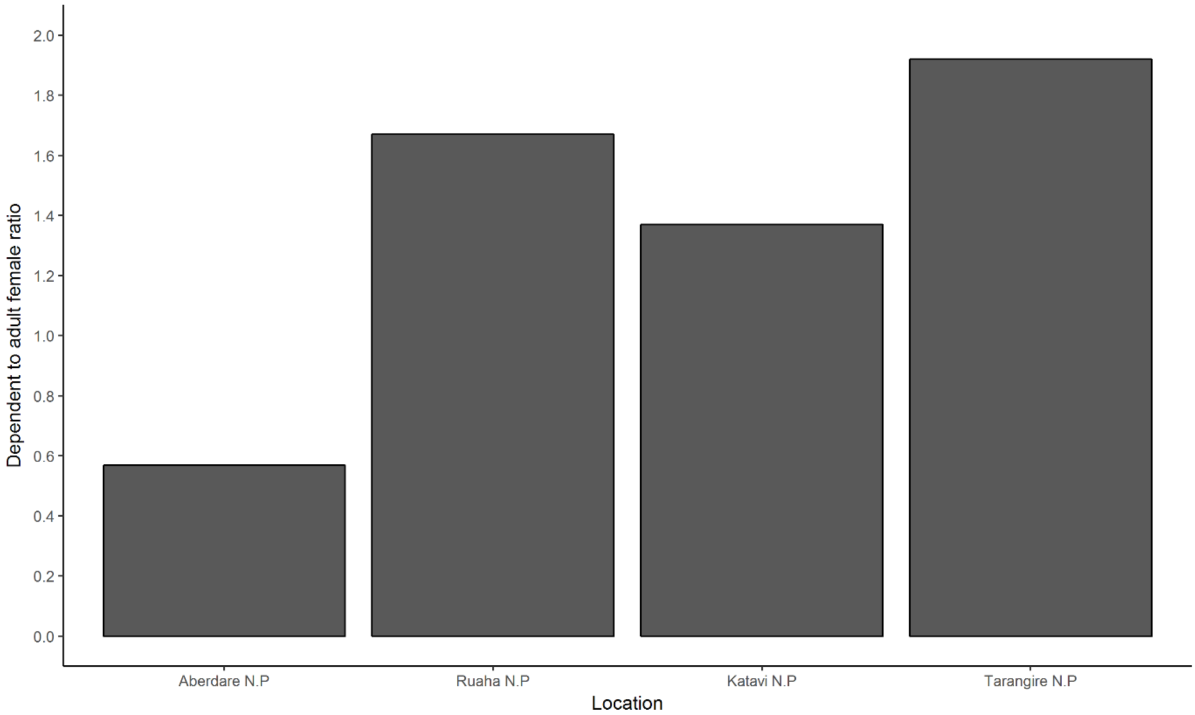


Figure 5.6 Ratio of dependent juveniles to adult breeding females in the Aberdare National Park, Ruaha-Rungwa, Katavi-Rukwa, and Tarangire populations

5.4 Discussion

The confined Aberdare Conservation Area population has a predominantly older age structure than many other elephant populations (Moss, 2001; Aleper and Moe, 2006; Jones et al., 2018). Distinct differences were observed between the confined population and all of the free-roaming populations of Samburu National Reserve, Ol Pejeta Conservancy, and the Mount Kenya Ecosystem. Similarly, when compared to the stable populations of Ruaha-Rungwa and Katavi-Rukwa, and the rapidly increasing population of Tarangire in 2006 (Jones et al., 2018), differences in the age structure were identified. With in-excess of 60% of the population aged 18 years and above, and only 2% calves under 1 year of age, the ANP population shows similar characteristics to the isolated Tarangire-Manyara population in 2012, which had a larger portion of adults, followed by sub-adults then juveniles (Kioko et al., 2013).

As population growth is governed by the potential rate of reproduction in females (Clutton-Brock and Vincent, 1991; Ogola and Omondi, 2005), female biased sex ratios are usually observed in growing populations due to the increased potential number of offspring that can be produced therefore resulting in a rapid population growth (Moss, 2001; Aleper and Moe, 2006). With an operational sex ratio of 0.8, the number of adult breeding males available to breeding females (adult and sub-adults) was highest in the confined population compared to all others, indicating that the population may be maintaining current growth rates, and not increasing (Hamilton, 1967). The high number of males in the confined ACA compared to all other populations, may be a result of restricting the dispersal of males from the area at the onset of puberty.

Age structure provides a measure of reproductive potential and future growth. Populations expanding at a high rate, are usually characterised by large reproductive cohorts, whereas populations considered to be stable, tend to exhibit approximately equal distributions of the age classes (Lebreton et al., 1992). The population pyramid of the Aberdare Conservation Area (Figure 5.3) shows a disproportionate age structure with a high number of individuals in the adult age class, and very few individuals in the juvenile classes, therefore implying there has been a reduction in reproductive output. This was also observed in a confined population in the Sweet waters reserve, Kenya, where 5-10 years after the installation of a fence, there was a hiatus in reproduction, indicated by a low number of elephants within the 5-10 year age group (Ogola and Omondi, 2005). Despite confinement the population experienced a rapid increase in growth, and approximately 9% of the population were calves aged 1 year and under. Authors suggested that the increase in population growth may have been attributed to a combination of increased security via the fence and ground patrols, reducing the number of illegal killings, and as a result of break-ins of free-ranging male elephants from outside of the reserve which continued to be recruited to the population (Ogola and Omondi, 2005).

Similar to the Sweet Waters population, the skewed age-structure observed in the Aberdare Conservation Area, suggests a significant decline in reproductive output during the final 7 years of the fence build (2002-2009). In this period, the ‘Salient’, an area of high elephant density in the East of the park, which is also a key area of historical migration (KWS 2016, pers.comm), was fenced. This decline continued for a further 8 years, as the proportion of individuals in the juvenile age class (1-8 years) is low, a further decline was observed, with calves under 1 year representing only 2% of the population (Figure 5.3). Even though there is evidence of a hiatus in breeding, the elephant population in the Aberdare Conservation Area has a substantial proportion of reproducing individuals (>32%), and has the potential to increase reproductive output. However, at present, age structure, and the low ratio of dependents to adult females, which is much lower than the free-roaming populations, infers that the population is not growing, and is possibly in decline (Lebreton et al., 1992).

The future status of the confined population is a concern, as when senescence occurs in the current adults, and the young age classes mature, there will be a period when there is only a small number of elephants of reproductive age. However, elephant populations have demonstrated great flexibility in reproductive strategies. Although the average age of first reproduction in females is 11-14 years (Calef, 1988; Lee et al., 2016), under ideal conditions, females can ovulate between the ages of 8-10 years (Calef, 1988), and the earliest reported age of sexual maturity observed at just 7 years old (Laws and Parker, 1968). Additionally, in disturbed populations, it is suggested that males have entered musth prematurely, and begun mating at approximately 20-25 years old (McKnight, 2000). Elephant populations under pressure, have demonstrated the ability to recover by reaching maximum intrinsic growth rates when conditions are favourable (Foley and Faust, 2010; Fritz, 2017). Given these flexible reproductive strategies, combined with their long reproductive potential of breeding until ~65 years of age (Lee et al., 2016), it is possible that a large decline may not occur, however favourable conditions in order to maximise reproductive potential are required (Bender, 2008).

Populations can fluctuate due to intrinsic and extrinsic drivers (Young and Van Aarde, 2010). Density independent environmental effects could be a potential cause of the skewed age distribution in the Aberdare Conservation Area population, as effects could be impacting differently on the different age classes. During periods of resource stress, juvenile survival is impacted first, followed by a reduction in reproduction, then finally a decrease in adult survival (Eberhardt, 2002). As with many large mammals, younger age classes are more sensitive to variations in climatic conditions (Gaillard et al., 2000; Moss, 2001; Coulson et al., 2002), whereas adults tend to be reasonably tolerant to temporal variations (Gaillard et al., 1998; Young and Van Aarde, 2010). The low proportion of juveniles in the confined ANP population since approximately 2002, could be as a result of decreased survival in the younger age classes due climatic conditions. During the years of 2001, 2005-06, 2008 – 2011, and 2016-17, Kenya experienced dry/drought conditions. High calf mortality has previously been reported during dry conditions, 20% of calves died within 9 months of a drought in Tanzania (Foley et al., 2008), and all calves were lost in Namibia during a drought (Leggett, 2003). Adding further to the issue could be the physiological response of elephants during these conditions, including delayed conception (Lee and Moss, 2011), and a reduction in conception rates (Wittemyer et al., 2007).

Although the complex relationship between climate and survival /fecundity (Fritz, 2017) provides an explanation for the age-skewed structure of the ACA population, it could be further compounded by chronic physiological stress in response to the curtailment of dispersal. In African elephants, high concentrations of stress hormones (Glucocorticoids), have been associated with a number of factors including translocation (Millspaugh et al., 2007; Viljoen et al., 2008; Pinter-Wollman et al., 2009), poaching (Gobush et al., 2007), and habitat disturbance (Jachowski et al., 2012). High concentrations of glucocorticoids that have been maintained for a long period of time, have been associated with a reduction in reproductive function, due to reduced fertility, low libido, and reduced conception rates (Liptrap, 1993; Dobson & Smith, 2000; Fernando, 2006; Dickens et al., 2010; Mason & Veasey, 2010). Evidence also suggests that exposure to stress early in life, decreases longevity, and reduces reproductive rates, this has further implications for the future reproductive potential of the population.

5.5 Conclusion

The isolation of wildlife populations is an increasing concern in conservation management, as many populations worldwide are becoming fragmented. The modelling of life-history traits is an effective method to assess the future viability of a population, however in many populations, a population viability analysis (PVA) is not possible due to a lack of long-term data. Examining the demographic structure of the confined elephants in the Aberdare Conservation Area, and comparing to various other free-roaming populations, particularly to the published populations of known status, has provided an indication to the growth potential, and subsequent conservation status of the population. Age, and sex structure of a population, are influenced by demographic processes that maintain population equilibrium.

The ACA population has a highly skewed age-structure, with 83% of the population being comprised of adults and sub-adults, and the ratio of dependents to breeding females is significantly low, suggesting a reduction in calving. Although the confined ACA population exhibits a significantly different population structure compared to the populations of known status, it shows similar characteristics to the montane forest population (Mount Kenya Ecosystem) that has a wildlife corridor connecting the forest to the lowland savannahs. Whilst results indicate that the current growth trajectory of the confined population is reasonably low, this may not necessarily be attributed exclusively to confinement, and may be the result of a number of other environmental factors, such as resource availability in the montane habitats. Annual monitoring of the demographic structure of ACA population, combined with annual estimates of elephant density, will enable effective modelling of the future viability of the population.

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Chapter 6

Physiological effects of confinement

6.1 Introduction

Many species are declining at an alarming rate through human induced influences (Baillie et al., 2004; Alonso et al., 2008; Ceballos et al., 2015) including overexploitation (Nelson et al., 2013), and loss of habitat (Gibbons et al., 2000). An expanding human population and subsequent conversion of land use has led to a competition for resources between people and wildlife. Many wildlife populations now exist isolated between a matrix of human settlement (Haddad, et al., 2015), or confined in protected areas as a result of fencing to reduce conflict (Hoare, 1992; Williams et al., 2001), conserve biodiversity (Short and Turner, 2000), or to prevent hunting practices (Dunham, 2001). There is now an unprecedented level of fragmented populations (Reed, 2004; Haddad, et al., 2015), and with the increasing utilisation of fencing in conservation management, it is imperative that we understand the full extent of isolating animal populations (Hoare, 1992; Haywood and Kerley, 2008).

For the past few decades the primary focus has been to determine the genetic implications of isolation, and these negative impacts are now widely understood (Shaffer, 1981; Frankham et al., 2017). More recently, there has been an increasing interest in identifying the ecological effects of confinement, such as the capacity of some species to permanently modify their habitat by altering vegetation structures in the absence of a period of regeneration whereby animals would seasonally disperse (Kerley and Landman, 2006; Pringle, 2008; Morrison et al., 2018). However, there is a paucity of information examining the physiological impact of curtailing dispersal, and the potential ramifications of this may have on the demographic structures that influence population growth in already vulnerable species such as elephants.

Increasing habitat fragmentation and human-elephant conflict (HEC) are amongst a number of drivers that threaten the status of the African elephant *(Loxodanta africana),* resulting in its ‘Vulnerable’ classification on the IUCN Red list (Archie et al., 2007; Blanc et al., 2010). With some of the highest reported incidences of conflict in East Africa (Jenkins and Hamilton, 1982; Graham et al., 2010; Evans and Adams, 2016), Kenya embarked on a strategy of fencing its montane forests, and in 2009, the world’s largest electric wildlife fence was completed, prohibiting the dispersal of the elephant population.

Dispersal plays a fundamental role in population regulation and has many drivers. The dispersal of males at the onset of puberty (Hollister-Smith et al., 2007), not only assists in regulating resource-dependent population density (Chaine and Clobert et al., 2015; Chamaillé-Jammes et al., 2007), but is a mechanism for inbreeding avoidance (Archie et al., 2007). Immigration of individuals between populations has been evidenced to reduce aggression between males during the search for mates (Whitehouse and Kerley, 2002). Elephants have a spatial-temporal ustilisation of the landscape, staying in the higher altitudes with permanent water sources during the dry season, and dispersing to the lowland savannahs during the wet season (Douglas-Hamilton et al., 2005; Lendrum et al., 2014). Although there are several suggestions explaining these seasonal migrations, ranging from thermoregulation (Fryxell and Holt, 2013) to reduced competition for resources (Fryxell and Sinclair, 1988), a general consensus is that seasonal migrations enable individuals to cope with a heterogeneous landscape that experiences changes in vegetation phenology, and the availability of forage (Murwira et al., 2005; Loarie et al., 2009; Lendrum et al., 2014).

In contrast to the efficient ruminant digestive system of species such as giraffe, elephants are hind gut fermenters digesting only 22 to 45 percent of their intake (Rees, 1982; O'Meissner et al., 1990). During the dry season when the mature grass is fibrous and un-palatable, they consume large volumes of abundant low-quality browse, in a trade-off between the limited availability of high-quality forage (van Soest, 1996; Bergman et al., 2001; Clauss et al., 2003; Clauss et al., 2007). Despite the year-round availability of browse, during the wet season, when the young grass has a higher crude protein, and is easily digestible, elephants disperse to the lowland savannahs (van Soest, 1996; Seydack et al., 2000; Cerling et al., 2006). Evidence documents a strong relationship between the availability of wet-season vegetation and its influence on conception rates (Wittemyer et al., 2007), and a number of studies have demonstrated that elephants are motivated towards these seasonal vegetation changes by dispersing from the higher altitudes, and rarely returning whilst green vegetation is available in the lowlands (Loarie et al., 2009; Young et al., 2009; Bohrer et a., 2014). A critical question, is what impact does the curtailment of dispersal have on the physiology of confined elephant populations?

Whilst fencing has become a common management strategy (Haywood and Kerley, 2008), a failure to perform seasonal migrations may illicit a physiological stress response. The release of glucocorticoids, steroid hormones (cortisol and corticosterone), are an important mechanism for short-term survival, enabling an individual to cope with a stressor by balancing the expenditure of energy (Sapolsky et al., 2000; McEwen and Wingfield, 2003; Romero and Butler, 2007; Sheriff et al., 2011). However, maintaining high concentrations of glucocorticoids for prolonged periods induces chronic stress, and as such, is linked to a number of pathological dysfunctions including decreased growth rates, reduced body condition, suppression of the immune system resulting in increased parasite loads, poor wound healing and premature death (Munck et al., 1984; Romero, 2004; Dickens et al., 2010; Mason & Veasey, 2010). Conversely, prolonged periods of low glucocorticoid concentrations have adverse effects, indicating a suppression of the adrenal system and preventing activation of the stress response (Sapolsky, 2015). Furthermore, elevated glucocorticoids can have negative effects on reproduction, by reducing fertility and lowering libido (Liptrap, 1993; Dobson & Smith, 2000; Romero, 2004; Dickens et al., 2010; Mason & Veasey, 2010). In isolated populations with no immigration, a reduction in reproductive output could considerably alter a populations demographic structure, further exacerbated in long-lived species including elephants due to long periods of sexual immaturity, and long inter-calving intervals (Whitehouse and Hall-Martin, 2000; Moss, 2001). In an ageing population with reduced calving, a decline in population growth will have negative ramifications for the sustainability of the population.

Glucocorticoids are metabolised and excreted in faeces. As a non-invasive technique of measuring stress, faecal glucocorticoid metabolites (FGMs) have become a useful tool in conservation, particularly in endangered species as there is no disruption to animals (Millspaugh and Washburn, 2004), and have been used in a variety of species (Wasser et al., 2000; Touma and Palme, 2005). FGM concentrations have been measured in elephants in various applications including; poaching, translocation, injury, the loss of matriarchs, and identifying refuge behaviours (Millspaugh et al., 2007; Gobush et al., 2008; Viljoen et al. 2008; Ganswindt et al., 2010; Jachowski et al., 2012; Jachowski et al., 2013). However, a significant gap remains in measuring the impact of confinement, and subsequent curtailment of dispersal.

Within this context, the aim of this chapter was to examine the physiological impact of confinement on elephant populations, which may have wider implications to the demographic structure, and population viability. The application of endocrinology techniques measuring glucocorticoid metabolite concentrations in faeces, provided a measure to assess adrenal activity in a population that has been confined by an electric fence since 2009. To interpret the FGM concentrations in the confined population, and assess the concentrations of FGMs determined and its relevance to confinement, direct comparisons were made to two free-roaming populations. One comparative population is located in the lowland savannah that free-roaming elephants migrate to during the wet season. The remaining population has the inclusion of a wildlife corridor, enabling the seasonal migration of elephants from a montane forest to the lowland savannahs, additionally allowing the examination on the use of wildlife corridors from a physiological perspective. The importance of understanding the drivers of dispersal and spatial-temporal utilisation have been highlighted (Berger, 2004; Schick et al., 2008), but restriction of dispersal has received little attention. Results aim to inform management strategies regarding the impact of confinement on elephant physiology and to examine whether in the inclusion of wildlife corridors can minimise the physiological stress response by enabling dispersal.

6.2 Materials and Methods

6.2.1 Study areas and subjects

The Aberdare Conservation Area (ACA) covers 1,748 km^2 and is comprised of the Aberdare National Park (ANP) and the surrounding Aberdare Forest Reserves. Located in the Central Province of Kenya, lying southwest of Mount Kenya, it is a montane forest with altitudes between 1885m and 4000m which provides a uniform climate all year, with daily temperatures ranging between 16 ^{0}C and 21.8 ^{0}C. Having commenced in 1989, the world’s largest electric wildlife fence was completed around the perimeter in 2009, resulting in the permanent confinement of savannah elephants in the forest.

To the north of Mount Kenya in the Isiolo province lies the 250 km^2 Lewa Wildlife Conservancy (LWC). This area is connected to the Mount Kenya montane forest and lower-lying Ngare Ndare forest by a 14-km-long wildlife corridor. Widths of the corridor vary between 1km and just 7m at an underpass. The Mount Kenya Elephant Corridor (MKEC) enables the passage of migrating elephants from the montane forest to the lowland savannahs, and north towards Samburu County. Daytime temperatures throughout the ecosystem range between 10^{0}C in the montane forest, to in excess of 30^{0}C in the northern Counties.

The Samburu National Reserve (SNR) covering 165 km^2 is located in the Samburu District, north of Lewa Wildlife Conservancy. This reserve in the lowland savannah has no perimeter fences between it and the surrounding reserves, and provides a wildlife corridor that is paramount for migrating elephants between the northern and southern conservation areas of Kenya. Average daytime temperatures vary between 18^{0}C and 30^{0}C (see Chapter 2 for further information on study locations).

6.2.2 Body Condition

To evaluate the physical condition of elephants in the various locations, a body condition score between 1 and 5 that was developed for adult African elephants (Morfeld et al., 2014) was assigned to adults and sub-adults in the population. Due to the dense vegetation in some of the study sites, this data collection was limited only to elephants that were clearly visible from a distance not exceeding 50m (Pinter-Wollman et al., 2009), as the method requires an index from multiple parts of the body (Ribs; Pelvis; Backbone).

6.2.3 Sample Collection

Data collection took place between June 2016 and July 2018. Sample collection was carried out either by direct observation of elephants defecating or by opportunistic collection on encountering dung piles in the study locations. Samples were only collected if they were estimated to be within 8 hours of defecation, determined by bolus consistency, temperature, and the presence of flies, as several studies have identified fluctuations in steroid concentrations as a result of metabolism over time, although FCMs are considered stable within 8 hours of defecation (Mostl et al., 2005; Wong et al., 2016; Yarnell and Walker, 2017; Yarnell and Walker, 2018). To avoid cross contamination gloves were worn to randomly collect a total of ~10g of faeces per bolus, with sub-samples taken across the bolus (each corner and the centre) and placed into plastic zip-lock bags. Date, time, location, and age class (adult, sub-adult, juvenile) which was determined by bolus size (Morrison et al., 2005) and has been used in several other studies (Burke et al., 2008; Woolley et al., 2008) were recorded. When age class could not be accurately assessed due to a damaged bolus or non-agreement between sample collectors, it was recorded as 'unknown'. Samples were immediately frozen in the field at ~ -10^{0}C using a portable car freezer (Dometic CDF-11) until stored in the research facility freezer (~-20^{0}C) until further processing.

6.2.4 Sample Extraction

Steroids in faecal samples are not evenly distributed (Palme et al., 1996; Millspaugh and Washburn, 2004), therefore, to ensure a representative random sample, all samples (*n*=451) were thawed and homogenised by mixing thoroughly in the bag. Adrenal hormones were extracted following a field-based extraction method (Edwards et al., 2014) adapted from Walker et al (2002) using 0.5g (±0.05g) wet weight of faecal material suspended in 4ml of methanol (90%) and vortexed for 5 minutes in a 5 ml glass vial. Sediment was separated by first attaching a 0.2um syringe filter (Thermo Fisher Scientific, 42225-NPL) to a 5 ml syringe and transferring all of the liquid portion of the extract into the syringe and leaving any large portions of faecal material in the glass vial. The liquid extract was then pushed though the filter into a 12 x 75 mm plastic tube. As samples were required to be exported from Kenya to the UK for analysis, FGMs needed to be preserved for prolonged periods (>2 years) on SPE silica cartridges (HyperSep™ C8). To achieve this, the cartridges were first primed following manufacturer protocol (Thermo Scientific, 2011), with 4ml methanol (100%) followed by 4ml of distilled water at an average rate of 1ml/min. Then, 5ml of distilled water was added to the filtered extract bring the methanol concentration from 90% to 40%. Cartridges were then loaded with the extracted sample at a rate of 1ml/min, washed with 2ml distilled water, and sealed with Parafilm® to prevent dehydration during storage. Once the samples were imported to the UK, a manifold was used to elute from the cartridge by pushing 5ml of methanol (100%) through the column at an average rate of 1ml/min collecting the sample. Samples were dried in a water bath (Grant Instruments) then re-suspended in 1ml of methanol (100%), placed in a sonicator (GT Sonic manufacturer) for 15 minutes and stored at -20^{0}C until analysis.

6.2.5 Biochemical and biological validation

Faecal glucocorticoid metabolite concentrations were extracted using the corticosterone enzyme immunoassay kit (DetectX®, Arbor Assays®) according to manufacturer guidelines. Parallelism tests were conducted to validate the polyclonal antibody (Donkey Sheep polyclonal) of the enzyme immunoassay (EIA) kit to accurately measure FGMs in the African elephant (Millspaugh et al., 2007; Jachowski et al., 2012). Twenty samples that were representative of all the samples (location and age classes) were chosen at random and an equal amount of extract was pooled from the Hypersep C8 cartridges (Section 6.2.4). The pooled extract was serially diluted 'two-fold' in assay buffer and compared to a serial dilution of the corticosterone standard. Displacement curves parallel to the standard curve indicated that the FGMs in the sample, were comparable immunologically to the standards in the assay. Interference of the sample matrix were measured via recovery of the assay standards with an equal amount of the pooled sample (100µl), and comparing the observed recovery to the expected concentration. Physiological biological validation to determine the suitability of the assay in detecting faecal corticosterone metabolites (FGMs) was performed by assessing adrenal activity after a potentially stressful event (Palme, 2005; Watson et al., 2013). Faecal samples were collected before, during, and after an institutional transfer of African elephant (n=1) from Knowsley Safari Park, UK for another study. Samples used for the biological validation were not loaded onto Hypersep C8 cartridges. All data analysed had an inter-assay coefficient of variation (CoV) less than 15%, and intra-assay CoV less than 10%.

6.2.6 Statistical Analysis

Parallelism and matrix interference data were analysed using linear regression. FGM concentrations for the biological validation (institutional transfer) were $\log_{10}$ transformed to fit a normal distribution. Generalised linear mixed models were used to enable analysis of a repeated measures design (repeated observations of the same elephant over time). FGM concentrations from the sampled populations (ACA, MKE, SNR) were $\log_{10}$ transformed to normal distribution, tested for equal variance using the Levene's test, and analysed using linear models to measure differences in FGM concentrations between then populations, and between the various age classes (Adults, Sub-adults, Juveniles) between the populations. Post-hoc pairwise comparisons between conditions (location and age class), were analysed with p value adjustment using Tukey's method to reduce type I error. The Log_{10} transformed data was back transformed to calculate the geometric mean with corrected confidence limits (Package 'lsmeans', R Core Team, 2017) to provide an original scale interpretation. Effect sizes (Cohen's d) were calculated (Package ‘effsize’, R Core Team) of statistically significant pairwise results. The Mann-Whitney U test was used to examine body condition scores between the confined ACA elephant population and the free ranging SNR population. All statistical analysis were carried out in R statistical environment (Version 3.4.3; R Core Team, 2017).

6.3 Results

6.3.1 Validation

Following the biochemical validation, results determined that the enzyme immunoassay (EIA) was able to accurately measure African elephant FGM’s, $R_2 = 0.9464$, $F = 88.27$, $p < 0.001$ (Figure 6.1), with no matrix interference, $R_2 = 0.9975$, $F = 2391$, $p < 0.001$ (Figure 6.2). Results from the biological validation demonstrated that FGM concentrations differed significantly during the institutional transfer of elephants ($t = -4.381$, $df=7$, $p < 0.01$), with higher FGM concentrations (0.9 ng/g, sd=0.2ng/g) observed during the transfer phase, compared to (0.02 ng/g, sd=0.06 ng/g) in the post transfer phase 5 weeks later (Figure 6.3). Mean FGM concentrations during the pre-transfer phase (0.5 ng/g, sd=0.3 ng/g) did not differ statistically to the transfer phase ($t = -2.227$, $df= 7$, $p > 0.05$). This may be the result of a number of potentially stressful management factors (i.e. enclosure maintenance/ health checks) that were completed during this period which were logged in the institutional Zoological Information Management Software (ZIMS), potentially increasing ‘baseline’ FGMs during the pre-transfer period (Figure 6.3).

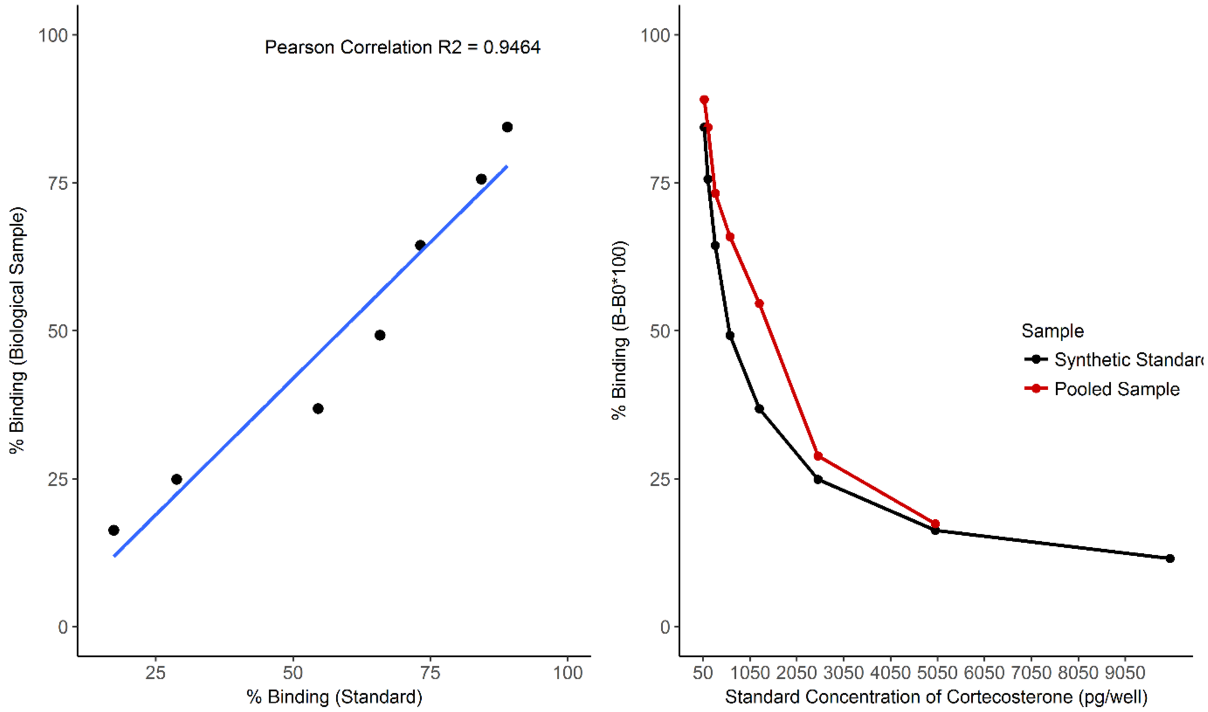

Figure 6.1 African Elephant faecal extract demonstrates parallelism with corticosterone standard curves on corticosterone enzyme immunoassay kit (DetectX®, Arbor Assays®).

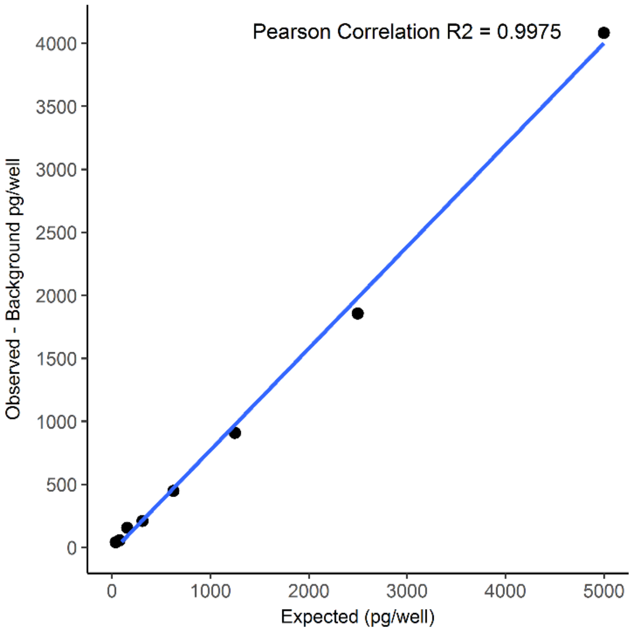

Figure 6.2 Assessment of matrix interference of African Elephant faecal extract on corticosterone standards with corticosterone enzyme immunoassay kit (DetectX®, Arbor Assays®).

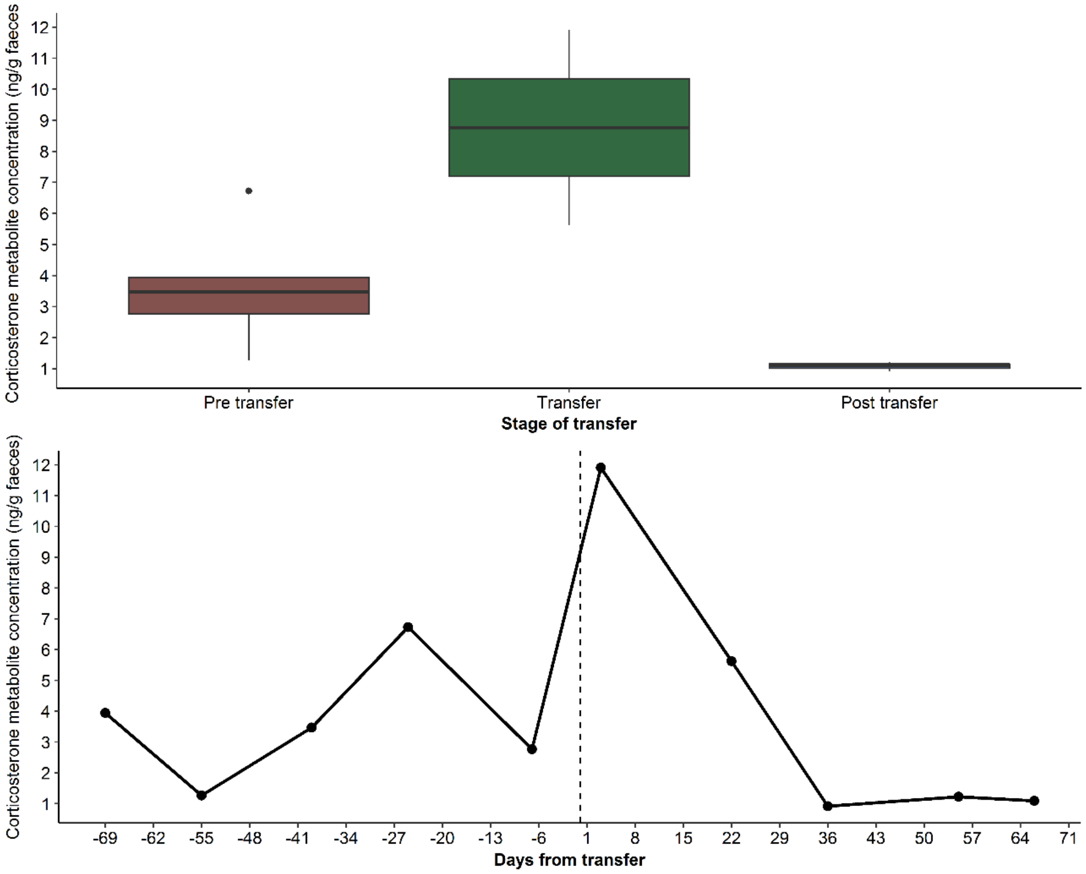

Figure 6.3 Faecal glucocorticoid metabolite concentrations (n/g) measured on the corticosterone enzyme immunoassay kit (DetectX®, Arbor Assays®) following the inter-zoo transfer of a African Elephant (n=1) which demonstrates biological validation. The dashed line represents the day of transfer, day 0.

6.3.2 Faecal Glucocorticoid Metabolite Concentrations

A total of 438 samples were collected and extracted during the wet and dry season between 2016 and 2018. However, 204 samples were damaged during exportation, which resulted in 234 samples from the wet season to be in included in the current statistical analysis. Significant differences in FGM concentrations were observed between the population locations (F=35.1, $p < 0.001$) (Table 6.1 and Figure 6.5). Overall, the confined ACA population has increased FGMs compared to both free roaming populations. FGM concentrations of 3.73 ng/g (95%CI, 3.35-4.16) is a 91% increase in compared to the LWC population (1.95 ng/g, 95% CI, 1.72-2.21) that use the wildlife corridors between the montane forest of Mount Kenya and North to Samburu, and 68% higher concentrations than the Samburu National Reserve population (2.22 ng/g, 95% CI, 1.98-2.59). No significant differences in FGMs were observed between the two free-roaming (LWC and SNR) populations (Table 6.1).

Any individuals recorded as age class ‘unknown’ (*n*=30) were omitted from the age class analysis. Age class data (*n*=204) were analysed to examine whether FGM concentrations varied between the different age classes (Adults; Sub-adults; Juveniles). Overall there was no significant differences in FGMs between the different age classes (F=2.084, p >0.05; figure 6.5). However within populations, significant differences in FGMs were detected between the adult elephants in the confined ACA population and both free-roaming populations (F=4.46, p < 0.05) (Table 6.2 and Figure 6.6). The average concentration in the ACA population (3.35 ng/g 95% CI, 2.59-4.33) was 60% higher than in LWC (2.09 ng/g, 95% CI, 1.70-2.56), and 47% greater than in the SNR population (2.28 ng/g, 95% CI, 1.86-2.79). No significant differences were observed between the adults in the free-roaming populations. The greatest difference in FGM concentrations between the confined ACA population and free-roaming populations was observed in the sub-adult age class (F=26.92, p < 0.001) (Table 6.3 and Figure 6.5). The elephants in the ACA had FGMs averaging 4.13 ng/gm (95% CI, 3.58-4.76), a 121% increased concentration compared to the LWC population (1.87 ng/g, 95% CI, 1.59-2.19), and 51% higher than SNR (2.74 ng/g, 95% CI, 2.28-3.30). In contrast to results from the overall differences in FGMs by location and the adult age class, whereby the free-roaming populations were not significantly different to each other, significant differences were also observed between the LWC and SNR populations. Elephants in the SNR exhibited a 32% increase in FGMs than the LWC population. Although the general linear model highlighted significant differences (F = 4.104, p < 0.05) in FGM concentrations in the ACA juveniles compared to the other populations, pairwise contrasts with adjusted P values revealed no significant differences. Sample size for this age class however, was likely too small (*n*=22) to detect an effect and may be the result of a type I error.

Table 6.1 Summary of the General Linear Model and Tukey pairwise comparisons of concentrations of faecal glucocorticoid metabolites between the Aberdare Conservation Area and non-fenced control populations.

Population	**Sample size (*n*)**	**Test Statistic**	**Test Statistic**	**Df**	**P value**	**Effect Size (Cohen’s d)**
All (GLM)	234	R^2 =0.2331	F = 35.1	(2), 231	< 0.001 ***	
LWC	157	T =7.689			< 0.001 ***	-1.22 (Large)
SNR	167	T = 6.395			< 0.001 ***	-0.97 (Large)
LWC ~ SNR	111	T = -1.485			> 0.05	

Table 6.2 Summary of the concentrations in faecal glucocorticoid metabolites in adult elephants in Aberdare Conservation Area and non-fenced control populations.

Population	Sample size (*n*)	Test Statistic	Test Statistic	Df	P value	Effect Size (Cohen's d)
All (GLM)	71	R^2= 0.116	F = 4.46	(2), 68	< 0.05 *	
ACA ~ LWC	53	T = 2.893			< 0.05 *	-0.88 (Large)
ACA ~ SNR	44	T = 2.362			< 0.05 *	-0.66 (Medium)
LWC ~ SNR	54	T = -0.603			> 0.05 *	

Table 6.3 Summary of the concentrations in faecal glucocorticoid metabolites in sub-adult elephants in Aberdare Conservation Area and non-fenced control populations.

Population	Sample size (*n*)	Test Statistic	Test Statistic	Df	P value	Effect Size (Cohen's d)
All (GLM)	111	R^2 = 0.3327	F = 26.92	(2), 108	< 0.001 ***	
ACA ~ LWC	83	T = 7.320			< 0.001 ***	-1.59 (Large)
ACA ~ SNR	74	T = 3.471			< 0.01 **	-0.88 (Large)
LWC ~ SNR	65	T = -3.131			< 0.01 **	0.752 (Medium)

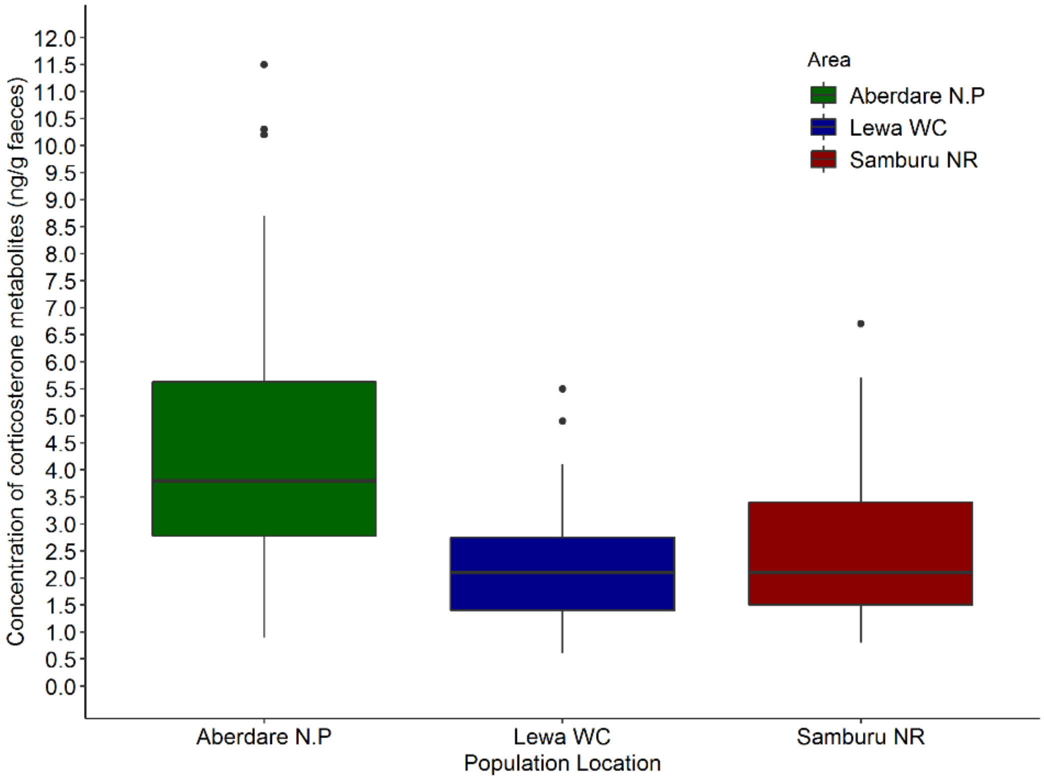

Figure 6.4 African Elephant corticosterone metabolite concentrations (non-transformed data) in each population

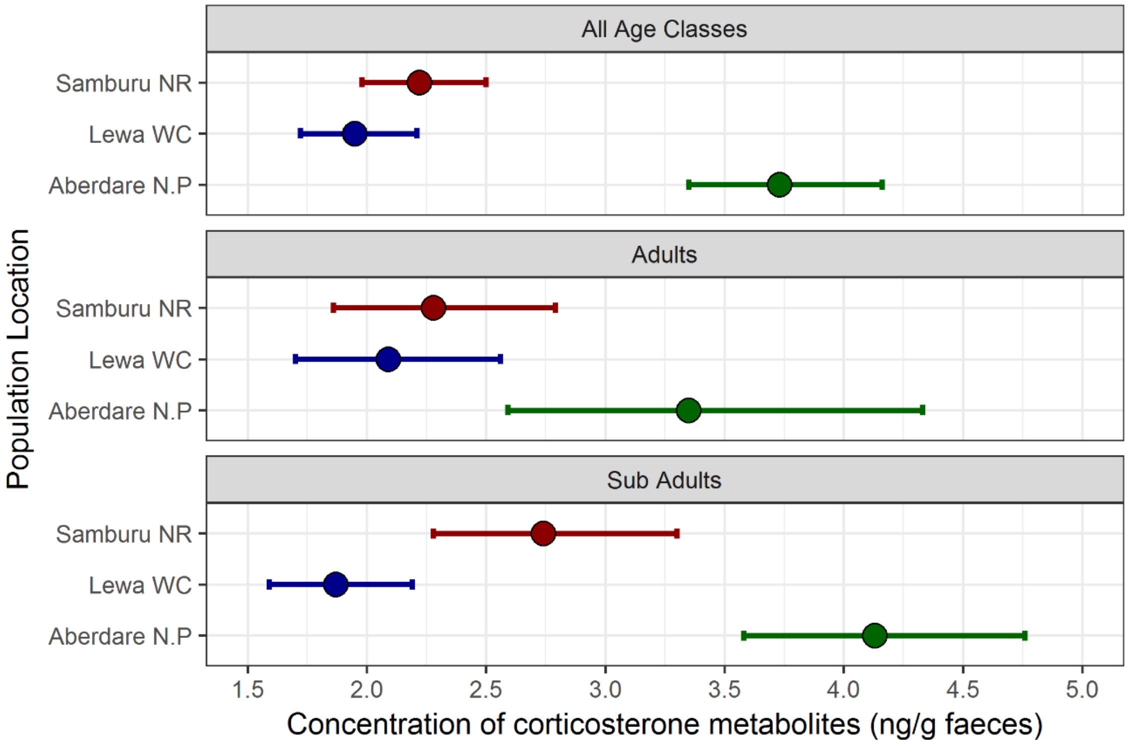

Figure 6.5 Pairwise comparisons of $\log_{10}$ transformed data (back-transformed) showing the geometric mean and 95% confidence limits of statistically significant differences in African Elephant faecal corticosterone metabolites across populations

6.3.3 Body condition

No significant differences were found (W= 1747.5, $p > 0.05$) between the body condition scores of the confined ACA and free roaming LWC population. Although the sample size (*n*=124) was relatively small, a power analysis based on unequal sample sizes from each population, with a medium (*d*=0.5) effect size and alpha level of 0.05, resulted in a power of 0.78, suggesting that the non-significant result may not be as a result of a type II error.

6.4 Discussion

Results indicate that the confined elephants in the Aberdare Conservation Area have significantly elevated concentrations of FGMs compared to both of the free-roaming populations, with between 68% and 91% increase on average across the population. Whilst the confined population showed significant differences in FGM concentrations, with the exception of the sub-adults, no significant differences were observed between the free roaming populations, indicating that the Aberdare Conservation Area population is under the influence of a potential stressor. The largest differences between the confined and free-roaming populations were observed in the sub-adult age class, whereby the confined population had FGM concentrations over double to the Lewa Wildlife Conservancy, and in excess of 50% higher than the Samburu National Reserve population. These higher concentrations may be driven by social influences, including the inability of sub-adult males to disperse from family groups at the onset of puberty, a motivated behaviour and mechanism for inbreeding avoidance (Archie et al., 2007). Additionally, nutritional requirements of elephants vary dependent on life-history stages, e.g. lactating females have approximately 30% increase in energy demands. The increased concentration of FGMs in the sub-adult age class may be attributed to the inability to disperse and access the higher quality vegetation during the wet season (Meissner et al., 1990; du Toit & Owen-Smith, 2002; Woolley et al., 2009). Although there may be an automatic assumption that these higher concentrations are negative, caution must be exercised in their interpretation, and a better understanding of what range, and over what duration of time does higher concentrations of FGMs have negative effects on welfare (Millspaugh and Washburn, 2004). The secretion of glucocorticoids play a critical role in maintaining homeostasis, preparing for challenge, and to supress immune system responses that may be detrimental to the body (Munck et al., 1984; Romero, 2004; Sapolsky et al., 2000). Therefore, an increase in glucocorticoids in the Aberdare Conservation Area population, does not necessarily mean that they are in a state of distress. Furthermore, it is more important to quantify whether concentrations of FGMs observed, have significant biological costs to the individuals by diverting energy away from normal processes (Moberg, 2000). Moreover, there is also a general consensus that not just an over-stimulation, but an under-stimulation of the adrenal system in which FGM concentrations are low, negatively impacts health (Busch and Haywood, 2009). This has been observed in some elephant populations that have been translocated, whereby there is a long-term suppression of adrenal activity (Wong, 2016). With this in mind, although the confined population has elevated FGMs compared to the free-roaming populations, the most important factor is not that they are elevated, but that they do not lie within the same range as either of the control populations. Importantly, the duration of time that the FGMs have been elevated for, is a factor in their long term effect on welfare. Despite being completely confined since 2009, the higher FGM concentrations in the ACA population may have remained higher than those in the free-roaming populations, possibly indicating a continuous stressor without acclimation to conditions. As with the ACA elephant population, a study measuring the long-term concentrations of FGMs after translocation, found that concentrations can remain high in excess of 10 years (Jachowski et al., 2013). In contrast however, another study monitoring FGMs in translocated elephants, reported that after the stressful event, FGMs returned to baseline after approximately 2 months. This would suggest that after the initial stressor, the elephant population acclimatised to the site, and there would unlikely be any negative long-term effects on health (Millspaugh et al., 2007).

Previous studies have identified fluctuations in FGMs due to a range of factors, including human disturbance (Pretorius, 2004), hunting practices (Burke et al., 2008), stochastic events (Woolley et al., 2008), and quality of forage (Woolley et al., 2008). The latter may be a factor in the confined ACA population due to the inability to perform seasonal migrations to the lowlands for the nutritious grasses during the wet season. Although there is a constant abundance of browse in the montane forests, elephants have demonstrated a desire to access the lowlands during the wet season by avoiding the higher altitudes whilst the lower savannahs are green (Loarie et al., 2009; Young et al., 2009; Bohrer et a., 2014). Failure to access nutritious seasonal vegetation however may not elicit a physiological response. A comparative study examining FGM concentrations in two elephant populations in South Africa, found that whilst both populations had seasonal variances in forage quality, only the population that had limited access to water exhibited a physiological stress response (Woolley et al., 2009).

Elevated FGMs observed in the adult age class in the confined population may be a result of both social and resource-driven factors. Female elephants have been observed to have higher adrenal activity in a number of studies (Goymann and Wingfield 2004; Wittemyer et al. 2005). Matriarchs and mature females have the responsibility of leading the herd, they develop various foraging strategies to secure resources for the group and move quickly through an area in search of high-quality forage (Woolley et al., 2008). Confinement within an area of low-quality browse, as such could be the case for the ACA population, higher FGM concentrations observed in the adult age class, may be explained by the social responsibility of the adult females inability to secure nutritious forage for the group.

6.5 Conclusion

Although other studies have measured FGMs in populations of elephants that have been confined (Jachowski et al., 2013), this is the first to examine the adrenal activity of a fenced population in direct comparison to both free-roaming savanna populations, and a population that has a wildlife corridor allowing the seasonal passage of migrating elephants. The results from this chapter demonstrate a significant difference in corticosterone concentrations in the confined elephant population in comparison to all other populations. Elephants in the sub-adult and adult age classes, exhibit considerably higher concentrations of FGMs. Despite the factors underlying these differences presently unknown (social and/nutritional deficit), the disruption elevated FGMs cause to the physiological systems, can result in immune suppression and a reduction in reproductive output. Higher mortality rates, and reduced fecundity, could cause a decline in population numbers, and threaten the future viability of the population. The direct comparison of the confined population and the population utilising a wildlife corridor, provides the first physiological evidence to support the benefits of connecting areas of habitat for migratory species such as elephants.

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Chapter 7

Conclusion

This thesis reports results on the impact of confining African savannah elephants (*Loxodanta Africana*) in montane forests in Kenya. With the increasing use of wildlife fencing, this thesis is the first to examine the physiological effects of confinement on the demographic structure of a population, which may present future implications for population viability. Furthermore, this thesis quantifies the impact of confinement, and subsequent curtailment of migration on the integrity of the forest habitat. Results aim to provide an understanding of the effects of population fragmentation via restricting dispersal, to inform the future management of elephant populations that exist within a matrix of human settlement.

The majority of the work was undertaken in the primary study site, the Aberdare Conservation Area, a montane forest with an elephant population that has been fenced since 2009. Whilst the genetic effects of population fragmentation have been well studied, there's a paucity of information examining the physiological impact of curtailing animal dispersal, and its potential ramifications on demographic processes that influence a populations viability. With this in mind, the work consisted of collecting faecal samples to undertake an analysis on the concentration of faecal glucocorticoid metabolites (FGMs), a measure of physiological stress (via adrenal activity), recording the body condition scores of elephants, and collecting data on the current demographic structure of the population. The inefficient feeding strategies of elephants can have detrimental impacts on vegetation communities, whilst studies have examined the impact of confining elephants within savannah ecosystems, to the best of my knowledge no study has assessed the effects in a forest environment. Remote sensing techniques were applied to monitor habitat degradation and map changes in the forest canopy. To provide a comparative analysis on the impact of confinement, data was also collected from control sites under various management practices. A free-roaming lowland savannah population formed one control site, and an elephant population from a montane forest that is currently in the process of being fenced but includes a wildlife corridor enabling seasonal migrations formed another. This approach provides a unique opportunity, not only in understanding the impact of fragmentation, but also the impact of the demographic structure and physiology of elephant population existing within a habitat connected by a wildlife corridor.

Results presented on the ecological effects of confinement revealed that both the Aberdare Conservation Area (ACA) and the Shimba Hills National Reserve (SHNR), a coastal forest of smaller size that has been fenced since 1999, experienced lower annual rates of forest loss than other East African montane forests that are not fenced. This is perhaps due to the positive effects of fencing on reducing anthropogenic disturbances which predominantly cause large scale deforestation. In the case of the study sites, analysis found that both the Aberdare National Park and the Shimba Hills National Reserve primarily exhibit smaller scale, subtle changes of gradual degradation of the forest canopy. The smaller of the forests, Shimba Hills National Reserve, experienced significantly larger areas of disturbance, possibly suggesting that smaller, fenced areas are more susceptible to changes in the forest as a result of confining elephants. Although 'greening events' signifying regeneration were observed, this is likely to be the growth of young vegetation and consequently alters the vegetation structure of the canopy from primary forest, to new growth. Ideally, it would have been preferable to monitor the annual rates of degradation in the forests prior to the start of the fence builds. This would have enabled a comparison of the annual rates of forest disturbance both before and after the confinement of elephants, however, due to a significant gap in Landsat satellite data during this period, and the launch of the MODIS satellite being post fence build, such analysis were not possible. Fortunately, the Aberdare National Park is the first of 5 montane forests in Kenya scheduled for fencing, and results from this thesis have documented the suitability of applying the BFAST method to be able to detect changes in the forest canopy from various drivers including that of elephant damage. With the recent advances and opening of the Landsat satellite archive, this provides an opportunity in the future to monitor changes in the forest canopy of further montane forests that are due to be fenced, this can be completed both prior to the implementation of a fence, and after fencing is complete. This will provide a direct analysis on the impact of fencing on the integrity of these montane forests by comparing annual rates of forest loss whilst elephants are able to disperse, compared to their confinement after the implementation of fencing.

Currently there are relatively few studies assessing the impact of fragmentation. To examine whether restricting dispersal and prohibiting the recruitment of individuals has resulted in a change in the demographic structure of the elephant population, demographic data was collected from the Aberdare Conservation Area and compared to a free-roaming savannah population, a montane forest population with a wildlife corridor, and additionally to the demographic structure of 3 populations of known status from published data. Many authors have reported that population numbers are regulated via demographic processes which assist in maintaining an equilibrium and ensure that an area does not exceed its maximum ecological carrying capacity. Results from Chapter 5 indicate that the fenced Aberdare Conservation Area population has a significantly different demographic structure to all other sampled control populations and that of the three populations of known status (stable and rapidly increasing) from published literature. The confined population has a highly skewed adult age structure with very few individuals in the juvenile or calf age classes, furthermore, the ratio of dependents juveniles to adult females is also significantly lower than all other populations suggesting that there has been a hiatus in reproduction over several years. The Aberdare Conservation Area population exhibits the characteristics of a population with low growth rates. Although this could be due to a number of processes including an increase in juvenile mortality rates, and a decrease in reproductive rates, it is most likely to be a result of reduced fecundity. If there had been an increase in juvenile mortality, the Kenya Wildlife Service (KWS) rangers that intensively monitor the area would have recorded elephant carcasses during patrols. Interestingly, results from Chapter 5 of this thesis found a significant decline in reproductive output occurred during 2002 to 2009, during which, an area of the National Park that has a high density of elephants was fenced. This area has historically included key seasonal migration routes and since being fenced, has prohibited the dispersal and recruitment of individuals to the population.

It was postulated that the restriction of dispersal and subsequent isolation of the elephant population may elicit a physiological stress response. Results from the analysis did in fact reveal that the confined elephant population in the Aberdare Conservation Area has significantly higher concentrations of faecal glucocorticoid metabolites (FGMs) than either the free-roaming savannah population or the population with a wildlife corridor connecting a montane forest to the lowland savannahs. Increased concentrations were particularly evident in both the adult and sub-adult age classes and FGMs in the fenced population were over twice the concentration of all of the free-roaming populations that were sampled. Whilst glucocorticoids are an important survival mechanism that aid an individual to escape a threatening situation and adapt to challenging environments, prolonged periods of elevated concentrations have been linked to a number of pathological dysfunctions therefore reducing the fitness of an individual. Additional evidence has shown that they are also linked to a reduction in reproductive output by reducing fertility and lowering libido, thus potentially resulting in negative ramifications for projected future population persistence. The skewed age structure with very few juveniles that was observed in the Aberdare Conservation Area could therefore be attributed to the effect of elevated FGMs reducing female reproductive rates. At present, the cause of the elevated FGMs in the confined population is difficult to ascertain. For the sub-adult age class which displayed the highest concentrations, it may be in response to the social influences of the prohibited dispersal of males from family herds at the onset of reproduction. Alternatively, in both the adult and sub-adult age classes, it could be a consequence of the inability to seasonally migrate to higher quality vegetation during the wet season. Evidence from other studies has suggested a strong influence between the seasonal availability of high quality browse on conception rates in elephants (See Chapter 6). Future work to differentiate the influence of social stressors and nutritional stressors could involve measuring faecal triiodothyronine (T3) concentrations, a thyroid hormone that influences the basal metabolic rate during periods of nutritional deficit. Measuring T3 concentrations in conjunction with FGMs will provide an opportunity to separate physiological stress as a result of insufficient nutrition, or from the psychological stress from social influences.

In addition to examining the ecological and physiological effects of confining elephants in montane forests, this thesis evaluated the application of the Random Encounter Model (REM) and camera traps to estimate the density of elephants in a forest environment. Kenya, along with all other countries with elephants in their range, are required to continuously monitor the illegal killing of elephants (MIKE) under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and report their population status. Density estimates calculated in Chapter 4, highlight the ability of utilising the REM method and camera traps for the continuous monitoring of elephants over large spatial scales, in the particularly challenging forest habitat. Although the confidence intervals for the shrub-land vegetation class were large, presumably as a result of the variation in capture numbers across the camera traps in this vegetation category, this is not unique to this study or limited to camera trapping surveys. This method provides many benefits from the currently utilised methods of total counts and dung surveys as it can be employed by a small number of staff and yield density estimates in a much shorter time-frame, does not involve specialist training or require the purchase of large quantities of equipment. The density estimates that were calculated, lie within the expected density of elephants in protected areas.

Examination of the ecological and physiological effects of habitat fragmentation and the isolation of an elephant population has demonstrated significant differences in the demographic structure and physiology of the confined population compared to free-ranging populations. To curtail the negative effects of population fragmentation and the impact of a permanent elephant population on the integrity of the forest habitat, a potential solution could be the inclusion of wildlife corridors. The implementation of wildlife corridors to increase the connectivity of the Aberdare Conservation Area, Mount Kenya, Laikipia, and Samburu elephant populations would enable all of these populations to be managed as one meta-population. Corridors would provide a route of dispersion to core areas of habitat, allowing elephants and other migratory species to disperse from areas of higher density, and be 'recruited' to lower density areas to maintain the demographic stability of the regional populations. Access to seasonal resources may alleviate the physiological impact of confinement, and long-term benefits will also include increased gene-flow reducing potential detrimental effects of inbreeding and promote species fitness, and may also assist in mitigating some of the impacts of climate change by enabling the dispersal of individuals to procure resources outside of the fenced area, and enabling access to the ACA which includes permanent water sources to elephants outside of the protected area.

However, the inclusion of wildlife corridors are not without their own concerns. Firstly, the region would require extensive GIS mapping in order to identify viable areas for their location. Consideration for prime areas of connectivity may lie within regions of high human density which elephants have been documented to avoid, thus not only potentially limiting their utilisation, but additionally emerging issues regarding land-ownership rights. The topography in the region includes areas of steep slopes, and evidence has documented that elephants avoid these areas, therefore posing further concerns of whether the elephants will utilise any corridors implemented. Although many corridors are used by wildlife, their presence does not guarantee dispersal. Whilst corridors offer the dispersal of wildlife which may ease degradation of the forest habitat in the future, it may take a number of years for the confined ACA population to disperse. However wildlife outside of the protected area may use the corridors resulting in an influx to the area and in the process result in further degradation to the forest in the immediate period following their inclusion. Furthermore, connective corridors could potentially provide a route of access for human activity to the protected area and may result in an increase in illegal activities such as poaching, logging and charcoal kilns. The fence was erected around the ACA to protect the forest habitat and to mitigate human-wildlife-conflict (HWC), however evidence from other studies have shown that elephants can not only use corridors as a migration route, but as an extension of their habitat, should corridors lie within human settlements, this could in fact cause an increase in HWC.

This thesis has provided evidence that highlights the negative characteristics of an isolated elephant population in a montane forest, including a demographic structure that differs from populations considered stable, elevated concentrations of corticosterone metabolites, and degradation of the forest habitat. The skewed age distribution with a high proportion of adults, and elevated concentrations of stress hormones, have the potential to be detrimental in maintaining the viability of the population. Although it is not possible to ascertain that these results are due to confinement alone, as there may be other attributing environmental factors, they provide a valuable insight into the demographic and physiological differences between confined and free-roaming populations via a direct comparison which has not been previously examined. Results from this thesis can be used to inform the future management of elephant populations across their range, to enable successful conservation of the species.