Elephants in a landscape of risk:

Spatial, temporal, and behavioural responses to anthropogenic risk in African savannah elephants

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Abstract

African savanna elephant (*Loxodonta africana*) populations have declined due to poaching for the ivory trade. Elephants and humans also increasingly share ranges and resources. This thesis investigates whether and how human-mediated risk influences elephant space use, activity patterns, resource use, grouping patterns, and sex differences in responses to risk, in the Ruaha-Rungwa ecosystem, Tanzania. This area experienced multiple poaching surges and has increasing levels of human activity.

I applied occupancy models to elephant occurrence data to investigate space use in relation to risk and environmental factors. Elephant occurrence was negatively associated with human population densities and conversion to agriculture, as well as elephant carcass occurrence (a proxy for poaching risk) and illegal human use.

Using camera trap data I compared active periods, grouping patterns, and use of roads and water sources at one low-risk site and three high-risk sites. Male and female elephants were more nocturnal in high-risk versus low-risk sites, including use of water sources; this was more pronounced for cow-calf groups than for lone males. In the high-risk versus low-risk sites, elephants were active for less time overall, avoided movement on roads, and male elephants associated more with males and cow-calf groups.

I assessed how risk influences elephant use of water sources using camera trap data. Elephant use of a high-risk resource was driven by seasonal variation in water availability, and use of high-risk water sources was more nocturnal than use of low-risk water sources. Males, but not females, adjusted group size in relation to risk.

I discuss costs associated with risk-induced behavioural shifts, including a reduction in total active time and effects on body condition, and show that the consequences of elephant poaching in Ruaha-Rungwa extend beyond effects on population size and structure. I suggest that risk-avoidance behaviour may enable elephants to persist in increasingly human-dominated landscapes.

Ethical Approval

Ethical approval for this study was granted by the University of Stirling's General University Ethics Panel (Approval: GUEP136) and Animal Welfare and Ethical Review Body (Approval: AWERB 617/186/Non-ASPA).

Declaration

I declare that the thesis embodies the results of my own research and was composed by me. Where appropriate I have acknowledged the nature and extent of work carried out in collaboration with others included in the thesis. This thesis has not been submitted for any other degree at the University of Stirling or any other institution.

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General Introduction: Elephants in an anthropogenic landscape of risk

***Photo 1**: Tuskless matriarch fleeing into the bush at dusk. In the higher-risk areas of Ruaha-Rungwa, elephants are wary of people and vehicles.*

Chapter 1. General Introduction: Elephants in an anthropogenic landscape of risk

This thesis explores the behavioural responses of African savanna elephants to human-mediated risk. In this chapter, I introduce how predation risk is thought to influence animal behaviour and how behavioural responses to predation risk may affect animal populations and ecological communities. I then suggest that elephants respond to humans as predators and outline the aims and structure of this thesis.

1.1 The ecology of fear

The ecology of fear concept recognizes that predators not only kill prey but also change the behaviour of their prey (Brown, Laundré & Gurung, 1999) and that changes in prey behaviour under predation risk may have higher-level consequences for population and community ecology that are as, or more, important as the direct effects of predators killing prey (Preisser, Bolnick & Benard, 2005; Zanette & Clinchy, 2019). In many heterogeneous natural ecosystems, the risk of predation varies in space and/or in time because of factors such as predator density and activity as well as prey vulnerability (Gaynor et al., 2019; Laundré, Hernández & Altendorf, 2001; Laundré, Hernández & Ripple, 2010). When heterogeneity in predation risk is predictable, prey may perceive a 'landscape of fear' (Laundré et al., 2001), defined as an animal's *perception* of spatial variation in predation risk (Gaynor et al., 2019). Landscapes of fear can also be 'dynamic' when perceived predation risk varies in time as well as in space, such as across diel, seasonal, tidal, or lunar cycles (Palmer et al., 2022b). The landscape of fear is fundamental to understanding how prey respond to predators and how these antipredator responses influence prey population dynamics and wider community structure (Laundré et al., 2010).

Animals respond to predators through antipredator behaviours; these are actions taken by prey to reduce the risk of predation by lowering the chance of encountering a predator, enhancing predator detection, and/or increasing the chance of escape in the event of an encounter (Caro, 2005; Gaynor et al., 2019). Antipredator behaviour may be reactive, occurring during a predator encounter, such as flight, bunching, predator mobbing, vigilance, signalling, and vocalization (Makin, Chamaillé-Jammes & Shrader, 2019; Palmer & Packer, 2021; Say-Sallaz et al., 2023). Antipredator behaviour can also be proactive, occurring when prey have an expectation of predation risk based on cues in their environment or experience and memory (Creel, 2018; Gaynor et al., 2019). Proactive antipredator behaviour may include avoidance of risky places and risky times (Creel et al., 2005; Epperly et al., 2021; Schmitz, Beckerman & O’Brien et al., 1997; Valeix et al., 2009) as well as adjustment of behaviours such as ‘routine’ vigilance (Childress & Lung, 2003; Cresswell et al., 2003; Fortin et al., 2004), movement (Basille et al., 2015; Suraci et al., 2019b), foraging (Barnier et al., 2014; Christianson & Creel, 2010; Peckarsky et al., 1993; Shrader et al., 2008; Suraci et al., 2019b), and aggregation (Beauchamp, 2004; Hamilton, 1971; Hill & Lee, 1998; Moll et al., 2016; Vine 1971).

Behavioural responses to predation risk can be associated with physiological or opportunity costs that affect prey survival and reproduction (Allen, Clinchy & Zanette, 2022; Creel & Christianson, 2008; Creel et al., 2007; Creel, 2018; Laundré et al., 2010; Zanette & Clinchy, 2019) and may give rise to so-called ‘risk effects’ on prey population dynamics. Behavioural responses to risk can also impact community ecology through ‘behaviourally mediated trophic cascades’ if risk-induced changes in prey behaviour alter the composition and structure of lower trophic levels. A classic (but still debated, e.g., Ford & Goheen, 2015) example of such a trophic cascade is the changes observed following the reintroduction of wolves into Yellowstone National Park, USA (Ripple & Beschta, 2004). Wolves are thought to have reinstated a landscape of fear for elk, as elk increased their vigilance, reduced their foraging, and changed their use of the physical landscape following the return of wolves (Christianson & Creel, 2010; Frair et al., 2005; Hernández & Laundré, 2005; Laundré et al., 2001; White, Feller & Bayley, 2003). In turn, several plant species were released from elk browsing pressure (Ripple & Beschta, 2003), especially in riparian and upland areas, and this was associated with an increase in woody cover and songbird and beaver populations (Beschta & Ripple, 2016; Ripple & Beschta, 2012).

While scientific study of the ecology of fear originally focused on non-human predators in natural ecosystems (Brown et al., 1999; Laundré et al., 2001), it has become clear that humans are the apex ‘super predator’ in many ecological communities (Darimont et al., 2015). As with non-human predators, humans may affect animal populations and ecological communities not just through their direct lethal effects (e.g., hunting) but also through indirect risk effects resulting from animals’ behavioural responses to a human-induced landscape of fear (Clinchy et al., 2016; Clinchy & Zanette, 2020; Lasky & Bombaci, 2023; Moleón & Sánchez-Zapata, 2022; Palmer et al., 2022a; Suraci et al., 2019b). In support of this view, two meta-analyses have shown that terrestrial mammals shift to more nocturnal activity and reduce their movement in response to humans and their activities and that these responses were consistent across a range of taxa, body sizes, and trophic levels (Gaynor et al., 2018a; Tucker et al., 2018). Recent experimental work has provided further evidence that the perceived predation risk from humans can induce changes in wildlife movement, foraging, diel activity, and space use (Suraci et al., 2019b). Behavioural responses to humans in animals can be stronger than those to non-human predators (Ciuti et al., 2012; Clinchy et al., 2016) and have been linked to demographic consequences, including declines in abundance (Sawyer et al., 2017) and reduced reproductive success (French et al., 2011; Spaul & Heath, 2016). Human-induced behavioural responses can also alter predator-prey interactions and competitive interactions between species, with potential repercussions for the structure of wildlife communities (Gilbert et al., 2022; Manlick & Pauli, 2020; Moll et al., 2018; Suraci et al., 2019b). Human actions are driving unprecedented, far-reaching changes in many of Earth's systems (Lewis & Maslin, 2015), and it is important to understand not only the direct effects of humans on ecosystems but also how anthropogenic landscapes of fear influence animal behaviour and affect animal populations as well as wider ecological communities.

1.2 Elephants in an anthropogenic landscape of fear

There are three extant species of elephant: the African savanna elephant (*Loxodonta africana*) occurring in sub-Saharan Africa, the African forest elephant (*Loxodonta cyclotis*) of central and western Africa, and the Asian elephant (*Elephas maximus*) of South and South-east Asia. All elephant species are endangered, with the African forest elephant classified as critically endangered, and are declining in number due to human activities (Gobush et al., 2021, 2022; Willams et al., 2020). All species have large brains and are long-lived and social (Bates, Poole & Byrne, 2008; Hart et al., 2008). Elephants move over large distances to meet foraging and water requirements and to find social and reproductive partners and they are thought to have detailed and long-term spatial-temporal and social memory (Hart et al., 2008; McComb et al., 2000; Polansky, Kilian & Wittemyer, 2015; Poole & Granli, 2009; Rasmussen, 1995; Thouless, 1995; Tsalyuk et al., 2019; Wall et al., 2013). In this thesis, I focus on African savanna elephants but will on occasion make reference to or compare behavioural responses to anthropogenic risk observed in African forest elephants and Asian elephants.

The African savanna elephant once occurred across the African continent (Sikes, 1971). Due to expanding human populations and associated rapid land use change, elephant range has declined and become increasingly fragmented (Gobush et al., 2022). Africa savanna elephants are currently found in 24 countries (Gobush et al., 2022). The combined current range for African savanna and African forest elephants is estimated at 3,132,000 km^2 (Thouless et al., 2016), an estimated 15-17% of their historic range (Chase et al. 2016; Wall et al., 2021). African savanna elephants are large-bodied, generalist herbivores that occupy a wide range of biomes, including forest, grassland, savanna, shrubland, and desert.

It is estimated that African savanna elephants have declined by >50% in the past 75 years (Gobush et al., 2022). A major reason for this decline is the large-scale killing of elephants for the ivory trade (Thouless et al., 2016; Schlossberg, Chase, & Sutcliffe, 2019; Wittemyer et al., 2014), with major poaching surges in the 1970s-1980s and in the 2000s-2010s (Gobush et al., 2022). During the most recent poaching surge, African savanna elephant populations declined by an estimated 30% between 2007 and 2014 (Chase et al., 2016) – with Tanzania experiencing one of the most severe population declines (Thouless et al., 2016). The Great Elephant Census estimated a population of around 352,000 (95% CI 334,000–370,000) African savanna elephants in 18 countries (representing approximately 90% of African savanna elephants in those countries)[1] in 2014-2015 (Chase et al., 2016).

Due to their large body size, adult elephants face little predation risk from non-human predators (Owen-Smith & Mills, 2008). While lions and hyenas predate on elephant calves (Joubert, 2006; Loveridge et al., 2006; Power & Compion, 2007; Bere, 1966 in Ruggiero, 1991; Ruggiero, 1991), and elephants perceive lions as a risk (McComb et al., 2011), humans are by far the most important predator of elephants. Elephants are killed by humans for the ivory trade or in licensed hunting (Burke et al., 2008), in response to their impacts on humans, crops, and livestock (Brooks & Buss, 1962; Kangwana, 2011; Rodgers & Lobo, 1980; Thouless, 1994), for the preservation of vegetation (Laws, Parker & Johnstone, 1975; Savidge, 1968), or in rite-of-passage practices (Kangwana, 2011). Elephants may also sustain injuries or perish in encounters with humans and their activities and infrastructure (Kangwana, 2011; Langley & Mathison, 2008). As an estimated 50% of African elephant range lies outside of formal protected areas (Wall et al., 2021), elephants have to navigate these various human-mediated risks throughout much of their range.

Elephants can mitigate predation risk by reacting to immediate risks within their environment, such as by fleeing from hunting incidents (e.g., Burke et al., 2008), as well as proactively through behaviour, such as by avoiding high-risk areas or adjusting their activity. Proactive behavioural responses to human-mediated risk are expected if humans generate a landscape of fear for elephants. For humans to induce a landscape of fear, several conditions must be met (Gaynor et al., 2019). First, elephants must associate humans with risk and perceive such risk through reliable cues and/or through experience and memory; and second, anthropogenic risk must vary predictably in time and space (Gaynor et al., 2019).

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[1] The African Elephant Status Report 2016 estimated the population of African savanna and African forest elephants combined at 415,428 (±95% CI 20,111) (Thouless et al., 2016).

Previous work has shown that elephants identify humans as a potential threat using visual, olfactory, and auditory cues and can distinguish different human subgroups representing varying levels of threat (Bates et al., 2007; Kangwana, 2011; McComb et al., 2014). Playback experiments indicate that elephants identify differences in human voices associated with ethnic group, sex, and age that are relevant to the level of threat associated with different human subgroups (McComb et al., 2014). Elephants may also use olfactory cues to distinguish between human ethnic groups (Bates et al., 2007). While this experimental work has clearly shown that elephants associate risk with human cues including voices and scents, it is probable that elephants also have an expectation of risk that may exist as a 'mental map' (Gaynor et al., 2019). African savanna elephants are intelligent and have the capacity for learning and spatial-temporal memory (Hart et al., 2008; Polansky et al., 2015; Tsalyuk et al., 2019), suggesting that elephants have the cognitive capacity to remember and/or anticipate risk. Previous observational work also suggests that elephants have a memory or expectation of risk. During a poaching surge in Samburu-Laikipia, Kenya, elephants adjusted their movement behaviour as soon as they entered different core areas within their home range that were associated with lower or higher poaching risk, likely indicating that they were not just responding to real-time encounters with people, but to perceived longer-term spatial variation in poaching risk (Ihwagi, 2019).

Human-mediated risks are often structured in space and in time (Barrueto, Ford & Clevenger, 2014; Duporge et al., 2020; Green et al., 2023; Oberosler et al., 2017). Humans and their activities tend to be spatially clustered and diurnal, especially in areas where electric lighting remains limited (Beale et al., 2017; Foster & Roenneberg, 2008; Klepeis et al., 2001; Pilz et al., 2018; Yetish et al., 2015). Elephant poaching risk is heterogeneous in space and is often related to water (Beale et al., 2018; Shaffer & Bishop, 2016; Rashidi et al., 2016; Sibanda et al., 2016), roads (Shaffer & Bishop, 2016), protection infrastructure (Beale et al., 2018), and land use such as whether areas are state- or community-owned conservation areas or village land (Ihwagi, 2019; Kahindi et al., 2010; Zafra-Calvo et al., 2018) - features that elephants may learn to associate with risk. The extent to which spatial variation in poaching risk is predictable depends on how rapidly poaching pressure shifts across the landscape over time as poachers try to evade detection (Bastille-Rousseau et al., 2020), and on the level of organisation and arms. While it is difficult to know for certain at what time of day elephant poaching occurs given its covert nature, it is plausible that, in the absence of sophisticated night vision armaments, poaching occurs primarily during the daytime hours for reasons of visibility (Ihwagi, 2019), although the risk of detection by rangers may cause poachers to move more under the cover of darkness (Moreto & Williams, 2015). Poaching risk may also vary seasonally and has been reported to be greater in the dry season in some areas (Maingi et al., 2012; Rashidi et al., 2016; Sibanda et al., 2016), and higher in the wet season in other areas (Kyando, Ikanda & Røskaft, 2017).

Even when landscapes of fear do exist, behavioural responses to risk will depend on an animal's ability to modulate space use, movement and activity patterns, and social behaviour in relation to risk (Gaynor et al., 2019). Behavioural responses to risk may also vary by sex (see Section 1.3). As elephants are selective in their use of space and make movement decisions in relation to water and forage (Boult et al., 2018; Loarie, van Aarde & Pimm, 2009; Mashintonio et al., 2014; Shannon et al., 2006b; Stokke & du Toit, 2002), it is possible that risk also factors into elephant movement and space use decisions. Indeed, poaching risk and human footprint have been found to influence elephant ranging behaviour, habitat selection, and movement rates and directionality (Bastille-Rousseau et al., 2020; Bastille-Rousseau & Wittemyer, 2021; Douglas-Hamilton, Krink & Vollrath, 2005; Ihwagi, 2019; Roever, van Aarde, & Chase, 2013; Wall et al., 2021). While elephants are generally considered cathemeral (Bennie et al., 2014), meaning they are active both day and night, the timing of diel elephant activity has been found to vary seasonally and across different sites (Clauss et al., 2021; Du Preez & Grobler, 1977; Gaynor et al., 2018b; Guy, 1976; Tambling et al., 2015; Wyatt & Eltringham, 1974), suggesting that elephants have the flexibility and capacity to mitigate anthropogenic risk in time by adjusting their active periods and timing of resource access (e.g., Bucholtz et al., 2021; Graham et al., 2009; Ihwagi et al., 2018; Zvidzai et al., 2013). Another proactive risk mitigation behaviour is aggregation. Elephants have a fission-fusion social structure and exceptionally flexible aggregations, ranging in size from solitary to several thousand (Archie, Moss & Alberts, 2006; Wittemyer, Douglas-Hamilton & Getz, 2005). This variability is expressed in hourly, diel, and seasonal decisions made about when, where, and with whom to aggregate (Moss & Lee, 2011). Such variability challenges our ability to determine the costs and benefits of grouping in elephants, although elephants may benefit from aggregation in response to anthropogenic risk through risk dilution, enhanced risk detection, or access to knowledge and experience from conspecifics (Allen et al., 2020; Chiyo et al., 2014; Kangwana, 2011). Previous work suggests that elephants respond to humans in a manner consistent with a human-induced landscape of fear and that elephants may proactively mitigate human-mediated risks through behaviour.

1.3 Thesis aims and structure

The aims of this thesis are to investigate (a) whether and (b) to what extent elephants adjust their use of space, activity, resource access, and grouping patterns in response to human-mediated risk, and (c) if there are sex differences in responses to risk. These questions were explored in the Ruaha-Rungwa ecosystem in south-central Tanzania because it presents elephants with a heterogeneous landscape of anthropogenic risk. The elephants of Ruaha-Rungwa have faced intense pressure from poaching for the ivory trade, including most recently during a poaching upsurge in 2010-2015 (Thouless et al., 2016). Some human activities also occur illegally inside protected areas, including hunting for bushmeat, livestock grazing, mining, and charcoal and timber extraction (Tanzania Wildlife Research Institute [TAWIRI], 2016, 2019). Human footprint in the ecosystem is also expanding rapidly (Komba et al., 2021), requiring elephants to navigate increasingly human-dominated landscapes when accessing habitat and key resources such as water outside of protected areas.

I define human-mediated risk as the risk of mortality and disturbance from humans, as humans in the Ruaha-Rungwa ecosystem pose both lethal and non-lethal risks to elephants. Poaching for the ivory trade was the main lethal risk from humans in this ecosystem at the time of the study. Although elephants can also be killed for their impacts on crops or people, either legally under the Government's 'problem animal control' policies (The Wildlife Conservation Act, 2009) or illegally, this typically occurs outside of protected areas and is a less significant cause of mortality than poaching for ivory. I use the term disturbance to encompass human activities that are not lethal to elephants (Coetzee & Chown, 2016). These include illegal resource extraction within protected areas as well as human settlements and economic activities outside of protected areas. Even when humans and their activities are not a direct mortality threat, animals may respond to people as predators (Beale & Monaghan, 2004; Crawford et al., 2021; Lasky & Bombaci, 2023). As animals may respond similarly to lethal and non-lethal human activities (Beale & Monaghan, 2004; Crawford et al., 2022; Frid & Dill, 2002; Gaynor et al., 2018b; Gill, Sutherland & Watkinson, 1996), human-mediated risk, as used in this thesis, encompasses both mortality and disturbance risk to elephants. I examine elephant behavioural responses to a landscape of human-mediated 'risk' rather than a landscape of 'fear', given the difficulty in quantifying perceived risk and in assessing underlying cognitive mechanisms for fear responses. The degree of congruence between the landscape of anthropogenic risk and elephant behavioural responses to risk may provide insight into the perceived landscape of fear for elephants, as well as potential tradeoffs and constraints on behavioural responses to risk (Gaynor et al., 2019).

The approach used in this thesis is to describe how human-mediated risk varies in space in the Ruaha-Rungwa ecosystem and to compare multiple aspects of elephant behaviour between areas of low- and high-risk. While not as rigorous as an experiment, this approach allows for direct semi-controlled comparisons of behaviour as a function of risk within a single population and ecosystem where environmental conditions are more similar than studies of different populations or sites. While previous work has explored elephant responses to humans in mixed-use landscapes where humans pose both a mortality and competition risk (e.g., Bastille-Rousseau et al., 2020; Ihwagi, 2019; Kangwana, 2011), the Ruaha-Rungwa ecosystem has extensive protected areas where human economic activities such as farming and livestock-keeping are officially excluded, enabling investigation into elephant responses to humans as predators (largely) in the absence of competition. In addition, because elephants use water sources both within and outside of protected areas it is possible to compare elephant use of a key resource across a gradient of anthropogenic risk and investigate how they access a resource that they share with people.

Understanding if and how elephants respond to anthropogenic risk is important for several reasons. First, it is important to understand the full range of consequences of poaching on elephants, as elephant populations across the African continent have experienced dramatic population declines (Wittemyer et al., 2014). While the direct effects of poaching on population numbers and demography are relatively well understood and have been documented in a range of sites (Douglas-Hamilton, 1987; Foley, 2002; Jones et al., 2018; Poole, 1989b; Wittemyer, Daballen & Douglas-Hamilton, 2013), our understanding of elephant behavioural responses to poaching is more limited (but see Bastille-Rousseau et al., 2020; Goldenberg, Douglas-Hamilton & Wittemyer, 2018; Ihwagi, 2019). These behavioural consequences of poaching are important to understand because they may be associated with important costs on survival and reproduction that may have population-level consequences. In addition, because poaching disrupts elephant social structure and results in a loss of older males and females with important social and ecological knowledge (Archie & Chiyo, 2012; Gobush, Kerr, & Wasser, 2009; Jones et al., 2018; Onyango & Lesowapir, 2016; Poole, 1989b; McComb et al., 2011) - including appropriately assessing and responding to risk (McComb et al., 2014; Shannon et al., 2022) - it is important to understand whether proactive risk mitigation behaviours are seen in a population that has experienced such disruption (Jones et al., 2018). Finally, an understanding of if and how elephants avoid humans in shared landscapes and when using shared resources can help improve our understanding of spatial and temporal contact zones and inform efforts to enhance coexistence between people and elephants.

Due to the challenges associated with observing elephants in areas of higher perceived risk - where elephants are wary of and aggressive towards people - elephant behaviour and space use were investigated using methods that did not require direct observation, including track-based occupancy surveys and camera trapping. Chapter 2 provides an overview of the study area and the methods used in this thesis, including a discussion of the reliability and limitations of these indirect methods.

Chapter 3 aims to contextualise anthropogenic risks to elephants in the Ruaha-Rungwa ecosystem. To set the context for the range of human-mediated risks that elephants face in this ecosystem, I present a novel synthesis of the history of elephant poaching in the ecosystem and its previously documented impacts on elephant demography and behaviour, as well as an overview of the expanding human footprint in the ecosystem. The chapter also describes how these risks are distributed in space, thereby generating a landscape of risk that enables comparisons of elephant behaviour in areas of low- and high-risk in subsequent chapters. To describe variation in elephant mortality risk to humans within protected areas, I use existing models of elephant carcass occurrence probability developed from aerial surveys (Beale et al., 2018). The risk of human disturbance within protected areas is described using an existing model of illegal human use (Strampelli et al., 2022b), as well as maps of the spatial occurrence of illegal human activity within protected areas from aerial surveys (TAWIRI, 2016; TAWIRI; 2019). As data on elephant mortality in the ecosystem are largely limited to protected areas, outside protected areas, I use features of the human footprint (e.g., settlements, human population density, agriculture) as a proxy for human mortality risk and disturbance risk. I assumed that humans and their activities are generally diurnal so that risk was structured over the diel cycle and was generally higher during the day.

Elephant space use reflects movement decisions about resource acquisition, energy expenditure, thermoregulation needs, social and reproductive opportunities, and risk avoidance (recently reviewed in Burton-Roberts, 2022). As obligate drinkers, the availability and distribution of surface water are important drivers of elephant movement and space use. In areas or periods of reduced water availability, elephant space use is strongly tied to surface water, while in wetter areas or periods, elephants range over larger areas and are more exploratory in their movements (Bastille-Rousseau et al., 2020; Chamaillé-Jammes, Valeix & Fritz, 2007; de Beer & van Aarde, 2008; Loarie et al., 2009; Mashintonio et al., 2014; Shannon et al., 2010; Stokke & Du Toit, 2002; Wato et al., 2018; Wittemyer et al., 2008). Elephant space use is also strongly influenced by forage availability and quality. Elephants select for areas with higher primary productivity and vegetation greenness (Bastille-Rousseau et al., 2019; de Knegt et al., 2011; Harris et al., 2008; Loarie et al., 2009; Valls-Fox et al., 2018a; Young, Ferreira & van Aarde, 2009), and selection for predictable, less variable productivity appears to be more important in the dry season than in the wet season (Loarie et al., 2009). While the importance of water and forage in elephant movement decisions has been extensively documented since the 1960s (as reviewed in Burton-Roberts, 2022), the role of risk and its importance relative to water and forage on elephant space use across multiple spatial scales is comparatively less well-studied (but see Bastille-Rousseau et al., 2020; Bastille-Rousseau & Wittemyer, 2019; Wall et al., 2021).

Chapter 4 investigates the role and relative importance of risk and environmental factors on elephant space use at multiple spatial scales using track-based occupancy surveys. First, I assess the relative importance of environmental and risk factors on elephant space use at a coarse spatial resolution in the wider ecosystem (comprising protected areas and unprotected village land). In this analysis, anthropogenic risk is quantified using features of the human footprint (e.g., human population density, land use, and distance to settlements), as a proxy for mortality risk and disturbance risk. I then analyse the relative importance of environmental factors and risk factors on coarse-scale and fine-scale elephant space use within protected areas, using elephant carcass occurrence models (Beale et al., 2018) as an indicator of human-mediated mortality risk, and illegal human use models (Strampelli, 2021) as indicators of human disturbance risk. I also investigate the influence of natural predation risk on fine-scale space use within protected areas using a model of lion space use (Strampelli, 2021), under the assumption that lion predation risk is greater in areas with a higher probability of lion use. Finally, I examine the relative influence of environmental factors and human footprint on fine-scale elephant space use on unprotected village land.

While adjusting space use may be one way in which elephants respond to spatial variation in human-mediated risk, elephants may also respond behaviourally to risk through temporal or social strategies (Chiyo et al., 2014; Gaynor et al., 2018b; Ihwagi et al., 2018; Kangwana, 2011), or through avoidance or altered use of specific features within their environment that they may associate with risk, such as roads (Blake et al., 2008) or water sources (Kangwana et al., 2011). Chapter 5 therefore aims to investigate whether elephants adjust their activity patterns, use of roads and water sources, and grouping patterns in response to spatial variation in human-mediated risk within protected areas. Using camera trap surveys, I compare elephant diel activity, use of roads and water sources, and male grouping patterns between one low-risk and three high-risk sites.

In sexually dimorphic species, behavioural responses to risk may differ by sex (Lasky & Bombaci, 2023; Ruckstuhl & Neuhaus, 2000; Ruckstuhl, 2007; Shannon et al., 2008). The predation risk hypothesis predicts that females will be more risk-averse than males due to sex differences in susceptibility to predation risk and reproductive strategies (Bleich, Bowyer & Wehausen, 1997; Clutton-Brock & Harvey, 1978; Corti & Shackleton, 2002; Ruckstuhl & Neuhaus, 2000). The male bias in high-risk, high-reward crop foraging among elephants has been hypothesised to arise from these sex differences in reproductive strategies and risk aversion (Chiyo et al., 2011a; Sukumar & Gadgil, 1988). Male elephants were also less wary than females of playbacks of cattle bells and mooing and were slower to retreat from these sounds than female groups (Kangwana, 2011). Males are the dispersing sex in elephants and are more likely to engage in exploratory, long-distance movements than females (Lee & Moss, 1999), which may make them more risk-prone than females; in fact, males experience higher rates of mortality than females throughout the elephant lifespan (Moss, 2001).

Sex differences in behavioural responses to risk may also arise if males and females face different constraints and trade-offs due to sexual dimorphism in body size and social organization. Because of their smaller body size and the demands of pregnancy and lactation, females have higher relative energy requirements and higher water turnover rates than males, even though males likely have larger absolute water and energy requirements (Shannon et al., 2006a; Stokke & Du Toit, 2002). Females and dependent calves are also less tolerant than males of diets that are low in nutrients and thus forage more selectively on higher-quality food items, while males 'bulk-feed' and tolerate lower-quality food (Shannon et al., 2006a; Woolley et al., 2009). Females also have a higher rate of heat gain per unit mass from the environment due to their higher surface area to volume ratio and may therefore be more vulnerable to heat stress than males (Barnes, 1983; Laws, 1970). While females and dependent offspring live in family groups, males disperse from their natal family group at an average age of 14 years and thereafter spend time alone as well as in temporary and flexible associations with other males as well as family groups (Lee et al., 2011; Moss & Lee, 2011). Female groups may be more constrained than males in their ability to move large daily distances due to the presence of calves (Laws et al., 1975). As males can more flexibly adjust their ranging behaviour in relation to water and forage than females, they could face fewer constraints than females when responding behaviourally to risk (Evans & Harris, 2012; Shannon et al., 2010; Shannon, Mackey & Slotow, 2013), even if females are potentially more risk averse. I explore possible sex differences in responses to risk in elephants in Chapter 5 by assessing whether males and females differ in the extent to which they shift their active periods in response to risk. Sex differences in risk responses are explored further in Chapter 6 in the context of water access.

Behavioural antipredator responses are thought to be associated with physiological or opportunity costs (Creel, 2018), but the potential costs for elephants have yet to be studied. Chapter 5 therefore also explores whether behavioural responses to risk can be associated with potential costs related to foraging or increased risk from natural predators by comparing female body condition and the degree of temporal overlap between elephants and lions between the low- and high-risk sites. To further examine potential costs, I compare the types of activities that elephants are engaged in, and specifically, the relative occurrence of maintenance, relaxed, and stress behaviours between the low- and high-risk sites.

While Chapters 4 and 5 explore the extent to which elephants respond to risk at fairly broad spatial scales, elephants may also respond to more localised anthropogenic risks, particularly in the context of resource access. Elephants may proactively mitigate risk when using risky resources by adjusting the timing of resource use (Bucholtz et al., 2021) or through aggregation (Sitati et al., 2003; Kangwana, 2011). These behavioural responses to risk may be influenced by seasonal variation in resource availability, as resource shortages may induce greater risk-taking behaviour (Arias-Del Razo et al., 2012; Riginos, 2015; Tadesse & Kotler, 2011), as well as by sex. Chapter 6 explores these questions in the context of elephant water source use. Specifically, I compare the timing of elephant water access between low-risk water sources inside a protected area and higher-risk water sources inside a protected area and on village land. I also investigate whether sex and seasonality in resource abundance influence the frequency and timing of elephant use of risky water sources. I then explore whether elephants use aggregation as a strategy when accessing risky water sources, and if and how this differs for males and females. Lastly, I investigate whether elephants are more vigilant at high-risk water sources than at low-risk water sources.

In Chapter 7, I contextualise my findings and discuss the possible implications of risk avoidance behaviours for elephants. I then discuss how an understanding of the ways in which elephants respond to humans can inform efforts to enhance coexistence between people and elephants.

Chapter 2

Study area and methods

***Photo 2**: Miombo woodland in western Ruaha National Park.*

Chapter 2. Study area and methods

Author contributions

I present maps from Tanzania Wildlife Research Institute aerial census reports and Ruaha National Park's General Management Plan (2009-2019). Inter-observer reliability assessments of group type and activity type definitions were done with assistance from Dr. Trevor Jones (Southern Tanzania Elephant Program). Interobserver reliability assessment of body condition scoring was done with assistance from Suzanne Lawrie and Professor Phyllis Lee (University of Stirling). I analysed inter-observer reliability data and wrote the chapter. Professors Phyllis Lee and Hannah Buchanan-Smith (University of Stirling) provided supervision on methods, inter-observer reliability analyses, and drafts of this chapter.

2.1 Abstract

This chapter is an overview of the study area and methods. The study took place in the Ruaha-Rungwa of south-central Tanzania. Ruaha-Rungwa is one of the largest protected area complexes in Tanzania (>40,000 km^2) and is a key ecosystem for elephant conservation, being home to an estimated 30% of the country's elephants in 2015 (Thouless et al., 2016). An ecosystem description is provided here. Permission for the study was granted by the Tanzania Commission for Science and Technology (COSTECH), Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks Authority (TANAPA) and Tanzania Wildlife Management Authority (TAWA). Ethical approval was granted by the University of Stirling's General University Ethics Panel and Animal Welfare and Ethical Review Body. Data collection was done with collaborators listed below (see 2.5.2) and in relevant chapters. Data on elephant space use, activity patterns, grouping patterns, and behaviour were collected through track-based occupancy surveys and camera trapping. Data collection for Chapter 4 was conducted in the dry seasons of 2017 and 2018. Data for Chapter 5 were collected in the dry seasons of 2018 and 2019. Data collection for Chapter 6 was conducted between January 2019 and January 2020. Most data collection was therefore completed before the COVID-19 pandemic led to major disruptions such as declines in tourism and impacts on community livelihoods and activities in the ecosystem. Data collected under Southern Tanzania Elephant Program's elephant monitoring program in Ruaha National Park span the period 2015-2021 and are used to contextualize risks to elephants in Chapter 3. Ethical considerations and limitations of the study are discussed.

2.2 Study site

2.2.1 Protected areas

The Ruaha-Rungwa ecosystem in south-central Tanzania (approximate centre of the ecosystem: Latitude: -7.3, Longitude: 34.4) at present includes eight protected areas (44,000 km^2) along with village land (Figure 2.1). The protected areas (PAs) include Ruaha National Park (20,226 km^2), Rungwa-Kizigo-Muhesi Game Reserves (17,035 km^2)[2], MBOMIPA Wildlife Management Area (777 km^2), Waga Wildlife Management Area (344 km^2), Lunda-Nkwambi Game Controlled Area (1,720 km^2), and Rungwa South Open Area (3,873 km^2). Photographic tourism is permitted in the National Park (NP), licensed hunting is permitted in Game Reserves (GR), the Game Controlled Area (GCA), and Open Areas (OA), and both photographic and licensed hunting are permitted in Wildlife Management Areas (WMA). Village land has no protected status. Additional details on the management and levels of on-the-ground protection in these areas are provided in Sections 2.2.4 – 2.2.7. A brief history of protected area establishment is provided below.

The first protected area in the ecosystem was the Saba River Game Reserve, which was gazetted in 1910 under German colonial rule (Coppolillo & Dickman, 2007). The Saba River Game Reserve comprised much of present-day Ruaha National Park (but not the Usangu area) and Rungwa Game Reserve. In 1946, the area was re-gazetted as Rungwa Game Reserve (Savidge, 1968)[3]. In 1964, the area south of the Mzombe River was excised from the game reserve and gazetted as Ruaha National Park (G.N. No. 464 of 1964). In 1974, an 800 km^2 section southeast of the Great Ruaha River was added to the park (Mtahiko, 2007). In 2008, Usangu Game Reserve (originally gazetted in 1998, G.N. No. 436A of 1998) was incorporated into Ruaha National Park, increasing the size of the park to 20,226 km^2 (Tanzania National Parks Authority, 2009; G.N. No. 28 of 2008). However, part of the Usangu extension of Ruaha National Park comprises areas of large-scale agriculture, livestock ranching, and settlements (TAWIRI, 2019). Due to ongoing conflicts over park boundaries, part of the Usangu extension of Ruaha National Park is being proposed for degazettement in 2023 (Mlacha, 2023). Kizigo Game Reserve was gazetted in 1974 (G.N. No. 275 of 1974) and Muhesi Game Reserves in 1991 (G.N. No. 531 of 1991). Lunda-Nkwambi Game Controlled Area was

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[2] Rungwa Game Reserve covers an area of 9,175 km^2, Kizigo Game Reserve covers an area of 5,140 km^2, and Muhesi Game Reserve covers an area of 2,720 km^2. While some sources state that Muhesi Game Reserve covers an area of 4,550 km^2, ‘effective’ boundaries were revised in 2017-2018 by the Tanzania Wildlife Management Authority because of human encroachment into the reserve (Strampelli, 2021). This revised ‘effective’ boundary is used in the thesis.

[3] Note that there is inconsistency between sources on the date of this gazettement, as Williams (2005) states that Rungwa Game Reserve was established in 1937. Rungwa Game Reserve was re-gazetted in 1974 under GN. No. 275 of 1974.

gazetted in 1985 (G.N. No. 38 of 1985). Part of Lunda-Nkwambi Game Controlled Area came under village government management in 1997-1998 as part of the *Matumizi Bora ya Malihai Tarafa za Idodi na Pawaga* (MBOMIPA) project (Walsh, 2003). While the MBOMIPA Association was established in 2002 and the area became a pilot Wildlife Management Area in 2003, MBOMIPA Wildlife Management Area was not formally registered until 2007 (CWMAC, 2019). Waga WMA was formally registered in 2015 (CWMAC, 2019).

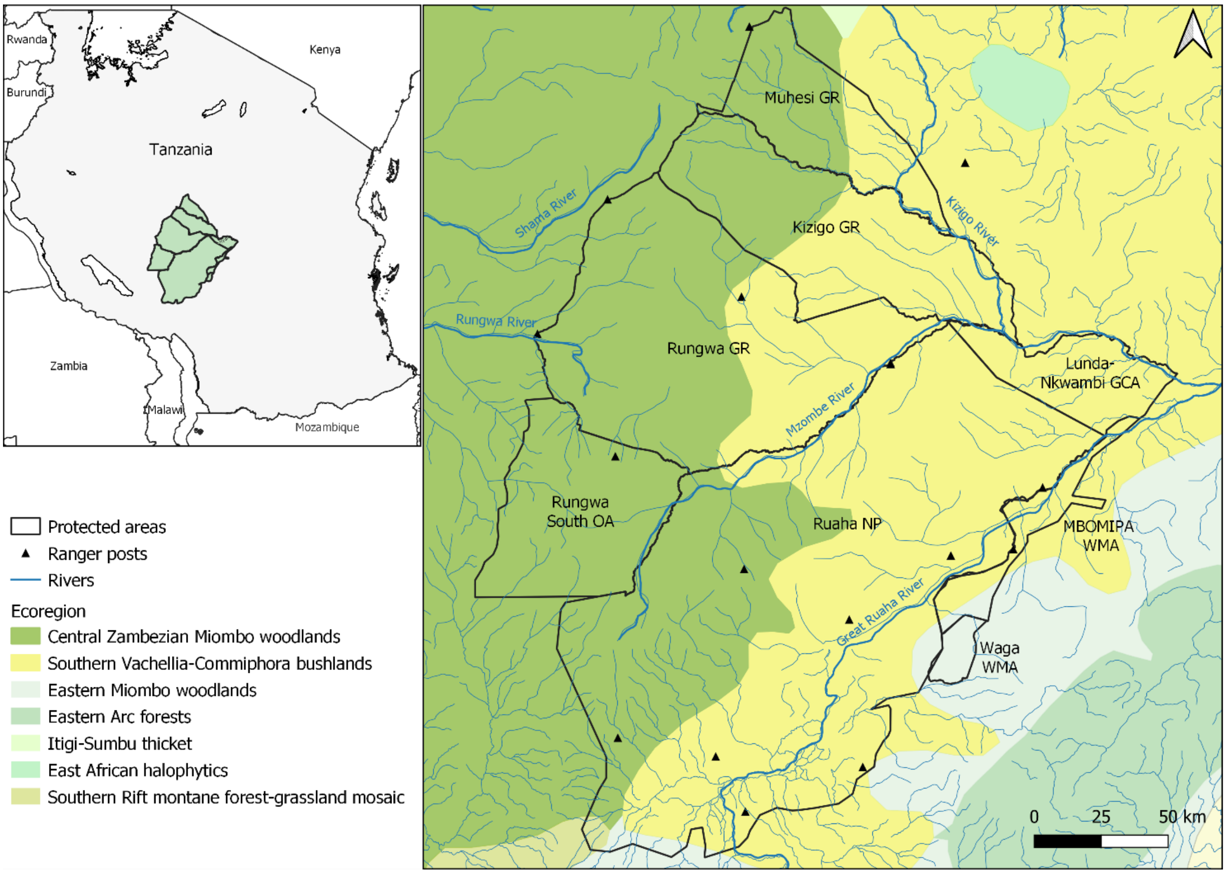

Figure 2.1 Map of the Ruaha-Rungwa ecosystem (right) with the location of the study area in Tanzania shown (top left). The ecosystem includes five types of protected areas, including three Game Reserves (GR), one National Park (NP), one Game Controlled Area (GCA), one Open Area (Rungwa South), and two Wildlife Management Areas (WMA). Major rivers (denoted by thick blue lines) and seasonal smaller rivers (denoted by light blue lines), ecoregions (Olson et al., 2001), and the locations of ranger posts are shown.

2.2.2 Habitat and climate

The two dominant ecoregions in Ruaha-Rungwa are Southern *Vachellia*[4]*-Commiphora* bushlands and thickets and Central Zambezian miombo woodlands and grasslands (Olson et al., 2001). A relatively small area in the southeast of the ecosystem comprises Eastern miombo woodlands and grasslands (Olson et al., 2001). Miombo refers to deciduous woodlands dominated by the genera *Brachystegia, Julbernardia*, and *Isoberlinia*, and it is the dominant ecotype in central and southern Tanzania (Frost, 1996). Miombo woodlands occur on highly weathered, nutrient-poor soils. Both woody plants and grasses in miombo woodlands are of low nutrient quality and faunal densities tend to be lower in miombo communities than in savanna communities with comparable climate and rainfall (Frost, 1996). Elevation varies from 700 m above sea level (asl) in the Great Ruaha River valley to >1800 m asl on the Isunkaviola Plateau in southwest Ruaha National Park (Bjørnstad, 1976).

The climate of the region is semi-arid to arid, with an average annual precipitation of 600 mm (Fick & Hijmans, 2017). Average annual precipitation increases across an east to west gradient in the landscape, from an average of 450 mm of rainfall per year in the east of Ruaha National Park to 900 mm of rainfall per year in Rungwa South Open Area (Fick & Hijmans, 2017). Mean daily temperatures range between 19°C and 26°C over the year (Martilla, 2011; Tanzania Wildlife Management Authority, 2023a; 2023c). Maximum daytime temperatures vary between 25°C and 40°C over the year, with October and November being the hottest months (Marttila, 2011). The area has one wet season, from December to April, and one dry season from May to November (Bjørnstad, 1976).

Important water sources include the perennial Great Ruaha and Mzombe Rivers, as well as seasonal sand rivers, springs, and wet grassy depressions and drainage lines in miombo areas (known as ‘korongos’, ‘mbugas’ or ‘dambos’). Other major seasonal rivers include the Kizigo, the Rungwa, and the Shama. Additional habitat characteristics relevant to elephants for each of the protected areas are provided in Sections 2.2.4 – 2.2.7.

2.2.3 Human presence in the ecosystem

There has been human presence in what is today the Ruaha-Rungwa ecosystem for at least 45,000 years (Willoughby et al., 2018). Before the establishment of the first protected area under German colonial rule, small and possibly seasonal human settlements occurred in the area (Coppolillo & Dickman, 2007; Williams, 2005). During protected area establishment, people living within these areas were moved out (Savidge, 1968; Williams, 2005), such that

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[4] Note that I use the current (2009) genus designation for the African *Acacia* group of species.

today, human settlements and cultivation are located along the edges of the protected areas in the ecosystem (see Chapter 3, Figures 3.19-3.20). As a result of a complex history of in-migration, resettlement under colonial policies (Kjekshus, 1977) and post-independence state-led villagization[5], and evictions during protected area establishment, villages around the protected area complex are home to at least 35 ethnic groups (Nahonyo, Mwasumbi, & Bayona, 1998) who are a combination of small-scale farmers, agro-pastoralists and transhumant pastoralists (Arnold, 2001; Sosovele, 2004; Williams, 1999, 2005). Some of the larger ethnic groups include the Sukuma, Gogo, Hehe, Bena, Nyaturu, Nyamwezi, Taturu, Maasai, and Barabaig. Additional settlements were moved out of Ruaha National Park in the mid to late 2000s following the addition of the Usangu extension to the park (although some settlements remain within legal park boundaries). In Tanzania's Population and Housing Census of 2022, the seven districts directly adjacent to the protected areas in the ecosystem were home to an estimated 2,410,000 people (URT, 2022). This represents an increase of 42% in the human population since 2012 and an increase of 83% since 2002 (URT, 2012). More information on human activities in the ecosystem is provided in Chapter 3.

2.2.4 Ruaha National Park

Ruaha National Park is situated within Iringa and Mbeya regions. The park consists of a lower basin (700-900 m asl) – an arm of the Great Rift Valley through which the Great Ruaha River flows– and a higher plateau area (1000-1500 m asl). *Vachellia-Commiphora* and *Combretum* bushlands are the dominant vegetation in the north and east of the park, while miombo woodlands cover much of the south and west of the park (Bjørnstad, 1976). The park is bounded by two major rivers which are important sources of water for wildlife year-round: the Mzombe River in the north and the Great Ruaha River in the south (Stolberger, 2012). Large-scale irrigation of agriculture upstream of Ruaha National Park has significantly reduced dry season water flow in the Great Ruaha River in the last three decades (Kashaigili, Mccartney, & Mahoo, 2007; Mtahiko et al., 2006). The park also has springs (e.g., Mwayembe, Mkwawa, Makindi) and seasonal sand rivers which form important dry season water sources, including the Mdonya, Mwagusi, Ikuka, Jongomero, Nyakapembe, Itiku, Lupati, and Kimbi (Stolberger, 2012). While these seasonal rivers only flow during the wet season, elephants access water in the dry season by digging in areas where water has accumulated due to bands of granitic rock that form underground dams (Stommel et al., 2016). Surface water in rain-fed wet-season pools disappears rapidly over the dry season (Stommel et al., 2016), such that perennial

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[5] Villagization (in Swahili, *Ujamaa Vijijini)* was a post-independence rural development policy (1968-1976) under which the majority of Tanzania's rural population was forcibly moved into nucleated settlements for the purposes of communal agricultural production and allocation of social services (Kjekshus, 1977; Schneider, 2004).

springs and sand rivers are key dry-season water sources. In the park's miombo zone, perennial springs occur along drainage lines and in mbugas (grassy wetlands).

Ruaha National Park is managed by the Tanzania National Parks Authority (TANAPA). Although the park has more resources for protection activities than other protected areas in the ecosystem, ranger presence and patrol effort vary and tend to be lower in the more remote, roadless areas of the park. Only non-consumptive use (photographic tourism) is permitted in the park. At the time of the study, Ruaha National Park was divided into six management zones where different types and levels of tourism were permitted (Figure 2.2; Tanzania National Parks Authority, 2009). The North High Use Zone comprises the northeastern part of the park along the Great Ruaha River. This zone receives the highest level of visitor activity and contains most of the park's tourism infrastructure and facilities (see Table 2.1). This zone includes an extensive road network for vehicle-based wildlife viewing, as well as four ranger posts and the park headquarters at Msembe. This zone is the safest area for elephants in the park as the extensive ranger and tourism presence deters illegal activities (Beale et al., 2018; Strampelli, 2021).

In the park's western miombo Wilderness Zone, only limited tourism and infrastructure development are permitted, and no tourism was occurring at the time of the study. Infrastructure is limited to access roads for use by park management and one ranger post. Challenges faced by TANAPA in managing and protecting wilderness zones in National Parks include difficult access, their large size, and limited financial resources (Mtahiko, 2007). Due to their low visitation rates, these wilderness zone areas are at higher risk of illegal activities than areas with higher tourism visitation (Mtahiko, 2007). As wilderness zones are not established for revenue generation, inadequate funding for their management is also a concern (Mtahiko, 2007).

The park's several Low Use Zones permit low-volume vehicle-based wildlife viewing and walking safaris. At the time of the study, there was no tourism investment in these zones, and these areas generally receive low numbers of visitors. The South High Use Zone, while designated as high use, also had no tourism investment at the time of the study.

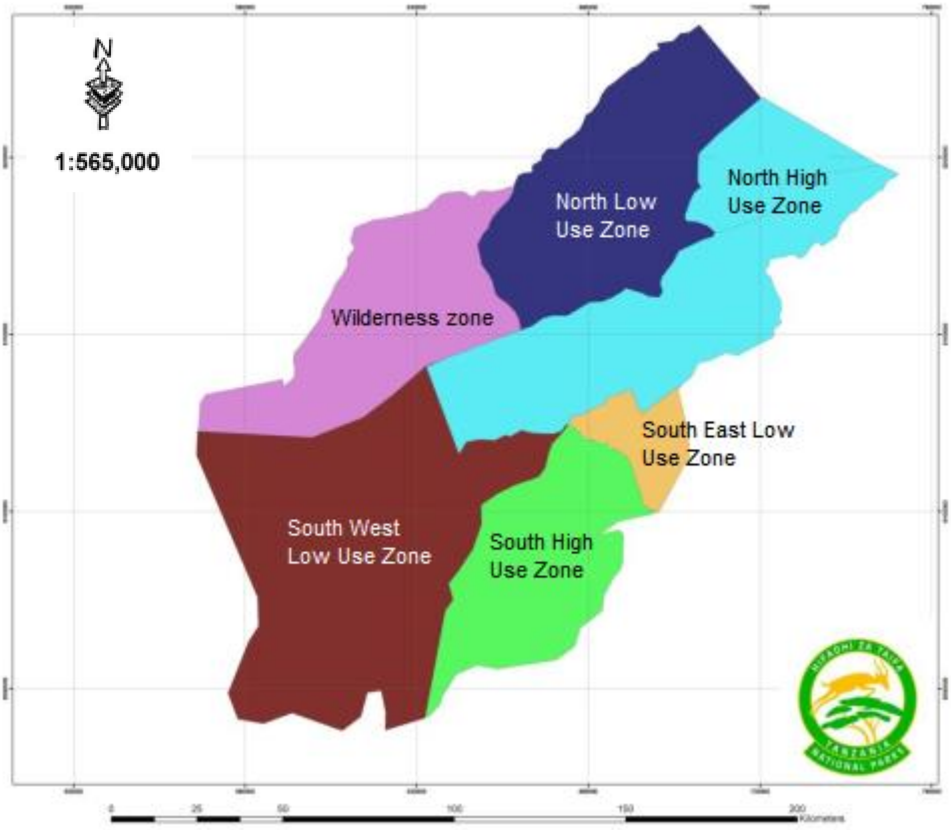

Figure 2.2 Management Zones in Ruaha National Park, 2009-2019. Reproduced from Tanzania National Parks Authority (2009). High-volume vehicle-based wildlife viewing is permitted in High Use Zones, while low-volume vehicle-based wildlife viewing is permitted in Low Use Zones. No vehicle-based tourism is permitted in Wilderness Zones; here, only walking safaris and scientific research are allowed.

2.2.5 Rungwa-Kizigo-Muhesi Game Reserves

The Rungwa-Kizigo-Muhesi Game Reserve complex is located in Singida, Mbeya, and Dodoma regions. At the time of the study, the three reserves were managed as one entity by the Tanzania Wildlife Management Authority (TAWA). Elevation ranges from >800 m asl at the confluence of the Kizigo and Mzombe rivers and >1800 m asl at Ikiri hill (Tanzania Wildlife Management Authority, 2023a; 2023b). Central Zambezian woodlands predominate in the west of the game reserves while *Vachellia-Commiphora* bushlands occur in the east. In addition to seasonal rivers (e.g., Kizigo, Rungwa, Mwakasumbi, Sabu, Musa), water is available in the perennial Mzombe River and in springs and mbugas. The Game Reserves are managed for licensed tourist hunting. At the time of the study, eight of the 12 hunting blocks within the reserves had active hunting operators (Strampelli, 2021). The hunting blocks with active operators were all in Rungwa and Kizigo; no operators were active in Muhesi. Licensed hunting of elephants did not occur in blocks without operators. Licensed hunting of elephants was also not occurring in Kizigo Game Reserve and the Rungwa-Ikiri hunting block in Rungwa Game Reserve at the time of the study (R. Ramoni, personal communications, 2019). While elephant hunting may have been occurring in other blocks in Rungwa Game Reserve, the number of elephant hunts during the study period was likely low[6]. Both TAWA and hunting operators conduct patrols, with TAWA being primarily responsible for law enforcement activities in areas without hunting operators. TAWA had four permanent ranger posts and one temporary post in the game reserves during the study period. Resources for protection are lower in Game Reserves than they are in Ruaha National Park (Strampelli, 2021).

2.2.6 MBOMIPA Wildlife Management Area

MBOMIPA Wildlife Management Area[7] (WMA) is located in Iringa Region. The WMA forms a narrow strip of protected community land and lies to the south of Ruaha National Park. V*achellia–Commiphora* and *Combretum* bushlands and grasslands predominate in the north of the WMA, while Eastern miombo woodlands occur in the south. Elevation ranges between 700 m asl to >1000 m asl. In addition to the perennial Great Ruaha River, which forms the WMA's northern boundary, several seasonal rivers (tributaries of the Great Ruaha) flow through the WMA. The WMA is currently managed by an Authorized Association, comprising two representatives from each of the 21 member villages. At the time of the study, however, no Authorized Association was in place and the Iringa District Natural Resources Advisory Body held a temporary caretaker role for the WMA. The WMA has four zones where different activities are permitted (MBOMIPA, 2013): Lunda (photographic tourism), Tungamalenga (officially, photographic tourism but this zone has also been used for licensed hunting), Mkupule-Kinyangesi (licensed hunting), and Nyaluu (licensed hunting but the area has been largely encroached by farmland). During the study period, neither photographic tourism nor licensed hunting took place in the WMA. Although the WMA has six village game scout posts, due to a lack of funds, no patrolling was occurring throughout 2015-2017. In 2018, the NGO Southern Tanzania Elephant Program (STEP) began supporting patrols in the Lunda zone of the WMA.

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[6] The number of elephants hunted in areas with active hunting operators during the study period is unknown. However, licensed elephant offtake for trophy hunting was likely low for several reasons: import of elephant hunting trophies was temporarily suspended in the United States of America (US Fish and Wildlife Service, 2014) and the European Union (European Commission, 2015), Tanzania's hunting quota was reduced from 100 to 50 elephants in 2017 (CITES, 2023), and male elephants of suitable age and with suitable tusks were rare because of poaching.

[7] MBOMIPA is a Swahili acronym for *Matumizi Bora ya Malihai Tarafa za Idodi na Pawaga*. This area is sometimes referred to as Pawaga-Idodi WMA.

2.2.7 Other protected areas

Several other protected areas were surveyed during track-based occupancy surveys (see Section 2.3.1). Waga Wildlife Management Area (WMA) lies in Iringa and Mbeya regions to the south of Ruaha National Park. The dominant vegetation is Eastern miombo woodlands. No photographic tourism nor licensed hunting was occurring in the WMA at the time of the study. Lunda-Nkwambi Game Controlled Area (GCA) is located in Iringa region to the northeast of Ruaha National Park. The dominant vegetation is *Vachellia-Commiphora* bushlands. The area is managed for licensed hunting and one hunting operator was active in the northern of the GCA's two hunting blocks at the time of the study. Rungwa South Open Area (OA) lies in Singida and Mbeya regions to the west of Ruaha National Park and south of Rungwa Game Reserve. The dominant vegetation is Central Zambezian miombo woodlands. The area is managed for licensed hunting, and the northern of the OA's two blocks had an active hunting operator at the time of the study. Licensed elephant hunting may have been occurring in Rungwa South OA and Lunda-Nkwambi GCA during the study period, but the number of elephants hunted is unknown. In general, these protected areas receive low levels of on-the-ground protection efforts (Strampelli, 2021), with periodic and seasonal patrols conducted by hunting operators and TAWA's Kikosi Dhidi ya Ujangili (KDU).

2.2.8 Elephants in Ruaha-Rungwa

In 2015, Tanzania was home to the third-largest population of African savanna elephants in Africa (Chase et al., 2016). The Ruaha-Rungwa elephant population is one of the largest in Tanzania, historically second only to the Selous-Mikumi ecosystem[8]. A detailed synthesis of elephant population and poaching trends for the Ruaha-Rungwa ecosystem is provided in Chapter 3, but elephant population estimates for the period 1977 to 2021 are shown in Figure 2.3 for context. In 2006-2009, the ecosystem held around 35,000 elephants (TAWIRI, 2007, 2010), but commercial ivory poaching reduced the population by more than half by 2015 (TAWIRI, 2016). During the study period, aerial censuses indicate that the elephant population was stable at around 15,500 elephants (Figure 2.3; TAWIRI, 2019, 2022).

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[8] Tanzania's Selous-Mikumi ecosystem was home to over 100,000 elephants in 1976 (Douglas-Hamilton, 1987). Multiple waves of poaching led to major population declines in this ecosystem such that, since 2015, Selous-Mikumi and Ruaha-Rungwa have held similar numbers of elephants (Thouless et al., 2016).

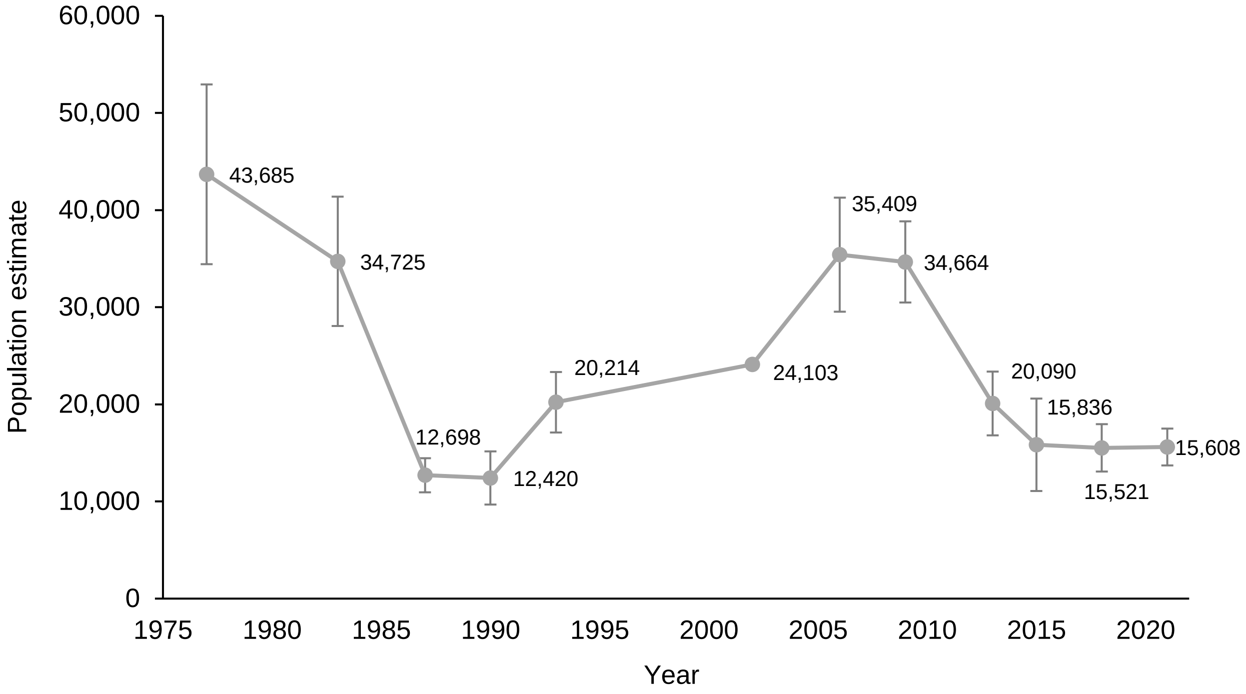

Figure 2.3 Elephant population estimates for Ruaha-Rungwa from aerial censuses for the period 1977 to 2021 with standard errors shown (note that the vertical error bar for the 1977 estimate is a 95% confidence interval and that a standard error for the 2002 estimate was not provided in the census report). See Chapter 3 for details of survey extents and elephant density estimates. Data from Barnes & Douglas-Hamilton, (1982); Borner & Severre, (1984); TWCM, (1990); TWCM, (1994); AED, (2002); TAWIRI, (2007); TAWIRI, (2010); TAWIRI, (2014); TAWIRI, (2016); TAWIRI, (2019); TAWIRI, (2022).

Aerial censuses provide a snapshot of elephant distribution in the ecosystem (Figure 2.4) and indicate that dry-season elephant densities are highest along the Great Ruaha River, the Mzombe River, and in western and central Rungwa and Kizigo Game Reserves (TAWIRI, 2013, 2016, 2019). As wet season aerial censuses have not been conducted in several decades (Savidge, 1968; TAWIRI, 1996), the current wet season distribution of elephants across the ecosystem is not well understood.

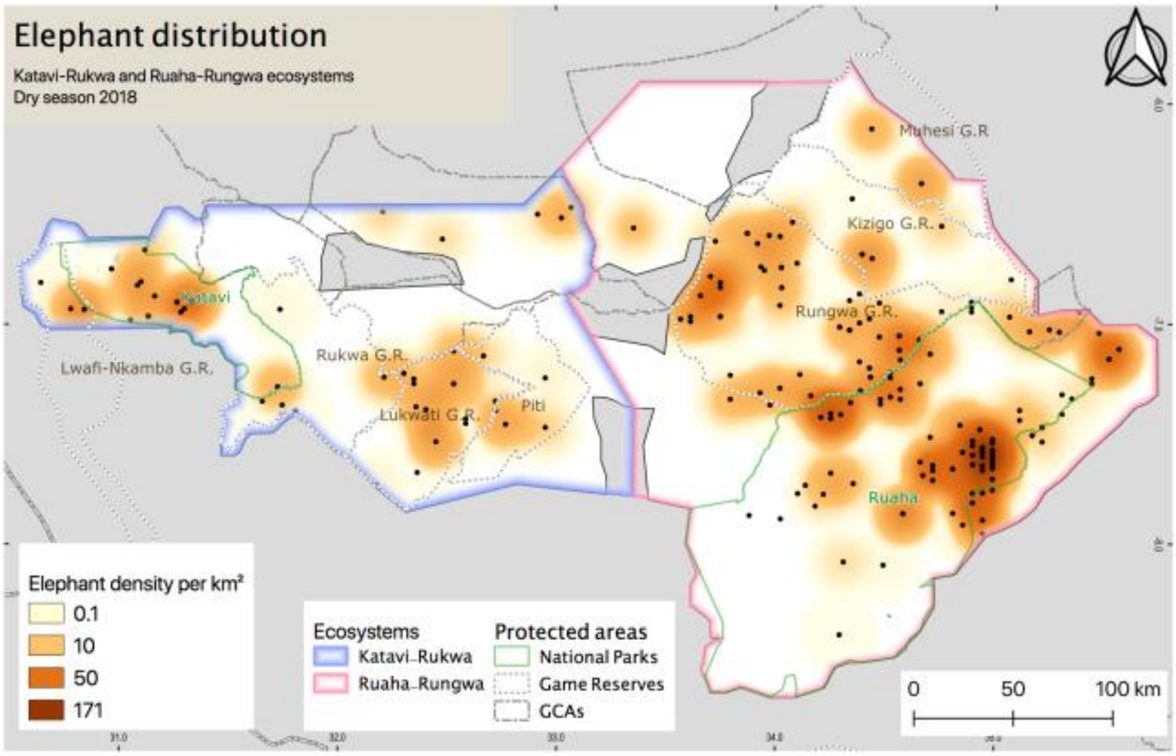

Figure 2.4 Distribution of elephants in the Ruaha-Rungwa ecosystem from the TAWIRI 2018 dry season aerial survey. Reproduced from TAWIRI, 2019. The census area denoted by a pink line is the Ruaha-Rungwa ecosystem. Black dots are the locations of elephant sightings on aerial transects. To the north-east of Ruaha National Park lies Lunda-Nkwambi GCA, to the south-east of Ruaha lie MBOMIPA WMA and Waga WMA (boundaries not shown), and to the west of Ruaha lies Rungwa South Open Area (boundaries not shown). The census area denoted by a blue line is the Katavi-Rukwa ecosystem, which was historically censused separately from the Ruaha-Rungwa ecosystem but is connected to Ruaha-Rungwa by wildlife corridors. Since 2018, TAWIRI aerial surveys have combined both ecosystems.

2.2.9 Anthropogenic changes in the ecosystem

The Ruaha-Rungwa ecosystem presents elephants with a complex landscape of anthropogenic risks, which are presented in detail in Chapter 3. While elephant poaching levels during the study period were lower than in 2010-2015 (Chapter 3), TAWIRI’s 2018 census report stated that the carcass ratio (the proportion of dead elephants to the sum of live and dead elephants, expressed as a percentage) remained high (above 8%, indicating a declining population, see Douglas-Hamilton & Burrill, 1991) and were “a cause for concern” requiring “ongoing attention by management authorities” (TAWIRI, 2019). It is therefore likely that poaching risk continued to influence elephant space use and behaviour in the ecosystem during the study period. Maps of poaching risk, as inferred from models of the probability of elephant carcass occurrence based on aerial census data (Beale et al., 2018) are provided in Chapter 3. Livestock keeping, timber extraction, charcoaling, fishing, and agriculture are legal on village land but also occur illegally within protected areas (see Chapter 3 for maps of human presence and resource use within protected areas derived from ground and aerial surveys). Key land use changes and human population distribution affecting the protected areas of the ecosystem are detailed in Chapter 3. While the Human Footprint Index (HFI; Venter et al., 2016) – an index of the aggregate influence of human population density, built-up areas, night-time lights, land use, coastlines, roads, railroads, and navigable rivers – has been used in some studies of elephant responses to humans and their activities (Beirne et al., 2021; Wall et al., 2021), the latest available version of the index at the time of the study was from 2009. Given that the human population in the study area has grown rapidly in the last ten years (see Section 2.2.3), I used measures of human pressure and presence (cropland, human population densities, building densities) that were more representative of the study period.

2.3 Data collection methods

Much of the Ruaha-Rungwa study area is covered in dense vegetation where direct observation of elephants is difficult and potentially unsafe (Barnes, 1983). In areas where elephants have experienced poaching, daytime observations of elephants are infrequent, and elephants tend to flee from observers (Chapter 3; Barnes, 1982d). This meant that direct observation of individuals or groups of elephants was seldom possible, especially in the higher-risk areas of the ecosystem. Here, I briefly outline the techniques that I used to collect data on elephant occurrence and behaviour and the definitions of elephant group types, activity types, body condition scores, age classes, and reaction indices used in the study.

***Photo 3**: A group of elephants in miombo woodland. Much of Ruaha-Rungwa is covered in dense vegetation where direct observation of elephant behaviour is difficult.*

2.3.1 Track-based occupancy surveys (Chapter 4)

In Chapter 4, I investigate the influence of risk and environmental factors on elephant space use in the Ruaha-Rungwa ecosystem using an occupancy study design. Occupancy studies require repeated surveys of pre-defined sampling units to estimate both the probability of occupancy or use of a sampling unit by a species and the probability of detecting a species given that is present in a sampling unit (MacKenzie & Royle, 2005). These repeated surveys provide a 'detection history' for the sampling unit, indicating whether a species was detected or not within each replicate survey (i.e., detection/non-detection data). Elephant detection/non-detection data used in this chapter were collected by a collaborator (Dr. Paolo Strampelli, University of Oxford) and two experienced trackers (Stivin Pangamwene and Hamis Dongo) via vehicle-based road transects as part of an ecosystem-wide, multispecies survey following jointly developed protocols. Data collection occurred during the dry season in 2017 and 2018 (7th July – 29th November 2017 and 29th June – 21st November 2018). As the survey team did not have experience with determining how long elephant dung had been present on the road surface (its 'age' since defecation in hours, days, or weeks), which is necessary for calculating dung decay and elephant densities (Barnes & Barnes, 1992), detection/non-detection records were based on elephant footprints. The locations of transects and the distribution of elephant detections are in Chapter 4 (see Figure. 4.1). Additional methodological details, including an overview of occupancy models and covariates used in analyses, are provided in Chapter 4.

2.3.2 Camera trap surveys (Chapter 5)

Chapter 5 investigates whether elephants adjust their activity patterns, grouping patterns, and use of roads and water sources in response to risk, and explores the potential costs of risk-induced shifts in diel activity. These questions were examined through camera trap surveys in four areas of the ecosystem representing one low- and three high-risk sites for elephants (see Chapter 3 for maps of poaching risk and human activities and Figure 5.1 for a map of the camera trap grids). Camera traps have been used to study diel activity in a range of mammals including elephants (Gaynor et al., 2018b; Gessner, Buchwald & Wittemyer, 2014; Rowcliffe et al., 2014) and to assess temporal overlap in activity patterns of animals and humans (Carter et al., 2015), predators and their prey, and competitors (Schuette et al., 2013). Camera traps are especially useful when direct observation is not feasible because of the study species' challenging habitat or terrain, wariness of humans, or nocturnal behaviour. Given the challenges of observing elephants in high-risk areas and the prohibitive costs of and ethical concerns around GPS telemetry (Soulsbury et al., 2020), camera traps were a feasible and less invasive method for studying elephant activity patterns in Ruaha-Rungwa. Data collection was done in collaboration with Dr. Charlotte Searle (University of Oxford) as part of a multi-species survey in the dry season of 2018 (June-November) and 2019 (July-October). Further details of the survey design and camera trap placement and settings are provided in Chapter 5. I used ExifPro Version 2.1 software to display and annotate camera trap images based on visual inspection (Kowalski & Kowalski, 2013). I defined independent elephant detection events as successive images of elephants that were separated by more than 15 minutes (Gaynor et al., 2018b; see 2.3.4). As camera traps record animal movement, each detection event represents ‘activity’ (Rowcliffe et al., 2014). In visualizing diel activity curves for elephants from camera trap detections (see Chapter 5), it was assumed that the rate at which camera traps detected elephant events at a given time of day was proportional to the activity level of the elephant (sub)population at that time (Rowcliffe et al., 2014). I coded group type for each event to enable comparison of grouping patterns and to investigate possible sex differences in diel activity shifts between the low- and high-risk sites (see 2.3.5). To explore possible costs associated with risk-induced behavioural shifts, I scored the types of activities that elephants were engaged in (see 2.3.6) and body condition of adult (≥ 10 years) female elephants (see 2.3.7). I focused on adult females because female condition affects conception rates and the survival of dependent calves (Foley, 2002; Lee, Lindsay & Moss, 2011), and because previous work indicates that risk effects on population dynamics may arise in part from risk-induced behavioural changes that reduce foraging efficiency and impact female condition (Christianson & Creel, 2010; Creel, Winnie & Christianson, 2009). I also compared elephant use of roads and water sources and the degree of temporal overlap between elephants and lions between the low- and high-risk sites (see Chapter 5 for methods of how these comparisons were made).

2.3.3 Camera trapping at elephant drinking points (Chapter 6)

Chapter 6 explores whether risk influences how elephants use water sources. I collected data on water source use via camera traps placed at low-risk and high-risk water sources (see Chapter 6 for how low- and high-risk water sources were defined). Camera trap sampling was conducted between January 2019 and January 2020 to capture 6 months of wet season data and 7 months of dry season data. Previous studies of elephant waterhole use and drinking patterns used direct 24-hour observations at waterholes (Weir & Davidson, 1965; Valeix, Chamaillé-Jammes & Fritz, 2007), or individual follows of elephants (Shannon et al., 2008; Wyatt & Eltringham, 1974). 24-hour observations are very time- and labour-intensive and there is a potential risk that observer presence may displace elephants from waterholes in areas where they are wary of humans. Individual follows are similarly time-intensive and challenging in the study area due to the paucity of roads and dense vegetation (Barnes, 1983). Camera traps thus provided a less intrusive and less time-intensive alternative. Camera traps have been used to study visitation patterns to bais in African forest elephants (Gessner et al., 2014) as well as for farmland in savannah elephants (Smit et al., 2019). Camera traps were placed on elephant trails to water and as close as possible to entry and exit points at known elephant drinking locations (see Figure 6.1). Further details of study design and camera trap placement and settings are provided in Chapter 6. Camera trap images were annotated using ExifPro Version 2.1 software (Kowalski & Kowalski, 2013). Independent elephant detection events were defined as successive images of elephants that were separated by more than 15 minutes (Gaynor et al., 2018b). In visualizing activity curves for elephant water source visits from camera trap detections (see Chapter 6), it was assumed that the rate at which camera traps detected elephant events at a given time of day was proportional to the elephant water source visitation rate at that time for a given water source. I coded group type (see 2.3.5), group size, and vigilance behaviour (see Chapter 6) for each elephant water use event.

2.3.4 Definition of independent elephant events from camera trap images used in this study

As camera traps capture sequences of images, it is common practice to cluster images of individuals of the same species at the same camera trap station into a single event in order to limit pseudoreplication and increase independence between observations (Rovero & Zimmerman, 2016). In this study, it was also necessary to define independent events as the unit for classifying elephant group types and activity types. Events are defined by the period of time between subsequent images of the same species (Meek et al., 2014). In this study, I have followed the definition of Gaynor et al. (2018b) in their camera trap study of elephant diel activity in Gorongosa National Park, Mozambique, whereby independent events were defined as successive images of elephants that were separated by more than 15 minutes. Gaynor et al. (2018b) based this definition on expert examination of camera trap footage which indicated that elephants in the same known group were rarely separated by more than 15 minutes at a given location. In addition to this event definition being the only one validated on known elephant groups, I opted for this definition because camera trap placement in this study closely reflected camera trap placement in the Gaynor et al., (2018b) study, suggesting that this definition is appropriate for cameras placed on roads, animal trails away from roads, as well as on animal trails to rivers[9].

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[9] In a camera trap study of elephant grouping patterns along trails to water sources in Botswana, Allen et al. (2020) defined independent elephant events as images separated by 11 minutes based on an analysis showing that most individuals were detected within 10 minutes of a previous individual. However, 98% of the elephants detected in the Allen et al. (2020) study were male. Given that initial inspection of camera trap photos indicated that both male and female groups used water sources, I opted for the Gaynor et al. (2018b) definition in Chapter 6.

2.3.5 Definitions of elephant group types used in this study

The group type definitions used to code group types in camera trap images (Chapters 5 & 6) are provided in Table 2.1. Elephant sex was determined through visual assessment of body shape, head shape, tusk shape, and external genitals (Moss, 1997). Inter-observer agreement in group type classification was assessed using percentage agreement (also termed simple concordance) and Cohen's kappa, a measure of inter-observer reliability that accounts for agreement due to chance (Landis & Koch, 1977). While there are no 'rules' on what constitutes an acceptable level of agreement, a percentage agreement of 70% (fair) to 80% (good) is generally considered acceptable (Barth et al., 2017; Jorgensen, Mallon & Kranioti, 2020) and a kappa above 0.7 is interpreted to represent good or substantial agreement (Cicchetti & Sparrow, 1981; Landis & Koch, 1977).

Both I and a second observer independently scored group type for a stratified random sample of 45 elephant detection events. At the time of this inter-observer agreement assessment, I had >4 years of experience observing elephants in the field as well as prior experience classifying elephant sex and broad age classes from camera trap images (Smit et al., 2019). The second observer had multiple years of experience with sexing and ageing elephants and was trained in the group type definitions used in this study. Percentage agreement for the two observers was calculated by dividing the number of events in agreement by the total number of events. Percentage agreement was 80% across the 45 events. Cohen's Kappa was 0.75, indicating substantial agreement in group type classification across the 45 events (Landis & Koch, 1977). Percentage agreement for individual group type categories was greater than 70% - and therefore acceptable - for four of the five group types (Table 2.2) but was 67% for the lone bull group type. Observers differed in whether they classified some events as a lone bull or unknown group type, with the second observer being more likely to classify an event as an unknown group type than I was. This likely reflects differing levels of experience in assessing sex and broad age classes for elephants from camera trap photographs and greater caution in assignments. In retrospect, more practice in assessing group type from camera trap images during training of the second observer in group type definitions would likely have improved interobserver reliability. Group type classification from camera trap images is likely to be challenging for observers without prior experience of assessing elephant group types through direct observation.

Table 2.1 Group type definitions used to classify group types. An elephant aged 10 years is approximately three-quarters of adult female size (Moss, 1997).

Group type	Group code	Definition
Lone bull	LB	One male elephant >10 years observed during an event.
Bull group	BG	More than one male elephant >10 years observed during an event.
Cow-calf group	CC	At least one adult female and/or calf <10 years observed during an event. Typically, multiple females and calves are observed.
Mixed group	M	Cow-calf group with one or more bulls of ≥ adult female height (17-18 years) present during an event.
Unknown group	U	Photographs for the event do not provide enough information to ascertain group type (e.g., only legs visible, elephants too distant in the image).

Table 2.2 Percentage agreement for group type classification between two observers from nine detection events for each group type (total N of events scored = 45).

Group type	Percentage agreement	N
Cow-calf	89%	9
Lone bull	67%	9
Bull group	78%	9
Mixed	89%	9
Unknown	78%	9

2.3.6 Definitions of elephant activity types used in this study

The activity type definitions used to code activities in camera trap images (Chapter 5) are given in Table 2.3. An activity type was considered present if at least one individual in the event displayed the activity. This means that more than one activity type could be present per event. Activity types were grouped into four categories (Table 2.3). Energy acquisition and movement behaviours were those that elephants use for basic subsistence. Relaxed behaviours were those that elephants use for comfort (e.g., wallowing, dusting) or display in the absence of stress or when not in the presence of a direct threat (e.g., play, lying). Suckling was included in this category despite its energy acquisition function because adult females must cease moving and adopt a specific 'suckle-stance' to allow the calf to suckle and may interrupt suckling by the calf if a threat is perceived (Lee, 1987; Poole & Granli, 2011). Stress behaviours included one activity type (running) and were those behaviours that elephants display in response to a perceived threat. The final category (other behaviours) were those behaviours whose function could not consistently be distinguished from camera trap images and included the pause activity type. Pauses may be a brief rest or be associated with attentive or vigilant behaviours such as listening, sniffing with the trunk, or moving the trunk toward the camera trap. While no specific function of pause was assumed in Chapter 5, in Chapter 6 I classify pauses to distinguish between vigilant and non-vigilant pauses (see Section 6.3.2). This was possible because water source camera traps (Chapter 6) were placed higher off the ground than camera traps used in the multi-species camera traps surveys (Chapter 5), and therefore provided more detail on behaviour.

Inter-observer reliability for activity type classification was assessed through percentage agreement. I and a second observer independently scored activity type for a stratified random sample of 45 elephant detection events. The second observer had prior experience observing elephant behaviour and was trained in the activity type definitions used in this study. As multiple activity types could be present in a single event, events in agreement were defined as events where both observers had recorded occurrences of the same activity types. I calculated percentage agreement for the two observers by dividing the total number of events in agreement by the total number of events. Percentage agreement was 82%, indicating good agreement.

Table 2.3 Activity type definitions and category classification.

Activity type	Definition
Energy acquisition and movement behaviours	
Walking	Movement into or out of the camera field of view, or from one area of the camera field of view to another in a series of camera trap photographs. In photographs that show elephants in the process of taking a stride, only one foot is completely off the ground at a time, but two feet may be partially off the ground at a time. In photographs where the visible feet are on the ground, the feet are extended as in walking motion. For events for which there was only one photograph, it was assumed the elephant(s) walked out of the field of view during the camera delay period.
Feeding while walking	Movement into or out of the camera field of view, or from one area of the camera field of view to another (see also definition for *Walking*), while eating or manipulating food items. A food item must be visible in the photograph (often branches, leaves, or grass). The elephant may be holding the food item in the mouth, in the trunk, or both. The trunk may be in the process of being used to grasp food items, to bring food items to the mouth, or to place food items in the mouth.
Feeding while standing	Eating or manipulating food items while stationary. The food item must be visible. The elephant does not take more than one step and does not show directed movement for at least two subsequent photographs. Feeding while standing occurs most often when an elephant is feeding on a tree, bush, or shrub.
Drinking	Using the trunk to take water to the mouth for swallowing.
Relaxed behaviours	
Suckling	A calf uses the mouth to gain fluids from an adult female’s teats. The adult female stands still with one front leg forward to facilitate suckling by the calf.
Lying	Resting on the ground on one side of the body and unless crouched, with no weight on any of the limbs and little movement (following Yon et al., 2019).
Dusting	Spraying or applying dust, water, mud, or sand to the body with the trunk while standing or lying down. Photographs show a cloud of dust.
Wallowing	Applying mud to the body while rolling or lying down. Mud must be visible on the elephant’s body.
Social Play	Engages in seemingly pleasurable interactions with another elephant involving exaggerated movements. Includes head-to-head sparring, trunk wrestling, mounting, chasing, and rolling on one another (adapted from Webber, 2017).

Object Play	Throwing, kicking, or manipulating debris or an object around in a non-aggressive, repetitive, exaggerated manner (Webber, 2017).
Stress behaviours	
Running	Rapid movement into or out of the camera field of view, or from one area of the camera field of view to another. In camera trap photos, running individuals typically have two feet off the ground, and there is often dust in the air which has been kicked up by the running elephant(s). The tail is usually raised, and the head may be raised with the ears held back.
Other behaviours	
Pause	The elephant stands in one position without taking more than one step (but may shift weight onto a different leg) for two or more subsequent photographs. The elephant may move the head or trunk.

2.3.7 Elephant body condition scoring

Body condition scoring (BCS) was done using the five-point index of Morfeld et al. (2014), where BCS=1-2 is underweight, BCS=3 is ideal/normal, and BCS=4-5 is overweight/obese[10]. Scores were based on visual assessment of the pelvic bone, ribs, and backbone in camera trap photographs. The extent to which these areas are visible beneath the skin is correlated with ultrasound measures of subcutaneous fat (Morfeld et al., 2014). While other body condition scoring indices exist (Foley, 2002; Poole, 1989a), the Morfeld et al. (2014) index had clear example photographs, high inter-observer reliability (73% to 93% agreement between observers in the original study) and had been verified against body fat measures. Body condition scoring was done for one individual per camera trap event for events with suitable images (between 16% and 20% of cow-calf group events per grid). Within a single event, condition was scored for the individual for which the best visual inspection of the pelvic bones, ribs, and backbone could be made.

In addition to myself (Obs1), two additional observers independently scored body condition for a stratified random sample of 28-30 elephant detection events. One observer (Obs2) had extensive prior experience with assessing body condition for elephants, while the other (Obs3) did not have prior experience. Percentage agreement between observers was calculated by dividing the total number of events in agreement divided by the total number of events. When using the five-point scale, percentage agreement was 63% between Obs1 and Obs3, but only 46% between Obs1 and Obs2 and Obs2 and Obs3. We therefore collapsed the five-point

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[10] This index was developed for female African elephants aged ≥ 10 years. This was a further reason for not scoring body condition for males and calves.

scale into a four-point scale to reduce the ambiguity between observers, which resulted in high percentage agreement (Table 2.4). The collapsed four-point scale was as follows:

- Category 1 = BCS 1
- Category 2 = BCS 2 or 3
- Category 3 = BCS 3 or 4
- Category 4 = BCS 5

Table 2.4 Percent agreement between the body conditions scores of three observers on 28-30 photos using a four-point scale adapted from Morfeld et al. (2014).

Observers	N	Percentage agreement
1 & 2	28	93%
1 & 3	30	93%
2 & 3	28	86%

***Photo 4**: Example camera trap images of adult females with a BCS of 2 (left, with pelvic bone clearly visible and a sunken area in front of the pelvic bone and a flattened area behind the pelvic bone) and a BCS of 4 (right, with pelvic bone not visible and backbone visible from taill head to mid-back).*

2.3.8 Elephant disturbance transects

To contextualize risks to elephants in the ecosystem, Chapter 3 of this thesis presents data on elephant responses to vehicles from elephant monitoring transects conducted in Ruaha National Park by Southern Tanzania Elephant Program (STEP). Transects were conducted between April 2015 and August 2018 along eight routes in Ruaha National Park. Transects followed existing park roads (Figure 2.5) and were conducted during the day, starting at 9:00 in the morning. Transects were opportunistic in that they followed roads, but they were generally stratified across regions with both high and low densities of elephants (see Figure 2.4). A total of 279 transects were conducted between April 2015 and August 2018 (Table 2.6), resulting in 1,224 observations for which elephant responses to a research vehicle were recorded. Elephant responses to the research vehicle were coded as: calm, initially nervous but calmed down, nervous and avoiding vehicle, or terrified and running away (Table 2.5).

Table 2.5 Reaction index used in this study to describe elephant responses to a research vehicle. Adapted from the reaction index used by Save the Elephants in northern Kenya (Goldenberg et al., 2017).

Response type	Definition
Calm	Elephants continue uninterrupted with the activity they are engaged in.
Initially nervous but calmed down	Elephants initially interrupt the activity they are engaged in and monitor the vehicle, but eventually resume their activity.
Nervous and avoiding vehicle	Elephants interrupt and do not resume the activity they are engaged in. Elephants monitor the vehicle and increase the distance between them and the vehicle by walking away from the vehicle.
Terrified and running away	Elephants run away from the vehicle, often with their tails raised and their ears held back.

Transect codes are in Table 2.6. The Mdonya (MD) and Mwagusi (MW) transects are in an area used intensively for tourism and is the most protected part of the ecosystem. The MK transect follows a road with very infrequent tourism use. The Magangwe (MG), Maji Moto (MJ), and Mpululu (MP) transects begin in areas with tourism presence and end in areas with no tourism presence. The Jongomero to Msembe (MT-1) and Msembe to Lunda (MT-2) transects follow the Great Ruaha River and bisect areas with and without tourist use. Roads outside the main tourism area were used by rangers and occasionally, researchers. Although not quantified, it was the perception of park rangers and a park assistant ecologist that illegal human use tended to be greater in areas with little tourism presence (H. Xavier, personal communication, 2021).

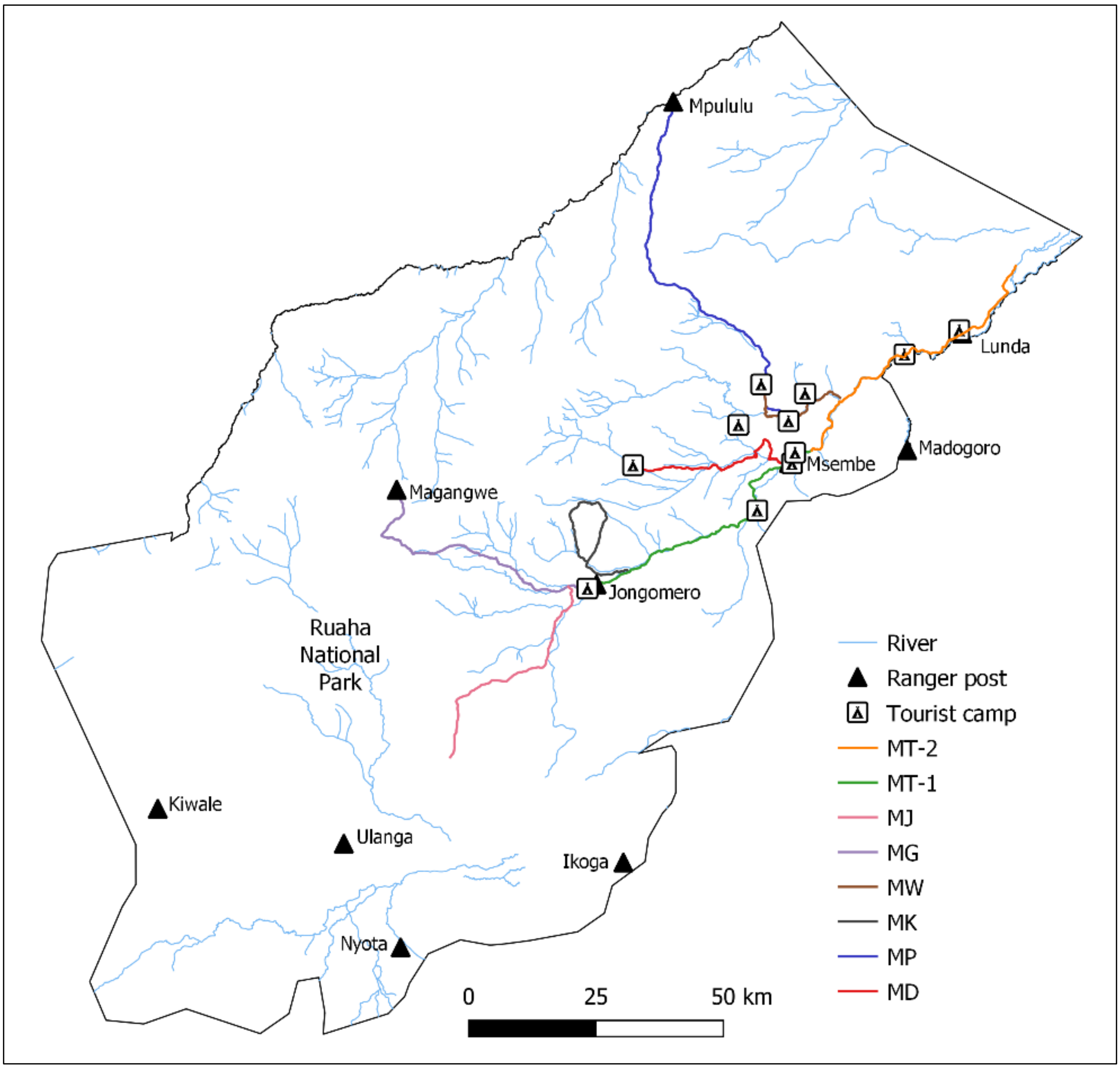

Figure 2.5 Location of vehicle transects in Ruaha National Park. Rivers, tourist camps, and park ranger posts are also shown (see Table 2.5 for transect codes).

Table 2.6 STEP elephant monitoring transects routes, distances, codes, and number of repeats.

Transect code	Route	Number of repeats
MT-2	Great Ruaha River from Msembe to Lunda (82.7 km)	42
MT-1	Great Ruaha River from Jongomero to Msembe (65.7 km)	44
MJ	Jongomero woodland to Ilamba Itali via maji moto (50.3 km)	12
MG	Jongomero ranger post to Magangwe ranger post (62.6 km)	36
MW	Mwagusi river (20.9 km)	42
MK	Nyahulunzi circuit via Makinde springs (44.2 km)	20
MP	Mpululu ranger post to Mwagusi river via Ikuka flats (85.7 km)	41
MD	Mdonya river (45.1 km)	42

2.3.10 Elephant age and sex assessments

In 2009, the Tanzania Wildlife Research Institute conducted ‘rapid demographic assessments’ of six elephant populations in Tanzania to quantify their age and sex structure (Mduma et al., 2010). These assessments followed the methodology developed by Poole (1989b) and used modified age class definitions from Moss (1997). These demographic assessments involved estimating the age and sex of as many different individuals as possible. Age class and sex assignment were based on visual assessment. As elephants grow for extended portions of their lives, shoulder height and back length are reliable indicators of absolute age (Croze, 1972; Laws, 1966; Lee & Moss, 1995; Western, Moss & Georgiadis, 1983). Thus, it is possible to estimate the ages of living elephants using these relative proportions and sizes, which tend to generalise across populations (Shrader et al., 2006). Male head shape also changes with age and can be used for age estimation (Moss, 1997). The age classes used were 0–4.9 years, 5–9.9 years, 10–14.9 years, 15–19.9 years, 20–24.9 years, 25–39.9 years and >40 years. These age classes should be understood as general indicators of an elephant falling within the defined class, rather than an absolute age assignment, as they are subjective assessments rather than measurements. Elephant sex was determined through visual assessment of body shape, head shape, tusk shape, and external genitals (Moss, 1997).

The 2009 TAWIRI survey provided baseline data for the Ruaha-Rungwa elephant population before the poaching upsurge. Assessments were repeated in 2015 (Jones et al., 2018) and in 2021 (led by me and Loyce Majige) to coincide with TAWIRI aerial censuses being conducted in these years and used a similar methodology to enable comparison with the 2009 survey[11]. My field assistants and I were trained in ageing techniques on elephants of known ages in Amboseli National Park, as part of the Amboseli Elephant Research Project’s scheme to assist elephant biologists, while data collectors participating in previous assessments were trained on elephant ageing in Tarangire National Park by the Tarangire Elephant Project (Mduma et al., 2010).

Population age structure was visualized using a bar chart depicting the proportion of the population in each age class. In an undisturbed population, the number of individuals in each age class shows a general downward gradient from left to right, while populations that have experienced high levels of disturbance from poaching often show altered age-and-sex structures characterised by fewer calves (<5 years) and older individuals (Poole, 1989b), as

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[11] The 2009 demographic assessments were conducted by Dr. Trevor Jones, Dr. Charles Foley (Wildlife Conservation Society), Dr. Alex Lobora, Dr. Simon Mduma, and Paul Baran (TAWIRI). The 2015 demographic assessments were conducted by Dr. Trevor Jones, Josephine Smit, and Lameck Mkuburo (STEP), and Dr. Jeremy Cusack and Dr. Rocio Pozo (at the time at the University of Stirling). The 2021 assessment was conducted by Josephine Smit and Loyce Majige (STEP).

older individuals tend to be targeted by poachers for their larger tusks (Chiyo, Obanda & Korir, 2015; Poole, 1989b; Raubenheimer & Miniggio, 2016). The proportion of calves (<5 years) and the proportion of adult elephants aged ≥40 years were therefore compared by year (2009, 2015, and 2021).

As an indicator of recruitment, the mean calf to adult female ratio at the group level was calculated. This is the ratio of elephants aged 0-4.9 years to adult females ≥10 years (Poole, 1989b). The ratio was calculated for each cow-calf group observed, and then a mean was calculated. This parameter is an indicator of recruitment potential at the group level given that the group is the unit at which calf recruitment and survival operates (Jones et al., 2018). In populations disturbed by poaching, the calf to adult female ratio is lower than in undisturbed populations (Poole, 1989b). The ratio of breeding age males (aged ≥25 years) to breeding age females (≥10 years) was also calculated (Poole, 1989b). These age classes represent the breeding proportion of the population, which are important indicators of a growing or declining population. Breeding males are considered to be those entering the reproductive state of musth, which typically occurs when males are between 25 and 30 years old (Poole, 1989a). Breeding age females were defined as ≥10 years following Poole (1989b), as females tend to become reproductively mature between the ages of 10-15 years (Moss, 1983; Smith & Buss, 1973). A higher breeding adult sex ratio indicates a healthy breeding population. The ratio typically declines in populations impacted by illegal killing, because adult males are often selectively killed first (Rodgers & Lobo, 1980; Dobson & Poole, 1998; Mondol, Mailand & Wasser, 2014). A caveat to this interpretation is that there are possible sampling biases, i.e., that areas of high concentrations of cow-calf groups may be sampled more intensively than 'bull areas' (Croze, 1974; Poole, 1982), resulting in underestimates of male numbers.

2.4 Analysis

I used a combination of frequentist and information theoretic approaches to statistical inference. Each analysis is detailed in the relevant chapters. Code for activity patterns analysis, statistical tests, and generalized linear mixed models (Chapters 5 & 6) was written in RStudio 1.4.1106 (RStudio Team, 2021) and RStudio 2022.02.2 (RStudio Team, 2022). Occupancy analyses (Chapter 4) were conducted in R as well as in PRESENCE version 2.13.39 (Hines, 2006). Data and code for Chapters 4, 5, and 6 are available in the university of Stirling DataSTORRE at the link below: https://datastorre.stir.ac.uk/browse?type=author&value=Smit%2C+Josephine.

2.5 Ethical approval and considerations

2.5.1 Approvals and permits

Ethical approval for the study was granted by the University of Stirling's General University Ethics Panel (Approval: GUEP136) and Animal Welfare and Ethical Review Body (Approval: AWERB 617/186/Non-ASPA). Approval for the study was also granted by the Tanzania Wildlife Research Institute, Tanzania Commission for Science and Technology, Tanzania National Parks Authority, and Tanzania Wildlife Management Authority. Vehicle transects and age-and-sex assessments of the Ruaha-Rungwa elephant population (Chapter 3) were conducted under permits 2015-122-ER-2009-229, 2016-315-NA-2009-229, 2017-268-NA-2009-229, 2018-414-NA-2018-184, and 2021-456-NA-2018-184. Occupancy surveys (Chapter 4) were conducted under permits 2017-210-NA-2017-107 and 2018-367-NA-2017-107**.** Camera trap surveys (Chapter 5) were conducted under permits 2018-368-NA-2018-107, 2018-414-NA-2018-184, and 2019-424-NA-2018-184. Camera trapping at water sources (Chapter 6) was conducted under permits 2018-414-NA-2018-184 and 2019-424-NA-2018-184.

2.5.2 Collaborators and fieldwork support

Data collection was done in collaboration with several other researchers (Dr. Charlotte Searle, Dr. Paolo Strampelli) and with support from Tanzanian colleagues (Lameck Mkuburo, Dr. Victor Kakengi, Dr. Edward Kohi, Loyce Majige), field assistants from Southern Tanzania Elephant Program (Kephania Mwaviko, Peter Mtyana, Kelvin Madege, Athumani Mndeme, Edmund Yalimba), camera trap monitors (Ramadhani Mduda, Kinyozi Madinda, Innocent Kisanyage, Leonard Fidelis) and trackers (Stivin Pangamwene and Hamis Dongo, who assisted Dr. Paolo Strampelli). Where data were collected by collaborators, I have personally analysed the elephant data and I have acknowledged collaborator and field assistant contributions in each chapter. Inter-observer reliability assessments of elephant group type, activity type, and body condition scoring were done with assistance from Dr. Trevor Jones (Southern Tanzania Elephant Program), Professor Phyllis Lee, and Suzanne Lawrie (University of Stirling). TANAPA, TAWA, and MBOMIPA WMA rangers or village game scouts accompanied all fieldwork in their respective management areas. Southern Tanzania Elephant Program (STEP) and Lion Landscapes provided logistical support during fieldwork.

2.5.3 Ethical considerations for the study

As observational studies of wild animals can raise ethical issues associated with disturbance (Lane & MacDonald, 2010), I minimized disturbance to elephants by using indirect techniques to gather data on elephant occurrence and behaviour. Data on elephant responses to vehicles from transects conducted by STEP (see 2.3.8) provided information on disturbance that we used as an indicator of perceived risk (Chapter 3, Figure 3.17). These transects and demographic surveys were collected by experienced observers and field assistants from STEP who received training in how to safely approach elephants and how to minimize disturbance to elephants once a startle response had been observed.

Camera traps may inadvertently capture images of people engaging in illegal activities within protected areas. As camera traps were placed for the sole purpose of research, images of people within protected areas were not shared with protected area staff or law enforcement agencies.

When placing camera traps on village lands to collect data on elephant use of village water sources, (Chapter 6), I obtained prior permission from village governments, and village residents were informed of the purpose of the study and the placement of cameras through village meetings. Village governments also advised on the appropriate placement of camera traps and asked that camera traps at some water sources be removed during daytime hours for privacy reasons; this request was complied with. I worked with camera trap monitors based in each village who were compensated for their time and transport costs and who received training in study protocols. Images of people obtained from these cameras were not used for any purposes. No attempts were made to recover camera traps that were presumably lost to theft.

All STEP field assistants were paid employees and had medical and emergency evacuation insurance. STEP field assistants were trained in safety procedures.

2.6 Potential limitations of the study

A key limitation in the study of elephant responses to risk is that direct observation of elephants is challenging in areas of higher risk. Elephants in the high-risk areas of Ruaha-Rungwa are difficult to observe during the daytime hours and are wary of humans (see Chapter 3). This necessitated the use of methods that did not require direct observation to gather information on elephant distribution, active periods, use of water sources, grouping patterns, and behaviour in relation to risk. The methods used assess population or sub-population level responses but do not provide insight into individual variability in these responses. I am thus unable to comment on the degree and importance of individual variability in risk responses. Other work indicates that there may be substantial individual variability among elephants in space use and movement decisions in response to risk (Bastille-Rousseau & Wittemyer, 2019), but that this variability may be less important in temporal responses to risk (Duporge et al., 2022; Ihwagi et al., 2018). Further, the cognitive mechanisms underlying the processes of detection, memory of, and responses to risk cannot be examined by these methods.

As the study began two years after the most recent poaching surge of 2010-2015, elephant behaviour and space use may have reflected reduced risk relative to the period of intense poaching. However, as demonstrated in Chapter 3 and discussed in Chapter 7, low-level poaching continued to occur during the study period and the elephant population showed no signs of rapid rates of reproduction which have been observed after severe poaching events in other sites (e.g., Foley & Faust, 2010).

Although the study was designed as a controlled comparison between areas of high and low risk, other variables such as food and water availability and distribution were not constant between sites. With the caveat that habitat type is a crude measure of food availability/quality, I was able to control for habitat type for one of the risk comparisons in Chapter 5, as both the low-risk RNP:LR grid and the high-risk MBO:HR2 grid were in *Vachellia-Commiphora* habitat. Furthermore, in both sites, the primary perennial water source was the Great Ruaha River and its seasonal tributaries. As discussed more in Chapter 5, there is unfortunately no low risk miombo site for comparison. In Chapter 6, I was able to control for habitat type, as the low- and high-risk water sources were all within the *Vachellia-Commiphora* zone of the ecosystem. Some insight into the potential effect of food and water availability on elephant risk responses could be obtained through comparisons of the frequency of elephant water use, timing of water access, and grouping patterns at low and high-risk water sources between the wet and the dry season (see Chapter 6).

Occupancy analyses (Chapter 4) provide insight into how the probability of use is associated with risk and environmental factors, not how risk influences use intensity or selection. The extent to which risk influenced use intensity, resource selection, and other movement properties (e.g., speed and directionality) of elephants were therefore not investigated in this thesis, but these may be important behavioural strategies that elephants use to mitigate risk in space (Bastille-Rousseau & Wittemyer, 2021; Ihwagi et al., 2018; Ihwagi et al., 2019). Although elephant space use is known to be sexually segregated (Shannon et al., 2008; Stokke & Du Toit, 2002), sex differences in space use could not be explored as elephant occurrence records collected during track-based occupancy surveys did not differentiate between footprints of male and female groups.

Possible seasonal differences in space use (Chapter 4) and diel activity (Chapter 5) were not investigated; as such, our findings on the influence of risk on elephant space use and activity patterns are limited to the dry season, a period of relative resource scarcity. Seasonal differences were however investigated in the context of water source use (Chapter 5).

In comparisons of elephant group types between areas of low and high risk, I assumed that groups reflect choices to associate based on a variety of push and pull factors; however, it may be that co-occurrence represents simple propinquity rather than sociability/social attraction (Ward & Webster, 2016). Group types were assessed from camera trap images. As camera traps have a defined field of view, elephants not moving through the field of view may go undetected. Camera traps may therefore underestimate the degree of sociality relative to direct observation. However, as camera placement was consistent between low and high-risk sites, I expect that any under-detection bias was consistent across sites and that comparisons of group composition and group size between sites are valid. Furthermore, in the context of water access (Chapter 6), elephants often use well-defined pathways and travel in close spatial proximity to each other, making it less likely that individuals were missed (Allen et al., 2020).

Chapter 3

Anthropogenic activities and risks to elephants in the Ruaha-Rungwa ecosystem

***Photo 5**: Large aggregation of elephants seen in the Lunda area of Ruaha National Park in February 2015. Over 100 elephants, including males and family groups, were estimated to be in this aggregation (note that this photo captured only a portion of the aggregation).*

Chapter 3. Anthropogenic activities and risks to elephants in the Ruaha-Rungwa ecosystem

Author contributions

I conceived the structure of this chapter and led the collation of the data presented. I led data collection on elephant age-and-sex structure (in 2015 and 2021) and elephant behavioural responses to a research vehicle (2015-2018). Assistance with data collection was provided by Lameck Mkuburo (Tanzania Elephant Foundation), Loyce Majige, Kephania Mwaviko, Athumani Mndeme, Peter Mtyana, Kelvin Madege, Edmund Yalimba (all from Southern Tanzania Elephant Program). Elephant carcass occurrence models were provided by Dr. Colin Beale (University of York). Models of illegal human use were provided by Dr. Paolo Strampelli (University of Oxford). I present maps and novel summaries of data from Tanzania Wildlife Research Institute aerial census reports and findings from previous studies on elephant demography and behaviour in Ruaha-Rungwa. I conducted all analyses and wrote the chapter. Professors Phyllis Lee and Hannah Buchanan-Smith (University of Stirling) provided guidance on analyses and drafts of this chapter.

3.1 Abstract

This chapter establishes the current context and history of anthropogenic risks to elephants in the Ruaha-Rungwa ecosystem, an area where humans and elephants have likely interacted for millennia. Humans pose both a mortality risk and a disturbance risk to elephants. The most important mortality risk is poaching for ivory. Elephants in the Ruaha-Rungwa ecosystem experienced major poaching disruption in 1978-1987 and again in 2010-2015. Thus, over the potential lifespan of an individual elephant (70+ years), they would have experienced successive waves of poaching, with social, behavioural, and reproductive consequences. Human use of the ecosystem, which may pose a disturbance risk (as well as a mortality risk) to elephants, has increased substantially over the past 30 years. I show that anthropogenic risks are spatially structured - with disturbance risk generally being greater outside of and near the edges of protected areas, and mortality risk being higher in the game reserves and other less strictly protected areas as well as in the more remote areas of Ruaha National Park - enabling comparisons of elephant behaviour between areas of lower and higher risk.

3.2 Introduction

This chapter aims to contextualise human-mediated risks to elephants in the Ruaha-Rungwa ecosystem. I define human-mediated risks as the risk of mortality and disturbance from humans, as humans in the Ruaha-Rungwa ecosystem pose both lethal and non-lethal risks to elephants. As both current and past interactions with humans may shape the elephant risk responses investigated in this study, I provide historical context on human-driven elephant mortality and anthropogenic change in the ecosystem and summarize how human-mediated risks were spatially distributed during the study period, thereby generating a landscape of risk which enables comparisons of elephant behaviour in areas of low- and high-risk in subsequent chapters.

I begin with a brief overview of human use of the Ruaha-Rungwa ecosystem and elephant hunting prior to the 1970s, before the commencement of systematic aerial surveys that provide data on elephant population trends for the past 50 years. I then present evidence that the Ruaha-Rungwa elephant population has experienced two poaching surges in the past 50 years using data from aerial surveys and the Monitoring the Illegal Killing of Elephants (MIKE) program, and then summarize what is known about the demographic and behavioural impacts of poaching on this population. I present maps of elephant carcass occurrence probability developed by Beale et al. (2018) from aerial survey data as an indicator of spatial variation in elephant mortality risk to humans during the period relevant to this study.

I then provide an overview of human use of the ecosystem, both within and outside of protected areas, and how this has changed over the past 30 years. As data on elephant mortality in the ecosystem are largely limited to protected areas, outside protected areas, I use features of the human footprint, including settlements, human population density, agriculture, and livestock as a proxy for human disturbance risk and mortality risk (because elephants may be killed for their impacts on human property and crops) for elephants. The risk of human disturbance within protected areas during the study period is described using maps of the spatial occurrence of illegal human activity within protected areas from aerial surveys (TAWIRI, 2016, 2019) and an existing model of illegal human use developed by Strampelli et al. (2022b).

3.3 Human-driven mortality of elephants in the Ruaha-Rungwa ecosystem

3.3.1 Elephant hunting prior to 1970

In pre-colonial and colonial times, small human settlements existed in present-day Ruaha National Park and MBOMIPA WMA, many of them located along rivers (Williams, 2005). Indeed, humans have formed part of the ecosystem for at least 45,000 years (Willoughby et al., 2018). While the scale of elephant hunting in prehistory remains unclear, available evidence suggests that this may have been localized and relatively small-scale (Lupo & Schmitt, 2023). The scale and frequency of elephant hunting in East Africa increased in the eighteenth and nineteenth centuries (especially in the period 1840-1890) with the introduction of firearms and the ivory and slave trade (Beachey, 1967; Spinage, 1973). In the 1800s, present-day Ruaha-Rungwa was used by slave and ivory traders, both for the extraction of ivory and humans and as a major trade route to the coast (Beachey, 1967; Håkansson, 2004).

Ivory trade decreased in the 1890s after colonial administrations brought in ‘game laws’, regulated elephant hunting, and gazetted the first game reserves (Beachey, 1967; Spinage, 1973). Beginning in the 1920s, colonial administrations in Tanzania brought in ‘elephant control’ programs involving routine shooting of elephants to ‘manage’ elephant impacts on agriculture and to generate revenue for the government game department through ivory sales (Rodgers & Lobo, 1980). Although little is known about elephant populations during colonial times, Savidge (1968) reported that before 1945, there was “much elephant hunting” in the area. As a result of the colonial gazettement of protected areas, protection from tsetse fly and sleeping sickness, and resettlement programs under colonial policies and Tanzania’s post-independence villagization scheme, human settlements were moved out of Ruaha National Park and Rungwa Game Reserve in the 1950s, 1960s, and 1970s (Kjekshus, 1977; Savidge, 1968; Williams, 1999, 2005).

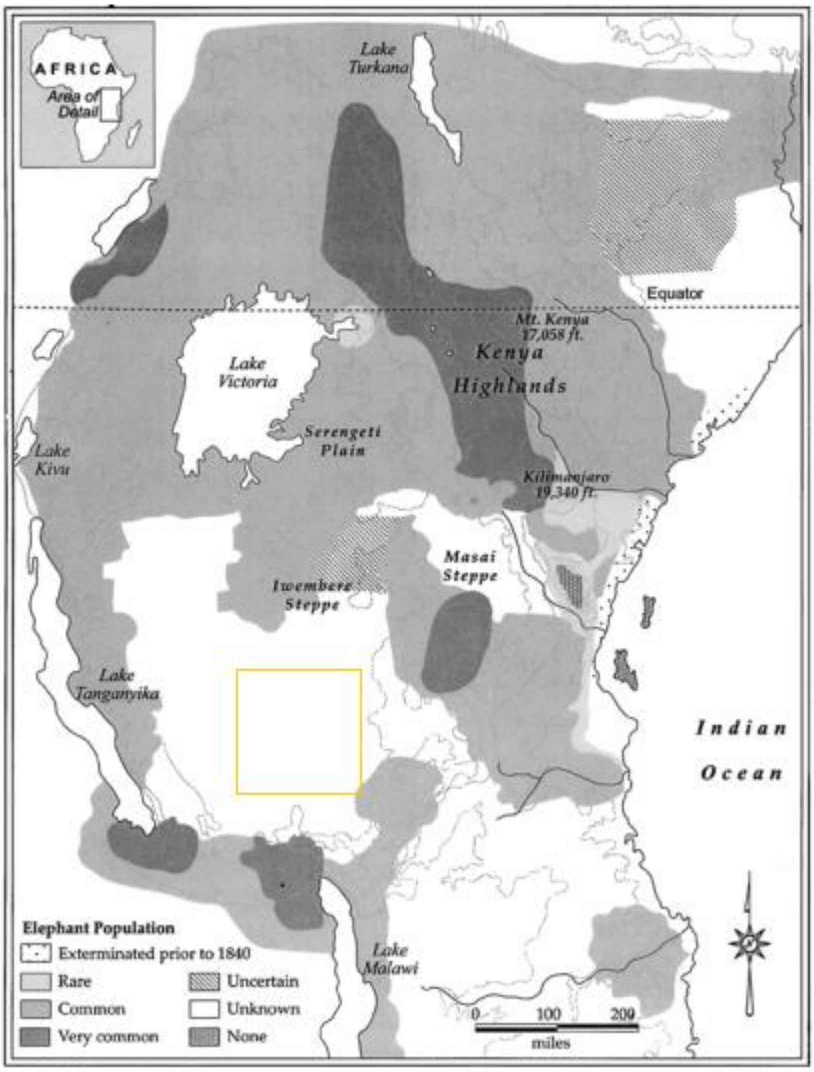

Figure 3.1 Map of elephant distributions circa 1840 early in the period of ivory and slave trade in East Africa, with approximate location of the present-day Ruaha-Rungwa ecosystem denoted by a yellow square. Reproduced from Håkansson (2004), who based this map on 19th century sources and oral histories.

3.3.2 Elephant poaching for ivory since 1970

Between 1965 and 1977, the elephant population in Ruaha National Park was thought to be increasing due to ten years of higher-than-average rainfall and in-migration to the relative safety of the park by elephants from unprotected areas experiencing low-level offtake (Barnes & Kapela, 1991; Savidge, 1968). The elephant densities estimated from this period are the highest ever recorded for the ecosystem (Table 3.1).

A first elephant poaching[12] surge inside the protected areas occurred between 1978 and 1987, resulting in a population decline of 70% (Figure 3.2). Poaching was initially more severe within Ruaha National Park, which had higher carcass ratios than the adjacent game reserves in 1983 (Figure 3.3). Between 1977 and 1983, the elephant population in Ruaha National Park declined by more than 60% (Barnes & Kapela, 1991), although it is possible that some elephants moved into Rungwa and Kizigo Game Reserves, where the elephant population estimate was stable between 1977 and 1983 (Borner & Severre, 1984). The game reserves were not spared, however, as aerial surveys in Rungwa and Kizigo Game Reserves indicate a >50% population decline between 1983 and 1987. The severity of poaching in this period is also evidenced by carcass ratios (the proportion of dead elephants to the sum of live and dead elephants, expressed as a percentage) and elephant carcass densities from aerial surveys (Figures 3.3-3.4). A carcass ratio >8% is considered indicative of a declining population, while a carcass ratio ≤8% is typical of a stable or increasing population (Douglas-Hamilton & Burrill, 1991); carcass ratios were more than double this in 1983-1987. Elevated carcass densities are also evident for the years with intense poaching (Figure 3.4).

With the imposition of a ban on the international ivory trade in 1989, the Convention of Trade in Endangered Species (CITES) established elephant and ivory monitoring programs called ETIS (Elephant Trade Information System) and MIKE (Monitoring the Illegal Killing of Elephants) across 70 sites in 32 African countries. Ruaha-Rungwa became one of these specific MIKE sites in 2003, allowing for an assessment of long-term trends in poaching. Following increased anti-poaching efforts under the Tanzanian government's Operation *Uhai* and the international ban on trade in ivory coming into effect in 1990, poaching decreased and the elephant population in Ruaha-Rungwa began to recover (Barnes & Kapela, 1991; TWCM, 2002). The elephant population apparently increased from around 12,000 individuals in 1990 to around 35,000 individuals in 2009, an annual sustained rate of increase of 6% (Table 3.1). Although carcass densities were not reported for the aerial surveys in this period, carcass ratios in 1993 and 2009 were less than 1%. Nevertheless, even by 2009, elephant densities had not recovered to those seen before the poaching crisis of 1978-1987.

Ruaha-Rungwa experienced a second poaching surge in 2010-2015, resulting in a >50% decline in the elephant population. The genetic assignment of large ivory seizures to Ruaha-Rungwa suggested that poaching rates increased later than in the nearby Selous-Niassa ecosystem, where the increase in poaching began around 2006 (Wasser et al., 2015). In 2010-

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[12] I use the term poaching to describe the illegal killing of elephants, i.e., the killing of elephants without a government-issued license and not for government-sanctioned 'elephant control'. Licensed hunting of elephants and killing of elephants under 'elephant control' policies continued post-1970.

2015, there was a spike in the observed proportion of illegally killed elephants (PIKE) and an increase in elephant carcass ratios and carcass densities estimated from aerial surveys (Figures 3.3-3.6). Observed PIKE is an index of poaching pressure that is calculated as the number of illegally killed elephants divided by the total number of elephant carcasses per site and year (Schwarz, 2020). An observed PIKE value of 0.5 is considered to represent unsustainable levels of illegal killing (CITES, 2014), and PIKE was above 0.5 between 2010 and 2015. In the aerial surveys of 2013, 2014, and 2015, carcass ratios ranged between 15% and 19% (Figure 3.4). PIKE, carcass ratios, and carcass densities declined after 2015, indicating that the intensity of elephant poaching fell post-2015 (Figures 3.2 to 3.8). Elephant poaching did not cease entirely, however. PIKE levels, carcass ratios, and patrol records from MBOMIPA WMA (Appendix A3.2) indicate that some elephant poaching continued to occur after 2015, albeit at much lower levels. In the 2018 aerial census, the carcass ratio was 12% (TAWIRI, 2019). The carcass ratio did not drop below 8% until the 2021 aerial census (TAWIRI, 2022). Spatial analyses of elephant carcass locations from aerial census data conducted by Beale et al. (2018) indicate that in the period 2013-2015, elephant carcass densities were highest in the game reserves, in western Ruaha National Park and in MBOMIPA Wildlife Management Area (Figure 2.7). Beale et al. (2018) found that elephant carcasses were more likely to be encountered near water sources and in areas of intermediate travel costs from villages. Across the extent of the whole ecosystem, Beale et al. (2018) found no correlation between carcass density and distance to ranger posts. However, when carcass densities were analysed by separate zones patrolled by each ranger post, the relationship between distance to ranger post and carcass density differed with post identity. While most ranger posts had no effect on carcass densities, some ranger posts were associated with higher carcass densities, and others had a strong negative effect on carcass densities, including the park headquarters at Msembe (Beale et al., 2018).

Table 3.1 Elephant population and density estimates (with standard errors or 95% confidence intervals shown) and survey extent for the Ruaha-Rungwa ecosystem from dry season aerial surveys conducted between 1968 and 2021. Carcass ratios are also shown. Aerial counts were conducted for the Greater Msembe Area (414 km^2) of Ruaha National Park in the dry season of 1965-1966 by Savidge (1968). Aerial surveys of Ruaha National Park were conducted in 1972 by Norton-Griffiths (1975). Aerial surveys of Ruaha National Park, Rungwa and Kizigo Game Reserves, and Lunda-Nkwambi Game Controlled Area were conducted in 1977 by Barnes & Douglas-Hamilton (1982) and in 1983 by Borner & Severre (1984). Dry season aerial surveys of the Ruaha-Rungwa ecosystem were conducted by the Tanzania Wildlife Conservation Monitoring (TWCM) project in 1987,1990, and 1993, and by the Tanzania Wildlife Research Institute (TAWIRI) in 2002, 2006, 2009, 2013, 2014, 2015, 2018, and 2021. Elephant population estimates for the 2014 aerial census were not considered representative (a public census report was never published) and were likely an undercount, and are therefore not presented below (TAWIRI, 2015). Where discrepancies existed between population estimates and survey extents, I present the figures from the published survey report or the African Elephant Database and have indicated in footnotes figures seen in other reports. Utengule swamp was originally a hunting block that was gazetted as Usangu Game Reserve in 1998. Usangu Game Reserve was annexed to Ruaha National Park in 2008, doubling the size of the park to 20,226 km^2. Although Lunda-Nkwambi Game Controlled Areas was not gazetted until 1985, the 1977 and 1983 aerial surveys included this area as it had been proposed for gazettement (originally under the name Mloa-Ilambi Game Controlled Area) and I use the present-day name of the area in this table.

Year	Elephant population estimate (standard error or 95% confidence interval)	Survey extent (km^2)	Areas surveyed	Density (elephants per km^2)	Carcass ratio (%)	References
1968[1]	451 (10,889 if extrapolated to entire Ruaha NP)	414	Greater Msembe Area of Ruaha NP	1.53	-	Savidge, 1968; Barnes & Douglas-Hamilton,1982
1972	15,966 (SE ±1,172)	10,000	Ruaha NP	1.60	-	Norton-Griffiths, 1975
1977	43,685 (95% CI ±9,254)	31,500	Ruaha NP, Rungwa & Kizigo GRs, Lunda-Nkwambi CGA	1.39	5.5 in NP, 9.7 in GRs, 9.5 in GCA	Barnes & Douglas-Hamilton,1982
1983	34,725 (SE ±6,659)	Estimated as 31,500[2]	Ruaha NP, Rungwa & Kizigo GR, Lunda-Nkwambi GCA	1.10	16 (higher in NP than in GR)	Borner & Severre, 1984
1987	12,698 (SE ±1,756)	27,765	Ruaha NP, Rungwa & Kizigo GR, Lunda-Nkwambi CGA	0.46	41 (higher in NP than in GR)	TWCM, 1990
1990[3]	12,420 (SE ±2,737)	26,895	Ruaha NP, Rungwa & Kizigo GR, Lunda-Nkwambi CGA	0.46	19.5	TWCM, 1991

Year	Elephant population estimate (standard error or 95% confidence interval)	Survey extent (km²)	Areas surveyed	Density (elephants per km²)	Carcass ratio (%)	References
1993[4]	18,864 (SE ±1,826)	41,297	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Utengule swamp, Itigi thickets	0.46	1	TWCM, 1994
2002[5]	24,103 (SE not available)	43,391	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Usangu Game Reserve, Itigi thickets	0.56	-	AED, 2002
2006[6]	35,409 (SE ±5,871)	45,800	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA	0.77	-	AED, 2007; TAWIRI, 2007
2009[7]	34,664 (SE ±4,178)	43,641	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA	0.79	0.1	TAWIRI, 2010
2013	20,090 (SE ±3,282)	50,889	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA	0.39	14.6	TAWIRI, 2014
2015	15,836 (SE ±4,759)	52,464	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA	0.30	16.6	TAWIRI, 2016
2018	15,521 (SE ±2,439)	52,637	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA, Out West of GRs	0.29	10.9	TAWIRI, 2019
2021	15,608 (SE ±1,897)	57,809	Ruaha NP, Rungwa, Kizigo & Muhesi GRs, Itigi thickets, Lunda-Nkwambi CGA, Out West of GRs, Wembere GR	0.27	1.4	TAWIRI, 2022

1. Elephant population estimate for the Greater Msembe area of Ruaha NP is the average of several counts conducted over several dry season months in 1965 and 1966. The density is the mean of dry season elephant densities from several months in 1965 and 1966.

2. The exact survey area is not stated in Borner & Severe (1984). As Borner & Severe (1984) based their methodology “as close as possible” on the methodology of Barnes & Douglas-Hamilton (1982), the same survey area was assumed.
3. 1990 estimate is 11,712 (SE ±5,481) and survey extent is 26,763 km^2 in TAWIRI (2013).
4. 1993 estimate is 19,284 (SE ±3,150) and survey extent is 41,297 km^2 in TAWIRI (2013).
5. 2002 estimate is 24,685 (SE ±3,314) and survey extent is 36,071 km^2 in TAWIRI (2003), but 24,993 (SE ±3,027) and 36,063 km^2 in TAWIRI (2013).
6. 2006 estimate is 35,461 (SE ±3,563) and survey extent is 43,601 km^2 in TAWIRI (2013).
7. 2009 estimate is 31,625 (SE ±2,890) and survey extent is 43,641 km^2 in TAWIRI (2013).

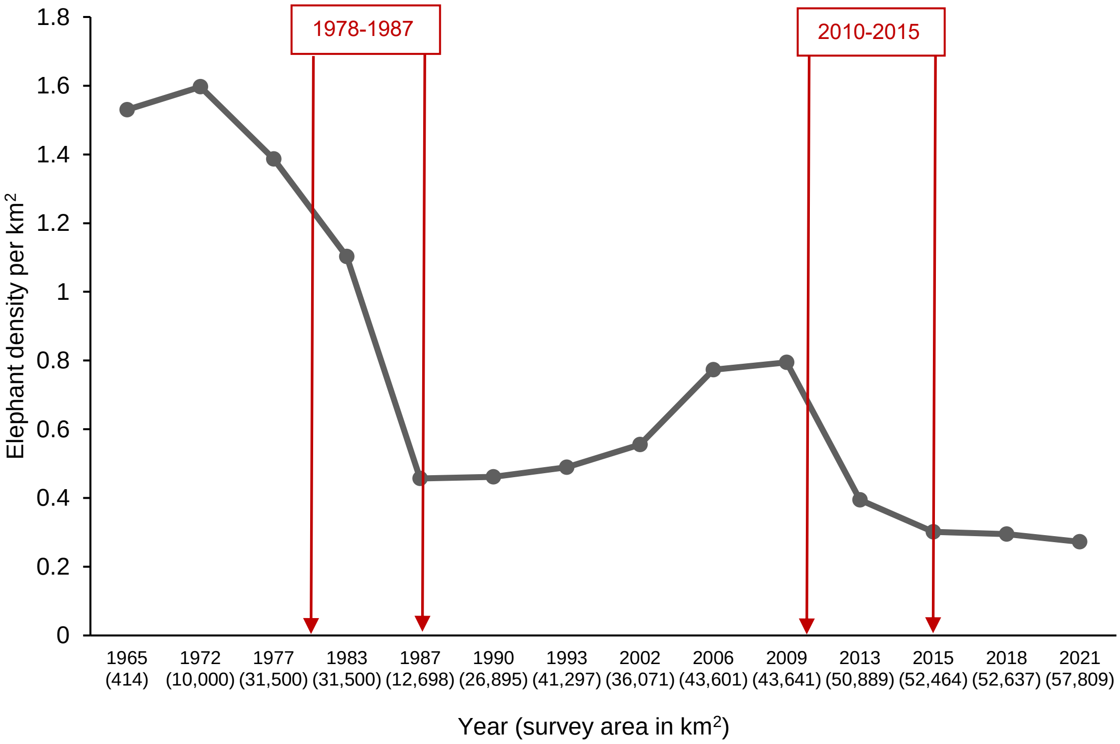

Figure 3.2 Elephant density (the estimated population size from aerial surveys divided by the survey extent) for the Ruaha-Rungwa ecosystem from aerial surveys conducted between 1965 and 2021. Two poaching crises (delineated by red arrows) occurred since the 1960s: one in 1978-1987, when the Ruaha-Rungwa elephant population declined by 70%, and a second in 2010-2015, when the elephant population declined by >50%.

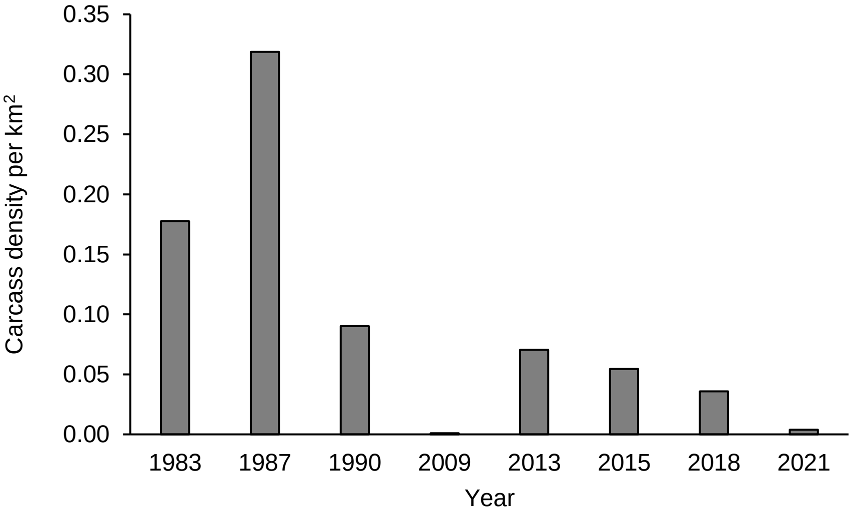

Figure 3.3 Elephant carcass densities (the estimated number of elephant carcasses from aerial surveys divided by the survey area) for the Ruaha-Rungwa ecosystem from aerial surveys conducted between 1983 and 2021. Carcass estimates were not reported for the 1993, 2002, and 2006 aerial surveys.

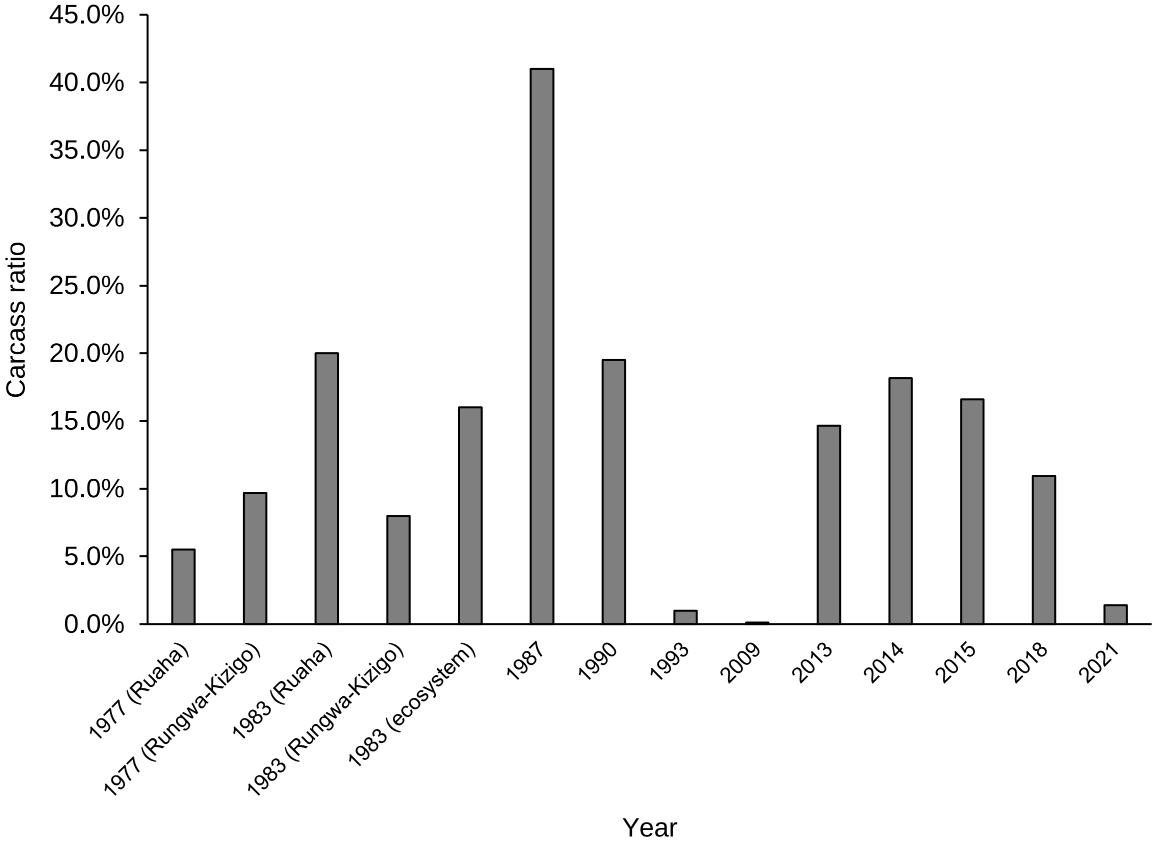

Figure 3.4 Elephant carcass ratios (the proportion of dead elephants to the sum of live and dead elephants, expressed as a percentage) for the Ruaha-Rungwa ecosystem from aerial surveys conducted between 1977 and 2021. Carcass ratios were not reported for the 2002 and 2006 TAWIRI aerial surveys.

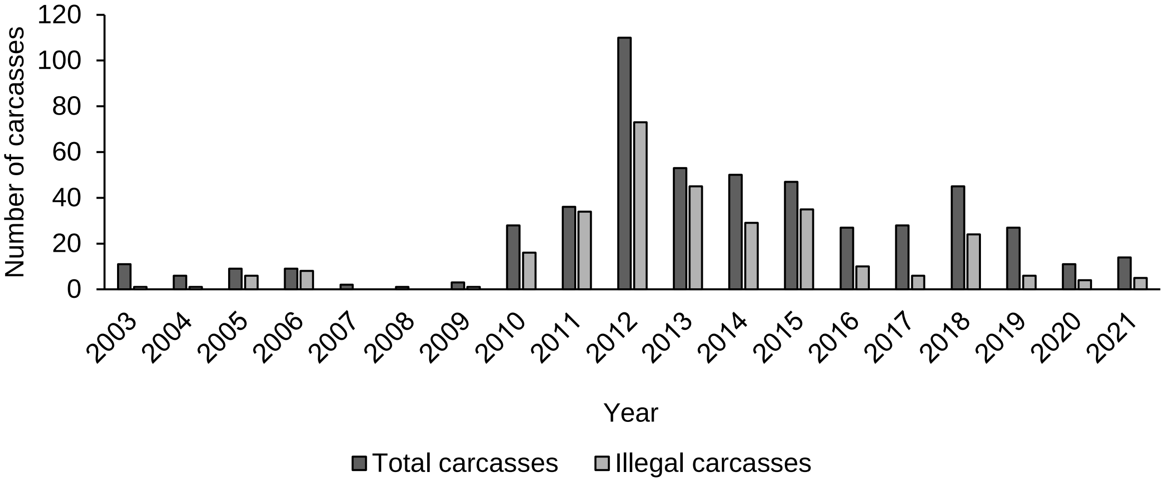

Figure 3.5 The total number of elephant carcasses (dark grey) and illegally killed elephant carcasses (light grey) reported from the Ruaha-Rungwa ecosystem via the Monitoring of Illegally Killed Elephants (MIKE) program between 2003 and 2021. The total number of elephant carcasses includes illegally killed elephants and carcasses due to other sources of mortality, such as drought or disease. No disease or severe drought events are known to have occurred in Ruaha-Rungwa from 2003-2021.

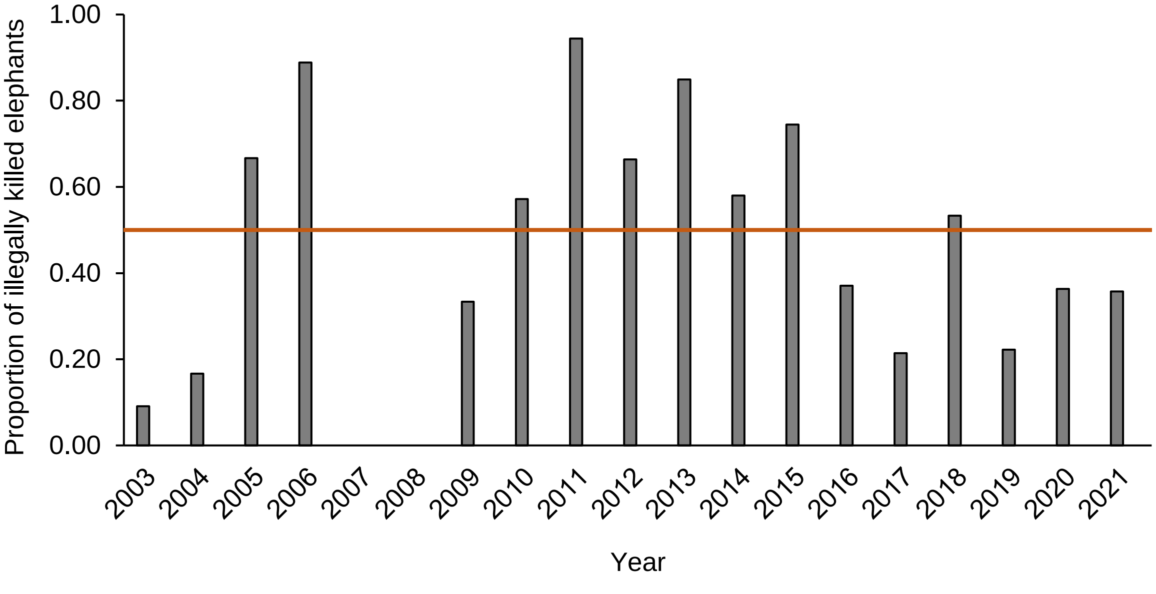

Figure 3.6 The observed proportion of illegally killed elephants (PIKE) for the Ruaha-Rungwa ecosystem for the period 2003 to 2021. Observed PIKE is calculated as the number of illegally killed elephants divided by the total number of elephant carcasses per site and year (Schwarz, 2020). An observed PIKE value of 0.5 (red line) is considered to represent unsustainable levels of illegal killing (CITES, 2014). The total number of carcasses is shown in Figure 3.5 above.

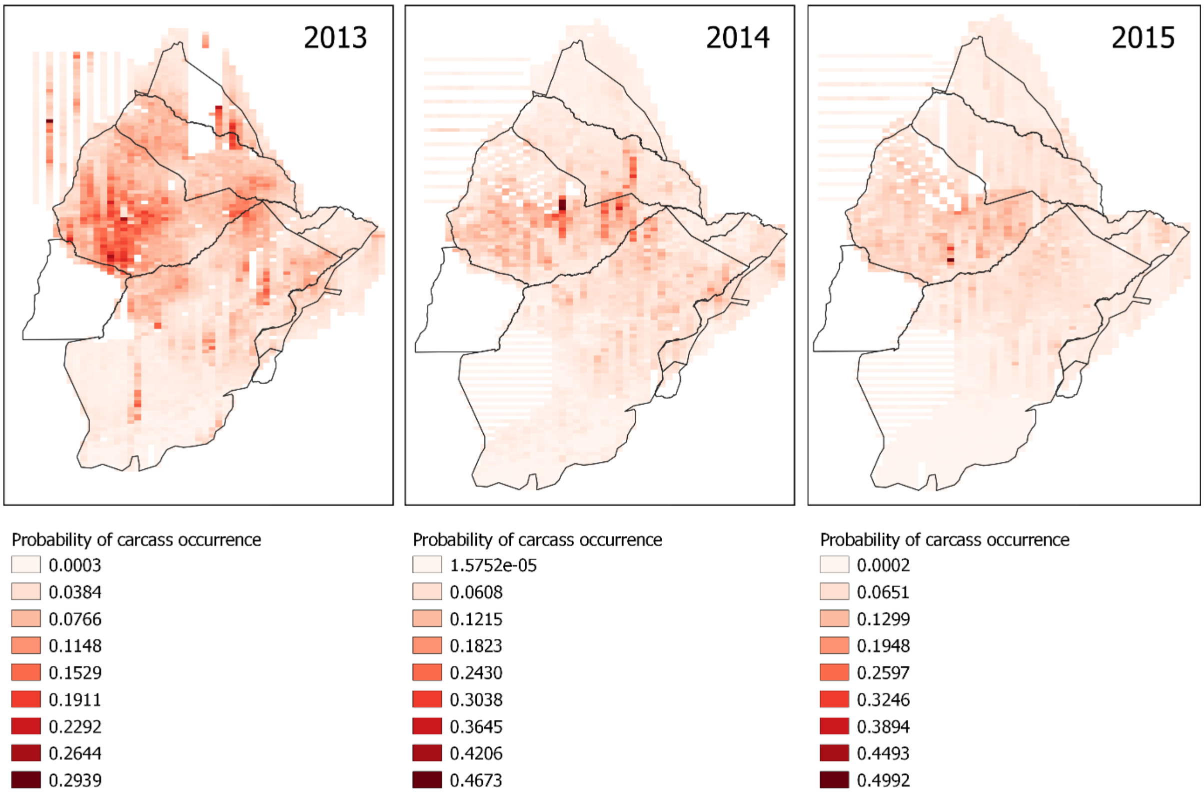

Figure 3.7 Probability of elephant carcass occurrence (at a resolution of 12.5 km^2) in the Ruaha-Rungwa ecosystem from Beale et al. (2018), derived from TAWIRI aerial surveys conducted in 2013, 2014, and 2018. Areas with darker shades of red have a higher probability of carcass occurrence. White areas have no value.

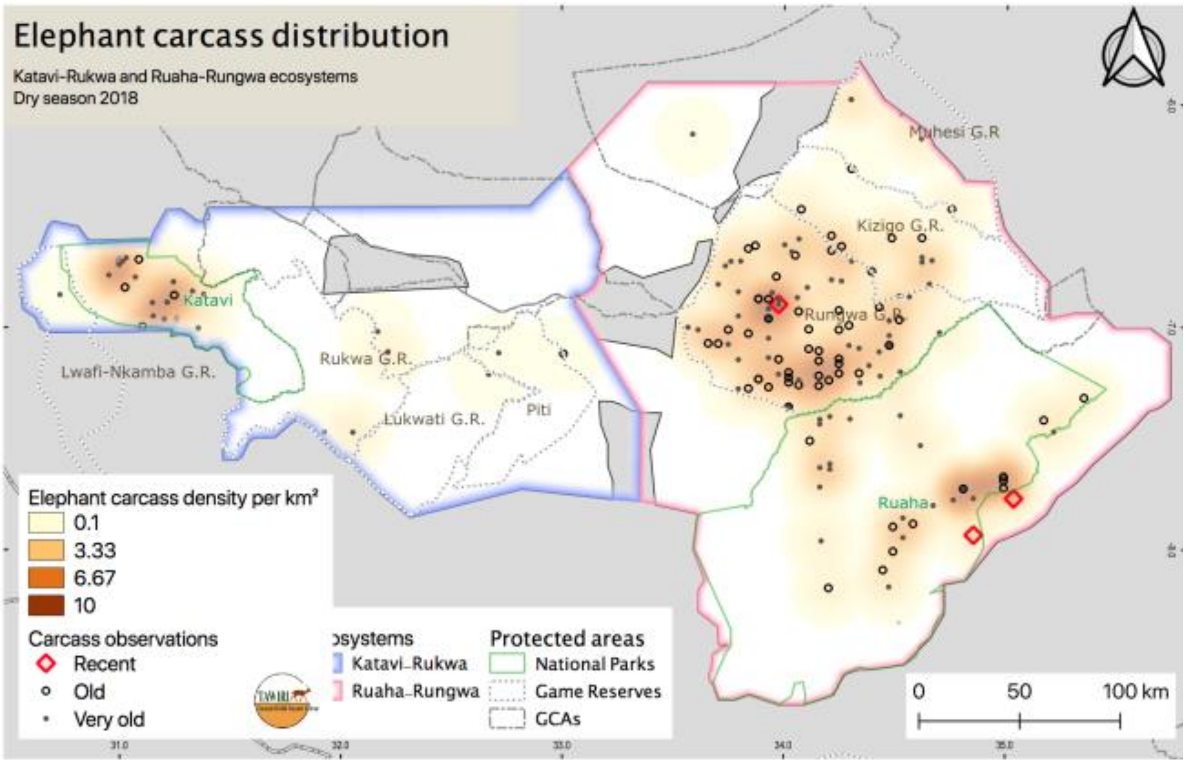

Figure 3.8 Distribution and density of elephant carcasses in the Ruaha-Rungwa ecosystem (right) and Katavi-Rukwa ecosystem (left) from the TAWIRI aerial census for the dry season of 2018. Carcass classes were defined as follows: recent: <1 year, old: > 1 year, very old: up to 10 years. Reproduced from TAWIRI (2019).

3.4 Demographic impacts of poaching

As has been documented for other elephant populations with a history of poaching (Abe, 1994; Foley, 2002; Gobush et al., 2008; Parker et al., 2021), poaching has affected the demography of the Ruaha-Rungwa population. Barnes & Kapela (1991) documented changes to the age distribution of the Ruaha elephant population following the first poaching surge in 1978-1987 by analysing the weight of tusks recovered by rangers in Ruaha National Park. The weight distribution of recovered ivory was significantly different in the pre-poaching (1973-1977) and poaching (1984-1988) periods, suggesting a shift in the age structure of the population, specifically a reduction in the number of males aged >16 years and females aged >35 years (Figure 3.9). Based on hind footprint measurements, Barnes & Kapela (1991) observed that there were also few individuals aged 2-9 years (born 1987-1980) in 1989, suggesting low recruitment during the poaching and first post-poaching years (Figure 3.10). Hind footprint surveys were repeated in 1992, which indicated improved infant survival relative to the poaching and early post-poaching years (Figure 3.10; Barnes, Barnes & Magombi, 1992).

In surveys conducted in the Msembe area of Ruaha National Park in 1992, of a sample of 299 elephants, Barnes et al. (1992) estimated the proportion of infants (<1 year) as 6%. No old adult bulls were observed. Young adult bulls comprised only 2.7% of the sample. The ratio of immature elephants to adult female elephants was 0.49 in 1992, relative to 1.4 in the mid-1970s[13]. Barnes et al. (1992) also noticed an increase in tuskless and one-tusked elephants relative to the 1970s, although they were unable to quantify change in the prevalence of tusklessness. Of a sample of 71 sub-adult and adult elephants observed in 1992, 18% were tuskless and 4% had one tusk. Although Barnes et al. (1992) did not provide the sex composition of their sample, the sample was likely skewed towards females. Balozi (1993) estimated the proportion of infants (<1 year) in the Msembe area in 1993 as 11.4%, and the proportion of 1–3-year-olds as 8.4% (Figure 3.11). The ratio of immatures (≤12 years) to adult females (>12 years) was 1.10 and adult males to adult females was 0.22 in 1993 (Balozi, 1993).

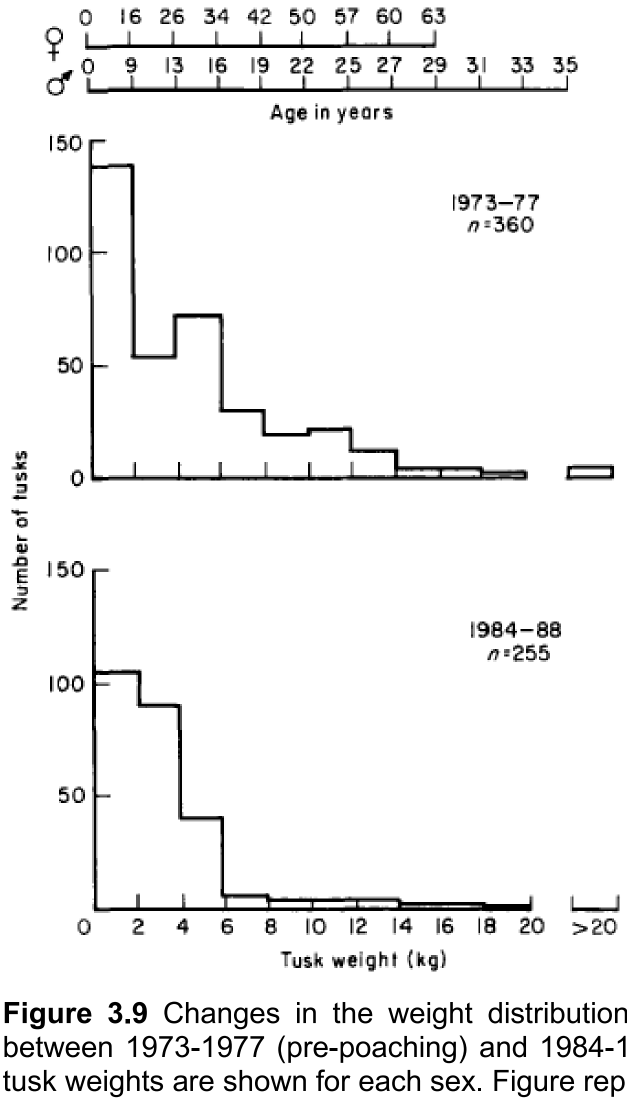

Figure 3.9 Changes in the weight distribution of ivory recovered by Ruaha NP rangers between 1973-1977 (pre-poaching) and 1984-1988 (poaching). The ages corresponding to tusk weights are shown for each sex. Figure reproduced from Barnes & Kapela (1991).

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[13] The Barnes et al. (1992) paper does not indicate how ‘immature’ and ‘adult’ were defined, but as age criteria were based on Laws (1966), immatures likely included elephants aged ≤12 years and adults were defined as >12 years).

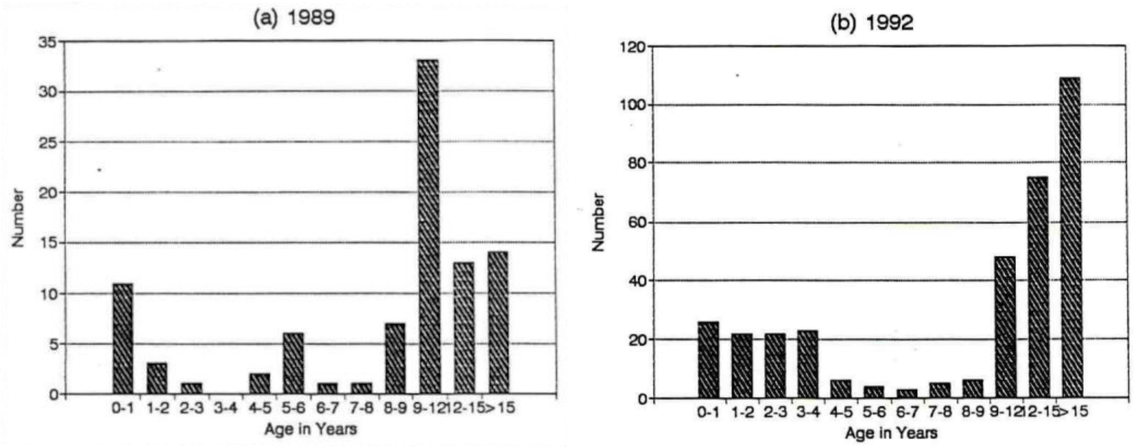

Figure 3.10 Age distribution of elephants in Ruaha National Park based on hind footprint measurements in a) 1989 (n=92) and b) 1992 (n=349). In 1989, all samples were from Msembe. In 1992, the sample included measurements from Msembe, Mpululu, and Lunda. Figures reproduced from Barnes et al. (1992).

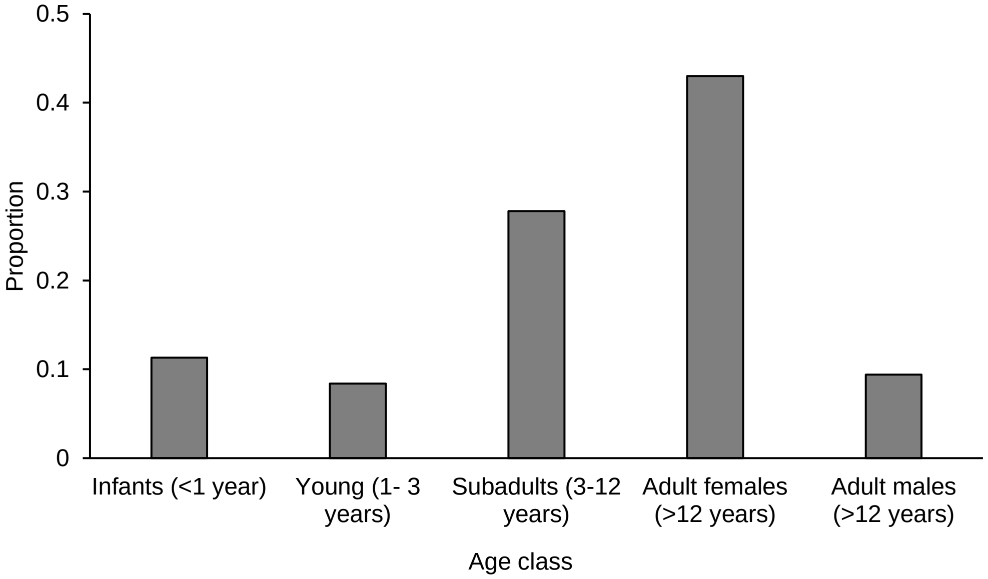

Figure 3.11 Age distribution of elephants in Ruaha National Park in 1993 based on visual assessment of ages (n=796 individuals). Data from Balozi (1993), obtained from TWCM (1994).

Demographic impacts were also assessed during the second poaching surge (See Chapter 2, Section 2.3.5 for methods for ageing). Age and sex assessments of the elephant population in the Greater Msembe Area of Ruaha National Park were conducted in 2009 before the poaching surge (Mduma et al., 2010), in 2015 near the end of the poaching surge (Jones et al., 2018), and in 2021, when the level of poaching had declined. It should be noted that the Greater Msembe Area (the area between the Mdonya, Mwagusi and Great Ruaha Rivers) represents the best-protected part of the ecosystem (Beale et al., 2018) and that assessments conducted in this area may underestimate the impacts of poaching in the less-protected areas of the ecosystem.

Between 2009 and 2015, there was a decrease in the proportion of calves (0-4.9 years of age) and a loss of individuals in older age classes, with lower proportions of adult females aged ≥25 years and males aged ≥40 years (Figure 3.12; Jones et al., 2018). As in the first poaching surge, the 2010-2015 poaching surge affected both ends of the age distribution (Barnes & Kapela, 1991; Jones et al., 2018). In 2015, 7.5% of individuals aged >5 years were tuskless (Jones et al., 2018). Between 2015 and 2021, in the years after the poaching period, there was an increase in the proportion of individuals in the ≥40 years age class, suggesting improved adult survival. However, in 2021, the Ruaha population still had a lower proportion of adults ≥40 years (2.6%) than observed for better-protected elephant populations in Tanzania (e.g., 5.2% in Tarangire and Serengeti: Jones et al., 2018) or elsewhere (e.g., 5.8% in Amboseli, Kenya, AERP long-term data). Between 2015 and 2021 there was a slight decrease in the breeding adult sex ratio (the ratio of males aged ≥25 years to females aged ≥10 years; Figure 3.14)[14]; however, this indicator is sensitive to sampling bias resulting from potential under-sampling of bull areas. Breeding age males (≥25 years) constituted a similar proportion of the population in 2015 (3.8%) and 2021 (3.3%).

While increases were observed in the 5-9.9 and 10-14.9-years age classes, there was no noticeable change in the proportion of individuals in the 0-4.9 years age class between 2015 and 2021 (Figure 3.12). The proportion of individuals in the 0-4.9 years age class in 2021 (29%) remained lower than in 2009 (36%) and is below what has been observed for undisturbed populations (e.g., 40% in Tarangire and Serengeti, Jones et al., 2018). The mean calf (0-4.9 years) to adult female (≥10 years) ratio at the group level decreased between 2015 and 2021 and remained lower in 2021 than in 2009 (Figure 3.13). These results suggest that six years after the end of the 2010-2015 poaching period, recruitment had not markedly improved.

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[14] Breeding males were considered to be those entering the reproductive state of musth, which typically occurs between 25-30 years old (Poole, 1989a). Younger males (18-25 years) are active in pursuing matings (Ganswindt et al., 2005; Poole, 1989c), but (older) musth males are more likely to sire offspring (Hollister-Smith et al., 2007). Breeding females were defined as ≥10 years following Poole (1989b), as females tend to become reproductively mature between the ages of 10-15 years (Moss, 1983; Smith & Buss, 1973)

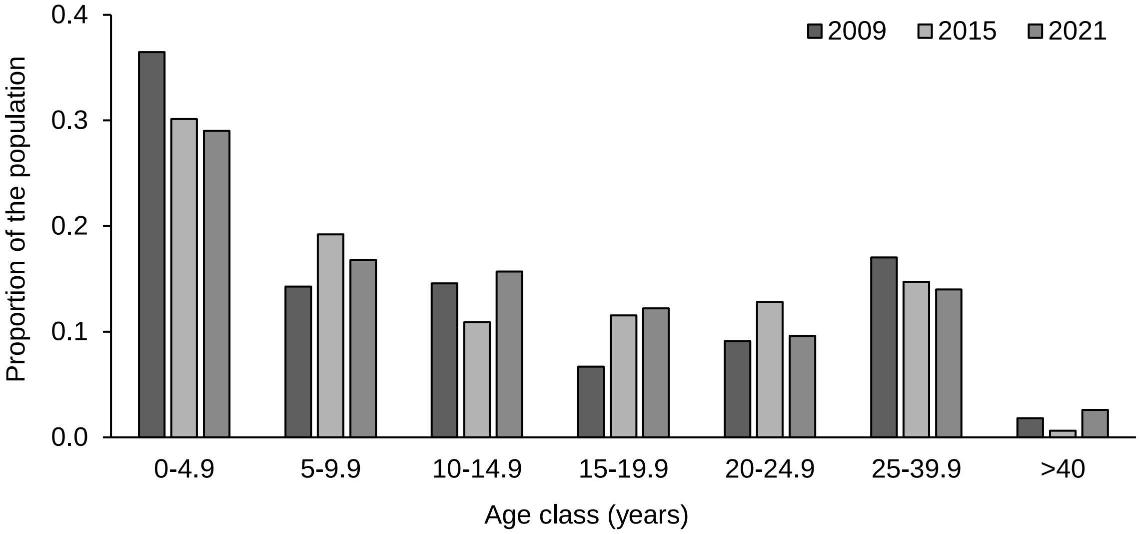


Figure 3.12 Age distribution for elephants in 2009 (n=329 individuals), 2015 (n=309 individuals), and 2021 (n=458 individuals); based on visual assessment of ages.

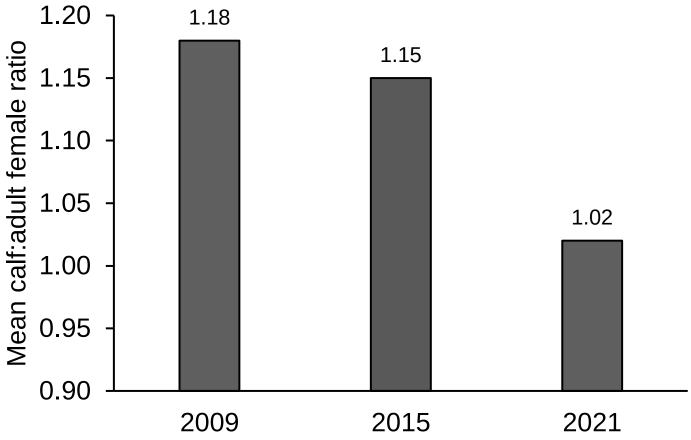


Figure 3.13 Mean calf (<5 years) to adult female (≥10 years) ratio in 2009 (n=30 cow-calf groups), 2015 (n=38 cow-calf groups), and 2021 (n=46 cow-calf groups).

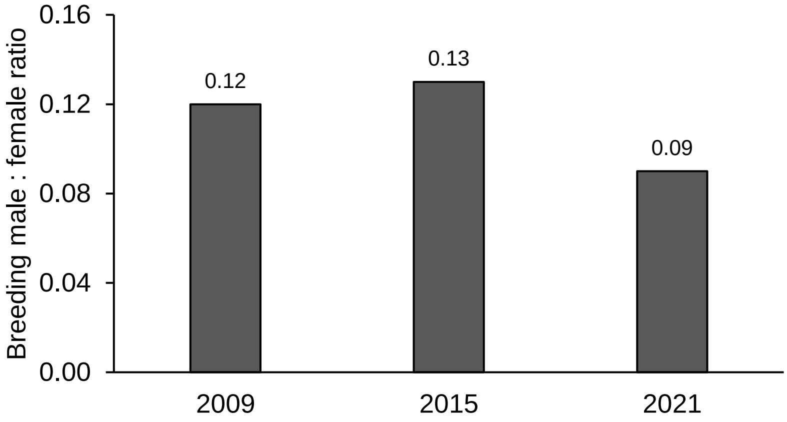


Figure 3.14 Breeding adult sex ratio in 2009, 2015, and 2021 (males ≥25 years, females ≥10 years).

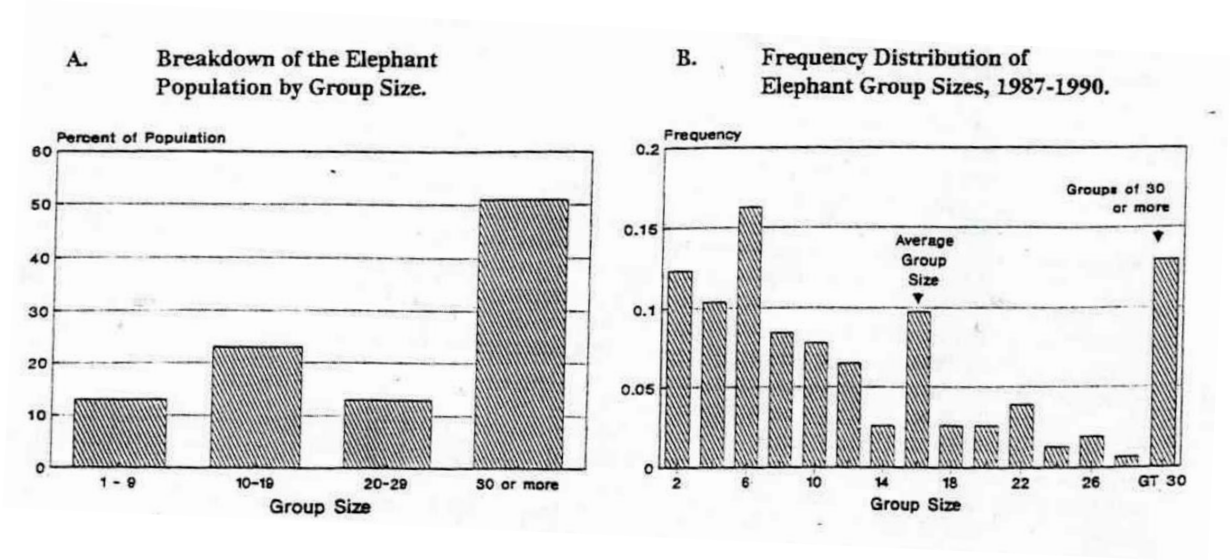
A note on drought events

Other than poaching, severe drought events are known to increase elephant mortality, especially among younger and older individuals, and affect population age-and-sex structure (Dudley et al., 2001; Foley, Pettorelli & Foley, 2008; Lee et al., 2022; Ndlovu et al., 2023; Wato et al., 2016). The extent to which drought has affected the Ruaha-Rungwa elephant population is poorly documented. Oral histories collected by Williams (2005) indicate that moderate to severe droughts occurred in Idodi area (village land southeast of Ruaha National Park) in 1940, 1946, 1967, and 1969, and a prolonged drought occurred in 1972-1974 (some margin of error around exact years is expected with oral histories). Rainfall data from Madibira (60 km from Msembe in Ruaha National Park) between 1924 and 1991, indicate that the years with the lowest rainfall (400 mm or less) were 1924, 1936, 1943, and 1953 (Barnes et al., 1992). Mean wet season rainfall in Madibira was higher in 1955-1970 (861 mm) and 1971-1991 (741 mm) than in 1924-1955 (577 mm). Only a drought in 1976 was documented to increase elephant mortality, especially among young individuals (Barnes & Kapela, 1991). Barnes & Kapela (1991) stated that this drought was an unusual event that was not known to occur before or since in the park's history. Indeed, a long-term tourism operator who has spent more than 30 years in the park could not, apart from 1976, recall any other severe droughts that resulted in notable elephant mortality in the park (C. Fox, personal communication, 2023). Rainfall data collected between 1988-2021 on Kibebe Farms in Iringa, approximately 70 km from Ruaha National Park as the crow flies, reveal that there were only three wet seasons (spanning November-May) where the total rainfall was more than one standard deviation below the long-term average annual rainfall (R. Phillips, personal communication, 2023). These periods were 1999-2000, 2007-2008 and 2008-2009. There were four wet seasons with more than one standard deviation above the long-term average annual rainfall: 1997-1998, 2018-2019, and 2019-2020.

3.5 Elephant behavioural responses to poaching

In addition to the demographic impacts of poaching, several changes in elephant behaviour in Ruaha-Rungwa have been speculatively linked to poaching. Barnes, Barnes & Kapela (1989) noted a change in grouping patterns after the poaching surge of the late 1970s and 1980s. In 1975-1977, mean cow-calf group size in the dry season was 6.8 individuals. In the dry season of 1989, mean cow-calf group size was 10.2 individuals. While in 1975-1977, few groups larger than 20 individuals were observed, in 1989, 10% of all groups observed had more than 20 individuals. Barnes et al. (1989) attributed these changes to increased poaching pressure resulting in elephants associating with each other for protection. Barnes et al. (1989) also observed that in the late 1980s, elephants concentrated in the Msembe area where the park headquarters was located, presumably for safety. In aerial surveys from 1987-1990 (both wet and dry seasons), 50% of observed groups had 30 or more individuals (Figure 3.15; TWCM, 1991). Unfortunately, aerial data on elephant group sizes from before the poaching surge was not available for comparison.

Similarly, in 2015-2018 I observed large aggregations of elephants in Lunda and Jongomero in Ruaha National Park, areas associated with higher poaching risk (Beale et al., 2018). In Lunda, elephant aggregations exceeding 100 individuals were seen on multiple occasions in both the wet and the dry season, suggesting that these were not just wet-season aggregations. Park rangers in Lunda call this aggregation, which they believe to be somewhat stable, *Kadege*. Tourist guides estimate the aggregation in the Jongomero area to be around 100 elephants (G. Nyenza, personal communication, 2023). I have not observed or heard about potentially stable aggregations of these sizes in the safer high-use tourism areas in the park. However, in the absence of long-term data on the composition and stability of these aggregations, it is difficult to say to what extent poaching was a factor in the formation of these large groups.


A. Breakdown of the Elephant Population by Group Size.

B. Frequency Distribution of Elephant Group Sizes, 1987-1990.

Figure 3.15 Distribution of elephant group sizes observed during aerial surveys of Ruaha-Rungwa in the dry season of 1987, wet season of 1988, wet season of 1990, and dry season of 1990. Average group size was 16 individuals. Figures reproduced from TWCM (1991).

Barnes & Barnes (1993) observed that elephants in Ruaha were more aggressive and fearful of vehicles after the poaching crisis of 1978-1987, especially in areas further from ranger posts and outside of the Msembe area, including north of the Mwagusi and along the base of the escarpment (Barnes et al., 1992). Noticing similar skittish behaviour outside of the main area of tourist use in Greater Msembe, I and other researchers at STEP began collecting data in

2015 on daytime elephant responses to a research vehicle along eight transect routes in Ruaha National Park. These transects varied in the extent of tourist use (See Chapter 2, Section 2.3.8 for transect methods and Figure 2.5 for a map of transect locations), and Park rangers and a park assistant ecologist perceived that illegal human use was greater in areas with little tourism presence (H. Xavier, personal communication, 2021). Elephant encounters along the transects in areas with no tourism presence were very rare. While some areas along these transects appeared to have been used very little by elephants, in other areas, elephants were present (as evidenced by dung and tracks) but rarely observed. Elephant responses to the research vehicle were coded as: calm, initially nervous but calmed down, nervous and avoiding vehicle, or terrified and running away (See Chapter 2, Table 2.5 for definitions).

Along the transects in the high-use tourism area, elephants responded calmly to the vehicle in most encounters (Figure 3.16). Elephants encountered on transects in the areas of low-tourism presence reacted more nervously. On the MG and MJ transects, which transition from an area of tourism presence to no tourism presence, elephant responses varied with distance to the nearest tourism camp (Figure 3.17). Elephants encountered beyond 10 km of a tourism camp were more likely to flee from the research vehicle than elephants encountered <10 km of a tourism camp. It is, however, difficult to disentangle elephant habituation to vehicles and risk. Elephants may be less habituated to vehicles in areas that receive less (tourist) vehicle traffic, and areas with the least vehicle traffic likely experience higher levels of illegal human use. The vehicle transects also indicated that elephants were extremely difficult to observe in the higher-risk areas of the ecosystem, as actual elephant encounters were very rare, and elephants tended to flee from the vehicle. It is likely that even if elephants were present, the sound of an approaching vehicle which could be detected from several kilometres away would send them retreating to hide in the bush.

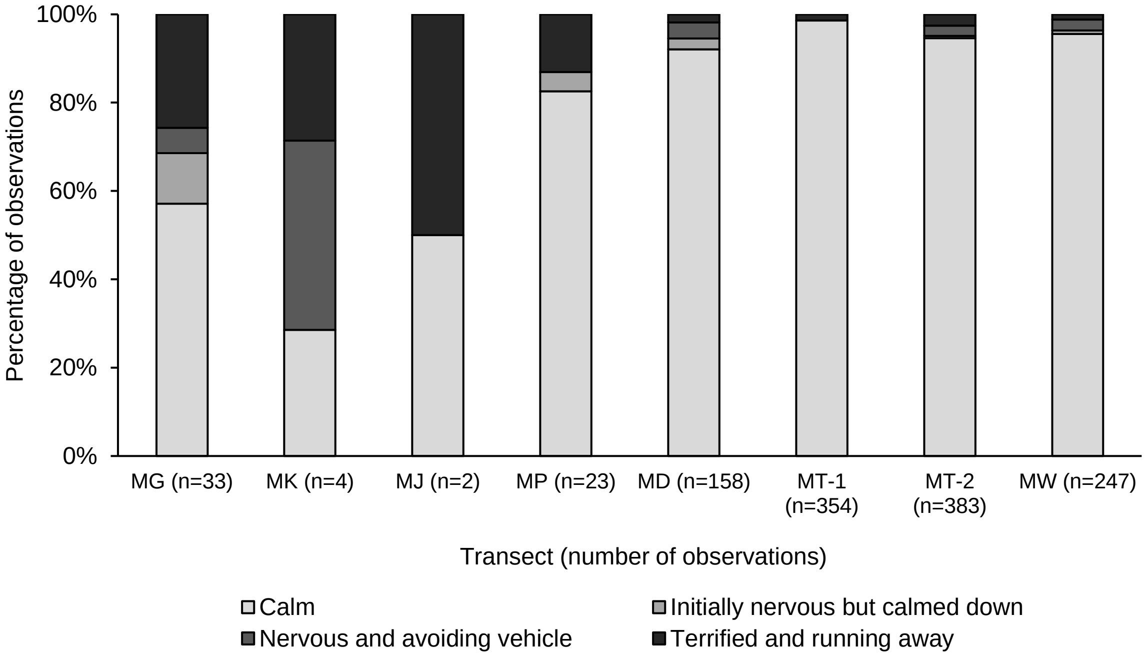


Figure 3.16 Elephant responses to a research vehicle along eight transect routes in Ruaha National Park (n=1,224 observations from transects conducted in 2015-2018). The MD and MW transects are in an area used intensively for tourism in the best-protected part of the ecosystem. The MK transect follows a road with very infrequent tourism use. The MG, MJ, and MP transects begin in areas with tourism presence and end in areas with no tourism presence. The MT-1 and MT-2 transects follow the Great Ruaha River and bisect areas with and without tourist use.

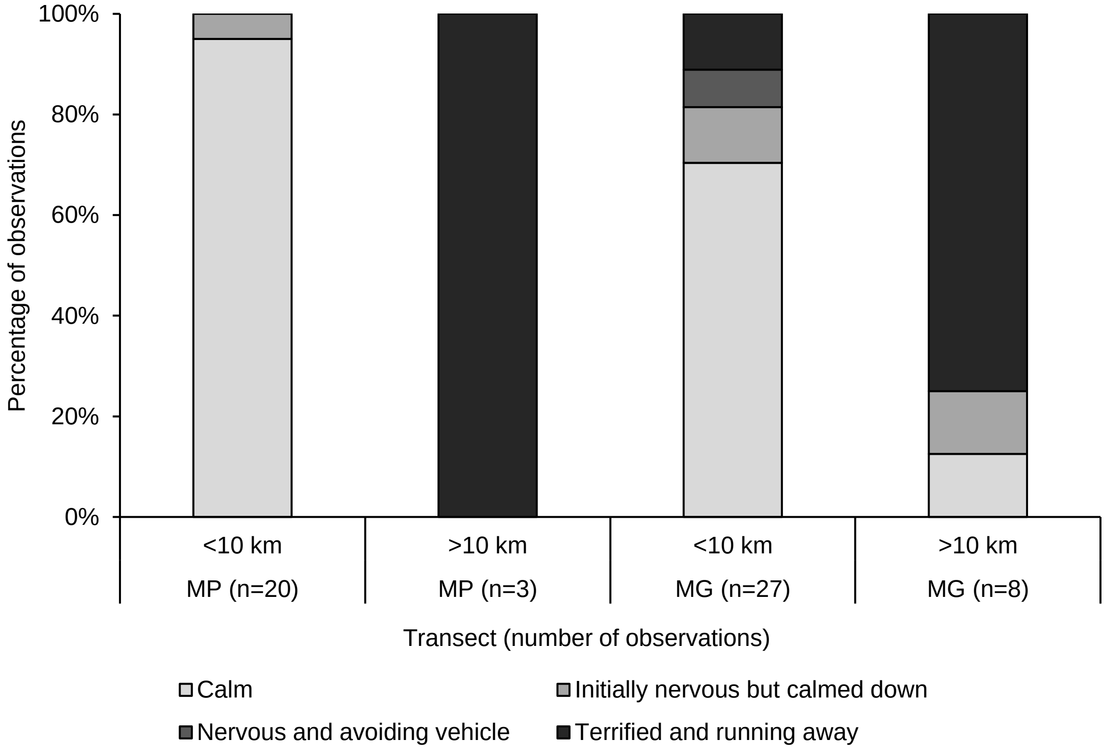


Figure 3.17 Elephant responses to a research vehicle along the MP and MG transects in Ruaha National Park, disaggregated by distance (<10 km or >10 km) to the nearest tourist camp (n=58 observations from transects conducted in 2015-2018). Note that the very infrequent detections may have been the result of elephants fleeing the vehicle prior to our approach. The MG and MP transects begin in areas with tourism presence and end in areas with no tourism presence.

3.6 Risks to elephants from human activities in the Ruaha-Rungwa ecosystem

Elephants use unprotected village lands in the Ruaha-Rungwa ecosystem in several ways. Elephants crop forage in cultivated fields and use water sources on village land (Hariohay, Munuo & Røskaft, 2020; Smit et al., 2016a, 2016b). Elephants from Ruaha-Rungwa also move west through human settlements towards the Katavi-Rukwa ecosystem (TAWIRI, 2019), and historical corridors are known to link Ruaha National Park with Mpanga-Kipengere Game Reserve and the Udzungwa Mountains (Jones, Caro & Davenport, 2009), also now dense agricultural lands.

Outside protected areas, elephants are at risk of poaching for ivory or killing in the context of human-elephant conflict (STEP, unpublished data). Elephants can also be killed legally by rangers and other authorized government officers if elephants have caused damage to property or injury or loss of human life (The Wildlife Conservation Act, 2009). Some spearing of elephants is known to occur in Iringa District, either as a rite-of-passage practice by Barabaig pastoralists or in crop protection. In some areas, farmers have enlisted Barabaig pastoralists for the protection of their farms against elephants (B. Cascio, personal communication, 2021). Elephant killing of livestock is not known to occur. Spearing and/or killing of elephants in retaliation for elephants killing livestock, which occurs elsewhere in East Africa (Kangwana, 2011), has not been recorded in this area. One further source of mortality of elephants on village land is elephants becoming trapped in wells dug by humans (STEP, unpublished data).

3.6.1 Human use of the ecosystem

Human populations in the administrative districts encompassing the Ruaha-Rungwa ecosystem have grown at an average annual rate of 3.5% between 2012 and 2022 (Wizara ya Fedha na Mipango, 2022). Human settlements and cultivation are located along the edges of the protected areas (Figures 3.18-3.19, Appendix A3.1). On the western side of the ecosystem, settlements and cultivation are clustered along the Itigi to Chunya road. In the south and east of the ecosystem, human settlements are clustered along the Iringa to Mbeya road and in Mbarali district (Mbeya region) and Iringa District (Iringa Region). There are also some settlements and cultivation inside less strictly protected areas, including in Rungwa South Open Area (settlement and farming are not prohibited in Open Areas). In southwest Ruaha National Park, where there is a contested boundary, large-scale commercial rice plantations and agro-pastoralist settlements are still present in an area that, according to current official park boundaries, is inside the park.

Komba et al. (2021) analysed the loss of natural vegetation in the Ruaha–Rungwa landscape for the period 2000–2019 using remote sensing methods (Figure 3.20). In this period, they estimated that an area of 18,023 km^2 or some 20% of the wider Ruaha-Rungwa ecosystem (including a 50 km buffer around the protected area complex) was converted to cultivated or bare land. Most of this conversion occurred on village land around the protected areas, with only minimal disturbance inside Ruaha National Park and Rungwa, Kizigo, and Muhesi Game Reserves. An estimated 30% of the land within 0-20 km of the protected area boundaries was converted to cultivated or bare land between 2000 and 2019. Although conversion was evident in most areas of the ecosystem, the western edge of the Rungwa-Kizigo-Muhesi Game Reserves complex, an area east of Kizigo Game Reserve, and two areas east of Ruaha National Park experienced particularly severe degradation. Conversion rates were lowest in 2000-2009 and accelerated in 2010-2019.

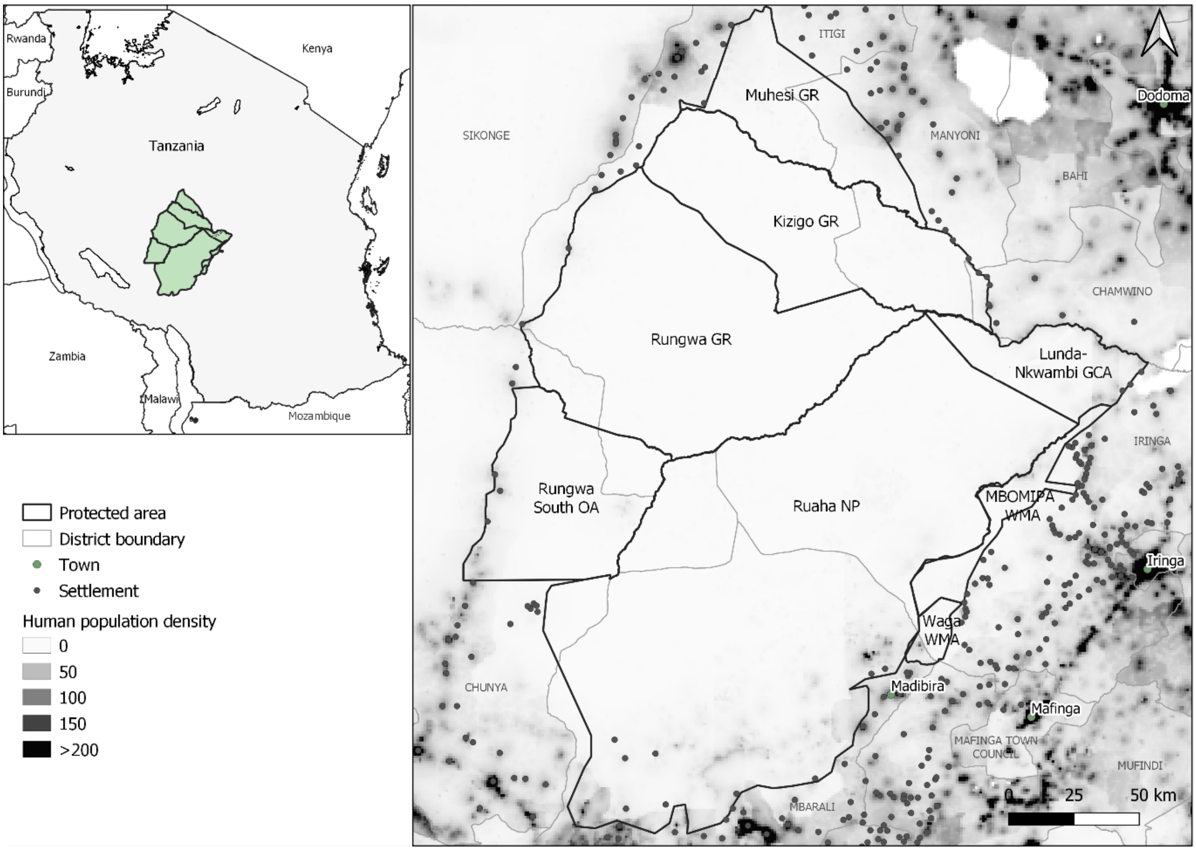


Figure 3.18 Location of human settlements, district boundaries, major towns, and human population density (people per km^{2,} in the year 2017; WorldPop, 2020) in the Ruaha-Rungwa ecosystem. The major population centres are the towns of Dodoma (national capital) and Iringa.

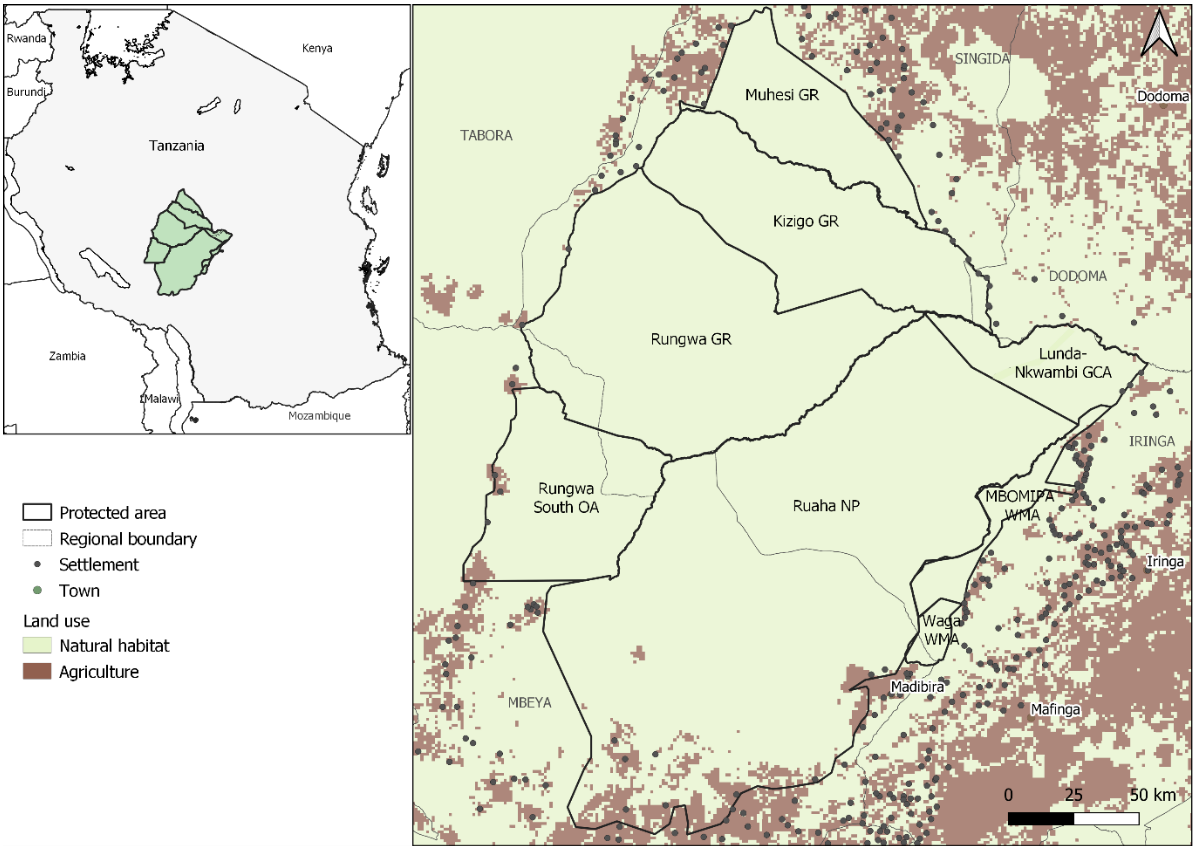


Figure 3.19 The distribution of natural habitat and areas converted to agriculture in the Ruaha-Rungwa ecosystem in approximately 2010 (Jacobson et al., 2015). Location of human settlements, regional boundaries, and major towns are also shown. See Appendices A3.1 for maps of the distribution of cultivation from aerial surveys.

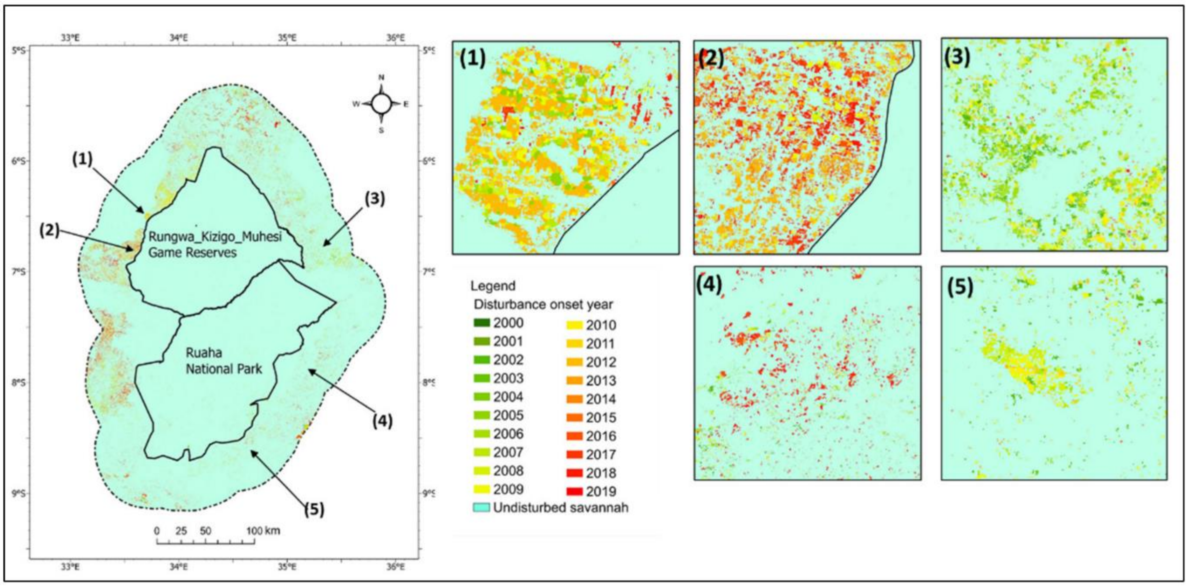


Figure 3.20 The spatial and temporal distribution of land conversion to agriculture or bare land in the greater Ruaha-Rungwa landscape (including a 50 km buffer around the protected area complex) from 2000 to 2019. Areas 1), 2), 3), 4), and 5) were considered as having experienced significant conversion during the study period. Reproduced from Komba et al. (2021).

Cattle densities in the ecosystem increased six-fold between 1993 and 2021[15], while the density of sheep and goats increased seven-fold in the same period (Figures 3.21-3.22). The major livestock owners in Ruaha-Rungwa are ethnic groups who first began moving into the area in the 1920s and in larger numbers in the 1960s and 1970s in search of grazing areas and farmland, particularly Sukuma, Barabaig, and Maasai (Coppollilo, 2004; Hariohay et al., 2017; Walsh, 2012), although traditionally agricultural ethnic groups such as Hehe and Bena also own cattle and smallstock (Dickman, 2008). Concurrently, the amount of land under cultivation has increased (Komba et al., 2021), reducing access to grazing land for pastoralists on village land, and increasing livestock grazing in protected areas (Coppollilo, 2004; Kessi, 2020). Livestock are widespread but some of the highest densities occur in the south (Mbarali District), east (the Idodi-Pawaga area in Iringa District), and north of the ecosystem (along the boundaries of the Game Reserves in Itigi and Manyoni Districts).

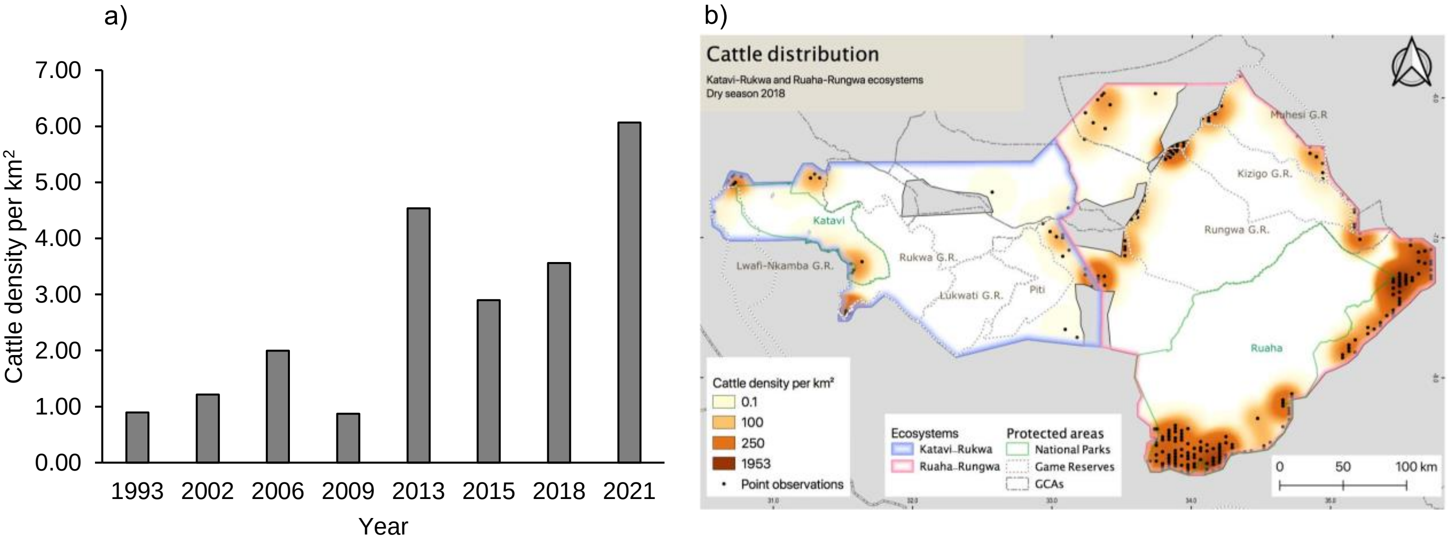


Figure 3.21 a) Cattle density (the estimated number of cattle from aerial surveys divided by the survey area) for the Ruaha-Rungwa ecosystem from TAWIRI aerial surveys conducted between 1993 and 2021. b) Cattle distribution and density in the Ruaha-Rungwa ecosystem from TAWIRI dry season aerial surveys in 2018. Reproduced from TAWIRI (2019). Cattle have primarily economic, cultural, and social value among pastoralist groups in the area, while for traditionally agricultural ethnic groups such as the Hehe and Bena, cattle are both a source of income and meat (Dickman, 2008).

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[15] The decrease in livestock densities in 2009 likely reflects the eviction of (agro)pastoralists and their cattle from Usangu Game Reserve and Mbarali District in 2006-2007 (Walsh, 2012).

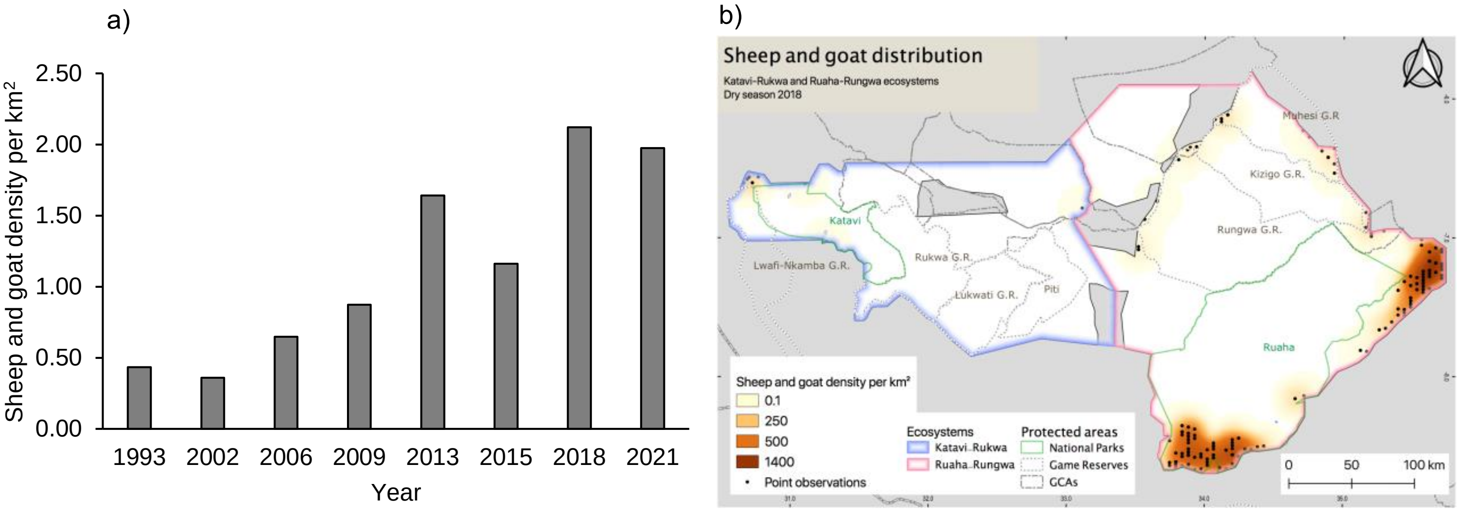

Figure 3.22 a) Sheep and goat density (the estimated number of sheep and goats from aerial surveys divided by the survey area) for the Ruaha-Rungwa ecosystem from TAWIRI aerial surveys conducted between 1993 and 2021. b) Distribution and density of sheep and goat in the Ruaha-Rungwa ecosystem from TAWIRI dry season aerial surveys in 2018. Reproduced from TAWIRI (2019). Sheep and goats are consumed as well as sold for income (Dickman, 2008).

3.6.2 Illegal human use of protected areas

Levels of illegal human use area vary across the ecosystem but are generally more prevalent close to protected areas boundaries and in the less-strictly protected areas (some timber extraction and hunting of wildlife in Game Controlled Areas and Open Areas is legal if an official permit has been issued). Other than elephant poaching (discussed in Section 3.3.2), illegal human activities inside protected areas include grazing of livestock, bushmeat poaching, timber logging, charcoaling, mining, and fishing (Hariohay et al., 2019; Mrosso et al., 2022b). Below, I summarize what is known about the spatial distribution of these activities in the ecosystem and, where data are available, an overview of temporal trends. Although most of these illegal human uses of the ecosystem (other than poaching of elephants for ivory or meat) do not directly cause elephant mortality, they may contribute to disturbance, impede access to water and/or food resources, and damage habitat. Elephants may avoid, in space or in time, people inside protected areas that are engaged in these activities.

Herders take livestock into the protected areas for grazing and watering. Livestock herders believe that wetland areas, especially the Ihefu wetland in Ruaha National Park, are especially nutritious and may induce cows to calve twice a year (Kessi, 2020). A lack of clarity and awareness around certain protected area boundaries and rules, especially in south-west Ruaha, also contributes to livestock being grazed inside the protected areas (Kessi, 2020). Aerial surveys indicate that livestock densities inside protected areas are highest in Muhesi Game Reserve, in southwest Ruaha National Park, in MBOMIPA Wildlife Management Area, and Lunda-Nkwambi Game Controlled Area (Figures 3.21-3.22). Between 2012 and 2019, 549 herders and 30,728 livestock were apprehended by rangers in Ruaha National Park (Kessi, 2020). The number of livestock apprehended by park rangers generally increased between 2012 and 2019 (Figure 3.23). Although information on ranger effort is lacking, livestock incursions into the park are perceived to be increasing (Kessi, 2020). Illegal livestock grazing accounted for 6.3% of arrests made on ranger patrols in Rungwa-Kizigo-Muhesi Game Reserves between January 2014 and April 2015 (Hariohay et al., 2019).

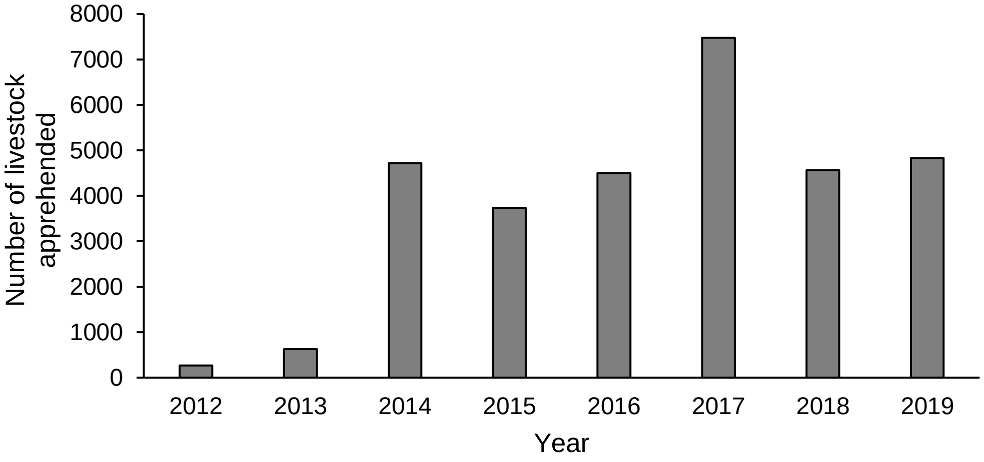

Figure 3.23 The number of livestock apprehended by rangers in Ruaha National Park between 2012 and 2019. Data from Kessi (2020).

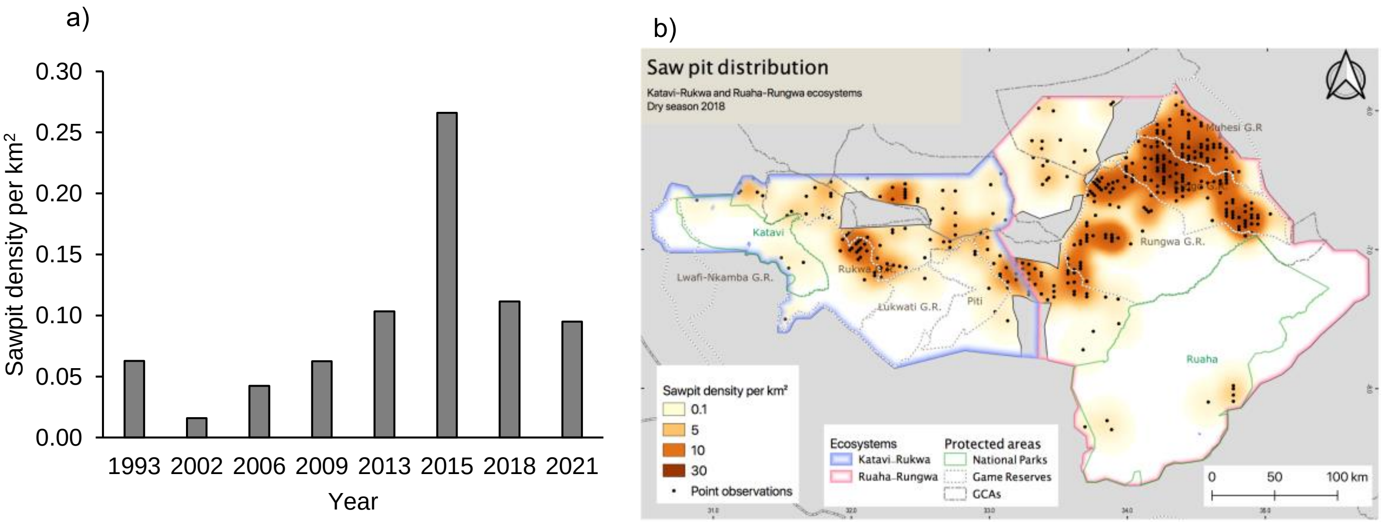

Figure 3.24 a) Density of sawpits in the Ruaha-Rungwa ecosystem from TAWIRI dry season aerial surveys conducted between 2009 and 2021. Note that the 2021 density estimate includes sawpits and tree felling. b) Distribution and density of sawpits in the Ruaha-Rungwa ecosystem from TAWIRI dry season aerial surveys in 2018. Reproduced from TAWIRI (2019).

Illegal timber logging, particularly the extraction of valuable timber species such as *Pterocarpus angolensis* (bloodwood), *Afzelia quanzensis* (pod mahogany), and *Dalbergia melanoxylon* (rosewood), is most prevalent in the Rungwa-Kizigo-Muhesi Game Reserve complex. Sawpit densities from aerial surveys suggest that logging increased between 2002 and 2013, peaked in 2015, and declined (to levels like those in 2013) in 2018 and 2021 (Figure 3.24). Timber logging accounted for 71.5% of arrests on ranger patrols in Rungwa-Kizigo-Muhesi Game Reserves between January 2014 and April 2015 (Hariohay et al., 2019). Many poachers' camps observed on aerial patrols conducted by STEP in the game reserves were located at timber logging sites (STEP, unpublished data), and some degree of hunting of wildlife for the pot is likely associated with these camps.

Another form of human resource extraction in protected areas is bushmeat poaching (Hariohay et al., 2019; Mrosso et al., 2022b), although little is known about spatial and temporal trends. Bushmeat poaching accounted for 39% of arrests in MBOMIPA Wildlife Management Area in 2018-2021 (STEP, unpublished data) and 10.8% of arrests in Rungwa-Kizigo-Muhesi Game Reserves in 2014-2015 (Hariohay et al., 2019). Several villages adjacent to MBOMIPA Wildlife Management Area and Ruaha National Park were identified as being sources of bushmeat (with meat obtained from MBOMIPA Wildlife Management Area and Ruaha National Park; Mrosso et al., 2022a), but studies are lacking for other parts of the ecosystem. Mammal species targeted for bushmeat include impala, dik-dik, buffalo, greater kudu, eland, warthog, giraffe, and occasionally, elephant (Mrosso et al., 2022b; STEP, unpublished data). Hunting is done primarily with home-made muzzleloaders (*goboles*) and dogs, but spears, snares, steel traps, and poison are also used (Coppollilo, 2004; Mrosso et al., 2022b; STEP, unpublished data).

Illegal artisanal gold mining occurs in Kizigo and Muhesi Game Reserves, MBOMIPA Wildlife Management Area, and Ruaha National Park. Mining occurs along rivers and in hills. Known locations of mining include Iluma hill in Muhesi GR, Ikiri hill and Issawa river in Rungwa GR, the Kizigo River, Ituli and Chambalasi hills in MBOMIPA WMA (Leader-Williams, Kayera & Overton, 1996; STEP, unpublished data). While the direct disturbance from digging may be minimal, miners establish camps and likely hunt for subsistence while in protected areas (Coppollilo & Dickman, 2007). Mercury used to extract gold is also leached into the environment. Illegal mining accounted for 6.0% of arrests in Rungwa-Kizigo-Muhesi Game Reserves in 2014-2015 (Hariohay et al., 2019).

Other resource extraction activities include fishing and honey gathering. Little is known about the spatial and temporal trends of these activities, although fishing is naturally concentrated around major rivers. Fishers establish temporary camps along rivers, from which fish is taken out by bicycle or motorcycle. Some large fishing camps were recently (2022) closed in Ruaha National Park, in which over 100 motorcycles were confiscated (personal observations). Honey gathering targets natural beehives in large trees, especially baobabs. While the direct effects of honey collecting are likely minimal, the indirect effects of fires set by honey gathers and associated hunting may be significant, but these have not been formally quantified (Coppollilo & Dickman, 2007).

As spatial data on these various resource extraction activities was not readily available, I used an occupancy model of illegal human use of the ecosystem developed by Strampelli et al. (2022b) to investigate elephant use of the ecosystem (Figure 3.25). This model was developed from human sign (footprints, bicycle tracks) observed during surveys in 2017-2018. This occupancy model likely captures various types of illegal human use. The probability of illegal human use captures patterns in livestock presence in protected areas, and, to a lesser extent, patterns of sawpit distribution in protected areas from aerial surveys.

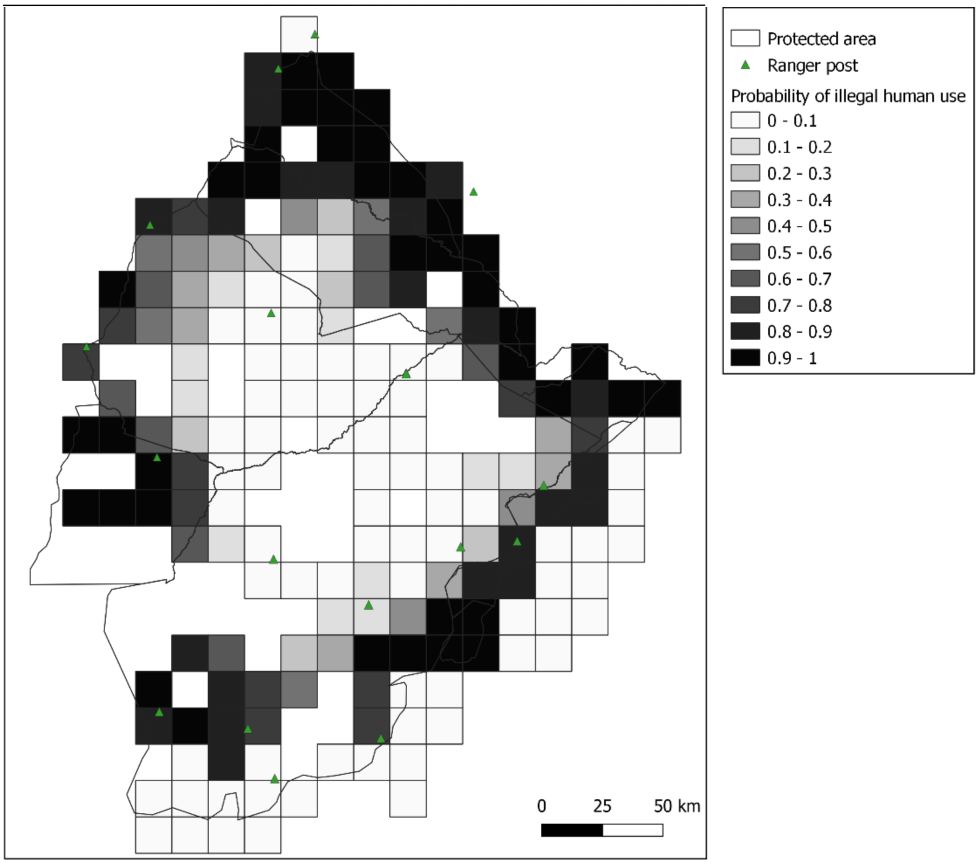

Figure 3.25 Illegal human use occupancy model developed by Strampelli et al. (2022b) showing site-specific probabilities of illegal human activity (each ‘site’ is a 225 km^2 grid cell). This model was developed using detection/non-detection data on illegal human use collected during occupancy surveys of the Ruaha-Rungwa ecosystem in 2017-2018.

3.7 Conclusions

Elephants in the Ruaha-Rungwa ecosystem have interacted with and been hunted by humans for thousands of years. Although most human settlements were moved out of protected areas in the 1950s, 1960s, and 1970s (apart from some settlements in southwest Ruaha National Park), this did not eliminate human hunting of elephants or other natural resource use within protected areas.

In the last 50 years, the Ruaha-Rungwa elephant population experienced two poaching crises which resulted in major population declines. These poaching waves have impacted the demography of the population, resulting in the loss of older individuals and poor recruitment during the poaching and first post-poaching years. Poaching has also been linked to changes in elephant grouping and ranging patterns, and to aggressive and fearful behaviour towards vehicles.

Adult elephants alive in 2010 at the start of the second poaching wave were likely to have experienced the first poaching surge (elephants aged >26 years in 2010 were born during the first poaching wave while elephants aged >32 years in 2010 were born before the first poaching wave). It is therefore likely that a memory of previous poaching remained at the time of the 2010-2015 poaching crisis, which may have shaped the elephant responses investigated in the subsequent chapters. Both current and past interactions with humans likely contribute to the behaviour, sociality, distribution, and reproduction of the elephants in the Ruaha-Rungwa ecosystem.

While elephant numbers have decreased by nearly 65% over the past three decades, human use of the ecosystem, both legal and illegal, has increased. Growth in human populations and the conversion of natural vegetation to agriculture have likely reduced available elephant habitat outside protected areas.

Human-mediated risks to elephants in the Ruaha-Rungwa ecosystem are spatially structured. Mortality risk from ivory poaching in 2010-2015 was greatest in the game reserves, in the Lunda area of Ruaha National Park and MBOMIPA Wildlife Management Area, and in the more remote areas of Ruaha National Park, such as in the western wilderness zone of the park and along the Mzombe River. Elephants are also killed on village land in hostile interactions with people, such that elephants likely associate village land with mortality risk. Human disturbance risk to elephants is greatest on village land outside protected areas, where most human settlements and cultivation are located, as well as in those areas where humans use natural resources illegally within protected areas. Illegal human use within protected areas is more common near protected area boundaries and in the game reserves, other less strictly protected areas, and the more remote areas of the park.

Elephant use of space within the ecosystem in relation to human population densities, settlements, and cropland (Figures 3.18-3.19) is investigated in Chapter 4. How poaching (based on carcass maps, Figures 3.7-3.8) and other illegal human use within protected areas (Figure 3.25) have shaped elephant use of the ecosystem is investigated in Chapters 4, 5, and 6.

Appendix 3.1 Cultivation distribution from aerial surveys

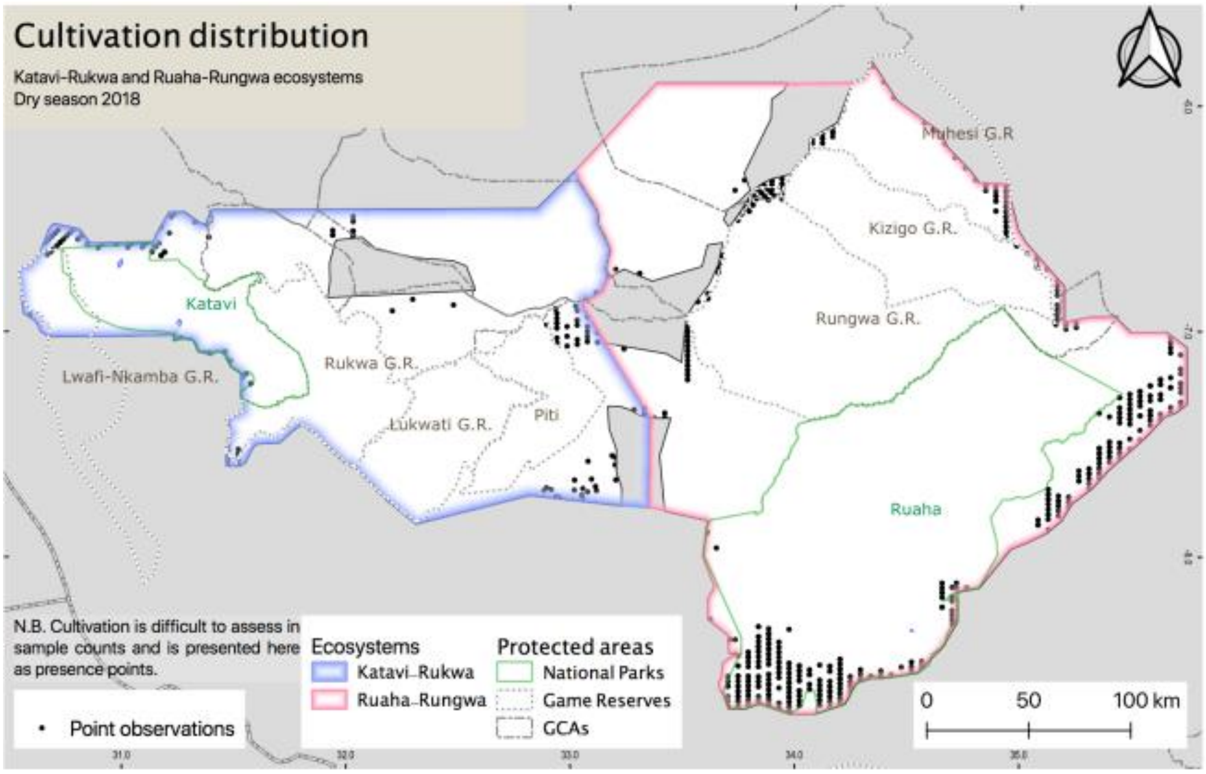

Figure A3.1 Observations of cropland from TAWIRI dry season aerial surveys in 2018. Reproduced from TAWIRI (2019).

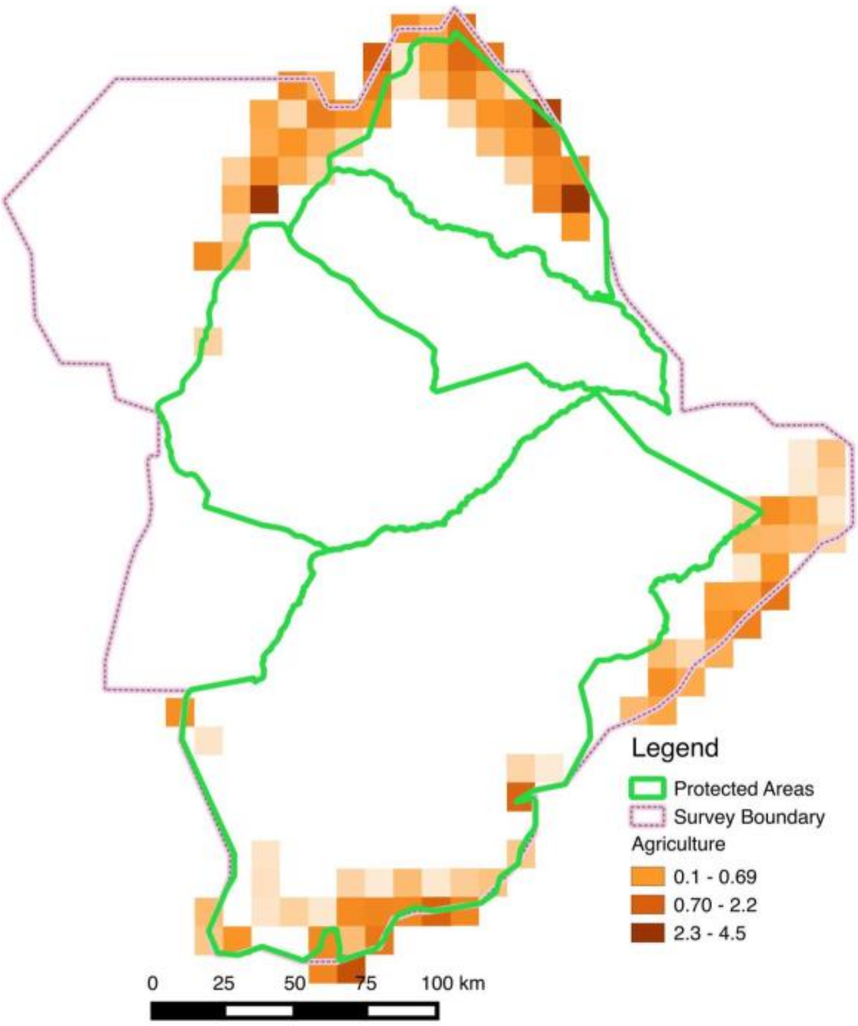

Figure A3.2 a) Cropland density from TAWIRI dry season aerial surveys in 2015, reproduced from TAWIRI (2016).

Appendix 3.2 Elephant mortality data for MBOMIPA WMA, 2018-2022

In 2018-2022, 70% of elephant carcasses encountered on village game scout patrols in MBOMIPA WMA and adjacent village land were attributed to ivory poaching, while 20% of carcasses were related to human-elephant conflict, where elephants were killed in retaliation for crop damage (STEP, unpublished data). A total of 27 elephant carcasses were encountered on village game scout patrols in MBOMIPA WMA and adjacent village land between 2018 and 2022 (STEP, unpublished data).

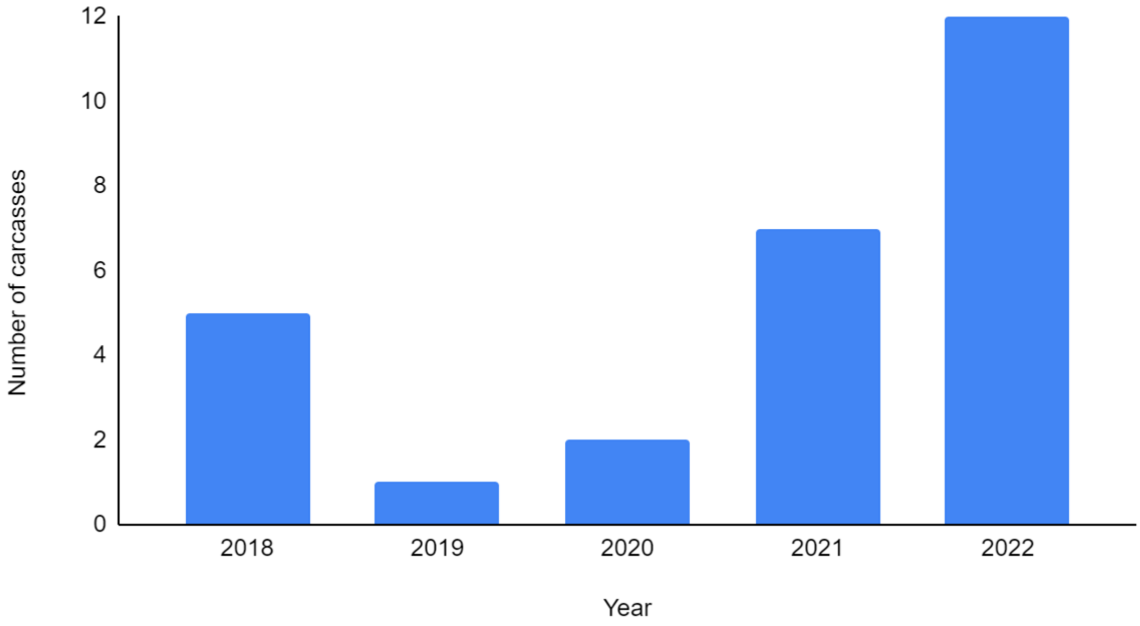

Figure A3.3 Number of elephant carcasses encountered by village game scouts in MBOMIPA WMA and adjacent village land (STEP, unpublished data).

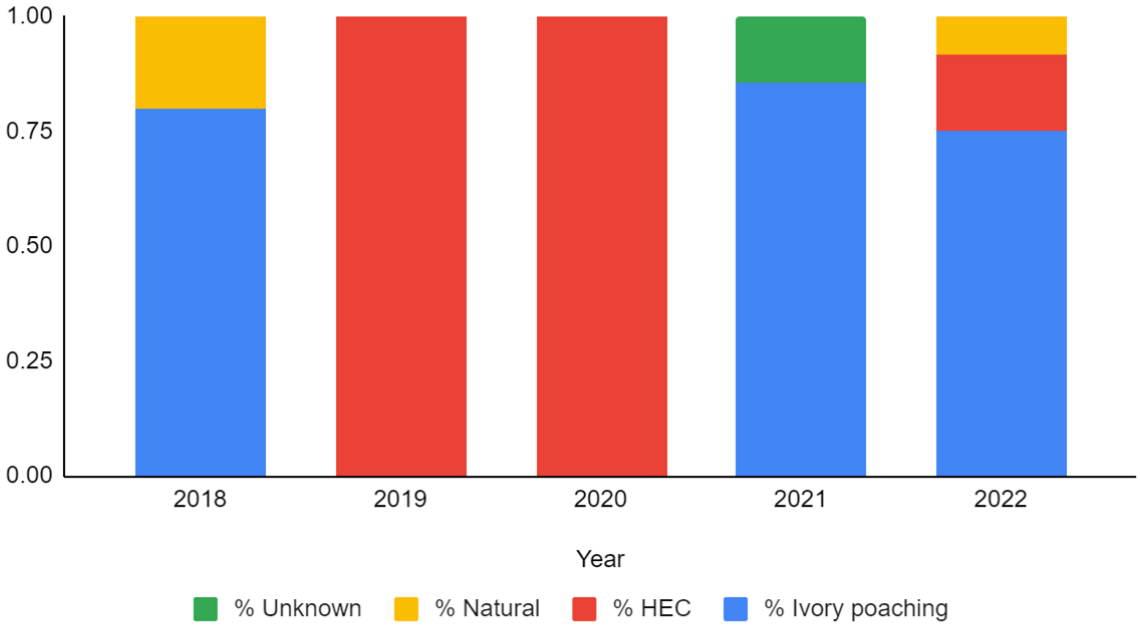

Figure A3.4 Cause of mortality of elephant carcasses encountered by village game scouts in MBOMIPA WMA and adjacent village land (STEP, unpublished data). HEC stands for human-elephant conflict and includes mortalities related to hostile interactions between people and elephants.

Chapter 4

The influence of anthropogenic risk and environmental factors on elephant space use across multiple spatial scales in the Ruaha-Rungwa ecosystem

Photo 6: *Dry season aggregation of elephants near Jongomero ranger post in the Vachellia-Commiphora zone of Ruaha National Park.*

Chapter 4. The influence of anthropogenic risk and environmental factors on elephant space use across multiple spatial scales in the Ruaha-Rungwa ecosystem

Author contributions

I conceived the study as part of a research collaboration with Dr. Paolo Strampelli (University of Oxford). Elephant occurrence data for the study were collected by Dr. Strampelli, Stivin Pangamwene, and Hamis Dongo. Dr. Strampelli provided data for covariates used in occupancy analyses (published in Strampelli, 2021), as indicated in Tables 4.2 and 4.3. Dr. Colin Beale (University of York) provided a spatial layer for the probability of elephant carcass occurrence (published in Beale et al., 2018), derived from aerial censuses of the Ruaha-Rungwa ecosystem conducted by the Tanzania Wildlife Research Institute in 2015 (TAWIRI, 2015). I extracted all other covariate data from open-access sources. I conducted all analyses and wrote the chapter. Professors Phyllis Lee and Hannah Buchanan-Smith (University of Stirling) provided guidance on analyses and drafts of this chapter.

4.1 Abstract

This chapter investigates elephant space use in the Ruaha-Rungwa ecosystem of Tanzania, with a focus on the influence and relative importance of environmental and anthropogenic risk factors at multiple spatial scales. Using detection/non-detection data from vehicle-based road transects, I modelled elephant space use in relation to environmental and risk factors in an occupancy framework for 1) the entire ecosystem, including protected areas and unprotected village land; 2) protected areas only; and 3) village land, at two spatial resolutions (coarse and fine). At the coarse spatial resolution (225 km^2 sites), elephant use of the entire ecosystem was most strongly predicted by and negatively associated with conversion to agriculture and human population density, while elephant space use within protected areas was positively associated with tree cover and proximity to riparian habitat. At the fine spatial resolution (1 km^2 sites), both risk and environmental factors predicted elephant site use within protected areas, and elephant site use was negatively associated with elephant carcass occurrence and distance to ranger posts. I found no evidence that elephants avoid areas also used by lions, their primary natural predator, at the fine spatial resolution. No predictors emerged as having a significant influence on fine-scale elephant space use on village land, likely because of the low number of elephant detections on village land. These findings indicate that in an ecosystem which recently experienced a poaching surge and faces threats from multiple anthropogenic activities, elephants are sensitive to risk in their use of the ecosystem.

4.2 Introduction

This chapter explores how anthropogenic risk and environmental factors influence elephant use of their environment. How elephants use their environment has consequences for their survival and reproduction and is thought to be influenced by resource acquisition and energy expenditure (Barnes, 1983; Boult et al., 2018; Harris et al., 2008; Loarie et al., 2009), thermoregulation needs (Kinahan et al., 2007; Mole et al., 2016; Thaker et al., 2019), mineral needs (Wheelock, 1980), access to mates (especially for males, Barnes, 1982c; Poole, 1987), social opportunities (Chiyo et al., 2014), and risk (Harris et al., 2008; Roever et al., 2013; Wittemyer et al., 2017).

Certain environmental factors related to resource acquisition are well-established drivers of elephant space use (see also Chapter 1; reviewed in Burton-Roberts, 2022). This includes access to water for hydration and thermoregulation, as well as food availability, quality, and distribution. Elephant habitat use is strongly influenced by proximity to water sources, particularly during dry periods (Chamaillé-Jammes et al., 2007; Harris et al., 2008; Loarie et al., 2009; Pittiglio et al., 2012; Stokke & du Toit, 2002), and is often positively associated with indicators of food availability such as primary productivity, vegetation greenness, and tree cover (Boult et al., 2018; Loarie et al., 2009; Pittiglio et al., 2012; Valls-Fox et al., 2018a; Young et al., 2009).

Elephant space use is also influenced by human modification of landscapes, human-induced mortality risk, and legal protection. While elephants do make use of areas without formal protection, including accessing agricultural fields for crop foraging (Graham et al., 2009), they have been shown to avoid (close proximity to) human settlements (Graham et al., 2010; Hoare & du Toit, 1999; Harris et al., 2008; Songhurst, McCulloch & Coulson, 2016) and to move rapidly through human-dominated landscapes, often under the cover of darkness (Douglas-Hamilton et al., 2005). There is also some evidence that elephant space use is sensitive to human-induced mortality risk (Bastille-Rousseau et al., 2020; Goldenberg et al., 2018; Roever et al., 2013). The potential safety afforded by protected areas and their infrastructure may also influence elephant space use, as elephant occurrence has been found to be positively associated with legal protection and ranger posts (Beale et al., 2018; Nahonyo, 1996; Rich et al., 2016).

Although risk has been shown to influence elephant space use in several contexts, the importance of risk relative to environmental factors such as water and forage across multiple spatial scales remains a pertinent question. It is important to understand how species-habitat associations vary with spatial scale, as the factors that influence use at coarse spatial scales may differ from those that influence use at fine scales and may even vary in their strength and direction (e.g., Altmoss & Henle, 2010; de Knegt et al., 2011; Elith & Leathwick, 2009; Wiens, Rotenberry & Van Horne, 1987). For instance, lions have been shown to avoid bushmeat poachers at fine spatial scales but not at coarse spatial scales (Everatt, Andresen & Somers, 2015). Spatial scale is characterized by resolution (the grain or cell size) and extent (the total study area) (Elith & Leathwick, 2009). By investigating space use at both a coarse and fine spatial resolution, insight may be gained into the factors that impact long-term and short-term elephant space use (e.g., Strampelli et al., 2022b). By varying the extent at which space use is investigated, insight may be gained into the relative importance of risk and environmental factors on elephant space use at the extent of the whole ecosystem (comprising both protected areas and village land), within protected areas, and on village land (see Table 4.1).

In this chapter, I investigate the influence and relative importance of anthropogenic risk and environmental factors on dry-season elephant space use in the Ruaha-Rungwa ecosystem at both a coarse spatial resolution (225 km^2 sites) and a fine spatial resolution (1km^2 sites), and within multiple spatial extents. Ruaha-Rungwa experienced severe elephant poaching in 2010-2015 (see Chapter 3). Poaching risk was unevenly distributed across the ecosystem and was higher in the less-strongly protected game reserves and wildlife management areas, enabling investigation into elephant space use in relation to recent poaching risk. Ruaha-Rungwa's protected areas are also affected by illegal human resource use (Strampelli, 2021), making it possible to explore how elephant space use is impacted by illegal human presence inside protected areas, as well as the protection afforded by law enforcement presence and infrastructure (specifically, ranger posts). As the ecosystem is undergoing conversion of natural habitat to agriculture and rapid human population growth (see Chapter 3), it is also timely and important to understand how elephant use of the ecosystem is affected by this expanding human footprint.

The specific aims of this chapter are to identify predictors of elephant space use at a coarse scale and fine scale, and to do so at the extent of a) the entire ecosystem, b) within protected areas and c) unprotected village lands, and 2) to understand the relative importance of risk and environmental variables on elephant space use across multiple spatial scales. To address these aims, I analyse dry season elephant occurrence data from vehicle-based road transects in an occupancy modelling framework.

4.2.1 Overview of occupancy models

Occupancy models are widely used in studies of species distribution and species-habitat relationships (Bailey, MacKenzie & Nichols, 2014; MacKenzie et al., 2002). In this framework, the detection of a species at a site is considered to arise from two processes: 1) the biological process that causes a species to be present at a site, and 2) the observation or sampling process that causes the species to be detected at a site. It is important to account for imperfect detection when modelling species-habitat relationships to ensure that models are not simply a representation of an observer's ability to detect the species (MacKenzie, 2006). Occupancy models allow the biological and observation processes to be modelled simultaneously, thereby explicitly accounting for detection biases (MacKenzie et al., 2017), while other approaches such as modelling species occurrence using logistic regression or resource selection functions (Manly et al., 2002) do not.

Occupancy models use data on detection and non-detection of a species over multiple surveys (sampling occasions) within a sampling unit (site) to estimate probabilities for the detection (p) and occupancy (ψ) of a species (Mackenzie et al., 2002). Heterogeneity in detection and occupancy can be modelled using covariates, thereby enabling investigation of the factors influencing habitat use by species, as well as factors influencing detection of a species during surveys (MacKenzie et al., 2017). Below, I define some key terms used in occupancy modelling:

- *Site*: the sampling unit of interest at which species occupancy or use is being assessed. Sites can be defined arbitrarily (e.g., a square or 'grid cell' within a regular grid overlaid on the study area) or naturally (e.g., for species naturally occurring in defined patches). This study used two levels of cell size, coarse and fine.

- *Sampling occasion*: replicate surveys within a site to determine species presence or absence. Sampling occasions can be either temporally replicated (i.e., the same area sampled multiple times over the course of a survey) or spatially replicated (i.e., different areas within the site sampled once). In this study, a spatial replication approach was used.

- *Detection history*: the pattern of detections (presence) and non-detections (absence) across sampling occasions within sites. Detection histories are recorded as matrices by site (rows) and sampling occasion (columns) with detection coded as 1 and non-detection coded as 0.

- *Closure assumption*: the assumption that sites are closed to changes in species occupancy during the sampling period (i.e., sites are either occupied or unoccupied by the species for the duration of the sampling period). In this chapter, the closure assumption is relaxed so that ψ is interpreted as the probability of site use rather than occupancy, and p is interpreted as the probability of detecting a species given that the site was used by the species. As recommended by Mackenzie et al. (2017), I relax the closure assumption because elephants are a highly mobile species with large home ranges relative to the size of the sampling units at which elephant habitat use is being investigated.

- *Detection probability* (p): the probability of detecting a species given presence in a site[16]. Detection probability is estimated using the detection history for sites where the species was detected. In sites where the species was detected in at least one sampling occasion, variation in detections between sampling occasions within a site is assumed to arise from the detection process alone, separate from the processes that influence use or occupancy of a site.

- *Detection covariate*s: covariates hypothesised to explain heterogeneity in detection of a species among sites and/or sampling occasions. See Section 4.3.4 for detection covariates used in this study.

- *Occupancy or site use probability* (ψ): the probability of a site being occupied (when the closure assumption is met) or used by the focal species (when the closure assumption is relaxed). In this chapter, the closure assumption is relaxed and ψ is interpreted as the probability that a site is used by the species, i.e., at any point in the sampling period, a site has a non-negligible probability of containing at least one individual of the focal species, but the species is not always present (MacKenzie et al., 2017).

- *Occupancy or site use covariates*: covariates hypothesised to explain heterogeneity among sites in species occupancy or use. I investigated the influence of environmental and risk covariates on elephant site use (see Section 4.3.5).

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[16] Strictly speaking, this is how the detection probability is defined when the closure assumption is met. In this study, I relax the closure assumption, so detection probability (p) is interpreted as the product of the probability that the site was used by the species at the time of the survey, and the probability of detecting the species given that the site was used by the species at the time of the survey.

- *Naïve occupancy*: the proportion of surveyed sites at which a species was detected. This measure of occupancy is uncorrected for detection biases.

Occupancy models estimate the probability of detection and occupancy by identifying values for these parameters that maximise the likelihood of the observed detection histories. In brief, likelihood terms (a probability statement for the observed detection history per site) are defined for each site and linked in a single model likelihood, which is then maximised to obtain maximum likelihood estimates for detection and site use probabilities (MacKenzie et al., 2002). The maximum likelihood estimates of detection probability and occupancy probability are the values of these parameters for which the observed data are the most likely, given the underlying model (MacKenzie et al., 2017), and are the ones that are therefore estimated and reported.

4.3 Methods

4.3.1 Study area

The study area comprised the Ruaha-Rungwa ecosystem in south-central Tanzania and included protected areas as well as adjacent unprotected village land (for an ecosystem description, see Chapter 2). Survey coverage in village land was the most extensive in the southeast of the study area (Figure 4.1). Elephant space use was investigated within multiple spatial extents in the ecosystem (Table 4.1).

4.3.2 Survey design

I investigated elephant space use at two spatial resolutions (coarse and fine) and within multiple spatial extents. The data on elephant occurrence used in this study were collected as part of a multispecies survey of the Ruaha-Rungwa ecosystem (Strampelli, 2021).

At the coarse spatial resolution, sites were defined as 225 km^2 grid cells. Grid cell size was informed by previous studies indicating that this size was small enough to provide insight into habitat associations for a range of species[17] and to have relevance for conservation management (Henschel et al., 2016; Petracca et al., 2020), while also large enough to enable sufficient sampling within sites. Elephant space use has been investigated at a similar spatial resolution in other occupancy studies (Jathanna et al., 2015; Petracca et al., 2020). Elephant

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[17] The multispecies survey sought to investigate the distribution of large carnivores and their prey within the Ruaha-Rungwa ecosystem. The size of the 225 km^2 grid cell - originally based on average lion home range size (Henschel et al., 2016) - was considered representative of the scale at which large carnivores make second order (home-range scale) habitat-use decisions (Strampelli, 2021).

home range sizes are highly variable as a function of gross habitat, sex, and season, ranging anywhere from 10 km^2 to >10,000 km^2 (Benitez et al., 2022; Douglas-Hamilton et al., 2005; Ngene et al., 2017; Wall et al., 2021). However, occupancy modelling does not require the sites at which occupancy or use are investigated to match the size of species' home range (MacKenzie et al., 2017). I interpret elephant use of sites at the coarse resolution to represent higher-level habitat use choices resulting from elephant selection for or against the use of a site. At the coarse spatial resolution, I investigated the effect of environmental and anthropogenic risk factors on elephant habitat use within two spatial extents: 1) the entire ecosystem comprising protected areas and village land, and 2) protected areas only (Table 4.1). Elephant space use on village land was not investigated at the coarse spatial resolution because the number of coarse-resolution sites within village land was low and these sites had few elephant detections.

At the fine spatial resolution, sites were approximately 1 km^2 cells. Sites were defined as a 2 km segment of road with a 250 m buffer around each segment for covariate extraction purposes (Figures A4.1-A4.3). In the fine resolution analyses, I only used transects from 225 km^2 sites where elephants had been detected, to ensure that absence at the fine resolution did not reflect elephant avoidance of sites at the coarse resolution (following Strampelli, 2021). I interpret elephant use of sites at the fine spatial resolution to reflect fine-scale, short-term habitat use decisions. I investigated elephant habitat use at the fine spatial resolution within protected areas and on unprotected village land (Table 4.1). I also assessed if there was evidence for elephants avoiding sites also used by lions, one of their non-human predators (Joubert, 2006), at the fine spatial resolution by using transects from the subset of 225 km^2 sites in which lions were detected (this sampling grid is referred to hereafter as natural predation risk).

Table 4.1 Summary of the spatial resolutions and extents at which elephant space use was investigated.

Sampling grid	**Spatial resolution (number of sites)**	**Spatial extent**	**Rationale**
Coarse resolution, entire ecosystem	225 km^2 (185 sites)	The entire ecosystem (approx. 50,000 km^2), comprising formal protected areas and unprotected village land.	Assess the effect and relative importance of environmental and anthropogenic risk factors on broad-scale elephant space use within the entire ecosystem.
Coarse resolution, protected areas	225 km^2 (139 sites)	Protected areas only (approx. 40,000 km^2).	Assess the effect and relative importance of environmental and anthropogenic risk factors on broad-scale elephant space use within protected areas.
Fine resolution, protected areas	1 km^2 (1005 sites)	Sites within protected areas (>50% of the site was protected area) where elephants were detected at the coarse spatial resolution (in 225 km^2 sites).	Assess the effect and relative importance of environmental and anthropogenic risk factors on fine-scale, short-term elephant space use within protected areas.
Fine resolution, village land	1 km^2 (42 sites)	Sites on unprotected village land (sites which were <50% protected area) where elephants were detected at the coarse spatial resolution (in 225 km^2 sites).	Assess the effect and relative importance of environmental and anthropogenic risk factors on fine-scale, short-term elephant space use on village land.
Fine resolution, natural predation risk	1 km^2 (652 sites)	Sites within protected areas where both lions and elephants were detected at the coarse spatial resolution (in 225 km^2 sites).	Assess fine-scale, short-term elephant space use with respect to natural predation risk (defined as the probability of lion site use).

4.3.3 Data collection

Detection/non-detection data for elephants were collected via vehicle-based sign transects. Sign consisted of tracks (elephant footprints) visible on the road surface (see also Chapter 2). Transects were divided into 500m segments. If within a 500 m segment of transect, elephant tracks were observed on the road surface, this was considered a detection. A non-detection was defined as a 500m segment of transect on which no elephant tracks were observed. Elephants could leave tracks when following a road and travelling on it, or when crossing a road. Both cases were considered a detection if observed during a 500m segment of transect.

***Photo 7**: Examples of elephant footprints on roads in Ruaha National Park. Photos by Mustapha Mohamed. Note that these photos were not from the time of surveying.*

Surveys were carried out by Dr. Paolo Strampelli and two experienced observers (Stivin Pangamwene and Hamis Dongo) over two dry seasons (7th July – 29th November 2017 and 29th June – 21st November 2018). Due to the extensive size of the ecosystem, it was necessary to survey over two years, but the data are treated as representing a single survey period during occupancy modelling.

During surveying, observers were seated on the front of the survey vehicle to maximise their view of the road surface. The vehicle was driven at a maximum speed of 10 km per hour. Surveys were conducted between dawn and 10 a.m. when tracks on the road surface were most visible. Transects were postponed if a vehicle had driven the target stretch of road during the previous night. The transect was ended if another vehicle was encountered during surveying, as this could have erased tracks on the road surface.

A spatial replication sampling approach was used whereby transects were driven within each site. Transect length per site varied with the distance of available roads in each site. In 225 km^2 sites, transect length varied between 6 and 20 km (average: 15.1 km). Transects within each site comprised mutliple 500 m segments. For each 500 m segment, observers recorded whether elephant tracks were detected (coded as 1) or not detected (coded as 0), as well as road quality and vehicle use intensity. Road quality was classified on a scale from 1 (best, sandy roads where animal tracks are easily visible) to 4 (worst, roads with harder/rocky surfaces). Vehicle use intensity was graded as 0 (no vehicles in the previous 4 days or more), 1 (no vehicles in the previous day), or 3 (a vehicle passed on the survey day; transect is ended). A total of 185 225 km^2 sites and 1,484 1 km^2 sites were surveyed (via 2,789 km of transects), covering >80% of the ecosystem.

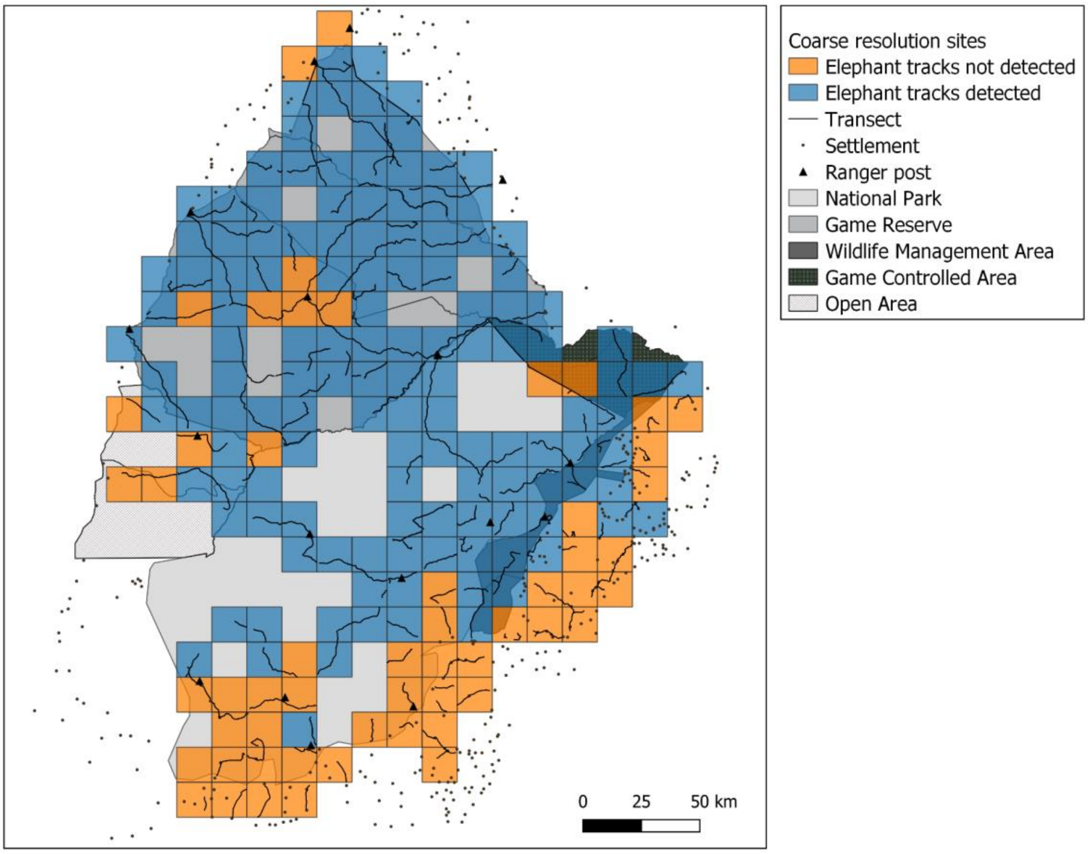

Figure 4.1 Map of the study area showing survey coverage and the pattern of elephant detections at the coarse spatial resolution. Grid cells (225 km^2) are the sites at which elephant space use was investigated at the coarse spatial resolution. Sites where elephant tracks were detected during surveying are shaded blue. Sites where elephants were not detected are shaded orange. Black lines show the coverage of road transects. See Figures A4.2-A4.3 for maps of the distribution of elephant detections at the fine spatial resolution.

4.3.4 Detection covariates

Heterogeneity in detection was modelled using covariates thought to influence the probability of detecting elephant tracks given elephant presence in a site (hereafter referred to as detection covariates). Some detection covariates were used to model heterogeneity in detection among sampling occasions within a site, while other detection covariates were used to model heterogeneity in detection among sites (see below).

4.3.4.1 Coarse spatial resolution

In the coarse spatial resolution analyses (225 km^2 sites), sampling occasions within sites were defined as 4 km segments of road in order to reduce spatial autocorrelation in elephant detections (see 4.3.6). I accounted for variation in survey effort between sampling occasions by including segment length (defined as the number of 500m sections in a sampling occasion, ranging from 1 to 8) as a detection covariate. I also included an index combining road quality and vehicle use intensity (following Strampelli et al., 2022b) as a detection covariate, hereafter referred to as substrate quality, as the ability to detect elephant footprints on roads can be affected by road traffic or substrates that are too hard for the retention of tracks.

Several covariates that are known to impact elephant use of roads, and which may therefore affect the ability to detect elephant tracks along road transects (given elephant presence at a site), were included as detection covariates. Elephants may avoid roads in high-risk areas or outside of protected areas (Blake et al., 2008; Scheijen et al., 2019; Smit et al., 2023; Stokes et al., 2010). In the entire ecosystem analysis, I hypothesise that elephants are more likely to use roads, and thus more likely to be detected by road-based transects given presence at a site, inside protected areas than on village land. I, therefore, included whether or not the sampling occasion was predominantly located in a protected area (coded as 1 for inside PA or 0 for outside PA) as a detection covariate. In the protected areas analysis, I hypothesise that elephants may be less likely to use roads – and therefore less likely to be detected given presence – in areas with a higher probability of elephant carcass occurrence and illegal human use as well as further away from ranger posts and closer to protected area boundaries (as this reflects greater proximity to village land). Elephant use of roads may also differ with habitat structure (e.g. if elephants are more likely to use roads for ease of movement in closed habitat types than open habitat types). For this reason, dominant vegetation type (with more closed miombo woodland coded as 1 and more open *Vachellia-Commiphora* coded as 0) and percentage tree cover were included as detection covariates.

Variation in abundance is also known to cause heterogeneity in detection probabilities: a species is more likely to be detected in sites where it is more abundant (MacKenzie et al., 2017). At the coarse spatial resolution, variation in local abundance is more likely to be reflected in detection probabilities than in site use probabilities. Many of the detection covariates used may therefore be associated with local variation in elephant abundance rather than, or as well as, variation in how elephants use roads. For example, elephants may be less abundant (and therefore less likely to be detected given their presence) at sites in high-risk areas where elephants are also less likely to use roads. Variation in local elephant abundance could also be associated with water availability; for this reason, water availability and distance to riparian habitat were also included as detection covariates.

Effort, substrate quality, legal protection, and dominant vegetation type were measured at the sampling occasion level (i.e., could vary between sampling occasions within a site). All other detection covariates were extracted at the site level (i.e., each sampling occasion within a site assumed the mean value of each covariate for that site). More information on how covariates were measured is provided in section 4.3.5, and a summary of the detection covariates used in each analysis is provided in Table 4.2.

4.3.4.1 Fine spatial resolution

In the fine spatial resolution analyses (1 km^2 sites), sampling occasions within sites were defined as 500m sections of road. As sampling effort was constant between sites (all sites had four sampling occasions), effort was not included as a detection covariate in these analyses. At the fine spatial resolution, substrate quality was the only covariate hypothesised to impact detection.

Table 4.2 Covariates hypothesised to influence the detection of elephant tracks on roads, given elephant presence at a site.

Covariate	**Handle**	**Relationship to detection**	**Hypothesised effect** (+ enhanced detection, - lower detection)	**Measurement**	**Data source**	**Evidence of effect on detection for elephants, if any**	**Spatial resolution and extent**
Sampling effort	Effort	Greater effort per sampling occasion should increase the probability of detection.	+	Number of 500m sections in sampling occasion (ranges from 1 to 8)	Strampelli et al. (2022b)	Petracca et al. (2020)	Coarse resolution, entire ecosystem, protected areas
Substrate quality	Substrate	Better road quality and less vehicle use should increase the probability of detection.	+	Index combining road surface quality and vehicle use intensity	Strampelli et al. (2022b)		Coarse resolution, all extents Fine resolution, all extents
Legal protection	PA	Elephants may be more likely to use roads as movement corridors in PAs than outside PAs, and elephants are more abundant inside PAs. Sampling occasions inside PAs are expected to have a higher probability of detection than those outside of PAs.	+	Whether or not the sampling occasion is predominantly within a protected area (0=not PA, 1=PA)	Strampelli et al. (2022b)		Coarse resolution, entire ecosystem
Illegal human use	Hum	Elephants may be less likely to use roads in high-risk areas, and elephants may be less abundant in areas with illegal human use. Detection probability is expected to decrease with greater illegal human use.	-	Mean probability of illegal human use (measured at site level)	Strampelli et al. (2022b)	Petracca et al. (2020)	Coarse resolution, protected areas
Probability of elephant carcass occurrence	Carcass	Elephants may be less abundant and less likely to use roads in high-risk areas. Detection probability is expected to decrease with higher probabilities of elephant carcass occurrence.	-	Mean probability of elephant carcass occurrence (measured at site level), extracted from a layer developed from aerial census data from 2015.	Beale et al., 2018		Coarse resolution, protected areas

Covariate	**Handle**	**Relationship to detection**	**Hypothesised effect** (+ enhanced detection, - lower detection)	**Measurement**	**Data source**	**Evidence of effect on detection for elephants, if any**	**Spatial resolution and extent**
Distance to ranger post	Post	Elephants may be less likely to use roads and may be less abundant in high-risk areas further from ranger posts. Detection probability is expected to decrease with increasing distance to ranger post.	-	Mean Euclidean distance to ranger post (measured at site level)	Strampelli et al. (2022b)		Coarse resolution, protected areas
Distance to PA boundary	Bound	Within PAs, elephants may be less likely to use roads and may be less abundant in high-risk areas closer to PA boundaries as this reflects greater proximity to village land. Detection probability is expected to increase with increasing distance to PA boundary.	+	Mean Euclidean distance to PA boundary (measured at site level)	Strampelli et al. (2022b)		Coarse resolution, protected areas
Dominant vegetation type	H	Elephants may be more likely to use roads as movement corridors in more closed habitats. Detection probability is expected to increase in areas with a greater percentage of miombo woodland.	+	Whether the sampling occasions is predominantly *Vachellia-Commiphor*a (0) or miombo woodland (1). The Central Zambezian miombo woodland and Eastern miombo woodland types were combined into a single habitat category of miombo woodland.	Strampelli et al. (2022b)	Goswami et al. (2014): for Asian elephants, detection probability varied with habitat type.	Coarse resolution, entire ecosystem, protected areas
Tree cover	C	Elephants may be more likely to use roads as movement corridors in areas with thick cover. Detection probability is expected to increase in areas with thicker cover.	+	Percentage tree cover (measured at site level)	Strampelli et al. (2022b)	Jathanna et al. (2015): for Asian elephants, detection probability varied with forest cover.	Coarse resolution, entire ecosystem, protected areas

Covariate	Handle	Relationship to detection	Hypothesised effect (+ enhanced detection, - lower detection)	Measurement	Data source	Evidence of effect on detection for elephants, if any	Spatial resolution and extent
Distance to riparian habitat	R	As a water-dependent species, elephants may be more abundant closer to rivers. Detection probability can be affected by variation in abundance. If local elephant abundance decreases with increasing distance to rivers, then detection probability may decline with increasing distance to rivers.	-	Mean Euclidian distance to nearest river or drainage line (measured at site level)	Strampelli et al. (2022b) (Rivers & drainage lines, hand digitised)		Coarse resolution, entire ecosystem, protected areas
Water availability	W	As a water-dependent species, elephants may be more abundant in areas with greater dry-season water availability. Detection probability can be affected by variation in abundance. If local elephant abundance increases with water availability, then detection probability may increase with water availability.	+	Mean probability of water availability (mean pixel value, measured at site level)	Strampelli et al. (2022b) (hand-digitised from Google Earth)		Coarse resolution, entire ecosystem, protected areas

4.3.5 Site use covariates

4.3.5.1 Choice of site use covariates

A range of environmental and anthropogenic risk factors were hypothesised to explain variation in elephant site use (defined as the probability of a site being used by elephants). Table 4.3 summarises the covariates used to model heterogeneity in site use in each analysis, and their hypothesised effect on elephant site use.

Environmental variables hypothesised to influence elephant site use in the coarse resolution (225 km^2 sites) analyses included distance to riparian habitat, water availability, tree cover, dominant vegetation type, and vegetation productivity. Analyses at the fine spatial resolution (1km^2 sites) included the same environmental covariates as the coarse resolution analyses, except for dominant vegetation type, which was excluded as this covariate did not exhibit variation at the fine spatial resolution.

The risk factors hypothesised to influence elephant site use varied with spatial extent. For analysis of the entire ecosystem at the coarse spatial resolution, risk factors included human population density, building density, distance to settlement, conversion to agriculture, and legal protection. For analyses within protected areas at both spatial resolutions, risk covariates included the probability of illegal human use (on a scale from 0 to 1), the probability of elephant carcass occurrence (on a scale from 0 to 1), distance to protected area boundary, and distance to ranger post (see Section 4.3.5.2 for details on how covariates were calculated). For village land analyses at the fine spatial resolution, risk factors included human population density, building density, and conversion to agriculture (distance to settlement was excluded as it exhibited little variation at this spatial resolution).

Due to sample size constraints, I only tested for a limited number of biologically plausible interactions between risk variables and environmental variables in the fine spatial resolution, protected areas analysis to investigate if risk influenced elephant responses to natural habitat features. Specifically, I tested for interactions between the probability of elephant carcass occurrence and tree cover (Carcass * C), elephant carcass occurrence and NDVI (Carcass * NDVI), elephant carcass occurrence and water availability (Carcass * W), and elephant carcass occurrence and distance to riparian habitat (Carcass * R). Table 4.2 explains abbreviation handles.

To assess whether natural predation risk influenced elephant use within protected areas at the fine spatial resolution, the probability of lion site use was included as a site use covariate to approximate predation risk.

4.3.5.2 Calculation of site use covariates

Covariates were extracted at the site level, whereby each covariate was assigned a mean value per site. Distance to riparian habitat was measured as the mean Euclidean distance (in km) of each 30 x 30-m pixel in each site to the nearest river or drainage line (using the HydroRIVERS layer; https://www.hydrosheds.org/page/hydrorivers) with the Spatial Analyst tool in ArcMap 10.4.1. Note that rivers and drainage lines vary in their likelihood to hold water during the dry season; this variation is not captured by the distance to riparian habitat covariate but is instead accounted for in the water availability covariate.

A layer for water availability in the ecosystem was developed by Strampelli et al. (2022b) to account for the fact that rivers and drainage lines of different sizes have different likelihoods of holding water during the dry season. Strampelli et al. (2022b) scored each 1 km segment of river/drainage line based on its width and annual average rainfall, with higher scores reflecting a higher likelihood of dry season water. This layer was rasterized and used to generate a map of predicted water availability across the study area, in which each pixel value represents a water availability score (with higher values representing greater likelihood of availability of dry season water). Predicted water availability per site was measured as the mean value of all pixels within the site using the Zonal Statistics tool in QGIS 3.6.3 (unless indicated otherwise, this same procedure was used to extract a site-specific value for each of the covariates below).

Tree cover was quantified by rasterizing a 20 m resolution land cover product (ESA CCI Land Cover, http://2016africalandcover20m.esrin.esa.int/), and assigning pixel values of ‘1’ to all pixels within the ‘Trees cover areas’ categories, and a value of ‘0’ to all pixels within other land cover categories. Site-specific measures of tree cover were then obtained as the percentage of pixels within each site classified as containing tree cover.

The dominant vegetation types in the Ruaha-Rungwa ecosystem are *Vachellia-Commiphora* bushland and miombo woodland (Olson et al., 2001). The two miombo woodland ecoregions that occur in the ecosystem (Central Zambezian miombo woodlands and Eastern miombo woodlands, see Chapter 2) were combined into a single habitat category of miombo woodland. Dominant vegetation type was quantified using a 30 m resolution raster developed by Strampelli et al. (2022b) from existing layers (Olson et al., 2001; https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world) in which pixels were assigned a value of ‘1’ if in miombo woodland, and a value of ‘0’ if in *Vachellia-Commiphora*. Site-specific measures of dominant vegetation type were then obtained as the percentage of pixels within each site classified as miombo woodland (higher values indicate a greater percentage of miombo woodland within the site).

Primary productivity was measured as the mean NDVI and standard deviation in NDVI for each site during the survey period, using raster layers (at 250 m resolution) for mean and standard deviation of NDVI developed by Strampelli et al. (2022b) using the MOD13Q1 product from NASA Earthdata (NASA LP DAAC, https://lpdaac.usgs.gov) to obtain 16-day NDVI imagery for both survey periods (July 1-November 30th 2017; July 1-December 16th 2018). These were then averaged to obtain a single mean and standard deviation NDVI value for each pixel, before obtaining a mean value per site by calculating an average of the pixel values within each site.

Site-specific measures of human population density were obtained from a human population layer for Tanzania for the year 2017 from the WorldPop database (WorldPop, 2020). In this layer, pixel values represent the number of people at a resolution of 30-arc seconds (approximately 1 km at the equator). The mean human population density (i.e., the mean pixel value) per site was extracted using the Zonal Statistics tool in QGIS 3.14.

Distance to settlement was quantified from a hand-digitised layer of settlements developed by Strampelli et al. (2022b) from Google Earth satellite imagery and OpenStreetMap layers, which was subsequently converted to a raster (30 m resolution raster) of distance to nearest human settlement using the Spatial Analyst tool in ArcMap 10.4.1. The natural logarithm (ln) of distance to settlements was used as I expected the strength of any effect on elephant space use to decrease with distance. Site-specific measures of distance to settlement were defined as the mean natural logarithm (ln) of distance to settlement per site.

Building density was quantified using a settlement layer (data resolution of 1 arc-second, approximately 30m) developed for Tanzania for the year 2015 by the Facebook Connectivity Lab and Center for International Earth Science Information Network at Columbia University (https://www.ciesin.columbia.edu/data/hrsl/#data). In this layer, a pixel is assigned a value of 1 if at least one building was detected, and a value of 0 if no building was detected. Site-specific measures of building density were calculated as the sum of the number of pixels containing one or more buildings using the Zonal Statistics tool in QGIS 3.14.

Legal protection was measured as the proportion of each site occurring within a protected area. A modified protected areas layer (from the IUCN World Database on Protected Areas, with the Muhesi Game Reserve boundary modified to reflect current effective boundaries) was converted into a 30 m resolution raster in which pixels within a protected area were assigned a value of 1, and pixels outside a protected area were assigned a value of 0.

The modified protected areas layer (converted to a raster with 30 m resolution) was also used to obtain site-specific distances to protected area boundaries. The distance of each pixel to the nearest protected area boundary was calculated using the Spatial Analyst tool in ArcMap 10.4.1. Site-specific measures of distance to protected area boundary were defined as the mean distance to protected area boundary per site.

Measures of conversion of natural habitat to agriculture (cropland) were obtained from Google Earth Grids (Jacobson et al., 2015), a 1-km resolution raster of cropland. Site-specific measures of cropland conversion were defined as the percentage of pixels within each site classified as cropland, with higher values indicating a greater percentage of cropland within the site.

The probability of illegal human use (on a scale from 0 to 1) was the probability that a site within protected areas was used by humans. Site-specific probabilities of illegal human use were obtained from an occupancy model of illegal human activity (Strampelli et al., 2022b). This model was developed using detection/non-detection data on illegal human use (footprints and bicycle/motorcycle tracks) collected during the multispecies survey of the Ruaha-Rungwa ecosystem.

The probability of elephant carcass occurrence for each site was derived from a layer developed by Beale et al. (2018) for Ruaha-Rungwa using data from TAWIRI aerial surveys conducted in 2015. Each pixel (pixel size 5 x 2.5 km) in this layer is associated with a modelled probability of elephant carcass occurrence (on a scale from 0 to 1). The systematic reconnaissance flight aerial survey method involves sampling along narrow strip transects at 5-10 km spacing, such that data on direct observations of carcasses are only available for a small fraction of the survey zone. Beale et al. (2018) used observations of elephant carcasses along these transects to model the distribution of elephant carcasses as a function of covariates and generate modelled probabilities of carcass occurrence for the whole survey zone. The mean probability of carcass occurrence (i.e., the mean pixel value) per site was extracted using the Zonal Statistics tool in QGIS 3.14. As the proportion of illegally killed elephants (PIKE) in Ruaha-Rungwa was 0.74 in 2015 (see also Chapter 3), indicating that substantially more elephant carcasses were due to poaching rather than natural mortality, the probability of elephant carcass occurrence was used as an indicator of recent poaching risk.

Distance to ranger post was measured as the mean Euclidean distance of each 30 x 30 m pixel in each site to the nearest ranger post using the Spatial Analyst tool in ArcMap 10.4.1.

Natural predation risk from lions was included as a covariate in one of the fine-resolution analyses. I used probabilities of lion use for each site (on a scale from 0 to 1) from a lion use occupancy model developed by Strampelli et al. (2022b). This model was developed using detection/non-detection data on lion occurrence collected during the multispecies survey of the Ruaha-Rungwa ecosystem.

Table 4.3 Covariates hypothesised to influence elephant site use at the coarse and fine spatial resolutions.

Covariate	**Handle**	**Relationship to use**	**Hypothesised effect** (+ enhanced use, - less likely to use)	**Measurement (at site level)**	**Data source**	**Evidence of effect**	**Spatial resolution and extent**
Legal protection	PA	Elephants are more likely to occur within protected areas where they and their habitat are legally protected, than outside protected areas.	+	Percentage of site that is legally protected.	IUCN World Database on Protected Areas, modified (https://protectedpprot e.net/), Riggio et al. (2019)	Goswami et al. (2014) for Asian elephants; Petracca et al. (2020)	Coarse resolution, entire ecosystem
Habitat conversion to agriculture	Crop	Areas where natural vegetation has been converted to agriculture may be unsuitable habitat. Elephants may avoid agricultural areas due to risk of persecution and disturbance.	-	Percentage of habitat converted to cropland	Jacobsen et al. (2015)	Hoare & du Toit (1999); Songhurst et al. (2016)	Coarse resolution, entire ecosystem Fine resolution, village land
Human population density	Pop	Elephants avoid areas with greater human population density due to risk of persecution and disturbance. Habitat in areas with higher human population density may also be unsuitable.	-	Estimated number of people per pixel at a resolution of 30 arc seconds (approximately 1 km resolution at the equator, equivalent to a 1 km^2 grid cell) with country totals adjusted to match corresponding official UNDP population estimate, for 2017.	WorldPop (2020) (10.5258/SOTON/WP00671)	Graham et al. (2010); Hoare & DuToit (1999)	Coarse resolution, entire ecosystem Fine resolution, village land
Building density	Settlement	Elephants may avoid built-up areas due to risk of persecution and disturbance. Habitat in built-up areas is likely to be unsuitable.	-	Sum of the number of pixels containing one or more buildings (pixel is 1 if building detected, 0 if no building detected). Data resolution of 1 arc-second (approximately 30m resolution) for the year 2015.	Facebook Connectivity Lab and Center for International Earth Science Information Network, Columbia University (2016). https://www.ciesin.columbia.edu/data/hrsl/#data		Coarse resolution, entire ecosystem Fine resolution, village land

Covariate	**Handle**	**Relationship to use**	**Hypothesised effect** (+ enhanced use, - less likely to use)	**Measurement (at site level)**	**Data source**	**Evidence of effect**	**Spatial resolution and extent**
Distance to human settlements	DistV	Elephants avoid areas close to human settlements due to risk of persecution and disturbance. Habitat near human settlements may also be unsuitable.	+	Natural logarithm of mean distance to nearest settlement, with asymptote (Ln)	Strampelli et al. (2022b): settlements & hamlets, hand digitised	de Boer et al. (2013); Douglas-Hamilton et al. (2005); Clark et al. (2009); Graham et al. (2010); Petracca et al. (2020); Roever et al., 2013; Yackulic et al. (2011); Songhurst, et al. (2016)	Coarse resolution, entire ecosystem
Distance to PA boundary	Bound	Within PAs, elephants may avoid areas near the boundary (closer to village land) where mortality risk and the risk of disturbance are likely to be greater.	+	Mean Euclidian distance to nearest PA boundary (in km)	IUCN World Database on Protected Areas, modified (https://protectedplanet.net/), Riggio et al. (2019)	Pittiglio et al. (2012); Rich et al. (2016)	Coarse resolution, protected areas Fine resolution, protected areas
Illegal human use	Hum	Within PAs, elephants may avoid areas which are used by humans to reduce mortality risk and disturbance.	-	Mean probability of illegal human use. Data availability is limited to protected areas.	Strampelli et al. (2022b)	Beale et al. (2018): elephant occurrence positively associated with increasing poacher travel cost from villages; Buij et al. (2007) for African forest elephants; Petracca et al. (2020)	Coarse resolution, protected areas Fine resolution, protected areas

Covariate	**Handle**	**Relationship to use**	**Hypothesised effect** (+ enhanced use, - less likely to use)	**Measurement (at site level)**	**Data source**	**Evidence of effect**	**Spatial resolution and extent**
Probability of elephant carcass occurrence	Carcass	Elephants may avoid areas of higher poaching risk to reduce mortality risk.	-	Mean probability of elephant carcass occurrence, extracted from a layer developed from aerial census data for the ecosystem (year 2015) Data availability is limited to protected areas.	Beale et al. (2018)	Goldenberg et al. (2018); Roever et al., (2013)	Coarse resolution, protected areas Fine resolution, protected areas
Distance to ranger post	Post	Elephants may use areas in proximity to ranger posts where they are afforded greater protection from poaching and disturbance.	-	Mean Euclidian distance to nearest ranger post (in km)	Strampelli et al. (2022b)	Beale et al. (2018)	Coarse resolution, protected areas only Fine resolution, protected areas only
Water availability	W	As a water-dependent species, elephants are more likely to use areas with greater dry season surface water availability.	+	Mean probability of water availability (mean pixel value)	Strampelli et al. (2022b): hand-digitised from Google Earth	Pittiglio et al. (2012); Roever et al. (2013); Smit et al. (2007)	Coarse resolution, entire ecosystem, protected areas only Fine resolution, protected areas and village land
Distance to riparian habitat	R	As a water-dependent species, elephants are more likely to use areas closer to rivers. Riparian habitat also provides shade and foraging resources.	-	Mean Euclidian distance to nearest river or drainage line (in km)	Strampelli et al. (2022b): rivers & drainage lines, hand digitised)	Anderson et al. (2016); Snyder et al. (2021); Roever et al. (2013); Smit, Grant & Whyte (2007)	Coarse resolution, entire ecosystem, protected areas only Fine resolution, protected areas and village land
Dominant vegetation type	H	Elephants are more likely to use the more productive *Vachellia-Commiphora* habitat than miombo habitat. The nutrient content in the foliage (leaves and grass) of miombo plants is low Frost, 1996).	-	Percentage of site that is miombo woodland. The Central Zambezian and Eastern miombo woodland types were combined into a single habitat category of miombo woodland.	WWF Terrestrial Ecoregions of the World (Olson et al., 2001) https://www.worldwildlife.org/publications/terrestrialecoregions-of-the-world)		Coarse resolution, entire ecosystem, protected areas only

Covariate	**Handle**	**Relationship to use**	**Hypothesised effect** (+ enhanced use, - less likely to use)	**Measurement (at site level)**	**Data source**	**Evidence of effect**	**Spatial resolution and extent**
Tree cover	C	Elephants are more likely to use areas of intermediate or greater tree cover. In the dry season, when elephants are primarily browsers, wooded areas provide greater forage resources.	+	% cover (woodland only)	ESA CCI Land Cover – S2 prototype land cover 20m map of Africa (http://2016africalandcover20m.esrin.esa.int/)	Anderson et al. (2016) (intermediate and dense tree cover); Beale et al. (2018); Roever et al. (2013) (intermediate tree cover); Smit et al. (2007)	Coarse resolution, entire ecosystem, protected areas only Fine resolution, protected areas and village land
NDVI (mean)	NDVIave	Elephants are more likely to use areas with greater forage resources; NDVI is a measure of vegetation productivity used to approximate the availability of forage resources.	+	Mean NDVI value at site during survey period (mean pixel value)	MCD43A4_NDVI (NASA LP DAAC, https://lpdaac.usgs.gov/)	Anderson et al. (2016); Pittiglio et al. (2012); Thapa, Kelly & Pradhan (2019) for Asian elephants; Young et al. (2009)	Coarse resolution, entire ecosystem, protected areas only Fine resolution, protected areas and village land
NDVI (standard deviation)	NDVIstd	Elephants are more likely to use areas with greater forage resources; I use the standard deviation of NDVI, a measure of variation in vegetation composition and growth, to approximate the availability of forage resources.	+	Standard deviation of NDVI values at site during survey period (mean pixel value)	MCD43A4_NDVI (NASA LP DAAC, https://lpdaac.usgs.gov/)	Anderson et al. (2016); Pittiglio et al. (2012); Thapa et al. (2019) for Asian elephants; Young et al. (2009)	Coarse resolution, entire ecosystem, protected areas only Fine resolution, protected areas and village land
Natural predation risk	Lion	At the fine spatial resolution, elephants may avoid areas that are used by lions to reduce predation risk.	-	Probability of lion site use	Strampelli et al. (2022b)		Fine resolution, protected areas only, using the subset of sites where lions were detected at the coarse spatial resolution

4.3.6 Occupancy modelling

For each analysis, I constructed matrices for elephant detection/non-detection data, detection covariates, and site use covariates (Smit & Strampelli, 2023).

At the coarse spatial resolution, I analysed elephant detection/non-detection data using single-season, single-species occupancy models using the *unmarked* package (Fiske & Chandler, 2011) in R version 2022.02.2 (RStudioTeam, 2022). Separate analyses were conducted for each spatial extent. For the coarse scale analyses, I could not use occupancy models which account for spatial correlation in detections (Hines et al., 2010), because transects in some sites were noncontinuous. Instead, I removed spatial autocorrelation in detections by increasing the sampling occasion length until detection in one sampling occasion was independent of detection on the previous sampling occasion (following Henschel et al., 2016, Searle et al., 2020 & Strampelli et al., 2022b). This was done in program PRESENCE (Hines, 2006) by increasing sampling occasion length by 500m increments until the standard single-season occupancy model ranked higher than the correlated detections model (Hines et al., 2010), and the probability of presence on a sampling occasion given absence on the previous sampling occasion ($\theta^{[0\}}$) was approximately equal to the probability of presence on a sampling occasion given presence on a previous sampling occasion ($\theta^{[1\}}$). Spatial independence was reached at a sampling occasion length of 4 km.

At the fine spatial resolution, I analysed elephant detection/non-detection data using single-season occupancy models that account for spatial autocorrelation in detections (Hines et al., 2010; see Box 4.1). It was possible to use the correlated detections model for the fine spatial resolution analyses because sampling occasions consisted of multiple continuous 500m segments along a transect. Analyses were conducted in PRESENCE, as the Hines et al. (2010) correlated detections model was not available in the *unmarked* package for R.

In all analyses, I used a two-step process to model detection (p) and site use (ψ). First, I modelled covariates hypothesised to influence detection while holding site use constant using the most parameterized model of non-correlated site use covariates to identify which of the competing models best explained the observed heterogeneity in detection (see Appendix A4.3 for detection model rankings). The highest-ranked detection model was then used to identify the best model for site use. I did this by fixing the best model for detection and varying all possible combinations of non-correlated site covariates. Models were ranked using the Akaike Information Criterion (AIC) for the fine spatial resolution analyses and AICc (AIC adjusted for small sample sizes, defined as the number of sites) for the coarse spatial resolution analyses. All models were fit using maximum likelihood estimation.

Box 4.1 Correlated detections model

Standard single-season, single-species occupancy models assume that there is independence in survey outcomes (detection or non-detection) between survey occasions (MacKenzie et al., 2017). When the survey outcomes are not independent, the probability of detecting the species in one survey depends on whether or not it was detected in another survey; this is a common feature of occupancy studies using spatially replicated surveys. The Hines et al. (2010) correlated detections model deals with the lack of independence between detections within a site by modelling the availability of a species for detection as a first-order Markov process, such that the probability of the species being available for detection in a survey depends on whether the species was available (or not) for detection in the previous survey. The following probabilities are defined for modelling the availability of a species for detection:

- θ_1, the probability that the species is available for detection in the first sampling occasion
- $\theta^{[0]}$, the probability that species is available for detection in a sampling occasion given it was not available in the previous sampling occasion
- $\theta^{[1]}$, the probability that the species is available for detection in a sampling occasion given it was available in a previous sampling occasion

Probability statements including the above probabilities for the availability process are defined for each detection history (for each site), and linked in a single model likelihood which can be maximised to obtain maximum likelihood estimates of psi, p, θ_1, $\theta^{[0]}$, and $\theta^{[1]}$. In this model, detection probability is conditional on availability and is defined as the probability of detecting the species given the species is available for detection.

Covariates were tested for collinearity using Pearson's correlation test (see Appendix A4.2 for correlation plots). Covariates were not included in the same model if $r \geq 0.45$. There is no formal rule or cutoff value at which covariates are considered highly collinear. I opted for this conservative cutoff to reduce the risk of issues arising from multicollinearity, as a cutoff of $r \geq 0.45$ indicates a moderate correlation where >20% of the variation in one variable is explained by variation in the second variable.

Covariates were standardised on the z-scale to facilitate model convergence (Mackenzie et al., 2017). The number of possible covariates included within a single model was informed by the rule of thumb of 15-25 observations (defined as detections) per predictor variable (Green, 1991). Univariate models were employed in the fine-scale, village land analysis due to the low number of elephant detections on village land.

I considered all models <ΔAIC or ΔAICc of <2 to be the final model set, as these are considered to have substantial support (Burnham & Anderson, 2004). All models with ΔAIC of 7, considered to have some but substantially less support (Burnham & Anderson, 2004), can be found at https://datastorre.stir.ac.uk/browse?type=author&value=Smit%2C+Josephine.

The untransformed coefficients (β) for detection and site use covariates are presented from the highest-ranked model in which they appear. The direction and strength of influence of covariates on site use and detection were determined from the sign and value of the β coefficients. Covariates were considered to have a statistically significant impact if the 95% confidence interval of the β coefficient did not span zero (Mackenzie & Bailey, 2004). For the coarse resolution analyses, 95% confidence intervals for β coefficients were generated using asymptotic normal approximation using the *unmarked* package. For the fine resolution analyses conducted in PRESENCE, confidence intervals were calculated manually as $\beta \pm 1.96$ SE (Mackenzie & Bailey, 2004). I present plots showing the influence of statistically significant covariates on elephant site use and detection probability in the main text of this chapter, while plots for non-significant covariates are presented in Appendix A4.5.

Model-averaged site-specific estimates of detection probability (p) and site use (ψ) were obtained using the *MuMin* package (Bartoń, 2013) in R for the coarse resolution analyses and the model averaging tool in PRESENCE for the fine resolution analyses. These model-averaged estimates are a weighted average of the detection and site use probabilities for each site from the models in the final model set, which are weighted by the AIC or AICc weights (Burnham & Anderson, 2004; MacKenzie et al., 2017). Model-averaged mean site use ($\bar{\hat{\psi}}$) and detection probabilities ($\bar{\hat{p}}$) for each of the spatial extents investigated were then obtained by averaging across the model-averaged site-specific detection and site use probabilities.

Model fit was assessed for the top-ranked and most parameterized models within each final model set (see Appendix A4.4 for results of model fit tests) using the Mackenzie and Bailey goodness-of-fit test (Mackenzie & Bailey, 2004). If the final model set included more than one model with the largest number of parameters, model fit was tested for the highest-ranked model. If there was evidence of overdispersion ($\hat{c} > 1.5$), model selection was done using the modified AIC or AICc criterion (QAIC or QAICc) and standard errors for β coefficients were adjusted following Mackenzie et al. (2017) by multiplying the standard error by the square root of the $\hat{c}$ value of the top-ranked model. These adjusted standard errors were then used to calculate confidence intervals adjusted for overdispersion.

I have already described how the assumptions of closure and independence in detection histories were met or dealt with (see 4.2.1). I am confident that the assumption that signs of species presence were correctly identified during surveys was met as data were collected by experienced trackers and elephant tracks are highly distinctive and difficult to confuse with those of any other species. Occupancy models also assume that the probability of use across sites and the probability of detection across sites and sampling occasions are either constant or can be modelled using covariates; I therefore assume that heterogeneity in the probability of detection and use has been sufficiently modelled using covariates.

4.4 Results

4.4.1 Coarse resolution, entire ecosystem

In the coarse resolution, entire ecosystem analysis, the probability of detecting elephant tracks given that elephants were present in the site (the detection probability) was influenced by sampling effort, legal protection, and dominant vegetation type. The detection probability increased with survey effort and was higher in sampling occasions in protected areas than on unprotected village land. Detection probability was higher in sites where *Vachellia-Commiphora* was the dominant vegetation type, and lower in sites where miombo woodland was dominant (Figure 4.4).

The final model set (all models within ΔAICc <2) for elephant site use (the probability of elephants using a site) in the coarse resolution, entire ecosystem analysis comprised five models (Table 4.4). Across the entire ecosystem, elephant site use was most strongly predicted by and significantly negatively associated with cropland ($\beta = -1.09$ [SE 0.30]; Table 4.5). A negative association between elephant site use and human population density ($\beta = -1.54$ [SE 0.53]) was also well supported (cropland and population density were highly collinear and therefore not included in the same models). Elephant site use was also positively associated with miombo woodland and increasing distance to riparian habitat, and negatively associated with NDVI, although none of these effects were statistically significant (Table 4.5, Figures A4.9-A4.11).

Using the final model set, I generated model-averaged mean estimates of the probability of detection ($\bar{p}$) and site use ($\bar{\psi}$) for the coarse resolution, entire ecosystem analysis (Table 4.14). The mean probability of detecting elephant tracks given presence at a site was 0.65. An estimated 78% of surveyed sites within the ecosystem were predicted to be used by elephants (Table 4.14). This was slightly higher than the naïve estimate of 70% (where the naïve estimate is simply the number of sites where elephants were detected during sampling divided by the number of sites sampled). Figure 4.5 shows that the probability of elephant use of sites within protected areas is predicted to be very high, while site use probability declines at the edges of protected areas and on unprotected village land, especially in the southeast of the ecosystem.

Table 4.4 Model rankings for elephant site use (ψ) and detection (p) in the coarse resolution, entire ecosystem analysis. Final set based on models with ΔAICc <2. Due to small sample size (n=185 sites), adjusted AIC (AICc) was used for model ranking. W_i: relative model weight. nPars: number of parameters in the model. −2*log: twice the negative log-likelihood. Crop (site use covariate): percentage of a site that is cropland. Pop (site use covariate): mean human population density. NDVI (site use covariate): mean NDVI. H (site use covariate): dominant vegetation type, measured as the percentage of miombo woodland in a site. R (site use covariate): mean distance to riparian habitat. Effort (detection covariate): the number of 4 km sampling occasions in a site. PA (detection covariate): whether the sampling occasion was predominantly inside a protected area (coded as 1) or outside a protected area (coded as 0). H (detection covariate): whether the sampling occasion was predominantly Vachellia-Commiphora (coded as 0) or miombo woodland (coded as 1).

Rank	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ(Crop) p(Effort + PA + H)	684.29	0	0.37	-335.91	6
2	ψ(Pop) p(Effort + PA + H)	685.46	1.16	0.21	-336.49	6
3	ψ(Crop + NDVI) p(Effort + PA + H)	686.13	1.83	0.15	-335.75	7
4	ψ(Crop + H) p(Effort + PA + H)	686.17	1.87	0.14	-335.77	7
5	ψ(Crop + R) p(Effort + PA + H)	686.26	1.97	0.14	-335.82	7

Table 4.5 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present), β-coefficient estimates, and associated standard errors and 95% confidence intervals of covariates explaining elephant site use (ψ) and detection (p) in the coarse resolution, entire ecosystem analysis. Only models retained in the final model set (ΔAICc<2) are presented. Bolded covariates have a significant effect in the top model in which they appear. For covariate definitions, see Table 4.5.

Covariate	Σw	β ($SE_β$)	**Confidence interval** (β ± 1.96 x SE)
Detection (p)			
Effort	1	0.31 (0.10)	0.12, 0.51
Legal protection (PA)	1	1.39 (0.19)	1.02, 1.75
Dominant vegetation (H)	1	-1.08 (0.14)	-1.36, -0.806
Site use (ψ)			
Conversion to cropland (Cropland)	0.79	-1.09 (0.30)	-1.67, -0.50
Human population density (Pop)	0.21	-1.54 (0.53)	-2.58, -0.49
Primary productivity (NDVI)	0.15	-0.16 (0.27)	-0.68, 0.37
Dominant vegetation (H)	0.14	0.14 (0.26)	-0.37, 0.64
Distance to riparian habitat (R)	0.14	0.12 (0.28)	-0.43, 0.67

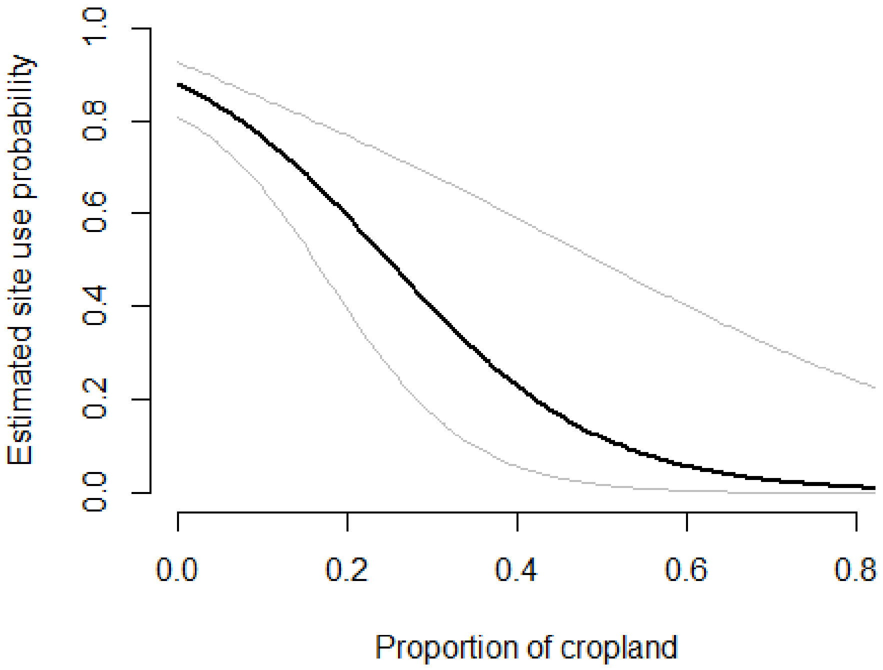

Figure 4.2 Relationship between the probability of elephant site use and the proportion of site converted to cropland with 95% confidence intervals shown as grey lines. The value of the covariate at which the probability of site use drops below 0.4 was estimated following Strampelli (2021). The probability of site use falls below 0.4 once approximately 30% of a site has been converted to agriculture. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value.

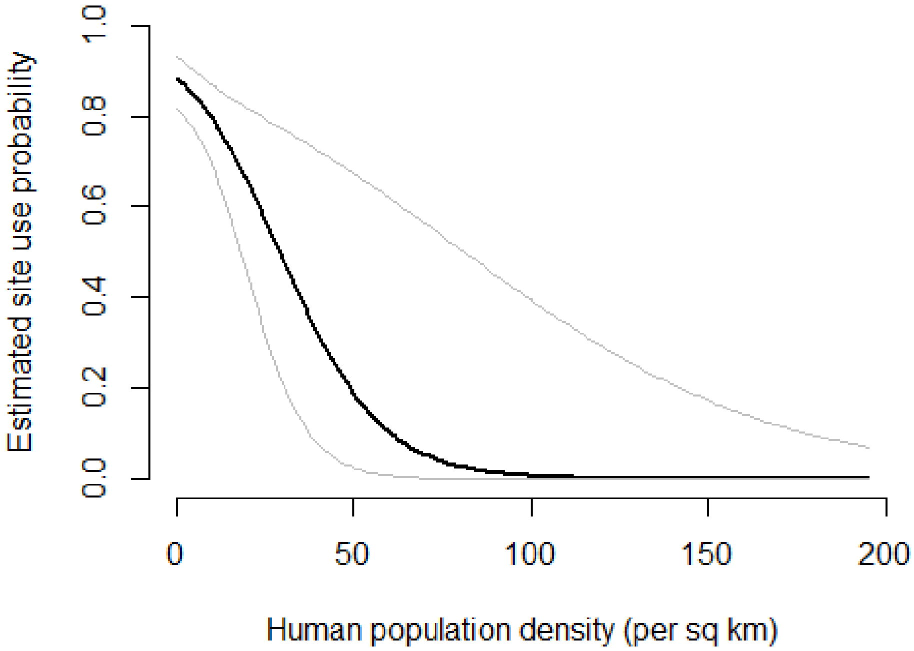

Figure 4.3 Relationship between the probability of elephant site use and mean human population density at a site, with 95% confidence intervals shown as grey lines. The value of the covariate at which the probability of site use drops below 0.4 was estimated following Strampelli (2021). The probability of site use falls below 0.4 at a human population density of approximately 40 people per km^2. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value.

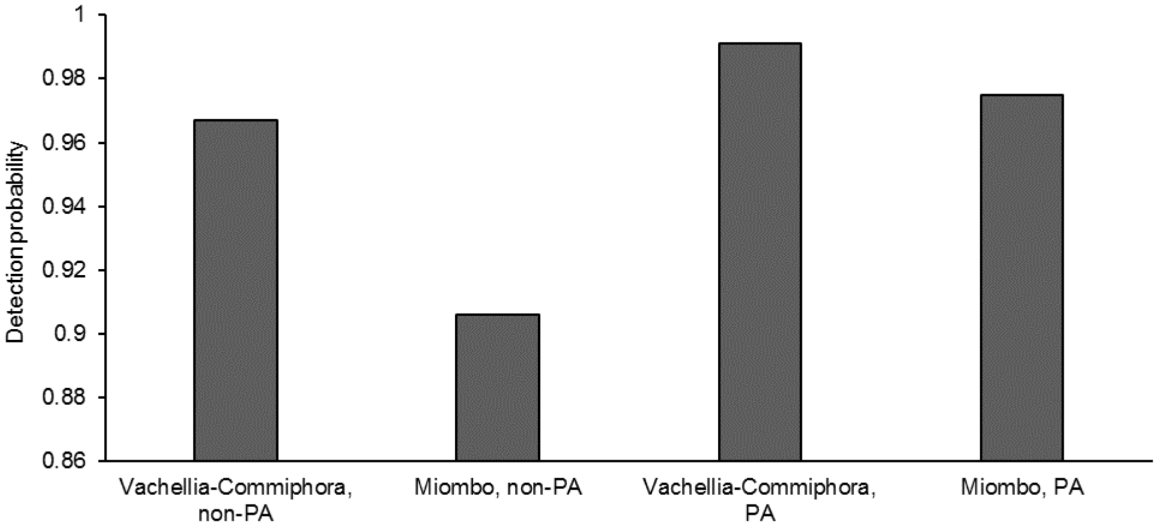

Figure 4.4 Predicted effect of dominant vegetation type (*Vachellia-Commiphora* or miombo) and legal protection (PA: inside a protected area or non-PA: outside a protected area) on the probability of detecting elephant tracks, when effort is held at its median value.

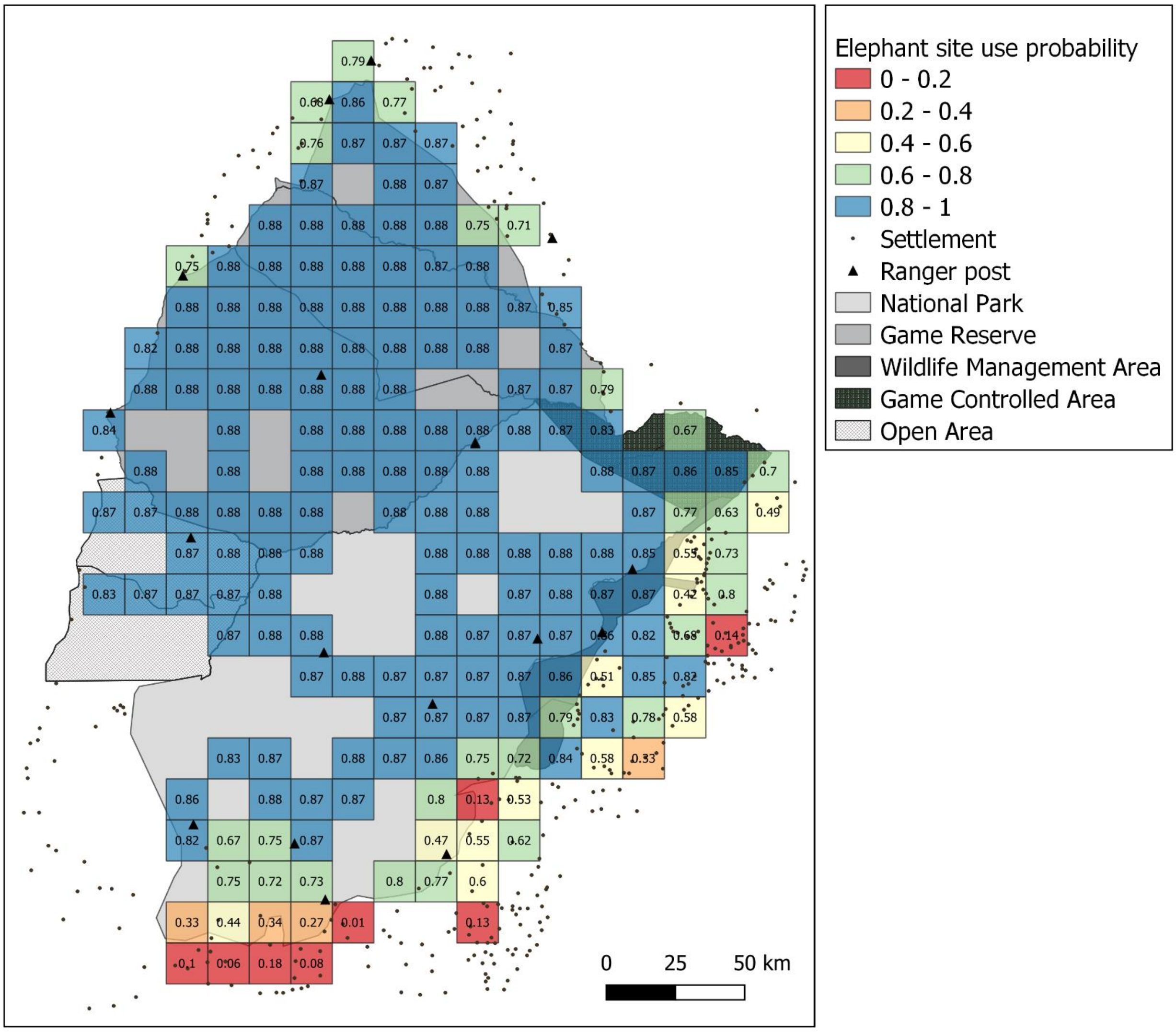

Figure 4.5 Model-averaged estimates of elephant site use probability per site for the coarse resolution, entire ecosystem analysis. Locations of ranger posts (black triangles) and settlements (black dots) are shown.

4.4.2 Coarse resolution, protected areas

Within protected areas at the coarse spatial resolution, the detection of elephant tracks was most strongly influenced by sampling effort, dominant vegetation type, and elephant carcass occurrence. As in the entire ecosystem analysis, detection probability increased with survey effort and was higher in sites where *Vachellia-Commiphora* was the dominant vegetation type (Figure 4.9 & Table 4.7). Detection of elephant tracks was significantly negatively associated with the probability of elephant carcass occurrence (Figure 4.10). Detection of elephant tracks increased with increasing distance to ranger post (Figure 4.11), although the effect was not statistically significant. Increasing distance to riparian habitat had a non-significant positive effect on detection.

The final model set for elephant site use within protected areas at the coarse spatial resolution comprised three models (Table 4.6). Within protected areas, elephant site use was most strongly predicted by elephant carcass occurrence, tree cover, and distance to riparian habitat (Figures 4.6-4.7 & Table 4.7). Site use was significantly positively associated with elephant carcass occurrence (β = 4.81 [SE 1.39]) and tree cover (β = 1.71 [SE 0.60]), and significantly negatively associated with distance to riparian habitat (β = -1.04 [SE 0.49]). There was also a non-significant positive association between elephant site use and water availability (Figure A4.12). None of the risk factors investigated (probability of illegal human use, distance to protected area boundary and ranger post) featured in any of the models in the final model set.

The model-averaged mean probability of detecting elephant tracks ($\bar{p}$) within protected areas at the coarse spatial resolution was 0.74 (Table 4.14). An estimated 92% of surveyed sites within protected areas at this spatial resolution were predicted to be used by elephants (Table 4.14). This was slightly higher than the naive estimate of 87%.

Table 4.6 Model rankings for elephant site use (ψ) and detection (p) in the coarse resolution, protected areas analysis. Final set based on models with ΔAICc <2. Due to small sample size (n=139 sites), adjusted AIC (AICc) was used for model ranking. Wi: relative model weight. nPars: number of parameters in the model. −2*log: twice the negative log-likelihood. Carcass (site use covariate): mean probability of elephant carcass occurrence for a site. C (site use covariate): percentage tree cover in a site. R (site use covariate): mean distance to riparian habitat in a site. W (site use covariate): mean water availability in a site. Effort (detection covariate): the number of 4 km sampling occasions in a site. H (detection covariate): whether the sampling occasion was predominantly Vachellia-Commiphora (coded as 0) or miombo woodland (coded as 1). Carcass (detection covariate): mean probability of elephant carcass occurrence, assessed at the site level. Post (detection covariate): mean distance to ranger post, assessed at the site level. R (detection covariate): mean distance to riparian habitat, assessed at the site level.

Rank	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ(Carcass + C + R) p(Effort + H + Carcass + Post + R)	581.86	0.00	0.50	-280.07	10
2	ψ(Carcass + C + W) p(Effort + H + Carcass + Post + R)	583.21	1.35	0.26	-280.75	11
3	ψ(Carcass + C + R + W) p(Effort + H + Carcass + Post + R)	583.33	1.47	0.24	-279.63	11

Table 4.7 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present), β-coefficient estimates, and associated standard errors and 95% confidence intervals of covariates explaining elephant site use (ψ) and detection (p) in the coarse resolution, protected areas analysis. Only models retained in the final model set (ΔAICc<2) are presented. Bolded covariates have a significant effect in the top model in which they appear. For covariate definitions, see Table 4.6.

Covariate	**Σw**	**β ($SE_β$)**	**Confidence interval** (β ± 1.96 x SE)
Detection (p)			
Effort	1	0.29 (0.11)	0.08, 0.50
Dominant vegetation (H)	1	-1.14 (0.15)	-1.44, -0.85
Probability of elephant carcass occurrence (Carcass)	1	-0.29 (0.11)	-0.51, -0.08
Distance to ranger post (Post)	1	0.21 (0.11)	-0.01, 0.42
Distance to riparian habitat (R)	1	0.06 (0.11)	-0.16, 0.27
Site use (ψ)			
Probability of elephant carcass occurrence (Carcass)	1	4.81 (1.39)	2.09, 7.53
Tree cover (C)	1	1.71 (0.60)	0.53, 2.88
Distance to riparian habitat (R)	0.74	-1.04 (0.49)	-1.99, -0.08
Water availability (W)	0.50	0.71 (0.42)	-0.11, 1.52

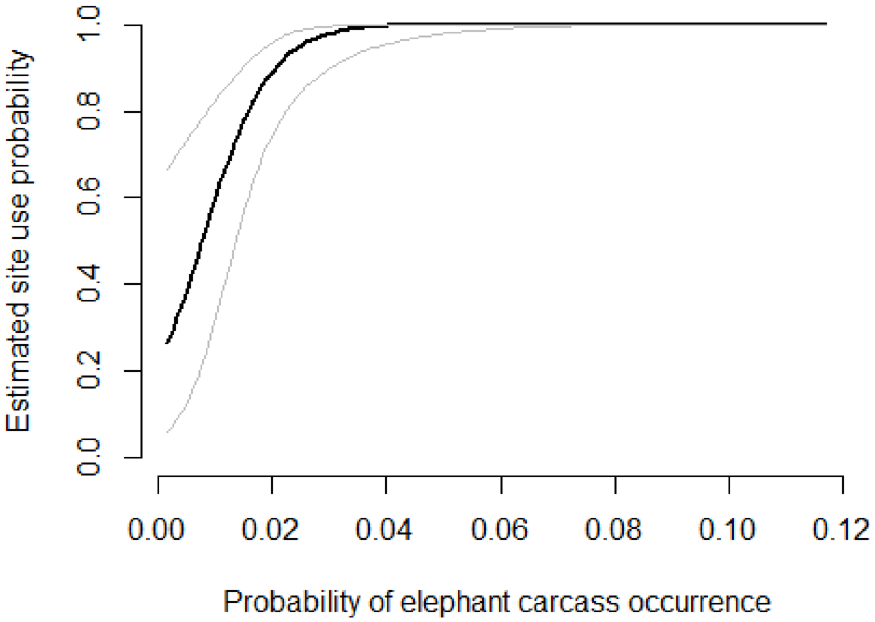

Figure 4.6 Relationship between the probability of elephant site use and mean elephant carcass occurrence probability in a site with 95% confidence intervals shown as grey lines. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value.

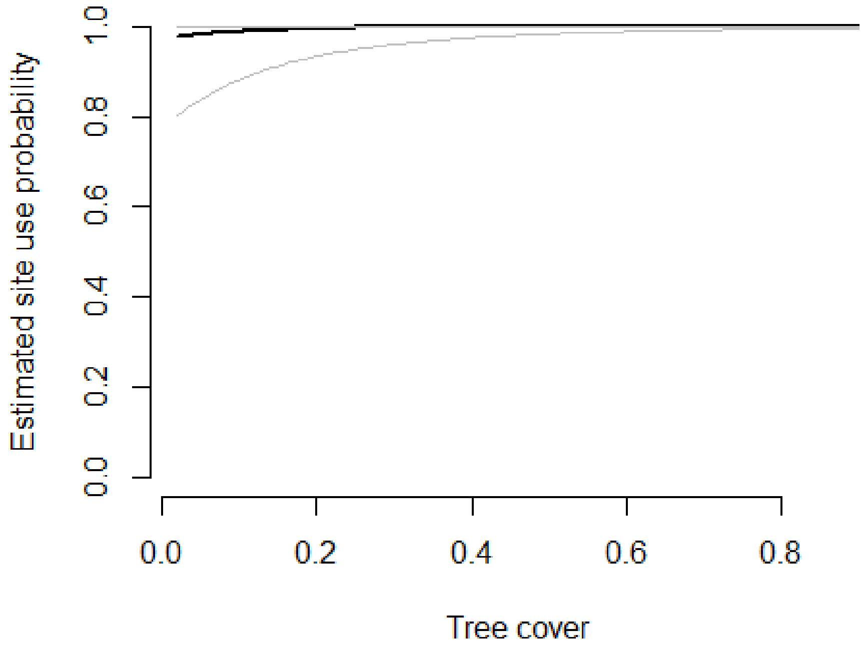

Figure 4.7 Relationship between the probability of elephant site use and the proportion of tree cover in a site with 95% confidence intervals shown as grey lines. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value.

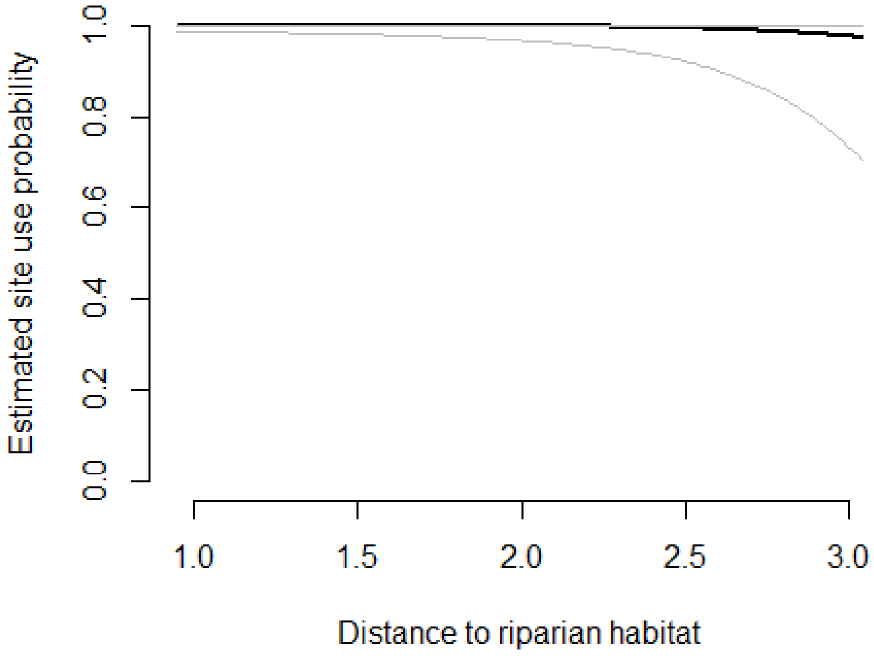

Figure 4.8 Relationship between the probability of elephant site use and mean distance to riparian habitat (in km) within a site with 95% confidence intervals shown as grey lines. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value.

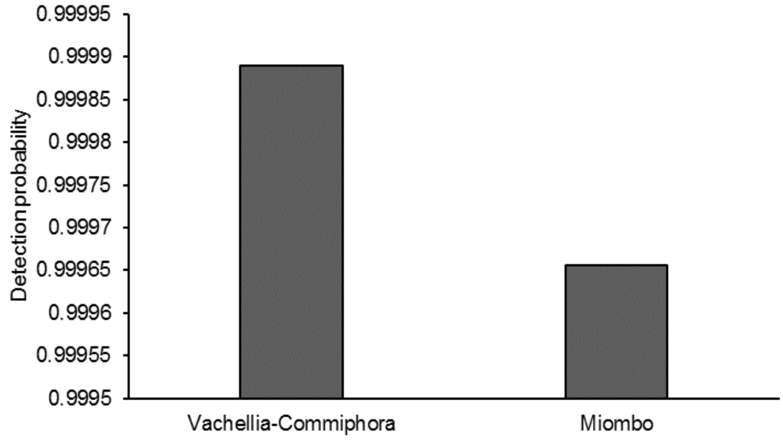

Figure 4.9 Predicted effect of dominant vegetation type (*Vachellia-Commiphora* or miombo) on the probability of detecting elephant tracks, when effort is held at its median value and other detection covariates (carcass occurrence probability, distance to ranger post, and distance to riparian habitat) are held at their mean value.

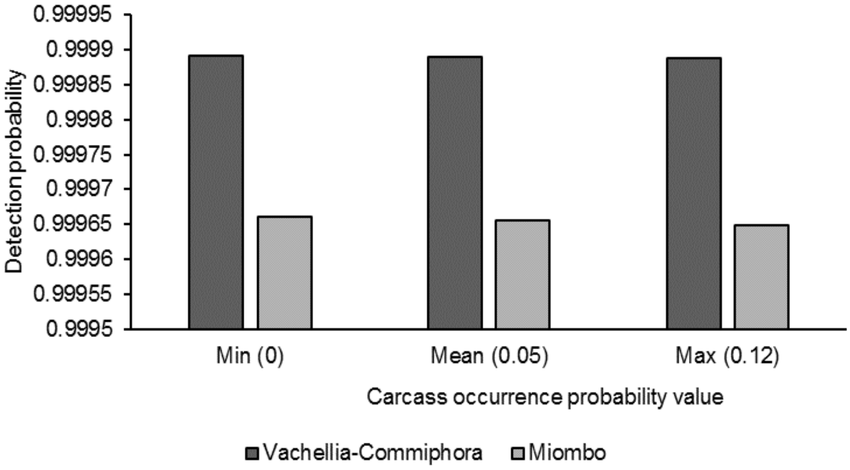

Figure 4.10 Predicted effect of dominant vegetation type (*Vachellia-Commiphora* or miombo) and carcass occurrence probability (assessed at its minimum, mean, and maximum values) on the probability of detecting elephant tracks, when effort is held at its median value and other detection covariates (distance to ranger post and distance to riparian habitat) are held at their mean value.

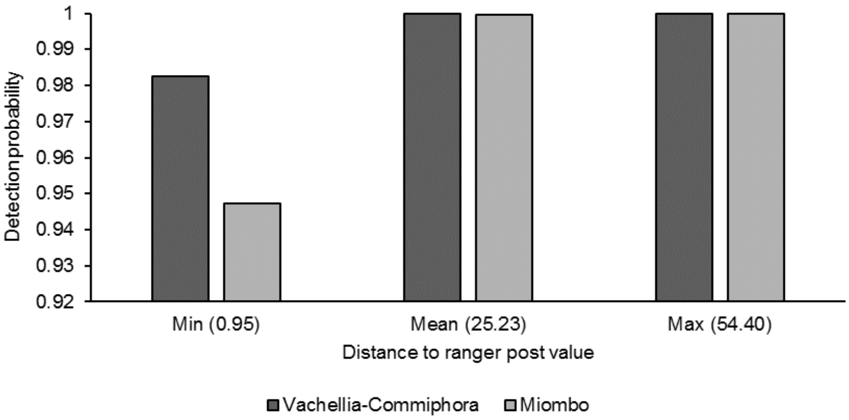

Figure 4.11 Predicted effect of dominant vegetation type (*Vachellia-Commiphora* or miombo) and distance to ranger post (in km, assessed at its minimum, mean, and maximum values) on the probability of detecting elephant tracks, when effort is held at its median value and other detection covariates (carcass occurrence probability and distance to riparian habitat) are held at their mean value.

4.4.3 Fine resolution, protected areas

For sites within protected areas at the fine spatial resolution, the probability of detecting elephant tracks was not significantly predicted by substrate type and the null model for detection (which assumes that the probability of detection is constant) received the most support. There was strong support for the Hines et al. (2010) correlated detections model over the standard single-season, single-species model (a difference of ΔQAIC >191), confirming that it was appropriate to use the Hines et al. (2010) model to account for spatial correlations in detections (see Box 4.1), rather than the standard single-season, single-species model.

The final model set for elephant site use within protected areas at the fine spatial resolution comprised five models (Table 4.8). Elephant site use at this spatial resolution was most strongly predicted by water availability, tree cover, distance to ranger post, and elephant carcass occurrence (Figures 4.12-4.15 & Table 4.9). Elephant site use was significantly positively associated with water availability ($\beta = 0.28$ [SE 0.05]). While tree cover had a positive effect on elephant site use at the coarse spatial resolution (Table 4.7), tree cover had a significant negative effect ($\beta = -0.29$ [SE 0.05]) on site use at the fine spatial resolution. At the coarse spatial resolution, elephant site use was positively associated with carcass occurrence (Table. 4.7), whereas at the fine spatial resolution, carcass occurrence had a significant negative effect on site use ($\beta = -0.17$ [SE 0.05], Table 4.9). Site use was also negatively associated with distance to ranger post ($\beta = -0.11$ [SE 0.05]) and probability of illegal human use (Figure A4.13), although only the effect of distance to ranger post was statistically significant.

There was some support for a non-significant interaction between tree cover and elephant carcass occurrence such that site use was more strongly negatively associated with tree cover in sites with a higher probability of carcass occurrence (Figure 4.16). An interaction between water availability and elephant carcass occurrence was included in one model within the top model set (Table 4.8; Figure A4.14), such that site use was less strongly positively associated with water availability in sites with a higher probability of carcass occurrence. However, the effect size was small, and the interaction was not statistically significant (Table 4.9).

The model-averaged mean probability of detecting elephant tracks within protected areas ($\bar{\hat{p}}$) at the fine spatial resolution was 1 (note that this definition varies from how detection is defined in the standard single-season, single-species model). The model-averaged estimate of $\theta^{[0]}$, the probability of a species becoming available for detection given that the species was not available in the previous segment, was 0.36 (SD 0.12). The model-averaged estimate of $\theta^{[1]}$, the probability of a species being available for detection given that the species was available in the previous segment, was 0.60 (SD 0.11), indicating that spatial autocorrelation in detections was present. An estimated 75% of surveyed sites were predicted to be used by elephants; this was slightly higher than the naive estimate of 63% (Table 4.14).

Table 4.8 Model rankings for elephant site use (ψ) and detection (p) in the fine resolution, protected areas analysis. Final set based on models with ΔQAIC <2. As model fit tests revealed overdispersion, the adjusted QuasiAIC (QAIC) was used for model ranking. Wi: relative model weight. nPars: number of parameters in the model. −2*log: twice the negative log-likelihood. W (site use covariate): mean water availability in a site. C (site use covariate): percentage tree cover in a site. Post (site use covariate): mean distance to ranger post in a site. Hum (site use covariate): mean probability of illegal human use in a site. Carcass (site use covariate): mean probability of elephant carcass occurrence in a site. At the fine spatial resolution, sampling effort within a site was constant, thus effort is not included as a detection covariate. The probability of detecting elephant tracks was not significantly predicted by substrate type, thus the null model for detection p(.) was used.

Rank	**Model**	**QAIC**	**ΔQAIC**	**W_i**	**-2*Log**	**nPars**
1	ψ,th0(W + C + Post + Hum + Carcass + Carcass*C), th1(), p(.), th0pi()	2481.98	0.0	0.26	4251.83	11
2	ψ,th0(W + C + Post + Hum + Carcass), th1(), p(.), th0pi()	2482.06	0.08	0.25	4255.43	10
3	ψ,th0(W + C + Post + Carcass + Carcass*C), th1(), p(.), th0pi()	2482.23	0.25	0.23	4255.72	10
4	ψ,th0(W + C + Post + Carcass), th1(), p(.), th0pi()	2483.13	1.15	0.15	4260.73	9
5	ψ,th0(W + C + Post + Hum + Carcass + Carcass*W), th1(), p(.), th0pi()	2483.62	1.64	0.11	4254.67	11

Table 4.9 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present), β-coefficient estimates, and associated standard errors and 95% confidence intervals of covariates explaining elephant site use (ψ) and detection (p) in the fine resolution, protected areas analysis. Only models retained in the final model set (ΔQAIC<2) are presented. Bolded covariates have a significant effect in the top model in which they appear. For covariate definitions, see Table 4.8. Standard errors and confidence intervals were adjusted for overdispersion. The covariates Hum and Carcass x C were not statistically significant after confidence intervals were adjusted for overdispersion.

Covariate	**Σw**	**β ($SE_β$)**	**Confidence interval** (β ± 1.96 x SE)
Site use (ψ)			
Water availability (W)	1	0.28 (0.05)	0.18, 0.39
Tree cover (C)	1	-0.29 (0.05)	-0.39, -0.19
Probability of elephant carcass occurrence (Carcass)	1	-0.17 (0.05)	-0.28, -0.06
Distance to ranger post (Post)	1	-0.11 (0.05)	-0.22, -0.01
Probability of illegal human use (Hum)	0.62	-0.08 (0.05)	-0.20, 0.03
Interaction between elephant carcass occurrence and tree cover (Carcass x C)	0.49	-0.07 (0.05)	-0.16, 0.03
Interaction between elephant carcass occurrence and water availability (Carcass x W)	0.11	-0.03 (0.05)	-0.13, 0.06

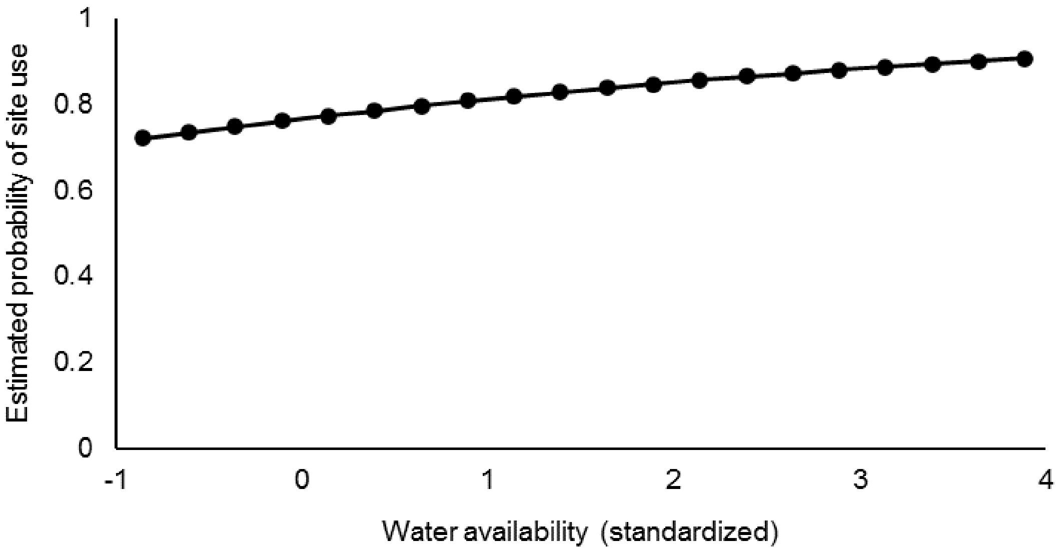

Figure 4.12 Relationship between the probability of elephant site use and mean water availability in a site within protected areas at the fine spatial resolution. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value. Covariate values were standardized as recommended by MacKenzie et al. (2017) by subtracting each covariate value from the mean of the covariate and dividing by the standard deviation.

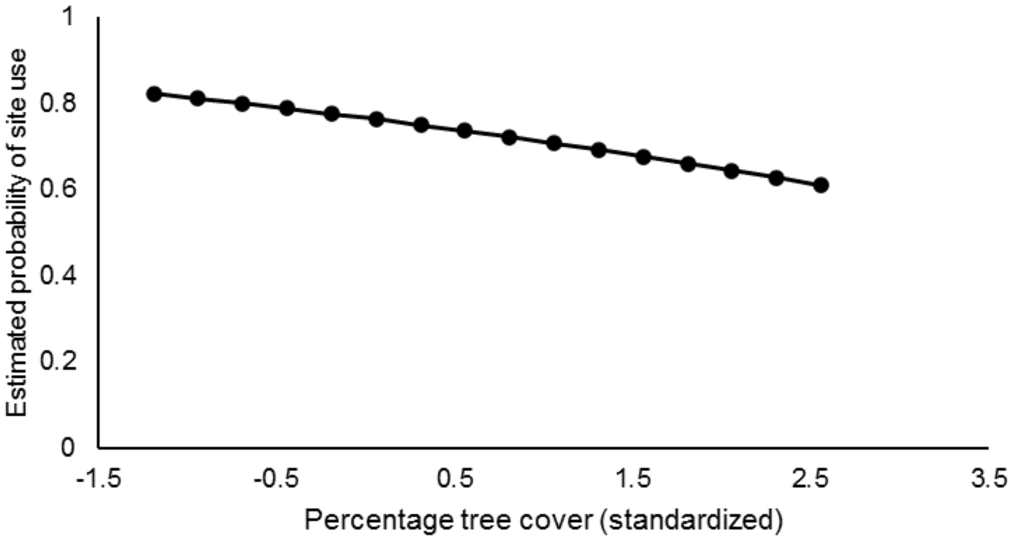

Figure 4.13 Relationship between the probability of elephant site use and percentage tree cover in a site within protected areas at the fine spatial resolution. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized).

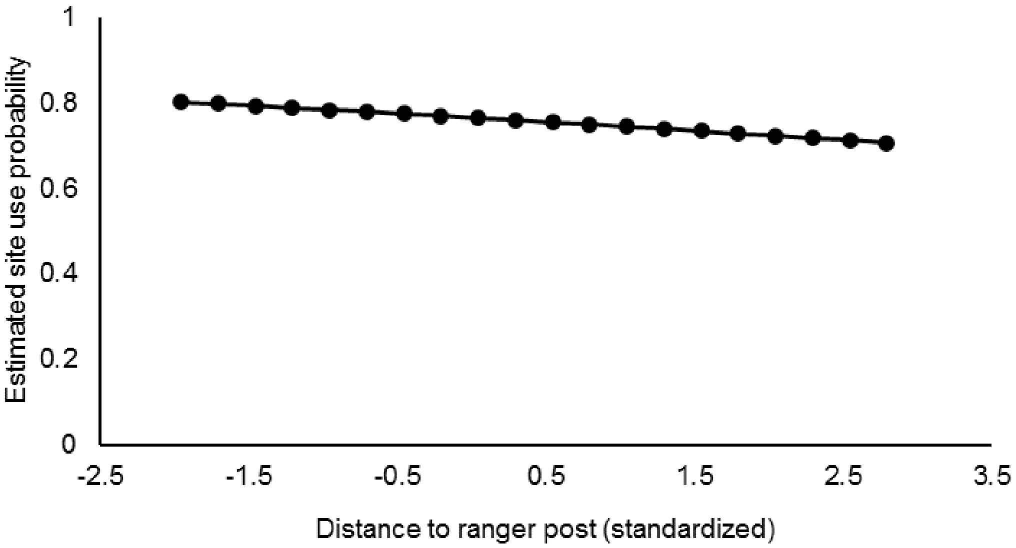

Figure 4.14 Relationship between the probability of elephant site use and mean distance to ranger post in a site within protected areas at the fine spatial resolution. Plots were produced using the top-ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized).

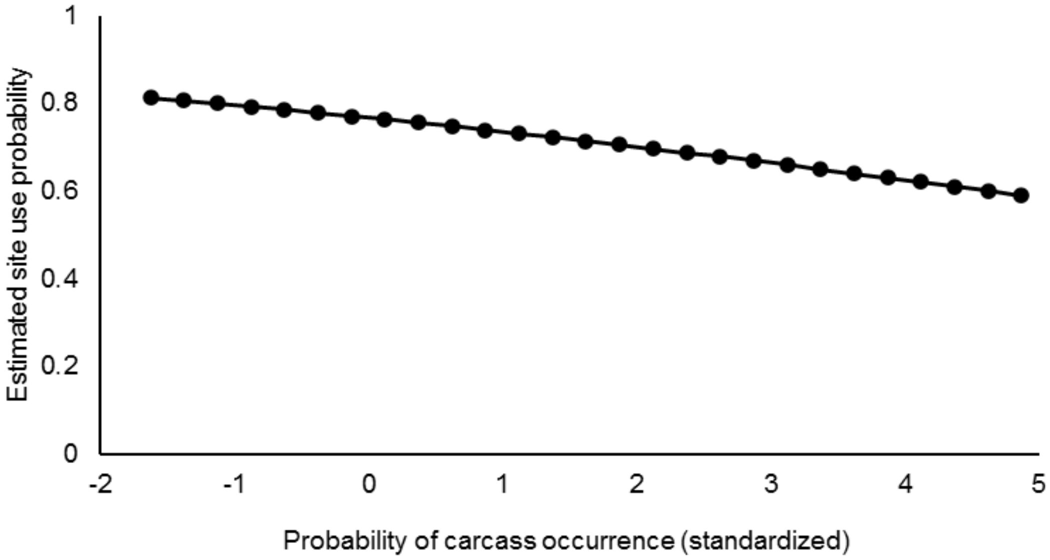

Figure 4.15 Relationship between the probability of elephant site use and mean probability of elephant carcass occurrence in a site within protected areas at the fine spatial resolution. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized).

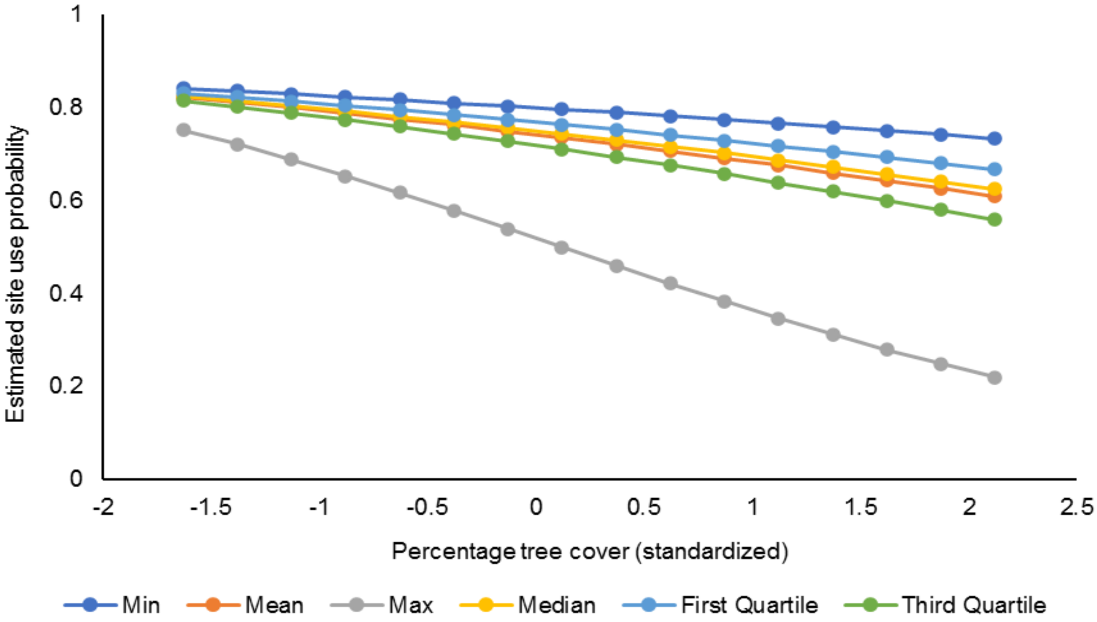

Figure 4.16 The interaction between tree cover and elephant carcass occurrence on the probability of elephant site use within protected areas at the fine spatial resolution. Each series shows the effect of tree cover on site use at a different value of carcass occurrence probability. The effect of tree cover on site use was assessed for the following values of occurrence probability: minimum, mean, median, first quartile, third quartile, and maximum. Plots were produced using the top ranked model containing the covariate. The series where carcass occurrence probability was held as its maximum value (Max, grey line) is near the bottom of the figure because the interaction between carcass occurrence probability and tree cover had a negative effect on elephant site use probability. All other site use covariates (water availability, distance to ranger post, probability of human use) in the model were held at their mean value (standardized).

4.4.4 Fine resolution, village land

In the fine-resolution, village land analysis, the standard single-season, single-species model performed as well as the correlated detections model (with a ΔAIC of 0.03). Due to the small number of sites (n=42) and detections (n=23) for the village land analysis, the single-season, single-species model was used as this requires estimation of fewer parameters than the correlated detections model. In addition, due to the small number of elephant detections, only univariate models for site use were tested.

The probability of detecting elephant tracks on village land sites was predicted by substrate quality for the retention of animal tracks, although the effect was not statistically significant. The final model set for elephant site use on village land at the fine spatial resolution comprised five models, and the null model for site use was ranked second-highest (Table 4.10). None of the site use covariates in the final model had a statistically significant effect on site use (Table 4.11). Elephant site use on village land was negatively associated with distance to riparian habitat, NDVI, and tree cover, and positively associated with water availability (Figures A4.15-A4.18).

The model-averaged mean probability of detecting elephant tracks ($\bar{\hat{p}}$) on village land at the fine spatial resolution was 0.41, and an estimated 39% of surveyed sites were predicted to be used by elephants (Table 4.14). Detection and site use probabilities were therefore substantially lower for village land sites than sites within protected areas.

Table 4.10 Model rankings for elephant site use (ψ) and detection (p) in the fine resolution, protected areas analysis. Final set based on models with ΔAICc <2. Due to small sample size (n=42 sites), adjusted AIC (AICc) was used for model ranking. Wi: relative model weight. nPars: number of parameters in the model. −2*log: twice the negative log-likelihood. R (site use covariate): mean distance to riparian habitat in a site. NDVI (site use covariate): mean NDVI in a site. C (site use covariate): percentage tree cover in a site. W (site use covariate): mean water availability in a site. Substrate (detection covariate): a measure of substrate quality for detecting tracks, higher values indicate better quality.

Rank	Model	AICc	ΔAICc	W_i	-2*Log	nPars
1	ψ(R) p(Substrate)	122.89	0.00	0.30	113.81	4
2	ψ(.) p(Substrate)	122.98	0.09	0.28	116.35	3
3	ψ(NDVI) p(Substrate)	123.98	1.09	0.17	114.90	4
4	ψ(C) p(Substrate)	124.53	1.64	0.13	115.45	4
5	ψ(W) p(Substrate)	124.75	1.86	0.12	115.67	4

Table 4.11 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present), β-coefficient estimates and associated standard errors and 95% confidence intervals of covariates explaining elephant site use (ψ) and detection (p) in the fine resolution, village land analysis. Only models retained in the final model set (ΔAICc<2) are presented. Bolded covariates have a significant effect in the top model in which they appear. For covariate definitions, see Table 4.10.

Covariate	**Σw**	**β ($SE_β$)**	**Confidence interval** (β ± 1.96 x SE)
Detection (p)			
Substrate	1	-0.78 (0.41)	-1.58, 0.02
Site use (ψ)			
Distance to riparian habitat (R)	0.30	-0.65 (0.44)	-1.51, 0.21
Primary productivity (NDVI)	0.17	-0.43 (0.37)	-1.16, 0.30
Tree cover (C)	0.13	-0.36 (0.39)	-1.12, 0.40
Water availability (W)	0.12	0.29 (0.36)	-0.42, 1.00

4.4.5 Fine resolution, natural predation risk

In this analysis, I investigated whether natural predation risk (defined as the probability of lion site use) impacted elephant site use within protected areas at the fine spatial resolution, using the subset of coarse-resolution sites where lions were detected.

The probability of detecting elephant tracks was not significantly predicted by substrate type. There was strong support for the correlated detections model over the standard single-season, single-species model (a difference of ΔQAIC >95 for the correlated detections model relative to the standard single-season, single-species model).

Only three site use models had strong support (Table 4.12). Lion site use probability was highly collinear with water availability and distance to riparian habitat. Of these collinear covariates, water availability, which had a statistically significant positive effect (β = 0.28 [SE 0.07]), was a better predictor of elephant site use than either distance to riparian habitat or lion site use probability. The highest ranked model including lion site use probability had a ΔQAIC >13 and therefore had no empirical support (in this model, elephant site use was positively associated with lion site use probability). Other statistically significant predictors of elephant site use were tree cover (β = -0.37 [SE 0.07]) and elephant carcass occurrence probability (β = -0.18 [SE 0.07]).

Table 4.12 Model rankings for elephant site use (ψ) and detection (p) in the fine resolution, natural predation risk analysis. Final set based on models with ΔQAIC <2. As model fit tests revealed overdispersion, the adjusted QuasiAIC (QAIC) was used for model ranking. Wi: relative model weight. nPars: number of parameters in the model. −2*log: twice the negative log-likelihood. W (site use covariate): mean water availability in a site. C (site use covariate): percentage tree cover in a site. Post (site use covariate): mean distance to ranger post in a site. Carcass (site use covariate): mean probability of elephant carcass occurrence in a site. At the fine spatial resolution, sampling effort within a site was constant, thus effort is not included as a detection covariate. The probability of detecting elephant tracks was not significantly predicted by substrate type, thus the null model for detection p(.) was used.

Rank	**Model**	**QAIC**	**ΔQAIC**	**W_i**	**-2*Log**	**nPars**
1	ψ,th0(W + C + Post + Carcass), th1(), p(.), th0pi()	1536.03	0.00	0.55	2795.91	9
2	ψ,th0(W + C + Post + Carcass + Bound), th1(), p(.), th0pi()	1537.78	1.75	0.23	2795.44	10
3	ψ,th0(W + C + Post + Carcass + Hum), th1(), p(.), th0pi()	1537.82	1.79	0.22	2795.53	10

Table 4.13 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present), β-coefficient estimates, and associated standard errors and 95% confidence intervals of covariates explaining elephant site use (ψ) in the fine resolution, natural predation risk analysis. Only models retained in the final model set (ΔAICc<2) are presented. Bolded covariates have a significant effect in the top model in which they appear. For covariate definitions, see Table 4.12. Standard errors and confidence intervals were adjusted for overdispersion.

Covariate	**Σw**	**β ($SE_β$)**	**Confidence interval** (β ± 1.96 x SE)
Site use (ψ)			
Water availability (W)	1	0.28 (0.07)	0.15, 0.41
Tree cover (C)	1	-0.37 (0.07)	-0.24, -0.08
Probability of elephant carcass occurrence (Carcass)	1	-0.18 (0.07)	-0.08, -0.05
Distance to ranger post (Post)	1	-0.14 (0.07)	-0.08, -0.01
Distance to PA boundary (Bound)	0.23	-0.03 (0.07)	-0.08, 0.10
Illegal human use (Hum)	0.22	0.03 (0.07)	-0.08, 0.16

Table 4.14 Model-averaged mean probability of detection ($\overline{\hat{p}}$), site use ($\overline{\hat{\psi}}$), and naïve occupancy (ψ, the proportion of surveyed sites as which elephants were detected, uncorrected for detection biases) for elephants at the different spatial resolutions and extents investigated, with associated mean of the standard errors in brackets (adjusted for overdispersion in the fine resolution, protected areas analysis). $\overline{\hat{\psi}}$ can also be interpreted as the proportion of sampled area used by a species. Note that for the fine resolution, protected areas analysis, detection (p) is defined as the estimated probability of detection given the species was available for detection in a survey, as the Hines et al. (2010) correlated detections model was used in this analysis. Detection probabilities for the Hines et al. (2010) model are usually higher than detection probabilities for the simple single-season model for this reason.

	Coarse scale, entire ecosystem	**Coarse resolution, protected areas**	**Fine resolution, protected areas**	**Fine resolution, village land**
Naive ψ	0.70	0.87	0.63	0.33
$\overline{\hat{p}}$ (SD) (95% CI)	0.65 (0.02) (0.59, 0.72)	0.74 (0.02) (0.66, 0.81)	1.0 (0.0)	0.41 (0.15)
$\overline{\hat{\psi}}$ (SD) (95% CI)	0.78 (0.03) (0.66, 0.90)	0.92 (0.06) (0.80, 0.97)	0.75 (0.12) (0.52, 0.99)	0.39 (0.06) (0.27, 0.51)

4.5 Discussion

This chapter investigated the relative importance of anthropogenic risk and environmental factors on elephant dry season space use in the Ruaha-Rungwa ecosystem within multiple spatial extents and at two spatial resolutions: first, at a coarse resolution (225 km^2 sites) representing higher-level, longer-term habitat use and, second, at a fine resolution (1 km^2 sites) representing fine-scale, short-term habitat use. Elephant space use was explored at the extent of the entire ecosystem, within protected areas, and on village land.

4.5.1 Site use

A large proportion of the sites (0.78) surveyed in the Ruaha-Rungwa ecosystem were predicted to be used by elephants, including protected areas as well as village lands. The probability of elephant site use was highest in sites within protected areas and considerably lower in unprotected village land (Figure 4.5).

At the coarse spatial resolution, elephant use of the entire ecosystem was strongly negatively associated with the conversion of natural habitat to agriculture and human population density. The probability of elephant use declined below 0.4 in sites where 30% of the land had been converted to agriculture and in sites with a human population density exceeding 40 people per km^2. Conversion to agriculture and human population density were better predictors of elephant habitat use than either legal protection or environmental factors, suggesting that elephant space use at the extent of the entire ecosystem was limited most strongly by human presence in and modification of the landscape. While the loss of suitable habitat (associated with the conversion of natural habitat to agriculture) is likely the primary limiting factor for elephants, avoidance of risks associated with more densely populated human areas may also play a role. These findings are similar to those of Hoare & du Toit (1999), who found that elephants largely avoided areas where 40-50% of the land was converted to human use as agricultural fields and settlements, and of Graham et al. (2010), who found that the likelihood of elephant crop use declines above human population densities of 94 km^2.

In the coarse resolution, entire ecosystem analysis, none of the environmental variables tested had a significant effect on elephant site use. There was some evidence that elephant site use at the extent of the ecosystem was negatively associated with NDVI and *Vachellia-Commiphora* habitat and with increasing distance to riparian habitat. These somewhat surprising results may be explained by the fact that conversion to cropland, the strongest predictor of elephant occurrence in the ecosystem at the coarse spatial resolution, was positively associated with rivers and *Vachellia-Commiphora* habitat (Figure A4.4). Furthermore, most of the variation in the probability of site use within this spatial extent arises from the sites on village land, and survey coverage of village land was biased towards the south-east of the ecosystem (Figure 4.5), an area dominated by *Vachellia-Commiphora* habitat.

Within protected areas at the coarse spatial resolution, the probability of elephant site use was high (Table 4.14). The limited variation in elephant site use within protected areas was predicted by environmental factors rather than risk factors. Although the strongest predictor of elephant site use was the probability of elephant carcass occurrence, at this scale, this is likely because elephant carcasses were more likely to occur in sites used by elephants (e.g., Rashidi et al., 2015). Elephant site use was predicted to be greater in sites with higher tree cover, in closer proximity to riverine habitat, and with greater dry-season availability of water. Although tree cover and distance to riparian habitat emerged as statistically significant predictors, it should be noted that they explained relatively little variation in the probability of site use: the probability of elephant site use declined marginally at very low values of tree cover, and at distances exceeding 2.5 km from riparian habitat.

At the fine spatial resolution, elephant space use within protected areas was influenced by anthropogenic risk and environmental factors, with environmental factors exerting a stronger effect on elephant space use than risk. Fine-scale elephant space use was associated with greater water availability, lower tree cover, and lower values of NDVI. Similarly to Beale et al. (2018), who investigated elephant distribution in the ecosystem at a similar spatial scale[18] using data from dry season aerial surveys conducted in 2013-2015, I found a negative relationship between elephant space use and NDVI. This is likely because higher dry season NDVI values are associated with miombo woodland where forage quality is low because of nutrient-poor soils (Frost, 1996), while better quality forage in *Vachellia-Commiphora* habitat is associated with lower NDVI values. The negative association between elephant fine-scale space use and tree cover may similarly be due to tree cover being higher in nutrient-poor miombo woodland (Figure A4.4).

Fine-scale space use in protected areas was negatively associated with carcass occurrence probability and illegal human use, and positively associated with ranger posts, suggesting that elephants are less likely to use areas associated with higher human-induced mortality and disturbance risk (e.g., Roever et al., 2013). These findings are consistent with other studies that have observed elephant range shifts and compression in response to poaching (Abe, 1993; Goldenberg et al., 2018; Western & Mose, 2023) and negative associations between elephant space use and human activity and (bushmeat) hunting in mixed-use landscapes (Clark et al., 2009; Petracca et al., 2020). Beale et al. (2018) similarly found a generally positive association between elephant occurrence and ranger posts across the ecosystem (although when investigated within the extent of smaller management zones, some ranger posts were associated with higher probabilities of carcass occurrence) and in areas of intermediate poacher travel cost from villages. I find some evidence that risk structures how elephants use natural features in their habitats, as elephants were predicted to use more open areas with less tree cover in areas with a greater probability of carcass occurrence. Elephant site use was also less strongly associated with water availability in sites with a greater probability of carcass occurrence, suggesting a degree of elephant avoidance of water sources in high-risk areas, although the effect was not statistically significant.

Natural predation risk (which was assumed to be associated with lion site use probability) did not influence elephant space use, suggesting that elephants did not avoid areas also used by lions at the spatial scale investigated. Camera trap surveys conducted in the Serengeti ecosystem of Tanzania similarly found no association between lion and elephant detections (assessed over 16-day intervals, Anderson et al., 2016).

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[18] In the Beale et al. (2018) study, elephant occurrence was recorded in sampling units measuring 2.5 km in length and 0.09-0.15 km in width.

Limited conclusions can be drawn about fine-scale elephant use of village land as the number of elephant detections was low, and no site use covariates emerged as statistically significant. With these caveats in mind, site use was positively associated with water availability and proximity to riparian habitats, and negatively associated with tree cover and primary productivity, likely because tree cover was lower near rivers on village land due to clearing for irrigated agriculture (Figure A4.7). The fact that no risk factors emerged as significant predictors may be due to the approach to selecting sites for inclusion in the fine-scale analysis, as coarse-resolution sites where elephants were not detected were excluded. This likely filtered out the effect of risk and unsuitable habitat.

4.5.2 Detection probability

In addition to factors associated with elephant site use, I investigated factors affecting the probability of detecting elephant tracks on roads given elephant presence at a site. In the coarse spatial resolution analyses, I hypothesised that detection probability would be influenced by covariates associated with variation in local elephant abundance (MacKenzie et al., 2017) and/or the extent to which elephants use or avoid roads. In the fine spatial resolution analyses, I only tested the effect of the quality of the road substrate for the retention of elephant tracks on the probability of detection.

The probability of detecting elephant tracks on roads was generally high and largely unaffected by substrate quality at either spatial resolution (Table 4.14). In the coarse-scale, entire ecosystem analysis, the probability of detecting elephant tracks was higher for sampling occasions in protected areas than on unprotected village land and higher in *Vachellia-Commiphora* habitat than in miombo woodland. This may be due to elephants being more abundant in protected areas and in the more productive *Vachellia-Commipora* habitat but could also be due to greater use of roads by elephants inside protected areas and in *Vachellia-Commiphora* habitat.

In the coarse scale, protected areas analysis, the probability of detecting elephant tracks given elephant presence at a site was influenced by risk and was significantly lower in areas of higher carcass occurrence probability. This may reflect variation in local elephant abundance and/or variation in the propensity of elephants to use roads, both of which could be lower in sites with higher historical poaching risk. Detection probability within protected areas was also negatively associated with proximity to ranger posts, although the effect was not significant. This result is somewhat unexpected, as ranger posts can afford safety (e.g., Beale et al., 2018; Jones et al., 2019; Nahonyo, 1996), but may reflect that ranger posts are situated at the edge of the protected areas where the risk of illegal human activity is higher (Strampelli, 2021). In these sites, elephants may be less locally abundant and/or less likely to use roads. Within protected areas, the probability of detection was positively associated with riparian habitats, which could reflect higher elephant abundance near rivers.

4.5.3 Limitations and Future Directions

Methodological limitations have been discussed in Chapter 2 (Section 2.6). Importantly, the findings in this study relate to the probability of site use, not the intensity of use. How the influence of risk and environmental factors on elephant space use may vary with season and sex (e.g., Shannon et al., 2008; Stokke & Du Toit, 2002; Bastille-Rousseau et al., 2020; de Knegt et al., 2011; Loarie et al., 2009) could not be examined here using only tracks (as sex/group type for a set of tracks was not recorded) and because surveying was limited to the dry season.

The application of occupancy models to large-bodied, mobile species with large home ranges such as elephants is somewhat challenging as they display more diffuse habitat occupancy compared to smaller-bodied, less mobile species, especially when habitat use is investigated at large spatial scales. In the Ruaha-Rungwa ecosystem, there was considerably more variation in elephant habitat use at the fine than at the coarse spatial resolution, and there was particularly little variation in broad-scale patterns of occupancy within protected areas. Despite these limitations, useful insight was obtained into factors influencing elephant use of the wider ecosystem, as well as fine-scale habitat use, from a multi-species survey. Occupancy studies of elephant space use are likely to be most useful when habitat associations are investigated at multiple spatial scales (e.g., Goswami et al., 2014; Jathanna et al. 2015).

I used standard single-season, single-species models to model elephant space use at the coarse scale. An alternative would have been to use the Royle-Nichols occupancy model (Royle & Nichols, 2003) to estimate site-level relative abundance based on heterogeneity in the detection probability, based on the assumption that detection probability increases with local abundance. However, I decided against using this model because it is typically used for solitary species (e.g., Fuller et al., 2022) and assumes that the detection of individuals is independent (Royle & Nichols, 2003), an assumption that it is likely violated given that elephants are a social species. Furthermore, heterogeneity in detection probability likely reflects not only variation in local elephant abundance but also variation in the propensity of elephants to use roads, thereby complicating the interpretation of site-level relative abundances.

I have interpreted the negative association between fine-scale dry season elephant space use and carcass occurrence as evidence of spatial avoidance of poaching risk. However, an alternative explanation for an apparent ‘mismatch’ between live elephant and carcass distributions in Ruaha-Rungwa was offered by Beale et al. (2018), namely that elephant carcass distributions reflect wet season elephant distributions. As no recent wet season aerial survey data are available for this ecosystem, the extent to which the distribution of elephants and poaching risk varies seasonally is unknown (although records from MBOMIPA WMA suggest that poaching risk may be higher during the dry season, see Chapter 3). In this study, elephant dry season space use at the coarse spatial scale was positively associated with the probability of elephant carcass occurrence, and there was no apparent mismatch between broad-scale elephant occurrence and carcass occurrence. This suggests that the observed negative association between fine-scale elephant space use and carcass occurrence is not merely driven by a wet season shift in elephant distribution, although this possibility cannot be excluded entirely.

This study has provided useful insight into the factors limiting coarse-scale elephant use of areas outside of formal protected areas, but only limited insight into fine-scale elephant space use on village land. The extent to which risk and environmental factors influence fine-scale elephant space use on village land would benefit from further study, as an understanding of these factors could inform efforts to enhance coexistence between people and elephants.

4.6 Conclusions

Elephant space use at the extent of the entire ecosystem was best explained by human presence in and modification of the landscape, which was likely associated with unsuitable habitat for elephants as well as elevated mortality and disturbance risk.

Within protected areas, risk influenced fine-scale but not coarse-scale elephant space use. Fine-scale space use was negatively associated with recent mortality risk from poaching, as inferred from elephant carcass distributions from aerial surveys conducted 2-3 years prior to this study. This suggests that elephants have a spatial understanding and memory of risk and were not merely responding to current cues (e.g., Ihwagi, 2019). Elephants have previously been shown to respond more strongly to long-term patterns of vegetation productivity than immediate forage, indicating that information on past environmental conditions influences current elephant space use (Tsalyuk et al., 2019). It further suggests that elephants may maintain behavioural responses to risk even after their environment has become more secure, as has been observed in Gorongosa, Mozambique, where elephants continued to be wary of and aggressive to humans years after the cessation of poaching (Poole & Granli, 2018). Short-term flight responses and temporary avoidance of certain areas have been observed in response to culling (van Aarde et al., 1999; Slotow et al., 2008), but sustained poaching may have longer-lasting effects on elephant habitat use and behaviour. Fine-scale elephant space use was also negatively associated with distance to ranger posts and illegal human use, although the effect of illegal human use was not statistically significant.

This study has shown that elephant space use was sensitive to anthropogenic risk, but that the influence and importance of risk varied with spatial scale (e.g., de Knegt et al., 2011). At the extent of the ecosystem, anthropogenic footprint and risk were more important predictors of coarse-scale elephant space use than environmental factors. Within protected areas, risk influenced fine scale but not coarse-scale elephant space use and environmental factors (water and forage) had a stronger effect on elephant space use than poaching risk (e.g., Bastille-Rousseau et al., 2020).

Elephants were most likely to occur inside Ruaha-Rungwa's protected areas, reiterating the importance of effective protected areas for conserving elephants in this ecosystem. Despite their importance to elephants, protected areas are not free of risk (as shown here and in Chapter 3), and in Chapter 5 I explore whether elephants respond to these risks by adjusting their temporal and social behaviour. Elephant space use was not limited to protected areas, and several (mostly unprotected) corridors link the Ruaha-Rungwa ecosystem with other protected-area complexes in Tanzania (Jones et al., 2009). Across Africa, >50% of elephant range is estimated to fall outside of formal protected areas (Wall et al., 2021), where the persistence of elephants relies on their ability to manage risks associated with people, and the willingness of people to coexist with elephants. How elephants manage such risks when accessing resources that they share with people is explored in Chapter 6.

Appendix A4.1 Maps of fine-scale survey effort and variation in elephant detection

Figure A4.1 An example of how fine-scale sites (road segments shaded grey if elephant tracks were detected along the segment during surveying and white if elephant tracks were not detected) were located within coarse-scale sites (grid cells, shaded blue if elephant tracks were detected during surveying and orange if elephant tracks were not detected).

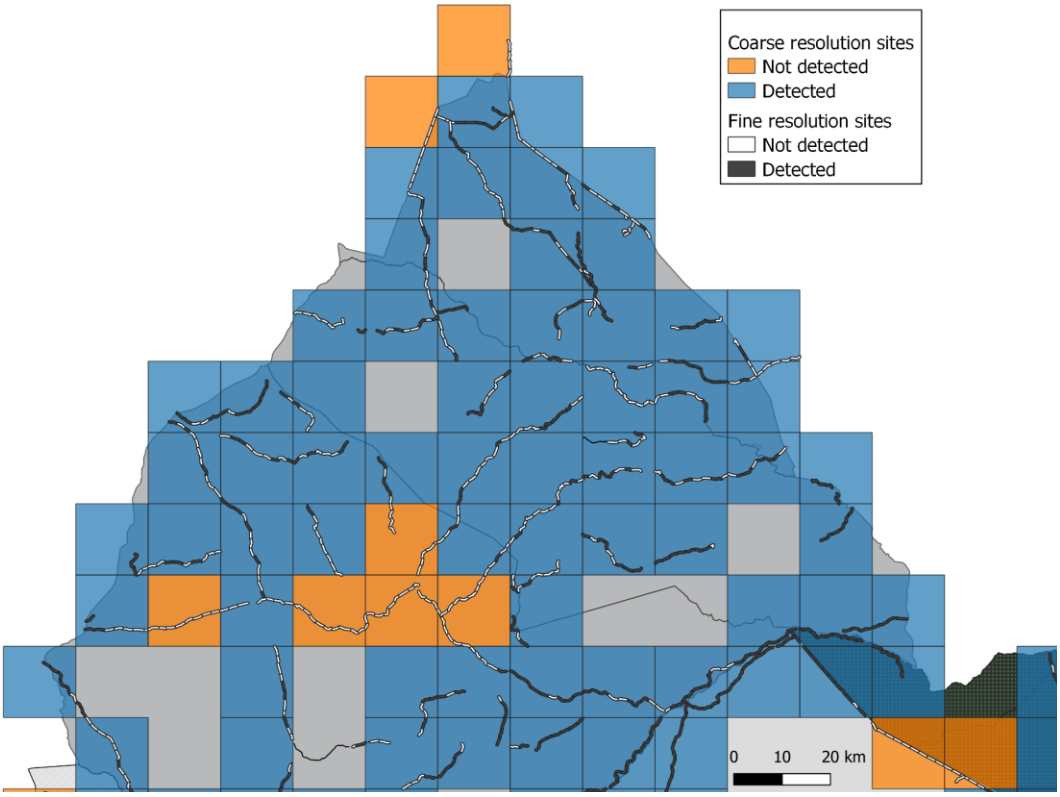


Figure A4.2 Variation in elephant detections at the coarse spatial scale (grid cells) and the fine spatial scale (road segments) in the game reserves comprising the northern half of the study area. Coarse-scale sites (grid cells) are shaded blue if elephant tracks were detected in the site during surveying and orange if elephant tracks were not detected. Fine-scale sites (road segments) are shaded dark grey if elephant tracks were detected in the site during surveying and white if elephant tracks were not detected.

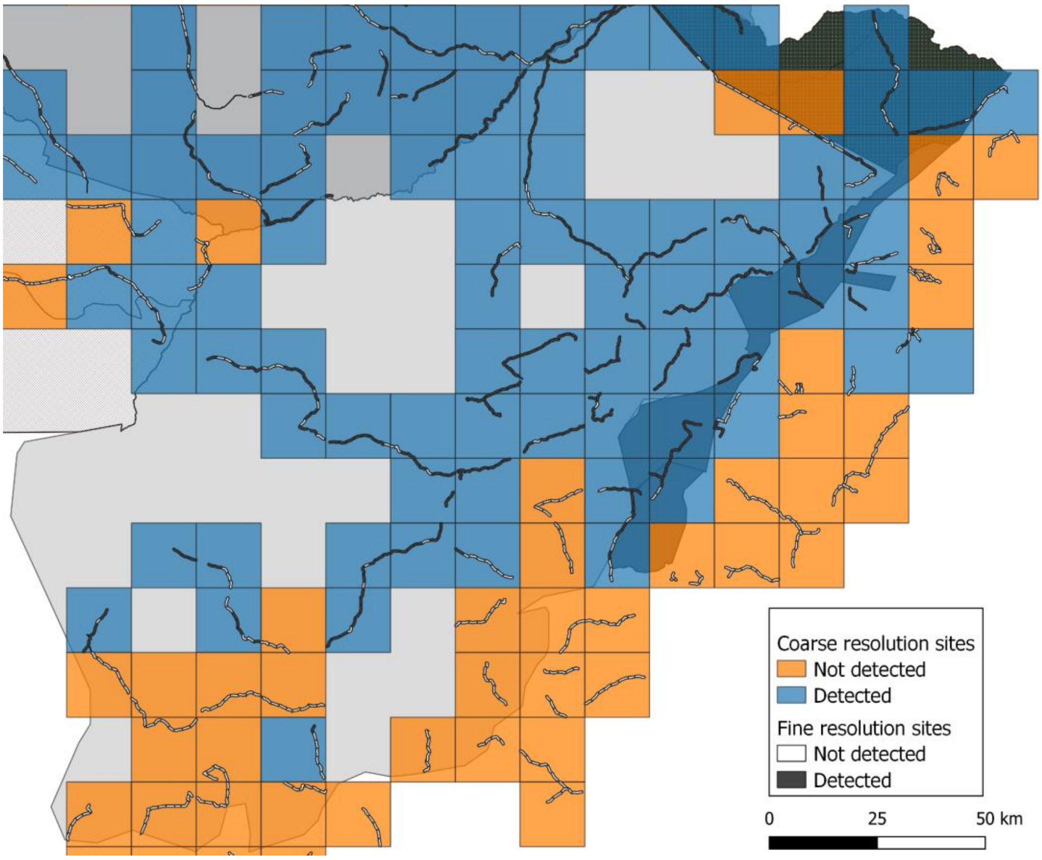
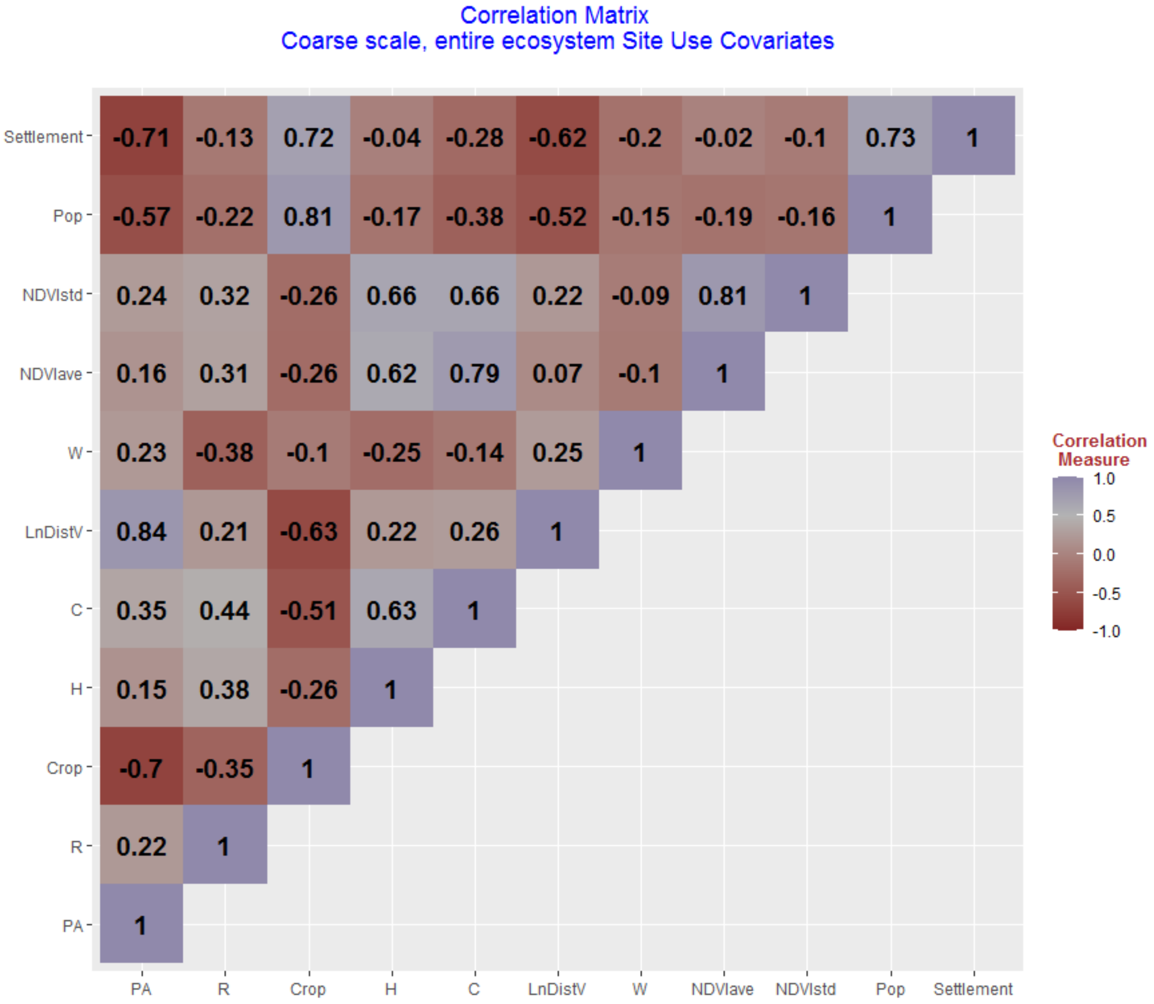


Figure A4.3 Variation in elephant detections at the coarse spatial scale (grid cells) and the fine spatial scale (road segments) in the national park, wildlife management areas, game controlled areas, and village land comprising the northern half of the study area. Coarse-scale sites (grid cells) are shaded blue if elephant tracks were detected in the site during surveying and orange if elephant tracks were not detected. Fine-scale sites (road segments) are shaded dark grey if elephant tracks were detected in the site during surveying and white if elephant tracks were not detected.

Appendix A4.2 Covariate correlation plots



	PA	R	Crop	H	C	LnDistV	W	NDVIave	NDVIstd	Pop	Settlement
Settlement	-0.71	-0.13	0.72	-0.04	-0.28	-0.62	-0.2	-0.02	-0.1	0.73	1
Pop	-0.57	-0.22	0.81	-0.17	-0.38	-0.52	-0.15	-0.19	-0.16	1	
NDVIstd	0.24	0.32	-0.26	0.66	0.66	0.22	-0.09	0.81	1		
NDVIave	0.16	0.31	-0.26	0.62	0.79	0.07	-0.1	1			
W	0.23	-0.38	-0.1	-0.25	-0.14	0.25	1				
LnDistV	0.84	0.21	-0.63	0.22	0.26	1					
C	0.35	0.44	-0.51	0.63	1						
H	0.15	0.38	-0.26	1							
Crop	-0.7	-0.35	1								
R	0.22	1									
PA	1										

Figure A4.4 Correlation plot for covariates used in the coarse resolution, entire ecosystem analysis.

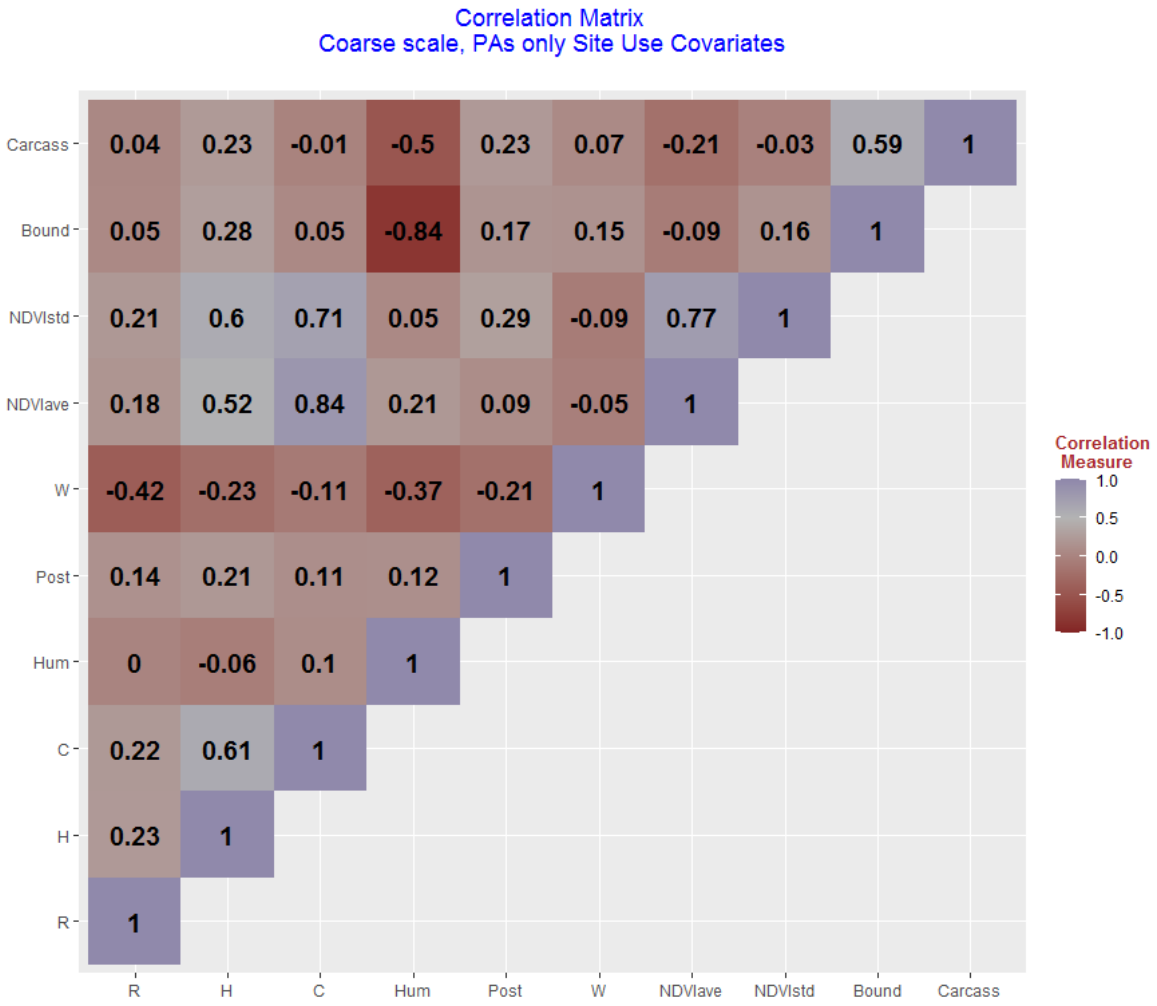


Figure A4.5 Correlation plot for covariates used in the coarse resolution, protected areas analysis.

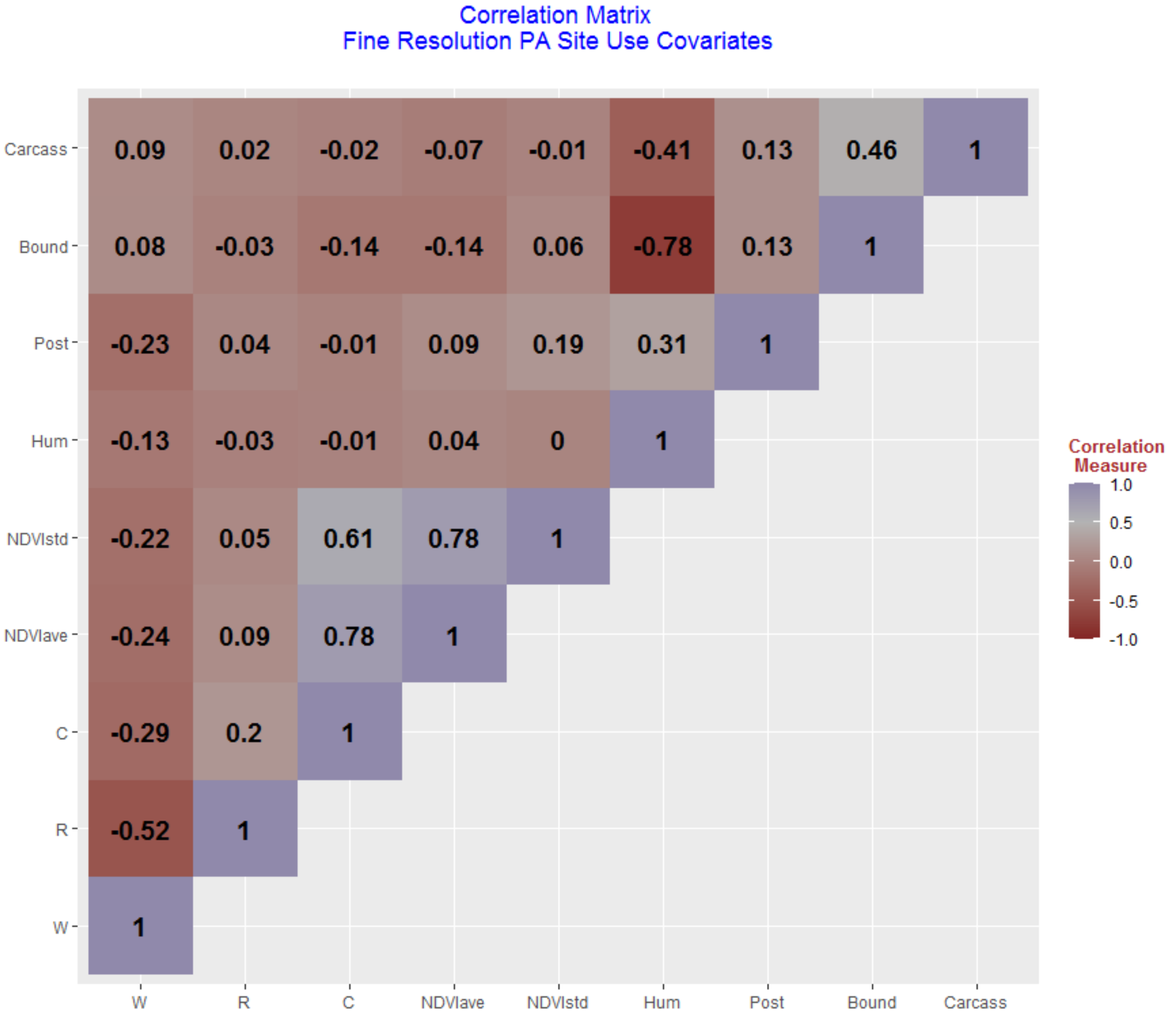


Figure A4.6 Correlation plot for covariates used in the fine resolution, protected areas analysis.

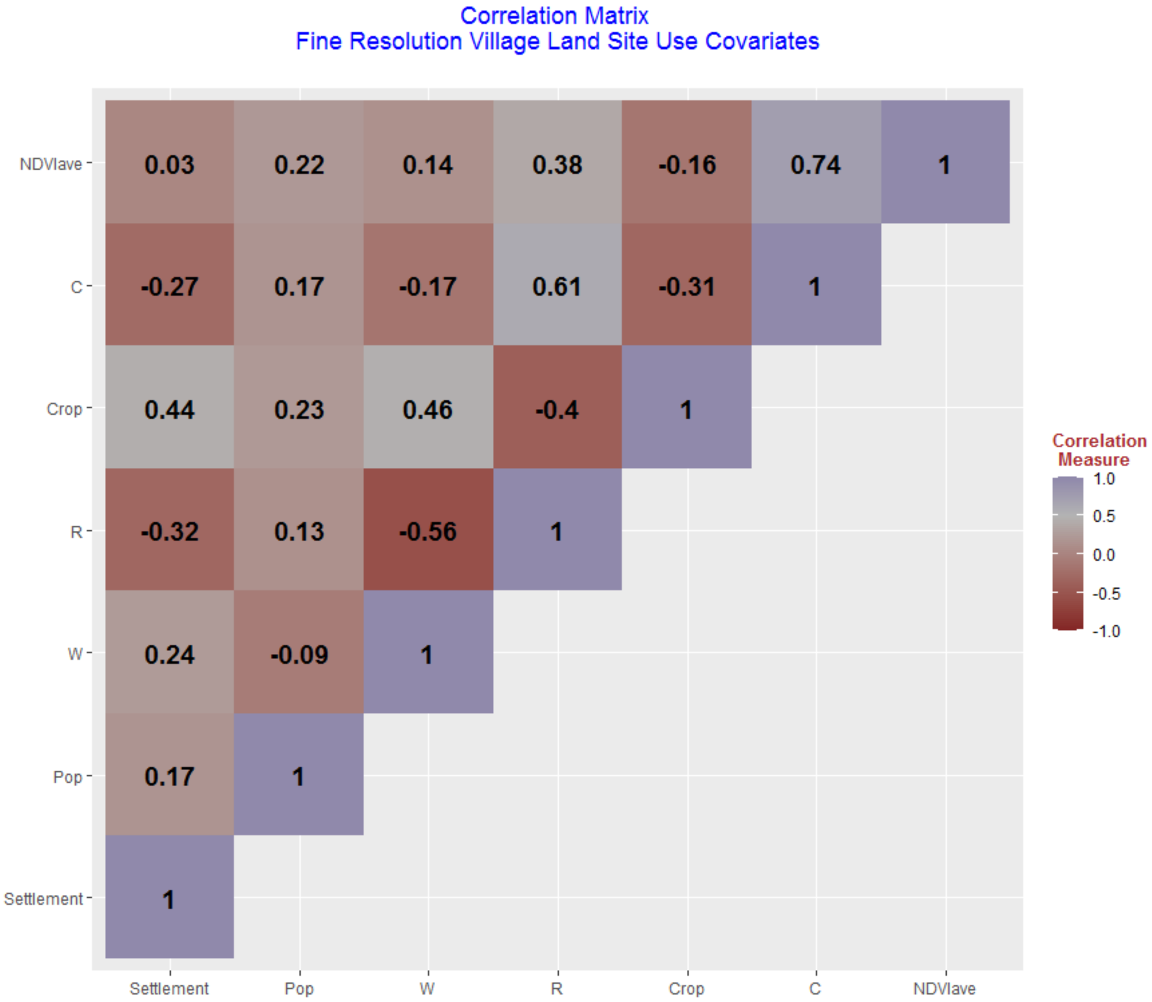
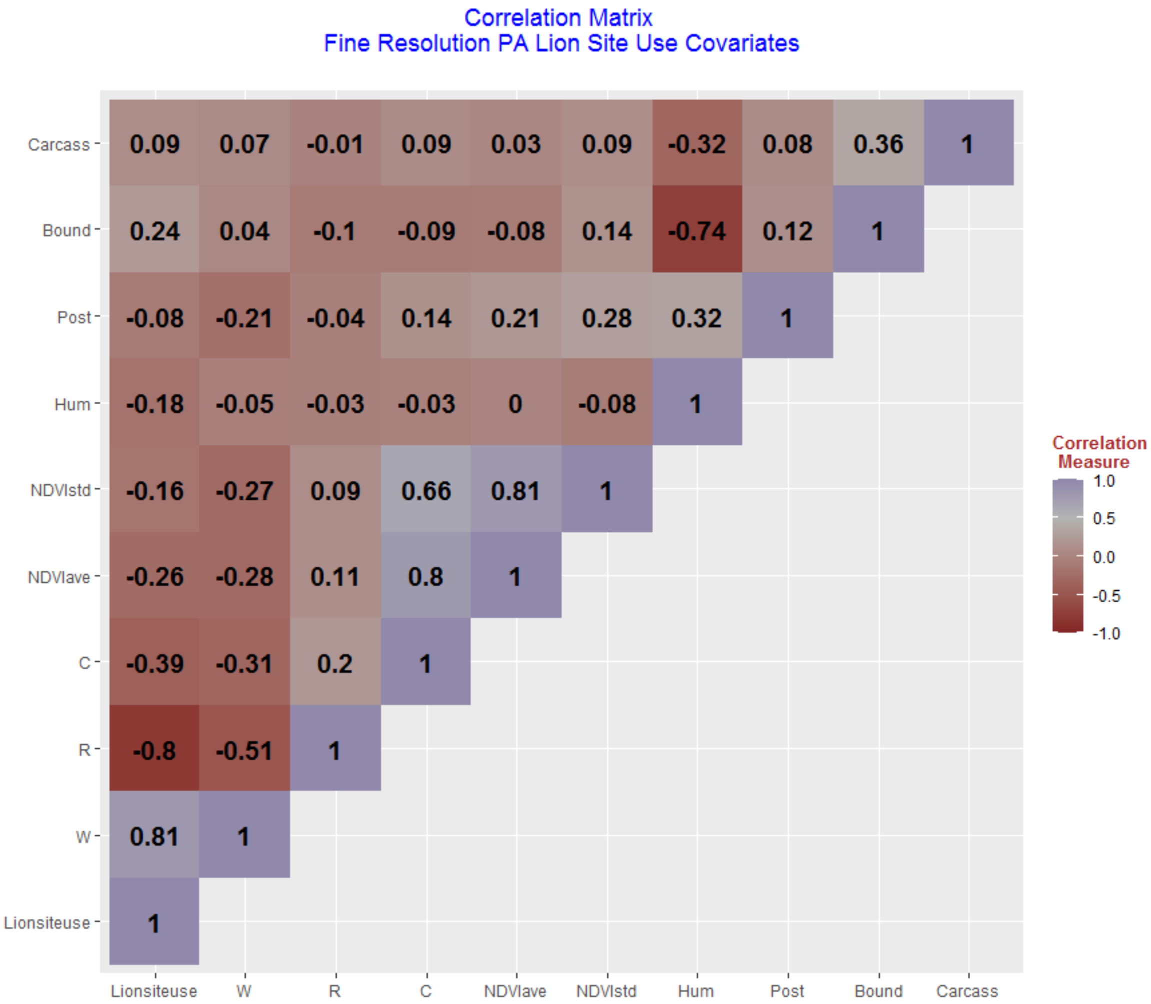


Figure A4.7 Correlation plot for covariates used in the fine resolution, village land analysis.



	Lionsiteuse	W	R	C	NDVIave	NDVIstd	Hum	Post	Bound	Carcass
Carcass	0.09	0.07	-0.01	0.09	0.03	0.09	-0.32	0.08	0.36	1
Bound	0.24	0.04	-0.1	-0.09	-0.08	0.14	-0.74	0.12	1	
Post	-0.08	-0.21	-0.04	0.14	0.21	0.28	0.32	1		
Hum	-0.18	-0.05	-0.03	-0.03	0	-0.08	1			
NDVIstd	-0.16	-0.27	0.09	0.66	0.81	1				
NDVIave	-0.26	-0.28	0.11	0.8	1					
C	-0.39	-0.31	0.2	1						
R	-0.8	-0.51	1							
W	0.81	1								
Lionsiteuse	1									

Figure A4.8 Correlation plot for covariates used in the fine resolution, natural predation risk analysis.

Appendix A4.3 Detection model rankings

Table A4.1 Model rankings of covariates influencing detection (*p*) for the coarse spatial resolution analyses. Final set based on models with ΔAICc <2. Effort: the number of 4 km sampling occasions in a site. PA: whether the sampling occasion was predominantly inside a protected area (coded as 1) or outside a protected area (coded as 0). H: whether the sampling occasion was predominantly *Vachellia-Commiphora* (coded as 0) or miombo woodland (coded as 1). Carcass: mean probability of elephant carcass occurrence, assessed at the site level. Post: mean distance to ranger post, assessed at the site level. R: mean distance to riparian habitat, assessed at the site level. Substrate: an index of the quality of the road substrate for detecting tracks, higher values indicate better quality.

Rank	Model	AICc	ΔAICc	W_i	-2*Log	nPars
Entire ecosystem						
1	p(Effort + PA + H)	690.12	0.00	0.50	-335.55	10
2	p(Effort + PA + H + W)	691.28	1.15	0.28	-335.01	11
3	p(Effort + PA + H + substrate)	691.78	1.66	0.22	-335.26	11
Protected areas only						
1	p(Effort + H + Post + Carcass + R)	589.51	0.00	0.51	-281.52	11
2	p(Effort + H + Post + Carcass + Substrate)	589.62	0.11	0.49	-281.57	11

Table A4.2 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present) and β-coefficient estimates, with associated standard errors and 95% confidence intervals, of covariates explaining detection in the coarse resolution, entire ecosystem analysis. Only detection models ranked within ΔAICc<2 were retained. Bolded covariates have a significant effect (β ± 1.96 x SE) in the top model in which they appear. For detection covariate definitions, see Table A4.1.

Covariate	Σw	β ($SE_β$)	Confidence interval (β ± 1.96 x SE)
Effort	1	0.31 (0.10)	0.12, 0.51
Legal protection (PA)	1	1.39 (0.19)	1.02, 1.75
Dominant vegetation (H)	1	-1.08 (0.14)	-1.36, -0.81
Water availability (W)	0.28	0.15 (0.15)	-0.14, 0.44
Substrate	0.22	-0.11 (0.14)	-0.39, 0.17

Table A4.3 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present) and β-coefficient estimates, with associated standard errors and 95% confidence intervals, of covariates explaining detection in the coarse resolution, protected areas analysis. Only detection models ranked within ΔAICc<2 were retained. Bolded covariates have a significant effect (β ± 1.96 x SE) in the top model in which they appear. For detection covariate definitions, see Table A4.2.

Covariate	**Σw**	**β (SE_β)**	**Confidence interval** (β ± 1.96 x SE)
Effort	1	0.29 (0.11)	0.08, 0.50
Dominant vegetation (H)	1	-1.14 (0.15)	-1.44, -0.85
Distance to ranger post (Post)	1	0.21 (0.11)	0.01,0.043
Probability of elephant carcass occurrence (Carcass)	1	-0.29 (0.11)	-0.51, -0.08
Distance to riparian habitat (R)	0.51	0.06 (0.11)	-0.16, 0.27
Substrate	0.49	0.02 (0.13)	-0.23, 0.27

Table A4.4 Model rankings of covariates influencing detection (*p*) for the fine spatial resolution analyses. Final set based on models with ΔAICc <2 or ΔQAIC (for models where overdispersion was present). As sampling effort was constant for sites at the fine spatial resolution, effort was not included as a detection covariate. Substrate: an index of the quality of the road substrate for detecting tracks, higher values indicate better quality. p(.) is the null model for detection, which assumes that the probability of detection is constant.

Protected areas						
Rank	**Model**	**QAIC**	**ΔQAIC**	**W_i**	**-2*Log**	**nPars**
1	p(.)	2482.23	0.00	0.73	4255.43	10
2	p(Substrate)	2484.06	2.00	0.27	4255.43	11
Village land						
Rank	**Model**	**AICc**	**ΔAICc**	**W_i**	**-2*Log**	**nPars**
1	p(Substrate)	122.89	0.00	0.73	113.81	4
2	p(.)	124.93	2.04	0.27	118.30	3
Natural predation risk						
Rank	**Model**	**QAIC**	**ΔQAIC**	**W_i**	**-2*Log**	**nPars**
1	p(.)	1598.1	0.00	0.73	2859.51	10
2	p(Substrate)	1598.42	2.00	0.27	2859.51	11

Table A4.5 Relative summed model weights (Σw, the sum of W_i for all the models in the top model set in which the covariate was present) and β-coefficient estimates, with associated standard errors and 95% confidence intervals, of covariates explaining detection in the fine resolution analyses. Only detection models ranked within ΔAICc<2 were retained. Bolded covariates have a significant effect (β ± 1.96 x SE) in the top model in which they appear. Substrate: an index of the quality of the road substrate for detecting animal tracks, higher values indicate better quality. Standard errors were adjusted for overdispersion in the protected areas and natural predation risk analyses.

Covariate	Σw	β (SE_β)
Protected areas		
Substrate	0.26	-0.26 (2215)
Village land		
Substrate	0.73	-0.78 (0.41)
Natural predation risk		
Substrate	0.73	-1.16 (31759)

Appendix A4.4 Model fit tests

There was no evidence of lack of fit (p-value > 0.05) or overdispersion ($\hat{c} > 1.5$) for any of the coarse resolution analyses (Table A4.6).

Table A4.6 Results of the MacKenzie-Bailey goodness-of-fit test tests for the coarse resolution analyses. A value of c-hat ($\hat{c}$) of around 1 indicates good model fit. A $\hat{c}$ value of >1.5 indicates overdispersion.

Spatial extent	Model	Model details	$\hat{c}$	p-value
Entire ecosystem	Top	ψ(Crop) p(Effort + PA + H)	1.10	0.28
Entire ecosystem	Most parameterized	ψ(Crop + NDVI) p(Effort + PA + H)	1.08	0.30
Protected areas	Top	ψ(Carcass + C + R) p(Effort + H + Carcass + Post + R)	1.06	0.36
Protected areas	Most parameterized	ψ(Carcass + C + R + W) p(Effort + H + Carcass + Post + R)	1.06	0.35

There was evidence for lack of fit and overdispersion for the fine resolution, protected areas analysis and fine resolution, natural predation risk analyses (Table A4.7). There was no evidence of lack of fit for the fine resolution, village land analysis (p > 0.05).

Table A4.7 Results of the MacKenzie-Bailey goodness-of-fit test tests for the fine resolution analyses. A value of c-hat ($\hat{c}$) of around 1 indicates good model fit. A $\hat{c}$ value of >1.5 indicates overdispersion.

Spatial extent	**Model**	**Model details**	$\hat{c}$	**p-value**
Protected areas	Top and most parameterized	ψ,th0(W + C + Post + Hum + Carcass + Carcass*C), th1(), p(.), th0pi()	1.73	0.02
Village land	Top and most parameterized	ψ(R) p(Substrate)	1.43	0.15
Natural predation risk	Top and most parameterized	ψ,th0(W + C + Post + Carcass), th1(), p(.), th0pi()	1.84	0.02

Appendix A4.5 Plots for non-significant site use covariate relationships

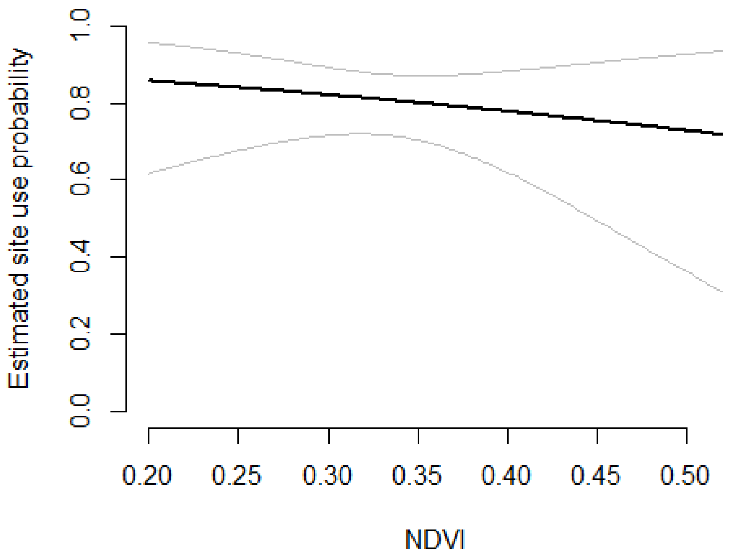


Figure A4.9 Relationship between the probability of elephant site use and mean NDVI for the coarse resolution, entire ecosystem analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value. The effect of NDVI was not significant in the highest-ranked model in which it occurred.

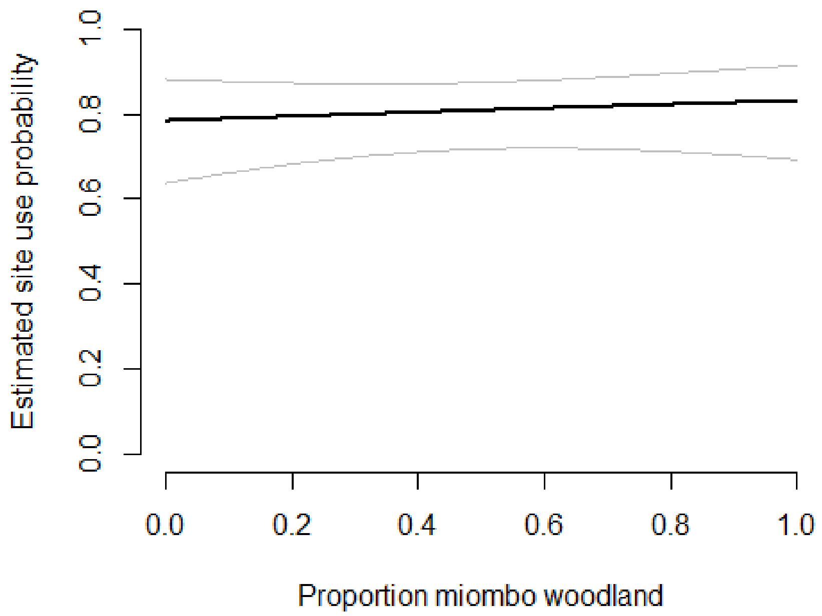


Figure A4.10 Relationship between the probability of elephant site use and dominant vegetation type (assessed as the proportion of a site that was miombo woodland) for the coarse resolution, entire ecosystem analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value. The effect of dominant vegetation type was not significant in the highest-ranked model in which it occurred.

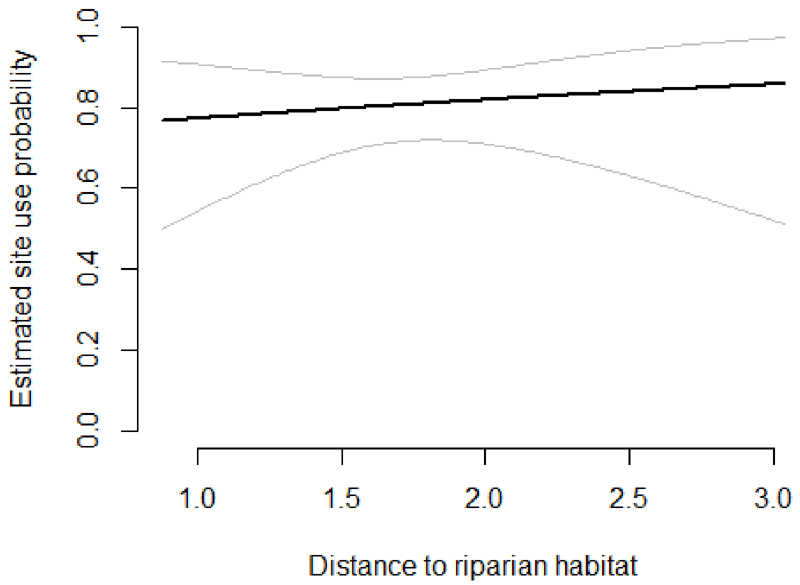


Figure A4.11 Relationship between the probability of elephant site use and distance to riparian habitat (in km) for the coarse resolution, entire ecosystem analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value. The effect of distance to riparian habitat was not significant in the highest-ranked model in which it occurred.

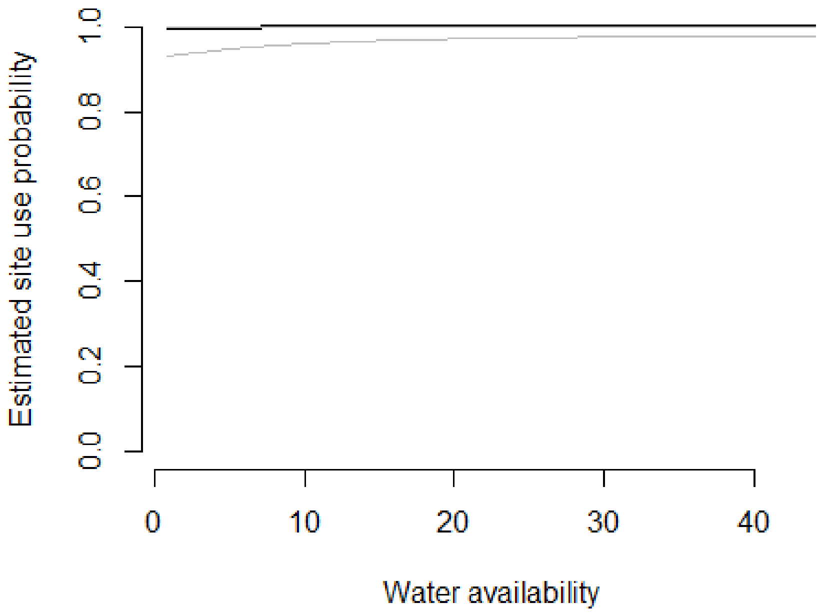


Figure A4.12 Relationship between the probability of elephant site use and water availability for the coarse resolution, protected areas analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value. The effect of water availability was not significant in the highest-ranked model in which it occurred.

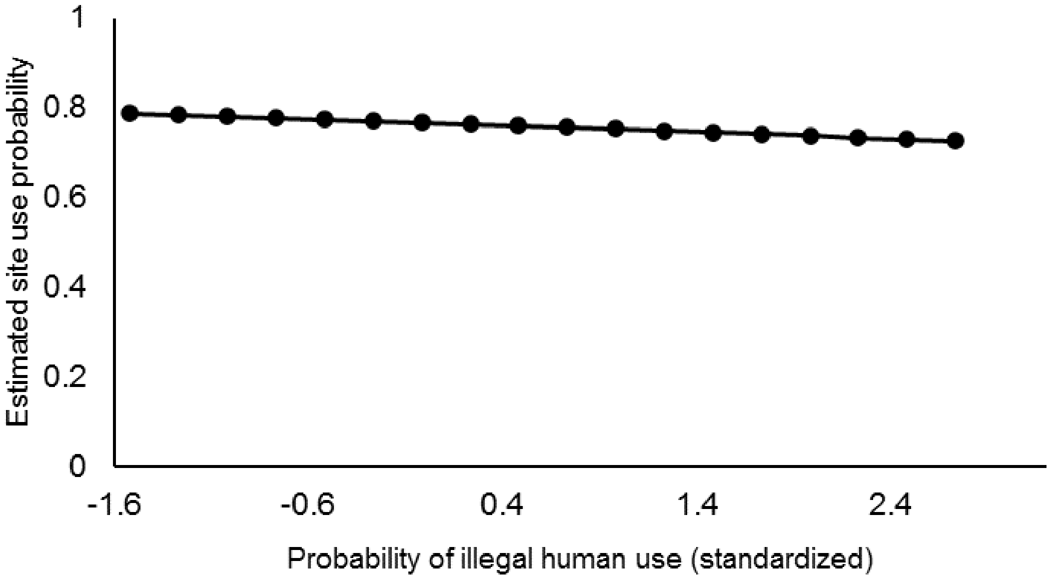


Figure A4.13 Relationship between the probability of elephant site use and mean probability of illegal human use in a site within protected areas at the fine spatial resolution. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized). The effect of illegal human use was not significant in the highest-ranked model in which it occurred.

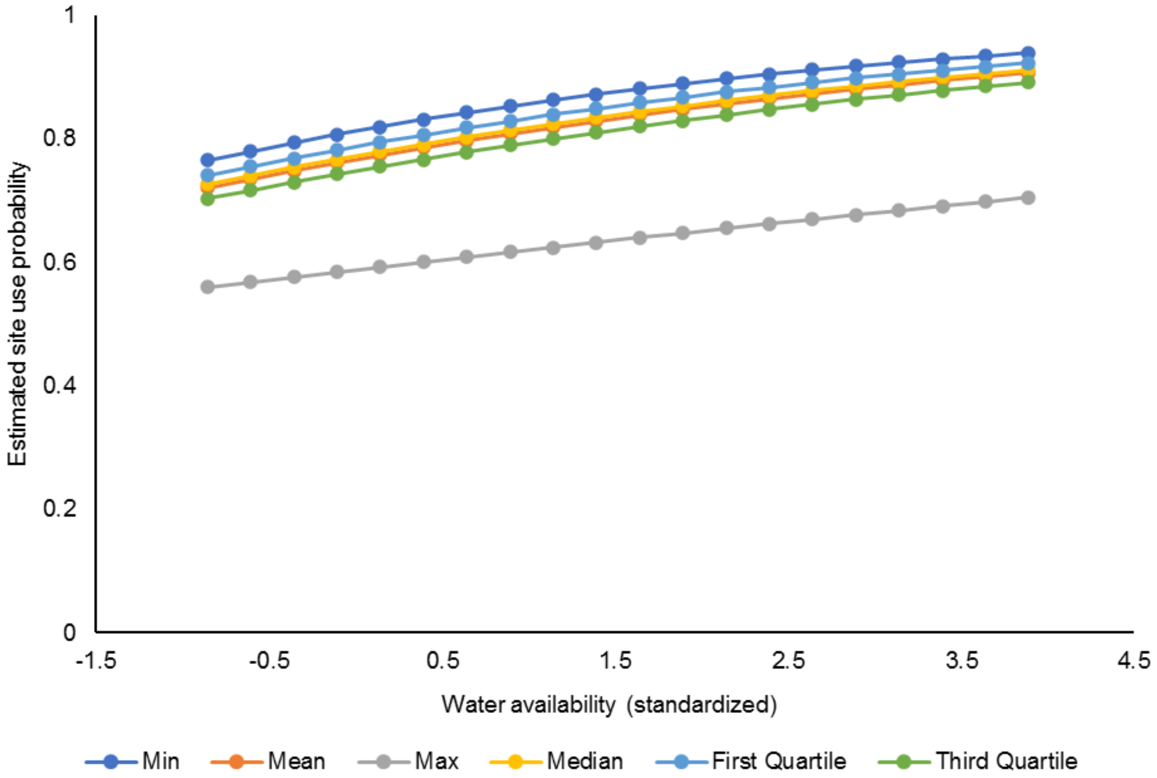


Figure A4.14 The interaction between water availability and elephant carcass occurrence on the probability of elephant site use within protected areas at the fine spatial resolution. Each series shows the effect of water availability on site use at a different value of carcass occurrence probability. The effect of water availability on site use was assessed for the following values of occurrence probability: minimum, mean, median, first quartile, third quartile, and maximum. Plots were produced using the top ranked model containing the covariate. All other site use covariates (tree cover, distance to ranger post, probability of human use) in the model were held at their mean value (standardized). The interaction between water availability and elephant carcass occurrence was not significant in the highest-ranked model in which it occurred.

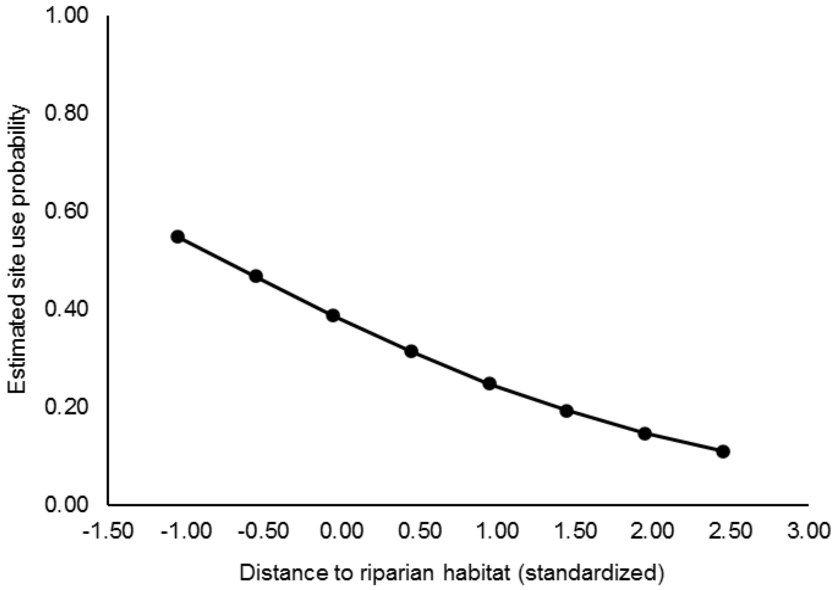


Figure 4.15 Relationship between the probability of elephant site use and mean distance to riparian habitat on village land at the fine spatial resolution. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized). The effect of distance riparian was not significant in the highest-ranked model in which it occurred.

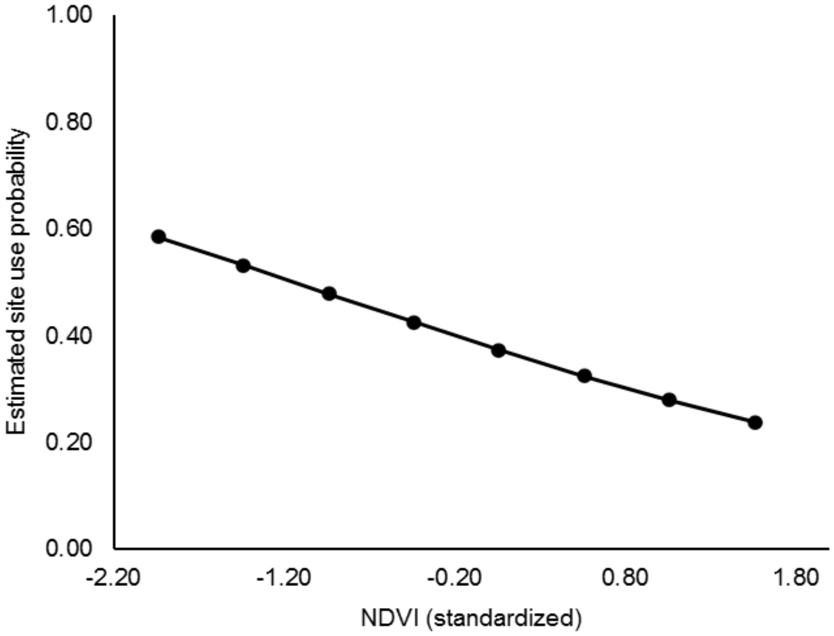


Figure A4.16 Relationship between the probability of elephant site use and NDVI on village land at the fine spatial resolution. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized). The effect of NDVI was not significant in the highest-ranked model in which it occurred.

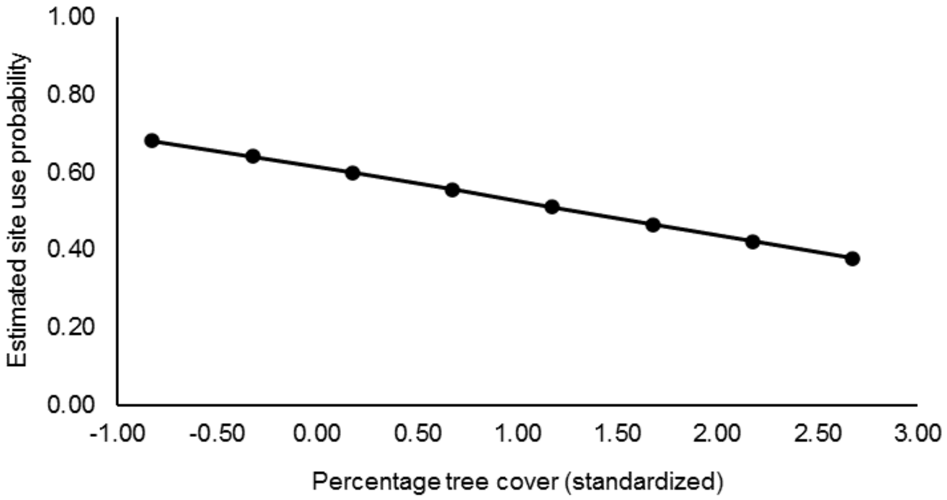


Figure A4.17 Relationship between the probability of elephant site use and percentage tree cover for the fine resolution, village land analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized). The effect of tree cover was not significant in the highest-ranked model in which it occurred.

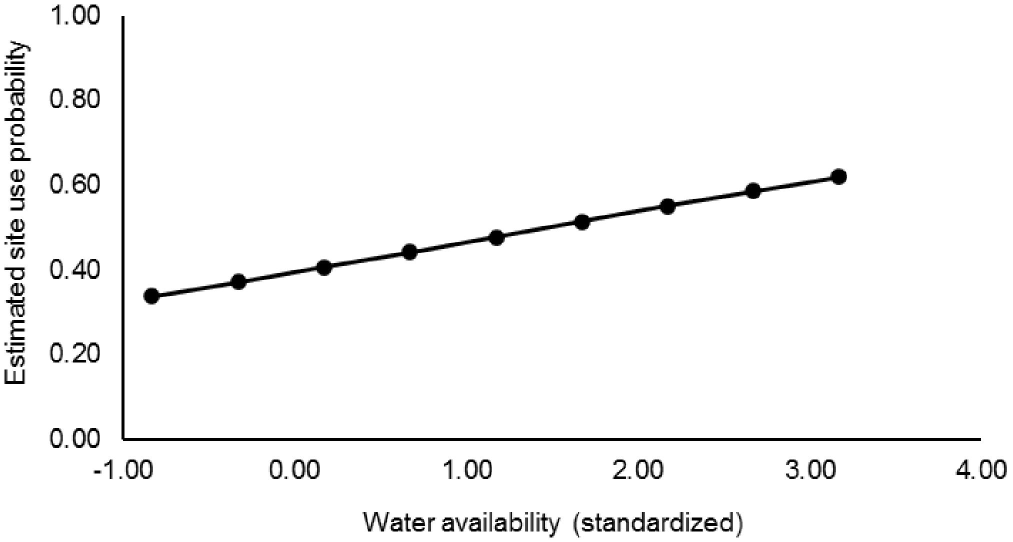


Figure A4.18 Relationship between the probability of elephant site use and water availability for the fine resolution, village land analysis. Plots were produced using the top ranked model containing the covariate. All other site use covariates in the model were held at their mean value (standardized). The effect of water availability was not significant in the highest-ranked model in which it occurred.

Chapter 5

The influence of risk on elephant diel activity, road and water source use, and grouping patterns

***Photo 8**: Camera trap image of a cow-calf group in Rungwa Game Reserve.*

Chapter 5. The influence of risk on elephant diel activity, road and water source use, and grouping patterns

This work was published in 2023 in the African Journal of Ecology (Smit et al., 2023) with the title below. I present here an expanded version incorporating some of the supplementary material from the publication into the main text and referencing other thesis chapters where relevant[19].

Anthropogenic risk increases night-time activities and associations in African elephants (*Loxodonta africana*) in the Ruaha-Rungwa ecosystem, Tanzania

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Author contributions

I conceived the study as part of a larger camera-trapping collaboration with Dr. Charlotte Searle and Dr. Paolo Strampelli (University of Oxford). I led the setup and management of two of the four camera trap grids, and Dr. Searle set up and managed the other two grids. During data collection, I was assisted by Lameck Mkuburo, Kephania Mwaviko, and Peter Mtyana (Southern Tanzania Elephant Program). I annotated all the elephant camera trap images used in the study. I conducted all analyses and wrote the chapter. Professors Phyllis Lee and Hannah Buchanan-Smith (University of Stirling) provided supervision on methods, analyses, and drafts of this chapter. All authors commented on the manuscript submitted to the African Journal of Ecology and agreed to publication.

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[19] In this chapter, I use the pronoun “we” because this work has been published as a multi-author study.

5.1 Abstract

Elephants face diverse threats from human activities and may adjust their temporal activity and social behaviour to reduce human-induced mortality risk. We used data from camera trap surveys in 2018-2019 (n=1,625 independent detection events from 11,751 sampling days) to investigate elephant responses to anthropogenic risk in the Ruaha-Rungwa ecosystem, Tanzania. The study was conducted in one low-risk and three high-risk sites using 26 to 40 paired camera trap stations per site. Risk influenced the active periods, use of roads and water sources, and grouping patterns of elephants. Elephants demonstrated significantly more night-time and reduced daytime activity in the high-risk sites relative to the low-risk site, and elephants were active for less time overall in the high-risk sites. Increased night-time activity in the high-risk sites was observed for both males and females, though it was more pronounced for cow-calf groups than for lone males. Foraging events and use of water sources were more frequent at night in the high-risk sites. Elephants used roads as movement routes in the low-risk site but avoided roads in the high-risk sites. Elephant activity on roads was more nocturnal in the high-risk sites than in the low-risk site, and there was less temporal overlap in elephant and vehicle activity in the high-risk sites than in the low-risk site. Males were significantly more likely to associate with other males and cow-calf groups in the high-risk sites. Fewer occurrences of relaxed behaviours were observed in the high-risk sites compared to the low-risk site. Mean female body condition was slightly lower in the high-risk sites than in the low-risk site but most females assessed were in normal condition in all four sites. There was greater temporal overlap between elephant and lion activity in the high-risk sites than in the low-risk site. We discuss the potential implications of our findings for elephant survival and reproduction.

5.2 Introduction

Since 2006, African savanna elephants (*Loxodonta africana*) have faced an upsurge in poaching resulting in marked population declines (Schlossberg et al., 2019; Thouless et al., 2016; Wittemyer et al., 2014). Poaching has demographic impacts, including the loss of older males and females and a reduction in the ratio of calves to adult females, resulting in populations consisting of adolescents and young adults (Jones et al., 2018; Poole, 1989b). In addition to these direct impacts of poaching, it is important to understand how elephants use behavioural strategies to adapt to risks associated with humans and identify the potential implications of these risk-mitigation strategies for elephant survival and reproduction (e.g., Adams et al., 2022; Buchholtz et al., 2021; Gaynor et al., 2018b; Ihwagi et al., 2018).

Elephants can identify humans in threatening contexts using visual, olfactory, and auditory cues (Bates et al., 2007; McComb et al., 2014). Elephants shift from daytime to crepuscular and nocturnal activity outside protected areas and near protected area boundaries (Gaynor et al., 2018b; Graham et al., 2009; Sitati et al., 2003; Wittemyer et al., 2017), allowing them to access areas where they are at higher risk of human encounters and associated threats such as injury or death, especially when they derive energetic benefits (e.g., access to agricultural crops, Chiyo et al., 2011b; Smit et al., 2019; Wilkie & Douglas-Hamilton, 2018). Increased nocturnal activity has also been observed in response to poaching (Breuer, Maisels & Fishlock, 2016; Ihwagi et al., 2018). Responses to risk may vary by sex due to differences between males and females in susceptibility to predation risk and reproductive strategies, or differences in energetic or thermoregulatory constraints (Ruckstuhl & Neuhaus, 2000; Ruckstuhl, 2007; see Chapter 1). For instance, males are more likely to engage in ‘high-risk, high-reward’ crop foraging than females, who tend to move through or avoid areas of high anthropogenic risk to reach foraging or water resources (Boult et al., 2018; Chiyo et al., 2011a; Kangwana, 1994; Sitati et al., 2003). Elephants may also use social strategies to mitigate risk by associating with other elephants to share knowledge or dilute mortality risk (e.g., Allen et al., 2020; Sitati et al., 2003; Smit et al., 2019). Understanding elephant behavioural responses to risk may help to develop behavioural indicators of anthropogenic pressure (Goldenberg et al., 2017; Ihwagi et al., 2018) and conservation strategies informed by an understanding of elephant behaviour and social structure.

We investigated elephant responses to poaching risk, as inferred from elephant carcass distributions (Beale et al., 2018; Chapter 3), in the Ruaha-Rungwa ecosystem of Tanzania. The Ruaha-Rungwa elephant population declined by >50% between 2006 and 2015 due to poaching for the ivory trade (Beale et al., 2018; Thouless et al., 2016; Wasser et al., 2015). This is reflected in a population with a disproportionate number of adolescents and young adults and high levels of tusklessness compared to sites that did not experience poaching (Jones et al., 2018; Chapter 3). Ratios of carcasses to live elephants suggested that low-level illegal killing of elephants continued to be a concern during the study period (TAWIRI, 2019). Poaching and other anthropogenic risks (Chapter 3) have likely influenced elephant space use (Chapter 4) and activity patterns in this ecosystem. Anthropogenic risk is distributed unevenly throughout the ecosystem, allowing for comparisons between high- and low-risk sites (Beale et al., 2018, Chapter 3). We used camera trap surveys to investigate whether elephants adjust their activity patterns, grouping patterns, and use of roads and water sources in response to spatial variation in human-mediated risk, and to explore potential costs associated with risk responses.

We hypothesized that anthropogenic risk would influence when elephants were active and how they used roads and water sources. We predicted that elephants would demonstrate greater night-time activity in high-risk areas as a strategy to reduce temporal overlap with humans (e.g., Gaynor et al., 2018b; Ihwagi et al., 2018). As cow-calf groups are thought to be more risk-sensitive than bulls (Chiyo et al., 2011a; Sukumar & Gadgil, 1988), we expected female groups to show a greater shift to night-time activity than males in response to risk. We predicted that elephants would make greater use of roads as movement corridors in the low-risk site than in the high-risk sites. We further predicted that elephants would visit water sources and use roads predominantly at night in high-risk areas and that there would be less temporal overlap between elephants and vehicles in the high-risk sites than in the low-risk site (e.g., Gaynor et al., 2018b). We also hypothesized that risk would influence elephant grouping patterns and predicted that male elephants would be more likely to occur in mixed groups (cow-calf groups with associated mature males) and bull groups in high-risk sites compared to the low-risk site. We also explored whether behavioural responses to anthropogenic risk may be associated with costs. We compared the types of activities that elephants were engaged in and expected that fewer relaxed behaviours and more stress behaviours would be observed in the high-risk sites compared to the low-risk site. Whether temporal responses to risk may be associated with foraging costs and increased predation risk from non-human predators was investigated by comparing adult female body condition and the degree of temporal overlap between elephants and lions, a non-human natural predator, in the low- and high-risk sites.

5. 3. Methods

5.3.1 Study site

The Ruaha-Rungwa ecosystem is located in south-central Tanzania. The study area comprised Ruaha National Park (20,226 km^2), Rungwa-Kizigo-Muhesi Game Reserves (17,035 km^2), and MBOMIPA Wildlife Management Area (777 km^2). For an ecosystem description, see Chapter 2.

Photographic tourism is conducted in the National Park, licensed hunting is permitted in the Game Reserves, and both photographic tourism and licensed hunting are allowed in the Wildlife Management Area (WMA). The road network in the ecosystem is designed primarily for ranger access. Only the high-use tourism area and hunting areas with active operators have extensive networks of minor roads, where tourism and hunting vehicle activity is largely restricted to daytime hours.

Camera traps were situated in grids within four sites representing different levels of risk to elephants. We categorized grids as low- or high-risk based on elephant carcass distribution (Chapter 3, Beale et al., 2018), with carcass density used as an indicator of poaching risk, as well as the distribution of illegal human activities (Chapter 3, Strampelli et al., 2022b; TAWIRI, 2016; TAWIRI; 2019). Camera trap surveys were conducted in the dry season of 2018 and 2019.

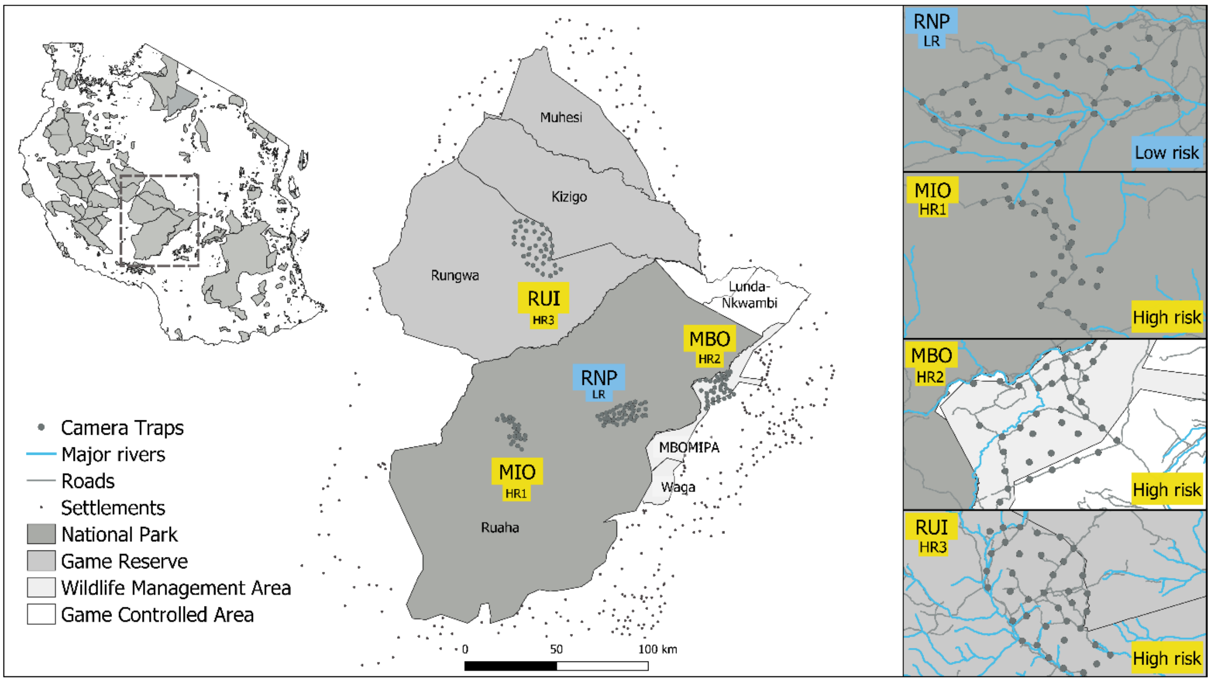


Figure 5.1 Location of the study area in Tanzania (left), study area with camera trap survey grid locations shown (middle), and location of camera traps (grey circles) and risk to elephants shown (right). The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2, and RUI:HR3 grids represent high-risk areas as determined in Chapter 3.

The Ruaha National Park core grid (RNP:LR, low-risk) was situated in the high-use tourism zone where the Park’s headquarters, three ranger posts, and tourism infrastructure are located, and where photographic tourism activity is concentrated. Due to established tourism and ranger presence, this area forms the safest part of the ecosystem for elephants (Beale et al., 2018). The dominant habitat is *Vachellia-Commiphora*.

The Ruaha National Park miombo grid (MIO:HR1, high-risk) was located in a ‘wilderness zone’ in the west of the park in an area dominated by miombo (*Brachystegia-Jubelnardia* woodland). Tourism activity in wilderness zones is restricted to walking safaris, though no tour operators were present at the time of the study (2018). Due to their low visitation rates, wilderness zone areas within the park were at higher risk of illegal activities than areas with established tourism presence (Mtahiko, 2007). The MIO:HR1 grid also had higher elephant carcass densities than the Ruaha NP core tourism area from 2013 to 2015 (Beale et al., 2018).

The MBOMIPA WMA grid (MBO:HR2, high-risk) was located in the Lunda zone of the WMA, where the dominant habitat is *Vachellia-Commiphora*. No tourism activities took place at the time of the study (2018). This area was a hotspot of elephant poaching from 2013 to 2015 (Beale et al., 2018) and the probability of illegal human activity was greater in the WMA than in Ruaha National Park at the time of the study (Strampelli et al., 2022b). The grid was also directly adjacent to cultivated and grazed village land.

The Rungwa-Ikiri grid (RUI:HR3, high-risk) was located in the Rungwa-Ikiri block of Rungwa Game Reserve, where miombo woodland was dominant. This area experienced elephant poaching from 2013 to 2015 (Beale et al., 2018). Human illegal activity was more prevalent in the Game Reserves than in the National Park (Strampelli et al., 2022b). Licensed hunting was actively occurring at the time of the study (2019), although not for elephants.

5.3.2 Data collection

We used camera traps to estimate elephant active periods (e.g., Gaynor et al., 2018b; Gessner et al., 2014; Rowcliffe et al., 2014). Elephant active periods have previously been described from camera trap surveys which varied in purpose, layout, and duration (Gaynor et al., 2018). Data were collected as part of a multi-purpose and multi-species research collaboration, with camera trap survey design initially guided by requirements for spatially explicit capture-recapture density estimation of carnivores (Searle et al., 2021). All surveys were conducted in the dry season to avoid possible confounding effects of seasonality on elephant activity patterns (Barnes, 1983).

A ‘grid’ was defined as the full complement of camera traps within each of the four survey areas. Grids consisted of between 26 to 44 stations with paired camera traps (Figure 5.1, Table 5.1). Camera stations were placed along roads as well as off-road on animal trails. Camera stations were defined as being near water if they were within 1 km of a water source. Grids were situated >30 km apart; as such, it is unlikely that the same elephant(s) would be captured at multiple grids in the same 24-hour period.

The low-risk RNP:LR grid contained 44 stations (88 paired cameras) deployed over an area of 223 km^2 (average spacing 1.96 km) in the core tourist area of Ruaha NP for 83 days between June and September 2018. 38 camera stations were placed on roads, and 6 camera stations were placed on animal trails off-road. 17 stations were placed near water (within 1 km of a water source).

The high-risk MIO:HR1 grid contained 26 stations (52 paired cameras) deployed in the miombo woodland of western Ruaha NP, covering an area of 152 km^2 (average spacing 1.88

km), for 90 days between August and November 2018. Due to the limited number of roads in this area, 12 stations were placed on animal trails off-road, and 14 stations were placed on roads. 12 stations were placed near water.

The high-risk MBO:HR2 grid comprised 40 stations (80 paired cameras) deployed across 270 km^2 (average spacing 2.08 km) in MBOMIPA WMA, for 70 days between September and November 2018. 30 camera stations were placed on roads, and 10 camera stations were placed on animal trails off-road. 17 stations were placed near water.

The high-risk RUI:HR3 grid comprised 40 stations (80 paired cameras) deployed over an area of 555 km^2 (average spacing 3.46 km) in the Ikiri hunting block of Rungwa GR, for 90 days between July and October 2019. 32 camera stations were placed on roads, and eight camera stations were placed on animal trails off-road. 19 stations were placed near water.

We used primarily Cuddeback Professional Color Model 1347 (Non Typical Inc., Wisconsin, USA) camera traps. A few stations used Cuddeback X-Change Color Model 1279 (Non Typical Inc., Wisconsin, USA) and/or Reconyx Hyperfire HC500 (Reconyx, Wisconsin, USA) cameras. All camera models used passive infrared (PIR) sensor systems. The trigger speed ranged from 0.2 seconds for the Reconyx Hyperfire HC500 camera to 0.25 seconds for the Cuddeback models. The Cuddeback cameras used white xenon flash and produced colour images day and night. The Reconyx cameras used infrared flash and produced colour images during the day and monochrome images at night.

Cameras were set to take still images, with one photograph per trigger. Cuddeback cameras were set to the minimum capture delay (Fast as Possible, <5 seconds). During the day, the recovery speed of the Cuddeback cameras was 1 to 2 seconds. During the night, owing to the time needed to recharge the capacitators in the white flash bulb, the recovery speed was 10 to 30 seconds depending on battery level (J. Peterson, personal communication, May 26, 2020). The Reconyx models had a recovery time of 0 seconds, and the capture delay was set to 1 second.

Neighbouring camera stations had a spacing of 1 to 5 km. Cameras were mounted on trees near roads and animal trails, perpendicular to the expected movement pathway of the target species. Cameras were positioned between 2 and 5 paces from the centre of the road or animal trail, at a height of 30-40 cm. Cameras positioned closest to centre of roads/trails primarily captured the legs and trunk of elephants moving through the field of view, while cameras positioned further away were able to capture the whole body of elephants. Cameras were positioned horizontally with the lens and sensor perpendicular to the ground.

Cameras were mounted in protective cases and secured with binding wire to prevent damage and loss to animals and humans. In high-risk areas for theft, protective cases were camouflaged with spray glue, soil, and vegetation and secured with padlocks. One camera was lost to theft (MBO:HR2 grid) and two cameras were lost to lions (MIO:HR1 grid). As stations were paired, at least one camera was always active at each station. We removed vegetation directly in the camera detection zone to reduce triggers from moving vegetation. In areas with fire risk, we cleared 1-metre diameter fire breaks around the cameras. Camera traps were serviced every one to four weeks to download photos and replace batteries.

Table 5.1 Summary of camera trap grid layout, events, and effort, where effort is measured as the total number of active days across all camera stations. Relative activity index (RAI) is defined as the number of detection events per 100 sampling days.

	Ruaha NP core zone (RNP:LR)	**Ruaha NP miombo zone (MIO:HR1)**	**MBOMIPA WMA (MBO:HR2)**	**Rungwa-Ikiri Block (RUI:HR3)**
Risk level	Low	High	High	High
No. of camera sites	44 (80 cameras)	26 (52 cameras)	40 (80 cameras)	40 (80 cameras)
Total survey area	223 km^2	152 km^2	270 km^2	555 km^2
Average spacing between camera stations	1.96 km	1.88 km	2.08 km	3.46 km
Camera placement on roads	38 stations on roads, 6 stations off-road	14 stations on roads, 12 stations off-road	30 stations on roads, 10 stations off-road	32 stations on roads, 8 stations off-road
Camera placement near water	17 stations near water	12 stations near water	17 stations near water	19 stations near water
Study period	June-September 2018 (83 days)	September-November 2018 (90 days)	August-November 2018 (70 days)	July-October 2019 (90 days)
Effort (camera trap days)	3,508	2,187	2,681	3,375
No. of camera sites with elephant detections	44 (100%)	24 (93%)	32 (80%)	38 (95%)
No. of elephant images	5,898	1,446	865	1,501
No. of elephant detection events	885	166	214	360
Relative Activity Index (RAI)	25.2	7.6	8.0	10.7

Camera trap images of elephants, lions, and vehicles were annotated based on visual inspection using ExifPro Version 2.1 software (Kowalski & Kowalski, 2013). We defined independent elephant detection events as images of elephants that were separated by more than 15 minutes (Gaynor et al., 2018b, see Chapter 2). This definition was based on expert assessment, including examination of camera trap video footage which demonstrated that elephants in the same known group were rarely separated by more than 15 minutes at a given location (Gaynor et al., 2018b). We noted the start time (the time of the first photograph in an event) and the midpoint for each elephant event. We coded group type for each event as cow-calf, lone bull, bull group, mixed group of cow-calf plus mature males, or unknown (see Chapter 2, Table 2.1), and whether elephants had visited a water source (determined from the presence of moisture on the trunk and/or legs or body). For each detection event, we visually inspected camera trap images to identify which activity types were present (see Chapter 2, Table 2.3 for activity definitions). An activity type was considered present if at least one individual in the event displayed the activity. More than one activity type could be present per event. See Chapter 2 for inter-observer reliability of group type and activity type scoring.

Lion detection events were defined as images of lions that were separated by more than 30 minutes, following common practice in camera trap studies of large carnivores (e.g., Yang et al., 2018; Saisamorn et al., 2019; Chaudhary et al., 2020). The event time for lion detections was the time associated with the first image in the event. Each camera trap image of a vehicle was defined as a vehicle detection event.

Body condition was scored for adult female elephants (≥10 years) in camera trap events where images were deemed suitable for assessing body condition, which ranged between 16% and 20% of cow-calf group events across the four grids. Body condition scoring (BCS) was done for one female elephant per event using the five-point scale in Morfeld et al. (2014), where BCS=1-2 is underweight, BCS=3 is ideal/normal, and BCS=4-5 is overweight/obese. See Chapter 2 for further details and inter-observer reliability of body condition scoring.

5.3.3 Data analysis

To visualize elephant active periods over 24 hours, we used the *overlap* package in R version 1.4.1106 to generate smoothed non-parametric kernel density distributions of independent elephant events (Ridout & Linkie, 2009). We used event start times following Gaynor et al. (2018b), as distributions using event start times and mid times were identical (Table A5.1; Figure A5.1). Since the sun's position in the sky ('sun time'), rather than clock time (the time on a 24-hour clock), has biological and environmental meaning, we accounted for geographic and temporal variation in the times of sunrise and sunset over the study area and study period by using the *SunTime* function to convert clock times to sun times (Nouvellet et al., 2012).

We compared 24-hour activity profiles for all elephant events and calculated the coefficient of overlapping between the low-risk site and each of the high-risk sites. The coefficient of overlapping represents the total proportion of area that is shared by two activity distributions. We determined if two activity distributions were significantly different using the *activity* package (Rowcliffe et al., 2014). We also compared the activity distributions and coefficient of overlapping between the low-risk and each of the high-risk grids for cow-calf group and lone bull events separately. We also used the *activity* package to estimate the proportion of the 24-hour diel period that elephants were active from the kernel density distributions of elephant events at each site (Rowcliffe et al., 2014).

To examine the effect of diel period, grid (a proxy for risk), group type, water, and roads on the number of elephant observations, we summed the number of elephant events for each group type and diel period by camera trap station (Smit, 2021b). Sample sizes for bull groups and mixed groups were too small to analyse independently (Table 5.3). We combined lone bull and bull group events into a single category of male events, as these two group types reflect male decision-making. We combined cow-calf and mixed group events into a single category of female events, as these two group types reflect primarily female decision-making. Each camera trap station was either near or far from water, on- or off-road, and in one of four grids (RNP:LR, MIO:HR1, MBO:HR2, RUI:HR3). Events were assigned to four diel periods: dawn (0.5 hours), day (12 hours), dusk (0.5 hours) and night (11 hours). Dawn and dusk were considered separately from day and night because they represent transition periods in brightness and temperature. Sunrise, sunset, and twilight times were extracted from *timeanddate.com*. We excluded the dawn and dusk diel periods (comprising 5% of detection events) from subsequent analysis to reduce zero-inflation resulting from small sample sizes.

We explored whether the degree of elephant nocturnality - defined as the percentage of nocturnal events - as a function of risk varied by group type (male/female), proximity to water (near/far) and camera placement relative to roads (on/off). This was done using the subset of day (07:00-18:59 hours) and night (19:00-06:59 hours) elephant detection events (n=1,262 events). We also explored whether male and female groups differed in the extent of their nocturnal use of water sources and roads as a function of risk by calculating the percentage of nocturnal events near and far from water and on- and off-road for male and female group types separately. To determine whether the degree of temporal overlap between elephant and vehicle activity varied with risk, we generated elephant and vehicle activity distributions (using the subset of elephant events from camera stations placed on roads) and calculated the coefficient of overlapping between elephant and vehicle activity curves for each site.

Data exploration was done prior to modelling following the eight-step protocol in Zuur, Ieno & Elphick (2010) and this exposed heterogeneity and overdispersion of the elephant event count data. To model the number of elephant events as a function of the covariates, a Negative Binomial Generalized Linear Mixed Model (GLMM) with a log link function was used. The log link function ensures positive fitted values, and the Negative Binomial distribution is typically used for overdispersed count data. Fixed covariates were *diel period* (categorical with two levels, with *Day* as the reference level), *water* (categorical with two levels, with *No* as the reference level), *road* (categorical with two levels, with *Off* as the reference level), *grid* (categorical with four levels, with *RNP:LR* as the reference level), and *group type* (categorical with two levels: with *Male* as the reference level). To account for repeated measures from cameras, camera station was used as a random intercept. We fit a global model with all biologically possible interactions informed by our hypotheses, including two-way and three-way interactions between *diel*, *group*, *water*, *road*, and *grid*. Those interactions which did not contribute to model fit were removed during model selection. To account for differences in camera trap sampling effort and differences in the duration of the day and night diel periods, the number of sampling hours was included as an offset in the model. For confirmatory purposes, we also fit the top random intercept-only model with *diel* and *group* as random slopes. Models were fit through Maximum Likelihood estimation using Laplace approximation and a BOBYQA optimizer in the *lme4* package (Bates et al., 2015).

Model selection was done using AIC, whereby all models within ΔAIC 6 were considered top models (Richards, 2008). We selected one model from the top model set which represented the best trade-off between explanatory power and complexity through a likelihood ratio test using the anova function in R, which performs an f-test to compare two nested models. We expressed model coefficients as incident rate ratios (IRRs) to compare the incidence rates of events between different levels of a categorical variable. IRRs were visualized using the *sjPlot* package (Lüdecke, 2020).

We examined whether there was a difference in the relative frequency of female and male events across the four grids using a chi-square test of homogeneity. We also used chi-square goodness of fit tests to determine if there was a significant difference in the number of 1) lone bull versus bull group events and 2) lone bull versus mixed group events between the low-risk grid and each of the three high-risk grids. We applied the Bonferroni correction to correct for multiple comparisons ($\alpha = 0.05 / 3 = 0.017$).

We investigated whether the range and frequency of elephant activity types detected by camera traps differed between the low- and high-risk sites. Activity types were grouped into three broad categories of 1) energy acquisition and movement behaviours, 2) relaxed behaviours, and 3) stress behaviours (Chapter 2). Events were classified as either day (07:00-18:59 hours) or night (19:00-06:59 hours). We compared the number of diurnal and nocturnal occurrences of energy acquisition and movement behaviours and visits to water sources between the low- and high-risk grids using chi-square goodness-of-fit tests. All probability tests were set to $p<0.05$.

We compared mean, median, and mode body condition scores for adult female elephants between the low- and high-risk sites. We visualized elephant and lion diel activity distributions and calculated the coefficient of overlapping between elephant and lion activity curves in all four sites.

5.4 Results

Camera traps detected 1,625 unique elephant events over 11,751 camera trap days (Table 5.1; Smit, 2021a). In the low-risk site, elephant activity was predominantly diurnal, with a peak around dusk. Elephant activity profiles for the three high-risk sites differed in the location of activity peaks, but all had reduced diurnal activity and increased nocturnal activity and were significantly different from the activity distribution for the low-risk site. Activity profiles for the high-risk sites had more compressed peaks of elephant activity relative to the low-risk site (Figure 5.2). The proportion of the 24-hour diel period that elephants were active was estimated as 0.53 (95% confidence interval: 0.47 – 0.60) for the RNP:LR grid, 0.40 (95% CI: 0.31-0.48) for the MIO:HR1 grid, 0.44 (95% CI: 0.36-0.49) for the MBO:HR2 grid, and 0.35 (95% CI: 0.29-0.40) for the RUI grid.

Activity profiles for cow-calf groups and lone bulls (Figure 5.2) demonstrated increased nocturnal activity in the high-risk sites relative to the low-risk site. For cow-calf groups, 79% of events were nocturnal in the high-risk sites compared to 47% in the low-risk site (Figure 5.3). For lone bulls, 81% of events were nocturnal in the high-risk sites compared to 59% in the low-risk site (Figure 5.3). Overlap between the cow-calf distributions in the low- and high-risk sites was lower than the overlap between lone bull distributions in the low- and high-risk sites. When the male and female group types were pooled, both male and female groups were more nocturnal in the high-risk sites than in the low-risk site, although the increase in nocturnality as a function of risk was slightly greater for female groups (Figure 5.4).

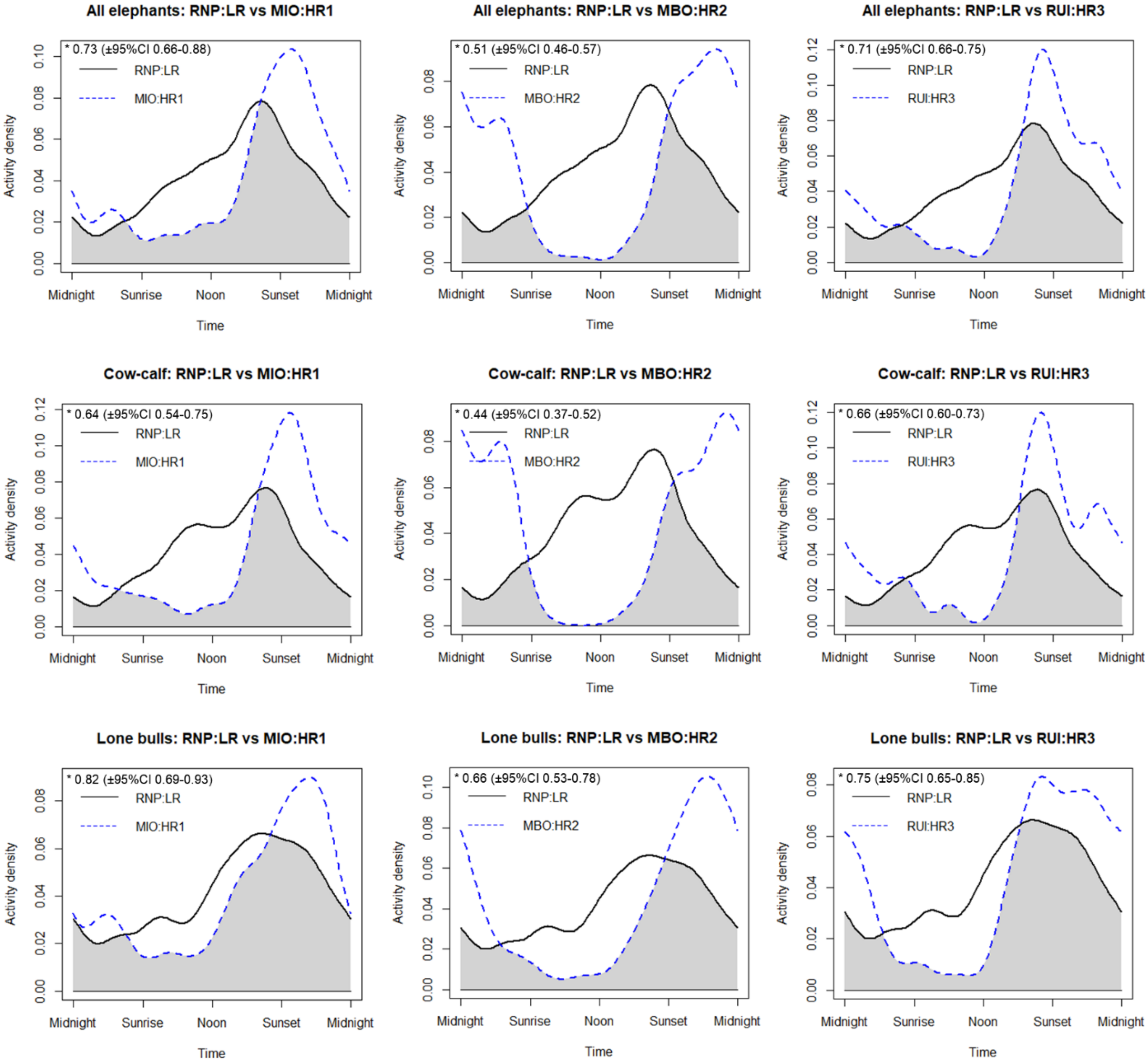


Figure 5.2 Elephant activity profiles for all events (top row) in the low-risk RNP:LR grid (n=885 events) and three high-risk grids: MIO:HR1 (n=166 events), MBO:HR2 (n=214 events), and RUI:HR3 (n=360 events); cow-calf events (middle row) in the low-risk RNP:LR grid (n=453 events) and three high-risk grids: MIO:HR1 (n=60 events), MBO:HR2 (n=104 events), and RUI:HR2 (n=170 events); and lone bull events (bottom row) in the low-risk RNP:LR grid (n=207 events) and three high-risk grids: MIO:HR1 (n=35 events), MBO:HR2 (n=41 events), and RUI:HR3 (n=59 events). Note the y-axes are not the same. The density of elephant events over a 24-h period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between the two distributions and is equivalent to the coefficient of overlapping. The coefficient of overlapping and 95% confidence interval is indicated for each pair of activity distributions. An asterisk indicates the two distributions are significantly different.

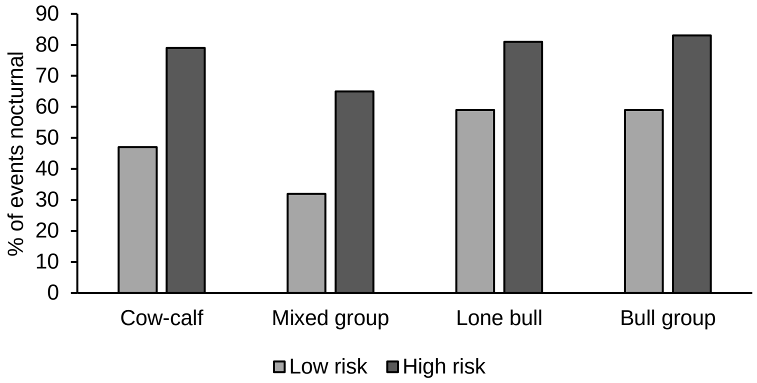


Figure 5.3 The percentage of nocturnal events for cow-calf groups (n=741), mixed groups (n=138), lone bulls (n=331), and bull groups (n=52) in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined.

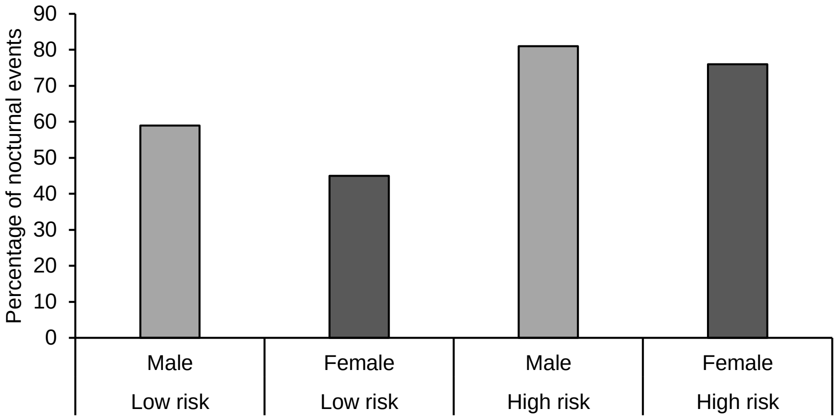


Figure 5.4 The percentage of nocturnal events for male (light grey, n=383 events) and female (dark grey, n=879 events) group types in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined. Male events include lone bull and bull group events. Female events include cow-calf and mixed group events.

There was a significant difference in the number of diurnal and nocturnal moving events between the low-risk grid and the high-risk grids, X^2 (1, N = 1549) = 174.0, p <0.005). In the low-risk site, 48% of moving events occurred during the day and 52% at night, compared to 23% and 77% respectively for the high-risk sites. There was also a significant difference in the number of diurnal and nocturnal feeding events between the low-risk site and the high-risk sites, X^2 (1, N = 345) = 8.3, p <0.005; Figure 5.3). In the low-risk site, 46% of feeding events occurred during the day and 54% at night, compared to 33% and 67% respectively for the high-risk sites. There was a significant difference in the number of diurnal and nocturnal visits to water sources between the low-risk sites and the high-risk sites, X^2 (1, N = 413) = 33.8, p <0.005). In the low-risk site, 45% of water source visits occurred during the day and 55% at night, compared to 18% and 82% respectively for the high-risk sites.

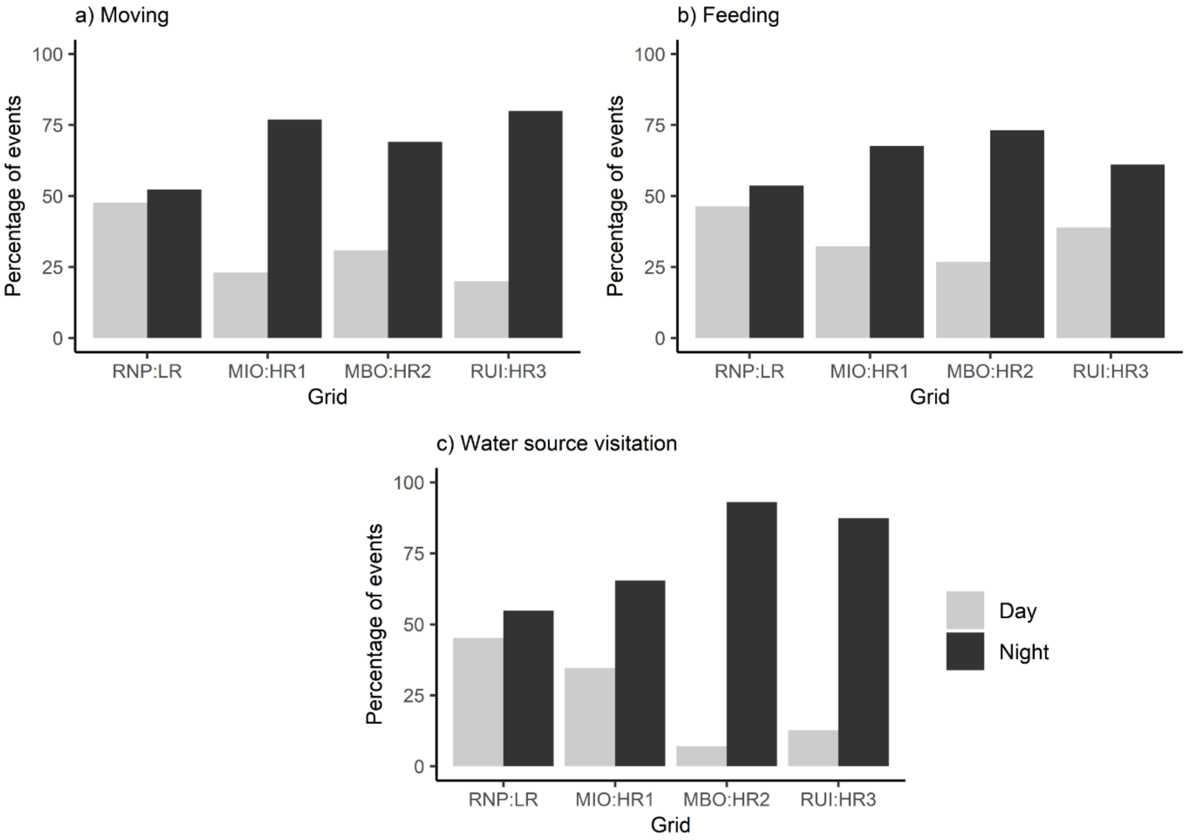


Figure 5.5 Percentage of daytime and night-time a) moving events (n=1,549), b) feeding events (n=345) and, c) visits to water sources by grid (n=413). The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2, and RUI:HR3 grids represent high-risk areas.

Proximity to water did not have a marked influence on the degree of elephant nocturnality as a function of risk, although camera stations near water detected a slightly higher percentage of nocturnal events than camera stations far from water (Figure 5.6). Both male and female groups were more nocturnal in the high-risk sites at cameras both near and far from water sources (Figure 5.7). This is consistent with the finding that elephant movement and energy acquisition activities (Figure 5.5), not just water use, were more nocturnal in the high-risk sites. In the high-risk sites, the degree of elephant nocturnality was similar on- and off-roads (Figure 5.8). There was, however, a greater increase in nocturnality at camera stations placed on roads in the high-risk site relative to the low-risk site. Both male and female groups increased nocturnal activity on roads in the high-risk sites relative to the low-risk site (Figure 5.9). There was less temporal overlap in elephant and vehicle activity in the high-risk sites than in the low-risk site (Figure 5.10).

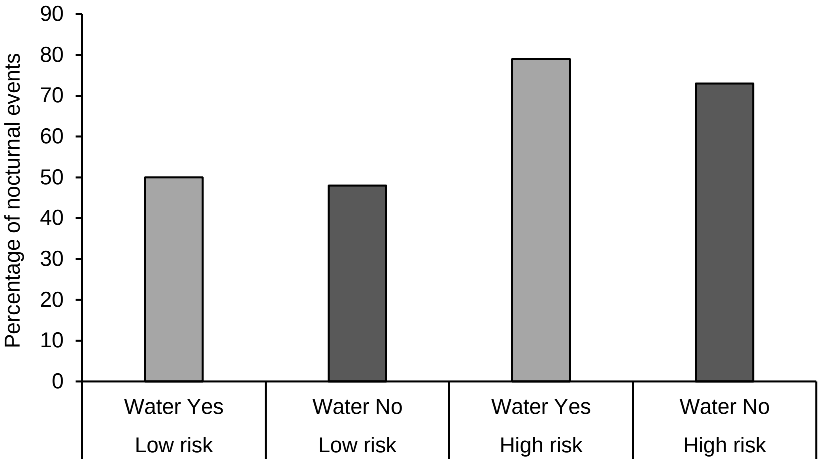


Figure 5.6 The percentage of nocturnal events near water (light grey, n=723 events) and far from water (dark grey, n=539 events) in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined.

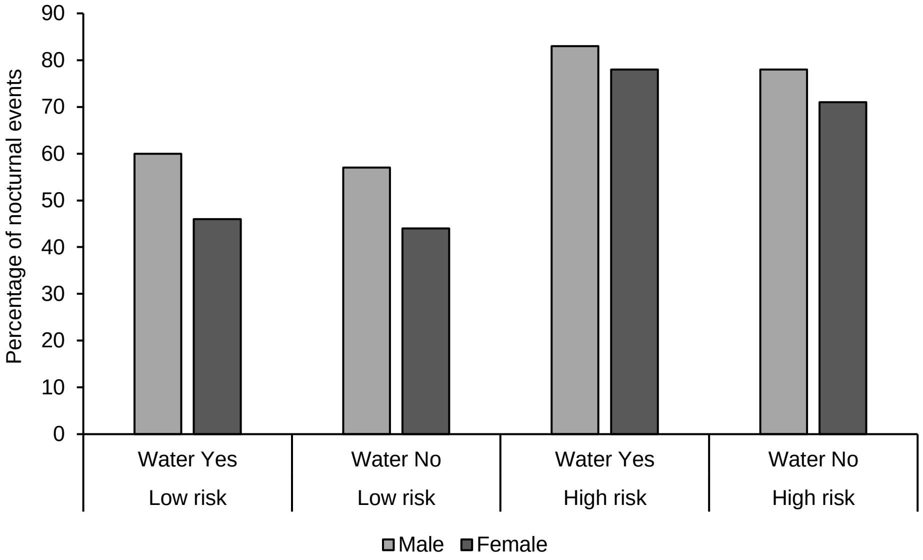


Figure 5.7 The percentage of nocturnal events near and far from water for male (light grey, n=383 events) and female group types (dark grey, n=879 events) in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined.

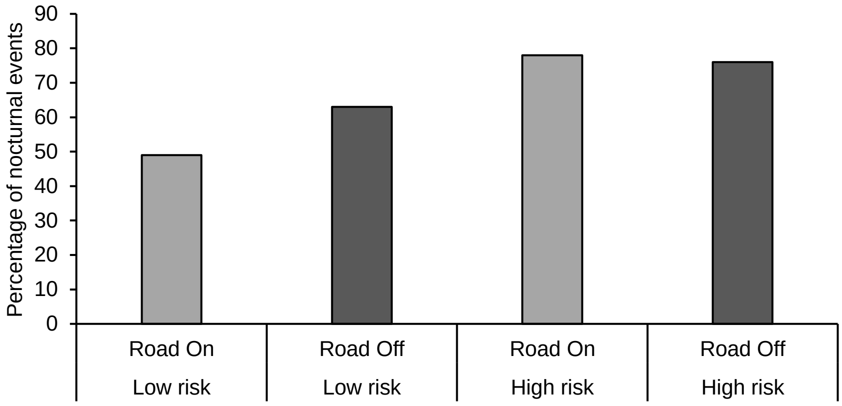


Figure 5.8 The percentage of nocturnal events on-road (light grey, n=1,032 events) and off-road (dark grey, n=230 events) in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined.

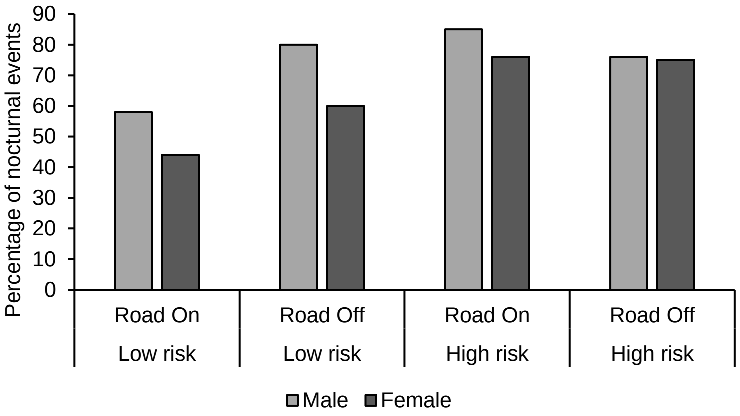


Figure 5.9 The percentage of nocturnal events on- and off-road for male (light grey, n=383 events) and female group types (dark grey, n=879 events) in the low-risk RNP:LR grid and all three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) combined.

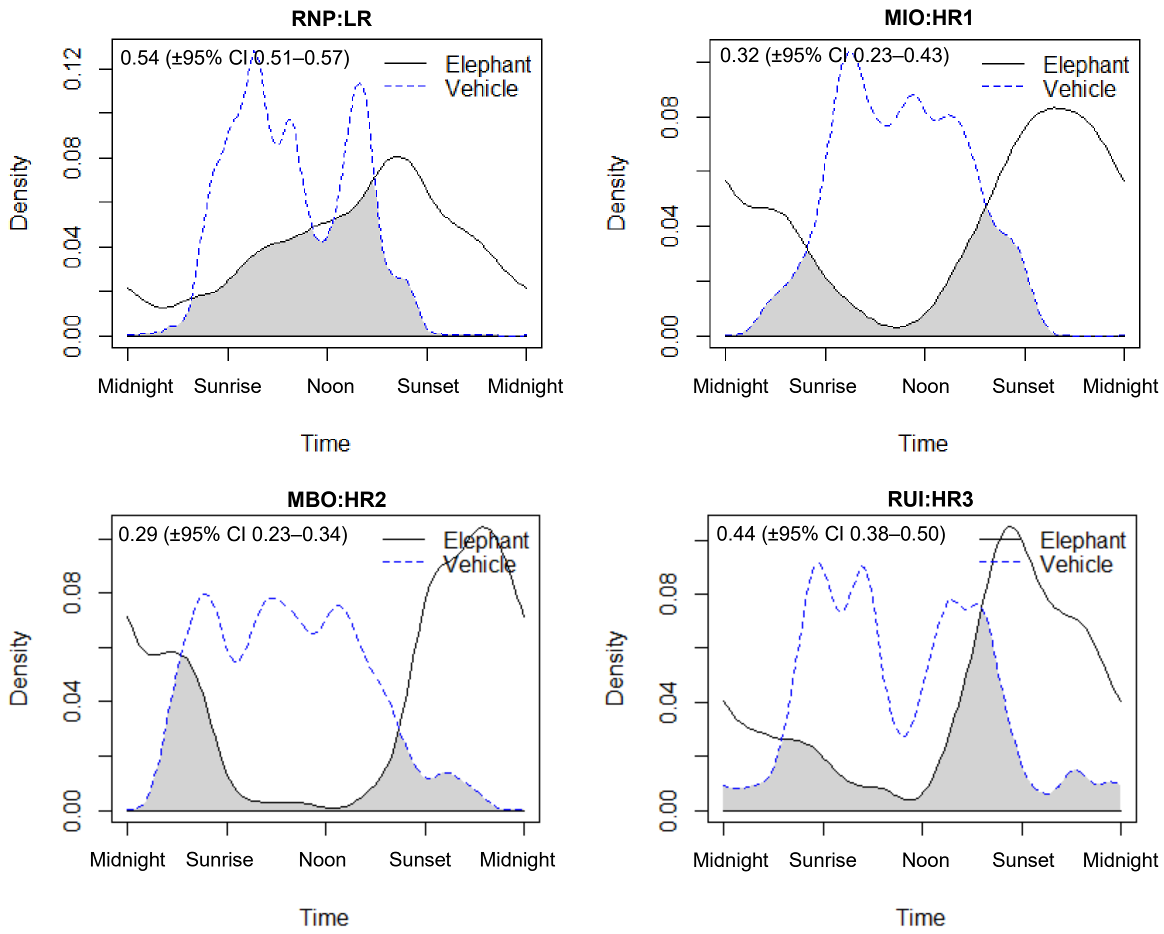


Figure 5.10 Elephant and vehicle activity profiles for the low-risk RNP:LR grid (n=15,955 vehicle images) and three high-risk grids: MIO:HR1 (n=1,016 vehicle images), MBO:HR2 (n=763 vehicle images) and RUI:HR3 (n=369 vehicle images). The elephant activity profiles for each grid are based on the subset of elephant events that occurred on roads: RNP:LR grid (n=847 events) and three high-risk grids: MIO:HR1 (n=45 events), MBO:HR2 (n=173 events) and RUI:HR3 (n=262 events). The density of elephant events and vehicle images over a 24-h period are expressed by the solid and dotted lines respectively. Note the y-axes are not the same. The shaded area represents the area that is shared between the two distributions and is equivalent to the coefficient of overlapping. The coefficient of overlapping and 95% confidence interval is indicated for each pair of activity distributions.

The effect of diel period, grid, group type, water, and roads on the number of elephant events was modelled using GLMM. The top random intercept-only model included the term *water* and interactions *diel x grid*, *road x grid* and *diel x group* (Figure 5.11 & Table A5.2, see Table A.5.3 for top model set). The random slopes model (Figure A5.5 & Table A5.4) had the same fixed effects structure as the intercept-only model. The top model included an interaction between diel period and grid, such that night had a positive effect on elephant event counts for the three high-risk grids. Water and roads had a significant positive effect on the number of elephant events. There was an interaction between road and grid, such that in the high-risk MIO:HR1 and RUI:HR3 grids, roads had a significant negative effect on elephant event counts. The top model included a non-significant interaction between group type and diel period. Neither the interaction between diel period, grid, and water nor the interaction between diel period, grid, and road featured in the top model.

Model validation showed mixed results (Figures A5.3 & A5.4). The top model had normally distributed residuals, though some heterogeneity was evident in the deviance residuals by grid and diel period. The top model was overdispersed (dispersion parameter 3.4).

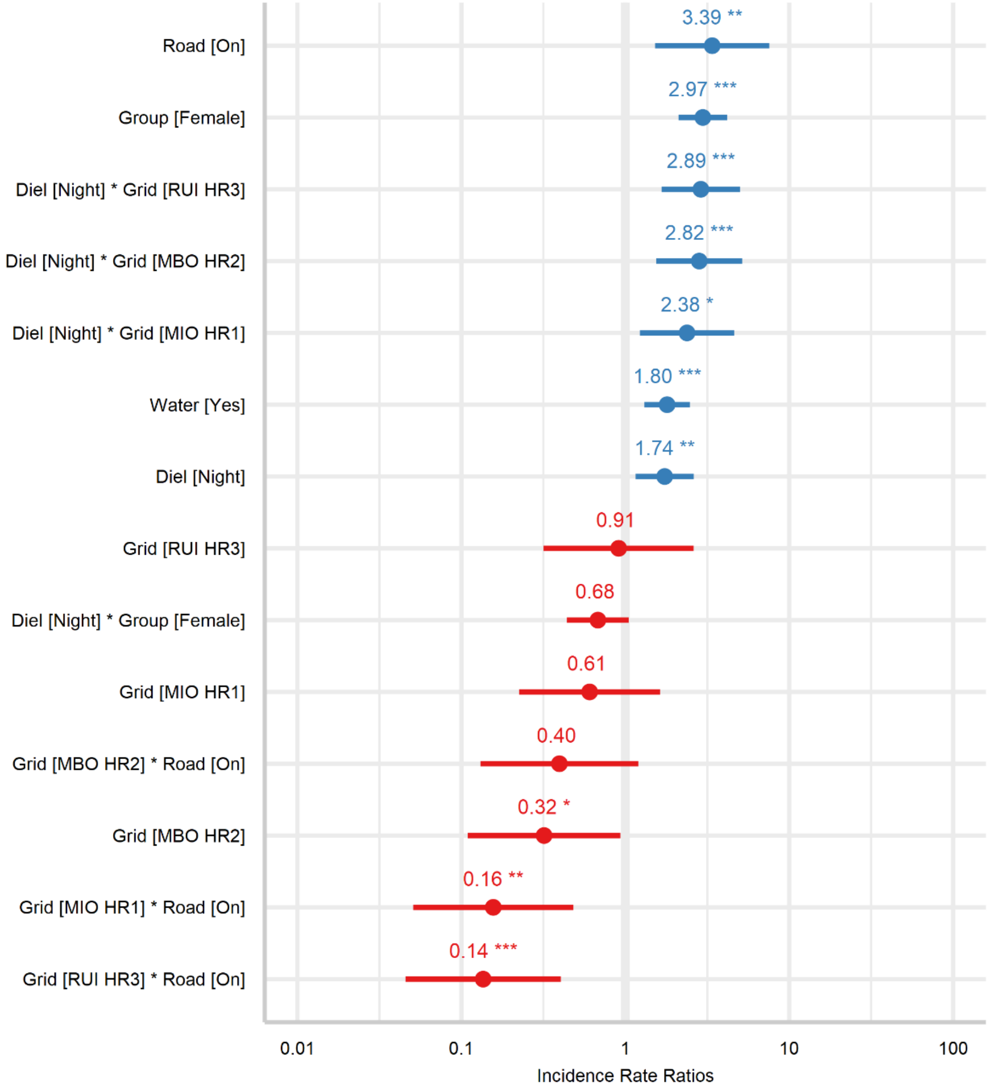


Figure 5.11 Elephant event incident rate ratios (dots) and 95% confidence intervals (bars) for model parameters. To express model coefficients as incident rate ratios, we raised the natural log to the power of each coefficient. The terms GridMBO HR2, RoadOn, WaterYes, GroupFemale, DielNight:GridMBO HR2, DielNight:GridMIO HR1, DielNight:GridRUI HR2, RoadOn:GridMIO HR1, and RoadOn:GridRUI HR3 were statistically significant. Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates. The RNP LR grid represents a low-risk area for elephants while the MIO HR1, MBO HR2 and RUI HR2 grids represent high-risk areas.

Cow-calf groups (787 events) and lone bulls (342 events) were the most frequently detected group types (Table 5.3). There was no significant difference in the relative frequency of female (cow-calf and mixed groups) and male (lone bull and bull group) events between the four grids, X^2 (3, N = 1,327) = 4.9, p >0.1) (Figure 5.12). Male associations differed between the low-risk and high-risk grids (Figure 5.13). There were significantly more bull group events than lone bull events in two of the high-risk grids (MIO:HR1, RUI:HR3) than in the low-risk grid: RNP:LR vs MIO:HR1, X^2 (1, N = 45) = 12.4, p <0.005) and RNP:LR vs RUI:HR3, X^2 (1, N = 78) = 28.4, p <0.005). There were also significantly more mixed group events than lone bull events in the three high-risk grids than in the low-risk grid: RNP:LR vs MIO:HR1, X^2 (1, N = 56) = 10.7, p <0.005), RNP:LR vs MBO:HR2, X^2 (1, N = 67) = 14.8, p <0.005) and RNP:LR vs RUI:HR3, X^2 (1, N = 106) = 39.2, p <0.005).

Table 5.2 Count of elephant events by group type.

Grid	Cow-calf	Lone bull	Bull group	Mixed group	Unknown
RNP: LR	453	207	17	52	156
MIO: HR1	60	35	10	21	40
MBO: HR2	104	41	6	26	37
RUI: HR3	170	59	19	47	65

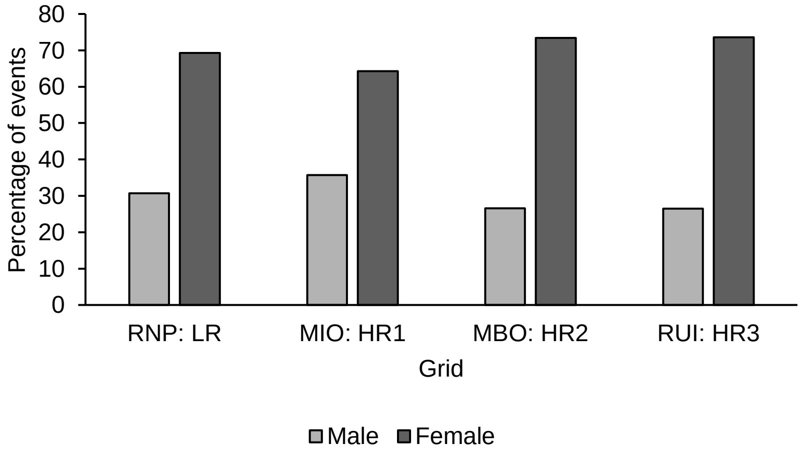


Figure 5.12 Percentage of male (light grey) and female events (dark grey) by grid, where RNP:LR is the low-risk grid and MIO:HR1, MBO:HR2 and RUI:HR3 are the three high-risk grids. Sample sizes were n=729 events for the RNP:LR grid, n=126 events for the MIO:HR1 grid, n=177 events for the MBO:HR2 grid, and n=295 events for the RUI:HR3 grid.

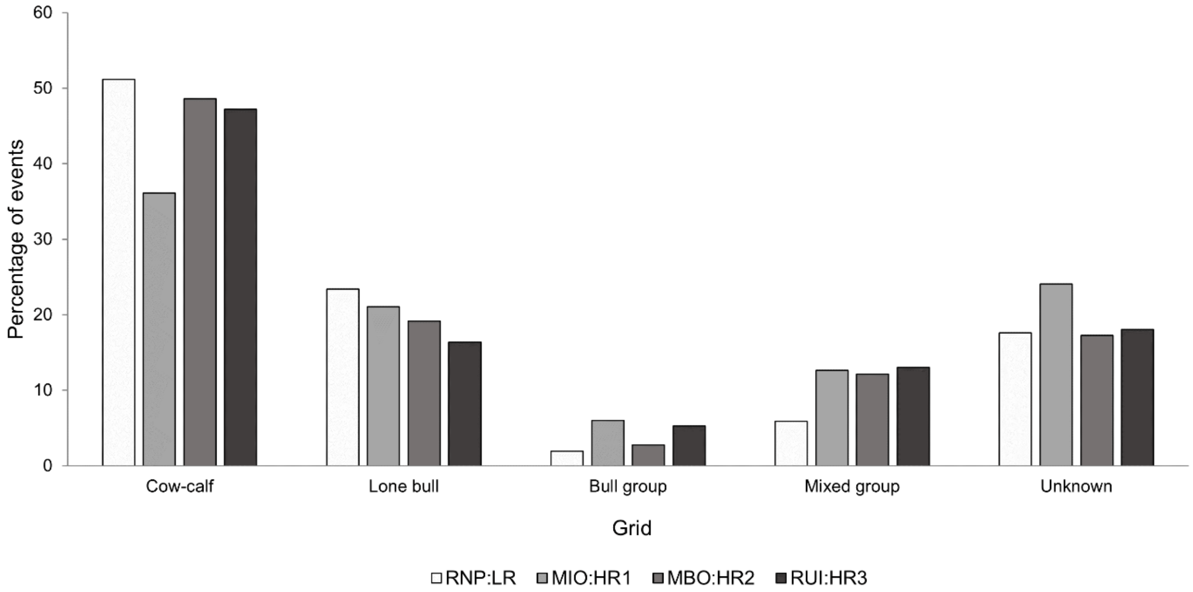


Figure 5.13 Percentage of events for each group type by grid. The RNP:LR grid (n=885 events) represents a low-risk area for elephants while the MIO:HR1 (n=166 events), MBO:HR2 (n=214 events), and RUI:HR3 (n=360 events) grids represent high-risk areas.

A total of 14 activity types were identified from camera trap images (Table 5.3). Movement and energy acquisition activities were dominant in camera trap detections of elephants. A greater diversity of activity types was observed for the low-risk site (14 types) compared to the high-risk sites (6-7 types). Relaxed behaviours were observed in 4% of elephant events from the low-risk site and in 0.8% of events from the high-risk sites. A single instance of play was recorded from the high-risk sites, compared to 11 instances of play in the low-risk site. Running, a stress behaviour, was recorded in 1.6% of events in the low-risk site and in 2.6% of events in the high-risk sites.

Table 5.3 Activity types observed from unique camera trap events of elephants for each grid. The RNP:LR grid represents a low-risk area for elephants while the MIO:HR1, MBO:HR2, and RUI:HR3 grids represent high-risk areas. More than one activity type may be observed per event. For activity type definitions, see Chapter 2. Total n=1,625 events.

Activity type (% of events)	**RNP:LR** n=885	**MIO:HR1** n=166	**MBO:HR2** n=214	**RUI:HR3** n=360
Energy acquisition and movement behaviours				
Walking	94.2	91.0	86.0	95.0
Feeding while walking	19.9	14.5	30.4	12.8
Feeding while standing	4.5	6.0	0.0	2.2
Drinking	0.6	1.2	0.0	0.0
Relaxed behaviours				
Dusting	2.3	0.0	0.0	0.0
Wallowing	0.1	0.0	0.0	0.0
Lying	0.7	0.0	0.5	0.0
Suckling	0.3	0.0	1.4	0.6
Social Play	0.2	0.0	0.0	0.0
Object Play	0.9	0.0	0.0	0.3
Lone play	0.1	0.0	0.0	0.0
Explore object	0.1	0.0	0.0	0.0
Stress behaviours				
Running	1.6	5.4	1.9	1.9
Other behaviours				
Pause	11.2	16.3	2.3	8.1

Most adult females assessed were in normal condition across the four grids, although mean body condition scores for adult female elephants were slightly lower in the three high-risk sites than in the low-risk site (Table 5.4). There was greater temporal overlap in elephant and lion activity in the high-risk sites than in the low-risk site (Figure 5.14).

Table 5.4 Summary of body conditions scored for adult female elephants by grid, where a score of 1-2 is underweight, 3 is ideal/normal, and 4-5 is overweight/obese (Morfeld et al., 2014).

Body condition score	RNP:LR	MIO:HR1	MBO:HR2	RUI:HR3
Mean	3.1	2.9	2.8	2.7
Median	3	3	3	3
Mode	3	3	3	3
Sample size	87	12	17	32
% of cow-calf events assessed	19	20	16	19

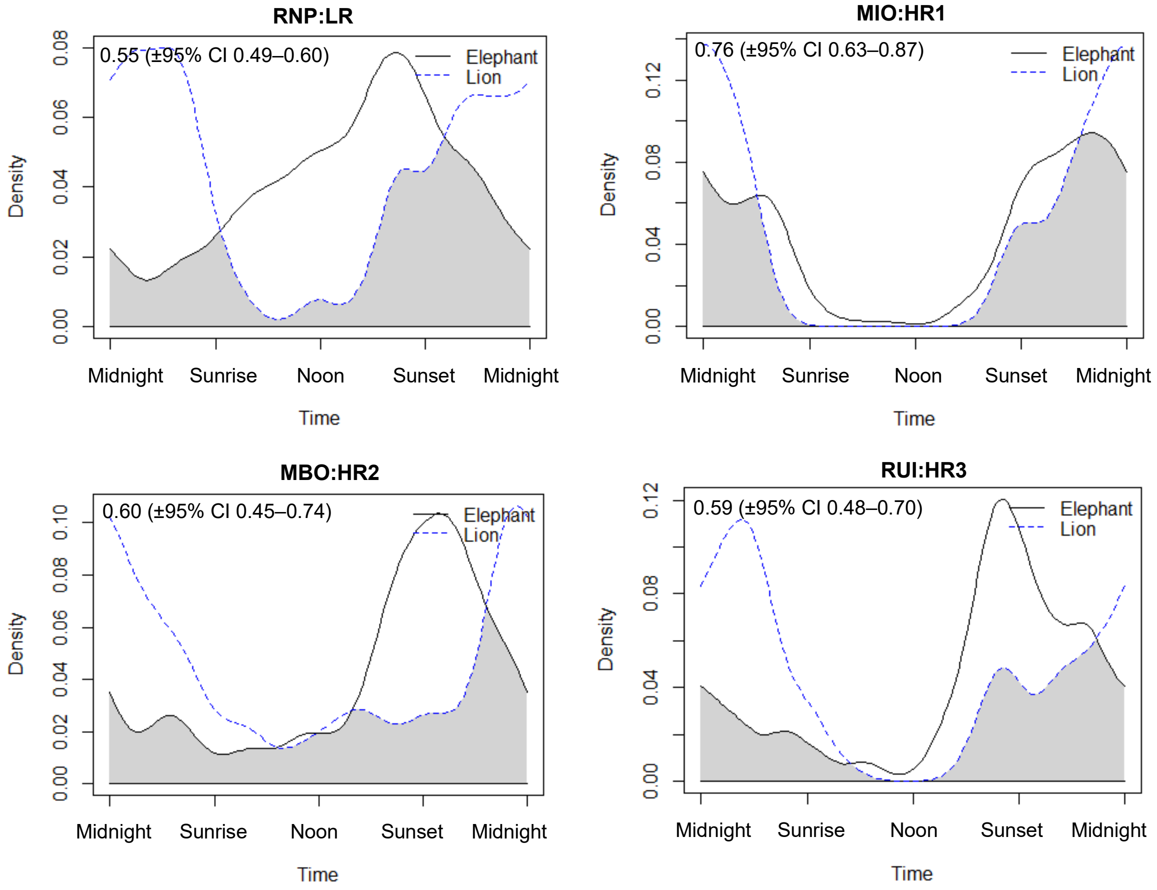


Figure 5.14 Elephant and lion activity profiles for the low-risk RNP:LR grid (n=242 lion events) and three high-risk grids: MIO:HR1 (n=29 lion events), MBO:HR2 (n=41 lion events) and RUI:HR3 (n=73 lion events). The density of elephant and lion events over a 24-h period are expressed by the solid and dotted lines respectively. Note the y-axes are not the same. The shaded area represents the area that is shared between the two distributions and is equivalent to the coefficient of overlapping. The coefficient of overlapping and 95% confidence interval is indicated for each pair of activity distributions.

5.5 Discussion

The African elephant has experienced widespread population declines over recent decades and was recently up-listed from *Vulnerable* to *Endangered* by the IUCN (Gobush et al., 2021). Understanding the longer-term impacts of anthropogenic pressure on elephant behaviour can help to reveal the consequences for at-risk populations. We provide evidence that elephants adjust their temporal activity and social behaviour in response to risk and shed light on differences in risk response among males and females. We also provide insight into possible costs associated with behavioural risk responses.

We found that elephants were more nocturnal in the high-risk sites, in line with findings of previous studies that elephants increase night-time activity in response to risk. Elephants tend to crop forage (Sitati et al., 2003; Smit et al., 2019) and move through areas outside of formally protected areas at night as a strategy to reduce temporal overlap with humans (Galanti et al., 2006; Gaynor et al., 2018b; Graham et al., 2009; Lewis, 1986; Wittemyer et al., 2007), and increased night-time movements in response to poaching in the Samburu-Laikipia ecosystem in Kenya (Ihwagi et al., 2018). In addition to risk, elephant active periods may be influenced by environmental temperatures (Mole et al., 2016) and the quality and distribution of forage and water resources (e.g., Guy, 1976). Average maximum daily temperatures in the study area varied with elevation and time of year (range 27°C to 33°C). Temperature increased over the course of the dry season, but as two of the high-risk sites were at higher elevations (MIO:HR1 at 1350m asl and RUI:HR3 at 1200m asl) than the low-risk RNP:LR site (800m asl), maximum daytime temperatures during the survey periods were comparable for these sites. As the RNP:LR and MBO:HR2 sites were both in *Vachellia-Commiphora* habitat, it is unlikely that the observed difference in elephant diel activity patterns was due to variation in habitat quality. The MIO:HR1 and RUI:HR3 sites were in more marginal miombo woodland habitat. As there was no low risk miombo site, it is uncertain to what extent habitat contributed to the observed activity patterns. However, risk was likely a more important driver of elephant activity patterns than habitat at the MIO:HR1 and RUI:HR3 sites. This is supported by the fact that contrary to what would be expected for more marginal habitats in which elephants spend more time feeding and moving to meet energetic requirements (Mramba et al., 2019), elephant active periods were compressed in these two high-risk miombo sites relative to the low-risk site in more productive habitat.

Both male and female elephants were more nocturnal in the high-risk sites, although the increase in night-time activity relative to the low-risk site was more pronounced for cow-calf groups than lone bulls (Figure 5.2). Similarly, in Samburu-Laikipia, both male and female elephants moved more at night when poaching levels were high, but the relationship between poaching levels and increased night-time movement was stronger for females than for males (Ihwagi et al., 2018). However, we did not find an interaction between group type, grid, and diel period because the risk-induced shift to night-time activity occurred for both male and female groups and was similar in magnitude with the different male and female group types pooled (Figure 5.4). While the greater shift in cow-calf activity patterns as a function of risk is consistent with the hypothesis that females are more risk-averse than males (Sukumar & Gadgil, 1988), the extent to which male and female activity patterns were (also) shaped by possible sex differences in foraging strategies and thermoregulatory requirements is unknown.

Elephants visited water sources more at night in the high-risk sites compared to the low-risk site. Although cameras near water had a marginally higher proportion of nocturnal events than did cameras far from water in the high-risk sites, we did not find a significant interaction between water, grid, and diel period because the shift to night-time activity in response to risk occurred both near and far from water (Figure 5.6). This pattern was consistent across male and female groups (Figure 5.7). Water is a key resource for elephants: family groups typically drink at least once a day with lactating females requiring water for milk production (Chamaillé-Jammes et al., 2013; Wyatt & Eltringham, 1974). Previous studies observed that elephant use of water sources peaked during the middle of the day (Leggett, 2009) or at dusk (Guy, 1976) in the dry season. In our study, elephants visited water sources primarily at night in the high-risk sites. Similarly, in Gorongosa National Park, Mozambique, elephants visited a risky water source (a river along the park boundary) almost exclusively at dusk and during the night (Poole & Granli, 2017), suggesting that risk influences the timing of elephant water access (see also Chapter 6).

Elephants used roads in the low-risk site but avoided roads in the high-risk sites. While elephant use of roads was more nocturnal in the high-risk sites than in the low-risk site (Figure 5.8), there was not a significant interaction between road, grid, and diel period as the shift to nocturnal activity in the high-risk sites occurred on- as well as off-road. This pattern was consistent for male and female groups (Figure 5.9). There was less overlap between elephant and vehicle activity profiles in the high-risk sites than in the low-risk site (Figure 5.10), suggesting that nocturnal use of roads in the high-risk sites enabled elephants to avoid vehicles. Our findings provide further evidence that elephant use of roads varies with risk: where elephants are well-protected, elephants may use roads for ease of movement (Granados, Weladii & Loomis, 2012), while in areas of higher risk, elephants may avoid roads (Blake et al., 2008) or time their use of roads to reduce interactions with humans and vehicles (Gaynor et al., 2018b; *Elephas maximus,* Katugaha, de Silva & Santiapillai,1999).

Camera traps detected significantly more mixed and bull groups in the high-risk sites compared to the low-risk site, contributing to evidence that anthropogenic risk is a driver of male associations (e.g., Chiyo et al., 2014; Srinivasaiah et al., 2019). While female elephants live in family groups composed of related adult females and their offspring, males disperse from their natal family group at an average age of 14 years (Lee et al., 2011). Independent males associate with other males for social partners and to reduce mortality risk, as observed in our study and elsewhere (Allen et al., 2020; Chiyo et al., 2014; Lee et al., 2011; Sitati et al., 2003). Males may also form associations to take advantage of the knowledge of other males (Allen et al., 2020; Chiyo et al., 2014; Srinivasaiah et al., 2019), potentially to problem-solve. Males also associate with cow-calf groups for companionship, knowledge, access to reproductive females, and, as observed in this study, to dilute mortality risk (Chiyo et al., 2014). Whether female groups aggregate in response in response to risk was not investigated here but is explored in the context of water source access in Chapter 6.

Elephant movement and activity patterns have implications for foraging, survival, and reproduction. The costs of risk-induced shifts in movement and energy acquisition activities are not fully understood, nor do we fully understand if risk-induced activity shifts result in a compression of the activity budget of elephants. With the caveat that camera traps are not appropriate for estimating activity budgets, we did find that the active period of elephants was compressed in the high-risk sites relative to the low-risk site. If risk-induced shifts in the timing and total time available for energy acquisition activities affect maternal food intake by limiting foraging duration or efficiency, this could potentially result in early calf mortality, poor growth rates, and reduced lifetime fitness, as has been observed for droughts (Lee et al., 2013). Mean body condition scores for adult female elephants were lower in the three high-risk sites than in the low-risk site, but females in all four sites had normal body condition overall (Table 5.5). We encourage other studies to explore the impact of activity shifts on condition by optimizing camera placement for body condition assessment. In addition, increased nocturnal activity in response to risk potentially exposes elephant calves to greater predation risk, as we found greater overlap in the active periods of elephants and lions in the high-risk sites than in the low-risk site (Figure 5.14).

Camera traps detected fewer occurrences of relaxed behaviours and more occurrences of stress behaviours in the high-risk sites than in the low-risk site. Although sample sizes were small, we suggest that elephants may engage less frequently in relaxed behaviours such as play in areas of higher risk (e.g., Lee & Moss, 2014), with potential implications for learning and acquisition of social experience (Lee & Moss, 1999; Shannon et al., 2022). This is an important area for further research through observational studies.

5.6 Conclusions

It is now clear that elephants adjust their active period in response to risk and we demonstrate that this can be a generalized response over large areas (e.g., 555 km^2 for the high-risk RUI:HR3 grid). We further demonstrate that this risk response is not limited to the boundaries of protected areas (as in Gaynor et al., 2018b) or in areas without formal protection status (e.g., Graham et al., 2009), but that it can occur inside protected areas where on-the-ground protection and tourism presence are low, and where elephants have experienced poaching. Our findings suggest that focused protection efforts and strategic distribution of tourism investments could help to make a larger part of the ecosystem safe for elephants.

Our study was conducted several years after the peak poaching period – although some illegal killing of elephants continued to occur (TAWIRI, 2019) – suggesting that elephants may maintain risk responses for a prolonged period, even after their environment has become more secure. This has been observed for African forest elephants (*Loxodonta cyclotis*) in Central Africa (Breuer et al., 2016) and savanna elephants in Gorongosa, where elephants continued to be wary of and aggressive to humans long after the cessation of intensive poaching during the country's 15-year civil war (Poole & Granli, 2018).

Human activities can profoundly influence elephant society, and the impacts of humans extend beyond direct effects on elephant population size and structure. Our study indicates that anthropogenic risk affects elephant decisions about when they move, when they forage and access water sources, how they use roads, and whom they associate with, resulting in potential indirect impacts on survival and reproduction. Importantly, however, our findings suggest that human presence in the form of tourism can contribute to making areas safer for elephants (e.g., Beale et al., 2018; Smit et al., 2017). Furthermore, the ability of elephants to make behavioural adjustments in response to risk might allow them to persist in increasingly human-modified landscapes. Understanding the broader impacts of human activities on elephants can help to design conservation strategies informed by elephant behaviour, movement decisions, and social requirements. While this chapter has shown that risk can impact the timing of water source use by elephants within protected areas, the next chapter investigates in more detail how elephants adjust the frequency and timing of use and the groups in which they access water as function of risk, and whether this varies by sex and season.

Appendix 5.1 Comparing the use of event start time versus event mid time

We examined whether using the start time or mid time of elephant detection events affected the shape of the activity profile. The coefficient of overlapping represents the total percentage of area that is shared by two kernel density distributions. Kernel density distributions using event start times and mid times were nearly identical, regardless of whether clock time or sun time was used (Figure S1; Table S4). The coefficient of overlapping for event start time and mid time distributions was close to the maximum value of 1 for all grids.

Table A5.1 Coefficients of overlapping for density distributions using event start time versus event mid time.

Grid	**Coefficient of overlapping (Δ_4) (Clock Time)**	**Coefficient of overlapping (Δ_4) (Sun Time)**
RNP:LR	0.998	0.997
MIO:HR1	0.996	0.996
MBO:HR2	0.998	0.998
RUI:HR3	0.997	0.997

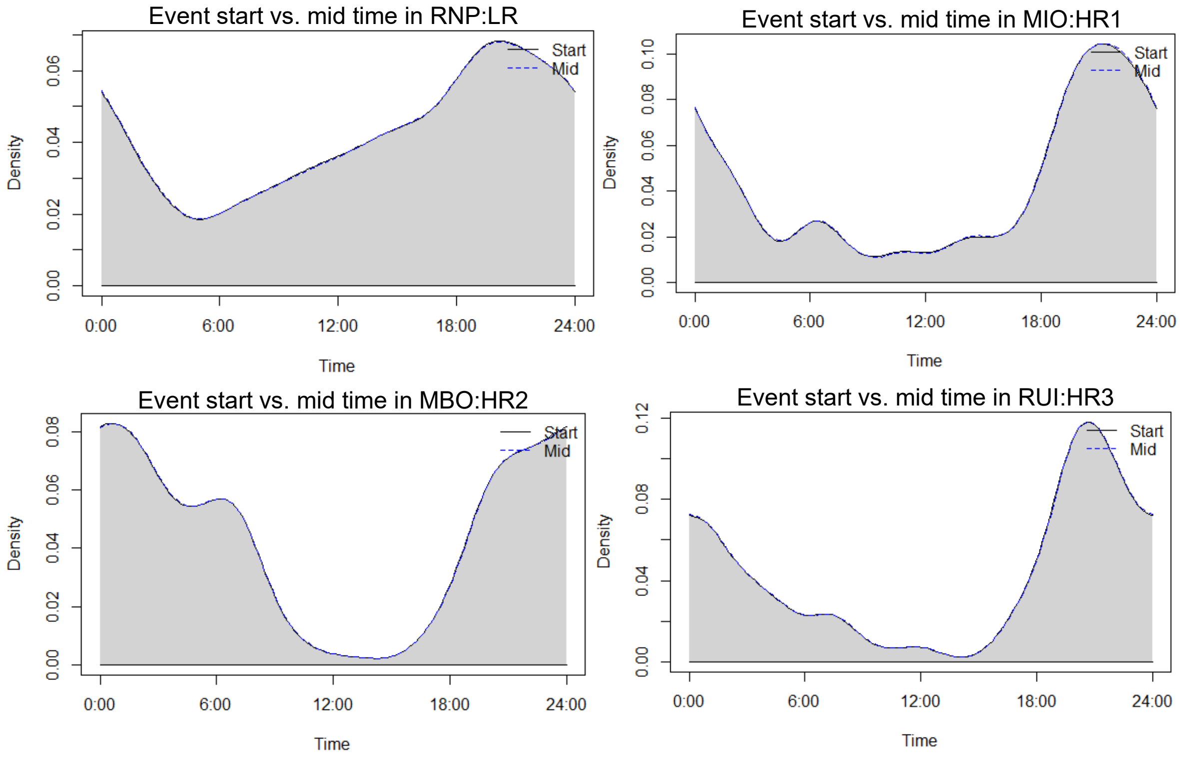


Figure A5.1 Density distributions of elephant events for the low-risk RNP:LR grid and three high-risk grids (MIO:HR1, MBO:HR2, RUI:HR3) using event start times (black curve) and mid times (blue curve), using clock time. Sample sizes were n=885 events for the RNP:LR grid, n=166 events for the MIO:HR1 grid, n=214 events for the MBO:HR2 grid, and n=360 events for the RUI:HR3 grid.

Appendix 5.2 Additional modelling results

Table A5.2 Estimated regression parameters for the fixed effects with their standard errors, z-values and p-values for the top random intercept-only model. The Wald chi-square test was used to test the statistical significance of the fixed effects. The MIO HR1, MBO HR2 and RUI HR3 grid represent high-risk areas while the RNP LR grid represents a low-risk area for elephants. Significance codes: 0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '

	Estimate	**Std. error**	***Z*-value**	***P*-value**
Intercept	-7.85	0.42	-18.70	<0.0001 ***
DielNight	0.55	0.21	2.66	0.008 **
GridMBO HR2	-1.14	0.55	-2.09	0.036 *
GridMIO HR1	-0.50	0.51	-0.99	0.321
GridRUI HR3	-0.09	0.54	-0.34	0.862
RoadOn	1.22	0.41	2.98	0.002**
WaterYes	0.59	0.16	3.60	<0.0001 ***
GroupFemale	1.09	0.17	6.27	<0.0001 ***
DielNight:GridMBO HR2	1.03	0.31	3.38	0.001 ***
DielNight:GridMIO HR1	0.87	0.34	2.56	0.01 *
DielNight:GridRUI HR3	1.06	0.28	3.78	<0.0001 ***
RoadOn:GridMBO HR2	-0.92	0.57	-1.64	0.100
RoadOn:GridMIO HR1	-1.85	0.57	-3.23	0.001 ***
RoadOn:GridRUI HR3	-2.0	0.56	-3.59	<0.0001 ***
DielNight:GroupFemale	-0.38	0.22	-1.74	0.080

Table A5.3 Top models for the effect of grid (a proxy for risk), group type (male/female), diel period, and camera placement relative to water and roads on elephant event counts.

Model	**Terms**	**AIC**
M1	Count ~ Grid*Diel + Grid*Road + Water + Diel*Group + offset(log(Hours)) + 1|Camera	1992.5
M2	Count ~ Grid*Diel + Road*Grid + Water + Group + offset(log(Hours)) + 1|Camera	1993.5
M3	Count ~ Grid*Diel + Road*Grid + Water + Diel*Group + Group*Water + offset(log(Hours)) + 1|Camera	1994.0
M4	Count ~ Grid*Diel + Road*Grid + Water + Diel*Group + Group*Road + offset(log(Hours)) + 1|Camera	1994.5

Figure A5.2 Elephant event incident rate ratios (dots) and confidence intervals (bars) for model parameters for models M2, M3, and M4. Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates. The RNP LR grid represents a low-risk area for elephants while MIO HR1, MBO HR2, and RUI HR3 grids represent high-risk areas. Significance codes: 0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.

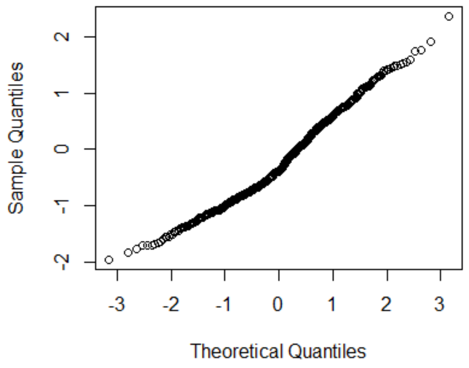


Figure A5.3 Quantile-quantile plot of model residuals. A correctly specified model would be expected to show an approximately straight diagonal line.

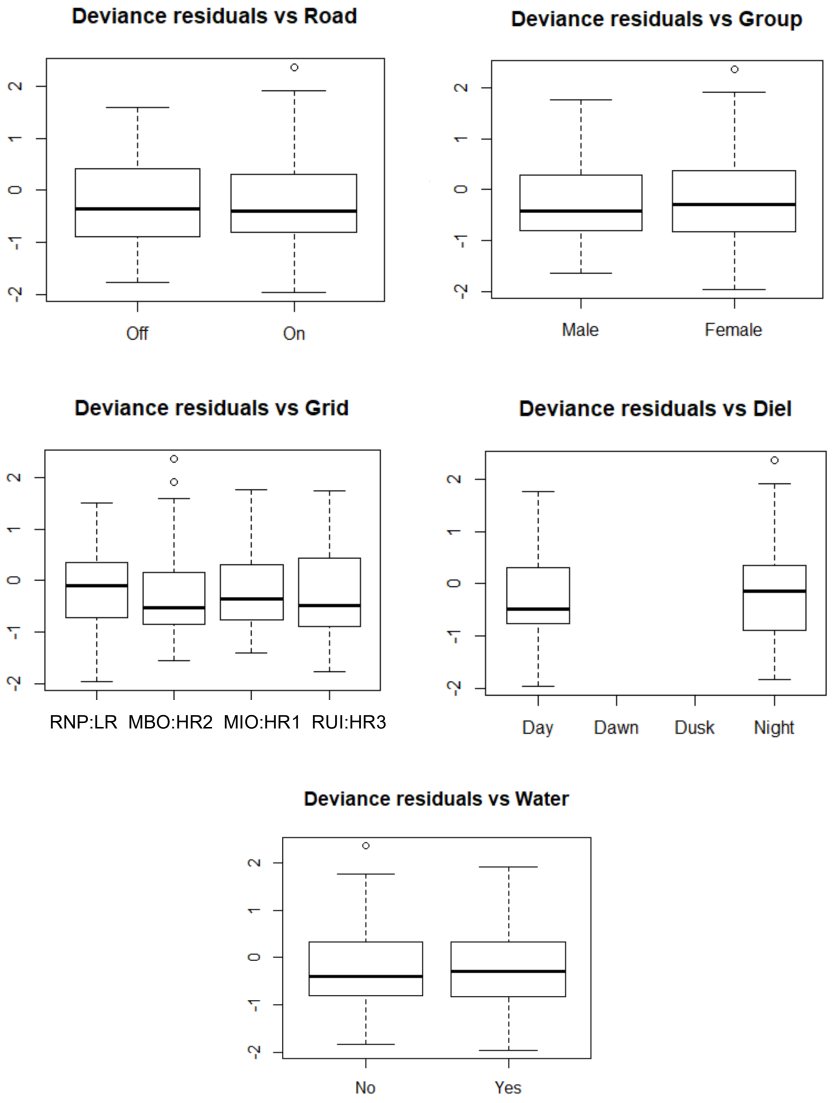


Figure A5.4 Boxplots of deviance residuals versus predictors (Road, Group, Grid, Diel period and Water). The RNP:LR grid represents a low-risk area, while the MIO:HR1, MBO:HR2, and RUI:HR3 grid represent high-risk areas. Due to small sample sizes, dawn and dusk diel periods were excluded to reduce zero-inflation. For a correctly specified model, boxes should be similar. Some heterogeneity was evident in the deviance residuals by grid and diel period.

For confirmatory purposes and to check for potential Type I errors in our top random intercept-only model (Harrison et al., 2018), we fitted the top random intercept-only model with *diel* and *group* as random slopes (*grid*, *water,* and *road* were not fitted as random slopes as these are properties of camera trap station, the random intercept term). With one exception, the same fixed effects were significant in the random intercept-only model and random slopes model. Model coefficients had the same sign in both models and values were similar. In the random slopes model, the interaction between *group* and *diel* is significant, while in the intercept-only model, this interaction is not significant.

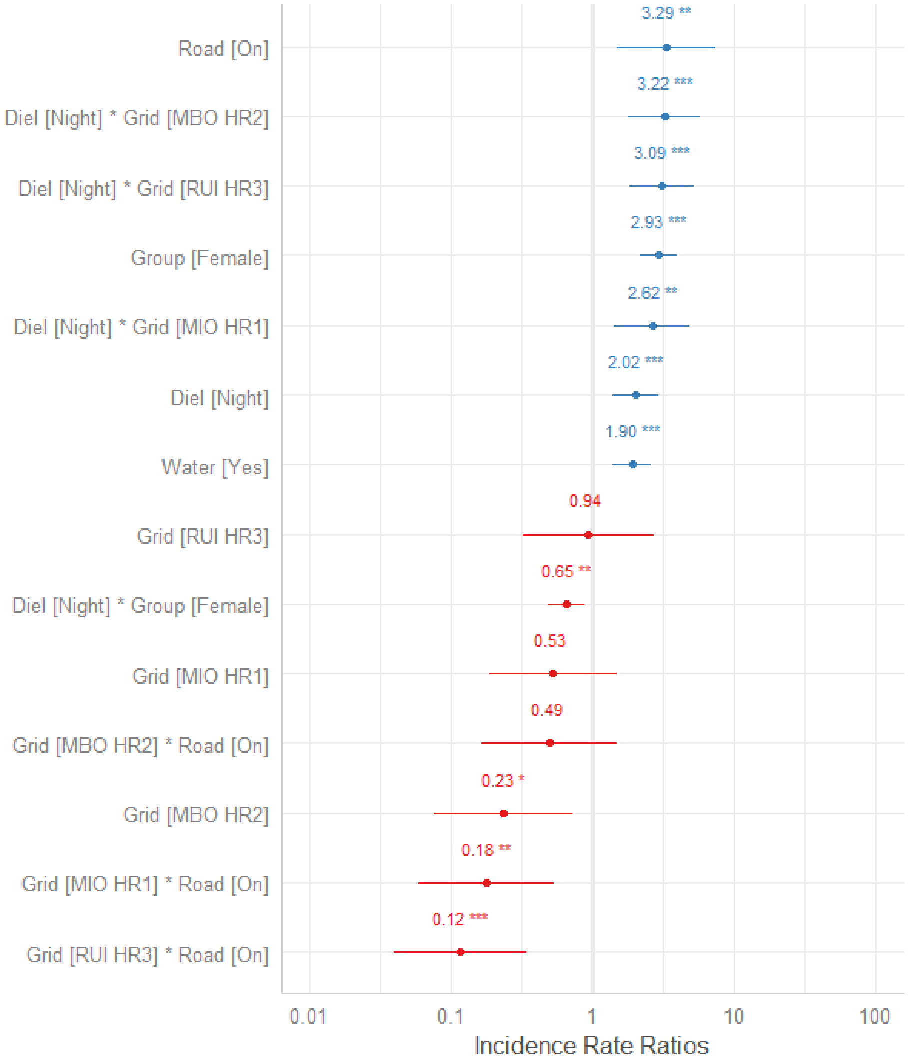
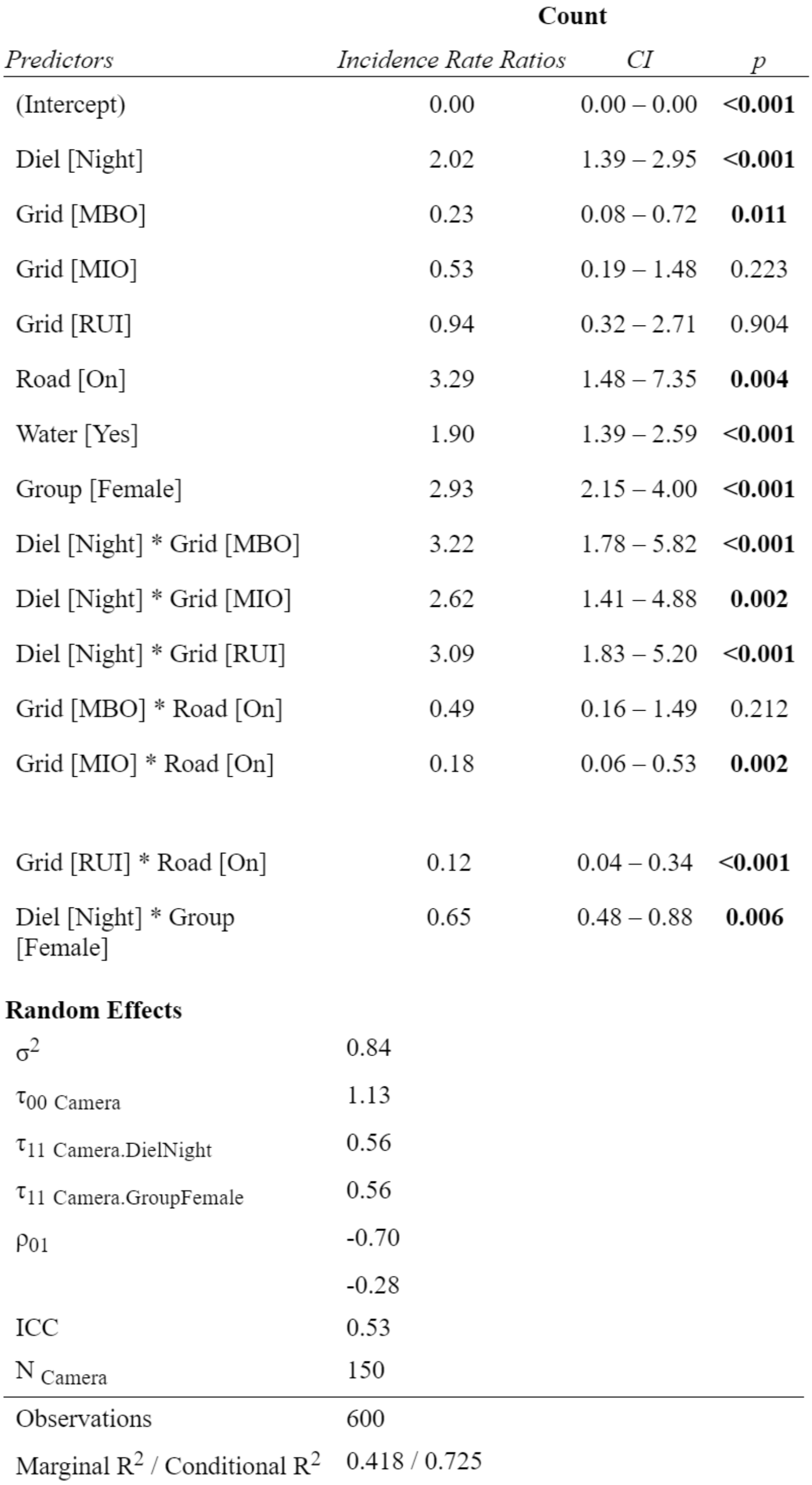


Figure A5.5 Elephant event incident rate ratios (dots) and confidence intervals (bars) for model parameters for the top model with *diel* and *group* fitted as random slopes. The random slopes model was specified as Count ~ Grid*Diel + Grid*Road + Water + Diel*Group + offset(log(Hours)) + (1 + Diel + Group |Camera). Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates. The RNP LR grid represents a low-risk area for elephants while MIO HR1, MBO HR2, and RUI HR3 grids represent high-risk areas.

Table A5.4 Model coefficients expressed as incident rate ratios with associated confidence intervals (CI) and p-values shown for the random slopes model. σ2 is the residual variance. τ00 is the between-subject variance. τ11 is the random-slope-variance. ρ01 is the random slope-intercept correlation. ICC is the intraclass correlation coefficient. NCamera is the number of camera trap stations. Observations is the sample size. The marginal pseudo R-squared considers only the variance of the fixed effects, while the conditional pseudo R-squared takes both the fixed and random effects into account (Nakagawa et al. 2017). The RNP LR grid represents a low-risk area for elephants while MIO HR1, MBO HR2, and RUI HR3 grids represent high-risk areas.



	Count		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.00	0.00 – 0.00	**<0.001**
Diel [Night]	2.02	1.39 – 2.95	**<0.001**
Grid [MBO]	0.23	0.08 – 0.72	**0.011**
Grid [MIO]	0.53	0.19 – 1.48	0.223
Grid [RUI]	0.94	0.32 – 2.71	0.904
Road [On]	3.29	1.48 – 7.35	**0.004**
Water [Yes]	1.90	1.39 – 2.59	**<0.001**
Group [Female]	2.93	2.15 – 4.00	**<0.001**
Diel [Night] * Grid [MBO]	3.22	1.78 – 5.82	**<0.001**
Diel [Night] * Grid [MIO]	2.62	1.41 – 4.88	**0.002**
Diel [Night] * Grid [RUI]	3.09	1.83 – 5.20	**<0.001**
Grid [MBO] * Road [On]	0.49	0.16 – 1.49	0.212
Grid [MIO] * Road [On]	0.18	0.06 – 0.53	**0.002**
Grid [RUI] * Road [On]	0.12	0.04 – 0.34	**<0.001**
Diel [Night] * Group [Female]	0.65	0.48 – 0.88	**0.006**
Random Effects			
σ^2	0.84		
$\tau_{00\ \mathrm{Camera}}$	1.13		
$\tau_{11\ \mathrm{Camera.DielNight}}$	0.56		
$\tau_{11\ \mathrm{Camera.GroupFemale}}$	0.56		
ρ_{01}	-0.70		
	-0.28		
ICC	0.53		
N_{Camera}	150		
Observations	600		
Marginal R^2 / Conditional R^2	0.418 / 0.725		

Chapter 6

The influence of risk, sex, and season on elephant water source use

Photo 9*: Camera trap image of a bull group heading towards a water source in Tungamalenga village.*

Chapter 6. The influence of risk, sex, and season on elephant water source use

Author contributions

I conceived the study and led data collection. Assistance with data collection was provided by Kephania Mwaviko, Peter Mtyana, Kelvin Madege (all from Southern Tanzania Elephant Program), Ramadhani Mduda, Kinyozi Madinda, Innocent Kisanyage, and Leonard Fidelis. I annotated all the camera trap images, conducted all analyses, and wrote the chapter. Professors Phyllis Lee and Hannah Buchanan-Smith (University of Stirling) provided guidance on analyses and drafts of this chapter.

6.1 Abstract

This chapter investigates whether risk influences elephant water source use and how risk responses vary by sex and season. I compare the frequency and timing of elephant water source use as a function of risk, sex, and season. I also investigate whether elephants adjust their grouping patterns when accessing a risky resource – and if this differs by sex – by comparing elephant group types and sizes between low- and high-risk water sources. I then explore whether elephants are more vigilant at high-risk water sources than at low-risk water sources. I used camera traps to collect data on elephant visits to low-risk water sources inside Ruaha National Park, high-risk water sources inside the park, and high-risk water sources located on village land adjacent to the park over a period of 13 months in 2019-2020 (n=1,287 elephant visits documented over 4,010.7 camera-trap sampling days). Elephants used high-risk water sources on village land almost exclusively in the dry season, suggesting that use of a risky resource was mediated by seasonal variation in water availability. Both male and female groups showed reduced use of high-risk water sources on village land during the wet season, although this pattern was stronger for females than for males. Elephant use of high-risk water sources was more nocturnal than their use of low-risk water sources, and this was true for both male and female groups. Males visited high-risk water sources in larger all-male groups than at low-risk water sources, with >30% of male groups at high-risk village water sources numbering ≥10 individuals. Females did not appear to adjust group size in relation to risk in the context of water access. Elephants were more likely to engage in vigilant pauses at high-risk water sources on village land relative to low-risk water sources in the park. These findings suggest that risk was an important factor in elephant decisions about when and how to access water, and that elephants adjusted their behaviour in multiple ways when accessing a risky key resource.

6.2 Introduction

Water is a key resource for elephants: they depend on it for hydration, metabolic processes such as lactation, and thermoregulation (Dunkin et al., 2013; Mole et al., 2016; Western, 1975). Water requirements for captive elephants in temperate conditions are estimated at 140-225 litres per day (Fowler & Mikota, 2008; Miller & Fowler, 2015). There are, however, no published water intake measures from wild African elephants as a function of age and sex, season, food water content, reproductive status, or ambient temperature. Water requirements must be met from environmental sources which are typically widely distributed across wild habitats. Estimates of how often African savanna elephants visit water vary between sites, but once every 24 to 36 hours may be typical (Chamaillé-Jammes et al., 2013; Purdon & van Aarde, 2007; Wyatt & Eltringham, 1974). In the high-elevation Rwenzori National Park, Uganda, it was most common for female elephants in family groups to drink once per day (Wyatt & Eltringham, 1974). In the hot, lowland Hwange National Park, Zimbabwe, it was most common for adult females in family groups to visit water sources within 36 hours of their last visit (Chamaillé-Jammes et al., 2013). In the mid-altitude, well-watered Amboseli National Park, Kenya, 50% of female groups (n=8), all with calves under 36 months of age, drank at least once during 24-hour follows (P. C. Lee & K. Lindsay, personal communication, 2022). In Kruger National Park, South Africa - where elephants have access to rivers and artificial water points - it was most common for adult females in family groups to access water sources at 12-to-24-hour intervals (Purdon & van Aarde, 2007). Due to water dependence, the availability and distribution of water strongly influence elephant ranging and movement decisions, especially in semi-arid and arid environments and during the dry season when water is less widely available (de Beer & van Aarde, 2008; Leuthold & Sale, 1973; Loarie et al., 2009; Stokke & Du Toit, 2002; Stommel et al., 2016; Wall et al., 2013; Western et al., 1975).

A range of interrelated factors are likely to influence the frequency and times at which elephants use water sources. Water use is influenced by the distribution and availability of water (Purdon & van Aarde, 2007), grouping dynamics and dominance hierarchies which can constrain or enhance individual access to water (Foley, 2002), and by the individual's sex and physiological state which affect motivation to drink or use water for thermoregulation (de Beer & van Aarde, 2008; Loarie et al., 2009; Mole et al., 2016; Poole & Granli, 2017; Rozen-Rechels et al., 2020; Valeix et al., 2007). Water access may also be influenced by predation risk (Crosmary et al., 2012; Zvidzai et al., 2013), especially when the risk of predation at water sources is high (e.g., Maingi et al., 2012; Rashidi et al., 2016), such that animals must trade off resource access with safety. Previous research indicates that the timing of water source use by elephants varies considerably between sites (see Table A6.1). The multiple factors influencing water use can be partially controlled by comparing water use in different risk contexts within a single population and area. As such, in this chapter, I investigate the influence of anthropogenic risk on the frequency and timing of water source use by elephants, and whether elephant use of risky water sources varies with sex and seasonal differences in water availability. I also explore whether elephants adjust their grouping patterns and vigilance behaviour when using risky water sources.

In the following sections, I briefly summarize previous work investigating how anthropogenic risk influences the timing of resource access and elephant grouping patterns and provide a rationale for why elephant use of risky water sources may be influenced by sex and seasonal differences. I then outline chapter aims and predictions.

Elephants perceive areas associated with humans as risky (see also Chapter 1). Elephants move through human-dominated landscapes primarily at night (Buchholtz et al., 2019; Graham et al., 2009) and increase nocturnal activity under elevated poaching risk (Chapter 5; Ihwagi et al., 2018). I therefore hypothesize that elephants demonstrate greater night-time use of high-risk water sources compared to low-risk water sources in order to reduce temporal overlap with humans.

Male and female elephants differ in their water requirements, foraging strategies, thermoregulatory requirements and, potentially, their tolerance to risk (see also Chapter 1). While males have higher total water requirements due to their larger size (Stokke & Du Toit, 2002), females and calves have higher rates of water turnover from evaporative and respiratory water loss (Gordon, 1977, as cited in Stokke & Du Toit, 2002; Beuchat, 1990). Lactating females also require water for milk production since elephant milk is dilute at between 50-80% water (Osthoff et al., 2007), calves suckle between 1-3 times per hour (Lee & Moss, 1986) and intake needs to sustain growth of ~385 g/day (Andrews, Mecklenborg & Bercovitch, 2005). Due to their smaller body size and higher surface area to volume ratio (Laws, 1970), females have a higher rate of heat gain per unit mass from the environment and may reach a critical temperature sooner than males (Barnes, 1983). Female groups are also thought to be less risk-tolerant than males (Sukumar & Gadgil, 1988). For these reasons, I hypothesize that the impact of risk on the frequency and timing of water source use may differ for males and females.

Season also shapes elephant movement decisions and activity patterns (Barnes 1983a; de Beer & van Aarde, 2008; Leggett, 2009; Stokke & Du Toit, 2002). In the Ruaha dry season, water and food availability and food quality decline. Elephants lose condition in the dry season, and mortality, especially of calves, increases (Barnes, 1982a, 1983a). In the wet season, elephants spend more time feeding and they gain condition as food and water are abundant and food quality is higher (Barnes, 1983). Ruaha elephants also experience a greater heat load in the dry season than in the wet season because of higher ambient temperatures and greater insolation (Barnes, 1983). Temperature is an important factor in elephant movement decisions and activity patterns, as elephants have been found to avoid thermal stress by concentrating their activity at cooler times of the day and by selecting for thermally stable landscapes (Kinahan et al., 2007; Mole et al., 2016; Purdon & van Aarde, 2017; Rozen-Rechels et al., 2020). For these reasons, I hypothesize that the impact of risk on the frequency and timing of water source use may differ by season.

Elephants may also use social strategies to mitigate risk. Elephants move through human-dominated landscapes in larger groups (Graham et al., 2009; Songhurst et al., 2016), and males associate with other males (forming bull groups) and with cow-calf groups (forming mixed groups) in risky areas (Chapter 5; Allen et al. 2020; Chiyo et al., 2014). Social strategies in resource and water use are marked in forest elephants (Fishlock & Lee, 2013; Fishlock, Caldwell & Lee, 2016) but aggregations at water occur for savanna elephants as well (Allen et al., 2020; O'Connell-Rodwell et al., 2011). I thus hypothesize that elephants visit risky water sources in larger groups than low-risk water sources.

Vigilance for threat detection or monitoring is thought to increase under predation (Lima, 1987) and anthropogenic risk (Matson, Goldizen & Putland, 2005; Proudman et al., 2020), as well as under increased risk from conspecifics (Allan & Hill, 2018). African ungulate species have been shown to increase vigilance at water sources in the presence of a predator (Creel et al., 2014; Périquet et al., 2010). A range of social, demographic, and ecological factors have been found to influence vigilance (Allan & Hill, 2018). Here, I investigate only the possible effect of anthropogenic risk on vigilance in elephants in the context of water access.

This chapter has four aims. The first aim (aim 6.1) is to assess whether seasonal differences in water availability and potential sex differences in risk tolerance influence the frequency of elephant use of risky water sources. I predict that elephants use high-risk water sources less during the wet season in comparison to the dry season (prediction 6.1.1) and that females make less use of high-risk water sources than males (6.1.2).

The second aim (aim 6.2) is to investigate whether elephants adjust the timing of water source use in response to risk, and if the timing of water access varies with sex and season. I expect that elephant use of high-risk water sources will be more nocturnal than their use of low-risk water sources (prediction 6.2.1), and that the timing of water access may influenced by season, as resource scarcity can induce greater risk-taking behaviour (prediction 6.2.2). As females may be more risk-averse than males, I predict a stronger shift to nocturnal use of high-risk water sources for female groups than male groups (prediction 6.2.3).

The third aim (aim 6.3) is to investigate whether elephants adjust their grouping patterns when using risky water sources, and how grouping patterns vary by sex and season. I predict that male elephants will visit high-risk water sources in bull groups or in mixed groups (cow-calf groups with associated mature males) more often than at low-risk sites (prediction 6.3.1) and that males will occur in larger all-male groups and mixed groups at high-risk water sources than at low-risk water sources (prediction 6.3.2). I expect that cow-calf groups visit high-risk water sources in larger group sizes in high-risk sites than in low-risk sites (prediction 6.3.3). I also explore whether male and female grouping patterns vary between the dry and the wet season.

The fourth aim (aim 6.4) is to assess whether elephants are more vigilant at high-risk water sources than at low-risk water sources**.** I compare the occurrence of vigilant and non-vigilant pauses to test the prediction that vigilance behaviour is more common at high-risk water sources than at low-risk water sources (prediction 6.4.1)

6.3 Methods

6.3.1 Study sites for water use

The study area comprised Ruaha National Park and adjacent village land in south-central Tanzania (see also Chapter 2). Only photographic tourism is permitted in the national park. Village land is a mosaic of settlements, agricultural land, and remaining natural habitat. The area has one wet season, from December to April, and one dry season from May to November (Bjørnstad, 1976). Mean daily temperatures range between 19°C and 26°C over the year (Martilla, 2011; Tanzania Wildlife Management Authority, 2023a; 2023c). Temperatures are higher and insolation is greater in the dry season than in the wet season. Water and food availability decline in the dry season and food availability is at its lowest in September and October (Barnes, 1982b, 1983a). Food and water are more widely available in the wet season.

Camera traps were deployed to capture elephant visits to water sources representing different levels of risk to elephants. I defined three risk categories: low-risk park, high-risk park, and high-risk village.

The low-risk park water sources were situated in the high-use tourism zone of Ruaha National Park where the park’s headquarters, three ranger posts, and tourism infrastructure are located, and where photographic tourism activity is concentrated. Due to established tourism and ranger presence, this area forms the safest part of the ecosystem for elephants (Beale et al., 2018; see Chapter 3). All low-risk cameras were placed either within 1 km of a ranger post or along the most-visited stretch of river in the park (River Drive), where tourism activity is concentrated.

The high-risk park water sources were located >10 km from ranger posts and/or in areas that were previously identified as elephant carcass density hotspots (Beale et al., 2018; see Chapter 3). Park ecologists also confirmed these high-risk areas as entry routes for poachers into the park (H. Xavier, personal communication, 2021). Furthermore, ten camera traps were lost to theft in these high-risk areas during the study period and a pre-study pilot phase, providing further evidence of human use of these high-risk areas.

The high-risk village water sources were all located on village land and were considered high-risk due to their proximity to humans. Camera traps were located along small rivers in three villages: Tungamalenga, Malizanga, and Kitisi.

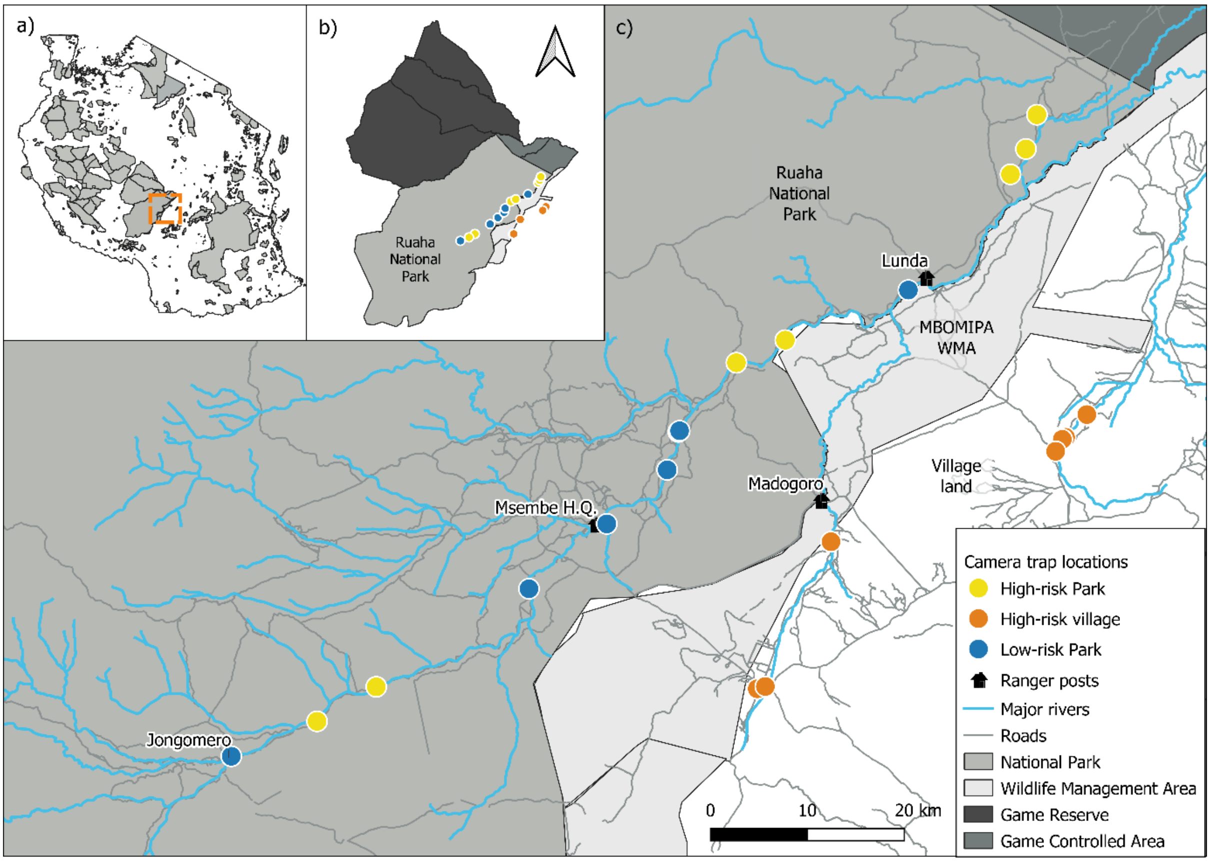


Figure 6.1 Inset map a) shows the location of the study site in the context of Tanzania's protected area network. Inset map b) shows the locations of camera trap locations within the Ruaha-Rungwa ecosystem and the location of national parks, game reserves, game controlled areas, and wildlife management areas within this ecosystem. Map c) shows the location of low-risk park (blue dots), high-risk park (yellow dots), and high-risk village (orange dots) camera traps in Ruaha National Park and adjacent village land. The locations of ranger posts, rivers, and roads are also shown.

6.3.2 Data collection

Camera traps were used to capture elephant visits to water sources. Camera traps were placed on elephant trails to rivers and as close as possible to entry and exit points. The low-risk park and high-risk park cameras were placed on wildlife trails leading to the Great Ruaha River, while the high-risk village cameras were placed on tributaries of the Great Ruaha River on village land. Camera trap sampling was conducted between January 2019 and January 2020 to capture 6 months of wet season data (January-April 2019 and December 2019-January 2020) and 7 months of dry season data (May to November 2019).

I used primarily Browning Dark Ops series camera traps (2018 Dark Ops Extreme, Browning Trail Cameras, USA). Two stations used Bushnell Trophy Cam HD (Bushnell, USA) camera traps. All camera models used passive infrared sensor systems. The trigger speed ranged from 0.38 seconds for the Browning Dark Ops model to 0.6 seconds for the Bushnell model. All cameras used infrared flash and produced colour images during the day and monochrome images at night. Cameras were set to take still images with three photographs per trigger and a 5-second trigger interval.

Cameras were mounted on trees along wildlife trails to rivers. In most cases, cameras were placed perpendicular to the expected movement pathway and were positioned at heights between 1.5-2 m so that the camera field of view could capture the whole body of elephants. However, in three of the high-risk sites in the park, cameras were placed at a height of 30-40 cm to make them less visible to humans and to reduce the likelihood of camera loss and inadvertent capture of images of humans. These cameras were positioned further back from the target wildlife trail, to ensure that the field of view captured the whole body of elephants. Cameras were positioned horizontally with the lens and sensor perpendicular to the ground.

In high-risk areas in the park, water trail cameras were camouflaged with spray glue, soil, and vegetation. On village land, I used two different approaches to camera deployment based on recommendations from village councils regarding both privacy concerns and the risk of camera loss. In Kitisi village, it was possible to deploy the camera-trap station full-time, and weekly checks of the camera were made by a local camera trap monitor to guard against camera loss. In Tungamalenga and Malizanga villages, the village government advised that the camera traps should be deployed in the late afternoon and removed in the morning. Trained camera trap monitors in these villages assisted with setting up and removing the cameras on a near-daily basis.

Camera traps were checked once per month to download photos and replace batteries. However, no camera trap checks could be conducted in Ruaha National Park in July and August 2019 due to delays in obtaining park entry permits.

There were differences between the three risk categories and between camera trap stations in sampling effort due to loss of cameras to theft, logistical differences between wet and dry season access for camera deployment and checks, and the daily camera deployment method used in Tungamalenga and Malizanga villages. For all low-risk park and high-risk park camera traps and one of the high-risk village camera traps (Kitisi), sampling effort was calculated both as the number of days a camera trap was active and the number of hours a camera trap was active per diel period (dusk, dawn, day, and night). For the remaining high-risk village camera traps (which were deployed on a near-daily basis), it was assumed that for each deployment day, the camera sampled a full night, a full dawn and dusk period, and one hour of the day.

Table 6.1 Summary of the number of camera traps, camera trap effort, and elephant events at the low-risk park, high-risk park, and high-risk village water source. Effort was measured as the total number of active days across all camera stations. Relative activity index (RAI) was defined as the number of detection events per camera trap sampling day. Camera traps captured a total of 61,397 elephant images.

	Low-risk park	**High-risk park**	**High-risk village**
No. of camera stations	7 dry season, 6 wet season	7 dry season, 4 wet season	7 dry season, 7 wet season
Total effort (camera trap days)	1,683.6	1,444.6	882.5
Dry season effort (camera trap days)	895.9	846.3	478.4
Wet season effort (camera trap days)	823.7	598.3	404.1
No. of elephant detection events	664 (352 dry season, 312 wet season)	217 (154 dry season, 63 wet season)	406 (373 dry season, 33 wet season)
Dry season relative activity index	0.393	0.182	0.780
Wet season relative activity index	0.379	0.105	0.082

I defined independent elephant detection events as images of elephants that were separated by more than 15 minutes (Gaynor et al., 2018b, see Chapter 2). Event time was defined as the time of the first photograph in an event. I coded group type for each event as cow-calf (CC), lone bull (LB), bull group (BG), mixed group (M) of cow-calf plus mature males, or unknown (U) (see detailed group type definitions in Chapter 2, Table 2.1). I also coded group size by reviewing camera trap images and counting the number of elephants in each event.

For each elephant event, I visually inspected camera trap images to classify what type of ‘pause’ was present. This was coded as vigilant pause, non-vigilant pause, no pause, or unknown pause. A vigilant pause was defined as an absence of walking by any individual between two subsequent photographs in an event, with the presence of one or more of the following vigilant behaviours: standing-tall, head-swinging, periscope-trunk, J-trunk, trunk-toward camera, look-at camera (ElephantVoices, n.d.). A non-vigilant pause was defined as an absence of walking between two subsequent photographs in an event with none of the aforementioned vigilant behaviours present. An unknown pause was an absence of walking between two subsequent photographs in an event but for which it could not be determined whether vigilant behaviours were present or not (e.g., because the elephant was facing away from the camera, or too close to or distant from the camera). No pause was coded when no individual in an event displayed an absence of walking between two subsequent photographs in an event. A type of pause was considered present if at least one individual in the event displayed that pause. More than one type of pause could be present per event. A caveat to this aspect of the study is that I do not distinguish between vigilance for the purpose of threat detection or monitoring of predators/humans versus conspecifics.

Table 6.2 Number of events by group type at low-risk park, high-risk park, and high-risk village water sources during the dry season (not corrected for camera trap sampling effort). Group types are cow-calf (CC), lone bull (LB), bull group (BG), mixed group (M), and unknown (U). Female events are cow-calf and mixed group events combined. Male events are lone bull and bull group events combined.

Risk	CC	LB	BG	M	U	Female events	Male events	Total events
Low-risk park	184	79	19	35	35	219	98	352
High-risk park	65	23	13	31	22	96	36	154
High-risk village	54	47	219	31	22	85	266	373
	303	**149**	**251**	**97**	**79**	**400**	**400**	**879**

Table 6.3 Daily relative activity index (number of elephant events divided by the number of camera trap sampling days) by group type at low-risk park, high-risk park, and high-risk village water sources during the dry season (n=879 events). Group types are cow-calf (CC), lone bull (LB), bull group (BG), mixed group (M), and unknown (U).

Risk	CC	LB	BG	M	U	Overall daily RAI
Low-risk park	0.205	0.088	0.021	0.039	0.039	0.393
High-risk park	0.077	0.027	0.015	0.037	0.026	0.182
High-risk village	0.113	0.098	0.458	0.065	0.046	0.780
	0.136	**0.067**	**0.113**	**0.044**	**0.036**	**0.396**

Table 6.4 Number of events by group type at low-risk park, high-risk park, and high-risk village water sources during the wet season (not corrected for camera trap sampling effort). Group types are cow-calf (CC), lone bull (LB), bull group (BG), mixed group (M), and unknown (U). Female events are cow-calf and mixed group events combined. Male events are lone bull and bull group events combined.

Risk	CC	LB	BG	M	U	Female events	Male events	Total events
Low-risk park	100	80	37	69	26	168	117	312
High-risk park	18	24	5	10	6	28	29	63
High-risk village	1	10	20	1	1	2	30	33
	119	**114**	**62**	**80**	**33**	**198**	**176**	**408**

Table 6.5 Daily relative activity index by group type at low-risk park, high-risk park, and high-risk village water sources during the wet season (n=408 events). Group types are cow-calf (CC), lone bull (LB), bull group (BG), mixed group (M), and unknown (U).

Risk	CC	LB	BG	M	U	Overall daily RAI
Low-risk park	0.121	0.097	0.045	0.084	0.032	0.379
High-risk park	0.030	0.040	0.008	0.017	0.010	0.105
High-risk village	0.002	0.025	0.049	0.002	0.002	0.082
	0.073	**0.070**	**0.038**	**0.049**	**0.020**	**0.250**

6.3.3 Data analysis

6.3.3.1 The influence of risk, sex, and season on the frequency and timing of water source use (aims 6.1 & 6.2)

To investigate how the frequency of elephant water source use varied with risk, sex, and season (aim 6.1), I calculated a daily relative activity index (daily RAI) for elephants at each water source. The daily RAI was defined as the number of elephant events (with events disaggregated by sex and season) divided by the number of camera trap sampling days, calculated per camera trap station (following Gaynor et al., 2018b). It was necessary to use the daily RAI as a direct comparison of elephant event counts between water sources would not have been appropriate due to differences in sampling effort between camera trap stations and between the wet and the dry seasons. Lone bull and bull group events were combined into a single category of male events, as these two group types reflect male decision-making. Cow-calf and mixed group events were combined into a single category of female events, as these two group types reflect primarily female decision-making. To test the prediction that female groups make less use of high-risk water sources than male groups (prediction 6.1.2), I used chi-square goodness-of-fit tests to compare the relative frequency of female and male events between the low-risk park and high-risk park water sources and between the low-risk park and high-risk village water sources. The low-risk park distribution was used to generate expected values for the higher-risk water sources.

To explore how the timing of water source use by elephants was influenced by risk, season, and sex (aim 6.2), I calculated an hourly relative activity index (hourly RAI) for elephants for the day and night diel periods at each water source. The hourly RAI was defined as the number of elephant events (disaggregated by sex and season) divided by the number of camera trap sampling hours, calculated per diel period and camera trap station (following Gaynor et al., 2018b). I then visualized the pattern of elephant water source use over 24 hours as a function of risk, sex, and season using the *overlap* package (Ridout & Linkie, 2009) in R to generate smoothed non-parametric kernel density distributions of elephant events (Ridout & Linkie, 2009). I used event start times following Gaynor et al. (2018b). Since the sun's position in the sky ('sun time'), rather than clock time (the time on a 24-hour clock), has biological and environmental meaning, I accounted for geographic and temporal variation in the times of sunrise and sunset over the study area and study period by using the SunTime function to convert clock times to sun times (Nouvellet et al., 2012). To explore whether the timing of elephant water source use varied as a function of risk and season (predictions 6.2.1 & 6.2.2), I compared elephant activity profiles for the low-risk park water sources, high-risk park water sources, and high-risk village water sources separately by season; and then compared wet and dry season elephant activity profiles by risk level. To explore whether the timing of water source use as a function of risk varied by sex (prediction 6.2.3), I compared the activity distributions for the low-risk and high-risk water sources by group type. This was done for the dry season only, as wet season sample sizes were too small. The coefficient of overlapping, which represents the total percentage of area that is shared by two density distributions, was calculated for all pairwise comparisons. The *activity* package (Rowcliffe et al., 2014) was used to determine if two activity distributions were significantly different. All analysis was conducted in R software (version 4.2.0).

I then sought to model the effect of diel period, risk, sex, and season on the number of elephant events at water sources (aims 6.1 & 6.2). As a first step, I summed the number of elephant events per diel period by camera trap station by sex (male/female) and season (wet/dry; Smit 2023a). Elephant events were originally assigned to one of four diel periods: dawn (0.5 hours), day (12 hours), dusk (0.5 hours) and night (11 hours). Dawn and dusk were considered separately from day and night because they represent transition periods in brightness and temperature. Sunrise, sunset, and twilight times were extracted from *timeanddate.com*. However, the dawn (8 events) and dusk (35 events) diel periods (comprising 3% of events) were excluded from subsequent analysis to reduce zero-inflation resulting from small sample sizes. The final dataset for modelling comprised 1,132 events.

Data exploration revealed heterogeneity and overdispersion of the elephant event count data. To model the number of elephant events as a function of the predictors, a Negative Binomial Generalized Linear Mixed Model (GLMM) with a log link function was used. The log link function ensures positive fitted values, and the Negative Binomial distribution was used for overdispersed count data. Fixed factors were Diel period (categorical with two levels, with Day as the reference level), Season (categorical with two levels, with Dry as the reference level), Risk (categorical with three levels, with low-risk park as the reference level), and Sex (categorical with two levels, with Male as the reference level). None of the model predictors were collinear. To account for repeated measures from camera trap stations, Station was fitted as a random intercept. Diel, Sex, and Season were fitted as random slopes to allow the effect of these factors to vary with Station and to reduce the risk of type I error associated with random intercept-only models (Harrison et al., 2018). To account for differences in camera trap sampling effort and differences in the duration of the day and night diel periods, the number of sampling hours was included as an offset in the model. Models were fit through Maximum Likelihood estimation using Laplace approximation and a BOBYQA optimizer in the *lme4* package (Bates et al. 2015). Inspection of residuals and assessment of model fit was done using the *performance (*Lüdecke et al., 2021), *sjPlot* (Lüdecke, 2020), and *DHARMa* packages (Hartig, 2022).

During model specification and selection, I worked backwards from a global model. Based on the predictions that the frequency of elephant use of high-risk water sources would vary by sex and season (predictions 6.1.1 & 6.1.2), that the timing of water source use would vary with risk (prediction 6.2.1), and that the timing of use of high-risk water sources would be influenced by sex and season (predictions 6.2.2 & 6.2.3), the global model included the interaction terms *Risk x Sex*, *Risk x Season, Risk x Diel, Risk x Diel x Sex, and Risk x Diel x Season*. Model selection was done using AICc (for small sample sizes) whereby all models ΔAICc<6 were considered top models (Richards, 2008). Within the set of nested top models, I selected one model which represented the best trade-off between explanatory power and complexity through a likelihood ratio test using the *anova* function in R, which performs an f-test to compare two nested models. I expressed model coefficients as incident rate ratios (IRRs) to compare the incidence rates of elephant events between different levels of a categorical variable. IRRs were visualized using the *sjPlot* package.

6.3.3.2 Elephant grouping patterns at water sources in relation to risk, sex, and season (aim 6.3)

To test the prediction that males would be more likely to visit high-risk water sources (versus low-risk water sources) in the company of other males or cow-calf groups (prediction 6.3.1), I used chi-square goodness-of-fit tests to determine if there was a significant difference in the number of 1) lone bull versus bull group events and 2) lone bull versus mixed group events between a) the low-risk park water sources and high-risk park water sources, and b) the low-risk park water sources and high-risk village water sources. The low-risk park distribution was used to generate expected values for the higher-risk water sources. I used two-sample Kolmogorov-Smirnov tests to examine if male and female group sizes were larger at the high-risk park and high-risk village water sources than at low-risk water sources (predictions 6.2.2 and 6.2.3). I then investigated the effect of season on elephant grouping patterns at low-risk water sources using a chi-square goodness-of-fit test to assess if the relative frequency of cow-calf group and mixed group events varied by season. The Kolmogorov-Smirnov goodness-of-fit test was used to examine possible seasonal differences in group size for cow-calf groups, bull groups, and mixed groups at low-risk water sources. Where indicated in the text, I applied the Bonferroni correction to correct for multiple comparisons.

6.3.3.3 Vigilance behaviour (aim 6.4)

To examine the prediction that elephants would be more vigilant at high-risk water sources than at low-risk water sources (prediction 6.4.1), I compare the percentage of elephant events with non-vigilant pauses, vigilant pauses, unknown pauses, and no pauses between the low-risk park, high-risk park, and high-risk village water sources.

6.4 Results

Camera traps detected 1,287 unique elephant events over 4,010.7 camera trap days (Table 6.1; Smit, 2023b). The number of elephant events and daily relative activity index by group type and season are shown in Tables 6.2-6.5.

6.4.1 Effect of risk, sex, and season on the frequency of elephant water source use (aim 6.1)

Comparisons of the median daily relative activity index (daily RAI) by water source indicate that males and females used low-risk water sources to a similar extent (Figure 6.2). The median daily RAI was slightly higher for females than for males at the high-risk water sources in the park, and lower for females than for males at the high-risk water sources on village land

(Figure 6.2). At the low-risk water sources in the park, the median daily RAI was higher in the wet season than in the dry season (Figure 6.3). In contrast, the median daily RAI was higher in the dry season than in the wet season at the high-risk park and high-risk village water sources (Figure 6.3). For both sexes, median daily RAIs were lower during the wet season than the dry season at high-risk water sources, although this pattern was stronger for females than for males at the high-risk village water sources (Figure 6.4).

In both seasons, there was a significant difference in the relative frequency of male and female events between the low-risk park and high-risk village water sources, but not between the low-risk park and high-risk park water sources (Table 6.6). Compared to the low-risk park water sources, there were fewer than expected female events at the high-risk village water sources.

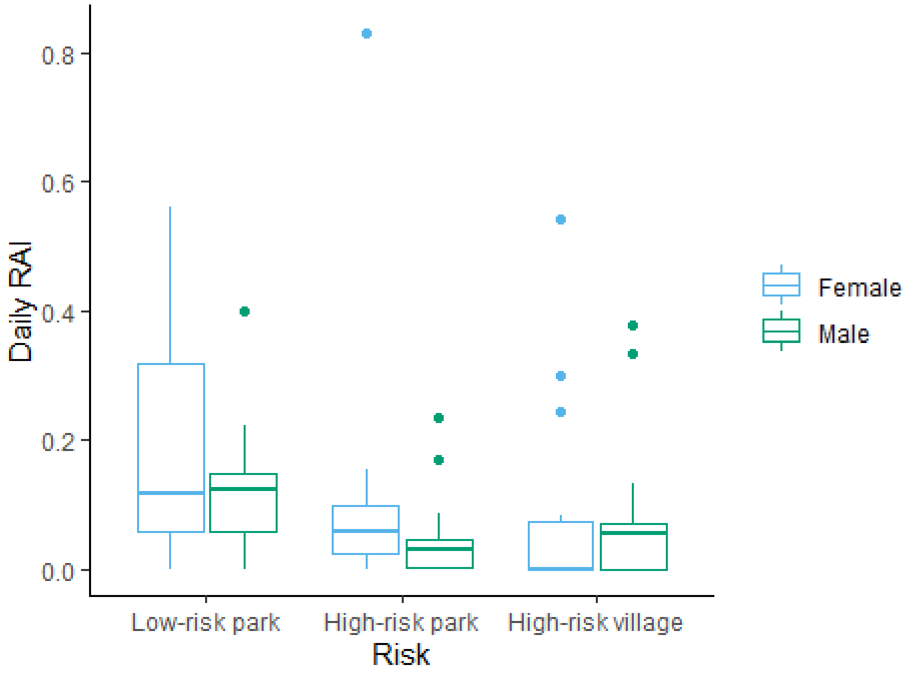


Figure 6.2 Daily relative activity index (daily RAI) by risk and sex. Daily RAI is the number of elephant events divided by the number of camera trap days, calculated per camera trap station. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Dots represent outliers. Sample sizes are 28 daily RAI measures (14 female, 14 male) for low-risk park water sources, 28 daily RAI measures (14 female, 14 male) for high-risk park water sources, and 27 daily RAI measures (14 female, 13 male) for high-risk village water sources. One outlier with a value of 3.08 (the high-risk village Tungamalenga Idelemle camera trap station, male dry season events) was removed to better show the main effects.

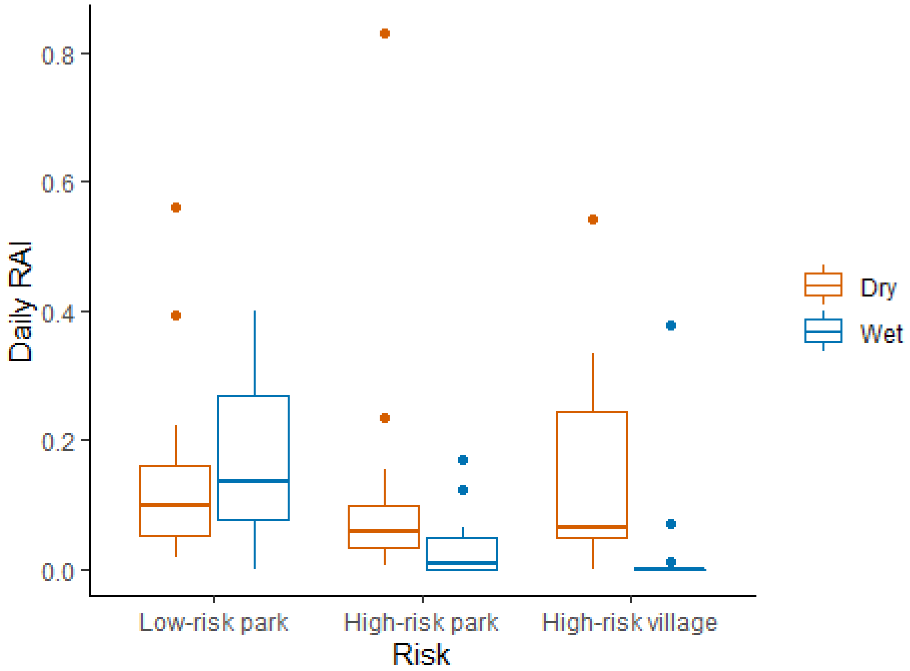


Figure 6.3 Daily relative activity index by risk and season. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Dots represent outliers. Sample sizes are 28 daily RAI measures (14 dry season, 14 wet season) for low-risk park water sources, 28 daily RAI measures (14 dry season, 14 wet season) for high-risk park water sources, and 27 daily RAI measures (13 dry season, 14 wet season) for high-risk village water sources. One outlier with a value of 3.08 (the high-risk village Tungamalenga Idelemle camera trap station, male dry season events) was removed to better show the main effects.

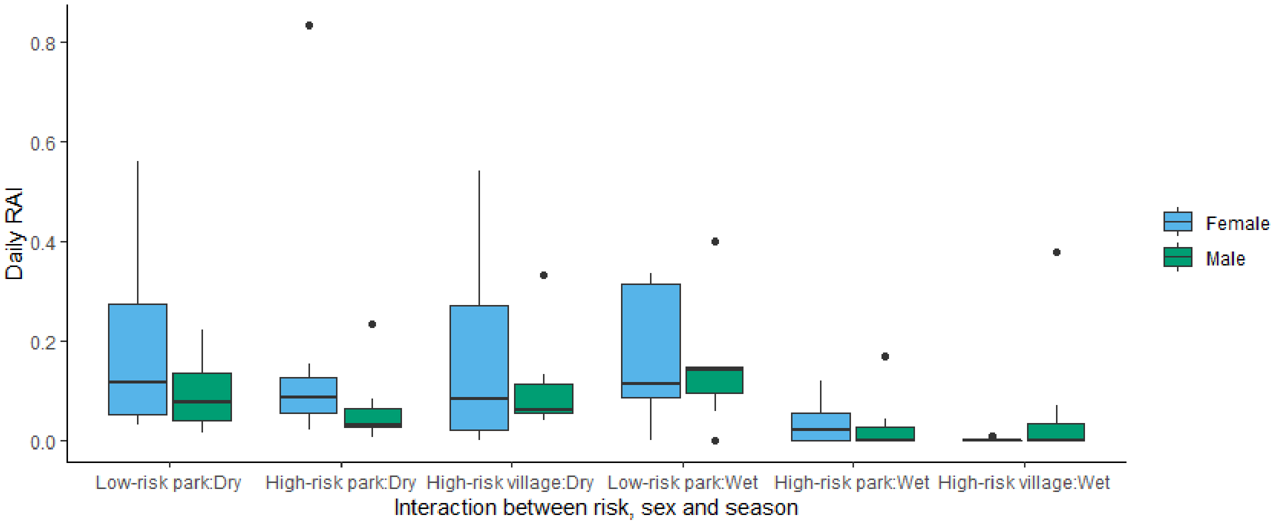


Figure 6.4 Daily relative activity index by risk, sex, and season. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Black dots represent outliers. Sample sizes are 28 daily RAI measures (split evenly by sex and season) for low-risk park water sources, 28 daily RAI measures (split evenly by sex and season) for high-risk park water sources, and 27 daily RAI measures (6 male and 7 female in the dry season, 7 male and 7 female in the wet season) for high-risk village water sources. One outlier with a value of 3.08 (the high-risk village Tungamalenga Idelemle camera trap station, male dry season events) was removed to better show the main effects.

Table 6.6 Results of chi-square goodness-of-fit tests to examine whether there are differences in the relative frequency of female and male events between low-risk park and high-risk park water sources, and between low-risk park and high-risk village water sources. Tests were done separately for the wet and dry season. For sample sizes, please refer to Tables 6.2 & 6.4. I applied the Bonferroni correction to correct for multiple comparisons (α = 0.05 / 2 = 0.025). Significant p-values have been bolded.

Risk comparison	**Season**	**Sex**	**Chi-square value**	**Degrees of freedom**	**p-value**
Low-risk park vs. high-risk park	Dry	Females vs. males	0.82	1	0.365
Low-risk park vs. high-risk village	Dry	Females vs. males	330.86	1	**<0.0001**
Low-risk park vs. high-risk park	Wet	Females vs. males	2.27	1	0.132
Low-risk park vs. high-risk village	Wet	Females vs. males	36.72	1	**<0.0001**

6.4.2 The effect of risk, sex, and season on the timing of elephant use of water sources (aim 6.2)

A comparison of the hourly relative activity index (hourly RAI) indicates that the frequency of elephant use of low-risk water sources in the park was similar during the day and night (Figure 6.5). In contrast, elephant activity was higher during the night than during the day at the high-risk water sources (Figure 6.5), and this was true for both males and females (Figure 6.6). Interestingly, the timing of female and male activity differed at low-risk water sources, with females showing greater nocturnal activity than males (Figure 6.6). At low-risk water sources, the median hourly RAIs for day and night did not vary much between the wet and dry seasons (Figure 6.7). At the high-risk water sources in the park, however, elephants had higher nocturnal activity during the dry season than during the wet season (Figure 6.7). Seasonal comparisons of the hourly RAI by diel period for the high-risk water sources on village land were challenging due to the low number of elephant visits to village water sources during the wet season.

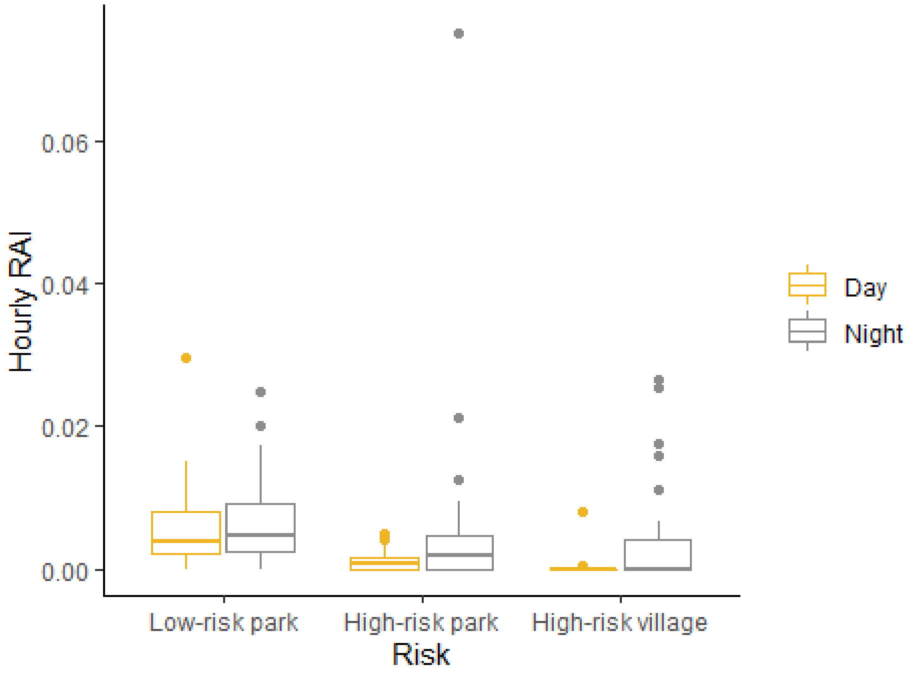


Figure 6.5 Hourly relative activity index (hourly RAI) by risk for the day and night diel periods. Hourly RAI is the number of elephant events divided per camera trap hour, calculated per diel period and camera trap station. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Dots represent outliers. Sample sizes are 56 hourly RAI measures for low-risk park water sources, 56 hourly RAI measures for high-risk park water sources, and 58 hourly RAI measures for high-risk village water sources. One outlier with a value of 0.15 (the high-risk village Tungamalenga Idelemle camera trap, nocturnal male events) was removed to better show the main effects.

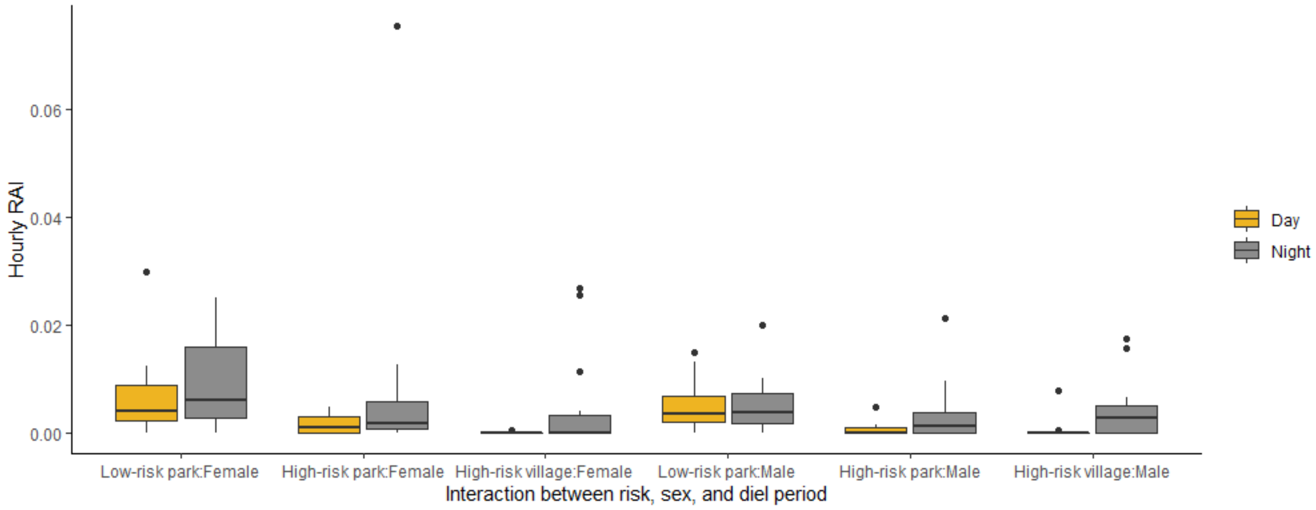


Figure 6.6 Hourly relative activity index by risk, sex, and diel period. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Black dots represent outliers. Sample sizes are 56 hourly RAI measures (28 female, 28 male) for low-risk park water sources, 56 hourly RAI measures (28 female, 28 male) for high-risk park water sources, and 58 hourly RAI measures for high-risk village water sources (30 female, 28 male). One outlier with a value of 0.15 (the high-risk village Tungamalenga Idelemle camera trap, nocturnal male events) was removed to better show the main effects.

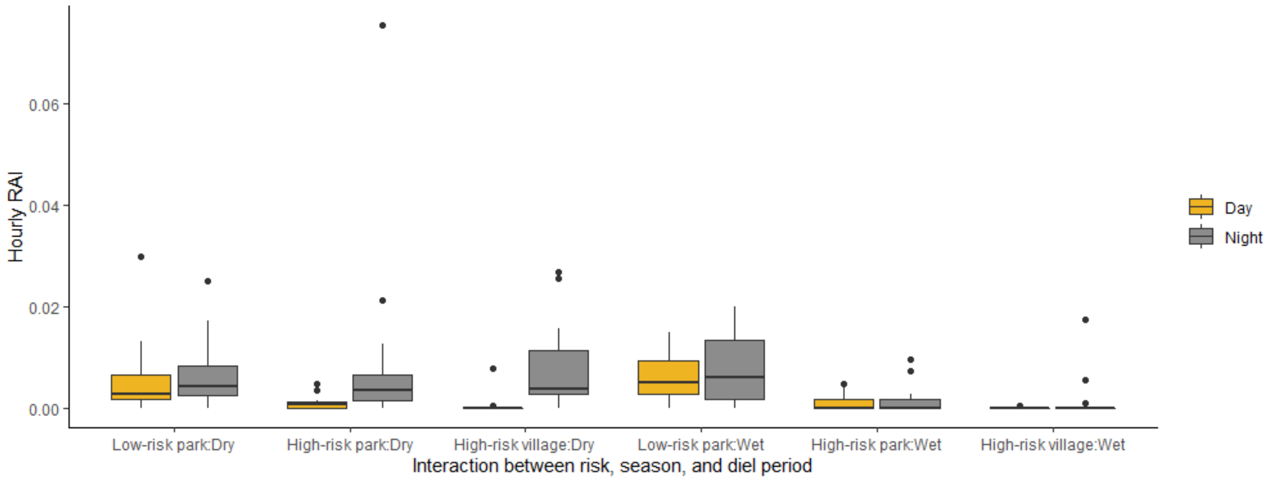
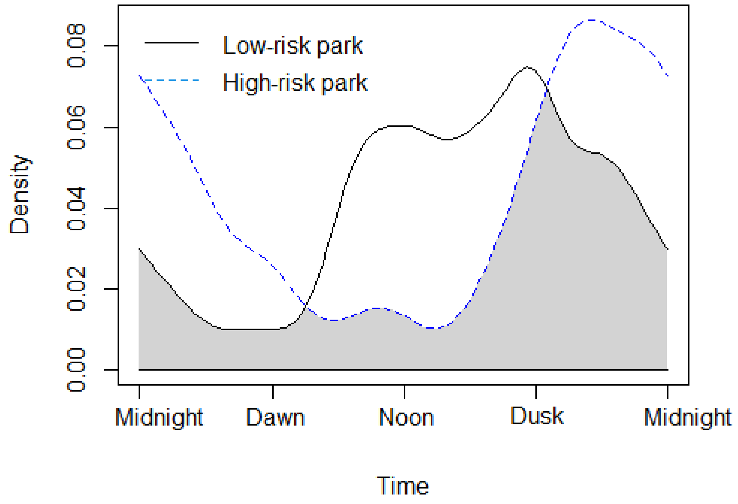


Figure 6.7 Hourly relative activity index by risk, season, and diel period. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Black dots represent outliers. Sample sizes are 56 hourly RAI measures (28 dry season, 28 wet season) for low-risk park water sources, 56 hourly RAI measures (28 dry season, 28 wet season) for high-risk park water sources, and 58 hourly RAI measures for high-risk village water sources (26 dry season, 32 wet season). One outlier with a value of 0.15 (the high-risk village Tungamalenga Idelemle camera trap, nocturnal male events) was removed to better show the main effects.

Activity profiles of elephant events at water sources (Figures 6.8-6.9) further indicate that elephant use of high-risk water sources was more nocturnal than their use of low-risk water sources, although this pattern was stronger for the high-risk water sources on village land than the high-risk water sources in the park. In both the wet and the dry season, elephants used high-risk water sources on village land more at night than during the day, and the activity profiles for the low-risk park and high-risk village water sources were significantly different in both seasons (Figures 6.8-6.9, Table 6.7). Elephant use of high-risk park water sources was more nocturnal than their use of low-risk park water sources in the dry season but not in the wet season, and the activity profiles for the low-risk park and high-risk park water sources were only significantly different in the dry season.



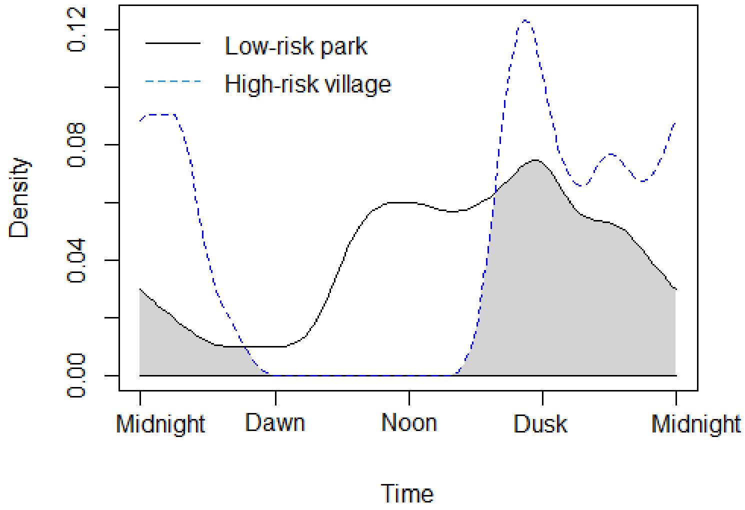


Figure 6.8 Activity profiles for dry season elephant events at low-risk water sources (n=352 events), high-risk water sources in the park (n=154 events), and high-risk water sources on village land (n=373 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same. The percentage of nocturnal events was 54% at low-risk park water sources, 79% at high-risk park water sources, and 97% at high-risk village water sources.

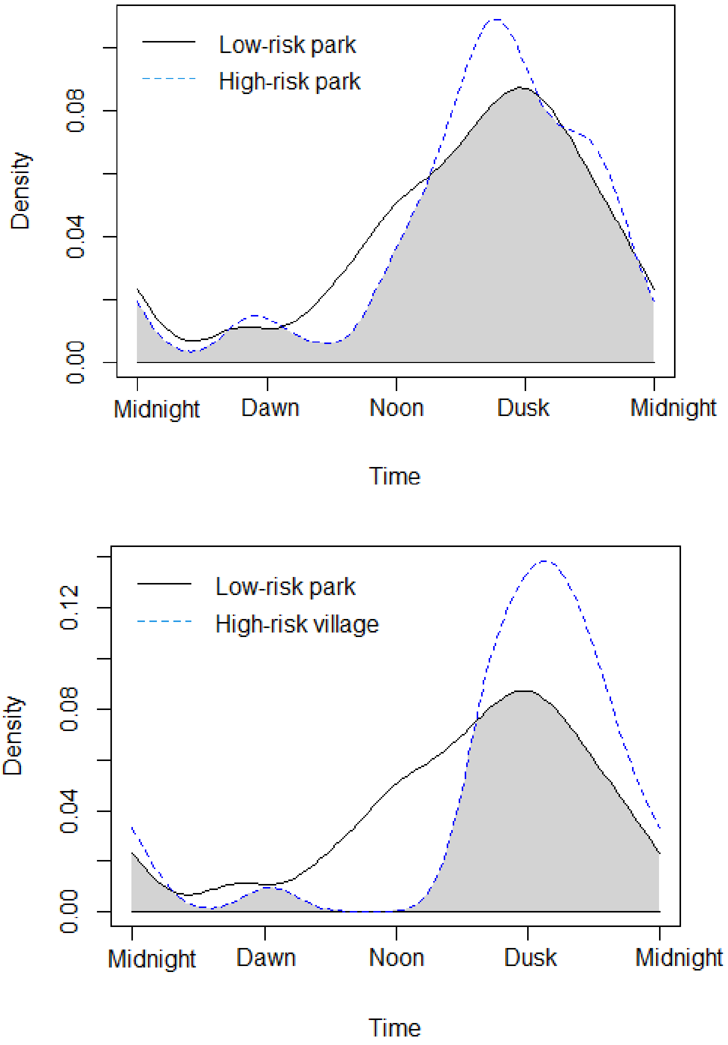
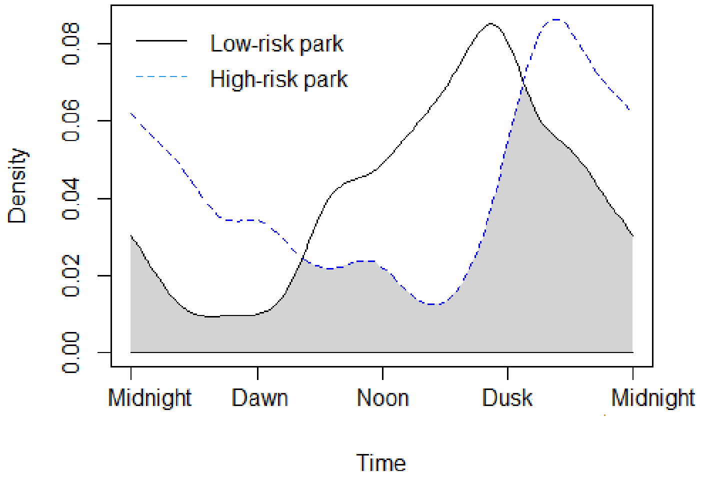


Figure 6.9 Elephant activity profiles for wet season elephant events at low-risk water sources (n=312 events), high-risk water sources in the park (n=63 events), and high-risk water sources on village land (n=33 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same. The percentage of nocturnal events was 50% at low-risk park water sources, 56% at high-risk park water sources, and 91% at high-risk village water sources.

Table 6.7 Coefficient of overlapping, 95% confidence intervals for the coefficient of overlapping, and statistical significance for pairwise activity distribution comparisons for the low-risk park, high-risk park, and high-risk village water sources by season. For sample sizes, please refer to Tables 6.2 & 6.4.

Season	**Comparison**	**Coefficient of overlapping**	**95% CI**	**p-value**
Dry	Low-risk park vs. high-risk park	0.616	0.542-0.692	**<0.0001**
Dry	Low-risk park vs. high-risk village	0.574	0.523-0.625	**<0.0001**
Wet	Low-risk park vs. high-risk park	0.880	0.790- 0.955	0.357
Wet	Low-risk park vs. high-risk village	0.689	0.576- 0.792	**0.001**

All group types were more nocturnal in their use of high-risk village water sources than low-risk park water sources (Figures 6.10-6.13, Table 6.8). The use of high-risk park water sources was more nocturnal than the use of low-risk water sources for cow-calf groups, lone bulls, and mixed groups, but not bull groups. There was less overlap between the low-risk and high-risk activity curves for lone bulls than cow-calf groups, indicating that there was a greater shift in the timing of water source use in response to risk for lone bulls than for cow-calf groups (Table 6.8). At low-risk water sources in the park, lone bull activity peaked around midday and decreased through the afternoon and evening, while cow-calf activity increased throughout the afternoon and peaked around dusk. Bull group activity at low-risk water sources peaked at noon and after dusk (Figure 6.12), while mixed group activity peaked before midday (Figure 6.13).



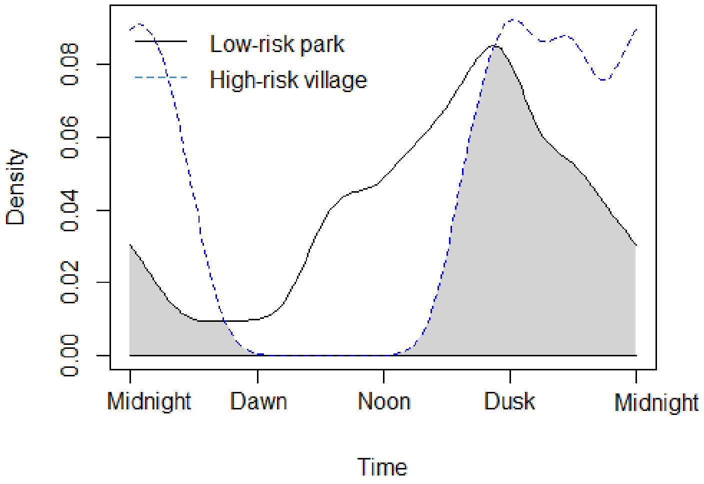


Figure 6.10 Activity profiles for dry season cow-calf group events at low-risk water sources (n=184 events), high-risk water sources in the park (n=65 events), and high-risk water sources on village land (n=54 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping.

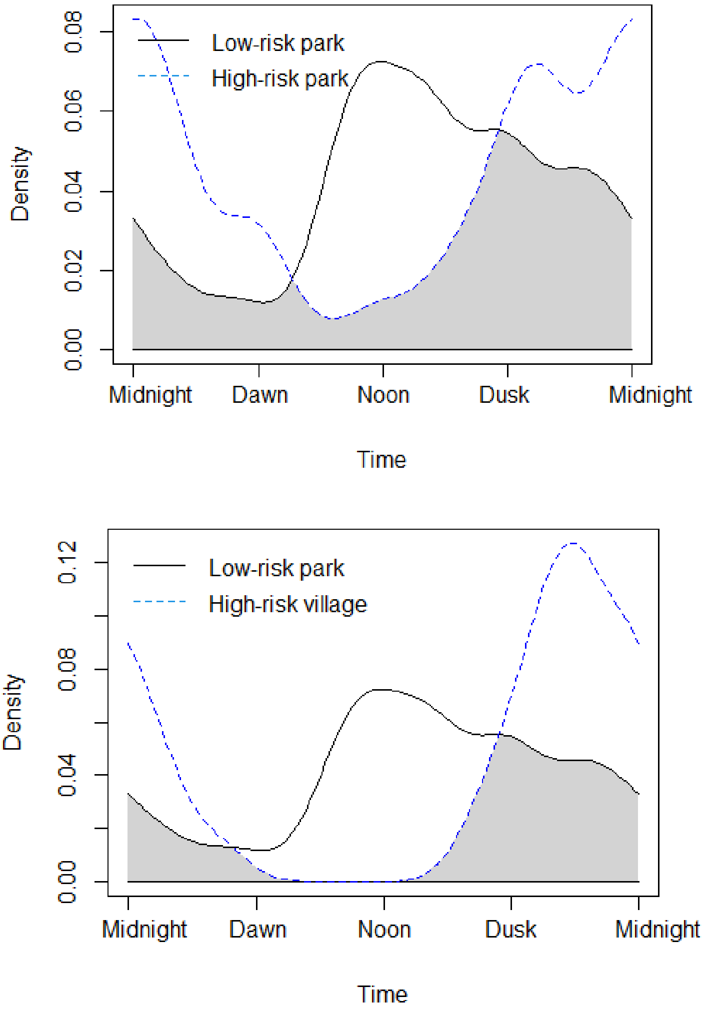


Figure 6.11 Activity profiles for dry season lone bull events at low-risk water sources (n=79 events), high-risk water sources in the park (n=23 events), and high-risk water sources on village land (n=47 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same.

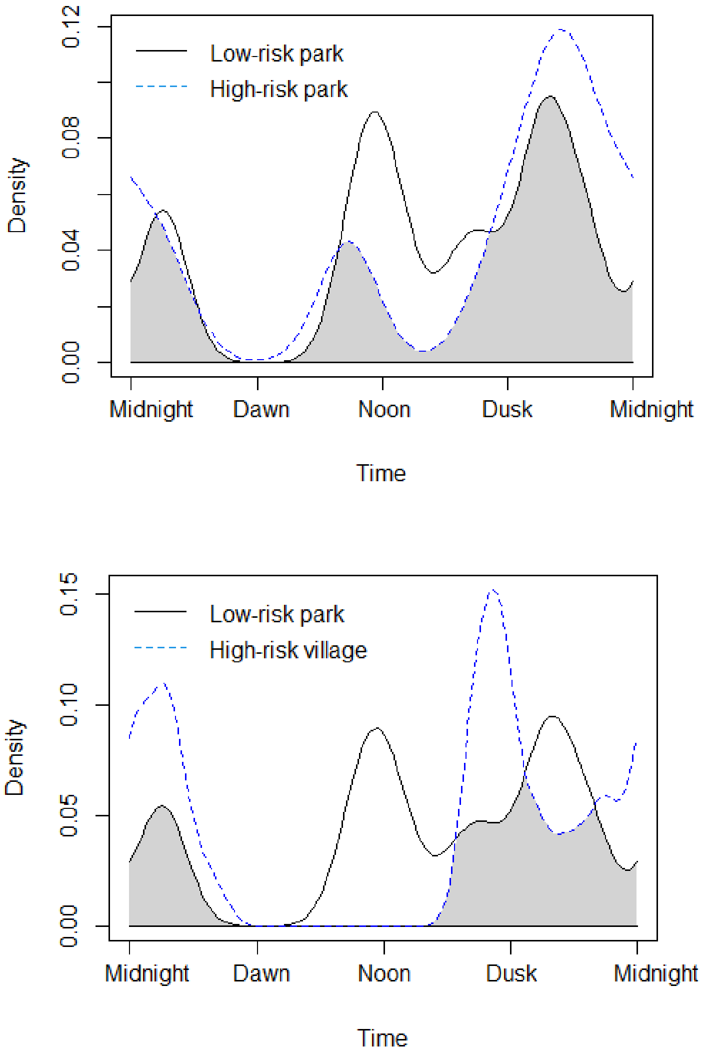


Figure 6.12 Activity profiles for dry season bull group events at low-risk water sources (n=19 events), high-risk water sources in the park (n=13 events), and high-risk water sources on village land (n=219 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same.

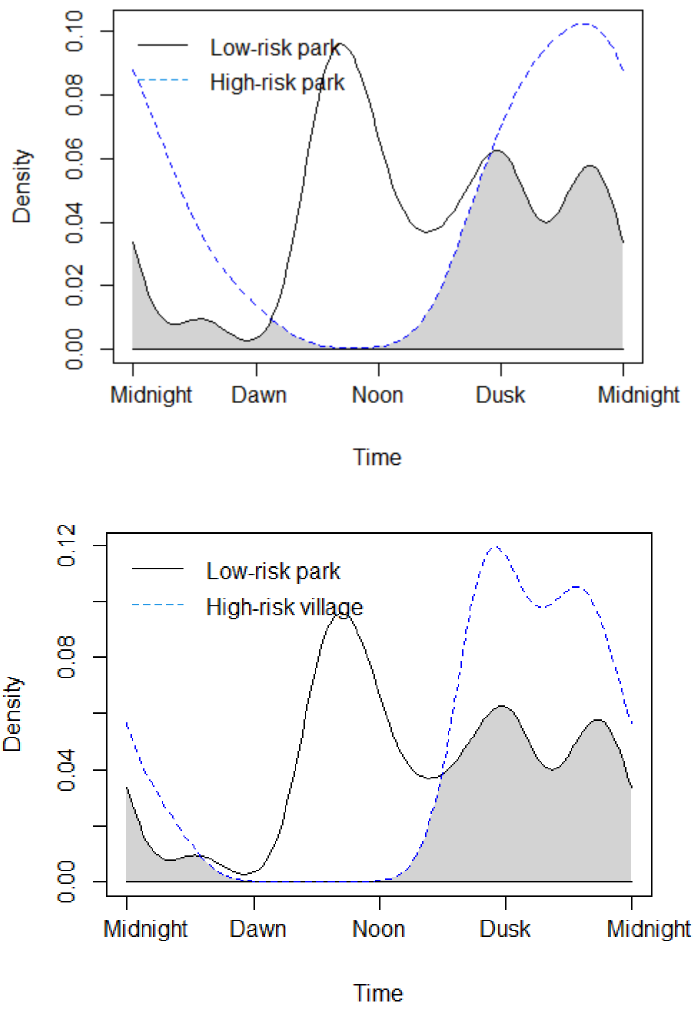


Figure 6.13 Activity profiles for dry season mixed group events at low-risk water sources (n=35 events), high-risk water sources in the park (n=31 events), and high-risk water sources on village land (n=31 events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same.

Table 6.8 Coefficient of overlapping, 95% confidence intervals for the coefficient of overlapping, and statistical significance for pairwise activity distribution comparisons for the low-risk park, high-risk park, and high-risk village water sources by group type (dry season only). For sample sizes, please refer to Table 6.2.

Group type	**Comparison**	**Coefficient of overlapping**	**95% CI**	**p-value**
Cow-calf	Low-risk park vs. high-risk park	0.632	0.524-0.739	**<0.0001**
Cow-calf	Low-risk park vs. high-risk village	0.603	0.503-0.699	**<0.0001**
Lone bull	Low-risk park vs. high-risk park	0.609	0.447-0.768	**<0.0001**
Lone bull	Low-risk park vs. high-risk village	0.491	0.375- 0.609	**<0.0001**
Bull group	Low-risk park vs. high-risk park	0.727	0.516-0.911	0.650
Bull group	Low-risk park vs. high-risk village	0.539	0.360-0.703	**0.001**
Mixed group	Low-risk park vs. high-risk park	0.514	0.345-0.674	**<0.0001**
Mixed group	Low-risk park vs. high-risk village	0.531	0.373- 0.684	**<0.0001**

Although differences between wet and dry season activity curves were statistically significant for all risk levels (Table 6.9), the percentage of nocturnal events only differed substantially between seasons for the high-risk park water sources (Figure 6.14b). At low-risk park water sources, dry season activity peaked around dusk with a secondary peak around noon, while wet season activity had a single peak around dusk (Figure 6.14). However, the percentage of nocturnal events differed only slightly by season (54% in the dry season versus 50% in the wet season). At high-risk park water sources, elephant activity peaked after dusk in the dry season but prior to dusk in the wet season, and elephant water source use was more nocturnal in the dry season (79% of events) than in the wet season (56% of events). Elephant activity at high-risk water sources on village land peaked around dusk during the dry season and after dusk in the wet season, but the percentage of nocturnal events varied little by season (97% in the dry season versus 91% in the wet season).

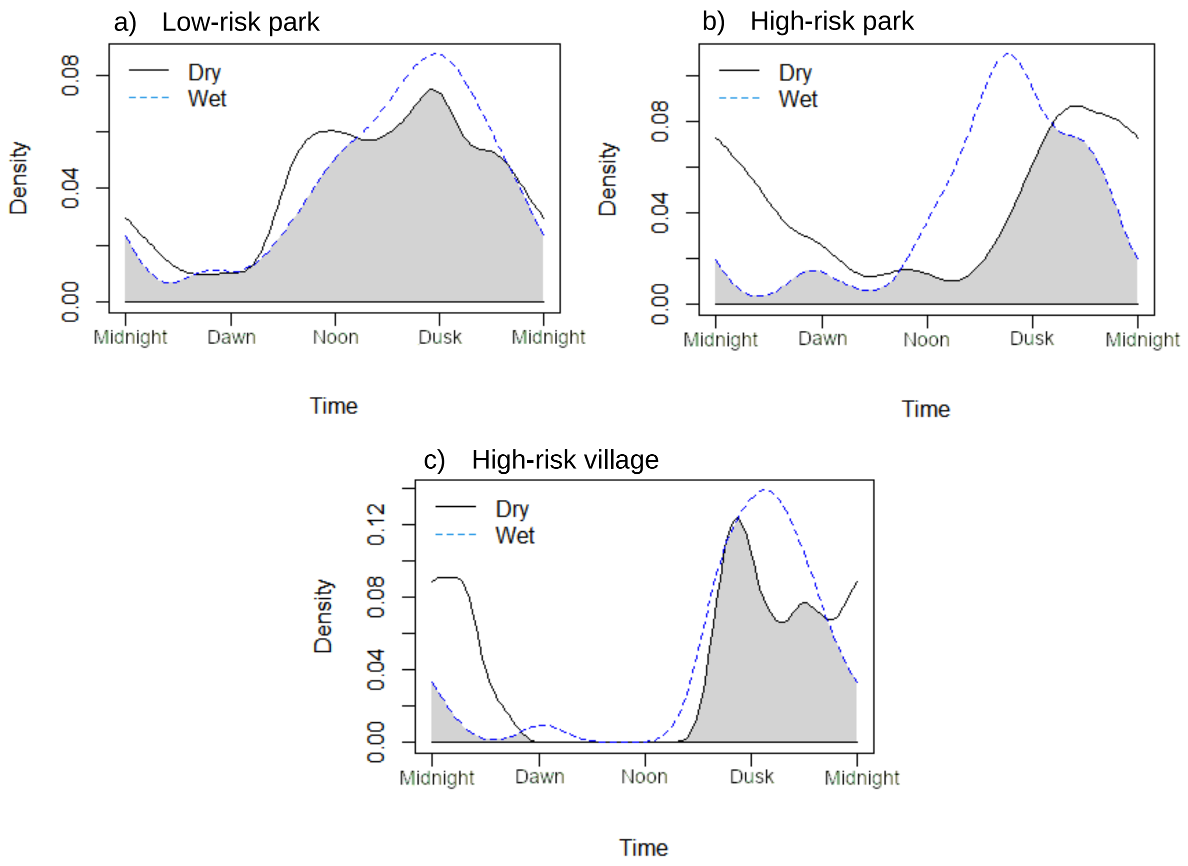


Figure 6.14 Activity profiles for a) low-risk park events by season (n=352 dry season and 373 wet season events); b) high-risk park events by season (n=154 dry season and 63 wet season events); c) high-risk village events by season (n=373 dry season and 33 wet season events). The density of elephant events over a 24-hour period is expressed by the solid and dotted lines. The shaded area represents the area that is shared between two activity distributions and is equivalent to the coefficient of overlapping. Note the y-axes are not the same.

Table 6.9 Coefficient of overlapping, 95% confidence intervals for the coefficient of overlapping, and statistical significance for pairwise activity distribution comparisons for the dry and wet seasons for low-risk park, high-risk park, and high-risk village water sources. For sample sizes, please refer to Tables 6.2 & 6.4.

Risk	Comparison	Coefficient of overlapping	95% CI	p-value
Low-risk park	Dry vs. wet	0.894	0.836-0.946	**0.040**
High-risk park	Dry vs. wet	0.612	0.507-0.728	**<0.0001**
High-risk village	Dry vs. wet	0.713	0.606-0.810	**0.014**

Next, I modelled the effect of risk, diel period, sex, and season on elephant event counts. The top model included the interactions *Risk x Diel* and *Risk x Season,* but not the interactions *Risk x Sex, Risk x Diel x Sex*, and *Risk x Diel x Season* (Figure 6.15 & Table 6.10; see Table A6.2 for top model set). There was consistency between the top models in which fixed effects emerged as significant. The top model's total explanatory power was substantial (conditional R^2 = 0.94), and the part related to the fixed effects alone (marginal R^2) was 0.58. The top model was not overdispersed. Diagnostic plots indicated good model fit (Figures A6.2-A6.4).

The terms *Risk:Highpark* and *Risk:Highvillage* were statistically significant and negative, indicating that fewer elephant events occurred overall at the high-risk park and high-risk village water sources than at the low-risk park water sources. The interaction between *Risk* and *Diel* was positive for the high-risk park and high-risk village water sources, but it was only statistically significant for the high-risk village water sources. Therefore, significantly more elephant events occurred at night at the high-risk village water sources compared to the low-risk park water sources, but the frequency of nocturnal events was not significantly different between the low-risk and high-risk water sources in the park. The interaction between *Risk* and *Season* was negative and statistically significant for the high-risk village water sources, indicating that significantly fewer elephant events occurred during the wet season than the dry season at high-risk village water sources. While the interaction between *Risk* and *Season* was also negative for the high-risk park water sources, it was not statistically significant. As the interactions between *Risk*, *Diel*, and *Sex* and *Risk*, *Diel*, and *Season* did not feature in the top model, shifts in the timing of water source use in response to risk were not significantly affected by sex or season.

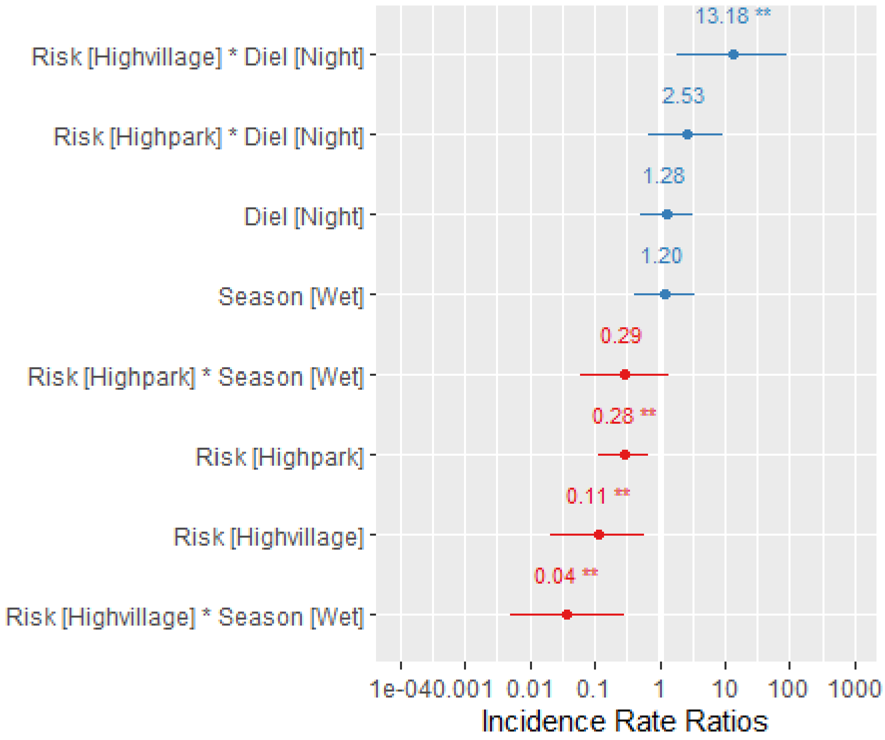
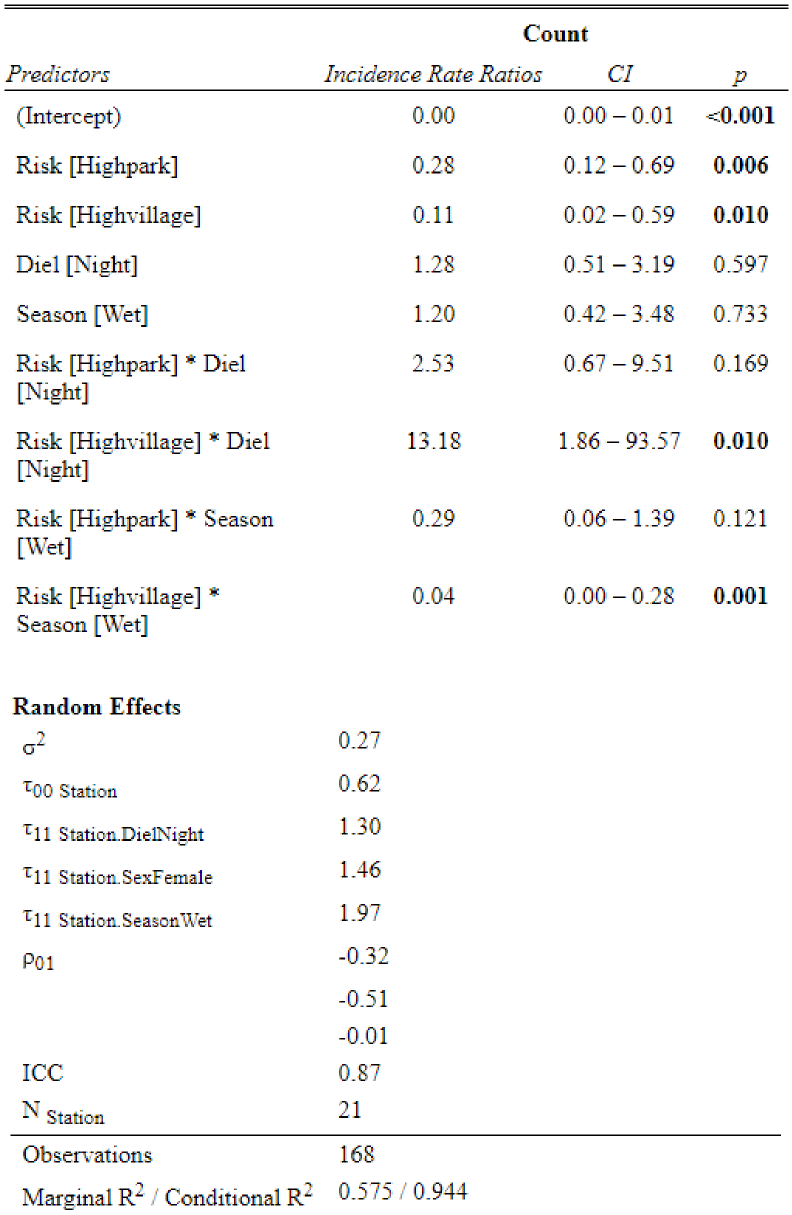


Figure 6.15 Elephant event incident rate ratios (dots) and 95% confidence intervals (bars) for model parameters for the top model. To express model coefficients as incident rate ratios, I raised the natural log to the power of each coefficient. Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates.

Table 6.10 Model coefficients expressed as incident rate ratios with associated confidence intervals (CI) and p-values shown. σ2 is the residual variance. τ00 is the between-subject variance. τ11 is the random-slope variance. ρ01 is the random slope-intercept correlation. ICC is the intraclass correlation coefficient. NStation is the number of camera trap stations. Observations is the sample size. The marginal pseudo R-squared considers only the variance of the fixed effects, while the conditional pseudo R-squared takes both the fixed and random effects into account (Nakagawa et al. 2017). Highpark represents the high-risk park water sources, and Highvillage represents the high-risk village water sources.



	Count		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	0.00	0.00 – 0.01	**<0.001**
Risk [Highpark]	0.28	0.12 – 0.69	**0.006**
Risk [Highvillage]	0.11	0.02 – 0.59	**0.010**
Diel [Night]	1.28	0.51 – 3.19	0.597
Season [Wet]	1.20	0.42 – 3.48	0.733
Risk [Highpark] * Diel [Night]	2.53	0.67 – 9.51	0.169
Risk [Highvillage] * Diel [Night]	13.18	1.86 – 93.57	**0.010**
Risk [Highpark] * Season [Wet]	0.29	0.06 – 1.39	0.121
Risk [Highvillage] * Season [Wet]	0.04	0.00 – 0.28	**0.001**
Random Effects			
σ^2	0.27		
τ_{00} Station	0.62		
τ_{11} Station.DielNight	1.30		
τ_{11} Station.SexFemale	1.46		
τ_{11} Station.SeasonWet	1.97		
ρ_{01}	-0.32		
	-0.51		
	-0.01		
ICC	0.87		
N Station	21		
Observations	168		
Marginal R^2 / Conditional R^2	0.575 / 0.944		

6.4.3 Elephant grouping patterns at water sources in relation to risk, sex, and season (aim 6.3)

Males were significantly more likely to occur in bull groups than as lone bulls at high-risk village water sources relative to low-risk park water sources in both seasons (Figures 6.16-6.17, Table 6.11). However, males were not more likely to occur in mixed groups than as lone bulls at high-risk village water sources compared to low-risk park water sources in either season. There were fewer mixed groups at high-risk village water sources in the wet season than in the dry season, likely because female use of high-risk village water sources was extremely limited during the wet season when only one cow-calf group event and one mixed group event were detected. At high-risk park water sources, males were significantly more likely to occur in bull groups and mixed groups compared to low-risk park water sources during the dry season but not in the wet season (Figures 6.16-6.17, Table 6.11). This may be because bull groups and mixed groups made up a greater percentage of events at the low-risk park water sources in the wet season than in the dry season.

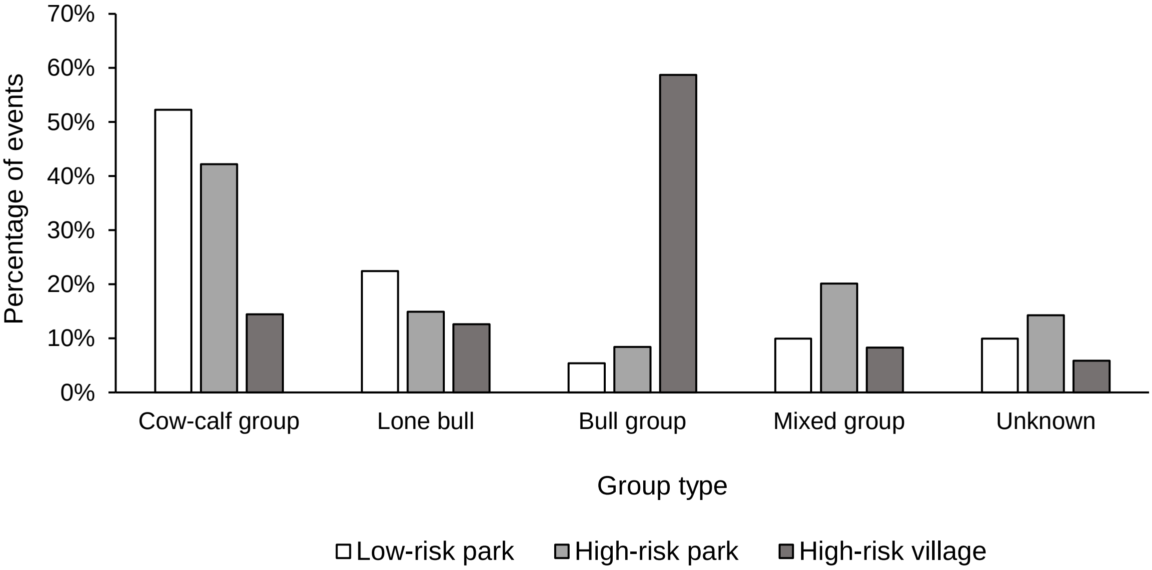


Figure 6.16 Percentage of cow-calf group (n=303 events), lone bull (n=149 events), bull group (n=251 events), mixed group (n=97 events), and unknown group type (n=79 events) events for the low-risk park, high-risk park, and high-risk village water sources during the dry season.

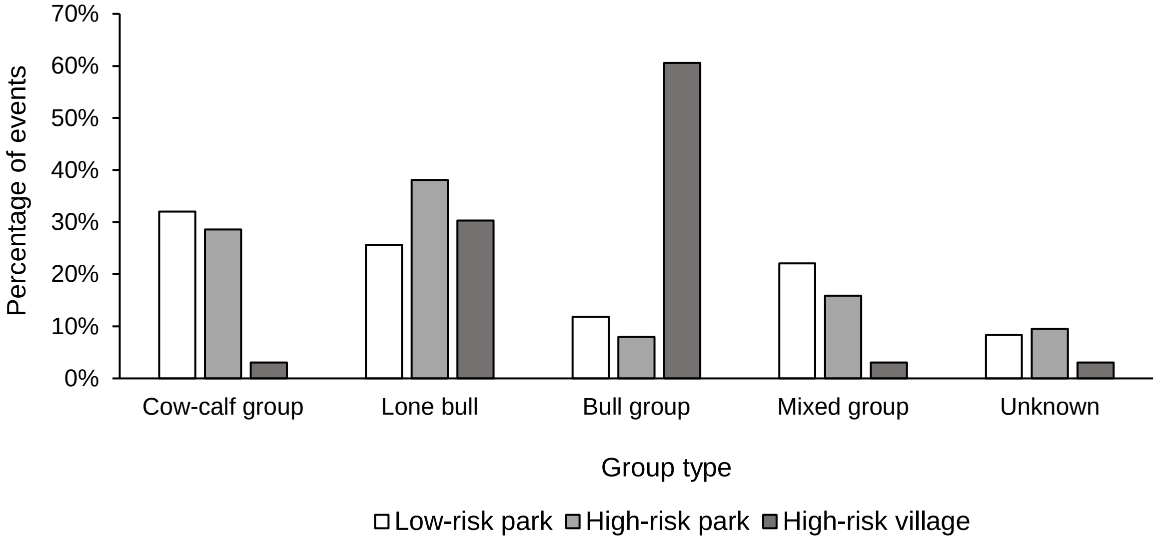


Figure 6.17 Percentage of cow-calf group (n=119 events), lone bull (n=114 events), bull group (n=62 events), mixed group (n=80 events), and unknown group type (n=33 events) events for the low-risk park, high-risk park, and high-risk village water sources during the wet season.

Table 6.11 Results of chi-square goodness-of-fit tests of the relative frequency of lone bull (LB) versus bull group (BG) events and lone bull versus mixed group (M) events between low-risk park and high-risk park water sources, and between low-risk park and high-risk village water sources. Tests were done separately for the wet and dry season. For sample sizes, please refer to Tables 6.2 & 6.4. I applied the Bonferroni correction to correct for multiple comparisons (α = 0.05 / 4 = 0.0125). Significant p-values have been bolded.

Risk comparison	Season	Group	Chi-square value	Degrees of freedom	p-value
Low-risk park vs. high-risk park	Dry	LB vs. BG	6.44	1	**0.011**
Low-risk park vs. high-risk village	Dry	LB vs. BG	674.29	1	**<0.0001**
Low-risk park vs. high-risk park	Dry	LB vs. M	18.10	1	**<0.0001**
Low-risk park vs. high-risk village	Dry	LB vs. M	3.00	1	0.083
Low-risk park vs. high-risk park	Wet	LB vs. BG	2.77	1	0.096
Low-risk park vs. high-risk village	Wet	LB vs. BG	17.04	1	**<0.0001**
Low-risk park vs. high-risk park	Wet	LB vs. M	3.74	1	0.053
Low-risk park vs. high-risk village	Wet	LB vs. M	6.02	1	**0.014**

Bull group sizes were significantly larger at high-risk village water sources than at low-risk park water sources in both seasons (Figure 6.18, Tables 6.12-6.13). There was no difference in bull group sizes between low-risk and high-risk water sources in the park in either season. There were no statistically significant differences in cow-calf and mixed group sizes between the low-risk park and high-risk park water sources in either season (Figures 6.19-6.20, Tables 6.12-6.13). Cow-calf and mixed group sizes did not differ significantly between the low-risk park and high-risk village sources in the dry season. It was not possible to compare cow-calf and mixed group sizes between low-risk and high-risk village water sources in the wet season, as only one cow-calf event and one mixed group event were detected at the village water sources in the wet season.

Table 6.12 Mean and median (in parentheses) group size for cow-calf groups, bull groups, and mixed groups for the low-risk park, high-risk park, and high-risk village water sources by season. Note that only one cow-calf event and one mixed group event were detected at the high-risk village water sources in the wet season.

	Dry season			**Wet season**		
	Low-risk park	High-risk park	High-risk village	Low-risk park	High-risk park	High-risk village
Cow-calf	5.9 (5)	5.0 (5)	6.7 (6)	7.2 (6)	4.7 (4)	5 (5)
Bull group	2.8 (2)	2.5 (2)	8.3 (6)	2.8 (2)	2.2 (2)	6.9 (6)
Mixed group	11.7 (10)	11.4 (8)	10.6 (9)	13.0 (11)	12.6 (12)	2 (2)

Table 6.13 Results of two-sample Kolmogorov-Smirnov tests of differences in the group sizes of bull groups, cow-calf groups, and mixed group sizes by risk and season. For sample sizes, please refer to Tables 6.2 & 6.4. I applied the Bonferroni correction to correct for multiple comparisons ($\alpha = 0.05 / 2 = 0.025$). Significant p-values have been bolded.

Risk comparison	**Season**	**Group type**	**p-value**
Low-risk park vs. high-risk park	Dry	Bull group	0.584
Low-risk park vs. high-risk village	Dry	Bull group	**<0.0001**
Low-risk park vs. high-risk park	Wet	Bull group	0.711
Low-risk park vs. high-risk village	Wet	Bull group	**<0.0001**
Low-risk park vs. high-risk park	Dry	Cow-calf	0.516
Low-risk park vs. high-risk village	Dry	Cow-calf	0.187
Low-risk park vs. high-risk park	Wet	Cow-calf	0.108
Low-risk park vs. high-risk park	Dry	Mixed group	0.321
Low-risk park vs. high-risk village	Dry	Mixed group	0.332
Low-risk park vs. high-risk park	Wet	Mixed group	0.892

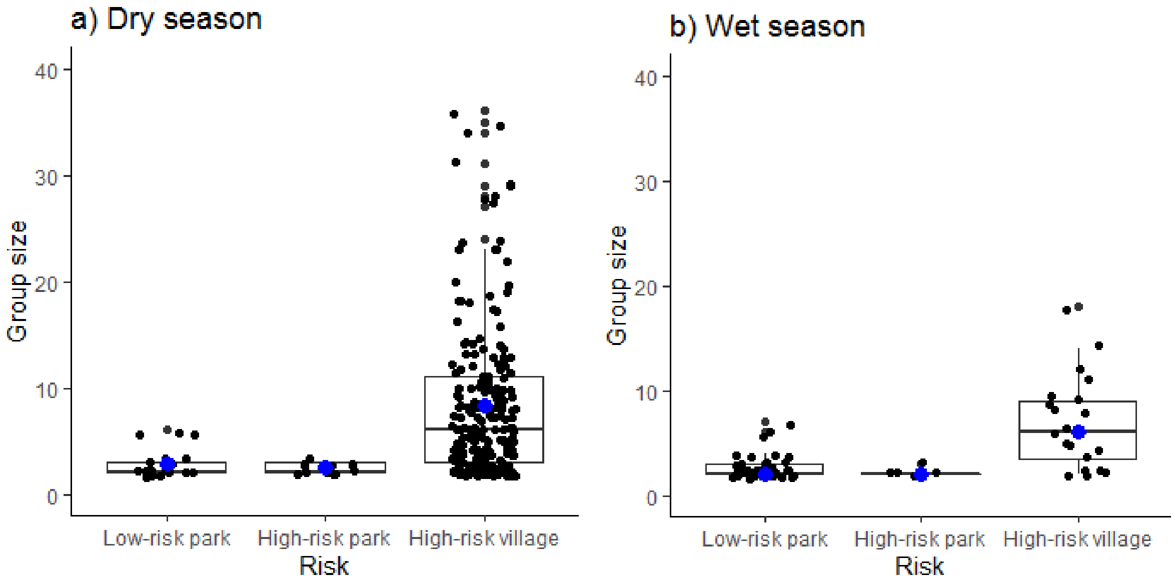


Figure 6.18 Bull group sizes for the low-risk park, high-risk park, and high-risk village water sources for a) the dry season (n=215 events) and b) the wet season (n=62 events). The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Mean group size is represented by a blue dot. Individual data points are represented by black dots.

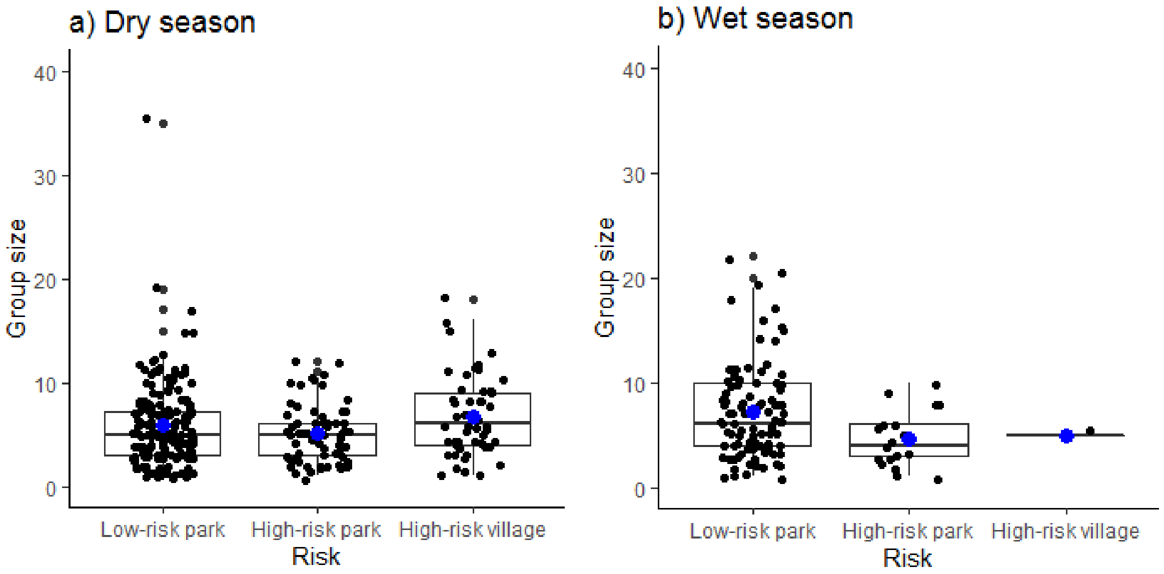


Figure 6.19 Cow-calf group sizes for the low-risk park, high-risk park, and high-risk village water sources in a) the dry season (n=303 events) and b) the wet season (n=119 events). The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Mean group size is represented by a blue dot. Individual data points are represented by black dots. There was a single observation of a cow-calf group at high-risk village water sources in the wet season.

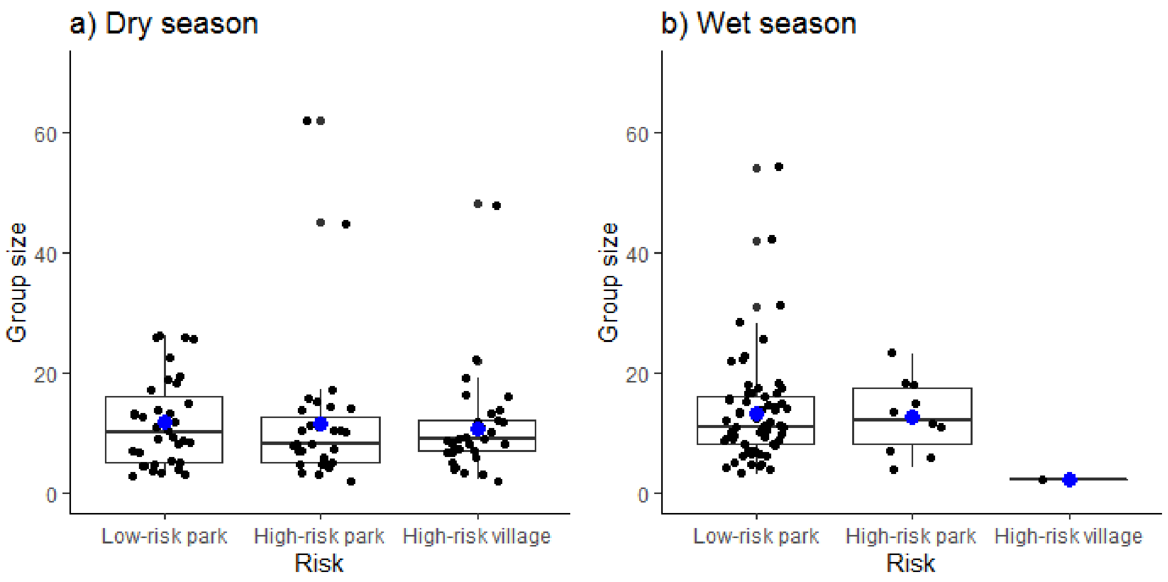


Figure 6.20 Mixed group sizes for the low-risk park, high-risk park, and high-risk village water sources for a) the dry season (n=97 events) and b) the wet season (n=79 events). The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Mean group size is represented by a blue dot. Individual data points are represented by black dots. There was a single observation of a mixed group at high-risk village water sources in the wet season.

I also examined the effect of season on elephant grouping patterns and group sizes for the low-risk park water sources only. There were significantly more mixed groups than cow-calf groups at low-risk water sources in the wet season than in the dry season (chi-square goodness-of-fit test, $\chi 2=75.07$, df=1, p-value <0.0001, n=387 events). Cow-calf group sizes were significantly larger during the wet season than the dry season at low-risk water park sources (Figure 6.21, Table 6.14). Bull group and mixed group sizes did not differ significantly with season at low-risk park water sources.

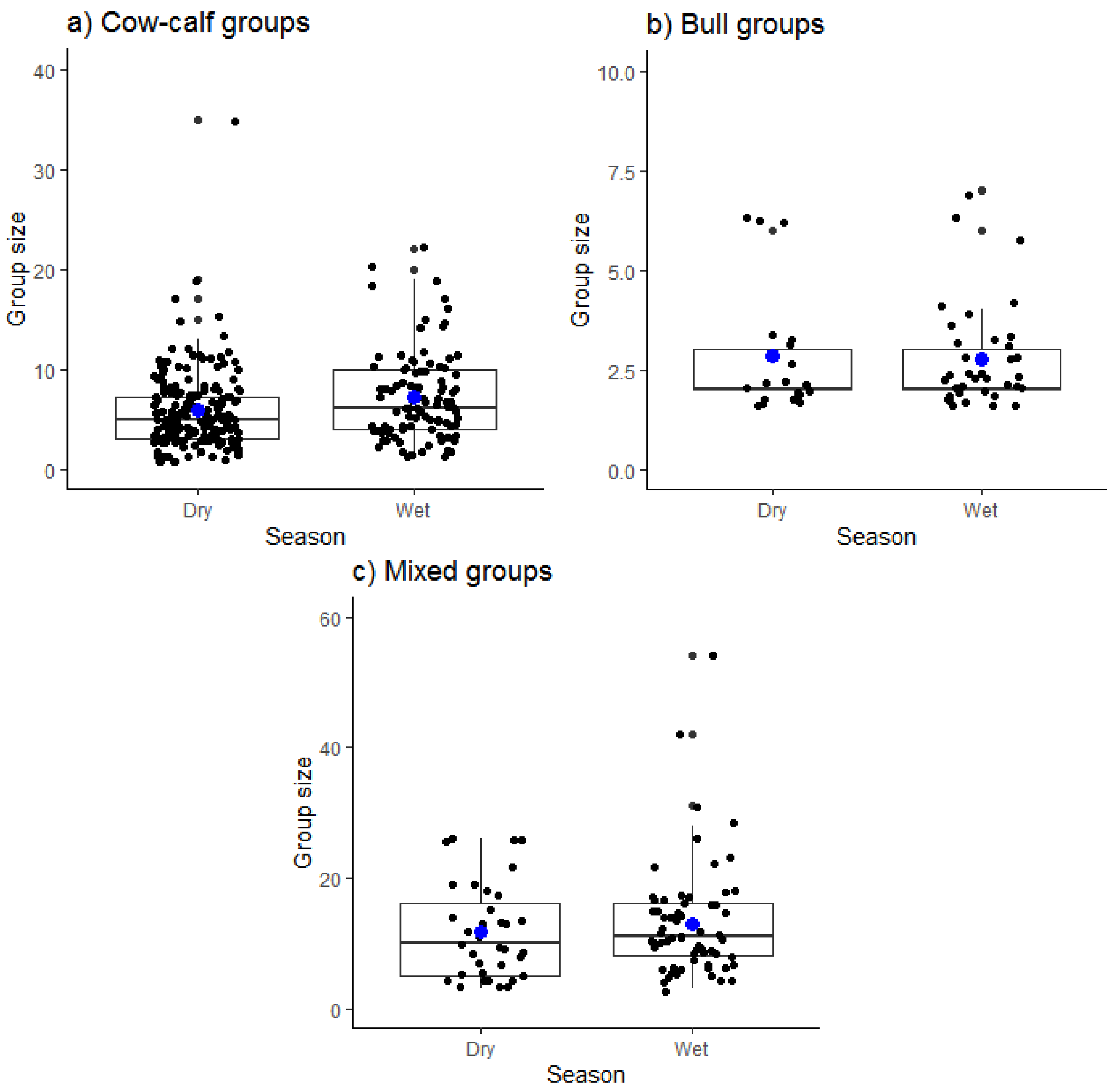


Figure 6.21 Distribution of dry and wet season group sizes for cow-calf groups (n=284 events), bull groups (n=56 events), and mixed groups (n=103 events) at low-risk water sources in the park. The central bar indicates the median. The box indicates the upper and lower quartile for the middle 50% and whiskers the upper and lower 25%. Mean group size is represented by a blue dot. Individual data points are represented by black dots. Note the y-axes are not the same.

Table 6.14 Results of two-sample Kolmogorov-Smirnov tests of differences in the group sizes of bull groups, cow-calf groups, and mixed group sizes between the dry and wet seasons at low-risk park water sources. For sample sizes, please refer to Tables 6.2 & 6.4. See Figure 6.21 for the distributions of group sizes by season.

Seasonal comparison	Group	p-value
Dry vs. wet	Cow-calf	**0.047**
Dry vs. wet	Bull group	0.876
Dry vs. wet	Mixed group	0.341

6.4.4 Vigilance behaviour at low-risk and high-risk water sources (aim 6.4)

Vigilant pauses were more frequent at high-risk village water sources than at low-risk park water sources (Figure 6.22). Vigilant pauses occurred in a similar percentage of events at the low- and high-risk water sources in the park. Non-vigilant pauses were more frequent at low-risk water sources than at high-risk water sources. It was more common to see elephant events with no pauses at the high-risk water sources relative to the low-risk water sources.

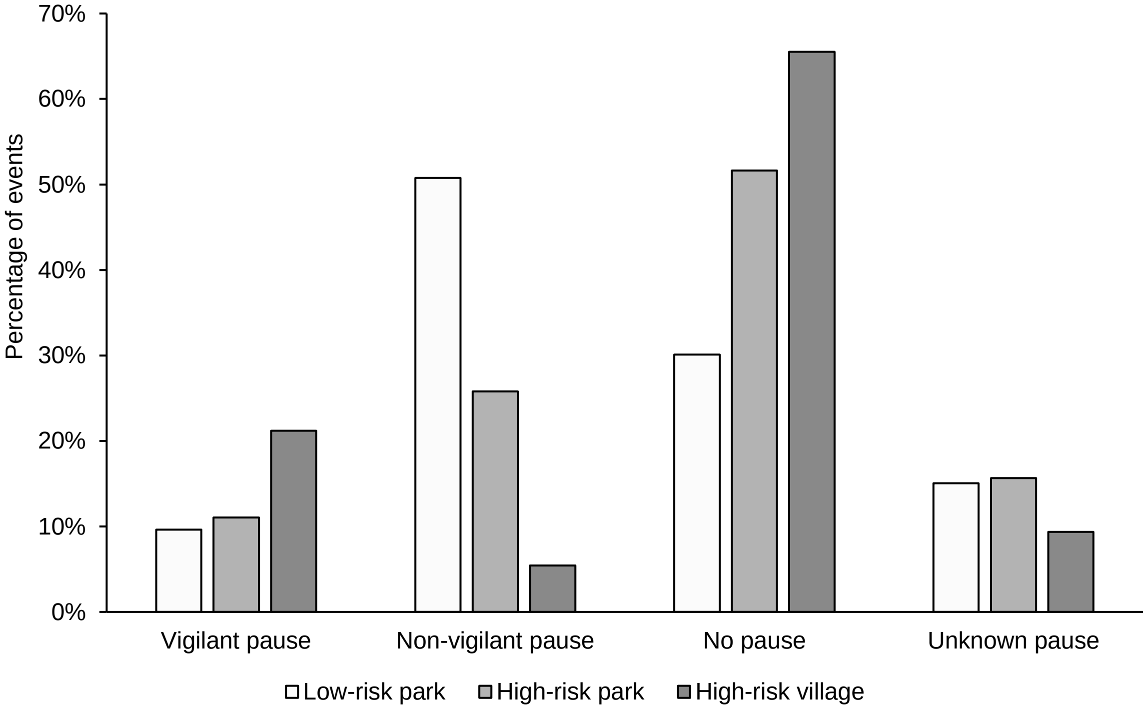


Figure 6.22 Percentage of elephant events with vigilant pauses, non-vigilant pauses, no pauses, or unknown pauses for the low-risk park (n=664 events), high-risk park (n=217 events), and high-risk village water sources (n=406 events). More than one type of pause (vigilant, non-vigilant, and/or unknown) could have been observed in a single event.

6.5 Discussion

6.5.1 Effect of risk, sex, and season on the frequency of elephant water source use (aim 6.1)

There were significantly fewer elephant events at the high-risk park and high-risk village water sources compared to the low-risk water sources, indicating that elephants used the higher-risk water sources less than the low-risk water sources in the park. I expected that elephant use of high-risk water sources would be lower in the wet season than in the dry season due to the greater availability of water at alternative and potentially lower-risk sites in the wet season (prediction 6.1.1). This prediction was partially supported. Although there was less elephant activity at both the high-risk park and high-risk village water sources during the wet season than the dry season, the interaction between risk and season was only significant for the high-risk village water sources in the top model. Elephants avoided the high-risk village water sources in the wet season, likely because there was less need for them to visit risky water sources on village land when water was more widely available in the ecosystem.

I further predicted (prediction 6.1.2) that female groups (cow-calf groups and mixed groups) would make less use of high-risk water sources than male groups (lone bulls and bull groups) because female elephants are thought to be more risk-averse than males (Chiyo et al., 2014; Sitati et al., 2003; Songhurst et al., 2016). This prediction was not supported at the high-risk park water sources, as the relative frequency of male and female events did not differ significantly between the low-risk park and high-risk park water sources. Sex differences in the use of high-risk water sources on village land were not straightforward. Overall, significantly fewer female than male events were observed at high-risk village water sources than would be expected from the proportion of female to male events at low-risk park water sources. The daily relative activity index was also lower for female groups than male groups at high-risk village water sources. However, the interaction between risk and sex was not included in the top model. This is likely because there was considerable variation between the high-risk village water sources in the relative proportion of female and male events detected, such that risk and sex did not interact in a consistent manner (see Figures A6.6-A6.8). The ‘expected’ usage also assumed that the ratio of males to females was similar in both high- and low-risk areas. While the camera traps in Tungamalenga village overwhelmingly detected males (98% of events were male versus 2% female), the Kitisi village camera trap detected more females than males (28% of events were male versus 72% female) and the Malizanga village camera traps detected male and female events in similar proportions (51% of events were male versus 49% female). Differences in the frequency of male and female use between the high-risk village water sources could be due to larger-scale differences in male and female ranges in the study area, especially as males have distinct bull areas (Poole, 1987), which could apply to Tungamalenga but not to the other villages. Factors specific to each village water source, such as availability of cover, proximity to buildings and building density (e.g., Bucholtz et al., 2021), proximity to roads, and proximity to a safe refuge might affect male and female selection of water sources, but these were not investigated here.

In other studies of elephant use of village or community land, females were observed to be less risk-tolerant than males. In the Amboseli ecosystem in Kenya, males comprised the majority of elephants sighted >10 km from a protected area boundary (Chiyo et al., 2014). In the Tarangire-Manyara ecosystem in Tanzania, male groups were more common than cow-calf or mixed groups on Manyara Ranch, an area with high poaching risk, compared to Lake Manyara National Park, where the risk of poaching was low (Kioko et al., 2013). In the Okavango panhandle, Botswana, female and male elephants differed in their use of pathways (leading to water) on community land, with some pathways closer to areas of high human activity used only by males (Songhurst et al., 2016). Females are also generally more likely than males to engage in crop foraging (Sitati et al., 2003; Smit et al., 2017, but see Hahn et al., 2022). The finding in this study that females use risky water sources on village land to a similar extent as males contrasts with these previous studies. It may be that in the context of access to a resource as critical as water, and especially in areas of limited water availability or during periods of water scarcity, both males and females use high-risk water sources rather than travel to low-risk water sources and incur time costs affecting foraging. In Ruaha, my findings suggest that both sexes used sparse and high-risk water sources to optimise between foraging and drinking during the resource-limited dry season.

6.5.2 The effect of risk, sex, and season on the timing of elephant water source use (aim 6.2)

I predicted that elephant use of high-risk water sources would be more nocturnal than their use of low-risk water sources (prediction 6.2.1). This prediction was supported for the high-risk water sources on village land, as elephants used these water sources almost exclusively at night in both seasons, and the interaction between risk and diel period was statically significant for high-risk village water sources in the top model. Seasonal differences in the times at which activity peaks occurred at high-risk village water sources were minor and the interaction between risk, diel, period and season was not included in the top model; as such, the prediction that season may influence the timing of water source use (prediction 6.2.2) was not supported for the high-risk water sources on village land. These results are similar to findings from several other sites. In the Okavango panhandle, elephants accessed water sources in areas with medium (1-100) to high (>100) building densities on community lands primarily at night but used water sources in areas with no buildings (on community land and in protected areas) to a similar extent during the day and night (Buchholtz et al., 2021). Similarly, while elephants in Gonarezhou National Park in Zimbabwe visited water sources in the park throughout the day, they visited water sources at the park boundary and in adjacent agricultural areas only at night (Zvidzai et al., 2013). In Gorongosa National Park in Mozambique, elephants visited a risky water source - the Pungue river which forms the boundary of the park - almost exclusively between sunset and sunrise (Poole & Granli, 2017).

Elephant use of high-risk water sources in the park was more nocturnal than their use of low-risk park water sources in the dry season but not in the wet season. The interaction between risk and diel period was not significant for the high-risk park water sources in the top model, indicating there was no significant difference in the relative frequency of daytime and night-time events at the low-risk park and high-risk park water sources, contrary to prediction 6.2.1. This study took place 4-5 years after the poaching surge of 2010-2015. While poaching of elephants continued to occur at a lower level (see Chapter 3), and human activity was present in the high-risk areas of the park (as evidenced by camera trap theft), it may be that elephants perceived these areas as less risky than the water sources on village land. Although the timing of elephant water use did vary between the wet and the dry season at the high-risk water sources in the park (prediction 6.2.2), it is not clear whether seasonal differences in ambient temperature or food availability drove these differences, as there was little seasonal variation in the timing of water use at the low-risk water sources. Alternatively, it may be that risk at the high-risk park water sources varied seasonally while risk at village water sources did not. For instance, in MBOMIPA Wildlife Management Area, which lies directly adjacent to the park, elephant poaching incidents were more common in the dry season than in the wet season (STEP, unpublished data for 2018-2022).

While I predicted that shifts in the timing of water access in response to risk would be greater for females than for males (prediction 6.2.3), both sexes were more nocturnal in their use of high-risk village water sources than low-risk water sources. Lone bulls, cow-calf groups, and mixed groups (but not bull groups) were also more nocturnal in their use of high-risk water sources in the park compared to low-risk water sources. The interaction between risk, diel period, and sex did not feature in any of the top models, indicating that, overall, males and females adjusted the timing of water source use in a similar way in response to risk. Similarly, in Gorongosa, both female and male groups predominantly visited a risky water source at the park boundary at dusk and during the night (Poole & Granli, 2017). Interestingly, in this study, activity curves indicated a greater risk-related shift in the timing of water source use for lone bulls than for cow-calf groups. This is because while both lone bulls and cow-calf groups used high-risk water sources nocturnally, lone bulls used the low-risk park water sources earlier in the day than cow-calf groups did, with lone bull activity at water sources peaking around noon and cow-calf activity peaking around dusk.

A possible reason for these differing lone bull and cow-calf activity peaks at low-risk water sources could be that heat stress was a greater factor in female decisions about the timing of water access than it was for males, and thus timed their movement to water sources around dusk when temperatures were cooler (e.g., Rozen-Rechels et al., 2020). Sex differences in dry season foraging requirements and strategies may also have influenced the timing of water source use by lone bulls and cow-calf groups. While males can subsist on large quantities of poor-quality food during the dry season, females need higher-quality food to maintain pregnancy and lactation as well as for their weaned offspring (Barnes, 1983; Shannon et al., 2010; Stokke, 1999). Barnes (1983) found that bulls in Ruaha National Park moved shorter daily distances during the dry season (June-October) and fed on abundant but poor-quality food items. In contrast, females travelled long distances in the mid-dry season (September-October), when food availability was lowest, but moved less in the early dry season (June-August) and at the end of the dry season (November). If females moved longer daily distances than males for foraging purposes, this could have contributed to the observed differences in their peak times of water source use. Water sources and drinking points may also serve as social arenas (Fishlock et al., 2016; Fishlock & Lee, 2013) and in Ruaha, it is common for elephants to form large, temporary aggregations around drinking points, especially in the dry season. The opportunity for social interactions with other elephants may therefore be another factor that influenced the timing of water source use, but this was not investigated here.

This thesis has shown that elephants are flexible not only in their overall activity patterns (as demonstrated in Chapter 5), but also in the timing of water access. Elephants can potentially visit water sources at any time of the day or night and although clear temporal peaks are observed in most studies, the timing of these peaks is highly variable (Table A6.1) and likely depends on habitat, environmental temperatures, the availability and distribution of water, sex-specific factors, and risk.

6.5.3 Elephant grouping patterns at water sources in relation to risk, sex, and season (aim 6.3)

I hypothesized that elephants adjust their grouping patterns when accessing risky sources. Specifically, I predicted that males would be more likely to associate with other males and with cow-calf groups (forming mixed groups) in response to risk (prediction 6.3.1) and that all-male and mixed groups would be larger at high-risk water sources than at low-risk water sources (prediction 6.3.2).

Males were significantly more likely to visit high-risk village water sources in bull groups than as lone bulls compared to low-risk water sources in the park. Bull groups were also significantly larger at high-risk water sources on village land than at low-risk water sources in the park. When accessing high-risk water sources on village land, all-male groups averaged 8.3 individuals during the dry season, and >30% of all-male groups comprised ≥10 individuals. Some very large bull groups were observed at high-risk water sources, including one group of 36 individuals. Males were, however, not more likely to associate in bull groups at high-risk park water sources than at low-risk water sources, and there was no difference in bull group sizes between high-risk park and low-risk park water sources.

The observed male grouping patterns at high-risk water sources on village land suggest that male elephants associate with other males to dilute mortality risk and perhaps to take advantage of the experience and knowledge of other males when accessing risky resources, as has been observed by others (e.g., Allen et al., 2020; Chiyo et al., 2014; Sitati et al., 2003; Srinivasaiah et al., 2019). While male associations are influenced by multiple factors including forage availability (Chiyo et al., 2014), age (Lee et al., 2011) and kin relationships (Chiyo et al., 2011), anthropogenic risk is clearly an important driver in the formation of all-male groups.

Contrary to expectations, males did not consistently associate more with cow-calf groups when accessing risky water sources. Males occurred in mixed groups to a similar extent at low-risk park and high-risk village water sources in the dry season, and mixed groups were not larger at high-risk village water sources. In the wet season, males were less likely to visit high-risk village water sources in mixed groups compared to low-risk water sources. There may simply have been fewer opportunities for mixed groups to form on village land, as female groups comprised only 23% of events at high-risk village water sources, compared to 64% at low-risk water sources. The opportunity for mixed groups to form on village land was even lower in the wet season when a single cow-calf group event and a single mixed group event were detected at high-risk village water sources and only 6% of high-risk village water source events comprised female groups.

At the high-risk park water sources in the dry season only, males were significantly more likely to associate with cow-calf groups compared to the low-risk water sources. Since fewer female groups were observed at the high-risk park water sources during the wet season, it could be that there were limited opportunities for mixed groups to form in the wet season. Mixed group sizes did not differ significantly between the low-risk and high-risk water sources in the park.

Similarly, in the Tarangire-Manyara ecosystem, mean mixed group sizes were not significantly different between an area of low poaching risk and high poaching risk (Kioko et al., 2013).

Overall, these findings suggest that males did not associate more with cow-calf groups at high-risk water sources, but that associations with other males were more likely. As such, predictions 6.3.1 and 6.3.2 were only partially supported by the data. In addition to the fact that opportunities for mixed groups to form were likely more limited at high-risk water sources than at low-risk water sources due to few female groups using the high-risk water sources, there may have been constraints or costs to forming mixed groups. Males forage less efficiently when associating with females in a mixed group than when foraging alone or with other males (Lindsay, 2011), though it is not clear if males experience a similar cost when drinking. Males join female groups for reasons other than risk, including for access to oestrous females and social partners (Lee et al., 2011). In the wet season, the largest mixed groups were observed at the low-risk water sources in the park. This is a time when males spend more time searching for and in the company of oestrous females (Barnes, 1982c, 1983), suggesting that in the wet season, male access to reproductive females was a more important driver of male associations and mixed group sizes than was risk. In the dry season, the largest mixed groups were observed at high-risk village and high-risk park water sources, suggesting that risk may have been a driver in the formation of mixed groups during this period since sexual behaviour is less common in the dry season in Ruaha (Barnes, 1982c, 1983a).

Contrary to prediction 6.3.3, cow-calf groups did not visit high-risk park and high-risk village water sources in larger groups than low-risk park water sources in either season. Larger groups may not have formed due to limited opportunities for cow-calf groups to join with other cow-calf groups as relatively few groups used high-risk village water sources. There may also have been constraints on forming larger groups, especially during the dry season, when cow-calf group sizes tend to be smaller due to resource constraints (Barnes, 1983; Moss & Lee, 2011). One study of female grouping patterns in relation to risk and water access suggests that females may adjust group size flexibly in response to risk (Kangwana, 2011). At a water source that elephants shared with Maasai in Amboseli, Kenya, cow-calf groups waited to access water in large groups when Maasai and livestock were present, likely affording them with safety in numbers, but then entered the water source in smaller groups, perhaps to reduce competition or the risk of actual contact with Maasai and their livestock (Kangwana, 2011).

Other studies of female grouping patterns in the context of risk relate to poaching, which means it is difficult to disentangle the direct mortality effects of poaching (e.g., altered age-and-sex structure including the loss of older matriarchs) from the indirect effects of risk on female grouping patterns. Indeed, a consistent female grouping response to poaching (risk) has yet to be shown. In several African sites that experienced heavy poaching and drastic elephant population declines, elephants formed large, year-round aggregations comprising multiple family groups and males. In Rwenzori National Park, Uganda, mean group size (not disaggregated by group type) increased from 7.2 individuals in 1971 to 10.8 individuals in 1976 while elephant densities declined by 74% (Eltringham & Malpas, 1980). In Kabalega Falls National Park, Uganda, mean group size increased from 16.9 individuals in 1967 to 23.7 individuals in 1976 while the population declined by 83% (Eltringham & Malpas, 1980). In Queen Elizabeth National Park, Uganda, all remaining elephants merged into one single large group following an 85% population decline due to a catastrophic poaching event (Abe, 1994). In Tarangire National Park, Tanzania, Foley et al. (2002) observed that family groups aggregated in large groups in the park's southern subpopulation, unlike other subpopulations in the park, and thought this was related to differences in poaching risk.

In contrast, in Manyara National Park, Tanzania, with constant groundwater access, Prins, Jeugd & Beekman (1994) observed no significant differences in mean elephant group size nor the distribution of group sizes prior to (1984) and following a poaching surge (1991). In a later study of the same area, Kioko et al. (2013) did not find a significant difference in mean cow-calf group sizes between areas of high and low poaching risk.

At yet other sites, smaller cow-calf group sizes have been linked to poaching, likely due to the effects of poaching on social bonds and reproductive output. In Mikumi National Park, Tanzania, cow-calf groups disrupted by poaching remained small and had relatively weak social bonds and low reproductive output 15 years after a severe poaching event (Gobush, Mutayoba & Wasser, 2008). In Ruaha National Park, mean and median cow-calf group sizes were smaller in areas that had experienced poaching relative to safer areas of the park, and cow-calf groups in poached areas had lower ratios of calves (<10 years) to adult females (≥ 10 years) (Mkuburo et al., 2020).

Female grouping is a function of too many factors to attribute group size to risk alone in most cases. Elephant females show a tendency to aggregate whenever possible, for social benefits such as calf care, for knowledge exchange, and to maintain relationships with distant kin (Moss & Lee, 2011; Mutinda, Poole & Moss, 2011). They tend to break into smaller units, often seasonally, when there is competition for food, or when individuals exhibit dominance or aggression (Moss & Lee, 2011). It may therefore be difficult to generalize about the influence of risk on female group sizes, including in part due to variation in the extent of 'social breakdown' caused by poaching (Bradshaw et al., 2005; Goldenberg & Wittemyer, 2017) at different sites. Female group sizes are also influenced by a range of other factors not explicitly investigated in this study, including kinship, personality, attributes of matriarchs, and environmental conditions (Moss & Lee, 2011).

I also explored the influence of season on elephant grouping patterns at the low-risk water sources in the park. Significantly more mixed groups were observed at low-risk water sources during the wet season than the dry season, as previously shown by Barnes (1983a). Cow-calf group sizes were significantly larger during the wet season than the dry season, again replicating work by Barnes (1983a). In both this study and in Barnes (1983a), males associated with other males year-round, but bull groups were slightly more common in the wet season. In this study, bull group sizes did not differ by season, unlike the finding of Barnes (1983a) that bull group sizes were significantly larger in the wet season. There were no significant seasonal differences in mixed group sizes in this study. Barnes (1983a) did not describe mixed group sizes in Ruaha, but in other sites, large mixed groups tend to be more common during the wet season and median elephant group sizes are larger in the wet season (Western & Lindsay, 1984).

6.5.4 Vigilance behaviour at low-risk and high-risk water sources (aim 6.4)

The prediction that elephants would be more vigilant at high-risk water sources than at low-risk water sources was generally supported by my findings (prediction 6.4.1). Non-vigilant pauses were more frequent at low-risk water sources than at high-risk water sources. Vigilant pauses were more common at high-risk village water sources than at low-risk park water sources, but not at the high-risk park water sources. Similarly, in Tarangire-Manyara, elephant vigilance behaviour (in this case, in response to a research vehicle) was more frequent in a partially protected area with higher poaching risk than in a national park with low poaching risk (Kioko et al., 2013). A caveat to my findings is that I was not able to identify whether vigilant pauses had a social monitoring or threat monitoring function, as camera trap images lacked sufficient context to make this distinction. I also did not account for other factors that have been shown to influence vigilance, such as group size and demographic factors (Allan & Hill, 2018). It was notable that elephants were more likely not to pause at all at the high-risk water sources, as elephants have been observed elsewhere to move rapidly through risky human-dominated areas (Douglas-Hamilton et al., 2005; Graham et al., 2009).

While classifying camera trap images, I observed several instances of elephants fleeing from water sources, and this appeared to be more common at high-risk water sources. In retrospect, it would have been interesting to compare the propensity of elephants to flee from water sources representing different levels of risk to elephants. Camera traps may provide an alternative to vehicle-based observation of vigilance and reactivity (e.g., Poole & Granli, 2017), especially in areas where elephants are habituated to vehicles and are therefore unlikely to associate vehicles with mortality risk, even under conditions of elevated poaching risk (Goldenberg et al., 2017).

6.5.5 Limitations and Future Directions

Elephant risk responses were very clear at the high-risk water sources on village land, but less so for the high-risk water sources in the park. This may be because this study was conducted 4-5 years after the end of the 2010-2015 poaching surge, such that elephants may have begun to perceive these areas as being less risky. Alternatively, anthropogenic risk to elephants may have varied seasonally at the high-risk water source in the park, but seasonal variation in risk was not quantified in this study.

To respect the wishes of village leaders (see 6.3.2), only one camera trap station on village land operated throughout the day and night, while at other stations, camera traps were deployed in the late afternoon and removed in the morning. This means some daytime events may have been missed at the high-risk village water sources where camera traps did not operate throughout the diel period. However, based on local knowledge and the results from the camera trap station that did operate continuously (which showed that only 2.5% of events occurred during the day, one just before dusk and one after dawn, see Appendix 6.3), it is unlikely that a meaningful number of daytime events were missed at the other high-risk village water sources.

I did not investigate potential costs associated with risk-related shifts in the timing of water access. Future work could explore whether such shifts are associated with thermoregulatory or metabolic costs or affect milk production in lactating females with possible consequences for calf growth or survival. Future research could also investigate whether risk influences the duration of elephant visits to water sources and the amount of time between subsequent visits to water.

6.6 Conclusions

This chapter has shown that anthropogenic risk influences elephant decisions about when and how to access water, including a shift to increased nocturnal use of risky water sources by both sexes and for males - but not females - a tendency to visit risky water sources in groups. While the frequency of elephant use of risky water sources was strongly influenced by season, likely because of seasonal variation in water availability, the timing of elephant use of risky water sources did not vary much by season.

By using village water sources at night, elephants were able to access a key resource in a risky human-dominated landscape. This study has shown considerable use of village water sources by elephants, especially in the dry season. These same water sources are used by village residents for domestic use as well as irrigation of farms and watering of livestock. As human populations and settlements adjacent to the park continue to grow, encounters between elephants and people at water sources may increase, and there is a risk that elephants lose access to these important dry-season water sources. A greater understanding of where, when, and how elephants access water sources on village land – to which this study contributes as a first step – may inform strategies for maintaining shared access to water sources by people and elephants, including recommendations for human safety when accessing water sources that they share with elephants.

This final data chapter has consolidated the previous chapters on how anthropogenic risk affects elephant behaviour by showing that elephants adjust the frequency and timing of resource access in response to risk and that males aggregate when using risky resources. In the next and final chapter, I integrate the findings across chapters and discuss them in a wider context highlighting the implications for elephant conservation and coexistence between people and elephants.

Appendix A6.1 Review of published studies on the timing of elephant water source use.

Table A6.1 Summary of published studies on the timing of elephant water source use. Protected area is abbreviated as PA.

Reference	Study location and period	Risk context	Type of water source	Study method	Sex(es) studied	Peak water use hours (dry season)	Peak water use hours (wet season)	Notes
Thaker et al. (2019)	Kruger National Park, South Africa 2007-2009	Low poaching risk, all water sources within PA.	Seasonal rivers/streams (considered in the wet season only). Artificial waterholes (dams, boreholes, troughs) with on average 4 km spacing.	Collar data	Adult females (n=14)	11:00-14:00	10:00-13:00	
Buchholtz et al. (2021)	Western Okavango Panhandle, Botswana 2014-2018	Botswana: non-protected area, community land with varying building density. Namibia: protected areas.	Okavango river (year-round), artificial waterholes in Namibian protected areas.	Collar data	Adult males (n=22) and adult females (n=15)	Zero buildings 12:00-18:00 1-100 buildings: 18:00-24:00 >100 buildings: 18:00-24:00	Zero buildings: No clear peak 1-100 buildings: 18:00-06:00 >100 buildings: 18:00-24:00	
Purdon & van Aarde (2017)	Kruger National Park, South Africa 2012-2014	All water sources in PA.	Five perennial rivers and point water sources such as springs, pans, pools in ephemeral rivers, boreholes, and earth-dams.	Collar data	Adult females (n=23)	Rivers: 11:00-22:00 Artificial water sources: 13:00-24:00 (combined wet and dry season data)	NA	More visits to water sources in the dry season than the wet season. Likelihood of a visit to water source increased with higher temperatures. Elephants typically returned to water sources at 12–36 hour intervals.

Reference	Study location and period	Risk context	Type of water source	Study method	Sex(es) studied	Peak water use hours (dry season)	Peak water use hours (wet season)	Notes
Tsalyuk et al. (2019)	Etosha National Park, Namibia 2008-2014	All water sources in PA.	Artificial waterholes.	Collar data	Males (n=7) and females (n=8)	Elephants preferred to be close to surface water mostly in the evening (around 19:00) and at night, and walked away from water around noon.	NA	
Ayeni (1975)	Tsavo National Park, Kenya 1973-1974	Some artificial water sources were at tourism camps.	Combination of rivers and artificial water sources (dams/reservoirs).	Direct observation at water sources (24-hour periods)	No differentiation made	17:00-21:00	NA	
Guy (1976)	Sengwa Wildlife Research Area, Zimbabwe 1973	No context was provided.	River, springs (natural water sources)	Direct observation (behavioural follows over 9 hours – diurnal only).	Males and females combined	Most time spent drinking between 16:00-17:00	Most time spent wallowing between 11:00-13:00; drinking between 10:00-11:00 and 15:00-16:00	Sometimes elephants drank more than once a day.
Weir & Davidson (1965)	Hwange National Park, Zimbabwe 1958-1960	All water sources inside PA. No context provided on poaching risk. Tourism was mentioned as a possible disturbance factor.	Artificial pans and water sources.	Direct observation at water sources (24-hour periods)	No differentiation made	18:00-22:00 (sharp increase between 16:00-18:00)	NA	
Valeix et al. (2007)	Hwange National Park, Zimbabwe 2003-2004	No context provided.	Seasonal natural water sources, artificial water holes.	Direct observation at water sources (24-hour periods)	No differentiation made	17:00-22:00 (peak at 19:00)	NA	

Reference	Study location and period	Risk context	Type of water source	Study method	Sex(es) studied	Peak water use hours (dry season)	Peak water use hours (wet season)	Notes
Loarie et al. (2009)	Khaudom Game Reserve, Namibia. Kafue National Park, Zambia. Ngamiland, Botswana. South and North Luangwa National Park, Zambia. Kasungu National Park, Malawi. Vwaza Marsh, Malawi. 2003-2006	Sites differ in the amount of anthropogenic disturbance, but this was not described in detail in the study.	Natural water sources and artificial water holes.	Collar data	Females and males (n=31)	Under drier conditions, elephants averaged about 4 km from water during the day and were significantly nearer to water sources at night (21:00–02:00).	Under wetter conditions, less strong diel pattern.	The patterns were similar when grouped by sex.
Du Preez & Grobler (1977)	Etosha National Park, Namibia 1971-1972	All water sources inside PA.	Primarily artificial water sources, some seasonal rivers and pans.	Direct observation at water sources (24-hour periods)	No differentiation made	18:00—24:00 (for wet and dry seasons combined)	NA	
Rozen-Rechels et al. (2020)	Hwange National Park, Zimbabwe 2013	All water sources were within a protected area. No context on poaching risk.	Artificial water sources and naturally occurring seasonal pans.	Collar data	Females (n=8 adult females)	18:00-20:00	NA	
Wyatt & Eltringham (1974)	Rwenzori National Park, Uganda 1970-1971	The study focused on an area within the protected area.	Wallows and river, water widely available.	Direct observation (behavioural follows)	Primarily females	Elephants were observed to drink at any time of the day or night	NA	The average number of times elephants were seen to drink during each 24-hour period in the present study was 1.3; the maximum number of times was three. On most days, elephants drank only once.

Reference	Study location and period	Risk context	Type of water source	Study method	Sex(es) studied	Peak water use hours (dry season)	Peak water use hours (wet season)	Notes
Leggett (2009)	Kunene region, northwestern Namibia 2002–2006	Civil war ended in 1990.	Ephemeral seasonal rivers. Arid, desert habitat.	Direct observation (behavioural follows) – diurnal only (7:00-19:00)	Males and females	11:00-15:00	07:00-11:00 and 15:00-19:00	Activities associated with water and resting increased to a maximum during the wet and hot dry seasons during the heat of the day (11:00–15:00). Adult females and juveniles spent longer periods engaged in water-based activities than either adult males or subadult elephants. Water-based activities were probably used to reduce heat stress.
Hayward & Hayward (2012)	Pilanesberg National Park, South Africa. Mashatu Game Reserve, Botswana. Kruger National Park, South Africa. Madikwe Game Reserve, South Africa. Tembe Elephant Park, South Africa. 2006-2007	Not described.	Artificial water sources, 4 out of 5 them lit at night.	Webcams were installed at five waterholes in different protected areas.	No differentiation was made.	Peak at 13:00-14:00, and 50% of observations between 13:00-17:00 (all sites and seasons pooled).	NA	
Rooney (2019)	Zambezi National Park, Zimbabwe 2018	Variation between waterholes in tourism use, park unfenced, hunting area and community land nearby.	Artificial waterholes	Camera traps at 6 waterholes	Did not differentiate by sex	Greater night-time (18:00-06:00) than daytime (06:00-18:00) use at 4 water sources; no difference between day/night use at 2 waterholes.	NA	There was no clear relationship between elephant and tourist presence – no evidence of spatial avoidance by elephants of water sources most visited by tourists.

Reference	Study location and period	Risk context	Type of water source	Study method	Sex(es) studied	Peak water use hours (dry season)	Peak water use hours (wet season)	Notes
Shannon et al. (2008)	Pongola Game Reserve (PGR), Pilanesberg National Park (PNG), Phinda Private Game Reserve (PPGR) 2002-2005	Small, private game reserves (except for PNG) with small elephant populations	Artificial water sources, river in PPGR.	Direct observation (behavioural follows) – diurnal only (6:00-18:00)	Males and females	Male peak drinking time was 10:00-14:00; female peak drinking times were 12:00-14:00 and 16:00-18:00	NA	Males spent more time at water points than females.
Mole et al. (2016)	Abu Camp, Okavango Delta, Botswana 2012-2013	Captive elephants taking part in tourism activities during early morning and late afternoon.	Rivers and seasonal swampland.	Direct observation (behavioural follows) – diurnal only (9:00-16:00).	Females	Probability of drinking peaked during the morning hours (09:00-12:00) and then decreased throughout the day.	NA	Temperature did not have a strong influence on drinking behaviour.
Poole & Granli (2017)	Gorongosa National Park, Mozambique 2015-2016	Pungue river along the park boundary (risky).	Natural river.	Camera traps	Male and female groups	Dusk and night-time use, almost no daytime use.	NA	Differences between male and female peaks in activity.
Zvidzai et al. (2013)	Gonarezhou National Park and adjacent agricultural areas, Zimbabwe. 2008-2011	Water sources inside a protected area, at the protected area boundary (also used by livestock), and in an agricultural area.	Natural rivers, artificial dams, and seasonal pans.	Direct observation at water sources (12-and 24-hour periods)	Male and female groups (no differentiation made)	Elephants used water sources within the national park throughout the day; but used water sources at the park boundary and in agricultural areas only between 22:00-02:00, while livestock used these water sources primarily between 13:00-16:00 (no differentiation made by season).	NA	Elephants used water sources at the park boundary in the wet and dry season.

Appendix A6.2 List of top models, table of fixed effects, and model fit diagnostic plots

Table A6.2 Null model (M0) and top models (within ΔAICc<6) for the effect of risk, diel period, season, and sex on event counts at camera trap stations at water sources.

Model	**AICc**
M0 <- glmer.nb(Count ~ 1 (1 + Diel + Sex /Station) + offset(log(Hours))	790.0
M7 <- glmer.nb(Count ~ Risk*Diel + Risk*Season + (1 + Diel + Sex /Station) + offset(log(Hours))	775.7
M6 <- glmer.nb(Count ~ Risk*Diel + Risk*Season + Sex + (1 + Diel + Sex /Station) + offset(log(Hours))	777.9
M5 <- glmer.nb(Count ~ Risk*Diel + Risk*Season + Risk*Sex + (1 + Diel + Sex /Station) + offset(log(Hours))	778.2
M9 <- glmer.nb(Count ~ Risk* Season + Diel + (1 + Diel + Sex /Station) + offset(log(Hours))	778.2
M4 <- glmer.nb(Count ~ Risk*Diel*Season + (1 + Diel + Sex /Station) + offset(log(Hours))	778.4
M10 glmer.nb(Count ~ Risk* Season + Diel + Sex + (1 + Diel + Sex /Station) + offset(log(Hours))	780.4
M8 <- glmer.nb(Count ~ Risk*Diel* + Season + (1 + Diel + Sex /Station) + offset(log(Hours))	780.7
M3 <- glmer.nb(Count ~ Risk*Diel*Season + Sex + (1 + Diel + Sex /Station) + offset(log(Hours))	780.8
M2 <- glmer.nb(Count ~ Risk*Diel*Season + Risk*Sex + (1 + Diel + Sex /Station) + offset(log(Hours))	781.2

Table A6.3 Estimated regression parameters for the fixed effects with their standard errors, z-values and p-values for the top model. The Wald chi-square test was used to test the statistical significance of the fixed effects. Significance codes: 0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '

	Estimate	**Std. error**	***Z*-value**	***P*-value**
Intercept	-5.62	0.30	-18.68	<0.0001 ***
RiskHighpark	-1.26	0.46	-2.76	0.006 **
RiskHighvillage	-2.20	0.85	-2.59	0.009 **
DielNight	0.25	0.47	0.53	0.597
SeasonWet	0.19	0.54	0.34	0.733
RiskHighpark:DielNight	0.93	0.68	1.37	0.169
RiskHighvillage:DielNight	2.58	1.00	2.58	0.009 **
RiskHighpark:SeasonWet	-1.24	0.80	-1.55	0.121
RiskHighvillage:SeasonWet	-3.29	1.04	-3.18	0.001 **

Figure A6.1 Elephant event incident rate ratios (dots) and 95% confidence intervals (bars) for model parameters for four of the best-ranked models after the top-ranked model (see Table A6.2). To express model coefficients as incident rate ratios, I raised the natural log to the power of each coefficient. Red indicates that a term has a negative effect on incident rates, while blue indicates that a term has a positive effect on incident rates. Significance codes: 0.0001 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 '.

I used the *DHARMa* package to assess model fit (Figure A6.2 and A6.3) and determine if there were issues with overdispersion/underdispersion and heteroscedasticity. The *DHARMa* package uses a simulation-based approach to create scaled residuals for generalized linear mixed models (GLMMs), as standard residual plots (i.e., those used for linear models) cannot be reliably used to diagnose model fit for GLMMs (Hartig, 2022). These scaled residuals can be interpreted in a similar way to residuals from a linear regression. Scaled residuals vary between 0-1, where a scaled residual value of 0.5 means that half of the simulated data are higher than the observed value, and half of them lower. For a correctly specified model, the scaled residuals should be uniformly distributed, and there should be uniformity in the vertical (y-axis) direction if scaled residuals are plotted against any predictor (Hartig, 2022).

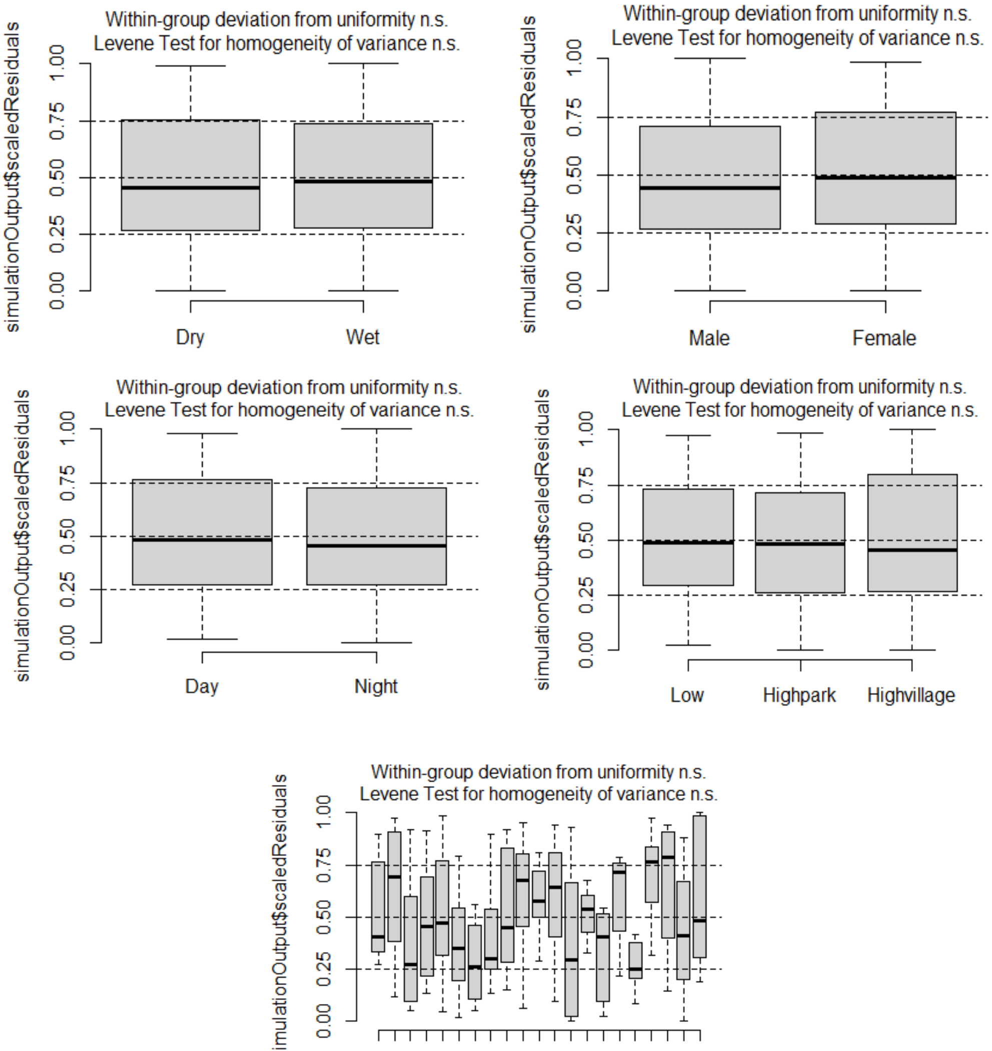


Figure A6.2. Boxplots of deviance residuals versus predictors (season, sex, diel period, risk, and camera trap station) for the top model. For a correctly specified model, boxes should range homogenously from 0.25-0.75. Tests for uniformity per box and tests for homogeneity of variances between boxes indicated that there were no deviations from this expectation. These boxplots indicate there was no systematic relationship between the residuals and the predictors for the top model.

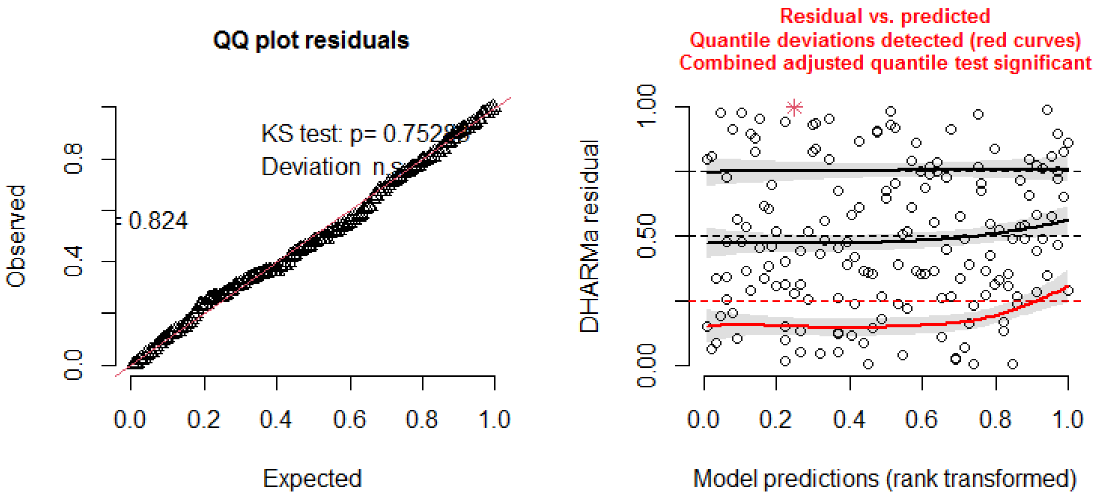


Figure A6.3 Quantile-quantile plot of model residuals (left) and plot of residuals versus predicted values (right) for the top model. A correctly specified model would be expected to show an approximately straight diagonal line in the quantile-quantile plot and to have a non-significant Kolmogorov-Smirnov (KS) test indicating a uniform distribution (left) and show visual homogeneity of residuals in the vertical and horizontal directions, i.e., that there is no pattern between residuals and model predictions (right). These plots indicate that the top model was neither overdispersed nor underdispersed and that, overall, the distributions of residuals did not deviate from uniformity. No zero-inflation was detected. Although the plot of residuals versus predicted values indicates there was some deviation from uniformity in the y-direction (for the 0.25 quantile), there was no systematic relationship between the residuals and the predictors (Figure A6.2).

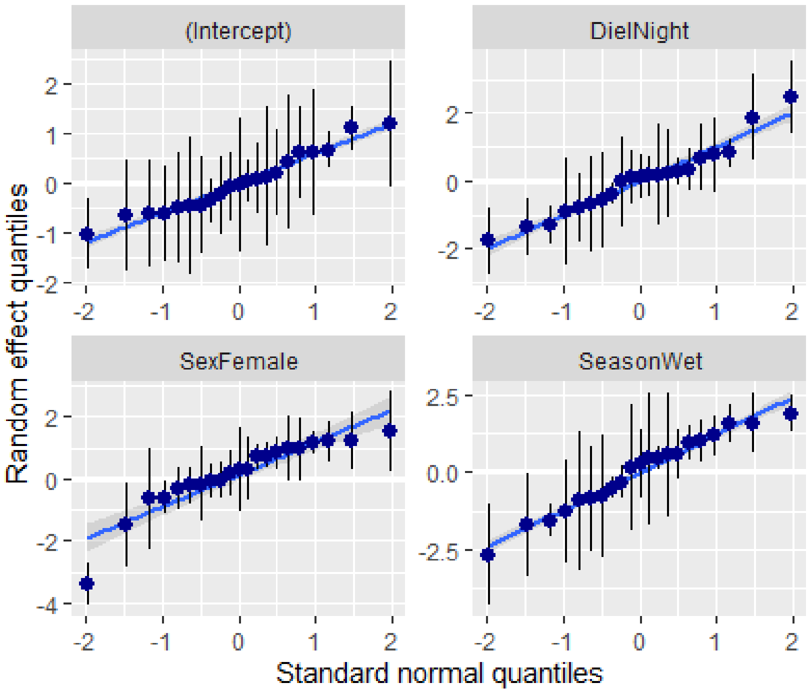


Figure A6.4 Quantile-quantile plot for random effects for the top model generated using the *sjPlot* package. A correctly specified model would be expected to show a straight diagonal line in the quantile-quantile plot.

Appendix A6.3 Comparison of elephant activity profiles between Kitisi (high-risk village water source) and low-risk park water sources

The Kitisi station was the only station on village land that operated throughout the day as well as the night. Of the 80 events detected by the Kitisi station, 92.5% occurred during the night, 5.0% at dusk, and 2.5% during the day (2 events). Based on these results and the knowledge and experience of the local camera trap monitors, it is unlikely that the camera traps in Tungamalenga and Malizanga villages missed a meaningful number of daytime events. Activity profile comparisons between the low-risk park water sources and Kitisi water sources show that, for most pairwise comparisons, there was little overlap between the low-risk park and Kitisi water source activity profiles. Only 15 events were detected at the Kitisi water source in the wet season (including one daytime event), which may explain why the low-risk park and Kitisi activity curves were not significantly different during the wet season.

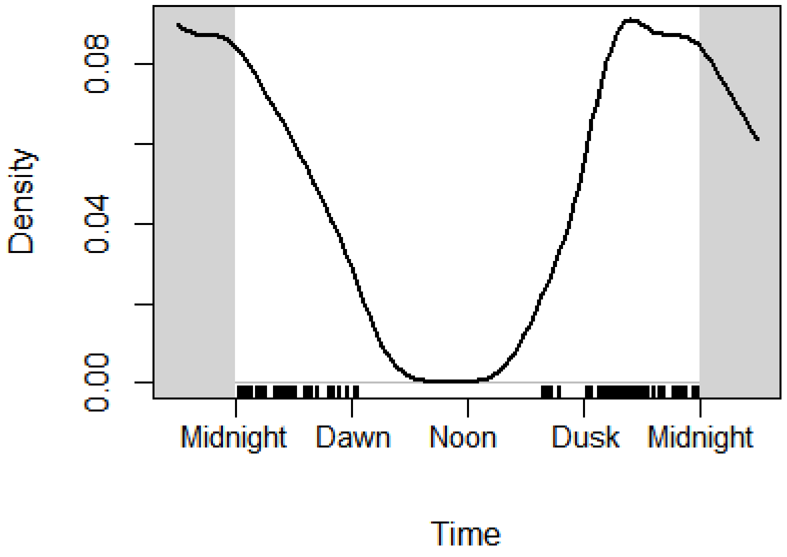


Figure A6.5 Distribution (black curve) of all elephant events (n=80 events) at the Kitisi high-risk village camera trap (dry and wet season data combined). The black vertical lines at the bottom of the figure represent individual events. The grey bar on the left side of the figure repeats part of the activity curve between dusk and midnight, and the grey bar on the right side of the figure repeats part of the activity curve between midnight and dawn.

Table A6.4 Coefficient of overlapping and associated 95% confidence intervals for activity curve comparisons between the low-risk park water source stations and the Kitisi camera trap station (on village land) for all elephant events in the dry and the wet season and by group type (dry season only). The p-value indicates whether the activity curves were significantly different.

Group	Season	Comparison	Coefficient of overlapping	95% CI	p-value
All	Dry	Low-risk park vs. Kitisi	0.435	0.363-0.507	**<0.0001**
All	Wet	Low-risk park vs. Kitisi	0.738	0.578-0.870	0.173
Cow-calf	Dry	Low-risk park vs. Kitisi	0.423	0.295-0.497	**<0.0001**
Lone bull	Dry	Low-risk park vs. Kitisi	0.214	0.062-0.380	**0.001**
Bull group	Dry	Low-risk park vs. Kitisi	0.334	0.068-0.661	Unable to run due to small sample sizes
Mixed group	Dry	Low-risk park vs. Kitisi	0.460	0.295-0.627	0.058

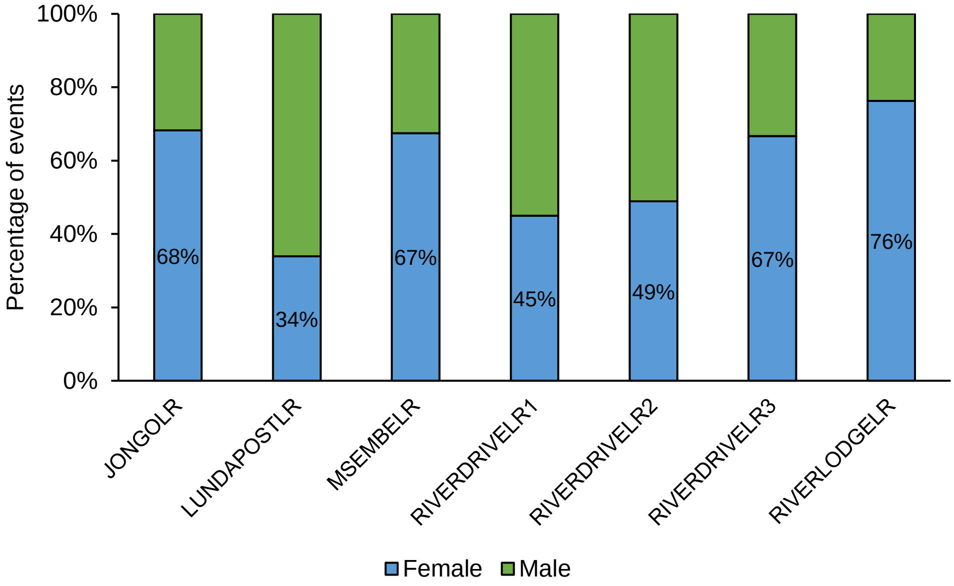


Figure A6.6 The percentage of female (blue) and male (green) events at individual camera trap stations at the low-risk park water sources (n=577 events). Data labels show the percentage of female events.

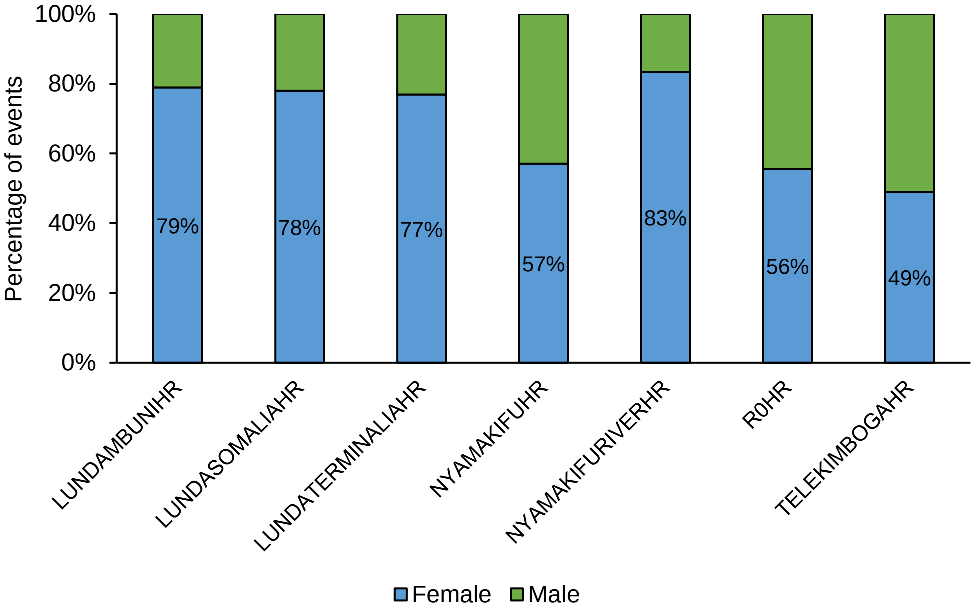


Figure A6.7 The percentage of female (blue) and male (green) events at individual camera trap stations at the high-risk park water sources (n=182 events). Data labels show the percentage of female events.

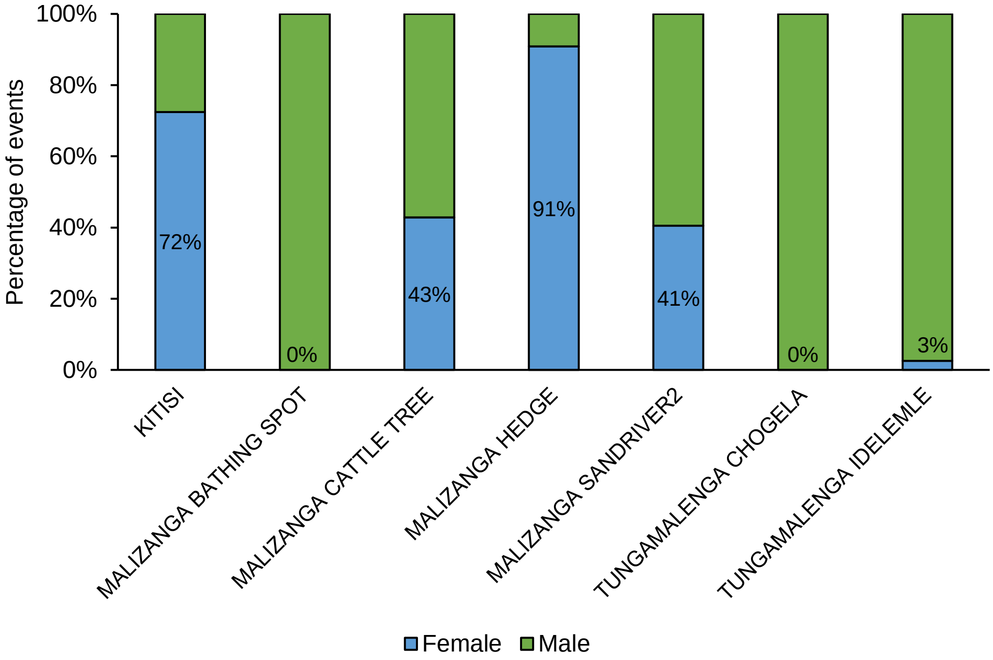


Figure A6.8 The percentage of female (blue) and male (green) events at individual camera trap stations at the high-risk park water sources (n=373 events). Data labels show the percentage of female events.

Chapter 7

General Discussion

***Photo 10**: Tuskless matriarch in Ruaha National Park, wet season.*

Chapter 7. General Discussion

The ecology of fear concept suggests that animals mitigate their risk of predation through behavioural responses when predation is a major source of mortality and is structured in space and time (Brown et al., 1999; Gaynor et al., 2019). Animals are predicted to behaviourally reduce their exposure to predation risk in space, in time, and through changes in behaviour such as aggregation. This thesis has explored the extent to which risk associated with humans, the most significant predator of elephants, shapes how elephants use their environment in space and time and influences elephant groupings. I used the Ruaha-Rungwa ecosystem in Tanzania, with a history of multiple waves of poaching and which is also undergoing rapid anthropogenic change, as a case study to investigate whether and how elephants adjust their space use, activity, resource access, and grouping patterns in response to human-mediated risk, and if and how risk responses vary by sex. The spatial distribution of human activities and elephant poaching in the Ruaha-Rungwa ecosystem were described in Chapter 3, setting the scene for comparisons of elephant behaviour between areas of low- and high-risk in the subsequent chapters.

7.1 Risk and elephant space use

Human-mediated risk and human footprint influenced elephant space use in Ruaha-Rungwa and structured how elephants used features within their environment. Elephant occurrence in the wider Ruaha-Rungwa ecosystem was primarily limited by agricultural areas and human population density, which are likely associated with unsuitable habitat as well as elevated mortality risk for elephants (Chapter 4). As observed elsewhere, I found that elephants in Ruaha-Rungwa used areas outside protected areas, but there appears to be a threshold of habitat conversion and human population density at which elephant use greatly declines (Graham et al., 2010; Hoare & du Toit, 1999; Sitati et al., 2003; Wall et al., 2021). I found that in Ruaha-Rungwa, as in many parts of their range, elephant space use was limited by an expanding human footprint (Beirne et al., 2021; Wall et al., 2021).

Within Ruaha-Rungwa's protected areas, elephant space use was investigated at a coarse spatial scale, representing broad, longer-term use, and a fine spatial scale, representing shorter-term, local-scale use. Risk influenced elephant space use within protected areas at the fine spatial scale but not at the coarse scale (Chapter 4). Fine-scale space use was significantly negatively associated with the probability of carcass occurrence (a proxy for poaching risk), positively associated with ranger posts, and weakly negatively associated with illegal human use. Importantly, my findings indicate that human-induced mortality risk can impact elephant space use within protected areas, where the risks of competition with humans and livestock are largely excluded. This thesis provides further evidence of spatial avoidance of poaching risk in elephants, as has previously been demonstrated through elephant range shifts (Goldenberg et al., 2018) and compression in response to poaching (Abe, 1994; Western & Mose, 2023). In Ruaha-Rungwa, space use at both spatial scales was influenced more strongly by environmental variables (water availability, tree cover) than risk, however, corresponding to findings from Samburu-Laikipia (Kenya) that poaching and other human-associated risks are less important drivers of elephant space use than water and food at the home range scale (Bastille-Rousseau & Wittemyer, 2020). In the mixed-use landscape of Samburu-Laikipia, elephant avoidance of poaching risk varied seasonally and individual elephants different in the extent to which they avoided poaching risk and other human-associated risks at the home range scale (Bastille-Rousseau & Wittemyer, 2019). Whether such seasonal and individual variability in spatial risk avoidance is present in Ruaha-Rungwa or at other sites that experienced heavy poaching would be an interesting topic for future research.

In Ruaha-Rungwa, risk also structured how elephants used features within their environment at a local scale. In areas of higher poaching risk, fine-scale space use was associated with areas of lower tree cover and less strongly associated with water availability, though the effect was weak (Chapter 4). Within protected areas, elephants used unpaved roads in areas of low risk, likely for ease of movement (Granados et al., 2012), but avoided roads in areas of higher risk (Chapter 5). While previous work has shown that elephants respond to roads as risky features (Gaynor et al., 2018b; Vidya & Thuppil, 2010; Wadey et al., 2018), my findings indicate that whether elephants perceive roads as risky depends on the broader risk context. Furthermore, elephants used defined pathways when accessing risky water sources on village land (Chapter 6), as observed elsewhere in the context of water use and crop foraging in risky landscapes (Allen et al., 2020; Songhurst et al., 2016; Von Gerhardt et al., 2014). Elephants may use pathways selectively in response to risk, as in the Okavango delta (Botswana), elephants preferred pathways to water located further from human settlements and in areas with less cultivated land (Songhurst et al., 2016). In this study, elephants used some village water sources more frequently than others. The extent to which risk structures selective use of certain pathways and water sources on village land in Ruaha-Rungwa merits further investigation.

The predation risk hypothesis predicts that females are more risk-averse than males (Corti & Shackleton, 2002; Ruckstuhl & Neuhaus, 2000). While sex differences in space use in relation to risk were not explicitly investigated in this thesis, both sexes used risky areas and risky resources. Camera traps detected a similar proportion of male and female groups in the low-and high-risk sites of Ruaha-Rungwa (Chapter 5) and both males and females used risky water sources (Chapter 6). Use of risky water sources was mediated more strongly by seasonal variation in water availability for females than for males, however (Chapter 6), suggesting that sex differences in risk tolerance may vary with resource abundance. In addition, the ability of female groups to avoid risk in space during periods of resource limitation may be influenced by their position within the female dominance hierarchy. While the role of social dominance was not investigated in this study, it has been shown elsewhere to impact access to water (Foley, 2002) and use of risky areas by female groups during the dry season, as in Samburu-Laikipia, low-ranking family groups spent more time outside protected areas than high-ranking groups (Wittemyer et al., 2007).

It should be noted that elephants have a range of behavioural strategies for mitigating risk in space other than simple spatial avoidance (Table 7.1). Elephants may mitigate risk by adjusting their speed (Douglas-Hamilton et al., 2005; Graham et al., 2009; Jachowski, Slotow & Millspaugh, 2013) and directionality of movement (Ihwagi et al., 2019; Vogel et al., 2020), as well as their intensity of use (Bastille-Rousseau & Wittemyer, 2021) and selection of areas with specific functions within the home range, as has been shown for rest sites outside protected areas (Wittemyer et al., 2017) and staging sites used prior to night-time crop use (Graham et al., 2010; Hahn et al., 2023). In addition to mitigating risk in space, elephants manage risk in time and through aggregation, as discussed in the subsequent sections.

Table 7.1 The influence of anthropogenic risk and human footprint on several space use and movement attributes of elephants. The human footprint index (HFI) is an index of the aggregate influence of human population density, built-up areas, night-time lights, land use, coastlines, roads, railroads, and navigable rivers (Venter et al., 2016). Results from this study are shown in bold.

Space use or movement attribute	**Influence of anthropogenic risk and human footprint**
Space use	Fine-scale space use was negatively associated with poaching risk, illegal human use, and increasing distance to ranger post (**this study**). Elephant space use within a human-inhabited landscape was negatively associated with human use (Angola; Petracca et al., 2019). Elephant occupancy was negatively associated with (bushmeat) hunting intensity (forest elephants, Republic of Congo; Clark et al., 2009). Probability of elephant use was lower in a wildlife management area, where elephants could be legally killed if they posed a threat to human life or property, than in a game reserve where elephants were fully protected (northern Botswana; Rich et al., 2016).
Range shifts/compression	In Samburu-Laikipia (Kenya), poaching induced a range shift among nine family groups monitored prior to and during an increase in poaching. These groups reduced their use of an area that experienced heavy poaching regardless of whether they had directly experienced the loss of a family member to poaching (Goldenberg et al., 2018). In Queen Elizabeth National Park (Uganda) survivors of a catastrophic poaching event (1979) coalesced into one aggregation concentrated in the safest area of the park and avoided areas where the heaviest poaching had occurred (Abe, 1994). In Amboseli (Kenya), poaching and hunting in the 1970s (and the exclusion of livestock when the park was created) resulted in compression of the elephant population into Amboseli National Park, resulting in a 90% range contraction relative to the 1960s (Western & Mose, 2023). Seasonal movements were also disrupted: elephants used the Amboseli basin year-round where previously they had used the area seasonally.

Use intensity	In Samburu-Laikipia, high-use areas within different elephants' home range (relative to areas of medium or low use intensity) were associated most strongly with higher and more predictable productivity, proximity to permanent water, and high-use by conspecifics (Bastille-Rousseau & Wittemyer, 2021). For females, areas of higher use intensity were associated with lower boma densities and were more likely to occur on elephant-tolerant private ranches or community conservancies; there was no effect of boma density or land use on use intensity for males (Bastille-Rousseau & Wittemyer, 2021). Seasonal use of water sources was influenced by human activities, such that risky water sources on village land were used less in the wet season than in the dry season (**this study**). Elephants avoided areas in close proximity to Maasai homesteads; relative use intensity increased at 0.5 to 2 km from homesteads (Amboseli, Kenya; Kangwana, 2011).
Resource selection	In a mixed-use landscape in Samburu-Laikipia, poaching risk and human footprint were less important drivers of population-level resource selection than were productivity and water (Bastille-Rousseau et al., 2020). Selection was significantly, albeit weakly, negatively associated with poaching risk in the dry season, but not in the wet season. In both seasons, elephants selected areas further from villages and with lower densities of human features. There was substantial individual variability in the extent to which elephants responded to poaching risk and human footprint at the home range scale, particularly in the degree of avoidance of poaching risk and human settlements (Bastille-Rousseau & Wittemyer, 2019; Cook, Parrini & Henley, 2015). During an increase in poaching and in the context of increasing populations, there was a shift to stronger avoidance of human settlements and poaching risk (Bastille-Rousseau & Wittemyer, 2019). Elephants selected for areas further from human settlements, which were strongly associated with higher human-induced mortality risk (Botswana; Roever et al., 2013). In Amboseli, elephants outside of protected areas were less selective of highly productive locations during the dry season (when

	the risk of mortality was highest) than during the wet season, suggesting that risk mediated the strength of selection for productive areas (Chiyo et al., 2014).
Home range size	Annual and 16-day home range size decreased with increasing human footprint index (assessed for African savanna and African forest elephants across 19 sites in sub-Saharan Africa, Wall et al., 2021). Monthly home range size decreased with increasing human footprint index (HFI), no effect of HFI on annual home range size (forest elephants in Gabon; Beirne et al., 2021).
Home range fidelity	Decrease in home range fidelity at the annual temporal scale but increase in fidelity at the monthly temporal scale with increasing human footprint index (forest elephants in Gabon; Beirne et al., 2021).
Displacement distance (Elephants may increase their displacement distance by increasing their speed, reducing their tortuosity, and/or reducing rest time.)	Daily (24-hour) displacement distance of female elephants increased with increasing proximity to bomas (Samburu-Laikipia; Duporge et al., 2022). Monthly movement distance decreased with increasing human footprint index (HFI), no effect of HFI on annual movement distance (forest elephants in Gabon; Beirne et al., 2021).
Movement speed	Faster movement speeds in riskier areas in a human-dominated landscape (e.g., elephant-intolerant ranches, Laikipia, Kenya; Graham et al., 2009) or when moving through corridors in human-dominated areas/outside protected areas (Douglas-Hamilton et al., 2005; Jachowski et al. 2013; Vogel et al., 2020). Faster movement speeds in proximity to villages (Great Limpopo Transfrontier Park, Zimbabwe and Mozambique; Cook et al., 2015). Movement speed did not increase in response to temporal or spatial variation in poaching risk (Samburu-Laikipia; Ihwagi et al., 2019). Fast movement corridors (as opposed to slow movement corridors) were associated with higher boma densities and proximity to villages for females, but not for males. However, forage and water were more important: corridors associated with fast movement were primarily

	associated with lower productivity and further distances from permanent water relative to corridors associated with slow movement speeds (Samburu-Laikipia; Bastille-Rousseau & Wittemyer, 2021).
Residency time	Shorter residency times in riskier areas in a human-dominated landscape (e.g., elephant intolerant and conflict-risk prone smallholder farmland, Laikipia; Graham et al., 2009).
Tortuosity	Reduced tortuosity (more directional movement) in response to temporal and spatial variation in poaching risk as well as in proximity to towns (for both males and females), though not in proximity to bomas (Samburu-Laikipia; Ihwagi et al., 2019). More directional movement when moving in corridors (to and from water) through human-dominated landscapes (Okavango; Vogel et al., 2020).
Exploratory vs. encamped states	Exploratory movement in corridors (to and from water) through human-dominated landscapes (Okavango; Vogel et al., 2020). A lower proportion of time spent in an exploratory state (vs. encamped state) in response to increasing HFI both at the annual and monthly temporal scale (forest elephants in Gabon; Beirne et al., 2021).
Resting sites	Rest sites outside of protected areas were further from rivers - likely to reduce encounters with people and livestock - and elephants showed greater repeat use of rest sites out of protected areas; this behaviour was more frequent in the dry season than in the wet season (Samburu-Laikipia, Wittemyer et al., 2017).
Staging sites	Staging sites - areas of low mobility that elephants use prior to incursions into cropland - were associated with greater vegetative cover and further from human settlements (Serengeti-Mara ecosystem, Tanzania and Kenya, Hahn et al., 2023).

7.2 Risk and the timing of elephant activity and resource access

This thesis has demonstrated that the risks associated with humans are an important driver of elephant diel activity and resource access in Ruaha-Rungwa. Risk induced a shift from cathemeral diel activity to predominantly nocturnal activity (Chapter 5) and increased nocturnal use of water sources (Chapter 6). Poaching risk has previously been shown to influence the diel pattern of movement in elephants (Ihwagi et al., 2018; Table 7.2). Here, using insights on behaviour from camera trap images of elephants, I show that risk affects the timing of feeding and water use in addition to movement (Chapter 5).

Risk also structured the timing of periods of inactivity associated with rest or sleep. In Ruaha-Rungwa, the trough in elephant activity occurred between midnight and sunrise in the low risk-site - corresponding to times of sleep observed for elephants in other well-protected areas (Gravett et al., 2017; Wyatt & Eltringham 1974) - and between sunrise and noon in the high-risk sites. A similar risk-induced shift to a more diurnal resting pattern was observed for elephants outside protected areas (Wittemyer et al., 2017; Table 7.2).

Risk also reduced total active time such that elephant activity peaks were narrower in the higher-risk areas of Ruaha-Rungwa (Chapter 5). Poaching risk similarly caused a reduction in total movement time for elephants in Samburu-Laikipia, Kenya (Ihwagi, 2019). A reduction in overall activity, with more time spent resting and less time foraging or in other fitness-enhancing behaviours, was also observed in sika deer and wild boar in response to hunting by humans (van Doormaal et al., 2015) and in skunks and opossums in response to playbacks of human vocalisations (Suraci et al., 2019b). The possible consequences of this reduction in total active time are discussed in Section 7.4.

Risk further structured seasonal variation in elephant use of water sources. Elephants used high-risk water sources on village land almost exclusively in the dry season and largely avoided them in the wet season, suggesting a trade-off between risk and resource availability (Chapter 6; e.g., Davies et al., 2021; Riginos, 2015 for ungulates). Elephants may also have responded to seasonal variation in risk, as they were more nocturnal in their use of high-risk water sources inside protected areas in the dry season - when poaching risk may be higher since poachers know that elephants will concentrate at water (Rashidi et al., 2016) - but not in the wet season (Chapter 6). Sensitivity to temporal variation in risk in the context of resource access is expected as shown for elephants in the context of crop foraging, since elephants are less likely to crop-forage on moonlit nights when farmers increase their guarding effort (Gunn et al., 2014). Seasonal variation in nocturnality near bomas (seasonal or temporary livestock enclosures used by pastoralists) further suggests that elephants may perceive variation in mortality risk or the risk of competition with pastoralists and their livestock (Duporge et al., 2022; Table 7.2).

Elephants of both sexes adjusted the timing of activity and resource access in response to risk in Ruaha-Rungwa. Cow-calf groups increased nocturnal activity in response to risk to a greater extent than lone males, but both females and males demonstrated a marked shift to nocturnal activity in the higher-risk areas of the ecosystem (Chapter 5). Similarly, in Samburu-Laikipia, elephants of both sexes became more nocturnal when poaching levels were high, although this was more pronounced for females than males (Ihwagi et al., 2018). In Ruaha-Rungwa, both sexes accessed risky water sources on village land at night (Chapter 6). Interestingly, lone males showed a greater shift in the timing of water access as a function of risk than cow-calf groups. This was the result of differences in the timing of use of low-risk water sources, which peaked at midday for lone males and at dusk for cow-calf groups, rather than differing responses to high-risk water sources. Similar to Shannon et al. (2008), I find that male and female diel activity curves were broadly similar (Chapter 5), except in the context of water use, where sex differences were obvious although only at low-risk water sources (Chapter 6). In sum, males and females mitigated their exposure to risk in time in broadly similar ways. Within this generalised response, differences in the magnitude of the response may be influenced by sex differences in foraging strategies and thermoregulatory requirements in addition to differences in their sensitivity to risk.

This thesis has demonstrated that elephants adjust their activity to risk in multiple ways. While it was known that elephants use risky human-dominated areas and croplands (Adams et al., 2022; Graham et al., 2009), the boundaries of protected areas (Gaynor et al., 2018b), areas near bomas (Duporge et al., 2022) and risky features such as roads (Gaynor et al., 2018b; Wadey et al., 2018) predominantly at night, I have shown that the timing of elephant activity, rest, and total activity time over the 24-hour diel period are reactive to risk, and provide further evidence that elephants avoid humans in time when using risky, shared resources (as also shown by Buchholtz et al., 2021; Wittemyer et al., 2007; Zvidzai, et al., 2013) suggesting that elephants trade off risk and resource availability. Previous work has often assessed elephant behaviour in landscapes that elephants share with humans where humans present both a mortality risk and a competition risk (e.g., exclusion from forage or water by people and livestock). By examining elephant activity within protected areas where livestock and associated human activities other than illegal poaching are largely excluded, I show that mortality risk alone, and crucially in the absence of competition with livestock, shapes elephant diel activity and resource access.

This thesis further points to the remarkable flexibility in elephant diel activity patterns. Important factors in this flexibility may be their baseline cathemerality as well as their low total sleep requirements (an estimated 2 hours per day, Gravett et al., 2017), which are likely a function of large body size and low trophic position (Owen-Smith, 1988; Ramesh et al., 2015; van Schaik & Griffiths, 1996; but see Clauss et al., 2021). A polyphasic sleeping pattern associated with cathemerality may enable elephants to adjust the timing and duration of rest and sleep in response to risk (Chapter 5; Wittemyer et al., 2017). Elephants have also been observed to forego sleep for periods exceeding 45 hours (Gravett et al., 2017); this ability may be linked to a further risk mitigation strategy of sustained movement away from direct disturbances, as has been observed in response to hunting incidents (Burke et al., 2008; Nobrega, 2015) or when dispersing through risky areas (Douglas-Hamilton et al., 2005).

It is clear that elephants proactively manage their exposure to human-mediated risks by reducing their temporal overlap with humans. This has been shown in several populations and in multiple contexts (Table 7.2), reiterating the importance of understanding elephant activity in the context of risk alongside thermoregulatory requirements, water availability, overall and seasonal variation in forage quality and abundance, social factors, and sex/age/reproductive status (Du Plessis et al., 2021; Poole & Granli, 2009). Available evidence suggests there may be limited individual variability in these temporal responses to risk among elephants, but this would be an interesting topic for further research (Duporge et al., 2022; Ihwagi, 2019). Temporal responses to humans are also not unique to elephants. A shift to increased nocturnality in response to human activity (both lethal and non-lethal) has been shown for diverse mammalian taxa (Gaynor et al., 2018a), suggesting that such activity shifts may be a generalised mammalian response to humans.

Table 7.2 The influence of anthropogenic risk on several attributes of activity in elephants. The human footprint index (HFI) is an index of the aggregate influence of human population density, built-up areas, night-time lights, land use, coastlines, roads, railroads, and navigable rivers (Venter et al., 2016). Results from this study are shown in bold.

Activity attribute	**Influence of anthropogenic risk and human footprint**
Diel activity	Increased nocturnal activity and reduced daytime activity in response to spatial variation in human-mediated risk **(this study**). Increased nocturnal activity/movement and reduced daytime activity/movement (change in the night:day speed ratio) in response to temporal and spatial variation in poaching risk: elephants became more nocturnal following a surge in poaching, and were more nocturnal in areas of higher poaching risk than low-risk areas (Samburu-Laikipia; Ihwagi et al., 2018). Increased nocturnal movement and activity in areas of higher livestock densities, though weaker effect than poaching (Samburu-Laikipia; Ihwagi, 2019). Exclusively nocturnal use of corridors leading to water in agricultural landscapes, while corridors in urban landscapes were used day and night, although predominantly at night (Okavango delta, Botswana; Adams et al., 2022). Nocturnal use of areas used by livestock during the day (Sikumi Forest, Zimbabwe; Valls-Fox et al., 2018b). Nocturnal use of riskier areas in human-dominated landscapes (e.g., smallholder farms, Laikipa; Graham et al., 2009; **this study**). Greater nocturnal activity and movement (change in night:day speed ratio) in proximity to bomas. This was more pronounced in the dry season than in the wet season. There was little individual variability in the response, which was assessed for female elephants only (Samburu-Laikipia; Duporge et al., 2022). No effect of human footprint index on diurnality (daytime movement versus night-time movement) at annual or monthly temporal scale (forest elephants in Gabon; Beirne et al., 2021).
Total time active	Reduction in total moving/active time in areas of higher poaching risk (Samburu-Laikipia; Ihwagi, 2019).

	More compressed activity peaks and a reduction in active time in areas of higher human risk **(this study**).
Timing of rest	Elephant activity throughs occurred between midnight and sunrise in the low-risk site and between sunrise and noon in the high-risk sites of Ruaha-Rungwa **(this study).** Elephants rested more frequently and for longer durations during the day and less during the night outside protected areas versus within protected areas (Samburu-Laikipia; Wittemyer et al., 2017).
Timing of resource access	Nocturnal access of risky water sources on village land (**this study**), in areas with higher human footprint (building density, Okavango delta; Buchholtz et al., 2021), and agricultural areas (Zimbabwe; Zvidzai et al., 2013). Crop use in risky agricultural landscapes is predominantly nocturnal across a range of African sites (Graham et al., 2009; Gunn et al., 2014; Smit et al., 2019; Wilkie & Douglas-Hamilton, 2018). Elephants used a water source shared with Maasai at times when they were less likely to meet Maasai and livestock (Amboseli; Kangwana, 2011).

7.3 Risk and elephant grouping patterns

This thesis has shown that anthropogenic risk was an important and consistent driver of all-male groupings in Ruaha-Rungwa but the influence of risk on the size of female groups was less clear.

Males associated more with other males in the higher-risk areas of Ruaha-Rungwa (Chapter 5). Risk also structured male groupings in the context of water access, as males were more likely to visit high-risk water sources on village land in the company of other males, and in significantly larger all-male groups than at low-risk water sources (Chapter 6). Similarly, in Makgadikgadi Pans National Park (Botswana), males accessed a river at the park boundary more often in all-male groups than alone, and this was most evident for adolescent males (Allen et al., 2020). In both sites, males walked in single file and in close proximity along defined pathways when accessing a risky water source (personal observations; Allen et al., 2020). The size of all-male groups has been shown to increase with distance from a protected area (Chiyo et al., 2014), and males often form groups when engaging in risky crop foraging (Sitati et al., 2003; Smit et al., 2019). In Ruaha-Rungwa, >30% of all-male groups at risky water sources on village land comprised 10 or more individuals and some groups exceeded 30 individuals (Chapter 6). These are larger all-male groups than have been reported elsewhere in the context of risk (Allen et al., 2020; Chiyo et al., 2014), sexual activity or food abundance (Lee et al., 2011), demonstrating that risk as well as opportunities can be a driver in the formation of very large all-male groups.

This study provides further evidence that risk is an important driver of all-male groups alongside other established factors such as reproductive state (Goldenberg et al., 2014) forage availability (Chiyo et al., 2014), age (Lee et al., 2011) and kin relationships (Chiyo et al., 2011b). Males likely associate with other males to dilute mortality risk as a proactive response (e.g., Creel, Schuette & Christianson, 2014) or to enhance vigilance or cooperative defence, but also to take advantage of the experience and knowledge of conspecifics (Allen et al., 2020; Evans & Harris, 2008). Older males are important sources of ecological and social knowledge, which may be especially valuable in risky contexts (Allen et al., 2020; Chiyo et al., 2011b; Evans & Harris, 2008; Wilke & Douglas-Hamilton, 2018). For instance, previous work showed that older males were more likely to travel at the front of all-male groups when using pathways to a river at a park boundary (Allen et al., 2020). While the age composition of all-male groups was not explicitly assessed in this study, both adolescent and adult males used the high-risk village water sources, and males occurred in mixed age groups. Whether older males similarly lead collective movements in all-male groups when accessing risky resources in Ruaha-Rungwa, where older males have been selectively removed by poaching (Jones et al., 2018), would be an interesting area for further study and could potentially be performed with the same camera trap dataset.

An alternative explanation of male aggregation could be that risk drove males to be more synchronised in their activity budgets - thereby facilitating social cohesion (Ruckstuhl & Neuhaus, 2001) - as males exclusively used risky water sources at night, while low-risk water sources were used throughout the day. This shared temporal response to risk may have been an important enabling factor in the formation and cohesion of large all-male groups, but it is unlikely to be the sole or main driver. Synchronised activity budgets have been found to be poor explanations of sex, size, and age-based associations in elephants elsewhere (Allen et al., 2020; Chiyo et al., 2011b; Shannon et al., 2008), and male groupings are reactive to anthropogenic risk at other sites during daytime hours (Chiyo et al., 2014).

Although male African elephants have weaker social bonds than females, they are gregarious and have been shown to have preferred social partners (Chiyo et al., 2011b; Lee et al., 2011).

Whether anthropogenic risk and the pressure to persist in increasingly human-dominated landscapes can drive larger and more stable associations among male elephants is an intriguing question. Among Asian elephants inhabiting a human-dominated landscape, Srinivasaiah et al. (2019) describe the emergence of large, stable all-male groups (which occur alongside more temporary groups) and suggest this may be a novel male strategy to mitigate risk and exploit foraging opportunities associated with humans. Although this was not the focus of the study, I observed repeat use of high-risk village water sources for several clearly identifiable males, who were often in the company of other males. Whether male African elephants have consistent associates when exploiting risky resources (e.g., water, crops) would be an interesting area for future research and could potentially be investigated in Ruaha-Rungwa with the same camera trap dataset.

While males associated with other males in response to risk, they did not necessarily associate more with female groups. Males occurred more often in mixed-sex groups in the higher-risk areas of Ruaha-Rungwa (Chapter 5), suggesting that male associations with female groups may respond to spatial variation in risk, as also seen by Chiyo et al. (2014). However, males were more likely to access risky water sources on village land in bull groups or alone than in mixed-sex groups. This may be the result of fewer opportunities to join female groups at risky water sources on village land, as females used these higher-risk water sources less often than males, compared to within protected areas. In Amboseli, Kenya, Chiyo et al. (2014) similarly observed that male opportunities to join female groups declined with increasing distance from a protected area boundary, as females used these “outside” areas less than males. Alternatively, males may have incurred costs when associating with cow-calf groups to access water sources, such as intra-specific competition or constraints on rates of movement and food intake (e.g., Lindsay, 2011), that possibly exceeded any risk mitigation benefits. Males were most likely to associate with female groups at low risk-water sources in the wet season, the time when most sexual activity occurs in the highly seasonal environment of Ruaha-Rungwa (Barnes, 1982c), suggesting that access to mates was a stronger driver of male associations with female groups than was risk, at least in the context of water access.

In this study, the influence of risk on female grouping patterns was only investigated in the context of access to water as opportunities to aggregate were available at rivers or waterholes, and potential predator risk (human and lion) was high at water. Neither cow-calf groups nor mixed-sex groups were significantly larger at risky water sources, suggesting that female groups did not consistently aggregate in this context in Ruaha-Rungwa (Chapter 6). Nevertheless, during the dry season, the largest mixed-sex groups (>40 individuals) were observed at risky water sources, suggesting that risk may have played a role in the formation of large groups comprising multiple cow-calf groups and multiple males. These results contrast with findings from other sites where female group sizes were reactive to risk. In the Okavango delta (Botswana), elephants adjusted group size to risk when accessing water (Songhurst et al., 2016). In Amboseli (Kenya), females adjusted group size depending on the competitive or cooperative context, using safety in numbers to mitigate risk when waiting to access a risky water source, followed by accessing water in smaller groups to reduce the risk of actual contact with people or livestock (Kangwana, 2011).

The female family structure is already a form of predator-response for calf protection (Moss & Lee, 2011), and thus average family size may be sufficient (or optimal) for countering most predation risks. Female group sizes are also influenced by a range of other factors not explicitly investigated in this study, including kinship, personality, attributes of matriarchs, and environmental conditions (Moss & Lee, 2011), which may override immediate risk. Furthermore, the unique social structure of elephants, with core cow-calf units embedded in kin families, that aggregate and break up at will (Mutinda et al., 2011), and which may include males as a function of those males' social decisions, predicts flexible social responses to risk on the part of elephants as seen in cetaceans (Mann et al., 2000), rather than simple rules for aggregation as seen in other birds and mammals (e.g., Conradt & Roper, 2005). It should be noted that this study was conducted in a population recently subject to intense poaching, which may have disrupted female social bonds (e.g., Gobush & Wasser, 2009) and removed experienced older matriarchs (Foley, 2002; Jones et al., 2018), potentially impacting the ability of surviving female groups to appropriately assess risk (e.g., McComb et al., 2011; Shannon et al., 2022) or use social knowledge (e.g., Shannon et al., 2013) and relationships to manage risk.

7.4 Responses to risk and their consequences for elephant survival and reproduction

Do elephants benefit from shifts in the timing of activities, resource access, use of space or aggregation in response to human-mediated risk? While survival benefits can be proposed but not demonstrated in this study, behavioural alterations that enable coexistence with humans are likely to have general adaptive consequences (e.g., Suraci et al., 2019a).

It is clear from studies in other taxa that behaviours used to mitigate predation risk are associated with costs (Preisser et al., 2005). In predator-prey systems in natural ecosystems, anti-predator responses have been shown to reduce foraging efficiency and energy intake (Christianson & Creel, 2008; 2010; Downes, 2001; Hernández & Laundré, 2005) and increase vulnerability to other predators (Losey & Denno, 1998, Eklöv & VanKooten, 2001). These costs impact prey growth, survival, and reproduction, and have been termed non-lethal predation effects (Creel & Christianson, 2008; Creel, Christianson & Winnie, 2011). Responding to humans as predators may have analogous costs and effects on survival and reproduction, as disturbance from humans has been shown to reduce foraging activity (Pirotta et al., 2015), increase energetic costs and resource requirements (McBlain, Jones & Shannon, 2020; Wang, Smith & Wilmers, 2017), and reduce reproductive rates and success (French et al., 2011; Spaul & Heath, 2016) in various species.

Costs of risk-induced shifts in ranging behaviour, activity budgets, and resource access have not yet been shown in elephants and require further investigation, but possible costs are discussed here. Behavioural shifts in elephants in response to risk may compromise their ability to meet thermoregulatory requirements and maintain energy balance and condition. Shifts in the timing of water access in response to risk (Chapter 6; Buchholtz et al., 2021) could be associated with thermoregulatory or metabolic costs, such as an inability to use water for rehydration and cooling at the hottest times of the day. Lactating females may experience water stress as a result of delayed or constrained access to water in risky areas; if this in turn affects milk production, calf survival during the two-year period before calves are weaned may be impacted.

Risk reduces the total time that elephants have available for activity, such that they have fewer hours for movement, feeding, and other fitness-enhancing behaviours (Chapter 5; Ihwagi, 2019). Risk may also induce heightened vigilance (Chapter 6) and flight responses, thereby reducing foraging efficiency and duration (Smith et al., 2017; Sönnichsen et al., 2013). Reduced foraging time and efficiency likely cause nutritional stress and impact body condition (de Klerk, 2009), with possible consequences for survival and reproduction (Mumby et al., 2015). In this study, mean body condition scores for adult females were lower in the three high-risk sites than in the low-risk site (Chapter 5), although most females were in normal condition across the four sites (Chapter 5). While these admittedly small differences in body condition could be due to risk-induced foraging costs, they could also result from variation in forage availability and quality in these high-risk areas. Future work should aim to systematically assess risk effects on body condition in elephants. If risk-induced behavioural changes affect maternal food intake and condition by limiting foraging duration or efficiency, consequences may include lower conception rates, reduced gestational success, lower calf survival, poor growth rates, and reduced lifetime fitness (e.g., Lee et al., 2022 in the case of reduced forage intake in the context of droughts).

A further cost of responding to humans may be increased temporal overlap with non-human predators, as seen for lions and elephants in the higher-risk areas of Ruaha-Rungwa (Chapter 5). While lion and hyena mortality are negligible sources of mortality for adult elephants

(Owen-Smith & Mills, 2008), calves and young dispersing males are vulnerable to predation (Joubert, 2006; personal observations). Evidence from lion and hyena reintroductions in Addo Elephant National Park, South Africa indicates that elephants are more diurnal in the presence of these largely nocturnal predators, possibly as a means to reduce predation risk (Tambling et al., 2015). Increased nocturnality in response to humans may therefore expose elephant calves and young males to greater lion and hyena predation risk, although in Ruaha-Rungwa, this may be mitigated somewhat by lower lion densities in the high-risk areas (Strampelli et al., 2022a). Predation risk is likely greatest in the context of nocturnal water access, as lion depredations on elephants often occur near water sources in Ruaha-Rungwa (personal observations).

A further intriguing result from this study was that fewer relaxed behaviours, such as play, were observed in camera trap images of elephants from the higher-risk areas of Ruaha-Rungwa than in the low-risk site (Chapter 5). If this finding reflects a trend towards less play among calves in response to human-mediated risk, either because of elevated or chronic stress, poor condition, or a reduction in the total time available for activity, there may be consequences for elephant social development. Whether through limited play or other forms of social interaction, lack of acquired social and physical knowledge of the environment and conspecifics can have long-term survival and reproductive consequences (Shannon et al., 2022).

An important implication of this work is that humans not only act as direct predators of elephants but also have behaviourally mediated, non-lethal, indirect effects on elephants. While poaching is known to alter the demography of elephant populations and suppress recruitment (Foley, 2002; Poole, 1989b; Wittemyer et al., 2013), including in Ruaha-Rungwa (Jones et al., 2018), this thesis demonstrates that poaching risk, even that removed in time by several years, also induces behavioural shifts in elephants including changes in diel activity, resource access, and space use. Poor recruitment in poached populations is often attributed to the direct lethal effects of poaching, including the loss of older, experienced matriarchs and allomothers due to poaching, and loss of older males, although the indirect effects of chronic stress levels have also been implicated (Gobush et al., 2008). My findings raise the possibility that potentially costly behavioural shifts induced by poaching risk may further contribute to poor recruitment by affecting female condition, fecundity, and calf survival.

7.5 Management and applications

This thesis resulted in several methodological innovations that could be used in other camera trap studies of elephants. While the use of camera traps to study elephant diel activity (Clauss et al., 2021; Gaynor et al., 2018b; Tambling et al., 2015) and resource access (Gessner et al., 2014; Smit et al., 2017) was not new, I developed reliable group type definitions tailored to camera trap images (Chapter 2, Section 2.3.5) that enabled novel investigation of grouping patterns and sex differences in diel activity and resource access from camera trap data. I also developed elephant activity type definitions for camera trap images (Chapter 2, Section 2.3.6) and scored elephant body condition in camera trap images (e.g., Bush et al., 2020 for African forest elephants) using an existing scale (Morfeld et al., 2014; Chapter 2, Section 2.3.7), enabling comparisons of activity and condition as a function of risk.

Conservation of the Ruaha-Rungwa elephant population should be informed by the understanding that this population has been impacted dramatically by poaching and has not yet shown signs of recovery. The poaching upsurge of 2010-2015 resulted in a loss of over half the population, suppressed recruitment and, critically, removed older males and females - who are important reservoirs of social and ecological knowledge - from the population (Allen et al., 2020; Chiyo et al., 2011b; Evans & Harris, 2008; Jones et al., 2018; McComb et al., 2011). In 2021, six years after the worst of the poaching, elephant numbers had not increased (TAWIRI, 2022) and recruitment had not improved (Chapter 3). This thesis further indicates that poaching resulted in behavioural changes that elephants maintained several years after the poaching peak. How long it will take for the Ruaha-Rungwa elephant population to recover is unknown, and evidence from elsewhere indicates that social and reproductive disruption from poaching can persist for more than a decade (Gobush et al., 2008), but it is clear that continued protection will be essential for recovery to occur. Continued, effective on-the-ground protection efforts will be important to mitigate a range of anthropogenic threats within protected areas: illegal human activity within Ruaha-Rungwa's protected areas was associated with increasing distance to ranger posts (Strampelli, 2021) and proximity to ranger posts had a positive effect on elephant occurrence (Beale et al., 2018; Chapter 4). In addition, strategic placement of low-impact tourism or research stations beyond the current core tourism area could make more of the ecosystem safer for elephants through increased tourism or researcher presence (e.g., Abdoulaye, Adama & Matthias, 2021; Laurance, 2013; Piel et al., 2015). Critically, any actions that would stimulate demand for ivory and bring about another poaching surge would be extremely detrimental to this population.

In recent years, hostile interactions between people and elephants have overtaken ivory poaching as the primary concern in elephant conservation. The future of elephants increasingly depends on human decisions about their populations and habitats and our willingness to coexist with elephants (Hoare, 2000; Lee & Graham, 2006). As demonstrated in this thesis and other work, elephants use a range of behavioural strategies to avoid humans in space and in time (Bucholtz et al., 2021; Graham et al., 2009; Songhurst et al., 2016). These behavioural risk responses can be incorporated into strategies to promote coexistence (Gaynor et al., 2021), help to maintain elephant access to shared resources, and inform effective land use planning and zoning to maintain networks of connected core areas for elephants while limiting elephant movement into human settlements and cropland (Guerbois, Chapanda & Fritz, 2012; Weaver, Paquet & Ruggiero, 1996; Graham et al., 2009; Poole et al., 2011; Songhurst et al., 2016). The elephant's capacity for long-distance movement, combined with risk-avoidance behaviour facilitates connectivity even through areas with human use or poor-quality habitat (Graham et al., 2009; Bastille-Rousseau & Wittemyer, 2021). Knowledge of elephant risk-avoidance behaviour and their specific movement routes through shared landscapes could therefore help to secure defined corridors and pathways that allow elephants free passage between different core areas and enable access to shared resources while minimising their contact with people (Songhurst et al., 2016). Risk avoidance behaviour by elephants could also be used to delineate and reinforce boundaries around human settlements or agricultural fields, by reinforcing perceived risks using appropriate non-lethal fear stimuli such as bees (King, Douglas-Hamilton & Vollrath, 2007), non-human predator cues (Thuppil & Coss, 2013) or irritants such as chilli (Parker & Osborn, 2006; Pozo et al., 2019). There may also be potential to reinforce elephant risk-avoidance behaviours using stimuli that evoke disgust responses (Sarabian et al., 2023). While the role of disgust and pathogen/disease avoidance in elephant foraging decisions remains poorly understood, it has been shown that elephants avoid water holes with high levels of *Escherichia coli* contamination (Ndlovu et al., 2018), and local farmers in Tanzania believe that applying elephant dung to crops makes these less attractive to elephants (W. Ngowi, personal communication, 2022).

Human emotions towards wildlife may represent barriers or opportunities for human-wildlife coexistence (Castillo-Huitrón et al., 2020; Jacobs & Vaske, 2019). In particular, whether people respond to a particular species with fear or with positive emotions influences attitudes to wildlife and support for conservation efforts (Ghasemi et al., 2021; Jacobs & Harms, 2014; Johanssen et al., 2012; Vaske, Roemer & Taylor, 2013). Personal experience and learned knowledge can affect emotional responses to wildlife, possibly reducing fear (Jacob & Vaske, 2019; Prokop & Fančovičová, 2016). Rural, protected area-adjacent communities are often fearful of elephants (Naughton-Treves, 1997; Mariki et al., 2015). It would be useful to understand whether contextualising elephant behaviour in shared landscapes, including an understanding of the risk-avoidance behaviours that elephants display towards humans, can reduce people’s fear of elephants and foster greater tolerance of elephants in shared landscapes, as this would have clear practical applications.

7.6 Conclusions

This thesis has shown that anthropogenic risk was an important driver of elephant space and resource use, temporal activity, and grouping patterns in Ruaha-Rungwa. Within Ruaha-Rungwa’s protected areas, risk influenced fine-scale elephant space use, diel activity, use of roads and water sources, and male grouping patterns. In the context of water access, risk induced changes in the timing of resource access and influenced male, but not female, grouping patterns. Critically, this work demonstrates that the impacts of severe poaching in Ruaha-Rungwa extend beyond previously documented effects on elephant population size and structure (Jones et al., 2018), and include marked behavioural shifts which may be associated with costs constraining population recovery. As with top predators in natural predator-prey systems, this thesis indicates that humans not only shape animal populations through their direct lethal effects but also through their indirect, non-lethal effects on animal behaviour (e.g., Suraci et al., 2019b). Risk-avoidance behaviour in elephants may also facilitate their coexistence with humans in an increasingly anthropogenic world.

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