

CONSEQUENCES OF A PASTORALIST INCURSION ON LARGE MAMMAL SPACE USE
IN LOISABA CONSERVANCY- NORTHERN KENYA

By

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ABSTRACT

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Pastoralists and large mammals regularly compete over access to grazing lands. This has been true historically and is particularly relevant in the present day. In the 21st century, competition between livestock and wildlife has increased in frequency given that grazing lands are rapidly dwindling (due to habitat fragmentation and human range expansion) and drying up (via the processes of desertification fueled by climate change). These dynamics are particularly apparent in East Africa and perhaps most obvious in northern Kenya. In February of 2017, a point source pastoralist incursion occurred in Laikipia County, Kenya. An estimated 40,000 livestock grazed onto Loisaba Conservancy by armed pastoralists. The livestock resided on the 226km² conservancy land for four months before departing to the north. Using a broad scale camera trapping system (53 sites distributed across the conservancy), I compared patterns in site visitation rates for large mammalian herbivores that rely on grazing, browsing, and mixed feeding life histories directly before, during, and after this livestock incursion. I found stark contrasts in patterns of site visitation rates for all large herbivores across the three time periods. My results indicate that the incursion considerably changed space use of large herbivores and altered their association with a variety of landscape features, including human settlements and water access points. Competition between pastoralists and wildlife is predicted to intensify in the future, emphasizing the importance of assessing the consequences of these interactions. I discuss the implications of this competition for wildlife conservation, pastoralist livelihoods, and the role of grazing lands in modulating interactions of pastoralist livestock and large mammals.

I am dedicating this thesis to a man who has meant and continues to mean so much to me. Although you are no longer on this world, your memories continue to regulate my life. My maternal uncle Shompole Ole Larpei, though you have gone away from me, leaving a void never to be filled in my lives. Though your life was short, I will make sure your memory lives on as long as I shall live. I love you all and miss you all beyond word.

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1.0. LITERATURE REVIEW

Pastoralism is a lifestyle in which people make their living by tending herds of livestock (i.e., cattle - *Bos taurus*, sheep - *Ovis aries*, goat - *Capra aegagrus hircus*, reindeer - *Rangifer tarandus*, horses - *Equus ferus caballus*, domestic yak - *Bos grunniens*, donkey - *Equus asinus*, camel - *Camelus dromedaries*, alpaca - *Vicugna pacos*, and llamas - *Lama glama*) and grazing the domestic animals on local rangelands (Blench, 2001; FAO, 2001). Livestock provide a number of quality proteins, in the form of meat, milk, and blood, to local communities (Sadler et al., 2009). These sources of nutrition are particularly important for children and lactating women (Sadler et al., 2009). Thus, condition of livestock influences human health and well-being. Though pastoralism occurs around the world, styles of livestock husbandry vary. There are two primary ways in which pastoralism has been defined. From a *productive perspective*, pastoralism can be organized to sell livestock. Here, care of livestock focuses on animal health, husbandry, and sustainable use of grazing on the rangelands (Blench, 2001). Pastoralism from a *subsistence perspective* shares many of these same values, but instead of commercialism, livestock-owners tend to live among their livestock and use them to feed their families and as an integral component to cultural practices (Blench, 2001; IFAD, 2008). Pastoralists have long overlapped and interacted with wildlife in rangelands across the world (Prins, 1992; Blench & Sommer, 1999; Butt & Turner, 2012; Homewood et al., 2012; Bedunah & Harris, 2016). The nature and strength of these interactions has reshaped the landscapes that wildlife and pastoralists share (Lankester & Davis, 2016; Butt & Turner, 2012). The spatio-temporal nature of these interactions depends on climate conditions, access to water, and the distribution and abundance of foraging resources (Prins & Voeten, 1999; Young et al., 2005; Averbeck et al., 2009; Low et al., 2009).

Interactions of pastoralists, livestock, and wildlife can be positive, negative, or indifferent. Where there is balance in the environment, livestock and wildlife can sustainably interact on rangelands. For instance, the act of livestock trampling soil can act as a tiller, stimulating growth of grass, forbs, and sedges (Maitra, 2010). Livestock also defecate and urinate on the soil which provides nutrients that promote both undergrowth and top growth of plants (Gordon, 1988; Odadi et al., 2011). Negative interactions typically occur through resource competition. Livestock compete with wildlife for forage, water, and access to rangelands. For example, grazers like African buffalo (*Syncerus caffer*) and zebras (*Equus quagga*) compete with cattle over grass which can result in overgrazing (Rowntree et al., 2004). This overgrazing subsequently affects natural composition of plant populations and their regenerative capacities (Stiling & Moon, 2005). Browsing species like giraffes (*Giraffa camelopardalis*) and eland (*Taurotragus oryx*) compete with livestock, such as camel and goats, with potentially destructive impacts on shrubs and woody plants (Goheen et al., 2010; O'Connor et al., 2016). Furthermore, species like African elephant (*Loxodonta africana*) and buffalo can be problematic to both pastoralists and their livestock as these large-bodied animals can become aggressive when competing with livestock for water and forage resources (Gadd, 2005). For example, both elephants and buffaloes have also been reported to chase, injure, and kill both livestock and herders (Gadd, 2005; Niamir-Fuller et al., 2012; Wiethoelter et al., 2015). Interactions of livestock and wildlife also facilitate disease transmission (Cleaveland et al., 2001). For instance, bovine malignant catarrhal fever, a virus that is carried mostly by sheep and wildebeest (*Connochaetes spp.*), is often highly adapted and non-lethal to the host, but can cause lethal infections when transmitted to vulnerable animals like cattle (Cleaveland et al., 2001; Catarrh, 2012). Foot-and-mouth is a disease that affects domestic cloven-hoofed animals (Jamal &

Belsham, 2013) including cattle, swine, sheep, and goats, as well as more than 70 species of wild animals such African buffalo, zebra, and warthog (*Phacochoerus africanus*; Fenner et al., 1993; Gortázar et al., 2007; Böhm et al., 2009). Diseases like these can increase the potential for negative interactions among pastoralists, livestock, and wildlife.

Excluding Antarctica, rangeland habitats occupy between 18 and 23% of global land area (Blench & Sommer, 1999; Follet & Reed, 2010). On these rangelands, pastoralism is practiced by approximately 200 million people (Blench, 2001). Many of these people maintain nomadic pastoralist lifestyles. In this case, the pastoralists move with their livestock following pasture resources in a pattern that varies from year to year (Blench, 2001). This type of nomadism is practiced in dryland and highland regions of the world, with low rainfall such as the Arabian Peninsula and Sahel of Africa (Dong, 2016). Transhumant pastoralism involves regular movement of livestock between fixed summer and winter sites so as to exploit seasonal availability of pastures annually (Dong, 2016; O'Neil, 2011; FAO, 2001). Lastly, agro-pastoralism involves supplementation of pastoralist livelihoods with small scale farming (Kerven et al., 2011; FAO, 2001). Some households grow feed crops and sell in local markets or to other households in exchange for livestock (Kerven et al., 2011).

In contrast to pastoralism, large scale livestock production is expanding across the world (Steinfeld et al., 2006; Thornton, 2010). As human populations grow globally, demand for meat and rangelands for grazing domestic animals has intensified (Herrero et al. 2010; Reid et al., 2010; Thornton, 2010). Thus, livestock-keeping is rapidly increasing, particularly in the Global South where a tripling in meat production occurred between 1980 and 2002 (World Bank, 2009; Thornton, 2010). Such growth in livestock production can negatively impact global biodiversity (Plachter & Hampicke, 2010; Schieltz & Rubenstein, 2016). These effects can be both direct and

indirect. Livestock can directly affect wildlife by interfering with the quality of habitat through influencing composition, structure, and productivity of plant communities (Krausman et al., 2009). This includes conversion of landscapes for agro-pastoralism. For example, livestock, aided by human herders, typically displace and outcompete wildlife for access to grassland forage (Kauffman & Pyke 2001). Livestock can indirectly impact wildlife by changing vegetation availability and quality (Putman et al., 1989; Eccard et al., 2000). Forage intake of large mammalian herbivores may decline in nutritional value when livestock grazing reduces vegetation species diversity and causes declines in rangeland quality (Holechek et al., 1995). Livestock can also affect wildlife indirectly by contributing to climate change (Gerber et al., 2013). Methane (CH₄) production, resulting from livestock digestion, flatulence, and defecation, can contribute to climate change phenomena (Olander et al., 2013; Pérez-Barbería, 2017). Climate change is a clear threat to wildlife forage quantity and quality, water scarcity, and biodiversity (Gerber et al., 2013). Thus, there are important effects of livestock production on the environment.

1.1. Pastoralism and wildlife competition globally

The consequences of livestock grazing vary spatially according to livestock space use, niche overlap with large mammalian herbivores, and availability of habitats offering palatable primary productivity (Mishra et al., 2004; Liu et al., 2015; Kinga et al., 2018). Interactions between livestock and wildlife are examples of interspecific sympatric competition, where individuals of different species contend for the same resources in an ecosystem (Prins, 2000). These interactions often take the form of competitive exclusion, in which two interacting species are sufficiently similar in resource use patterns and one has a competitive advantage in excluding the other (Gause, 1934). Ecological consequences of this competition are informed by the theory

of limiting similarity (MacArthur & Levins, 1967; Abrams, 1983), applied in the context of livestock and large mammalian herbivore interactions (Prins, 2000; Mishra et al., 2002). Owing to the importance of this theoretical principle, coexistence of livestock and wildlife is an area of scientific inquiry (see Moktan et al., 2008; Dettenmaier et al., 2017; Kinga et al., 2018).

According to the projections of Food Agriculture Organization (FAO, 2009; FAO, 2011), by 2050 the global demand for livestock will increase by 70% in accordance with predicted growth in the human population (Dettenmaier et al., 2017). This suggests that pastoralism will remain a major land use in the future.

Pastoralism is rapidly changing in the 21st century as a result of natural degradation of landscapes, varying weather patterns, human population growth, and labor restrictions. Furthermore, the practice of pastoralism is becoming endangered by sedentarization and the increasing criticism of cultural practices. For example, children among many pastoralist cultures may not pursue formal education (Krätli, 2001; Ole Seno & Tome, 2013; Schmidt & Pearson, 2016). This tendency lies in stark contrast to value systems that promote youth education. Furthermore, as pastoralist lifestyles become more sedentary (Ole Seno & Tome, 2013), the structure and function of landscapes previously suited for biodiversity conservation are altered (Galvin et al., 2008; Barnosky et al., 2011). The sedentary tendencies of many pastoralists are linked to habitat change (Archer, 2010), overgrazing of rangelands (Talbot, 1986), and increasing spread of invasive shrubs on rangelands (Witt & Nongogo, 2011).

Livestock are integral to sustaining rural livelihoods in variable and heterogeneous landscapes across the globe (Ellis & Galvin, 1994; Scoones, 1994). They also provide increased economic stability to pastoralist households (Devendra & Thomas, 2002) both in small and large scale forms (Reid et al., 2001; 2004). For instance, in areas of the world cohabited by wildlife

and livestock, wildlife and pastoralist cultures are important tourist attractions that can boost local economies. East Africa hosts some of the highest densities and distributions of large mammalian herbivores in the world (Sinclair & Arcese, 1995; Sinclair et al., 2008). In countries like Kenya and Tanzania, wildlife and pastoralism support tourism via wildlife viewing and cultural activities (Akama, 2002; Waithaka, 2004). However, expanding human populations, habitat fragmentation, climate change, and drought can increase conflict between wildlife and livestock. Understanding when and how competition occurs between pastoralists' livestock and wildlife can help communities, governments, and non-governmental organizations (NGOs) better realize the extent of this problem and determine how best to implement interventions.

Recent and swift changes in pastoralist grazing dynamics, especially during the dry season, has resulted in competition with wildlife for scarcer resources. These effects have been particularly apparent in northern Kenya where pastoralists use both unprotected and protected habitats to graze livestock. As a result of severe droughts and limited availability of forage on rangelands, thousands of livestock were driven to Laikipia County from the counties of Samburu, Isiolo, Baringo, Marsabit, and Turkana. In this incursion, ~40,000 livestock were grazed onto the protected area known as Loisaba Conservancy. Pastoralists and their livestock stayed for a period of three months. During that time, grazing occurred across the conservancy before herds moved to the north following local depletion of rangeland grasses. Research to understand the effects of this livestock incursion on wildlife occurrence is needed to better understand the dynamic interactions of wildlife and livestock in East African protected areas. In this thesis, I evaluated the nature of pastoralist-wildlife competition and assessed impacts of this pastoralist incursion on large mammalian spatial dynamics in Loisaba Conservancy.

2.0. INTRODUCTION

Competition between wildlife and pastoralist livestock over access to water and grazing lands is increasingly becoming a wicked problem in the 21st century (Kassahun et al., 2008; Ogutu et al., 2009; Otuoma et al., 2009; Papanastasis, 2009; Lankester & Davis, 2016). This problem lacks a clear solution given divergent values among stakeholders that differentially value wildlife conservation versus pastoralist well-being (Redpath et al., 2013; Mason et al., 2018). While competition of this type occurs worldwide, it is often most intense in the southern hemisphere (Verlinden et al., 1998; Western et al., 2009). Meat dependency has increased dramatically in the Global South, where a tripling in meat production occurred between 1980 and 2002 (World Bank, 2009; Thornton, 2010; Weiss et al., 2010; Bonny et al., 2015; Machovina et al., 2015). As livestock in the Global South are often grazed on open rangelands, rather than given provisions in confined spaces or enclosures, corresponding requirements to feed those livestock has increased the potential for resource competition with large mammalian herbivores (Rannestad et al., 2006; Odadi et al., 2007; Sitters et al., 2009). This competition has been associated with intensive overgrazing in some areas with subsequent negative consequences for livestock, wildlife, and the environment (Rowntree et al., 2004; Bilotta et al., 2007; Niamir-Fuller et al., 2012).

Overgrazing can negatively affect the natural composition of plant populations (Stiling & Moon, 2005; Walck et al., 2011) as root stocks that contain food reserves and promote regeneration in plants can be ruined (Keine, 2009). Thus, overgrazing can alter ecological succession, nutrient cycles, and landscape heterogeneity with subsequent fitness-related impacts on the wildlife that depend upon these rangelands (Kauffman & Pyke, 2001; Ceballos & Ehrlich, 2002; Balmford et al., 2003). The nature of wildlife-pastoralist interactions is further exacerbated

by climate change, including extreme weather and drought (Sinclair et al., 2008). Furthermore, competition between pastoralists and wildlife for forage negatively affects livestock milk and meat production, which in turn compromises human well-being and livelihood (Randolph et al., 2007; World Bank, 2009; Kimman et al., 2013). Thus, overgrazing and pastoralist-wildlife conflict represent important environmental challenges (Bilotta et al., 2007; Niamir-Fuller et al., 2012).

East African savannas are landscapes where pastoralists, livestock, and large mammalian herbivores have interacted for thousands of years (Otuoma, 2004; Ogutu et al., 2016). These landscapes support a high diversity of large mammals, including African elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), and African buffaloes (*Syncerus caffer*; Georgiadis et al., 2007; Shorrocks, 2007; Goheen et al., 2018), and are also populated with vast numbers of livestock including cattle, sheep and goats, donkeys, and camels (Nelson, 2012; Ogutu et al., 2016). Pastoralists inhabiting savanna landscapes typically provide livestock with resources by moving over large distances in search of water and grazing lands (Reid & Ellis, 1995; Butt, 2010). These movements are coordinated in accordance with seasonal shifts in forage and water availability (Niamir-Fuller, 1999; Thornton et al., 2014; Egeru, 2016). Movements and migrations of large mammals are similarly dictated by forage potential following spatio-temporal changes in resource abundance (Mose et al., 2013; Teitelbaum et al., 2015). Thus, migration facilitates large mammalian herbivores to exploit forage quality in ways that maximize intake rate over larger spatial scales (Fryxell et al., 2004; Hebblewhite et al., 2008). Consequently, there is strong potential for competition, and potentially conflict, between pastoralists and wildlife. This competition is intensified by the fact that both productive grazing lands and water

availability are dynamically changing given climate change and habitat fragmentation processes (Stiling & Moon, 2005; Walck et al., 2011).

Kenya is a global hotspot for pastoralist-wildlife competition (Gadd, 2005; Tyrrell et al., 2017). There are 17 different pastoralist tribes (KNBS, 2009) that almost completely depend upon livestock for their livelihoods and well-being (Thornton et al., 2002). These include the Maasai, Samburu, Turkana, and Pokot, among others (Ameso et al., 2018; Pas, 2018). Pastoralists move their herds and flocks over extensive areas annually in search of water and productive grazing lands (Western & Finch, 1986; Leff, 2009; Lengoiboni et al., 2011). In February 2017, pastoralists from northern Kenya forcibly grazed tens of thousands of livestock onto the Loisaba Conservancy. Movement of these pastoralists, many of whom were armed with assault rifles, was motivated by severe drought in adjoining counties. This pastoralist incursion resulted in a state of insecurity characterized by banditry, cattle rustling, proliferation of illegal firearms, poaching, and property vandalism (Ngeiywa, 2008; Manasseh et al., 2012). Pastoralists grazed their livestock on conservancy lands for approximately three months before moving northward following local depletion of green grasses. This incursion, and others like it, represent a potentially major disturbance for native wildlife communities. However, the consequences of pastoral incursions on the spatial dynamics of large mammalian herbivores are presently unclear.

Here, I examined the impacts of this point source pastoralist incursion on the spatial dynamics of large mammalian herbivores in Loisaba Conservancy. Using a camera trapping network, I evaluated site visitation rates of large mammals with browsing, grazing, and mixed feeding life history strategies in the periods preceding, during, and directly after the incursion. Given rapid growth in meat dependency and ongoing climate change dynamics, there is good reason to believe that pastoralist incursions will become more common in future. Thus,

documenting the impacts of livestock and pastoralist actions on large mammals will help fill important knowledge gaps yielding information that could be used to inform interventionist planning. Within this context, I discuss the implications of this study for conservation practice in savanna landscapes of East Africa.

3.0. METHODS

3.1. Study site

Loisaba conservancy (N 00 31.58.53, E 360 48.06.69, elevation range of 1,400 to 1,800 m) is a 226 km² protected area situated in Laikipia County, Kenya (Fig. 1). The conservancy sits within a broad matrix of other protected and community-owned lands. The northern portion of the conservancy consists of a relatively flat, open grassland with scattered shrubs and acacia bushes and trees. The Ewaso Narok and Ewaso Nyiro rivers meet at the southern and eastern edges of the conservancy (Fig. 1). The climate is semi-arid with a pronounced rainy season from April to May and lesser rainy seasons from July to August and October to November. The longer dry season is from December to March. During our study, annual rainfall at Loisaba Conservancy was 697 and 657 mm per year in 2016 and 2017, respectively.

3.1.1. Experimental design

I deployed camera traps at 53 sites across the Loisaba Conservancy between June 2016 and October 2017 (Fig. 1). I positioned each camera trap, affixed to a tree, in the centroid of a 2 km² resolution grid cell. I placed each camera at a height of 40–50 cm above the ground to capture large mammalian herbivores in the system. I programmed cameras to capture one photograph per trigger with re-triggers occurring every five seconds thereafter. I assessed large mammalian herbivore site visitation rates over a 15-month period. Specifically, I sampled; *i*) a 14-week period prior to the incursion (June – September 2016), *ii*) a three-week period during

the incursion (March – April 2017), and *iii*) a 14-week period that began two months after conclusion of the intense incursion (July – October 2017). I note that the sampling period during the incursion was limited to three weeks because of inherent dangers of field work, widespread vandalism, and physical damage to camera traps by pastoralists and livestock herds. I collated and managed all resultant camera trap photos in digiKam, an open-source digital management application (The digiKam Developer’s team, 2018) and examined all photos to identify large mammalian herbivores in the images.

3.2. Modeling framework

I used a Bayesian site visitation model (Kays et al., 2016; Moll et al., 2018) to evaluate large mammal spatial dynamics before, during, and after the incursion. Given our interest in pastoralist-livestock competition, I modeled the occurrence of wildlife species that were most likely to be directly affected by this incursion. These included browsing species, which forage on the leaves, shoots, or fruits of woody plants and shrubs; grazing species which predominantly consume grass; and mixed feeding species which forage on both grass and browse. The browsers included reticulated giraffes (*G. c. reticulata*) and eland (*Taurotragus oryx*; Codron et al., 2007). Grazers included African buffaloes, Plains zebras (*Equus quagga burchelli*), and Grevy’s zebras (*Equus grevyi*; Codron et al., 2007; Hibert et al., 2010). There were two types of mixed feeders in our study area. These included African elephants (Hibert et al., 2010) and impala (*Aepyceros melampus*; Landman et al., 2018). However, given the differences between these species in body size, predator avoidance strategies, and life history (Gordon, 2003; Anderson et al., 2016; Ross, 2016; Ashiagbor & Danquah, 2017), I modeled these two mixed feeders separately.

For each large herbivore group, I modeled the number of times per week any of the species within the group visited a given camera trap (hereafter referred to as *site visitation rate*)

as a function of incursion period (i.e., pre- during, and post-incursion) and spatial covariates. Site visitation rate can be interpreted as an index of the intensity of space use across the landscape (Kays et al., 2016; Moll et al., 2018). To avoid pseudo replication and help ensure temporal independence of the site visit data, I omitted site visits of the same species that occurred within 60 minutes of a previous visit by that species (Burton et al., 2015; Wang et al., 2015).

I modeled site visitation rates using a negative binomial distribution to account for overdispersion in the data (Greene, 2008). I included covariates that evaluated the effects of: *i*) incursion period, *ii*) four spatial covariates that I expected to influence large mammalian herbivore space use, and *iii*) interaction terms between incursion period and each of the four spatial covariates. I included these interaction terms to assess the possibility that relationships between large mammalian herbivores site visitation rate and spatial covariates might fundamentally shift during pastoralist incursion as wildlife sought forage and water resources while coping with this landscape-level disturbance event. The correlation coefficient between all covariates in all the seasons (preceding, during, and after incursion) was less than 0.64 indicating that the covariates that I considered were not collinear (Table 2).

3.3. Spatial covariates

I identified four spatial covariates, each expressed as rasters at a 30 m resolution across the study area, known to influence large mammal space use (Guo et al., 2017; Soofi et al., 2018; Table 1). I estimated proximity to two sources of water, human habitations, and the conservancy area boundary by calculating Euclidean distance (km) to the nearest dam, major river, human habitation, and conservancy boundary. I chose water-related covariates (i.e., distance to dams and rivers) based on the understanding that water is a basic requirement for large herbivores influencing their spatial distribution and intensity of site use (Rondinini et al., 2011). Loisaba

Conservancy owns several dams that form reservoirs for provision of water to livestock and wildlife. As human habitations are known to influence space use of large mammalian herbivores (Ogutu et al., 2017), I examined proximity to tented tourist camps, lodges, ranger posts, and the conservancy administrative headquarters. Finally, despite Loisaba Conservancy being unfenced, I calculated proximity to the boundary given that there may be important edge effects associated with large mammal occurrence in this system (Xavier et al., 2018).

3.4. Model analysis and predictions

I analyzed models in a Bayesian framework using Markov Chain Monte Carlo simulations in R (R Core Team 2017) and JAGS (Plummer, 2003) via the package *R2jags* (Su & Yajima 2012; see model code in Appendix A). For each model (i.e., one model each for grazers, browsers, and the two mixed feeding species), I ran three chains of 8,000 iterations, each following a burn-in of 2,000 iterations and thinned chains by four. I used diffuse priors for all covariates (Kéry & Royle, 2015) and checked for model convergence using R-hat statistics (values for all parameters were <1.1 ; Gelman & Hill, 2007). I assessed model fit using posterior predictive checks and Bayesian p -values by comparing a Chi-square discrepancy statistic calculated using the data with an analogous statistic calculated using data simulated from the fitted model (Kéry & Royle, 2015). Bayesian p -values near 0.5 indicate an excellent fit and extreme values near one or zero indicate poor fit (Kéry & Royle, 2015). I checked for spatial autocorrelation among model residuals by plotting spline correlograms of Pearson's residuals summed across sites (Rhodes et al., 2009; Moll et al., 2018). Finally, I used the fit model to produce spatially-explicit predictive maps of large mammal space use in the pre-, during, and post-incursion periods.

4.0. RESULTS

Across the 53 sites, camera traps were active for 379 camera-trap weeks (2,653 camera-trap nights). My cameras recorded 2,200 site visits of the focal large herbivore species. Impala were most commonly-detected ($n = 751$ site visits) while African buffalo were least-commonly detected ($n = 43$ site visits). Bayesian p -values indicated good to excellent fit for all models ($p_{\text{grazers}} = 0.60$, $p_{\text{browsers}} = 0.64$, $p_{\text{impala}} = 0.63$, $p_{\text{elephant}} = 0.56$). Spine correlograms indicated lack of spatial autocorrelation among the residuals in all models (Appendix A).

4.1. Spatial dynamics

4.1.1. Browsers

Distance to dam had little effect on the site visitation rates of the browsing large mammalian herbivores in the pre-, during, and post-incursion periods (Fig. 2a; Table 2). Site visitation rates of browsers demonstrated completely opposing patterns in the pre-incursion period when compared to during the incursion (Fig. 3a; Table 2). Site visitation rates increased closer to the boundary in the pre-incursion period (Fig. 3a). I detected a comparable effect in the post-incursion period (Fig. 3a; Table 2). Distance to human habitation had little effect on browser site visitation rate in the pre- and during incursion periods, but the pattern was pronounced in the post-incursion period when site visitation rate was considerably higher closer to human habitation (Fig. 4a; Table 2). Browsers preceding, during, and after the incursion showed little relationship with distance to the river (Fig. 5a; Table 2). The spatial maps demonstrate that browsers used the eastern edge of the conservancy in the pre-incursion period, the central portion of the conservancy during the incursion, and the center, north, and east of the conservancy in the post-incursion period (Fig. 6a).

4.1.2. Grazers

Patterns of site visitation rates in relation to distance to dam were non influential in pre-incursion period and completely opposing when compared between the during and post-incursions periods (Fig. 2b; Table 2). During the incursion grazers visited sites closer to dam and after incursion they visited sites father from the dam (Fig. 2b; Table 2). Across all three time periods, grazers tended to visit sites closer to the boundary of the conservancy (Fig.3b; Table 2). Grazer site visitation rates in relation to distance to human habitation changed considerably across the three time periods (Fig 4b; Table 2). For instance, grazer site visitation rates were considerably higher in sites near to human habitation in the post-incursion period (Fig. 5b; Table 2). Finally, grazers visited sites nearer to the rivers in the pre-incursion period and this pattern was completely opposite in the post-incursion period (Fig. 5b; Table 2). Grazers used the eastern portion of the conservancy in the pre-incursion period, their use was dispersed in the during incursion period, and they used the center, north, and east of the conservancy in the post-incursion period (Fig. 6b).

4.1.3. Mixed feeders

Distance to dam was an influential covariate for elephant site visitation rate in the pre-incursion period, but not so in the during and post-incursion periods (Fig. 2c; Table 2). Elephant site visitation rate increased nearer to dams in the pre-incursion period (Fig. 2c). This same pattern was evidential in relation to the distance to the boundary of the conservancy (Fig. 3c; Table 2). In the pre-incursion period, elephant site visitation rate was higher farther from human habitations, but there was relatively no effect of this covariate in the during and post-incursions periods (Fig. 4c; Table 2). Elephant site visitation rate was higher nearer to rivers across all three time periods, though this effect was diminished in both the during and post-incursion periods

(Fig. 5c; Table 2). Elephants widely used the conservancy in the pre-incursion period with very low site visitation rates in the during and post-incursion periods (Fig. 6c).

Distance to dam had a negligible effect on impala in the pre- and during incursion periods, though impala site visitation rate increased farther from the dams in the post-incursion period (Fig. 2d; Table 2). Impala site visitation rate was highly variable between the three time periods for the distance to boundary, distance to human habitation, and distance to river covariates (Fig. 3d; Fig. 4d; Table 2). Impala used the eastern edge of the conservancy in the pre-incursion period, the central portion of the conservancy during the incursion, and the center, north, and east of the conservancy in the post-incursion period (Fig. 6d).

5.0. DISCUSSION

My research sought to quantify the effects of a pastoralist incursion on the spatial dynamics of large mammals. The results indicated that large mammals were highly affected, but that the magnitude and extent of these effects differed depending on the large mammalian herbivore group. Before the incursion, large mammalian herbivores from all functional groups tended to avoid human habitations and used habitat closer to the river and the conservancy boundary. During the incursion, all functional groups were closer to human habitation and farther from rivers and dams. After the incursion, the functional groups of browsers, grazers and mixed feeders (impala) were closer to the conservancy boundary and river. These results highlight complex and often strong effects of a pastoralist incursion on the spatial dynamics of large mammalian herbivores. The underlying mechanisms associated with these patterns suggest that the livestock in this pastoralist incursion were able to competitively exclude large mammalian herbivores, or that large mammalian herbivores avoided pastoralists and their livestock as forms of disturbance. However, I acknowledge that water is also an important

variable given that the incursion itself was motivated by widespread drought in the region. Thus, the results of my study productively advance discourse on spatial dynamics of large mammalian herbivores in relation to a pastoralist incursion.

Water is an essential resource in the savannas of East Africa and a fundamental component of seasonally dynamic movement and land use among large mammals (Coppock et al., 1986; Fryxell et al., 2004; Hopcraft, 2010). The Ewaso Narok and Ewaso Nyiro rivers provide the only permanent sources of water in Loisaba Conservancy as well as the human communities that lie downstream. Thus, rivers act as a vital lifeline for wildlife, local people, and their livestock (Didier et al., 2011; Ontita, 2012). During the incursion, the Ewaso Nyiro river dried up and there was no water for both wildlife and livestock. This is likely yet another reason why we detected all large herbivore groups to move away from the river and concentrate on the central part of the conservancy during the incursion. The central part of the conservancy features dams where water was reliably located (Fig. 5a, b, c, d). The conclusion is that incursions such as the one documented here can dramatically alter animal-habitat associations to both natural and anthropogenic features.

Additionally, the incursion also was associated with declining forage availability. The livestock grazed onto the conservancy locally depleted the grass resources. During this study, I observed scores of large mammalian herbivores that died as a result of these conditions. Changes in availability and accessibility of forage was important to all large mammal herbivores and livestock, but manifested in different ways. Browsers, for instance, redistributed themselves across the conservancy probably in search of potential forage to maximize their nutritional requirements (Owen & Smith, 1982; Kinga et al., 2018). Wild grazers (buffalo and zebras) and cattle both depend on grass for their nutrition requirements (McNaughton & Georgiadis, 1986;

Beekman & Prins, 1989; Sitters et al., 2009). This can lead to competition and facilitation of grazers and livestock and was likely a mechanism associated with the pattern of grazers dispersing widely across the conservancy during the pastoralist incursion (Young et al., 2005; Odadi et al., 2011; Fig. 6b). I also found impala, as a mixed feeding species, to overlap with grazers along riverine areas and conservancy boundaries preceding the incursion (Fig. 6d, b). During the incursion, they moved to the central part of the conservancy and overlapped with browsers in habitat that was closer to human habitation (Fig. 6c, a). After the incursion period, impalas visited sites closer to the river and conservancy boundary increased and was once again overlapping with grazers (Fritz et al., 1996; Hibert et al., 2010). I suspect that these patterns, in part, derive from impalas' dynamic feeding style allowing them to adjust their spatial interactions with livestock, browsers, and grazers (Hibert et al., 2010).

My research provides additional evidence for the position that pastoralism can have pronounced effects on large mammalian herbivores (Hempson et al., 2017). Ultimately, the nature and intensity of these effects will vary according to numerous factors, including the life history characteristics of the large mammals, seasonality, climate, the number of livestock, and the style of livestock husbandry (Kinga et al., 2018). I acknowledge that assessments across a three-month period directly before and after a large livestock incursion are likely not long enough to fully comprehend the impacts of pastoralist-wildlife conflict. I suspect that different species might have varying periods of recovery to normal dynamics following such incursions. Nonetheless, my study illuminates the highly disruptive potential of pastoralist incursions on the spatial dynamics of large mammalian herbivores.

5.1. Implications for conservation

Although East Africa still supports some of the largest populations of large mammalian herbivores on earth (Ogutu et al., 2016), my analysis shows that spatial dynamics of these species in northern Kenya can be compromised by unmanaged pastoralist incursions. In northern Kenya, pastoral land continues to shrink. Land conversion into farming, human population growth, and the sedentarization of pastoralists have adversely affected grazing resources with coupled negative impacts on both wildlife and livestock.

My research describes the short-term effects of pastoralist incursions on the spatial dynamics of large mammal herbivores. Research of this type is needed for the creation of progressive policies and management decisions regarding pastoralist communities living adjacent to conservancies, as well as pastoralists who originate from other counties and move their livestock over broad spatial scales. This research also has potential applications in catalyzing new dialogues relating to the ways in which pastoralist perspectives can be actively involved in conservation practice. Overall, my research is needed to preserve pastoralist well-being while conserving important species of wildlife that share landscapes with livestock.

APPENDIX

Table 1. Description of covariates used in the site visitation models for large mammalian herbivores in relation to a pastoralist incursion in Loisaba Conservancy, Kenya, May 2016 – October 2017.

Covariate	Description
Distance to dam	Euclidean distance (m) of camera trap site to dam, There are a number of dams in the Conservancy that supply wildlife with water.
Distance to boundary	Euclidean distance (m) of camera trap site to boundary of the Conservancy.
Distance to human habitation	Euclidean distance (m) of camera trap site to closest human habitation. There are several areas of human habitation and use in the Conservancy including tented tourist camps, Loisaba star beds, Acacia campsite, an airstrip, ranger posts, and the Conservancy administration headquarters
Distance to river	Euclidean distance (m) of camera trap site to the main river, the Ewaso Nyiro. The river runs from the south western boundary to the mid-eastern boundary of the Conservancy (see Fig. 1)

Table 2. Posterior means and 95% credible intervals for parameters from site visitation models for the three large mammal herbivore groups browsers, grazers, and mixed feeders (elephant and impala) fit to data across 53 sites in Loisaba Conservancy, Kenya deployed between May 2016 and October 2017. See Table 1 for descriptions of the covariates.

	Browsers			Grazers			Elephant			Impala		
variable	mean	low	up	mean	low	up	mean	low	up	mean	low	up
Intercept*	-0.9	-1.28	-0.54	-0.18	-0.49	0.13	0.17	-0.09	0.42	-0.71	-1.07	-0.35
period_incursion	-0.27	-1.36	0.7	0.9	0.24	1.64	-4.46	-7.34	-2.36	0.66	-0.15	1.44
period_post_incursion	-0.2	-0.77	0.35	0.44	0.01	0.87	-1.72	-2.27	-1.19	1.09	0.64	1.55
Distance to dam_pre	0.04	-0.41	0.51	-0.07	-0.47	0.32	-1.11	-1.47	-0.75	-0.1	-0.58	0.42
Distance to dam_during	-0.51	-1.57	0.51	-0.18	-1.17	0.79	0.48	-1.83	2.64	0	-0.96	0.94
Distance to dam_post	0.46	-0.36	1.23	0.52	-0.08	1.11	0.41	-0.32	1.12	0.97	0.23	1.72
Distance to boundary_pre	-1.38	-1.85	-0.94	-1.28	-1.66	-0.92	-0.41	-0.7	-0.11	-0.63	-1.06	-0.2
Distance to boundary_during	2.63	1.53	3.86	1.1	0.11	2.02	1.32	-0.53	3.49	1.45	0.48	2.45
Distance to boundary_post	0.22	-0.61	1.05	0.5	-0.09	1.05	0.54	-0.11	1.24	-0.68	-1.36	-0.06
Distance to human_pre	-0.48	-1.01	0.05	0.13	-0.38	0.63	0.8	0.41	1.21	0.18	-0.39	0.69
Distance to human_during	1.18	-0.21	2.63	-0.04	-1.03	1.01	-0.71	-3.91	2.44	0.44	-0.63	1.56
Distance to human_post	-1.31	-2.36	-0.25	-1.31	-2.04	-0.57	-0.42	-1.28	0.51	-2.4	-3.3	-1.53
Distance to river_pre	-0.33	-0.66	0	-0.8	-1.08	-0.54	-0.69	-0.93	-0.45	-1.44	-1.85	-1.04
Distance to river_during	0.46	-0.79	1.77	0.77	-0.24	1.71	-2.01	-4.92	0.16	1.66	0.7	2.62
Distance to river_post	0.5	-0.08	1.07	1.52	1.05	2	0.19	-0.46	0.8	2.1	1.55	2.68

*The intercept represents the natural log of mean site visitation rate during the pre-incursion period. Thus, parameters for period effects (rows two and three) are relative to the pre-incursion

LIST OF FIGURES

Figure. A1. The 226 km² Loisaba Conservancy situated in Laikipia County, Kenya. Triangles indicate Human habitations, the blues V shaped images are Loisaba dams and blue lines indicate the Ewaso Nyiro and Narok rivers, the red stars show the distribution of camera traps. The two rivers meet at the Southeastern corner of Loisaba and form one Ewaso Nyiro river.

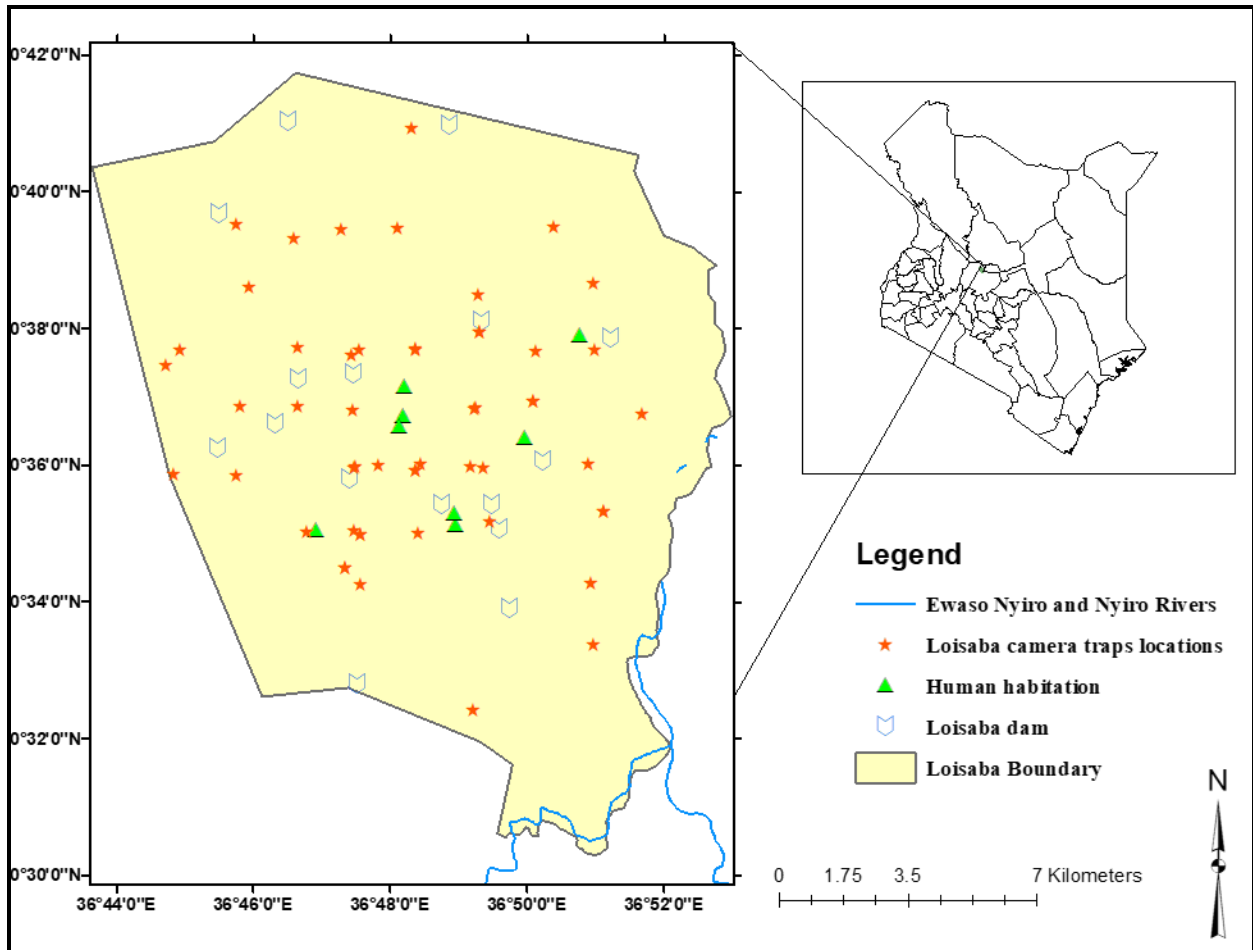


Figure. A2. Plots of effects of distance to dam on site visitation rates for a) browsers, b) grazers, c) mixed feeder – elephants, and d) mixed feeder - impala from the site visitation model fit to data across 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017. The gray lines represent predictions from a random posterior sample of 200 iterations to depict uncertainty.

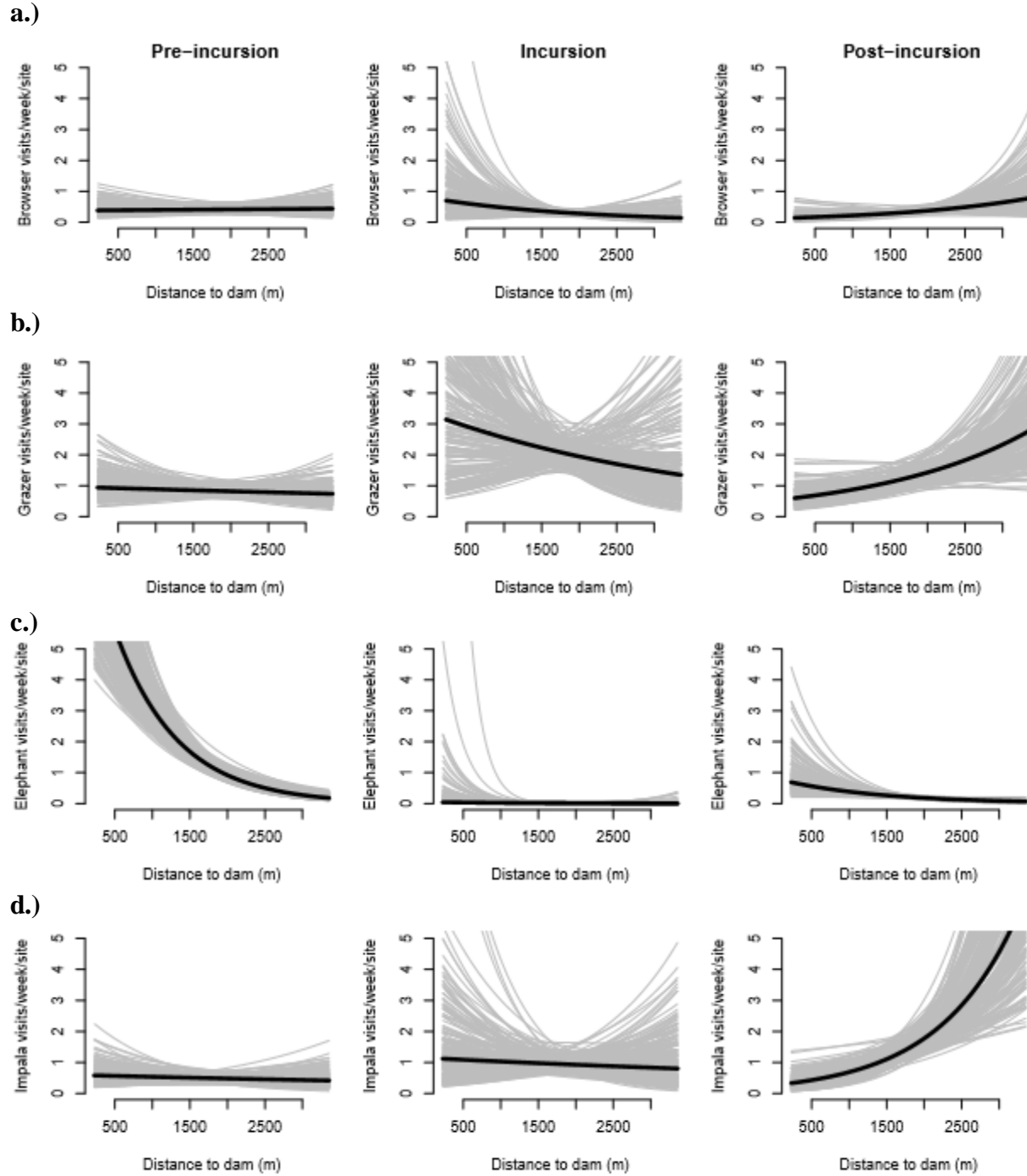
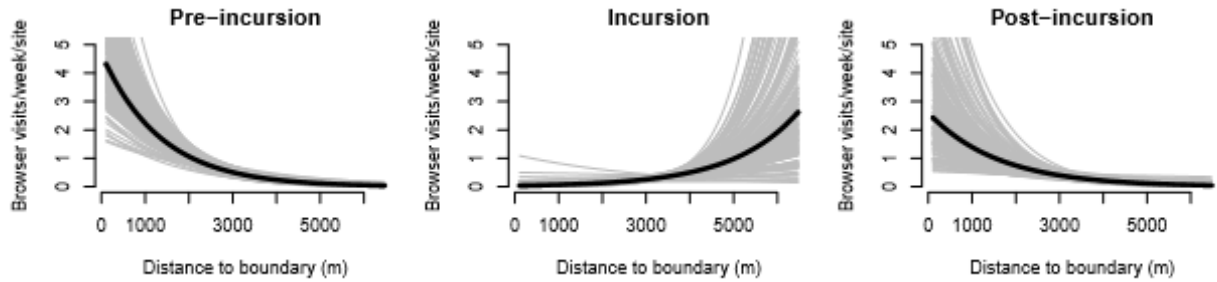
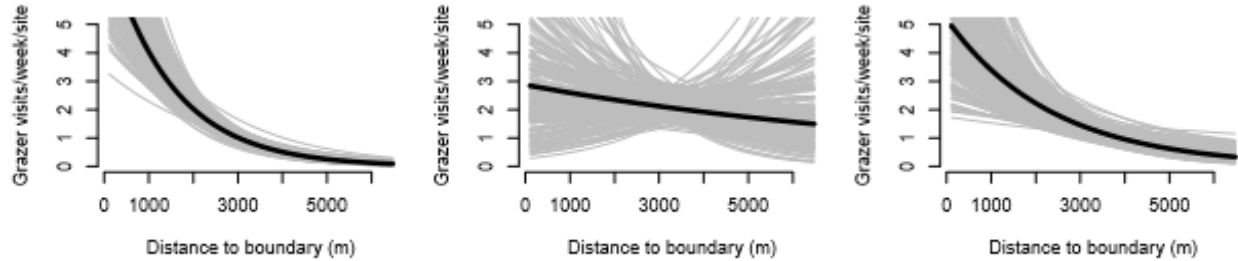


Figure. A3. Plots of effects of distance to boundary on site visitation rates for a) browsers, b) grazers, c) mixed feeder – elephants, and d) mixed feeder - impala from the site visitation model fit to data across 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017. The gray lines represent predictions from a random posterior sample of 200 iterations to depict uncertainty.

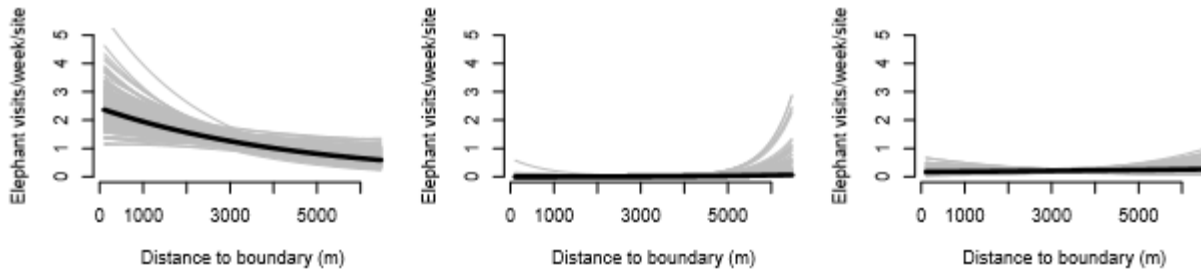
a.)



b.)



c.)



d.)

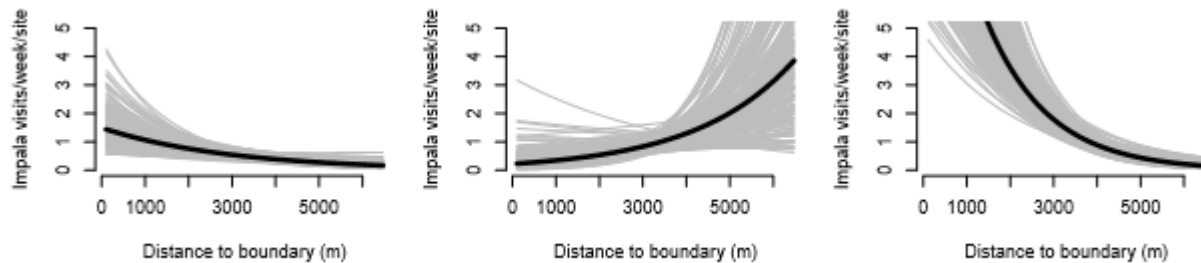


Figure. A4. Plots effects of distance to human habitation on site visitation rates for a) browsers, b) grazers, c) mixed feeder – elephants, and d) mixed feeder - impala from the site visitation model fit to data across 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017. The gray lines represent predictions from a random posterior sample of 200 iterations to depict uncertainty

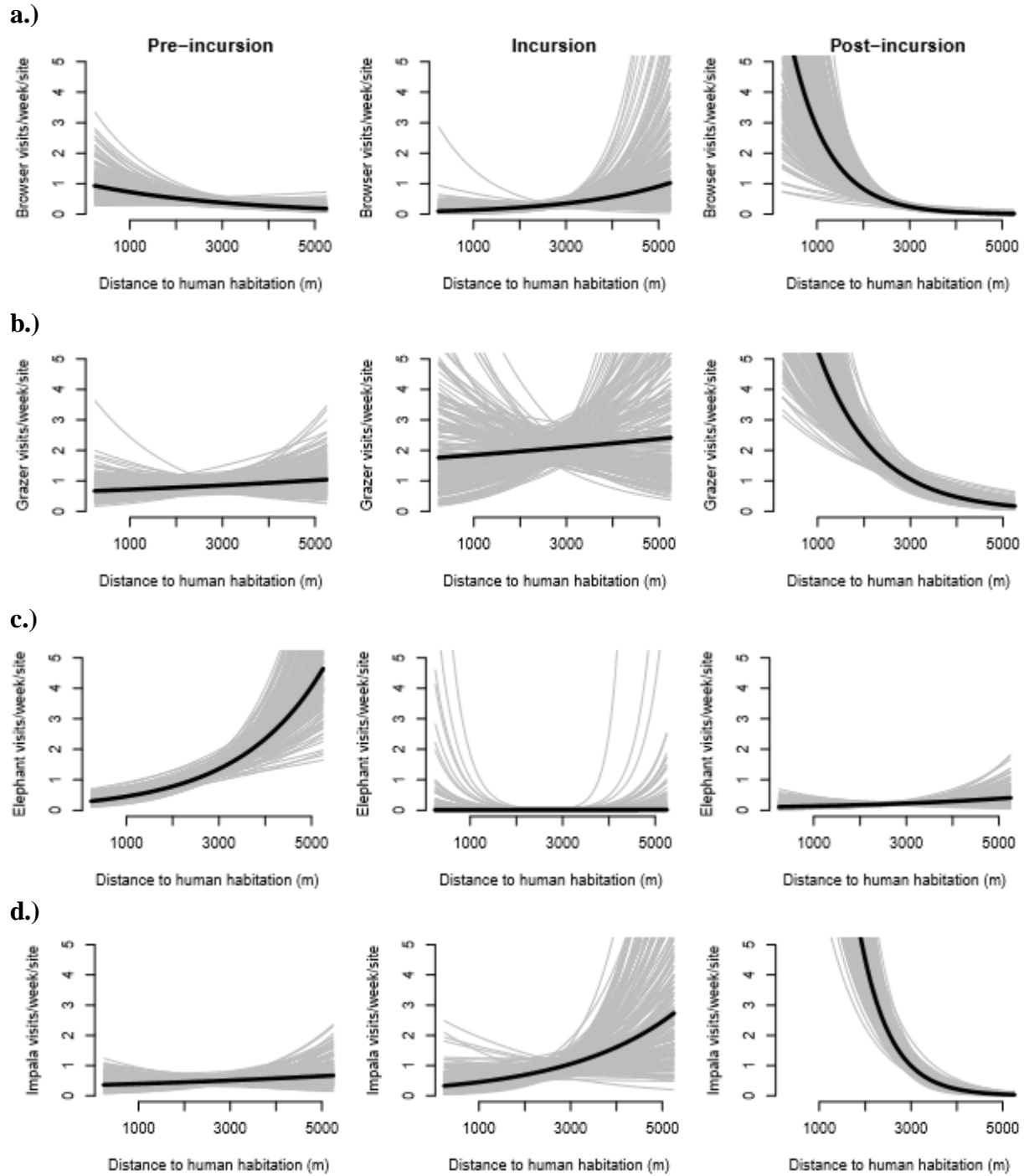


Figure. A5. Plots of the effects of distance to river on site visitation rates for a) browsers, b) grazers, c) mixed feeder – elephants, and d) mixed feeder - impala from the site visitation model fit to data across 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017. The gray lines represent predictions from a random posterior sample of 200 iterations so to depict uncertainty.

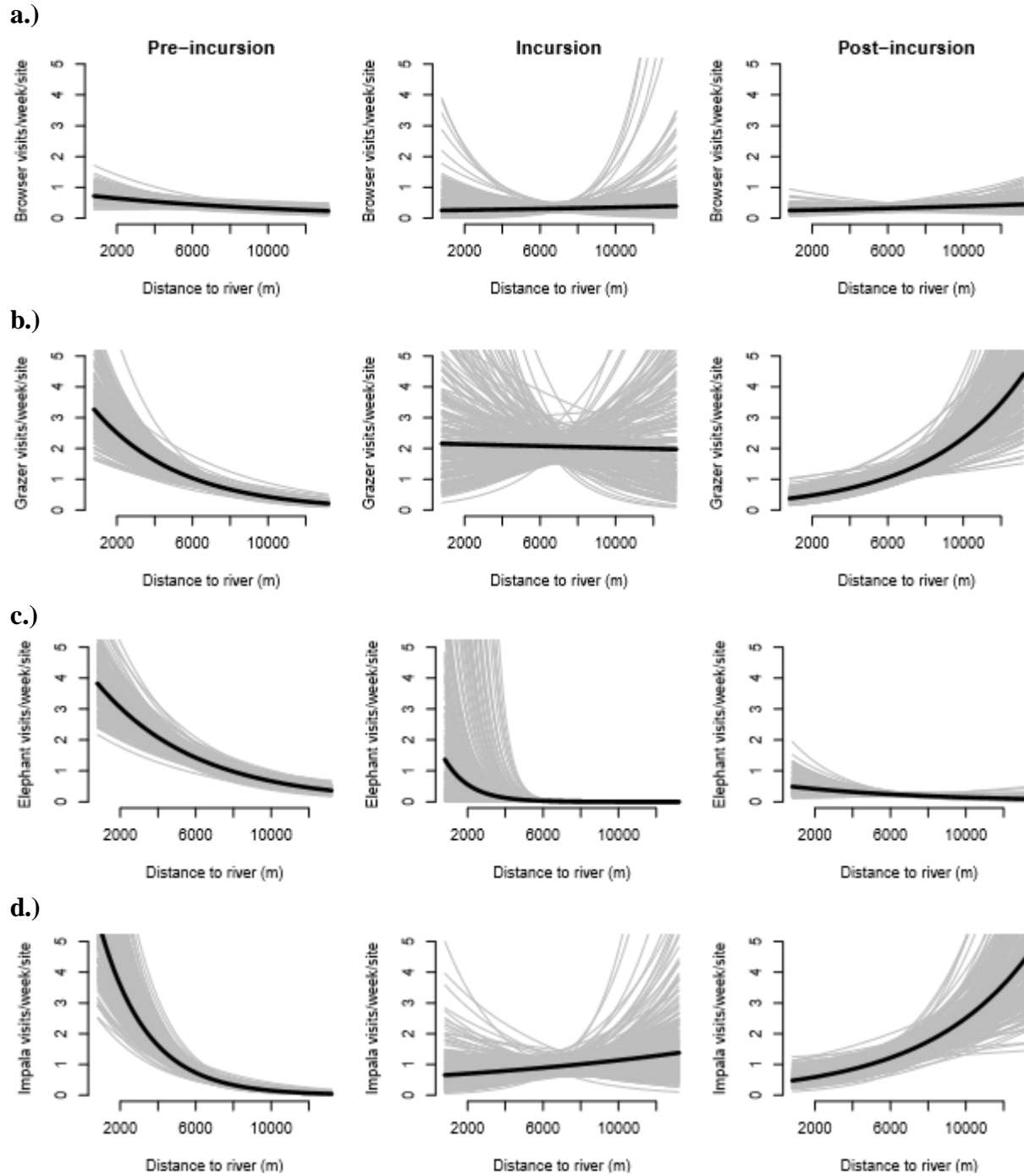
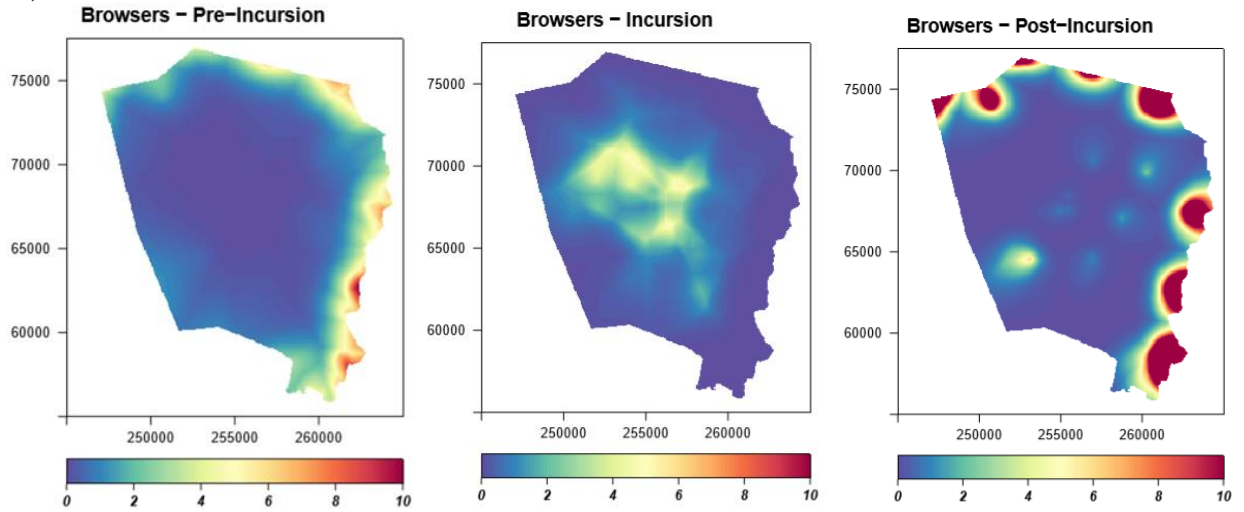


Figure. A6. Spatial predictions of site visitation rates for a) browsers, b) grazers, c) mixed feeder - elephants, and d) mixed feeder-impala from a model fit to data across 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017. The X and Y axes are representative of UTM coordinates. Site visitation rate axes vary among plots.

a.)



b.)

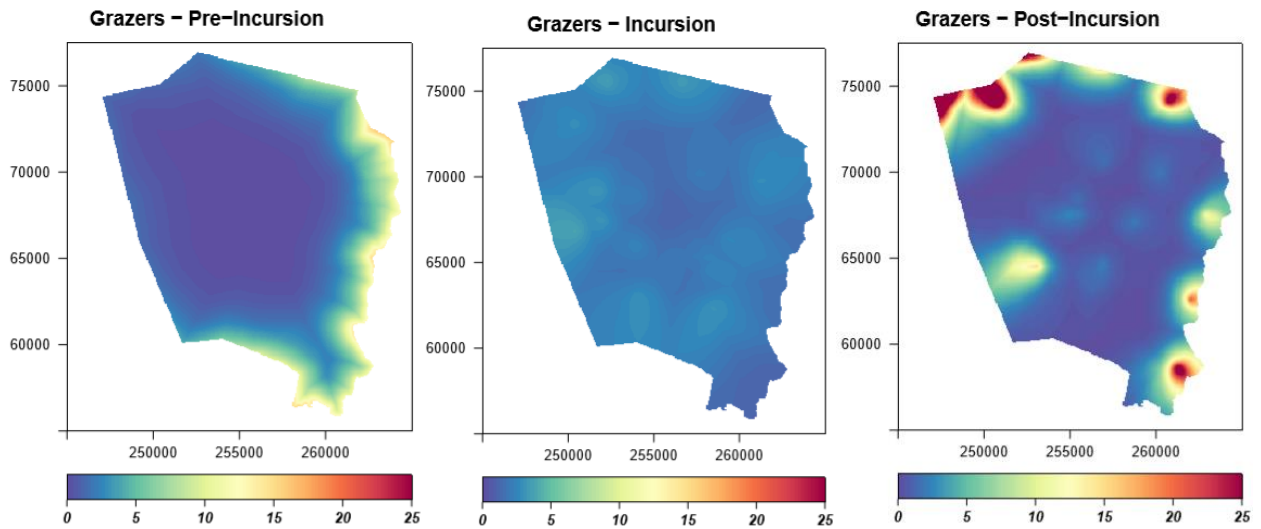
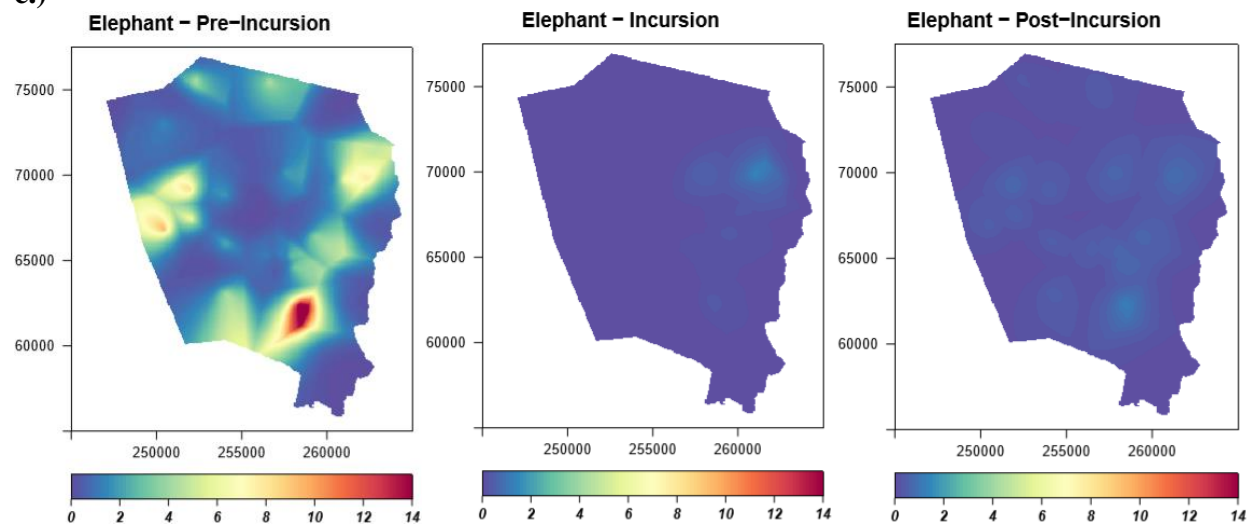
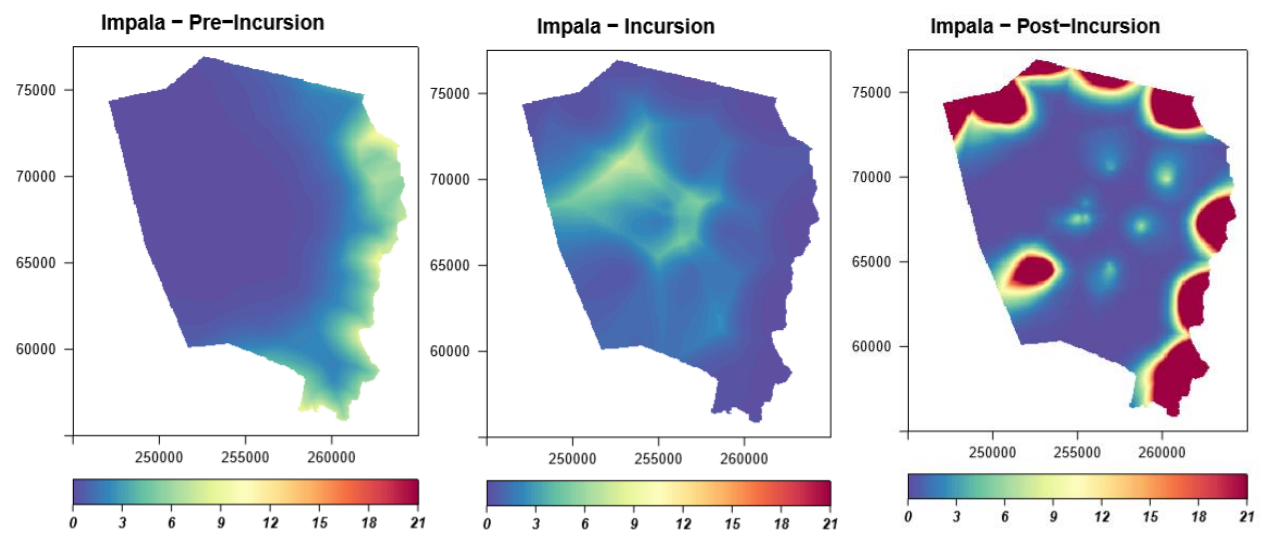


Figure A6. (cont'd).

c.)



d.)



Appendix A. JAGS model code and spline correlograms of model residuals from a Bayesian site visitation model fit to data from 53 sites in Loisaba Conservancy, Kenya, between May 2016 and October 2017.

```
# jags model
model {

  # Site visit priors
  int ~ dnorm(0,0.1)
  A_riv ~ dnorm(0,0.1)
  A_dam ~ dnorm(0,0.1)
  A_bound ~ dnorm(0,0.1)
  A_hum ~ dnorm(0,0.1)

  A_riv_dur ~ dnorm(0,0.1)
  A_riv_post ~ dnorm(0,0.1)

  A_dam_dur ~ dnorm(0,0.1)
  A_dam_post ~ dnorm(0,0.1)

  A_bound_dur ~ dnorm(0,0.1)
  A_bound_post ~ dnorm(0,0.1)

  A_hum_dur ~ dnorm(0,0.1)
  A_hum_post ~ dnorm(0,0.1)

  A_treat[1] <- 0 # Reference category
  for (k in 2:3) {
    A_treat[k] ~ dnorm(0,0.1)
  }

  # priors on gamma
  alpha<-exp(logalpha)
  logalpha ~ dunif(-5,5)

  # Likelihood
  # Loop over rows (sites)
  for (i in 1:R) {

    # Loop over columns (replicate periods)
    for (j in 1:T) {

      y[i,j] ~ dpois(mustar[i,j])
      mustar[i,j] <- rho[i,j]*mu[i,j]
      rho[i,j] ~ dgamma(alpha,alpha)

      log(mu[i,j]) <- int +
        A_treat[treatment[j]] +
```

```

A_riv * d_riv[i] +
A_dam * d_dam[i]+
A_bound * d_bounde[i]+
A_hum * d_hum[i] +

A_riv_dur* equals(TREATMENT[j],2) *d_riv[i] +
A_riv_post* equals(TREATMENT[j],3) *d_riv[i] +

A_dam_dur* equals(TREATMENT[j],2) *d_dam[i] +
A_dam_post* equals(TREATMENT[j],3) *d_dam[i] +

A_bound_dur* equals(TREATMENT[j],2) *d_bound[i] +
A_bound_post* equals(TREATMENT[j],3) *d_bound[i] +

A_hum_dur* equals(TREATMENT[j],2) *d_hum[i] +
A_hum_post* equals(TREATMENT[j],3) *d_hum[i]

} #j
} #i
}

```

Figure. A7. Spline correlograms of model residuals for a) browsers, b) grazers, c) mixed feeder – elephants, and d) mixed feeder - impala. The distance on the x-axis represents kilometers between paired locations. The plots depict mean correlation and a 95% confidence envelope. For all browser, grazer, and mixed feeder (elephant and impala) model residuals, the confidence envelope overlaps zero at all distances, indicating a complete lack of autocorrelation.

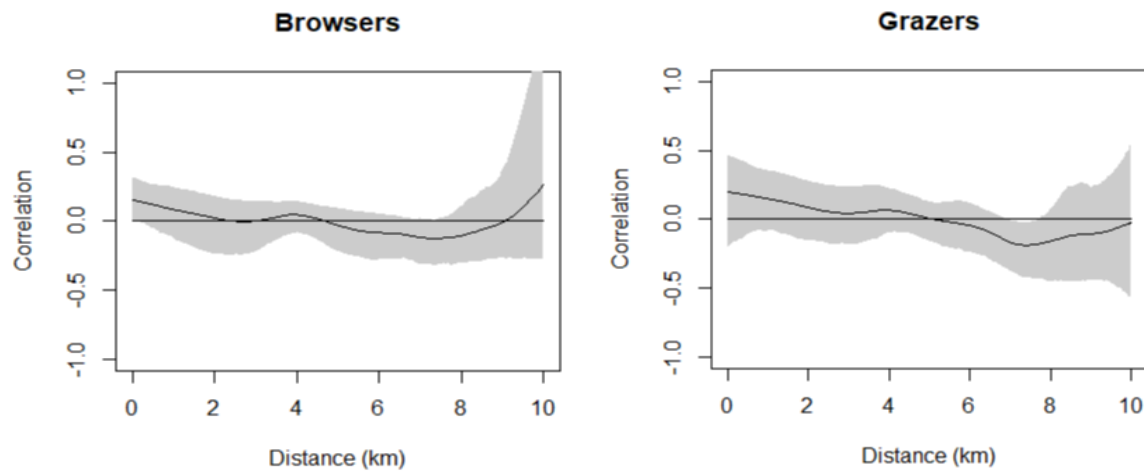
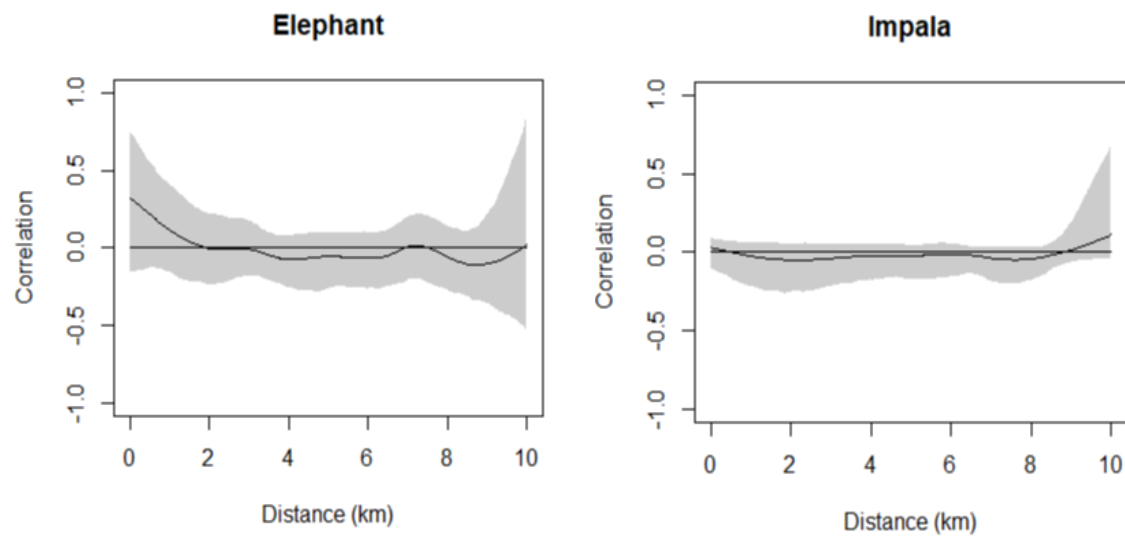


Figure. A7. (Cont'd)



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