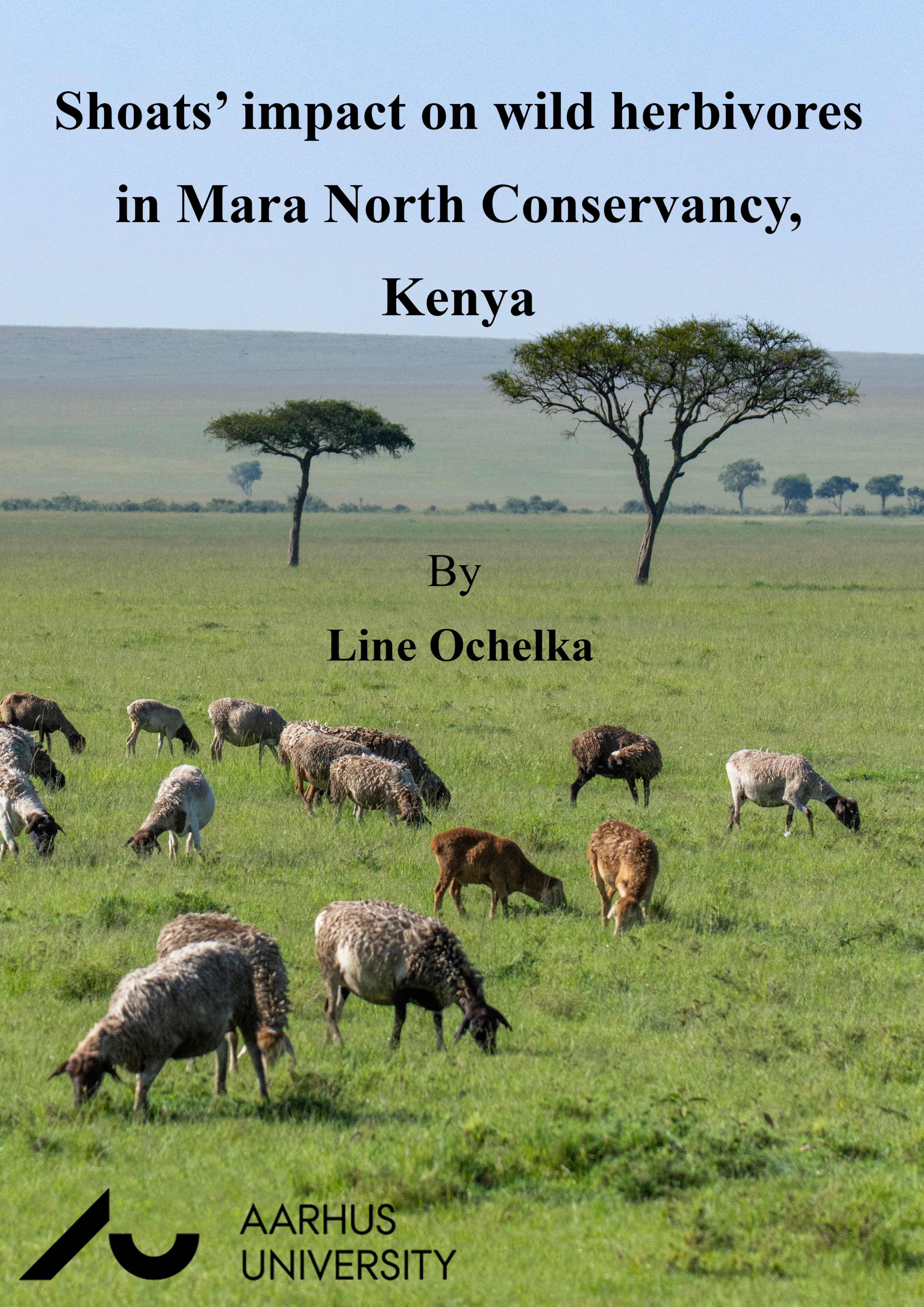

Shoats' impact on wild herbivores in Mara North Conservancy, Kenya

By

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AARHUS
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Shoats' impact on wild herbivores in Mara North Conservancy, Kenya

60 ECTS Master's Thesis

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Preface

This master thesis is the conclusion of my Master's Degree in biology at the Section for Ecoinformatics and Biodiversity – Department of Biology from the Faculty of Natural Science, Aarhus University. The master thesis is the product of 60 ECTS (10 months) work, including 2,5 months of fieldwork in Mara North Conservancy, Kenya. The master thesis is made in collaboration with Maasai Mara Science and Development Initiative and is meant to contribute to the science-based sustainable conservation approach in Mara North Conservancy.

During my research and work in the last 10 months, several people have helped me on different levels, and I would like to express my gratitude to all. My master thesis would not have been possible without the exceptional help from my supervisor Jens-Christian Svenning and co-supervisor Robert Buitenwerf. I would like to thank you for your help in developing this project. Furthermore, I would like to thank you for all your feedback throughout the entire process. I would also like to thank Karen Blixen Camp and Maasai Mara Science and Development Initiative. My project and field work in Mara North Conservancy would not be possible without them. A big thank you to all the staff at Karen Blixen Camp for the warm welcome and for hosting me, and thank you to Jesper Stagegaard for helping me with the arrangements for transportation and my stay at Karen Blixen Camp. One of my biggest gratitude's goes to the Maasai Mara Science and Development Initiative, Jully Senteu and David Noosaron. Without your help fieldwork in Mara North Conservancy would not have been possible.

This thesis consists of two parts – Part A and Part B. Part A is a general introduction to the project, the savanna ecosystem, Mara North Conservancy and the interactions between wildlife and livestock. Part B is an article manuscript for publishing in African Journal of Ecology.

Abbreviations

Maasai Mara National Reserve (MMNR)

Mara North Conservancy (MNC)

Sheep and goats (Shoats)

Serengeti-Mara Ecosystem (SME)

Serengeti National Park (SNP)

Human-wildlife conflict (HWC)

Part A

General introduction to the African savanna ecosystem and the interactions between wildlife and livestock.

Introduction

The savannas worldwide are vital for both socioeconomic and biodiversity values. Savannas are unique ecosystems continuously changing with an increase in human populations, settlements, human-wildlife conflicts (HWC), and livestock populations (Odadi et al. 2011, Løvschal et al. 2017, 2018). In savannas, worldwide domestic and wild herbivores commonly share food, habitat, and other resources. In these ecosystems, management decisions are based on the perception that wildlife and livestock compete for these resources, yet there are virtually no experimental data to support this assumption. To be able to protect both wildlife and pastoral lifestyle on savannas, it is essential to understand the interaction between wildlife and livestock, because of their shared land use (Odadi et al. 2011). An important interaction between different wildlife species, and also between wildlife and livestock, are resource competition. In order to study resource competition, it is important to understand the main drivers that structure the distribution of resources used by herbivores in space and time. To understand the main drivers, it is also important to understand the African savanna as an ecosystem, and which challenges both the savanna, wildlife and local people face on the modern savanna. To support this knowledge, it is also important to understand the specific area where the interactions occur due to the difference between protected and semi-protected areas.

In recent years, there has been a switch from cattle to shoats (sheep and goats), which have coursed the number of shoats to increase rapidly. The increase of shoats raise new questions about the influence of shoats on the savanna ecosystem and the interaction between shoats and wild herbivores (Bedelian and Ogutu 2017). It is therefore important to understand the drivers behind the switch from cattle to shoats, the shoats feeding behavior and how the wild herbivores respond to the presence of shoats.

The African Savanna

The defining feature of savannas is that they are dominated by species with two different growth forms and life histories – woody plants and grasses (Archibald et al. 2020). Savannas constitute one of the largest biomes of the world, which covers about 20 percent of the land surface and are composed of complex, multivariate relationships among vegetation, herbivores, predators and disturbance (Shorrocks 2007, Osborne 2012, Anderson et al. 2016). Savannas are tropical and subtropical grasslands with scattered bushes and trees. They are found around the world, including Africa, South America, India and Australia, with the most savanna in Africa, and occur around the equator, where it is warm, but relatively dry. Most experience seasonal drought, and the vegetation is influenced by rainfall, soil type, grazing, browsing, and fire. The vegetation is dominated by C_4 plants where the CO_2 is first combined into a 4-carbon compound in the mesophyll cells of the leaf and then passed to the cells around the leaf veins where the CO_2 is released at high concentrations. It then enters the photosynthetic carbon reduction pathway (PCR) or Calvin-Benson Cycle, also used by C_3 plants. C_4 plants are able to utilize higher light intensities than C_3 plants, have greater maximum photosynthesis, and use less water in the process, which makes them ideal for the savanna ecosystem (Young et al. 2005, Beerling and Osborne 2006, Shorrocks 2007, Osborne 2012).

Africa is home to more ungulates than any other continent, and the savannas are home to the world’s most abundant and diverse communities of large mammalian herbivores. It is therefore especially important to understand the different trophic levels on the savanna. Otherwise, the development of management plans could be flawed, and important species could be lost. The greatest species richness is found in the grass-dominated savannas of East Africa and it is therefore important to focus on this area (Anderson et al. 2016, Abraham et al. 2019). The African savannas are represented by several trophic levels. The first level is the primary producers which consist of a sparse tree cover underlain by a highly flammable C_4 grass layer. The primary producers are being consumed by the next tropic level – the primary consumers. The primary consumers include herbivores who graze or browse on the savanna vegetation. The herbivores can be divided into different categories according to their herbivore functional types. This includes small nonsocial browsers, medium-sized social mixed diets, large browsers, water-dependent grazers and nonruminants. Dividing the herbivores according to functional types gives a better understanding on their impact on the vegetation structure on the savanna (Hempson et al. 2015). The variation in predation risk also contribute to the spatial use of the herbivores and where they forage. Predators are therefore important to take into account when discussing herbivores and their impact on the vegetation structure (Burkepile et al. 2013). Predators are therefore a part of the next tropic level – the secondary consumers, which include hyenas, wild dogs, snakes, bird of prey, lizards, cheetahs, leopards and lions. Some species, such as lions, are also a part of the level tertiary consumers which prey upon both herbivores and other carnivores (Fritz et al. 2011, Anderson et al. 2016). Scavengers, which include vultures, storks, termites etc., and decomposers, which include insects, mushrooms and bacteria, also play an important role in the ecosystem by consuming carcasses and feces, which ends as nutrients for the savanna vegetation (McNaughton and Georgiadis 1986, Fritz et al. 2011, Anderson et al. 2016, Velado-alonso et al. 2020).

Determinants of the Savanna structure

In order to study resource competition between herbivores it is important to understand the main drivers that structure the distribution of resources used by herbivores in space and time. The key drivers of the African savanna include herbivory, fire, rainfall, and soil texture and nutrients, where fire and herbivory often act together to maintain the vegetation structure and are shown to influence the savanna vegetation composition (Archibald et al. 2005, Sankaran et al. 2008, Riginos et al. 2018). The two drivers also affect each other, where fire affects herbivores by altering large-scale foraging patterns through frequently burning areas so new, tender grass shoots and attracts herbivores, and herbivores affect fire by reducing fuel loads and altering fire spread in the savanna landscape through foraging (Archibald et al. 2005, Burkepile et al. 2013). Together they act to constrain tree cover in the landscape (Ratnam et al. 2020). Fire acts as a source of consumer control with implications for evolutionary adaptations, plant ontogeny, and the filtering of plants by functional traits adapted to prevailing fire regimes (Hoag and Svenning 2017). Fire is a strong predictor of the global distribution of the savanna biome and of tree cover within savannas (Staver et al. 2011), and maintain the tree–grass balance and 'compete' with herbivores for herbaceous vegetation (Anderson et al. 2016). The importance of fire as a driver varies and is typically greatest in mesic savannas, and fire-maintained savannas are typically found under wetter conditions such as in forests (>1000 mm). The spread of the fire depends on a continuous grass layer, to which tree cover act as a barrier. However, the tree cover has little effect on the spread of fire, frequency, or size until it reaches a specific threshold (45 to 50 %) (Staver et al. 2011). In forests, fire is limited by fuel loads, low probabilities of ignition and shorter dry seasons overall, whereas in arid and semi-arid savannas, fire is similarly limited to fuel loads but also to fuel contiguity (Sankaran et al.

2008, Ratnam et al. 2020). The plants in arid and semiarid savannas exhibit adaptions to fire, where trees and shrub have a thick, insulating, corky bark and can sprout from underground organs. Grasses also sprout from underground organs and utilizes the enriched soil from the ash (Osborne 2012). Globally, 3.6-4.6 million km^2 of land burns annually of which >80% comprises savannas, where Africa alone accounts for >60% of the global area burned annually. By burning these large areas across Africa, fire can also serve to extend the geographic distribution of savannas beyond their climatically determined limits (Ratnam et al. 2020). The natural fires are typically started by lightning during thunderstorms, but humans have also started fires to maintain the savanna vegetation, to improve pastures, to clear the land for cultivation, or to keep animals away from villages (Osborne 2012). Human impacts on fire are pervasive, altering the extent of fire and also its seasonal patterns. But fire has often been characterized as the ultimate non-selective herbivore, whereas different species of herbivores have different forage preferences (Archibald and Hempson 2016).

Herbivores influence the environment in a number of different ways. The savanna herbivores range in size from the dik-diks (*Madoqua kirkii*) (3 to 4 kg) to the adult male savanna elephant (*Loxodonta africana*) (2500 kg). All the different herbivores impact the vegetation differently (Cumming 1982). Herbivores can indirectly affect the vegetation by fueling fires, which leads to the regrowth of a high-quality vegetation layer. Herbivores often prefer to graze in areas which have been recently burned due to the high-quality vegetation. Grasses are fire adapted and therefore respond well to fire. When burned grasses have a rapid re-growth, improved seed germination and even providing their own fuel to carry fires in the form of litter (Keyser et al. 2015). Fire can therefore have a diverse range of effects on the savanna structure, from directly suppressing tree and shrub cover to facilitate encroachment of the trees and shrubs (Anderson et al. 2016, Ratnam et al. 2020). Grazers promote woody vegetation by removing the herbaceous competitors, exerting also a negative effect on fires that are fueled by herbs, whereas browsing has the opposite effect, promoting herbaceous plants and therefore promoting fire (Hoag and Svenning 2017). Megaherbivores (>1000 kg), such as elephants and Maasai giraffes (*Giraffa camelopardalis tippelskirchi*), have the potential to facilitate forage availability for smaller herbivores. Elephants push trees to the ground and thereby encourage resprouting, thus increasing availability to small herbivores (Anderson et al. 2016, Oliveras and Malhi 2016). The opening of the canopy also favors grasses, which again fuels fires and the fires inhibit tree recruitment by killing tree seedlings

(Osborne 2012, Ratnam et al. 2020). But the importance of fire and herbivory vary across rainfall and soil fertility gradients (Ratnam et al. 2020).

The seasonal rainfall also plays a critical role in driving the vegetation structure. The rainfall also has a role in determining what kind of vegetation can be found in a given area (Shorrocks 2007, Ogutu et al. 2020). Rainfall controls the quality and quantity of forage for the savanna herbivores, which, according to a study from Bartzke et al. (2018) and Ogutu et. al. (2020), gives a strong positive correlation between rainfall and animal biomass, abundance and population dynamics in African savannas (Bartzke et al. 2018, Ogutu et al. 2020). The distribution and seasonality of the rainfall also drives animal migration and dispersal. If rainfall is lacking, animals may alter their migratory routes and short-term movements as a consequence of the missing rainfall, but with low rainfall, animals are forced to travel longer distances in order to reach water and foraging grounds, thus making their offspring more vulnerable to predation (Bartzke et al. 2018). Savannas are unstable states that can transition between grassland and closed forest (Hoag and Svenning 2017). In a study by Oliveras and Malhi (2016), they display the ever-changing environment with the influence of rainfall on fire and herbivory. If the rainfall is low, it will enhance the probability of fire and herbivory with a small probability of survival for juvenile woody vegetation. Meanwhile, if the rainfall is higher it will result in a change from savanna to forest. The alternative stable state in the middle is an ever-changing environment controlled by the two positive feedbacks, which are acting in different directions (Figure 1) (Staver et al. 2011, Oliveras and Malhi 2016).

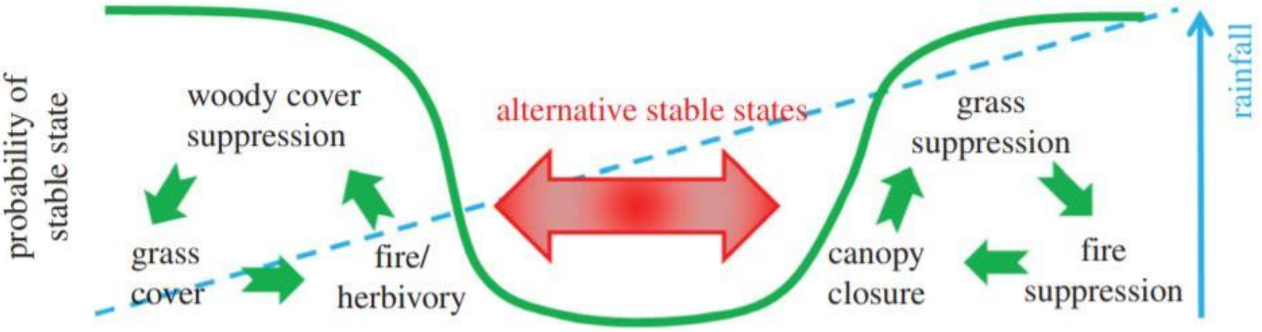

Figure 1 – From Oliveras and Malhi 2016: Illustrates the alternative stable states theory in forest-savanna transitions. Low rainfall levels lead to grasslands with limited woody cover which enhances the probability of consumption by herbivore and/or fire. High rainfall levels lead to a more closed canopy and a barrier for fire. Intermediate rainfall however leads to an ever-changing environment due to the two positive feedbacks acting in different directions.

Soil texture and nutrients are likewise important determinants of the savanna structure and can also influence the migratory routes and movements of animals. Sandier soils show higher densities of woody vegetation, but are lower in nutrients. The lower amount of nutrients reduce the competition from herbaceous vegetation because of the deeper water percolation (Archibald et al. 2009, Staver et al. 2017, Messina et al. 2018, Ratnam et al. 2020). This will, on the other hand, favor deep-rooted species and woodier savannas, while clay soil will have more herbaceous vegetation because of the higher water retention. Nitrogen and phosphorus can likewise shift the balance between woody and herbaceous elements. Savannas become less woody in N-rich soils and more woody in N-poor soils (Ratnam et al. 2020).

Challenges in the Savanna ecosystem

Different challenges can also have an impact on the interaction between herbivores and on the local communities on the African savanna. It is therefore important to address which challenges the wild herbivores and the local people face in the modern savanna.

Globally, tropical savannas are among the most threatened biomes (Ratnam et al. 2020). Over the past 50-100 years, Africa has seen a warming trend that will continue across the continent (Hoag and Svenning 2017). Rainfall are expected to decrease in the Northern Africa and the southwestern regions of Southern Africa, while Eastern and Western Africa could see an increase in rainfall overall including increases in the frequency of extremely wet and dry years (Hoag and Svenning 2017). The change in rainfall could have considerable consequences for crop and livestock production, and the survival of flora and fauna will be challenged (Hoag and Svenning 2017).

Interactions between modern humans and savannas stretch back to at least 200.000 years ago, and the savannas contain a wide spectrum of social systems with divergent population densities, land tenure systems, and land use practices. Worldwide the savannas deliver a range of supporting and provisioning ecosystem services that sustain the livelihoods of millions of people. This can either be indirectly by supporting key economic activities, or directly by providing for people’s everyday needs. Savannas provide forage for commercial and subsistence livestock farming, habitat to support the wildlife industry, timber and non-timber forest production such as food and medicin (Twine 2020). Human activities have influenced ecological characteristics of savannas for thousands of years. These activities are changing the nature of the fundamental driving variables with more intense climate change progresses due to rapid human population growth (Blackburn et al. 2016). The growth in human population has also led to an increase in human activities in rangelands bordering many reserves, leading to habitat loss and encroachment. Kenya has experienced exponential human population growth in recent decades. In 1960 Kenya's population was about 8 million people, but in 2018 this number increased to about 49 million people. Human activities have caused large wild herbivore populations to rapidly decline, often being replaced by livestock (Blackburn et al. 2016, Riginos et al. 2018, Twine 2020). Human settlements are expanding faster around protected areas due to enhanced economic activities and opportunities inside and around these areas. One example from Maasai Mara National Reserve (MMNR) in Kenya shows this rapid expansion. Rapid declining of wildlife numbers is associated with the progressive intensification of land use in pastoral systems in east Africa. The declines are related to increasing numbers of people, settlement poaching and land use changes on the pastoral ranches. Continuous land use change is predicted to erode grazing areas with an increase in competition between livestock and wildlife for resources, which can lead to declines in wildlife and livestock populations (Bhola et al. 2012, Blackburn et al. 2016, Twine 2020). But increasing numbers of livestock also lead to overgrazing which can have significant consequences for rural livelihoods and wildlife (Boles and Lane 2019).

The increase in human settlements and livestock leads to conflicts with wildlife. The wildlife found on savannas is not only making a massive contribution to national and regional economics, primarily through ecotourism, but also has a cost (Veldhuis et al. 2019, Twine 2020). The loss of human life, loss of livestock, crops and property which leads to a loss in income. This can lead to conflict between humans and wildlife called human-wildlife conflicts (HWC), which are conflicts between the specific interest of people living close to wildlife in rural areas. HWC is often caused by an increase in human population, high number of livestock and wildlife, climate and changes in land use, and often happens during severe droughts. HWC also has a cost for wildlife. Wildlife suffer from poaching, hunting, and habitat destruction and loss (Shorrocks 2007, Mukeka et al. 2019, Twine 2020). In the Maasai Mara, main predator species that caused conflict were spotted hyenas (*Crocuta crocuta*) (53%), African leopards (*Panthera pardus pardus*) (32%) and lions (*Panthera leo*) (15%), but cheetahs (*Acinonyx jubatus*) also occasionally predate on small stock (Broekhuis et al. 2018). Megaherbivores (>1000 kg) and megacarnivores (>100 kg) are rapidly declining, due to the threats including hunting, fencing and habitat destruction or fragmentation stemming from human activity (Hoag and Svenning 2017). The declines of large herbivores in savanna ecosystems may reduce beta diversity and the spatial heterogeneity of woody vegetation, particularly as fencing and artificial water points alter the way the large herbivores move through the landscape (Hoag and Svenning 2017). Furthermore, the change in movement from herbivores could reduce grass fuel and fires, weaken the capacity of soils to sequester nutrients and carbon, and decrease the responsiveness of primary production to rainfall (Veldhuis et al. 2019).

Many pastoralists in savannas are changing their lifestyle into a more sedentary one, thus combining pastoralism with agriculture. Since the 1980s group ranches have been subdivided, the results have been loss of wild herbivores, increasing HWC over natural resources and habitat fragmentation (Sitters et al. 2009), but fragmentation of rangelands also have a negative effect on pastoralist and wildlife (Hoag and Svenning 2017, Boles and Lane 2019). One of the major reasons for fragmentation is fencing. With land privatization and fencing of communal grazing areas, East Africa is struggling with one of the most radical cultural and environmental changes in its history. The use of fences has both benefits and costs to people and wildlife. Fences can be used to prevent poaching and other illegal activities, as well as to avoid the spread of diseases between wildlife and livestock. But fencing can also cause habitat fragmentation, which can have major consequences for wildlife (Hoag and Svenning 2017, Løvschal et al. 2017). One consequence of the increasing level of fencing is the redirection of wildlife migrations which have negative consequences on the population size of the migrating wildlife (Løvschal et al. 2017). One of the ungulate migrations in the Greater Mara ecosystem is the Mara-Loita migration. The Mara-Loita migration used to be concentrated around the Loita Plains, where up until the late 1970s, this migration involved the movement of wildebeest (*Connochaetes*), plains zebra (*Equus quagga*), Thomson’s gazelle (*Eudorcas thomsonii*) and eland (*Tragelaphus oryx*). However, during the last five years the Mara-Loita migration has virtually collapsed due to the dramatic increase in fences on the Loita Plains (Ogutu 2020). Fencing has also been used to remove people from wildlife areas, which can result in negative attitudes towards conservation, but this sort of fencing can be very important in dryland and migratory ecosystems such as the Maasai Mara in Kenya (Broekhuis et al. 2018).

Wild herbivores on the savanna

In order to study interactions between herbivores, it is also important to understand the herbivores feeding ecology and functional types to get a better understanding about how the herbivores impact the ecosystem. Another important subject is to understand the different types of interactions which can be observed between herbivores. This can give a better understanding about how the herbivores interact and behave in the same ecosystem. All this combined, give a clearer picture about how sheep and goats (shoats) can influence the wild herbivores and how the wild herbivores may either benefit or lose from the presence of shoats.

The wild herbivores on the African savanna have different feeding ecologies. Some herbivore species are pure grazers, while others are either mixed feeders or pure browsers (McNaughton et al. 1988, Lundgren et al. 2020). In the Mara the dominant grazers are Grant's zebra (*Equus quagga boehmi*), hippopotamus (*Hippopotamus amphibius*) and Western white-bearded wildebeest (*Connochaetes taurinus mearnsi*) (Owaga 1975), while black rhino (*Diceros bicornis*), eland and dik-dik are browsers and elephants, Thomson's gazelles and impala (*Aepyceros melampus*) are mixed feeders (Roosendaal 1973, McNaughton and Georgiadis 1986, Pansu et al. 2019). Other factors can also have an influence on the utilization of forage. These include body size, craniofacial anatomy, and gut architecture, herbivore distribution and vegetation heterogeneity, plant traits such as height, nutritional content, defenses and species interactions such as competition and predation (McNaughton and Georgiadis 1986, Pansu et al. 2019). When these traits or habitats overlap it can often lead to interspecific competition or facilitation (Butt and Turner 2012).

Interspecific competition

Interspecific competition is the competition between two animal species, which are often ecologically similar and is an important mechanism structuring ecological communities (Razgour et al. 2011). This is only possible when the following three conditions are met: (1) populations of the different species must share resources in the same habitat; (2) these resources must be limited, and; (3) the joint exploitation of those resources and/or interference interactions related to the resources must negatively affect the performance of either or both species (Sinclair and Norton-Griffiths 1982, de Boer and Prins 1990, Butt and Turner 2012). Interspecific competition predominates during the winter or dry season, when resources are less available (Arsenault and Owen-Smith 2002). There are only a limited number of ways of "making a living" within ecological communities, but the different herbivore species have different ways of dealing with competition

(Griffin and Silliman 2012). One way is through resource partitioning, which means that species change their use of resources in response to selection pressure from interspecific competition and facilitates coexistence in a variety of animal communities. In this way different species can coexist in a habitat with limited resources (Razgour et al. 2011, Kartzinel et al. 2015). Resource partitioning can be divided in two ways; dietary and spatial/temporal partitioning.

Consumptive competition is the most frequent from of competition observed in terrestrial animal studies. Dietary partitioning is an important mechanism of differentiation ecological niches and avoiding interspecific competition (Sutherland 2011). A known theory when discussing dietary partitioning is the grazer-browser spectrum. The grazer-browser spectrum divides species into three different categories; grazers, mixed feeders and browsers, which allows multiple of different species to co-exist because of the lack of competition (Van Der Merwe and Marshal 2012, Crego et al. 2020, Pringle 2021). Grazers forage on grasses, while browsers forage on trees and shrubs and mixed feeders both browse and graze, therefore foraging on a wide variety of vegetation (Shipley 1999, du Toit and Olff 2014). Mixed feeders tend to switch back and forth between grazing and browsing depending on availability of forage; browsing when the grass is limited during the winter or dry season and graze when grass is available (du Toit and Olff 2014). At the same time, species can be generalists, foraging on a broad range of plant species, or specialists, foraging on very few plant species, when it comes to their forage behavior (Pansu et al. 2019).

Other key factors in dietary partitioning are body size, gut morphology and mouth physiology (du Toit and Olff 2014, Fynn et al. 2016). Small-bodied herbivores require more energy per unit of body mass compared to large herbivores, which means they can only be sustained by highly digestible forage (Clauss et al. 2013). Their higher energy requirements constrain them to select rarer high-quality forage. Whereas, large-bodied herbivores have lower relative metabolic requirements which constrain them to a diet of more abundant but lower quality forage. The large-bodied herbivores also have a larger less selective mouth, which helps them have a greater food intake (Arsenault and Owen-Smith 2002, Fynn et al. 2016). Narrow-mouthed herbivores, such as reedbuck (*Redunca redunca*), hartebeest (*Alcelaphus buselaphus cokeii*) and Defassa waterbuck (*Kobus ellipsiprymnus*), are better able to select higher quality forage, whereas broad-mouthed herbivores, such as white rhino (*Ceratotherium simum*), are more efficient at foraging on short, dense swards of grass with small ability to select forage (Fynn et al. 2016). Arsenault and Owen-Smith (2002) investigated an increase in white rhino abundance in the Hluhluwe Umfolozi Park in South Africa. The increase was associated with declines by reedbuck and waterbuck, both dependent on tall grass. Whereas, species preferring short grass, such as wildebeest, zebra, impala and common warthog (*Phacochoerus africanus*) maintained or increased their abundance. This demonstrated that the white rhinos were competing with species who were dependent on tall grass, but were facilitating species favoring short grass (Arsenault and Owen-Smith 2002). Smaller species, and those with narrower mouths, have higher among-individual variation of forage than large-bodied and/ or broad-mouthed species (Pansu et al. 2019). Herbivores are also divided into ruminants and hindgut fermenters (non-ruminant). Ruminants include wildebeest, cape buffalo (*Syncerus caffer*), waterbuck and topi (*Damaliscus lunatus jimela*), while hindgut fermenters include zebra, warthog and elephant (Ogutu et al. 2014).

Herbivores tend to have a specific habitat use through spatial/temporal partitioning. Spatial partitioning can be accomplished with three different factors: (1) the occupation of different vegetation types and broad habitat; (2) the occupation of different areas at the same season, and; (3) the occupation of the same area at different seasons (Lamprey 1963). An example of spatial partitioning have been explained by Pringle (2021), where different herbivore species avoid competition with other species by occupying different habitat near a waterhole (Figure 2) (Pringle 2021).

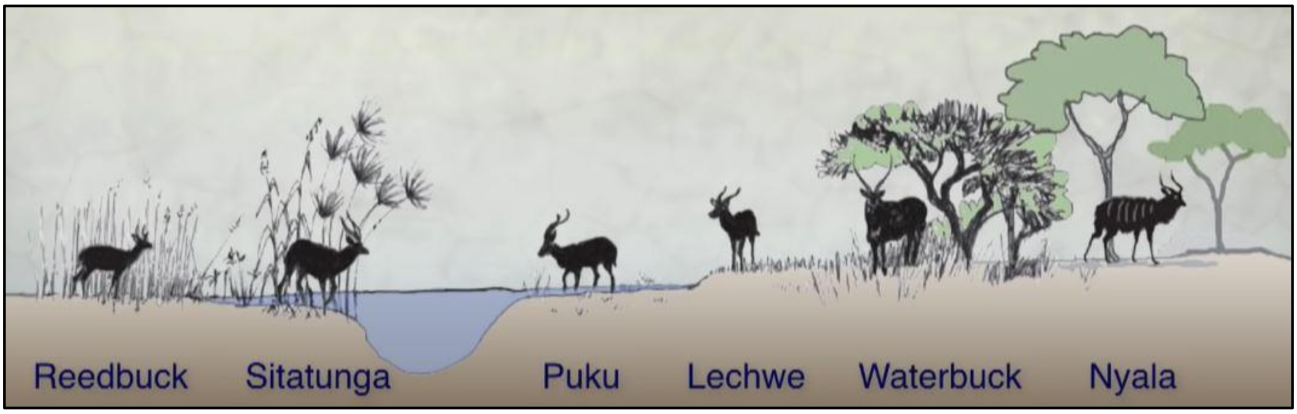

Figure 2 – adapted from Pringle 2021. An example of spatial partitioning. Habitat selection for different herbivore species to avoid competition near a waterhole.

Mouth physiology can also have an impact on spatial partitioning. Narrow-mouthed herbivores favor intermediate to tall-grass habitats, generally to avoid the higher risk of predation which is associated with large numbers of herbivores. On the other hand, broader-mouthed herbivores favor short-grass habitats, which are often found in heavily grassed pastoral areas (Fynn et al. 2016).

All the key factors discussed above are not the only factors which define the ecological niche of each species. Factors such as the interaction and influence between species; seasonal behavior, water needs and migration are also important in terms of resource partitioning (Lamprey 1963, Ogutu et al. 2014).

Facilitation

Positive interactions among herbivore species, such as facilitation, may occur when one species benefits from the actions of another species. Facilitation often occur during the wet season when grass is actively growing and forage quality may become limited if allowed to mature (Arsenault and Owen-Smith 2002, Sitters et al. 2009, Fryxell et al. 2014, Fynn et al. 2016). Facilitation can be divided into three different categories: (1) feeding facilitation; (2) population facilitation and; (3) habitat facilitation (Arsenault and Owen-Smith 2002).

Feeding facilitation may arise in two different ways: (1) when grazing by one species makes more grass accessible to another species, or; (2) when grazing by one species stimulates grass regrowth, thereby increasing the nutritional quality of forage for another species (Arsenault and Owen-Smith 2002). Large species have the ability to utilize high food biomass that is low in quality. Small species require high forage quality but can tolerate low food biomass levels. Small species may benefit from the grazing impacts of larger species (Arsenault and Owen-Smith 2002). Arsenault and Owen-Smith (2002) describes a study from Tanzania, where trampling and feeding by elephants exposed grass. The medium-height grass was eaten by buffaloes, while the short grass was eaten by topi. The elephants therefore facilitated several species (Arsenault and Owen-Smith 2002). In the MMNR, which has the highest density of wildlife in Kenya, heavy livestock grazing has led to facilitation of small and medium-sized herbivores in the wet season, but during the dry season a study by Odadi et al. 2011 showed that wild herbivores depressed cattle (*Bos taurus*) food intake and performance (Odadi et al. 2011, Bhola et al. 2012, Bedelian and Ogutu 2017).

Population facilitation states that feeding facilitation would translate into improved population performance for species grazing later in the same area. Although no evidence was found to confirm the translation in population abundance (Arsenault and Owen-Smith 2002).

Habitat facilitation happens when the vegetation changes induced by the feeding and destructive impacts of megaherbivores can alter habitat structure, to benefit other species (Arsenault and Owen-Smith 2002). Megaherbivores, elephants in particular, can facilitate forage availability for smaller bodied browsers by having a negative impact on woody vegetation by pushing over trees and encouraging re-sprouting, thus increasing availability for smaller-bodied herbivores (Sankaran et al. 2008, Anderson et al. 2016). Other megaherbivore on the African savanna are the white rhino and the hippopotamus. Rhinos and hippos can also transform the landscape through grazing, where they transform tall grass grasslands into extensive grazing lawns (Arsenault and Owen-Smith 2002).

Predation risk is another example of habitat facilitation and influence ungulates distribution (Burkepile et al. 2013). Evidence from ungulate-predator systems across several terrestrial habitats has also shown that prey species avoid areas frequented by predators or have higher perceived risk of predation. Ungulates must balance between the overlap of valuable foraging areas and areas of high predator use or predation risk, to obtain the resources needed to survive while avoiding predation (Burkepile et al. 2013). An increase in vegetation cover and tree density provides more cover for predators and increasing predator risk and decreasing visibility for prey species. Whereas, shorter grasses have lower predation risk. Prey species may avoid areas with denser woody cover or vegetation, or spend more time looking out for predators than feeding (Bhola et al. 2012, Burkepile et al. 2013). By moving seasonally between protected and pastoral areas, ungulates maximize their resource requirements while minimizing predation risk. The seasonal moving can be constrained by body size and are therefore not for all species due to its influence on food quality and quantity requirements (Bhola et al. 2012).

Humans and Livestock

Of all the mammals on Earth, 36 % are humans and 60 % are livestock. Only the last 4 % are wild animals as seen on figure 3 (Bar-On et al. 2018, The Guardian 2018). Globally, livestock grazing is the most dominant anthropogenic land use. On one-third of the global land surface livestock is grazing. It supports approximately 1.5 billion buffalo and cattle and 1.9 billion goats (*Capra spp.*) and sheep (*Ovis spp.*)

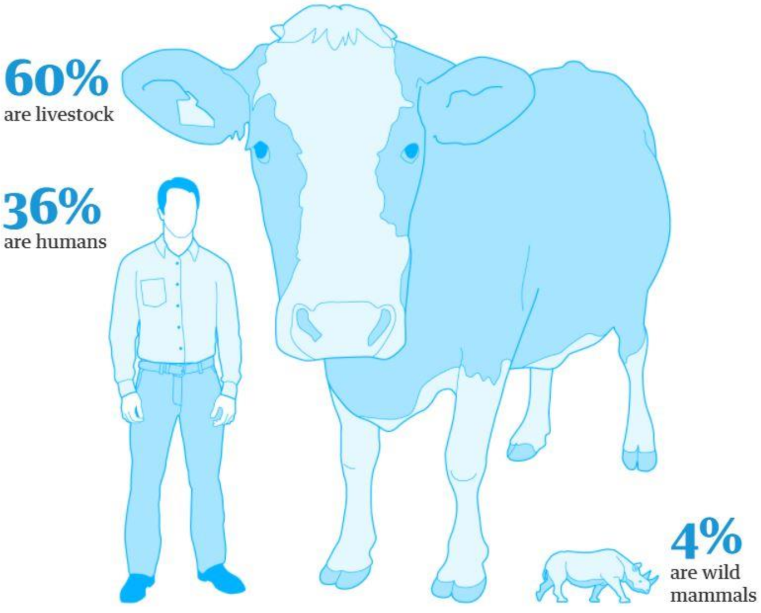

Figure 3 – Illustration of the percentage of livestock, humans and wild mammals on Earth (The Guardian 2018). Data from Bar-On et al. 2018.

(Dettenmaier et al. 2017, Bernardi et al. 2019). As seen on figure 4, different livestock species can be found around the globe. Especially cattle, sheep, goat and chicken (*Gallus gallus domesticus*) are the most abundant species. But figure 4 also assume no livestock to occur in IUCN protected areas, and imposing a density of zero in such areas. It is, however, known that livestock encroach on protected areas and the validity of these assumptions depends on how effectively these restrictions are enforced. This varies greatly from country to country and even within countries (Gilbert et al. 2018).

Since the 1960s, the global production of livestock for human consumption has more than doubled (Dettenmaier et al. 2017, Bernardi et al. 2019). The grazing livestock has a significant influence on the rangeland ecosystem services and the quantity and quality of wildlife habitat, resulting in consequences for the biodiversity (Dettenmaier et al. 2017). In the tropics, livestock ranching extends over 32 million km2, twice the area covered by tropical moist forest (Bernardi et al. 2019). Livestock grazing is one of the key drivers of the conversion of tropical forests into grasslands (Bernardi et al. 2019). Livestock grazing is also one of the factors resulting in 52 species moving one category closer to extinction each year. Dettenmaier, Messmer, and Hovick (2017) stated that in 2010, most indicators of the state of biodiversity declined, while the indicators of pressures on biodiversity increased such as the anthropogenic land use (Dettenmaier et al. 2017).

In the pastoral savannas of East Africa, wildlife have lived side by side for millennia with pastoralists and the domestic herbivores of Africa including cattle, sheep, goats, donkeys (*Equus asinus spp.*), horses (*Equus caballus spp.*) and camels (*Camelus sp.*) (Cumming 1982, Bedelian and Ogutu 2017). In savannas domestic herbivores often provide the only viable production alternative to crops and play an important role in cultural practices (Fynn et al. 2016). Wildlife and the ecological stability of the ecosystem are being pressured with the rapid human population growth and the increase in livestock densities and associated overgrazing (Crego et al. 2020). Ecosystem fragmentation is also promoted by development initiatives and agriculture in critical seasonal ranges. As a consequence of these fragmentation effects, many wild herbivore populations across Africa are in decline (Bhola et al. 2012, Fynn et al. 2016).

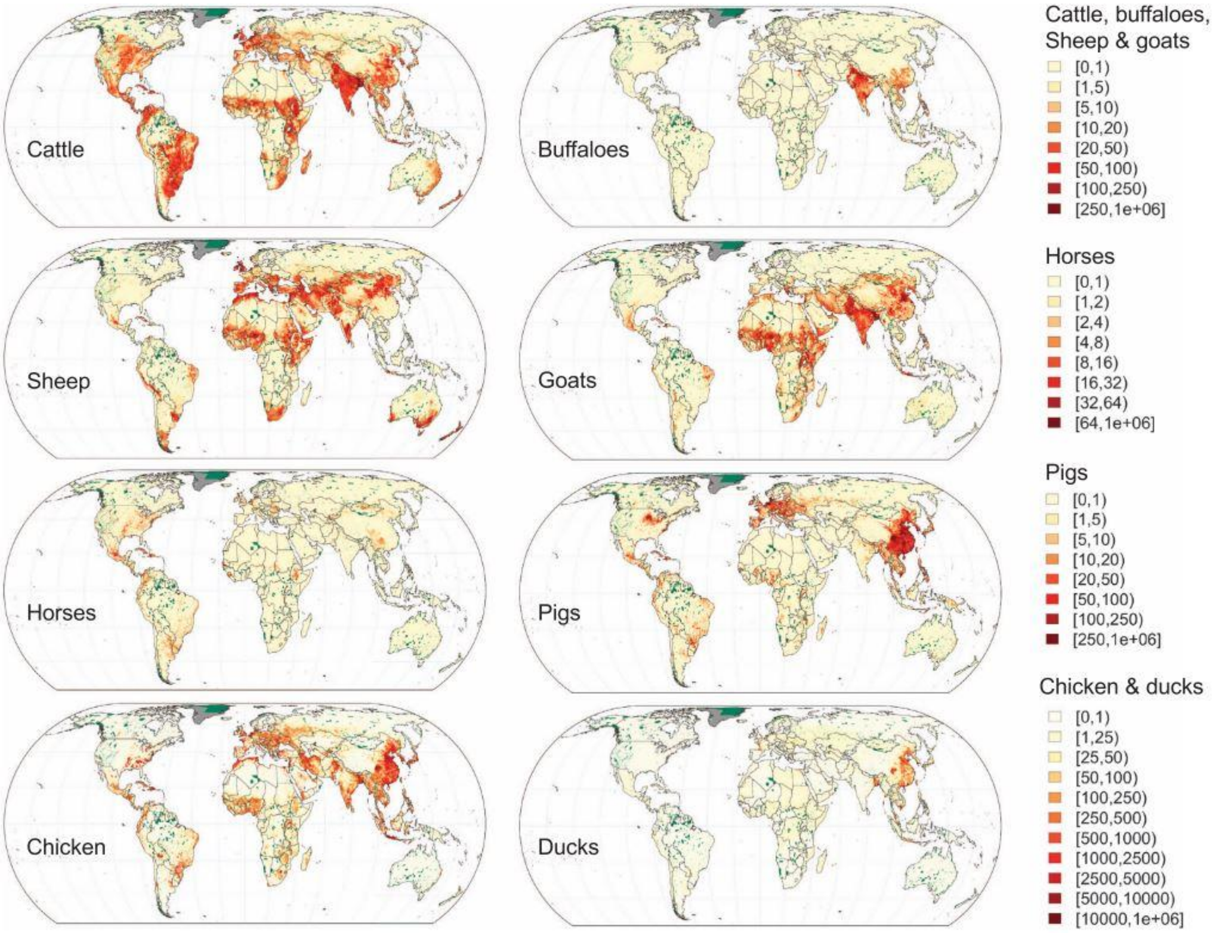

Figure 4 – Gridded Livestock of the World (GLW 3) based on the dasymetric model (Gilbert *et al.* 2018). Dark grey areas considered unsuitable and dark green areas correspond to IUCN protected areas. Number of animals pr. square kilometer.

Competition and facilitation between livestock and wild herbivores

For thousands of years pastoral societies on the African savannas and their livestock have interacted with wild herbivores. The livestock include goats, sheep, donkeys, cattle and camels, and often followed similar migration routes and seasonal foraging patterns (Fynn et al. 2016, Kimuyu et al. 2016). Management decisions for savannas worldwide, are based on the supposition that wildlife and livestock compete for forage resources, but there are little experimental data to support this assumption (Odadi et al. 2011). The interaction between wild herbivores and livestock are a particularly important topic due to; (1) livestock husbandry is often the primary land use type; (2) most savanna and grassland wildlife share part or most of their range with livestock, and; (3) interactions between livestock and wildlife are generally thought to be negative (Kimuyu et al. 2016, Ogutu et al. 2020). But the interactions might vary depending on different abiotic and biotic factors. Abiotic factors are, for instance, temporal variation in rainfall, which might affect interactions in terms of habitat use, and the interactions can also very depending on biotic factors such as the presence of megaherbivores (Kimuyu et al. 2016). Different scholars have over the years suggested, implied or stated that the following four statements have to be taken under advisement when discussing the interactions between livestock and wildlife: (1) livestock compete with wildlife over natural resources; (2) livestock facilitate wildlife; (3) livestock coexist or do not compete with wildlife; (4) livestock both facilitate and compete with wild herbivores.

Competition between livestock and wild herbivores is becoming an increasing problem on the African savanna, where e.g. food competition between livestock and wild herbivores is very common (Fynn et al. 2016, Kimuyu et al. 2016). Ogutu et al. (2016) reports an average decline of wildlife numbers by 68 % between 1977 and 2016 in Kenya's rangelands, though the magnitude of decline varied among species. The most extreme cases report declines of specific species by 72-88 %, and the competition for forage, space, and water have been a major contributor to the decline of 18 wildlife species across Kenya in the same period (Ogutu et al. 2016). Causes of the wildlife declines include exponential human population growth, increasing livestock numbers, declining rainfall and a striking rise in temperatures, but the fundamental cause seems to be policy, institutional and market failures (Ogutu et al. 2016). In Narok County (including MNC and MMNR) the population numbers of 13 out of the 18 wildlife species almost collapsed. Impala was reduced by 76.5 %, wildebeest by 50.2 %, topi by 73.3 %, and Grant's gazelle (*Nanger granti*) by 64 %. In the same period, livestock increased by 144.4 % in Narok County. Furthermore, the cattle numbers decreased by 3 %, which could suggest that sheep and goats (shoats) compete with wild herbivores (Ogutu et al. 2016).

Often, the primary mechanism by which competition between wildlife and livestock occurs is about habitat and dietary overlap in the distribution of both livestock and wildlife (Butt and Turner 2012). Diet overlap is higher among members of the same trophic guild than across guilds. For example, cattle are predominantly grazers and have a higher diet overlap with other grazers such as wildebeest and warthogs than with mixed feeders such as impala or with browsers such as elands. The cattle might therefore have a greater influence on wildebeest and warthogs than on impalas and elands (Ogutu et al. 2020). In a study by Odadi et al. (2011), it has been proved that cattle can both be affected by the presence of wild herbivores and can compete with them (Fig. 5). The study measured the weight gain of cattle within different treatment plots. The first treatment plot (C) was only accessible to cattle, the second (WC) was accessible to both cattle and meso-herbivores, and the third (MWC) was accessible to cattle, meso- and megaherbivores. The measurements were collected during the dry season (A) and the wet season (B). The study showed that wild herbivores were found to depress cattle weight during the dry season. The cattle gained 39-49 % less weight during this period, when they were sharing the habitat with wild herbivores. This changed in the wet season, where the wild herbivores facilitated the weight gain of the cattle, which can be observed in figure 5 (Odadi et al. 2011, Kimuyu et al. 2016).

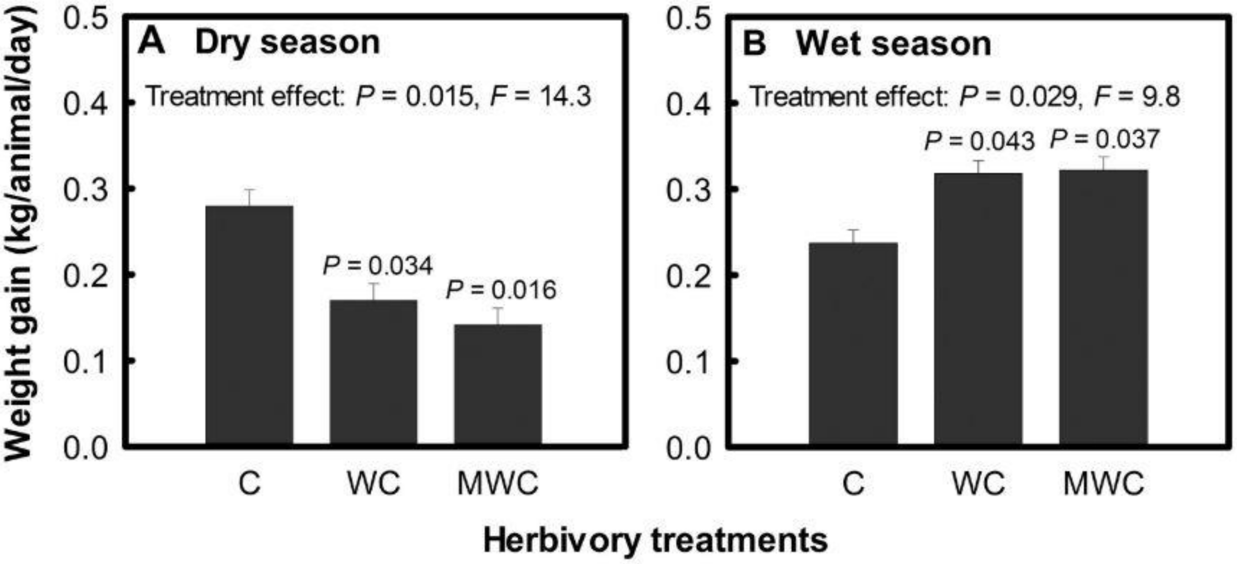

Figure 5 – Odadi et al. 2011: Weight gain of cattle within treatment plots they accessed exclusively (C) and those they shared with wild herbivores, with megaherbivores absent (WC) or present (MWC). (A) During dry season and, (B) During wet season. P-values over WC and MWC are for comparisons with treatment C.

Other examples of facilitation between livestock and wild herbivores have been stated when discussing fire. Higher livestock densities have been proved to be associated with lower fire frequency and a higher cover of shrubs and dwarf tress, but livestock can also prevent tree recruitment and growth through browsing and trampling. The increasing tree and shrub cover ensure protection for wild herbivores against predators due to the increasing number of hiding places, and the cover also ensures more forage for especially browsers (Bernardi et al. 2019). Young, Palmer, and Gadd (2005) also describe that elephants indirectly facilitate zebras in plots where cattle are grazing by increasing the grass cover (Young et al. 2005).

Interactions between wild herbivores and livestock change throughout the year, where competition are mostly observed during the dry season and facilitation are mostly observed during the wet season. However, high numbers of livestock for a longer period of time can increase the level of competition throughout the year (Odadi et al. 2011, Fynn et al. 2016).

The Serengeti-Mara Ecosystem

To understand the impact from the increasing number of shoats, it is also important to understand the ecosystem, where the shoats are found, and also to understand the local people keeping the shoats. The Serengeti-Mara ecosystem (SME) is an area expanding 40.000 km^2 on the border between Tanzania and Kenya in East Africa (Walpole et al. 2003, Veldhuis et al. 2019). The SME consists of protected areas and unprotected areas. The unprotected areas support ecotourism and harvesting of wildlife, whereas livestock keeping can create local nutrient hot spots that increase biodiversity. Protected areas, can on the other hand, provide mayor benefits for humans in the form of ecosystem services (Veldhuis et al. 2019). However, increase in human populations can result in unsustainable use and thus reduce wildlife populations both outside and along the edges of the core protected areas (Veldhuis et al. 2019). The entire SME supports an extremely diverse and abundant community of herbivores and carnivores, which is comprised of protected areas such as the Serengeti National Park (SNP) and MMNR. The ecosystem is reputed for the spectacular annual migration of 1.3 million wildebeest, 0.6 million zebra and Thomson’s gazelles, the high number of lions and the Maasai community (Aboud et al. 2011, Bartzke et al. 2018). The annual migration roams from the southern plains of the SNP to the northern grasslands of MMNR and back. The SME is a dynamic ecosystem, and both human and ecological elements are in a constant state of flux (Walpole et al. 2003). The Mara River, the only permanent river in the SME, serve as the only source of water for wildlife and livestock across the area. The river originates from the Mau forest complex and meanders alongside the Siria Escarpment before reaching the MMNR. The river bisects in the MMNR and the Mara Triangle, covering a distance of 60 km, before it reaches the border of the Maasai Mara and the plains of the Serengeti (Bartzke et al. 2018, KBC 2019a). Temperatures are moderate and range from 15-35 3. Annual rainfall varies from 600 mm to 100 mm with the long-wet season between March-June and a small wet season in November-December. January-February trends to be dry and hence is sometimes called the short dry season in contrast to the long dry season from July-October (Shorrocks 2007, Blackburn et al. 2016, Bedelian and Ogutu 2017, Bartzke et al. 2018). In regions with high human density, the sharp contrast in natural resources across protected areas boundaries leads to “hard edges”, which exacerbate HWC. This, however, leads to two opposing intervention strategies: Fencing protected areas as a form of “land sparring” from intensively used surrounding areas can solve some HWCs but also prevents beneficial temporary use of areas outside the reserve by wildlife and requires costly intensive management. An alternative strategy involves “land sharing”, which promotes coexistence between wildlife and humans, especially in the buffer zones between protected areas and non-protected areas (Veldhuis et al. 2019).

The Kenyan part of the ecosystem is located in the south-west of the country in the Rift Valley Province, forming part of two Districts: Narok and TransMara (Walpole et al. 2003). This area is also known as the Maasai Mara, which covers an area of 2.500 km^2 (Aboud et al. 2011). The MMNR, which are located at the southern border of Kenya, protects 1.510 km^2 of land and has the highest density of wildlife in Kenya, many of which spill out into and graze in neighboring conservancies and group ranch lands during the wet season. During the migration, the Mara provides dry season grazing and permanent water for the migratory species (Bedelian and Ogutu 2017, KBC 2019a). The high predator densities in the Maasai Mara together with the spectacle of the annual wildebeest migration have resulted in the MMNR being the highest earning wildlife area in Kenya (Broekhuis et al. 2018). However, during the past four decades, the density of livestock has increased, which likely has displacing wild herbivores into the SNP and leading to declining densities of wildlife in the MMNR. Human settlement and populations have increased enormously, especially close to protected areas. A study by Veldhuis et al. (2019) found that wildlife biomass inside the first 15 km of the core protected area was reduced by 75 % in the wet season and by 50 % in the dry season from the 1970s to the 2000s. The declines in the dry season were mostly due to the changes in the abundance of the Loita subpopulation of migratory wildebeest and zebras that traditionally use the MMNR during the dry season (Veldhuis et al. 2019, Ogutu 2020). Maasai pastoralists have also started to move their bomas closer to the protected areas or bring their herd into the protected areas on illegal multiday grazing trips, which also affects the migratory movements of large herbivores (Veldhuis et al. 2019). Data from GPS collaring of migratory wildebeest obtained from Veldhuis et al. (2019) show avoidance of the borders of the protected areas in the last two decades, which could be due to the increasing competition between migratory wildebeest and livestock.

The Maasai and Livestock

The major land use type in the Maasai Mara ecosystem is pastoralism which is also the economic mainstay of most inhabitants of grasslands of East Africa (Bhola et al. 2012, Bartzke et al. 2018). The Maasai Mara is also home to the Maasai people and it is therefore important to understand their culture, how they use the ecosystem and interact with wildlife (Ayiemba et al. 2015). The Maasai people are pastoralists who own of cattle and shoats. The pastoralists or the Maasai form 20 % of the Kenyan population and they occupy 74 % of the arid and semi-arid lands. Livestock are the living bank for most of the Maasai and are linked to the social and cultural lives of most of the Maasai community (Shorrocks 2007, MNC 2017a, KBC 2019a). The Maasai people are traditionally semi-nomadic pastoralists with a colorful and proud cultural heritage centered around their cattle. Today many Maasai are sedentary and are also keeping shoats. Their traditional beliefs towards wildlife have enhanced a generally peaceful and mutually beneficial coexistence between people, wildlife and the land, but this is all changing due to current pressures from increasing population density, economics, land competition and ownership (MNC 2017b, Li et al. 2020). The local people get their primary food from cattle, sheep and goats, and, to a lesser extent, donkeys. When the grazing resources grow scarce, they move their family and cattle to surrounding counties and to Tanzania. Therefore making both the migrating large mammals and the migrating Maasai tribes dependent on access to the resources in the SME (Bedelian 2014, Løvschal et al. 2017).

The local people, face many social, economic, political and environmental challenges. The level of poverty among the Maasai is very high and their culture is quickly eroding. Even in areas such as Narok County, where pastoralism is the major form of land use, the Maasai are struggling. Changing economic opportunities as well as culture and human immigration have led to substantial changes in the lifestyles of the local pastoralists (Ayiemba et al. 2015, Mukeka et al. 2019). In later years the patterns of land-use have principally changed from semi-nomadic pastoralism to sedentary agro-pastoralism, agropastrolism, and, in some cases, pure cultivation. Human population growth is accelerating the conversion of wildlife habitat to agriculture, and large swaths of land have been converted into large-scale farms for wheat and maize. This have resulted in a large increase of livestock, which makes the protecting of the nature and the use of conservancies so much more important (Nyariki et al. 2009, Broekhuis et al. 2018, Mukeka et al. 2019, KWCA 2020).

From cattle to shoats

Traditionally, Maasai predominantly kept cattle, but more recently there has been a switch to small stock, particularly sheep (*Ovis aries*) and goats (*Capra hircus*) (Broekhuis et al. 2018). The knowledge of shoats' impact on wild herbivores are limited, therefore it is important to understand the reasons for the switch from cattle to shoats. The switch is due to: 1) shoats are more drought resistant; 2) shoats have lower feeding requirements; 3) increase in demand of goat meat; 4) increase in conservancy income and; 5) shorter gestation time. In tropical regions, goats can breed every six-eight months, and tend to get one to three offspring, compared to the most dominant cattle type (Zebus). The Zebus have a gestation periods of approx. 12 months, and usually only get one calf. The introduction of a new sheep breed (Dorper) has also caused an increase in the number of sheep, since the Dorper has a high lambing percentage (can breed every eight months), is disease resistant, and mature early (Degen 2007, Ogutu et al. 2016, Bedelian and Ogutu 2017, Broekhuis et al. 2018, Løvschal et al. 2018). Shoats also serve as an increasingly important source to petty cash as they are more rapidly sold compared to cows that are more expensive (Løvschal et al. 2018). All these facts shows that shoats have greater capacity to recover more rapidly from droughts and show that they require smaller grazing rangers and less forage, and so are better able to forage in areas with short grass such as the areas close to bomas. Shoats are also thought to be getting increasingly preferred to cattle because they cannot move over long distances and hence are less likely to be stolen than are cattle (Ogutu et al. 2016). Meanwhile, are there no limits on shoat numbers, unlike for cattle, in the conservancies. This makes shoats more preferred over cattle in a landscape with limited mobility. Long-term datasets and figure 6 show a clear sign that shoats in the Mara are rapidly increasing in number, whereas cattle numbers are declining (Bedelian and Ogutu 2017). The number of shoats have increased by 210 % between 1977 and 2011 (Bedelian 2014), but as observed on figure 6, have also increased by 235.6 % between 1977 and 2014. This is evidence for a shift in which species of livestock are preferred (Bedelian and Ogutu 2017). The switch to small species of livestock is a common strategy where mobility is increasingly curtailed mostly due to climate change and habitat destruction, and it is expected to increase with climate warming. Recent restrictions in conservancies limit grazing areas and curtail mobility, which also can be contributing to the switch to small stock (Bedelian and Ogutu 2017).

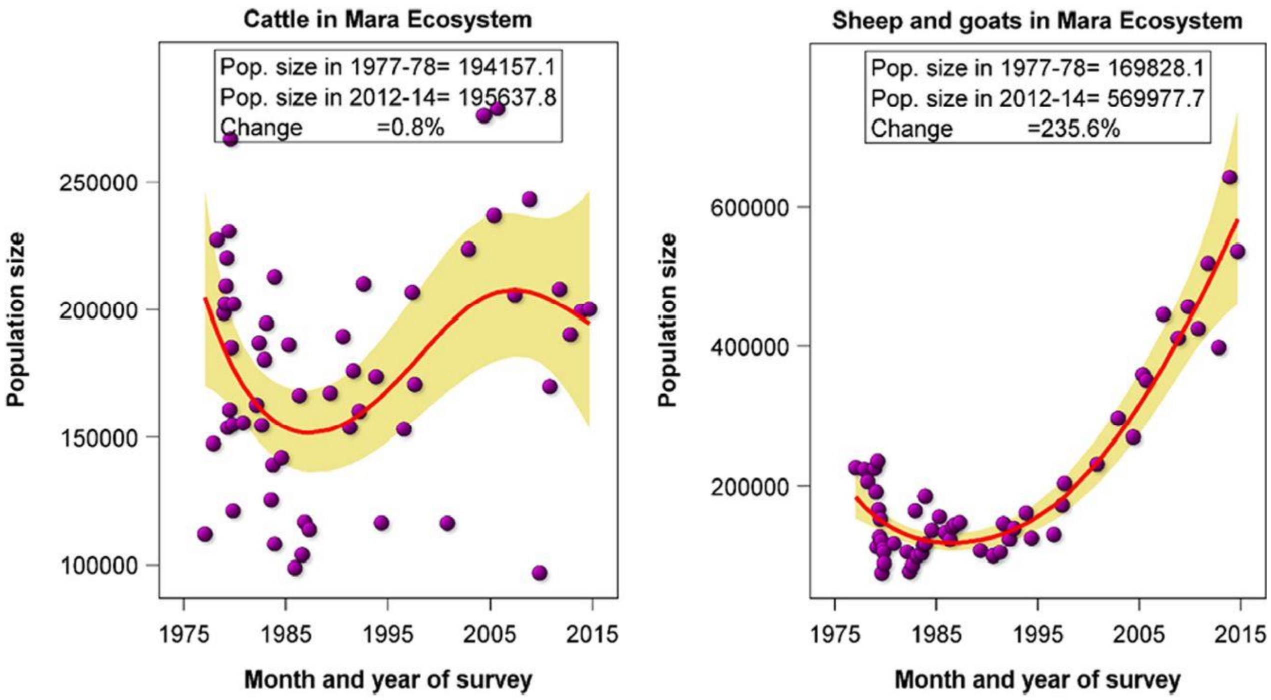

Figure 6 – Trends in cattle and shoat populations in the Mara ecosystem from 1977 to 2014 (Bedelian and Ogutu 2017).

Shoats' feeding behavior

Shoats have the potential to have a high negative impact on the vegetation and wild herbivores. To understand the impact by shoats, it is important to understand the feeding behavior of both sheep and goats. Both species are small ruminants and can consume a diverse diet based on native plants, which allows both species to present a greater flexibility in their forage and habitat selection. One of the most important traits in both species are their feed selectivity capacity, due to their narrower, longer muzzles, and their movable and cleft lips. Sheep and goats are both mixed feeder 'opportunists' (Lu 1988, Arslan 2007, Dias-Silva and Filho 2021). However, sheep tend to prefer grasses, while goats tend to prefer shrubs due to their higher tolerance towards more bitter feeds, but both species forage on grasses, broadleaf plants, herbaceous, and shrubs. The feeding behavior done by shoats are related to their mouths' anatomical adaptations, where goats have developed upper lips that enable them to pluck desirable leaves out from among thorns (Arslan 2007, Dias-Silva and Filho 2021). Goats' prehensile lips also enable them to eat grass close to the roots, thereby accelerating overgrazing (Løvschal et al. 2018). Goats can browse up to 2 meter in height and do also have the ability to climb trees where branch structures permit this. This behavior also reduces the risk of infection by parasite eggs found on surface vegetation and eye-level feeding is also considered a valuable mechanism for protection against predators (Dias-Silva and Filho 2021).

The daily grazing time is approximately 7-8 hours in sheep and 10-11 hours in goats. Grazing intensifies in the early morning and late afternoon (Arslan 2007).

Shoats are generally more drought resistant than cattle, but sheep are more negatively affected by drought than goats because herbaceous plants are more sensitive to periodic moisture stress than woody plants. In contrast, goats can better withstand drought periods with relatively fewer browse species in their diet because they are more nutritious (Lu 1988, Løvschal et al. 2018, Dias-Silva and Filho 2021). Sheep and goats are therefore the most widespread of all livestock. The sheep and goats raised by pastoralists are generally low-producing in terms of milk and offspring output but are well-adapted to the climatic conditions and are relatively tolerant of local diseases (Degen 2007). All these factors make shoats one of the most ideal livestock species for pastoralist in a changing environment.

Mara North Conservancy

Loss of space and connectivity, the increasing development pressures and impacts of climate change, are threatening Kenya’s iconic wildlife, its tourism industry and livelihoods for rural communities (KWCA 2020). This is where the conservancies become important. A conservancy is land managed by an individual landowner, a body or corporate, group of owners or a community for purposes of wildlife conservation and to establish a better livelihood for themselves. Conservancies provide connected landscapes with other conservancies, national parks and reserves, with no physical barriers between the wildlife areas and the surrounding community. This enables the wildlife to roam free. 15 conservancies are located in the Maasai Mara protecting over 450.000 acres of nature. One of these conservancies is the group conservancy Mara North Conservancy (MNC), which in the past was known as a part of the former Koiyaki-Lemek Group Ranch. A group conservancy is created by the pooling of land by private land owners who share a common border for the purpose of wildlife conservation (Blackburn et al. 2016, Bedelian and Ogutu 2017, Broekhuis et al. 2018, KWCA 2020).

MNC is a 27.680 ha not-for-profit public company natural wilderness in close partnership with Maasai communities. The conservancy was established on the 1st of January 2009. The partnership involves 13 tourism partners, 922 Maasai landowners and is one of the most densely populated wildlife areas within the Maasai Mara Ecosystem. MNC is located north of the MMNR, in the South-Western corner of Kenya (Ayiemba et al. 2015, MNC 2017c, KBC 2019b), with the Siria Escarpment to the west (Walpole et al. 2003). The ambition of the conservancy is to create a best-practice, world-class conservancy with long term commitments to the environment, the wildlife and the Maasai communities. The member camps pay a fixed monthly lease payment to the Maasai communities and is not subject to the number of conservancy tickets sold, and therefore not dependent on fluctuations in tourism. The lease payments provide the Maasai with the economic incentives to set aside their land for wildlife conservation. This lease gives the member camps the privilege to carry out game drives within the conservancy. The fixed lease also allows the community members to plan ahead for the future (Ayiemba et al. 2015, Broekhuis et al. 2018, KBC 2019b). The mission and goals for the MNC is to safeguard the Maasai Mara through professional wildlife management, have a direct and transparent revenue distribution to the Maasai landowners, promote eco-tourism practices and use of environmentally friendly technologies, control tourism and guarantee low vehicle density for lower environmental impact and fundraising for the betterment of the local communities. Twice a year, full community meetings are held whereby all landowners are able to voice their opinion on the planning of the grazing plans and other arrangements (KBC 2019a; Pers. comm. William Kipetu, conservancy manager in MNC, 2020).

A rotational grazing plan has been implemented in MNC to avoid HWC. The grazing plan dictates where and when cattle are allowed to graze. This is also done to secure tourists an amazing experience without seeing too much livestock (Bedelian and Ogutu 2017). The grazing rules within the MNC are monitored and enforced by conservancy rangers. If livestock herds are caught grazing in the conservancy outside of the specified time and place herd owners will be fined (Bedelian and Ogutu 2017). In August 2020, the number of cattle, which is a part of the rotational grazing plan, was 15.824, whereas the shoats were not counted (Pers. comm. William Kipetu, conservancy manager in MNC, 2020). A big part of the conservation work in MNC is also the MNC’s member camps numerous projects, which highly benefit the local communities. Several member camps are supporting women’s empowerment enterprises, including the development of new income-generating activities, such as handicraft projects. This makes the women more independent and makes sure that they can have an income if they are alone with children. There have also been established educational as well as health facilities with a focus on maternal and child disease, HIV/Aids, TB, malaria and waterborne diseases (MNC 2017b).

This Study

If shoats continue to not be a part of the current management plan, the numbers will continue to rise, due to the no limitation on shoat numbers and the benefits for keeping shoats instead of cattle. From all of the above it indicates missing understanding about the impact of shoats on the natural environment – especially in MNC. MNC is a unique conservancy with an important management plan to protect the local people and the wildlife. Shoats have the potential to impact the wild herbivores in different ways according to the herbivores functional type, body size and dietary requirements. These questions will be addressed with the help from fieldwork conducted in MNC and will be explained more in depth in the part B.

The knowledge gained from my research contributes to a broader understanding about the savanna ecosystem and interactions between herbivores, which can support the work on future management plans in MNC. The Maasai Mara Science and Development Initiative (MMSDI) gave their approval for my study and can also use the results for their future research.

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Part B

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The effect of shoats on wild herbivores in a semi-protected conservancy in Maasai Mara, Kenya

Abstract

A small part of East Africa is home to a pastoralist community called the Maasai. The Maasai traditionally keep cattle, but keeping sheep and goats (shoats) have become more common. The shift from cattle to shoats is due to several benefits by keeping shoats, as shoats are more drought resistant, have lower feeding requirements and they are being used as a living ATM because they are easier to sell than cattle. However, shoats do not have the same importance in a traditional Maasai household as cattle, thus, the increasing number of shoats are not being taking into account when planning conservation work. The increasing number of shoats have the potential to influence the savanna ecosystem and wildlife. If shoat numbers continue to rise, the competition for resources and space between shoats and wild herbivores will increase. Today, wildlife roams inside protected and outside in semi-protected areas. Maasai Mara National Reserve (MMNR), located in the southeastern part of Kenya, act as a fully protected area for wildlife, and Mara North Conservancy (MNC) is an adjacent semi-protected area. MNC has implemented a rotational grazing scheme in order to prevent overgrazing by cattle. However, shoats are not included in the grazing scheme and knowledge on shoats in African savannas are limited. This study aims to investigate if shoats have a positive, neutral or negative response on wild herbivores in MNC. However, a negative response could also be due to avoidance behavior from shepherds and dogs guarding shoats, and from the settlements. Therefore, the additional effect from shepherds, dogs and settlements will also be investigated. Strip transects were used to count all herbivores (both domestic and wild) to understand the spatial use of herbivores in MNC. We show that the overall density of wildlife is higher in the settlements, however, this varies from species to species and also in body size. Despite the influence from settlements and shoats, shepherds and dogs does not seem to be responsible for negative or positive responses from wild herbivores. Due to the negative response from settlement areas on Grant’s gazelle, topi and impala, and the negative trend from the presence of shoats on giraffes, eland, topi, wildebeest and zebra it would be advised to include shoats in the future management plans and use sustainable grazing management in savanna ecosystems, where both domesticated and wild herbivores can forage side by side.

Keywords: Africa | Livestock | Wildlife | Herbivores | Savanna | Interaction | Conservation

Introduction

Worldwide, competition for space and resources continues to rise. Biodiversity continues to battle with humanity and as a result, many species are therefore thrown into conflict with people, which results in extreme wildlife losses worldwide (Walpole et al. 2003, Ogutu et al. 2016, Løvschal et al. 2018). One of the ecosystems which are under massive threat are the savannas. Savannas are an important ecosystem, both for wildlife and people. African savannas support high densities of both domestic and wild herbivores (Abraham et al. 2019, Ogutu et al. 2020). However, South American, Australian and Asian savannas have fewer species of large herbivores than the African savannas. Particularly in South America and Australia large ground-living herbivores became practically extinct during the last c. 50.000 years (Skarpe 1991). Domestic animals (cattle, buffaloes, sheep, equids, camels and goats) now dominate the large herbivore fauna in most savannas (Skarpe 1991). African savannas support a high proportion of Africa's rural populations, livestock and wildlife. This makes the savanna vital for both socioeconomic and biodiversity values (Odadi et al. 2011, Marshall et al. 2018). Unfortunately, with the increasing human and livestock populations, wildlife and the savanna biome are more threatened than ever before (Ogutu et al. 2005). Categorizing several wildlife species on the African savanna as both endangered, and in some places, as pest species, are some of the consequences due to the rising competition (Walpole et al. 2003, Bedelian and Ogutu 2017). Beside the competition for space, conflicts arise due to crop destruction, livestock depredation and threats to human life caused by wildlife (Bedelian and Ogutu 2017). Protected areas are therefore important for the survival of wildlife. However, at low human population densities, local people can benefit from protected areas without compromising them, and the protected areas can also benefit from the presence of local people. Under such conditions, pastoralists with livestock and wildlife can coexist outside core protected areas (Veldhuis et al. 2019).

Pastoralists and wildlife have lived side by side for millennia (Cumming 1982, Bedelian and Ogutu 2017). Pastoralism emerged in East Africa around 4000 BP and primarily kept livestock (small ruminants, cattle (*Bovinae spp.*), camels (*Camelus sp.*)) (Lankester and Davis 2016). In Kenya, pastoralism is nomadic, where herders adapt to spatial-temporal variability in pasture and water availability through herd migration (Huho et al. 2011). Traditionally, the local people in southern Kenya in the Maasai Mara (the Maasai), predominantly kept cattle. However, more recently there has been a switch to small ruminants (sheep (*Ovis aries*) and goats (*Capra hircus*)) (Broekhuis et al. 2018). Sheep and goats (shoats) do not have the same importance in traditional

Maasai household as cattle, therefore the increase in shoat numbers can “fly under the radar” when conservation work and the traditional livelihood of the Maasai has to be maintained at the same time (Kuiper and Parker 2013). Due to loss of habitat, development pressure and impacts of climate change, 70 % of Kenya’s wildlife have been lost in the past 30 years (Ogutu et al. 2016). However, shoats have increased rapidly in the Mara region by 235.6 % between 1977 and 2014 (Bedelian and Ogutu 2017). Shoats have several benefits such as: 1) being more drought resistant; 2) have lower feeding requirements; 3) increase in demand of goat meat; 4) increase in conservancy income and; 5) shorter gestation time (Degen 2007, Ogutu et al. 2016, Bedelian and Ogutu 2017, Broekhuis et al. 2018, Løvschal et al. 2018). All these benefits have caused the local people to partly switch from their traditionally cattle to shoats (Broekhuis et al. 2018). However, the rapid increase in shoats have the potential to have a significant impact on the ecosystem (Bedelian and Ogutu 2017, Løvschal et al. 2018). Evidence suggests that current wildlife impacts on the vegetation are dominated by small-bodied mixed feeders, like shoats, which will likely continue into the future. However, this may also depend on changing climate, fire, and atmospheric CO_2 (Dias-Silva and Filho 2021, Staver et al. 2021).

Herbivory is a key process structuring vegetation in savannas, and decrease grass abundance by 57 % and tree abundance by 30.6 % across African savannas (Staver et al. 2021). Herbivores thereby potentially stabilize tree-grass coexistence (Staver et al. 2021). In African savanna, wild herbivores and livestock either compete or facilitate each other, or have a neutral relationship (Odadi et al. 2011). Competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species. While facilitation may arise if the actions of one species benefit another species (Arsenault and Owen-Smith 2002, Sitters et al. 2009, Fryxell et al. 2014). However, the distribution of species is the outcome of decisions that balance the trade-off between predation risk and resource richness, and therefore animals select habitats that minimize the ratio of mortality risk to net energy intake (Frid and Dill 2002). Furthermore, some species would exploit human activities, while others would avoid contact with people (Bar-Massada et al. 2014). Shoats could cause herbivores to either avoid or exploit the presence of shoats. By staying close to shoats, and thereby settlements, the risk of predation would decrease (Burkepile et al. 2013, Anderson et al. 2016). However, shoats’ prehensile lips enable them to eat grass close to the roots, thereby accelerating overgrazing. Their sharp hoofs can potentially have a negative impact on the soil due to prolonged high-intensity use of the same area, which can cause soil erosion and grassland deterioration (Løvschal et al. 2018). Prolonged high-intensity use of the same area by large flocks of shoats can therefore be much more damaging to grasslands than cattle (Løvschal et al. 2018). Furthermore, short and nutritious grasses are highly abundant near the settlement areas where grazing livestock keeps the grass short (Ogutu et al. 2010). The short grass also makes it easier for herbivores to detect predators. Especially smaller herbivores often face a higher predation risk, which makes them choose areas with better visibility and therefore the probability for predator encounters decreases (Burkepile et al. 2013, Anderson et al. 2016). Small herbivores require more energy per unit of body mass compared to large herbivores. A smaller size, thus smaller gut size and lower efficiency, imply that these animals need to select high-quality food to function (Bhola et al. 2012, Burkepile et al. 2013, Clauss et al. 2013, Anderson et al. 2016). Short and nutritious grasses are highly digestible forage and ideal for small herbivores, which could cause them to choose to stay near shoats and settlements (Bhola et al. 2012, Burkepile et al. 2013, Clauss et al. 2013, Anderson et al. 2016). However, herbivores could also exhibit fear or avoidance behavior in relation to shepherds and their guarding dogs, which could cause the herbivores to stay away from settlements and shoats (Gaynor et al. 2018b).

It is important to explore and to extend our understanding of the interaction between wildlife and livestock, in order to develop the most fitting management plan for wildlife-livestock coexistence in human-occupied savanna landscapes (Lamprey and Reid 2004, Odadi et al. 2011, Bhola et al. 2012, Løvschal et al. 2018). Furthermore, human population and the number of livestock are anticipated to increase intensely over the next decades (Bedelian and Ogutu 2017, Crego et al. 2020). Therefore, a better understanding of the interaction and impact between wildlife and livestock are needed; thus, this study aims to provide further information on the interaction between domestic and wild herbivores, with a focus on the domestic shoats. This study was conducted in MNC, a semi-protected conservancy, in Kenya, bordering the Serengeti-Mara ecosystem (SME). The SME supports an extremely diverse and abundant community of wild herbivores and carnivores, and are vital for the annual migration of wildebeest, zebra and Thomson's gazelle (Aboud et al. 2011, Bartzke et al. 2018). In MNC shoats are only permitted to graze in the settlement areas. A rotational grazing scheme has been implemented in the conservancy, which dictates where and when cattle are allowed to graze. No similar scheme has been implemented for the increasing number of shoats. This study investigates how the shoats impact the wild herbivores in MNC by testing the following hypotheses:

1) The shoats will be located inside the border of the settlement areas as agreed.
2) The overall density of wild herbivores would be higher in areas without shoats grazing.

3) Small herbivores will prefer areas with shoats, due to the nutritious grass and protection against predators.
4) The presence of shepherds with/or guarding dogs negatively affect the presence of wild herbivores.

Materials & Methods

Study Area

Data collection was conducted between October 2020 and December 2020 in the southwestern part of Kenya in MNC located at the northern border of the MMNR (Fig. 7). The area consist of more than 30,000 ha and receives an annual precipitation of 984 mm of rain, with a short rainy season in November and December and a long rainy season from March to May (Bartzke et al. 2018, KBC 2019). Temperatures range from a low of 7.3 °C to a high of 28.5 °C (Mukeka et al. 2019). Vegetation in the area is dominated by grasses, thicket, Acacia woodlands and riverine areas, and MNC offers habitat to a large diversity of wildlife. The ungulates include western whitebearded wildebeest (*Connochaetes taurinus mearnsi*), cape buffalo (*Syncerus caffer*), Grant's zebra (*Equus quagga boehmi)*, Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*), impala (*Aepyceros melampus*), Defassa waterbuck (*Kobus ellipsiprymnus*), topi (*Damaliscus lunatus jimela*), Coke's hartebeest (*Alcelaphus buselaphus*), eland (*Tragelaphus oryx*), Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), hippopotamus (*Hippopotamus amphibius*), common warthog (*Phacochoerus africanus*) and savanna elephant (*Loxodonta africana*). The large carnivores in MNC includes black-backed jackal (*Canis mesomales*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), leopard (*Panthera pardus*), and lion *(Panthera leo*).

MNC have implemented a rotational grazing plan that dictates where and when cattle are allowed to graze. The management plan is implemented to avoid overgrazing and human-wildlife conflicts. However, the shoats are not a part of the grazing plan, but are kept near settlements, where they are allowed to graze freely (William Kipetu, conservancy manager in MNC, pers. com. 2020). White rocks and trees mark the boundary for where the shoats are allowed to graze. The total number of cattle in August 2020 were 15824 cattle, however, MNC do not keep a record on shoats' numbers (William Kipetu, conservancy manager in MNC, 2020, pers. com.).

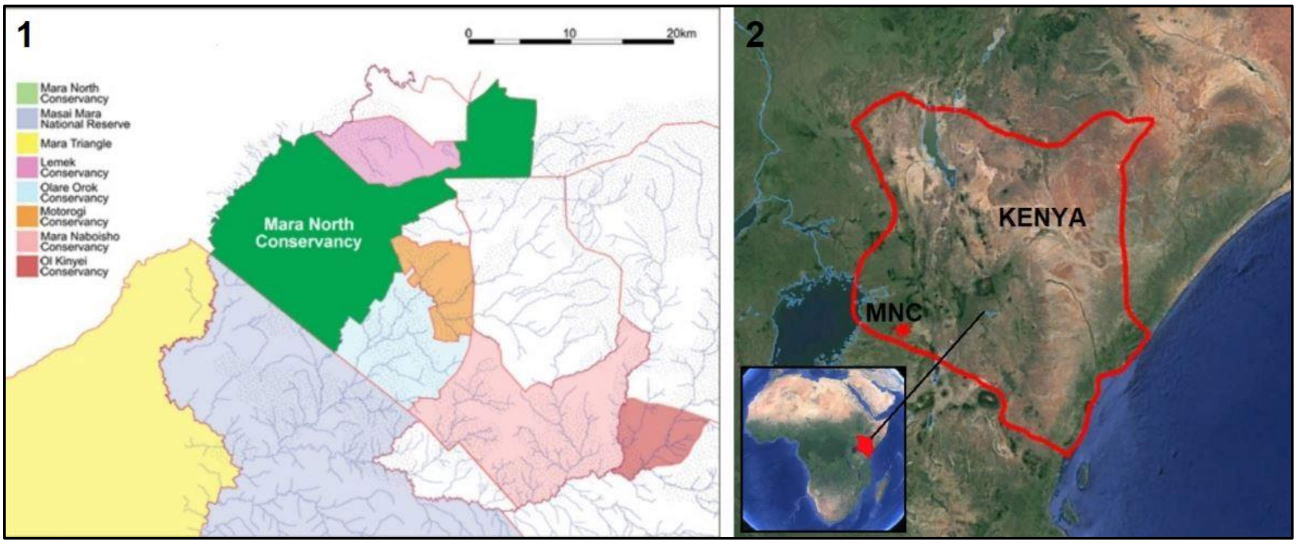

Figure 7 - Map 1: Mara North Conservancy and the surrounding conservancies and the Maasai Mara National Reserve. Adapted from Mara Predator Project (Project 2021). Map 2: The location of Kenya in Africa. Adapted from Google Earth.

Experimental Design

The data was collected by using strip transects which is a very long and thin quadrat of fixed width (Fig. A2). It is assumed that all objects within the strip are detected. In this case all the herbivores. All individuals are counted within this strip to estimate the density (Hill et al. 2005, Certain and Bretagnolle 2008). Strip transects are also a sampling method used to estimate density over a larger area. When using this method all the individuals are counted to get the correct estimated density of the transect area (Hill et al. 2005). The data consists of 155 strip transects, which were conducted from a car. The different strip transects vary in length due to vegetation being too dense in some areas to count all the individuals or that the car was not able to go any further. The transects were between 822 meters and 1239 meters in length and each transect was 200 meters wide to each side of the car (total of 400 meters in width). The preferred number of plots for each transect were 5 plots of about 200 meters to be able to identify each species, but due to vegetation challenges they were dived into 3 to 5 plots. The different distances were determined by a rangefinder (Nikon Forestry Pro II) and the GPS location was logged directly into ArcMap (10.6.1) by a GPS (Trimble Juno SB). All the herbivores inside the different transects were counted with or without binoculars and noted. The GPS location was noted at each end of the plots inside the transects (Table 1). Each transect was conducted in an average of 20 minutes, however, the time for each transect depended on the landscape and how many animals observed in the transect. Sheep and goats were grouped together as shoats because it is too time-consuming and difficult to count them separately in the field (Ogutu et al. 2014).

Table 1 – Functional grouping of the noted species by herbivore functionality and average weight. Augustine (2010) [1], Lundgren et al. (2020) [2] and Marker et al. (2003) [3].

Common name	Scientific name	Herbivore functionality	Average weight (kg)
Cape buffalo	*Syncerus caffer*	Grazer	450 [1]
Cattle	*Bos taurus*	Grazer	322 [1]
Common warthog	*Phacochoerus africanus*	Grazer	45 [1]
Defassa waterbuck	*Kobus ellipsiprymnus*	Grazer	160 [1]
Dik-dik	*Madoqua kirkii*	Browser	5 [1]
Donkey	*Equus asinus*	Grazer	250 [2]
Eland	*Tragelaphus oryx*	Browser	340 [1]
Goat	*Capra aegagrus hircus*	Mixed feeder	27 [3]
Grant's gazelle	*Nanger granti*	Mixed feeder	55 [2]
Grant's zebra	*Equus quagga boehmi*	Grazer	200 [1]
Coke's hartebeest	*Alcelaphus buselaphus cokeii*	Grazer	171 [2]
Impala	*Aepyceros melampus*	Mixed feeder	40 [2]
Maasai giraffe	*Giraffa camelopardalis tippelskirchi*	Browser	750 [1]
Maasai ostrich	*Struthio camelus massaicus*	Mixed feeder	111 [2]
Reedbuck	*Redunca redunca*	Grazer	44 [2]
Savanna elephant	*Loxodonta africana*	Mixed feeder	1.725 [1]
Sheep	*Ovis aries*	Mixed feeder	27 [3]
Thomson's gazelle	*Eudorcas thomsonii*	Mixed feeder	20.5 [2]
Topi	*Damaliscus lunatus jimela*	Grazer	136 [2]
Western white-bearded wildebeest	*Connochaetes taurinus mearnsi*	Grazer	180 [2]

The only herbivore species not observed was black rhino (*Diceros bicornis*). The Maasai do not want black rhinos near their settlements or livestock due to their aggressive behavior and also due to the risk of poaching. It is easier for the rangers to keep an eye out and protect the rhinos in the reserve (Leggat et al. 2000, David Noosaron, pers. com.). Kenya contains approximately 400 black rhinos, or 15% of the continental population (Emslie & Brooks, 1999). Within Kenya, MMNR is a key refuge for the endangered black rhinos. It currently holds around 23 rhinos, around 6 % of the Kenyan population (Walpole et al. 2003). Black rhinos will typically travel from MMNR to MNC, but the government will make sure to get the rhino back into the National Reserve (David Noosaron, pers. com.).

The strip transects where made throughout the conservancy and around the border of the three main settlements in MNC (Mara Rianta, Aitong and Nkorbob). The rotational grazing scheme was only executed outside the settlement areas. However, it does not include shoats, which were only allowed to graze near the settlement areas. To account for their spatial use, shoats were counted and noted on the GPS if they have not been observed in that area before. This would give a clearer picture of the whereabouts of the shoats and if they are staying around the border of the settlement areas. All the data were noted into Microsoft Excel (2016) and for the statistical analysis R 3.5.2 (2018) was used through the interface RStudio (version 1.1.456). Maps were created in ArcMap (10.5.1).

Statistical Analysis

Before the statistical analysis the density of all the species needed to be calculated. To calculate species density the total count of a species within each transect was divided by the total area in km^2 of the transect sampled.

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The *x* symbolizes a given species and the *s* symbolizes a given transect. The densities were calculated in Microsoft Excel (2016) and imported to RStudio (version 1.1.456) for further analysis.

A map of all the shoat observations was created in ArcGIS with GPS data from each shoat observation in MNC. To determine the distribution of the shoats a heatmap was also produced as a layer on the map. The heatmap was produced with help from the kernel density tool. The kernel density calculates the density of features in a neighborhood around those features, and can be calculated for both line and point features (Silverman 1986).

To determine the differences between shoats and wildlife in the two different land cover types (settlement and non-settlement), the densities were calculated. This is illustrated through a boxplot (Fig. 9). The data do not live up to normality assumptions, which means a non-parametric test needed to be used to test if there is a statistically difference between herbivore species' preference for non-settlement or settlement areas. The non-parametric test used was the Wilcoxon Rank Sum test, due to the categorical predictor, which is land cover. Due to the multiple tests with the same dataset, the Bonferroni correction was used. The Bonferroni correction is a method that is used to counteract the problem of inflated type 1 errors, while engaging in multiple pairwise comparisons between subgroups (Redfern et al. 2006). This approach was used to calculate the difference between the preference in land cover for overall wildlife density and also the density of the different wild herbivore species.

To get a broader understanding on the impact of shoats, wild herbivores were grouped into three different weight classes in R. The weight classes are small herbivores (<100 kg – 6 species – warthog, dik-dik, Grant’s gazelle, Thomson’s gazelle, impala and reedbuck), medium-sized herbivores (100-400 kg – 7 species – waterbuck, eland, zebra, hartebeest, ostrich, topi and wildebeest) and large herbivores (>400 kg – 3 species – giraffe, elephant and buffalo) (Marker et al. 2003, Augustine 2010, Hempson et al. 2015, Lundgren et al. 2020). The same approach as above was used to test for statistically significant differences between the preference in land cover.

Shepherds and dogs are guarding the grazing shoats and may therefore also impact wild herbivores with their presence. To test whether wildlife densities, a continuous variable, is affected by shepherd and dog density, another continuous variable, the Wilcoxon Rank Sum test cannot be used. However, a multiple linear regression model can attempt to describe the relationship between the different species, shepherds and dogs, and the land cover:

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The test allows to estimate how the dependent variable changes as the three independent variables changes. The model can answer how strong the relationship is between the different independent variables and the depend variable. The multiple linear regression model was used to test for land cover and also to determine the additional effect shepherds and dogs can have on the wild herbivores. The variables ‘Species’, ‘Shoats’, ‘Shepherds’ and ‘Dog’ showed a skewed distribution. By using square root transformation, the higher values are being compressed, so lower values become more spread out. The square root transformation therefore leads to normalizing of the skewed distribution. When examining the residuals, the plot does not look good for buffalo, hartebeest, waterbuck, dik-dik and reedbuck. This can be due to the lack of data for these species, and the results should therefore be interpreted with caution.

Results

The spatial use by shoats

Shoats primarily stay inside the settlement areas, but outliers were observed (Fig. 8). Density numbers for shoats outside the settlement areas are 7.8 animals/km^2, while the density numbers for shoats inside the settlement areas are 317.9 animals/km^2.

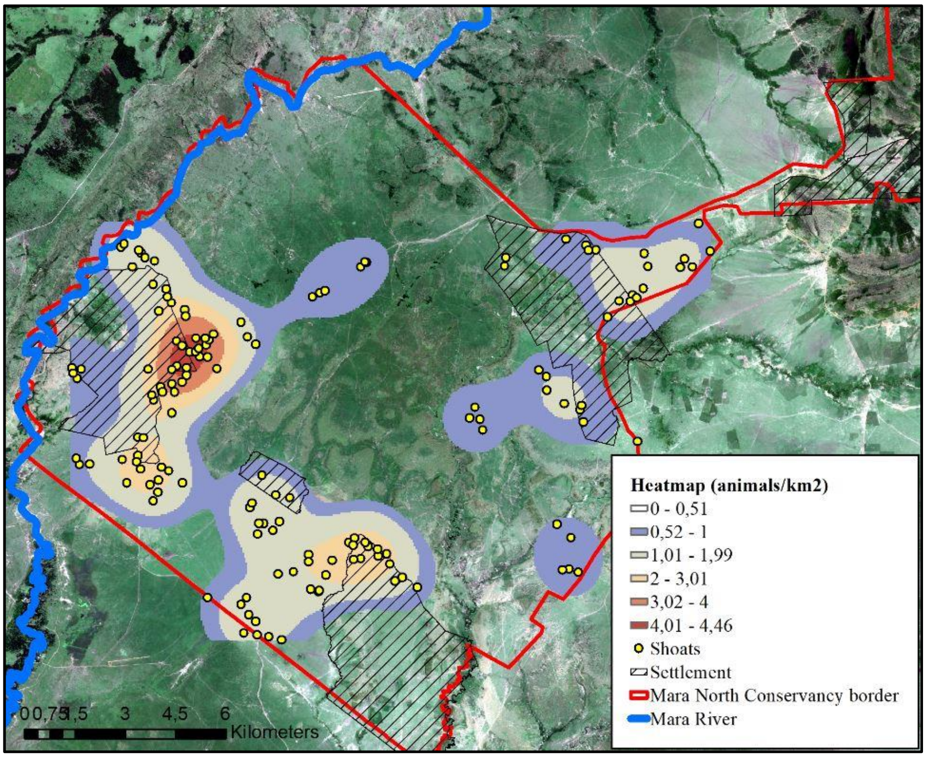

Figure 8 – Heatmap of the distribution of shoats. The yellow points and the heatmap mark the location of observed shoats in MNC. The observations are from individual GPS points and not from strip transects. From blue (low density of shoats) to red (high density of shoats), with the highest distribution of shoats around Mara Rianta (left settlement). The density is calculated as animals/km^2.

Density estimates of wild herbivores and shoats

The density for shoats outside the settlement areas is lower than inside the settlement areas, which supports that shoats stay near the settlement areas (Fig. 9, Table 2). Meanwhile are the density for wildlife outside the settlements lower than in the settlements (Fig. 9, Table 2). The boxplot with log10 also illustrates higher density for both wildlife and shoats in the settlements than outside the settlements (Fig. 9).

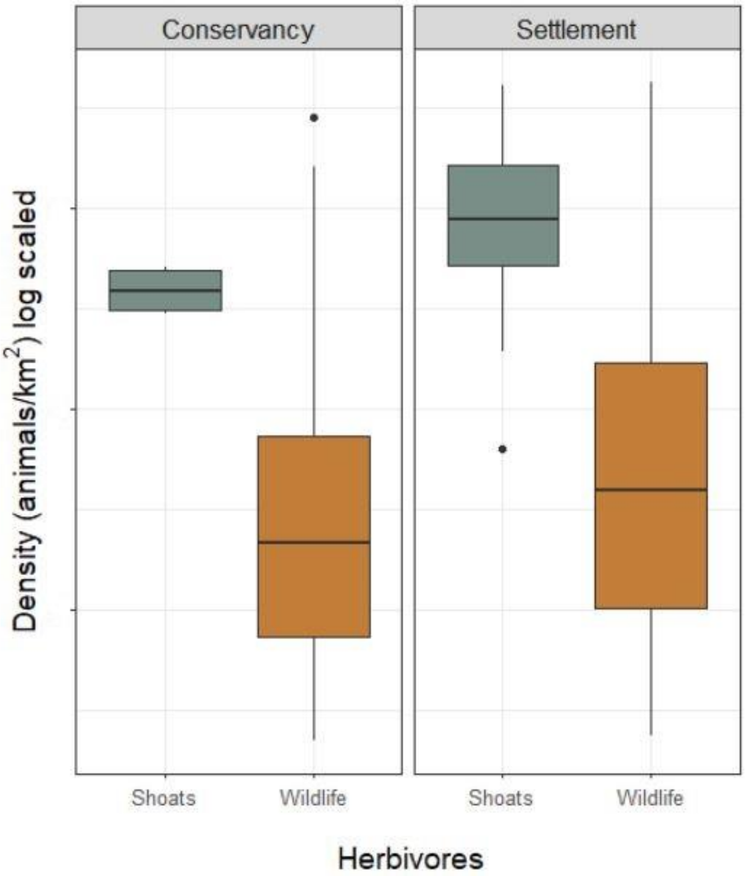

Figure 9 – Boxplot of the density of wildlife and shoats (log10) separated in two land cover types – settlement and non-settlement (classified as conservancy). The boxplot shows higher density of wildlife and shoats in the settlement areas than in the non-settlement areas. The densities were log transformed for better visualization and interpretation.

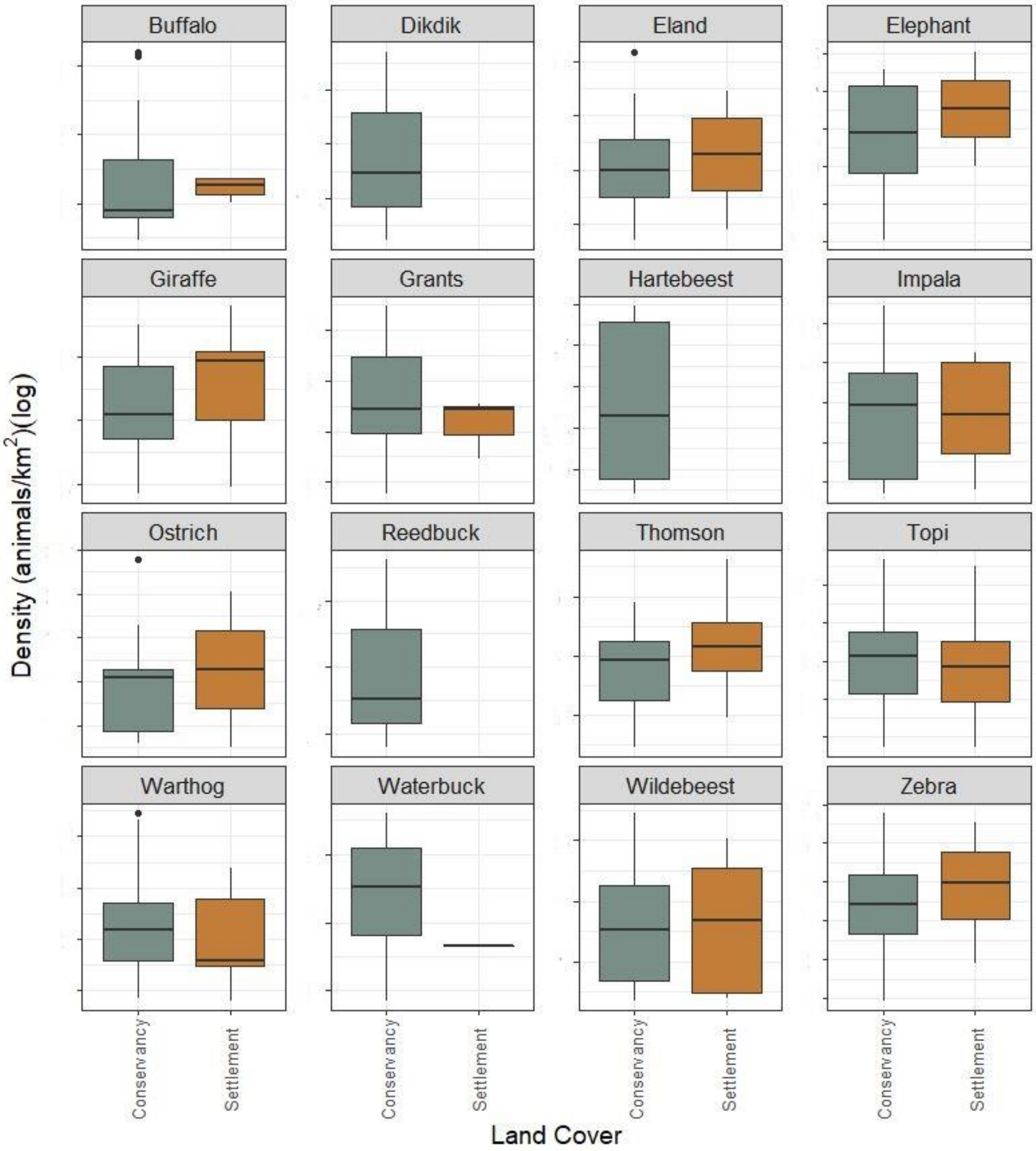

Figure 10 – Boxplot of the density of each species divided in land cover. Non-settlement is classified as conservancy. The boxplot illustrates that the overall wildlife density differs between non-settlement (conservancy) and settlement areas. The densities were log10 transformed for better visualization and interpretation.

Overall wildlife density differed between non-settlement and settlement areas (Wilcoxon Rank Sum test, non-parametric test, n=14312, p=0.0023). The Wilcoxon Rank Sum test was adjusted using the Bonferroni correction (p= 0.049) (Table 2). Furthermore, shoat density did also differ between non-settlement and settlement areas (Wilcoxon Rank Sum test, non-parametric test, n=8144, p=1.061e-15). The Wilcoxon Rank Sum test was adjusted using the Bonferroni correction (p= 2.33420e-14) (Table 2). Four species, Thomson’s gazelles, topi, Grant’s gazelle and impala, are statistically significant after the Bonferroni correction and therefore there is a difference between the species preference in land cover (Table 2).

Table 2 – Wildlife and shoat densities (animals/km^2) in settlement areas and outside settlement areas, Wilcoxon Rank Sum test raw p-values and Bonferroni adjusted p-values for the different species. The adjusted p-values were made with the Bonferroni correction. ‘*’ Statistically significant.

Species	**Density (Settlement)**	**Density (Non-settlement)**	**Raw p-value**	**Adjusted p-value (Bonferroni)**	**Sample size**
Thomson’s gazelle	134.32	53.08	**0.0001022***	**0.0017374***	5351
Wildebeest	55.97	53.64	0.07191	1	3364
Zebra	42.62	23.45	**0.02825***	0.48025	1936
Warthog	4.65	9.00	**0.005624***	0.095608	446
Topi	11.51	28.96	**0.00000563***	**0.00009571***	1338
Grant’s gazelle	0.43	6.59	**0.000005332***	**0.000090644***	248
Impala	3.67	14.70	**0.0001153***	**0.0019601***	623
Buffalo	0.78	15.59	0.07335	1	581
Elephant	0.70	0.58	0.3692	1	50
Giraffe	3.75	1.50	0.1237	1	150
Hartebeest	0	0.61	**0.0399***	0.6783	22
Ostrich	0.23	0.61	0.05331	0.90627	28
Eland	1.25	3.08	**0.01833***	0.31161	143
Reedbuck	0	0.11	0.1513	1	4
Dik-dik	0	0.17	0.1513	1	6
Waterbuck	0.08	9.00	0.338	1	22
Shoats	317.9	7.80	**1.061e-15***	**2.33420e-14***	8144
All wildlife	260.0	212.2	**0.002315***	**0.048615***	14312

Does size matter?

Small and medium-sized herbivores have a higher density in the settlement areas than outside settlements (Fig. 11, Table 3). In contrast, large herbivores have higher densities outside settlements, but not significant (Fig. 11, Table 3). The same tendency can be seen for the combination of the medium-sized and large herbivores, but again not significant (Fig. 11, Table 3).

Table 3 – Wildlife densities (animals/km^2) separated in land cover and weight class with Wilcoxon Rank Sum test p-values and Bonferroni adjusted p-values. '*' Statistically significant.

	Settlement	**Non-settlement**	**P-value**	**Adjusted p-value (Bonferroni)**
Small	143.06	83.65	**0.006597***	0.13194000
Medium	111.68	111.0	0.1304	1
Large	5.23	17.67	0.6611	1
Medium + Large	116.91	128.58	0.1071	1

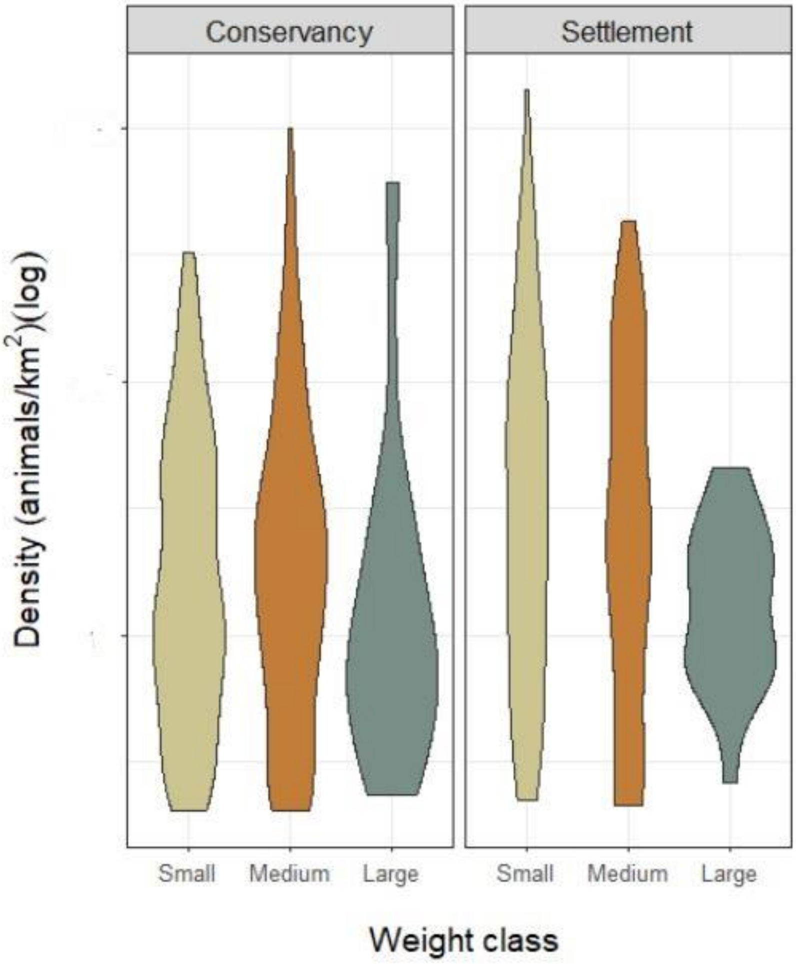

Figure 11 – Violin plot with the three weight classes shown in density (animal/km^2) and separated in land cover (settlement and non-settlement (classified as conservancy)). The figure shows the highest distribution between 0-10 for the non-settlement, and between 10-100 for the settlement. The densities were log10 transformed for better visualization and interpretation.

Anthropogenic disturbances on wild herbivores

The density for wild herbivores is lower (99.95 animal/km2) when shepherds and dogs are present than when they are absent (132.39 animal/km2) (Fig. 12).

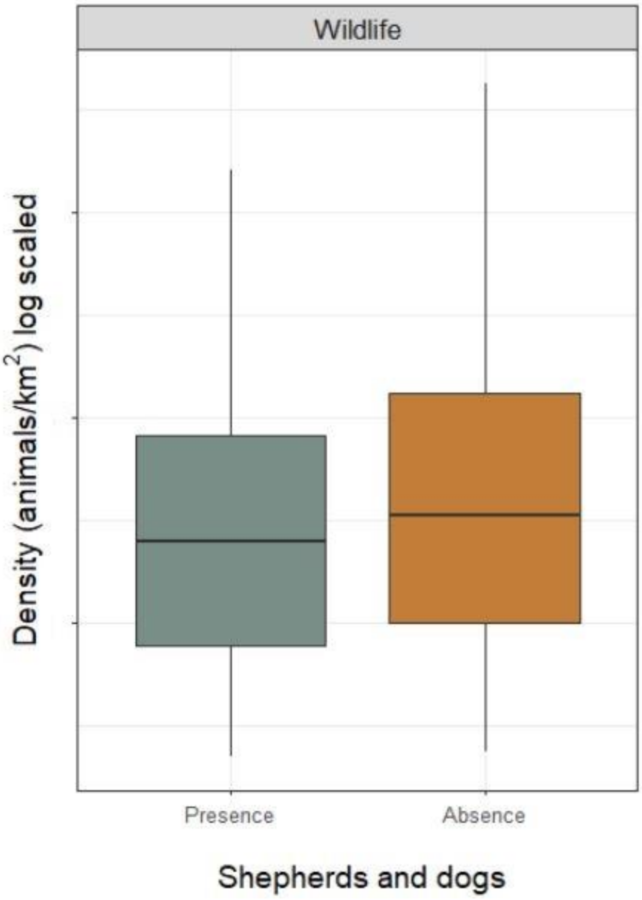

Figure 12 – Boxplot of the density of wildlife in the presence and absence of shepherds and dog. Higher density of wildlife when shepherd and dogs are not present. The densities were log10 transformed for better visualization and interpretation.

The multiple linear regression model included four independent variables: land cover, density of shoats, density of shepherds and density of dogs, and one dependent variable: the density of the wild herbivore species. Giraffes, Thomson’s gazelle, impala, Grant’s gazelle, topi and zebra were significantly different in their preference for habitat (Table 4). However, giraffes, Thomson’s gazelle and zebra prefer the settlements, while impala, Grant’s gazelle and topi prefer the non-settlements. Furthermore, only wildebeest is significantly different in their preference for habitat with or without the presence of shepherds, and zero species were significant for their preference for dogs (Table 4). Wildebeest and zebra have a positive response to shepherds outside the settlement, while giraffe, Grant’s gazelle, reedbuck, impala and topi have a negative response to shepherds (Fig. 13). The results also show that shoats had a negative impact on giraffes, zebra and warthogs

(Table 4). Giraffes and wildebeest also have a negative response to dogs outside the settlements, while warthogs and Thomson's gazelle have an overall negative response to dogs (Fig. 14).

Table 4 – multiple linear regression models to determine the additional effect on wild herbivores by shepherds and dogs. All densities have been square rooted. '*' Statistically significant.

Wildebeest				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.25255	0.67011	4.854	**0.00000304***
Land cover (Settlement)	0.24959	1.29601	0.193	0.8476
Shepherd	1.07979	0.43774	2.467	**0.0148***
Dog	-1.27131	0.82883	-1.534	0.1272
Shoats	-0.00379	0.07095	-0.053	0.9575
Buffalo				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.0736301	0.3299861	3.254	**0.00141***
Land cover (Settlement)	-0.7850885	0.6381971	-1.230	0.22059
Shepherd	-0.0398837	0.2155575	-0.185	0.85346
Dog	-0.0329372	0.4081410	-0.081	0.93579
Shoats	0.0003227	0.0349385	0.009	0.99264
Eland				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.783089	0.153072	5.116	**0.000000954***
Land cover (Settlement)	-0.379095	0.296044	-1.281	0.202
Shepherd	-0.010446	0.099992	-0.104	0.917
Dog	0.175435	0.189326	0.927	0.356
Shoats	-0.009924	0.016207	-0.612	0.541
Giraffe				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.36918	0.15242	2.422	**0.01664***
Land cover (Settlement)	0.79934	0.29478	2.712	**0.00749***
Shepherd	0.15716	0.09957	1.579	0.11658
Dog	-0.16467	0.18852	-0.873	0.38381
Shoats	-0.04085	0.01614	-2.531	**0.01242***
Ostrich				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.276042	0.072699	3.797	**0.000213***

Land cover (Settlement)	-0.146654	0.140601	-1.043	0.298628
Shepherd	-0.011991	0.047490	-0.252	0.801009
Dog	-0.040840	0.089918	-0.454	0.650357
Shoats	-0.001268	0.007697	-0.165	0.869378
Waterbuck				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.1725	0.07384	2.337	**0.0208 ***
Land cover (Settlement)	-0.1142	0.1428	-0.800	0.4251
Shepherd	-0.03.405	0.04824	-0.706	0.4813
Dog	0.07.386	0.09133	0.809	0.4200
Shoats	0.00003502	0.007818	0.004	0.9964
Thomson's gazelle				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	5.41534	0.63896	8.475	**0.0000000000000218***
Land cover (Settlement)	3.45221	1.23576	2.794	**0.0059***
Shepherd	0.31703	0.41739	0.760	0.4487
Dog	-0.08445	0.79029	-0.107	0.9150
Shoats	0.01587	0.06765	0.235	0.8149
Impala				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.151117	0.310779	6.922	**0.000000000126***
Land cover (Settlement)	-1.351005	0.601051	-2.248	**0.0261 ***
Shepherd	-0.060673	0.203011	-0.299	0.7655
Dog	-0.047710	0.384385	-0.124	0.9014
Shoats	-0.007937	0.032905	-0.241	0.8097
Grant's gazelle				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	1.364110	0.189484	7.199	**0.0000000000283***
Land cover (Settlement)	-0.962664	0.366465	-2.627	**0.00952***
Shepherd	-0.121943	0.123777	-0.985	0.32614
Dog	-0.061492	0.234362	-0.262	0.79339
Shoats	-0.004069	0.020062	-0.203	0.83954
Hartebeest				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.1949998	0.0647102	3.013	**0.00304 ***
Land cover (Settlement)	-0.1687958	0.1251504	-1.349	0.17948

Shepherd	-0.0271518	0.0422708	-0.642	0.52165
Dog	0.0040785	0.0800364	0.051	0.95943
Shoats	0.0009588	0.0068514	0.140	0.88889
Dik-dik				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.086443	0.038037	2.273	**0.0245***
Land cover (Settlement)	-0.074826	0.073564	-1.017	0.3107
Shepherd	-0.012036	0.024847	-0.484	0.6288
Dog	0.001808	0.047046	0.038	0.9694
Shoats	0.000425	0.004027	0.106	0.9161
Zebra				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.07464	0.45384	6.775	**0.000000000275***
Land cover (Settlement)	3.68117	0.87773	4.194	**0.0000470***
Shepherd	0.15476	0.29646	0.522	0.602443
Dog	0.61727	0.56133	1.100	0.273264
Shoats	-0.19076	0.04805	-3.970	**0.000112***
Topi				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	4.00682	0.37073	10.808	**<2e-16***
Land cover (Settlement)	-1.59956	0.71699	-2.231	**0.0272***
Shepherd	-0.09097	0.24217	-0.376	0.7077
Dog	-0.48560	0.45853	-1.059	0.2913
Shoats	-0.02085	0.03925	-0.531	0.5961
Elephant				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.197257	0.087108	2.265	**0.025***
Land cover (Settlement)	0.013704	0.168467	0.081	0.935
Shepherd	-0.036825	0.056901	-0.647	0.519
Dog	-0.024122	0.107738	-0.224	0.823
Shoats	-0.000842	0.009223	-0.091	0.927
Warthog				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.26383	0.20595	10.992	**<2e-16***
Land cover (Settlement)	-0.11993	0.39831	-0.301	0.7638
Shepherd	-0.01547	0.13453	-0.115	0.9086
Dog	-0.12007	0.25473	-0.471	0.6381

Shoats	-0.05393	0.02181	-2.473	**0.0145***
Reedbuck				
Coefficients:				
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.057246	0.028001	2.044	**0.0427***
Land cover (Settlement)	-0.057108	0.054154	-1.055	0.2933
Shepherd	0.014092	0.018291	0.770	0.4423
Dog	-0.018973	0.034633	-0.548	0.5846
Shoats	-0.001055	0.002965	-0.356	0.7225

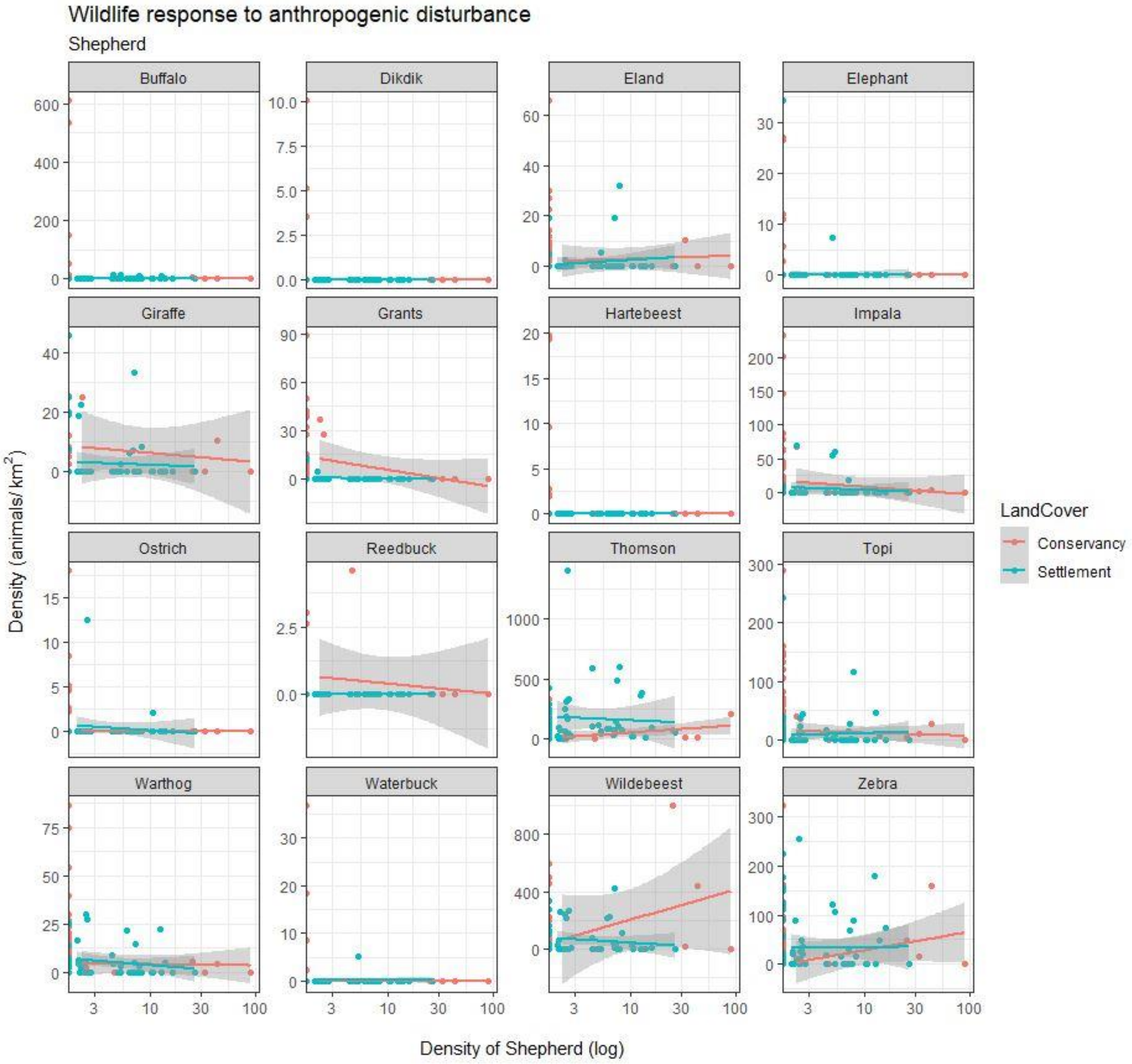

Figure 13 – Relationship plot between the density of each species and the density of shepherds. Non-settlement is classified as conservancy. Positive response in the non-settlement for wildebeest, zebra, Thomson's gazelle and eland. Negative response in the non-settlement for giraffe, Grant's gazelle, warthog, impala and reedbuck. Negative response

in the settlement for Thomson's gazelle, wildebeest and warthog. The densities for shepherds were log10 transformed for better visualization and interpretation.

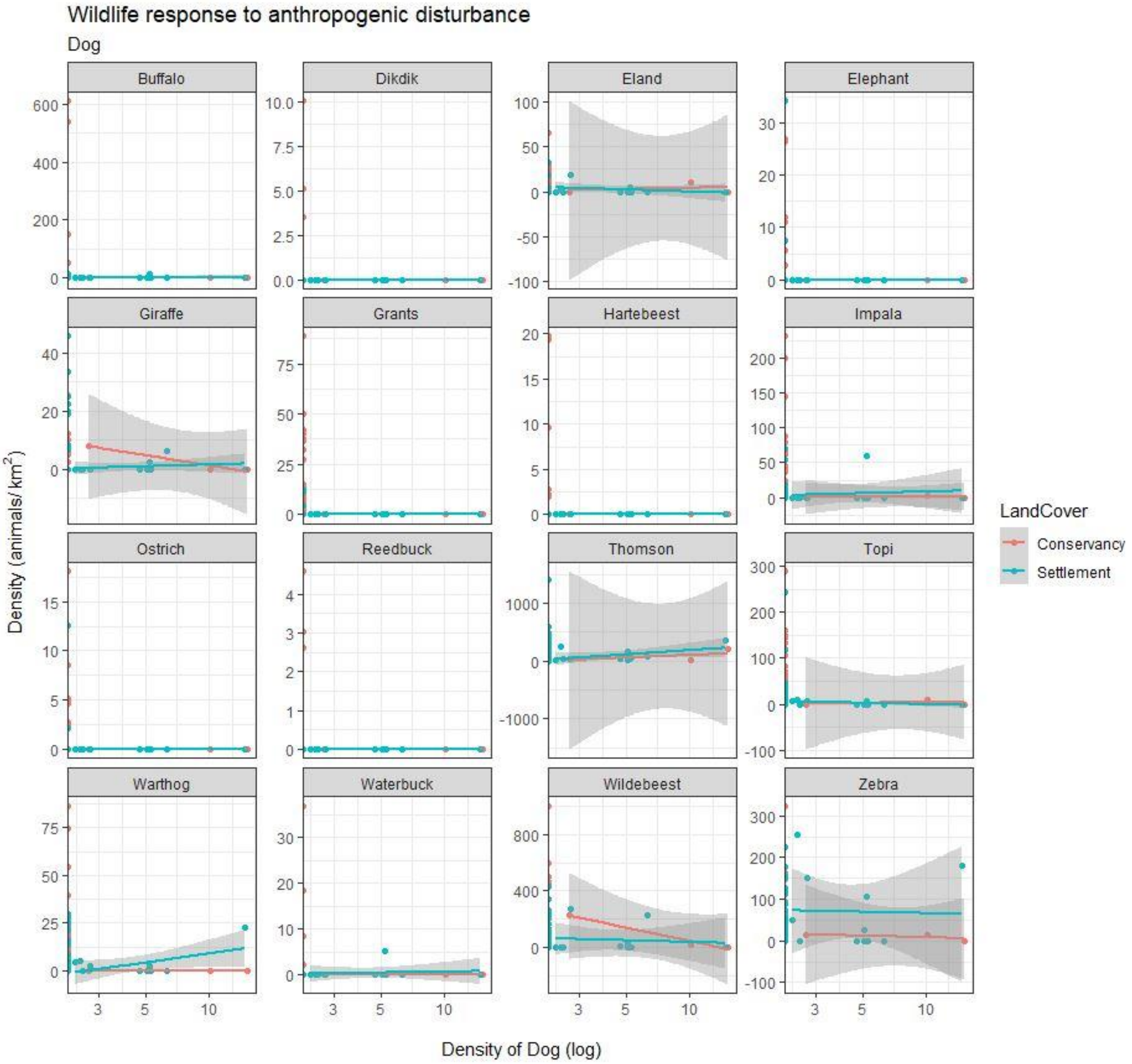

Figure 14 - Relationship plot between the density of each species and the density of dogs. Non-settlement is classified as conservancy. Positive response in the non-settlement for Thomson's gazelle. Negative response in the non-settlement for giraffe, wildebeest and zebra. Positive response in the settlement for Thomson's gazelle, giraffe and warthog. The densities for dogs were log10 transformed for better visualization and interpretation.

Discussion

The aim of this study was to investigate if the increasing number of shoats, guarded by shepherds and dogs, have an impact on the wild herbivores in a semi-protected East African savanna ecosystem. The results from this study demonstrates that the shoats are not always grazing where the current management plan states they are allowed to graze (Fig. 8). The results also indicate that the overall density of wildlife is higher in the settlement areas (Fig. 9), but with differences for the different species. Four species (Thomson's gazelles, topi, Grant's gazelle and impala) show a significant difference in preference in land cover, in which Thomson's gazelle prefer the settlements and topi, impala and Grant's gazelle prefers the non-settlements (Table 2). Furthermore, does the results indicate that small herbivores have a significant preference for the settlement areas, however, not after the Bonferroni correction. Medium-sized and large herbivores have no significantly preference in land cover (Fig. 10, Table 3). However, shepherds and dogs did not have a large impact on the wild herbivores. None of the wild herbivore species exhibited a significant response to dogs, however, wildebeest exhibited a positive response to shepherds. This leads to some interesting questions; why is there a difference between species in their preference for land cover? Why do small herbivores prefer the settlement areas? And why does shepherds and dogs not have a big impact on the wild herbivores? These questions will be answered in the following sections.

The spatial use by shoats

The first hypothesis, H_1, was that shoats would be located inside the border of the settlement areas as agreed. H_1 is overall supported by the findings (Fig. 8). According to the MNC management plan, shoats are only allowed to graze in and near the settlement areas (William Kipetu, MNC manager, pers. com.). The borders are marked with white rocks, trees and other markings along the border. The borders are approximately between 50 and 100 meters outside the actual settlement area to make room for grazing livestock. However, shoats have also rarely been observed grazing in grazing blocks in the rotational grazing scheme, where they are not allowed to graze (Sørensen 2020, unpublished). The distribution of shoats depended on the time of the day. The shoats were herded out by shepherds at around 10 o'clock and herded back into enclosures inside the settlements before sundown as predation risk increases after sundown and moist grass in the mornings is thought to cause disease (Mukeka et al. 2019, David Noosaron, local Maasai landowner, pers. com.). The moist grass causes a higher probability for infections from parasites, which can cause disease and an increase in mortality (Barger et al. 1994, Baker and Gray 2004). Shoats mainly graze inside the border of the settlements, but they tend to graze outside the borders as well (Fig. 8). Approximately 10 observations of shoats could have been classified as unauthorized grazing. Several observations of shoats were made along the road from Mara Rianta to Aitong (Fig. 8). This is due to the weekly outdoor market taking place in Aitong every Thursday. Every Wednesday several shepherds with livestock were observed walking towards Aitong to be able to reach the market in time (pers. obs.). Several of the observations of shoats were made outside the settlement areas but were connected to smaller houses which are not included in the management plan and therefore do not have to follow conservancy rules. The observations are also supported by the density numbers for shoats inside and outside the settlement areas, with a higher density of shoats inside the settlement areas. To understand if shoats are encroaching on wildlife areas, a better indicator would be the proportion of observations, or the number of counted shoats, grazing outside settlement areas that cannot be explained by weekly market trips or settlement areas which are not a part of the conservancy rules. The distance to settlement areas could furthermore be used as an indicator for shoats encroaching on the wildlife areas to understand how close to settlements wild herbivores forage. However, it is also important to keep track and regulate the increasing number of shoats in the Mara region to avoid the grazing of shoats outside of the settlement areas, which could cause a negative response from wildlife. Furthermore, by regulating the number of shoats, rangeland degradation through overgrazing, could be minimized (Ogutu et al. 2016, Bedelian and Ogutu 2017). The distribution of shoats on figure 8 are also supported by a study by Ogutu (2014), where shoats were observed in high numbers near Aitong and Mara Rianta (Ogutu 2014). Although, in the data set from Sørensen (2020, unpublished) unauthorized grazing by shoats was observed in 2019 with a density of 4.63 animals/km^2, which also was observed during fieldwork in the fall 2020 (pers. obs., Fig. 8).

If shepherds and their shoats do not follow the current management rules it could have negative impact on the surrounding vegetation, which can impact the wild herbivores. Shoats are mixed feeder ‘opportunists’, where sheep tend to prefer grasses and goats tend to prefer shrubs (Arslan 2007, Dias-Silva and Filho 2021). Goats prehensile lips enable them to eat vegetation close to the roots and thereby accelerate overgrazing (Løvschal et al. 2018). Furthermore, sharp hoofs can potentially have a negative impact on the soil due to prolonged high-intensity use of the same area, which can cause soil erosion and grassland deterioration (Løvschal et al. 2018). Prolonged high-intensity use of the same area by large flocks of shoats can therefore be much more damaging to grasslands than cattle (Løvschal et al. 2018). However, a rotational grazing plan (similar to the cattle) could be the answer to avoid grassland deterioration (Kuiper and Parker 2013).

Density estimates for wild herbivores and shoats

Hypothesis two, H_2, stated that it was expected that wild herbivores would have greater overall densities in areas without shoats grazing, due to the potential negative impact by shoats on wild herbivores (Løvschal et al. 2018). However, the density for the overall wildlife in the settlements was higher than outside the settlements, which is also supported with the boxplot (Fig. 9) and Wilcoxon Rank Sum test with the Bonferroni correction. To get a broader understanding about the species distribution, all species were investigated to understand their individual preference. Thomson's gazelles demonstrated a significant preference for settlements, while Grant's gazelle, topi and impala demonstrated a significant preference for the non-settlements.

Habitat choice is the outcome of decisions that balance the trade-off between predation risk and resource availability, and therefore animals select habitats that minimize the ratio of mortality risk to net energy intake. Animals also tend to shift their habitats if it benefits their survival, and even avoid habitats with richer resources if the habitat are associated with greater danger (Frid and Dill 2002). Different species have different resource requirements and react differently among predators. Some species will therefore choose to exploit the presence of human impact to avoid predators, while others will avoid such habitats due to the risk of human presence (Bar-Massada et al. 2014).

Thomson's gazelle and zebra were the only species with higher densities near the settlements, but only Thomson's gazelle had a significant preference for the settlements after the Bonferroni correction. Preference for staying near human settlements could be due to the improved shelter and fewer predators especially for small herbivores such as Thomson's gazelles (Ogutu et al. 2010, Bar-Massada et al. 2014). They have therefore greater predation risk, thus staying close to settlements could benefit their survival (Burkepile et al. 2013, Anderson et al. 2016, Lankester and Davis 2016). Staying close to livestock also increases the number of eyes detecting predators, and therefore decreasing the predation risk even more. A study by Riggio et al. (2018) investigated large African mammals and their human sensibility. He found that some species of large African mammals were being relatively unaffected by human presence. One of these species were the bushbuck and were also found in MNC. However, the bushbuck is very rare in MNC and was only observed a couple of times in the area and not when strip transect were conducted. However, other species of large African mammals were classified as human adapters. The human adapters were reedbuck, warthog, impala, hartebeest and savanna elephant (Riggio et al. 2018). Reedbuck were only observed in very low densities outside the settlements in MNC and not near the settlements (Table 2). However, due to the low amount of data for reedbuck it is impossible to interpreted the behavior of reedbuck in MNC. Warthog had higher densities outside the settlements than inside the settlements (Table 2), but results from Johansen (2021, unpublished) suggest that warthog exploits areas recently used by livestock, which supports the findings by Riggio et al. (2018). Hartebeest were also only observed outside the settlements in MNC (Table 2), but findings from Verlinden (1997) found that hartebeest were more regular found in higher numbers closer to settlements and were quite abundant between 10 and 40 km from settlements, due to their preference for green grass during the wet season. One of the reasons for why this cannot be seen in the data could be due to the high density of shoats near the settlements. Shoats forage on vegetation down to the roots and could therefore influence the number of hartebeest in the area (Løvschal et al. 2018). Savanna elephants also had higher densities outside the settlements (Table 2), but the different results can be due to the change in elephants behavior to avoid the presence of humans (Gaynor et al. 2018a). Recent results also suggest that wild herbivores prefer to feed in areas of intermediate biomass (Ogutu et al. 2010). However, some species tend to prefer short or long grass (Bhola et al. 2012, Lankester and Davis 2016). Forage biomass is related to its nutritional quality, but is positively related to dry matter intake rate. Animals will therefore choose patches containing intermediate biomass to maximize their rate of intake of digestible energy. Settlement areas create gradients with different levels of forage biomass extending away from these settlements, which therefore attracts animals (Ogutu et al. 2010). However, in dry years human settlements and livestock would extend this gradient and make it more difficult for herbivores to find intermediate biomass, thus making the no grazing zones in MNC very important (Johansen 2021, unpublished).

Herbivores were also observed staying around the settlement areas during the night and walking back outside the settlements in the morning (pers. obs.). This suggest that herbivores exploit the settlements when they are more vulnerable to predation. Other species change their behavior altogether to avoid people and are using areas of anthropogenic disturbance at night when people are less active (Gaynor et al. 2018a). With the increase in human population animals are forced to adapt in order to survive. In places where wild animals cooccur alongside humans, animals may minimize risk by separating themselves in time rather than in space (Gaynor et al.

2018b). There is growing evidence that mammal species across the planet adjust their diel activity patterns in response to human activities (which occur largely during daylight hours) by becoming more nocturnal (Gaynor et al. 2018a). Wild animals often perceive humans as a threat and therefore seek to minimize encounters with people. Studies have shown African elephants adjusting the timing of their movements at multiple spatial scales, and were therefore able to navigate a landscape of multiple anthropogenic activities and opportunities while minimizing direct contact with people (Gaynor et al. 2018a). However, this cannot be interpreted from the results from this study. Further fieldwork in MNC would be needed to determine if species in MNC have altered their behavior to be more active during the night.

Despite the ability to adapt, some species avoid anthropogenic activities altogether. Human settlements can also have a negative impact on wildlife. The results illustrate that wildebeest, warthog, topi, Grant's gazelle, impala, buffalo, elephant, hartebeest, ostrich, eland, reedbuck, dik-dik and waterbuck had greater densities outside the settlement areas, which could suggest avoidance of human settlements and shoats (Table 2). However, only impala, Grant's gazelle and topi had a significant difference after the Bonferroni correction (Table 2). Out of all the herbivores in this study, Riggio et al. (2018) found that eland is in the greatest danger of local extirpation in the face om human impacts, which are supported by a study by Verlinden (1997). The results from this study partially supports the findings from Riggio et al. (2018). The density of eland is higher outside the settlements than inside the settlements (Table 2). However, there was no significant difference between the two habitats, suggesting that eland have the ability to adapt to the presence of people. Other species, such as buffalo, wildebeest, giraffe and zebra, were classified as human avoiders (Riggio et al. 2018). This supports the densities for all the mentioned herbivores except from zebra, which had higher densities inside the settlements than outside the settlements (Table 2). However, according to the relationship plot (Fig. A3), shoats have a negative impact on zebras, which could suggest that other factors are playing a role in the habitat selection by zebras.

When further examining the relationship plot, shoats have a negative impact on eland, giraffe, wildebeest and zebra, whereas shoats did not seem to influence Thomson's gazelle and topi (Fig. A3). The impact on eland is supported by Verlinden (1997) and Riggio et al. (2018), which both suggest that eland tend to avoid areas affected by human impact (Verlinden 1997, Riggio et al. 2018). The impact on giraffes were also observed during fieldwork in MNC. When driving around in the morning or evening the giraffes were close to settlements. However, when shoats were grazing near the settlements the giraffes were not observed (Pers. obs.). The impact on wildebeest is also supported by Riggio et al. (2018), however, partially not by Verlinden (1997) and the densities from this study, which were higher outside the settlement areas. Verlinden (1997) explains that wildebeest are more regular found in higher numbers closer to settlements, which is also supported by Lankester and Davis (2016). Lankester and Davis (2016) states that wild herbivores use proximity to pastoralist homesteads to avoid non-human predators and exploit dams (built for livestock), as a source of water. Pastoralists utilize rich pasture for their livestock herds, providing nutritional benefits to wild herbivores. Lankester and Davis (2016) also suggests that species such as wildebeest and gazelles, which prefer short grass, actually benefit from the grazing livestock. Even the live fencing, build by planted trees, around livestock provide shade and cover for ungulates hiding from predators (Lankester and Davis 2016). However, wildebeest also avoid areas with overgrazing, which supports the relationship plot.

All of the results suggest that both settlements and the presence of shoats impact the selection of habitat by wild herbivores. However, the level of impact varies from species to species. Some species are only influenced by shoats, such as giraffe, while others are only influenced by settlements, such as wildebeest. Further research is however needed to fully understand shoats' impact on wild herbivores and how they impact the habitat selection by wild herbivores during the day. Do wild herbivores seek shelter and protection in the settlements in MNC and if so, what drives the herbivores to choose the settlements?

Does size matter?

The third hypothesis, H_3, was that small herbivores prefer areas with shoats, due to the nutritious grass and protection against predators. H_3 is supported by the findings (Fig. 11, Wilcoxon Rank Sum tests). The small herbivores demonstrate a significant higher preference for settlement areas than outside the settlements. However, medium-sized and large herbivores do not demonstrate a significant preference for any land cover, but medium-sized had a higher density inside settlements and large herbivores had a higher density outside the settlements. The distribution of herbivore species varies with the functional categories of the species based on body size, dietary guild (grazer, browser, and mixed feeder), gut morphology (ruminant vs. nonruminant), or foraging guild (resident vs. migratory) (Ogutu et al. 2010). Size is an important factor for the distribution of species, as difference in size leads to different requirements for the habitat. Small herbivores require more energy per unit of body mass compared to large herbivores, which means they need highly digestible forage to survive such as short and nutritious grasses (Bhola et al. 2012, Clauss et al.

2013). Short and nutritious grasses are highly abundant near the settlement areas where grazing livestock keeps the grass short (Ogutu et al. 2010). The short grass also makes it easier for herbivores to detect predators. Especially smaller herbivores often face a higher predation risk, which makes them choose areas with better visibility and therefore the probability for predator encounters decreases (Burkepile et al. 2013, Anderson et al. 2016). Staying close to settlement areas also keep predators away, as the predators refrain from human activities, due to the history of people killing large predators such as lions (Blackburn et al. 2016). Bhola et al. (2012) also observed that the proportion of newborn warthogs and juvenile topi were higher around ranches, which have shorter grasses and lower predation risk than in the reserve (Bhola et al. 2012). However, Kuiper and Parker (2013) states that intensive shoat grazing reduces the availability of suitable habitat (long grass) for small-mammal communities, such as rodents (Kuiper and Parker 2013). The data suggest that the reduction of grass height associated with grazing is the primary mechanism by which shoats affect rodents and mammal insect eaters in a savanna ecosystem. The species diversity, abundance and richness were significantly higher where grass was tallest than where grazing by shoats occurred (Kuiper and Parker 2013). This is not the case for small herbivores. The small mammals in the study by Kuiper and Parker (2013) included rodents and shrews are depended on tall grass for protection against predators whereas small herbivores are depended on short grass to improve visibility of predators (Bhola et al. 2012, Kuiper and Parker 2013). In some areas around the settlements the ground was barren due to the high grazing pressure from livestock, which could have a negative impact on wild herbivores and especially small herbivores who prefer to stay near the settlements (pers. obs.). Due to the small size of herbivores, they do not have the resources to move longer distances such as the medium-sized and large herbivores. Medium-sized herbivores are often seen moving seasonally between landscapes in their search for food for maximizing their resource requirements and to minimize predation risk (Bhola et al. 2012). However, large herbivores require large amounts of forage, but are less susceptible to predation. Large herbivores are therefore often observed in the reserves than in and around the ranches (Bhola et al. 2012).

Landscape features can also affect the preference in habitat, which also are depended on body size. Features such as recent burned areas, termite mound density, distance to rivers and woodland cover also play a role in herbivores choice of habitat (Burkepile et al. 2013, Anderson et al. 2016). Large herbivores, such as zebra and wildebeest avoided burned areas, whereas Thomson’s gazelle and impala were associated with burned areas (Anderson et al. 2016). Burned areas are used primarily for their nutritional properties, which are important for smaller herbivores (Anderson et al. 2016). Nutritional forage is also found on termite mounds, which are a preferred area for topi and other small herbivores. Topi also use termite mounds during mating display, to signal territoriality and to detect predators. However, hartebeest, which is similar in size to topi, avoid areas with termite mounds. Distance to rivers and woodland cover are important for herbivores due to the risk of predation. Smaller herbivores avoid areas with great predation risk, however, impalas are an exception (Burkepile et al. 2013, Anderson et al. 2016). Impalas are mixed feeders and are known to prefer woodlands. However, impala occur in large groups consisting of one male and up to 30 females, which may reduce the risk of predation by providing greater vigilance by the large group (Bhola et al. 2012, Anderson et al. 2016). Large herbivores may even facilitate the hunting success of predators when their foraging activities open up dense vegetation, making small herbivores more vulnerable to predation (Ripple et al. 2015, Anderson et al. 2016).

Dietary guild can also affect the presence of wild herbivores in different landscapes as well as body size (Ogutu et al. 2010). Figure A5 illustrate that there is a difference in preference in land cover according to body size and dietary guild. Small grazers more regularly forage outside the settlements and less inside the settlements. This can be due to the grazing livestock, especially shoats, who graze in large numbers near the settlements during the day and therefore compete with small grazers for forage (Løvschal et al. 2018). This can also be seen for the small browsers, who were not observed near the settlement areas. Although, the only small browser in the dataset is the dik-dik, so the result has to be carefully interpretated. However, small mixed feeders demonstrate a preference for the settlements, which can be seen for all weight class for mixed feeders. Mixed feeders tend to switch back and forth between grazing and browsing depending on availability of forage; browsing when the grass is limited during the winter or dry season and graze when grass is available (du Toit and Olff 2014). This means that mixed feeders can forage on the vegetation that is available, which the shoats are not foraging on. Medium-sized grazers demonstrate no preference in land cover, but can be observed in high numbers both outside and inside the settlements. However, large grazers, more regularly forage in the settlements, but less outside the settlements. Though large numbers of large grazers were observed outside the settlements, especially buffalo. However, buffaloes were only counted in very few transects, which can be the reason for this result. Elephants and buffalo prefer open grassland habitats found close to water but avoid cattle differently (Valls-Fox et al. 2018). This could also be the reason for the low density of buffalo and elephants around the settlement areas. Figure A5 is also supported by the densities in table 3, which also demonstrate that medium-sized and large herbivores do not have a significant preference in land cover.

When discussing management plans it is important to include how body size can affect the distribution of wild herbivores. Body size affects the resource requirements for the different species and it is therefore important to include both protected areas as well as semi-protected or pastoral lands adjoining protected areas. Bhola et al. (2012) agrees that this combination is important for seasonal dispersal and breeding grounds for wild herbivores.

Anthropogenic disturbances on wild herbivores

The last hypothesis suggested that the presence of shepherds with/or guarding dogs negatively affect the presence of wild herbivores. This was not supported by the results. The multiple linear regression model presented no significant negative response to the presence of either shepherds or dogs. However, wildebeest showed a significant positive response to the presence of shepherds (Table 4). Nonetheless, the boxplot (Fig. 12) and the relationship plots (Fig. 13, Fig. 14) illustrates that some species had a negative response to shepherds and dogs. The lack of significant negative results from wild herbivores, due to the response of shepherds, could be due to the lack of hunting in MNC. Furthermore, has MNC implemented rules for game drives to prevent harassment of wildlife. They only allow five cars at an animal sighting and have to keep a distance of 20 meters (MNC 2017). However, wildlife still have a natural fear for people and will avoid human contact (Gaynor et al. 2018b). The lack of significant negative results from wild herbivores, to the response of dogs, could be due to the small number of dogs in MNC (Jensen 2014). The dogs in MNC are free-ranging dogs, and they have the potential to have a negative impact on wild herbivores. They are used to protect livestock from predators (Gandiwa et al. 2013) and a study by Broekhuis et al. (2017) found that the likelihood of a depredation event occurring inside a boma decreased where more dogs were present (Broekhuis et al. 2017), which means the dogs are important for the locals to protect their livestock. However, dogs behavior tends to be both diurnal and nocturnal, and exhibit large variation in their home range sizes (1- 2500 ha), which potentially may have great disturbance effects on wild herbivores (Hughes and Macdonald 2013, Jensen 2014). Dogs may impact native wildlife through predation, competition, disturbance, hybridization and disease transmission (Young et al. 2011, Hughes and Macdonald 2013). It is therefore important to control the number of dogs in MNC to prevent further impact on wild herbivores.

Methods used

The data in this study were collected with strip transects. Strip transects, or transect surveys in general, are ideal for gathering presence data on species that are easily observable in the field and can provide accurate population trend data for species that are seasonably common. However, strip transects may miss rare or nocturnal species and species that are not easy to detect, which can overestimate population declines where species have changed their behavior to avoid anthropogenic disturbances, such as hunting pressure, livestock, dogs etc. (Riggio et al. 2018). MNC accommodate different habitat types from open savanna to closed forests and shrubs. Several of the no grazing zones were located in habitat with shrubs and forest, thus, making it difficult to detect species in that area, which means that not all transects were equally long and some herbivores may not have been detected (pers. obs.). To improve the understanding of the behavior and the distribution of the species, strip transect could have been made throughout the day to accommodate for different moving patterns. This would get a better understanding on the shoats' impact on all the wild herbivores.

This study should be reproduced in the following years to accommodate for changes in rainfall. High levels of precipitation were recorded in 2020, however, low levels of precipitation were recorded in 2019 (Johansen 2021, unpublished), which could change the impact by shoats. With the shoats' potential negative impact on wild herbivores, it could be possible that shoats would have a larger negative impact during dry years than in wet years.

Implications for future management

Shoats in the Mara region are rapidly increasing and have increased by 235.6 % between 1977 and 2014 (Bedelian and Ogutu 2017). They have the potential to have a high negative impact on vegetation and wild herbivores, thus it is important to keep track on the number of shoats in MNC and include them in future management plans. It is crucial to regulate livestock stocking levels to minimize rangeland degradation through overgrazing (Ogutu et al. 2016). By regulating livestock wildlife tourism income will be secured (Bedelian and Ogutu 2017). However, wildlife tourism can also be affected by other factors, such as political unrest, terrorism or epidemics/pandemics (Higginbottom 2004, Škare et al. 2021). The current pandemic, COVID-19, has had a large impact on the number of international travelers, and has therefore threatened the local economy (Lindsey et al. 2020, Škare et al. 2021). The crisis also threatens conservation efforts with reduced conservation funding, depleted management capacity, collapse of community-based natural resource management enterprises, and elevated threats (Lindsey et al. 2020). Furthermore, loss of income from tourism can increase opportunity costs of conservation and the risk of land conversion, which will threaten wildlife even further. Communities, private landowners and even governments could lose confidence in wildlife conservation as a reliable land-use option, due to the sudden loss of income from wildlife-based tourism (Lindsey et al. 2020). Wildlife tourism do not only result in positive effects for the local people, but also in a range of negative effects for wildlife. These effects vary from short-term changes to long-term effects. Short-term changes could be changes in physiology or behavior of individual animals, while long-term effects could be increased mortality or reduced breeding success (Higginbottom 2004). If the more ‘exciting’ species disappear, which are the major focus of wildlife tourism, the number of tourists decreases as well (Higginbottom 2004). It is also important to control the type, frequency and intensity of wildlife tourism, distance between people (or vehicle) and animals, and other stimuli from human activity such as sound and light (Frid and Dill 2002, Higginbottom 2004, Gaynor et al. 2018a, 2018b).

Veblen et al. (2016) found that it was the herbivory pressure and not the herbivory type (domesticated vs. wild herbivores) that was the main modifier of plant composition in the understory of a Kenyan savanna, thus, there is no need to remove the domesticated herbivores from the conservancy. Shoats do not have the same importance in traditional Maasai household as cattle, therefore the increase in shoat numbers can “fly under the radar” (Kuiper and Parker 2013). However, Kuiper and Parker (2013) demonstrated that wildlife may coexist with shoats in intensively grazed savannas if husbandry techniques are implemented to secure that suitable habitat persists. Such husbandry techniques could be rotational grazing, which is already implemented for cattle in MNC (Kuiper and Parker 2013). When stocking numbers for shoats were controlled Odadi et al. (2017) found that time-controlled rotational grazing (including shoats) were a positive conservation management method towards avoiding land degradation (Odadi et al. 2017). However, if stocking numbers were not controlled it would have a negative effect on forbs (Odadi et al. 2017). Shoats are currently not included in the conservancy management plans in MNC, but are kept near settlements (Løvschal et al. 2018). Furthermore, there is no record on how many shoats are kept in MNC (William Kipetu, conservancy manager, pers. com.). We would therefore advise MNC to keep a record of shoat numbers, and furthermore calculate the carrying capacity for shoats in the area to prevent overgrazing.

Shoats are not the only problem for future management. The local people are increasingly getting a higher education, which can act as a strong catalyst of livelihood diversification, that leads to land becoming fragmented and space for livestock grazing diminishes (Nkedianye et al. 2020). The younger people will likely venture into new, non-traditional areas from which parents would rather keep off. Land is also commonly sold to non-pastoralist who fence and convert it from pasture to other uses incompatible with pastoralism and conservation, including high-density settlements, ranching and cultivation (Nkedianye et al. 2020). It is therefore essential to involve local communities and the younger people in management plans, if they need to succeed (Mundia and Murayama 2009).

If shoat numbers are kept controlled and the local communities are involved, local management plans will have a larger chance of succeeding (Mundia and Murayama 2009, Veblen et al. 2016). However, larger conservation efforts are needed to secure the livelihood of the communities on East African savannas. The COVID-19 pandemic, like the Ebola epidemics, likely originated from human consumption of wild animals through wildlife markets. Effective conservation of species and habitats has been directly linked to decreases in the number of viruses that animals share with humans, thus making current and future conservation effort even more important (Lindsey et al. 2020).

Conclusion

This study revealed that shoats have the potential to have a negative impact on wild herbivores. According to this study shoats primarily stay near the settlements, but still compete with giraffes, zebra and warthog, and there were no signs of facilitation. However, it was found that small herbivores prefer to stay near settlement areas where the shoats are grazing, while medium-sized and large herbivores did not have a significant preference, although medium-sized herbivores tended to prefer settlements and large herbivores tended to prefer the non-settlements. The overall density of wildlife was higher near the settlements than outside the settlements, which could imply that wildlife is facilitated by the settlements, due to the lower predation risk and higher amount of nutritious forage. However, different species exhibited different preferences, which could in some cases imply competition between livestock and wild herbivores. Shepherds and dogs did not have a significant influence on the wild herbivores on the space use recorded in this study; however, further research is needed to understand their impact on wildlife.

The future of many wildlife populations on the African savanna is uncertain, making rotational grazing plans a very important management tool. For an effective rotational grazing plan, it is essential to include all the livestock found in MNC and that all guidelines are being followed, to avoid illegal grazing. Management plans needs to be based on well-informed studies and it is essential to include the local people, hereby the younger people, if the plans are to succeed (Mundia and Murayama 2009). Due to climate change and the increasing population in Kenya, it is important to have a flexible management plan for conservation work (Bedelian and Ogutu 2017). This study acknowledges its limitations and further research is needed to confidently extrapolate the results to other conservancies in the Mara region and other African savannas.

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Appendix

Table A1 – Overview of strip transects. The table illustrates the number of strip-transects within each area, the total area sampled within each area and if shoats were allowed to graze in the area.

Area	Nr. of strip transects	Total area of transects in km^2	Grazing shoats
Settlement	63	25.62	Yes
Non-settlement	92	35.98	No

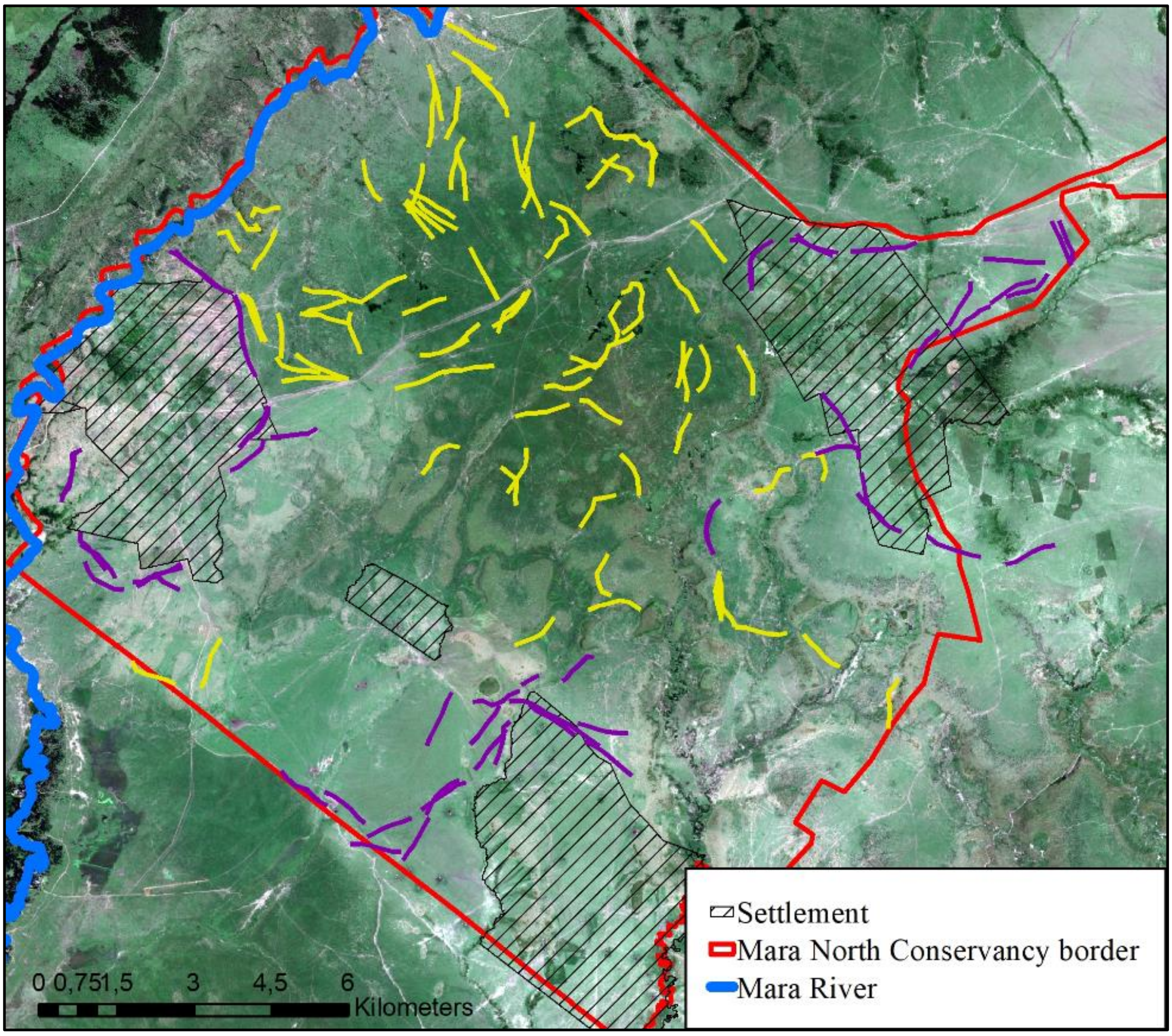

Figure A2 – A map of MNC with all the strip transects and settlement areas. Purple transects are conducted around settlement areas and yellow transects are conducted outside settlement areas.

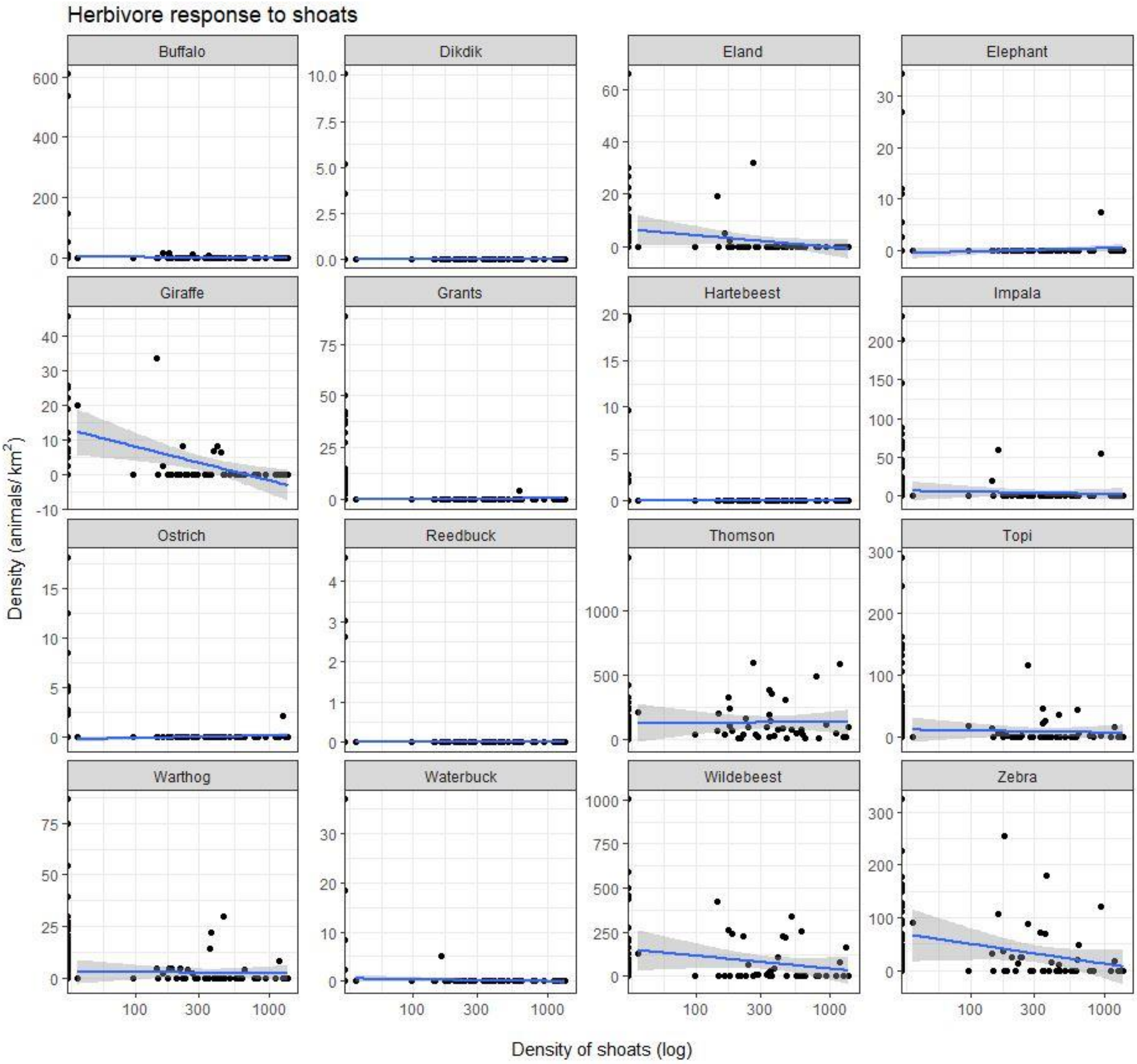

Figure A3 – Relationship plot of wild herbivore response to shoats in density (animals/km^2). Negative response for giraffe, wildebeest, zebra and eland. The densities for shoats were log10 transformed for better visualization and interpretation.

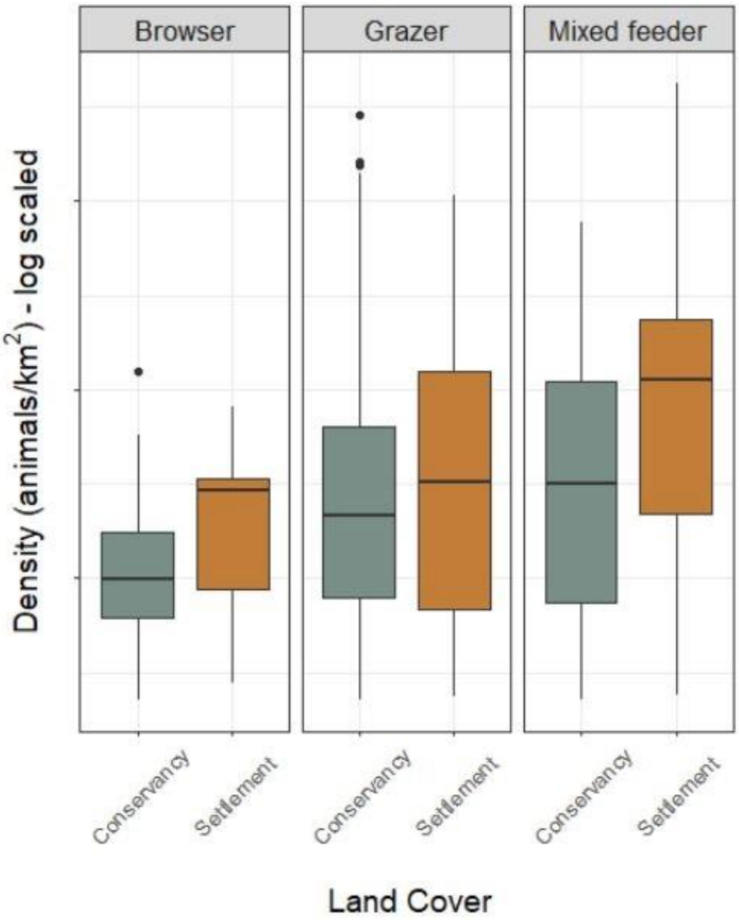

Figure A4 – The density of herbivores divided in land cover and their feeding ecology. Non-settlement is classified as conservancy. The densities were log10 transformed for better visualization and interpretation.

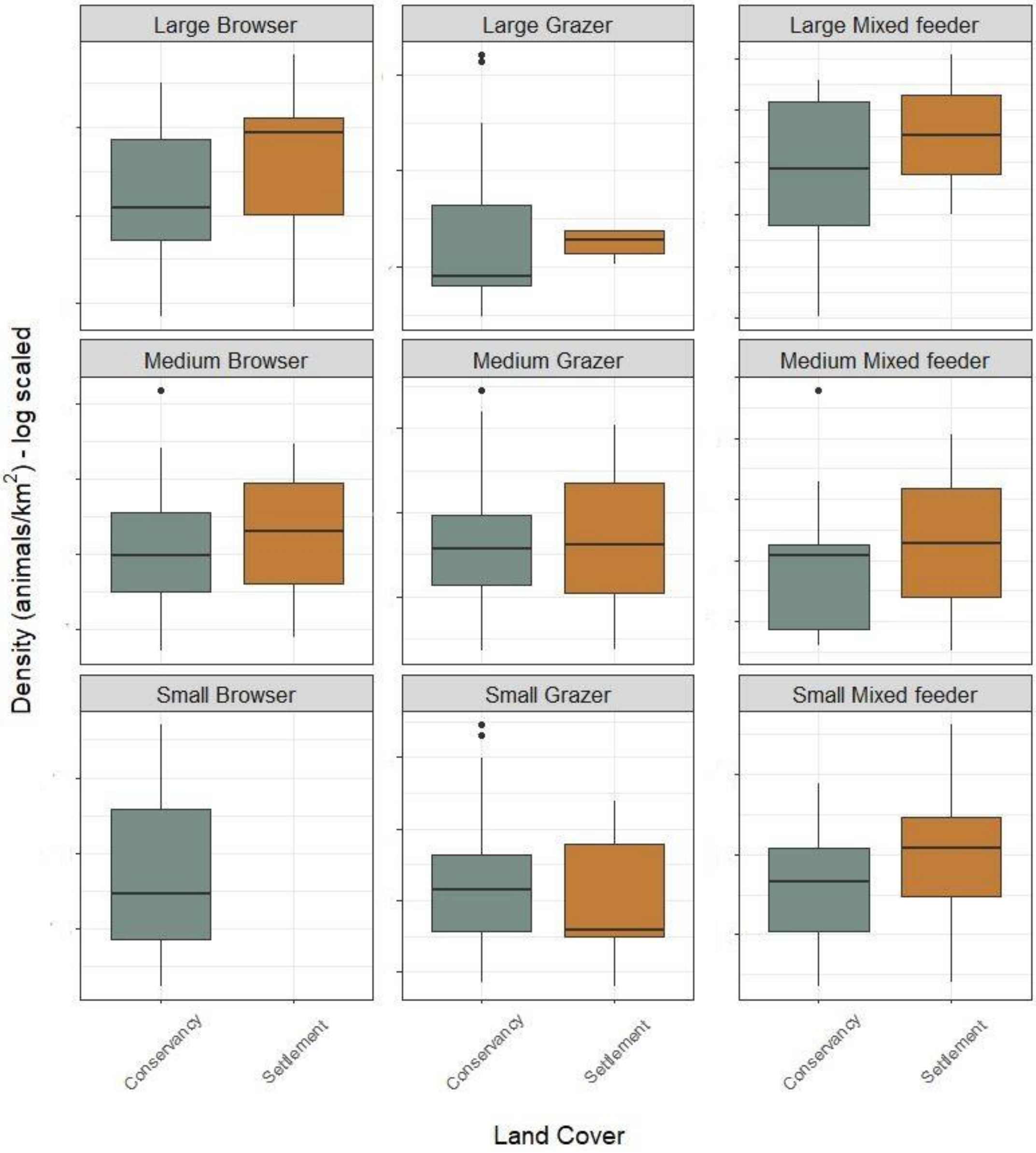

Figure A5 – The density of the different herbivore species divided in land cover, weight class and their feeding ecology. Non-settlement is classified as conservancy. The densities were log10 transformed for better visualization and interpretation.