Domestic Bliss or Trouble in Paradise Interactions Between Domestic and Wild Herbivores in the Mara Region of Kenya

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By

Domestic Bliss or Trouble in Paradise:

Interactions Between Domestic and Wild Herbivores in the Mara Region of Kenya

A 60 ECTS Master's Thesis

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Preface

This thesis is the final conclusion to my master's degree in Biology, from the faculty of Natural Sciences at Aarhus University, Denmark. The thesis was done at the section for Ecoinformatics and Biodiversity, and constitutes 10 months' work, equaling 60 ECTS, including 2.5 months of fieldwork in the Mara North Conservancy, Kenya. The project is likewise meant to contribute to the Maasai Mara Science and Development Initiative (MMSDI), to further sustainable and science-based conservation work within the Maasai Mara ecosystem.

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This work is divided into two parts. Part A that offers a lengthy and overall introduction into the African savanna and the remarkable ecosystem. Part B is a scientific manuscript for publishing in African Journal of Ecology.

Part A

General introduction to the African savanna ecosystem

Welcome to The African Savanna

Savannas exist across the tropics and subtropics on various continents, but none are more diverse and iconic than those found in Africa (Reid 2012). Approximately 44 % of all classified savannas are located on the African continent and these ecosystems support an immense biodiversity, rarely found elsewhere on the planet (Cumming 1982, Butt and Turner 2012, Fynn et al. 2016, Hempson et al. 2017). African savannas are at the epicenter of various indigenous and long-lasting cultures, effective land use practices and biodiversity hotspots, primarily because of their high productivity and unique plant and animal diversity (Reid 2012, Lomolino et al. 2017). It is one of the few ecosystems on Earth that still preserve much of its original species assemblages (Waldram et al. 2008, Hempson et al. 2015a). During recent years, the African savanna has been under massive anthropogenic pressure from a steadily growing human population, and many small- or regional-scale ecosystems have already collapsed fully. Today, only small fragments of a previously vast, species-rich savanna exist across the continent and as a result, several animal populations are either rapidly declining or have gone extinct (Bhola et al. 2012a, Fynn et al. 2016, Green et al. 2019). A primary contributor to many wildlife declines have been the increasing livestock production that follows a larger human abundance (Georgiadis et al. 2007, Ogutu et al. 2016). 10,000 years ago, 99 % of all terrestrial, vertebrate weight mass on the planet consisted of wildlife where humans accounted for the remaining 1 %. Today, humans now represent 32 % while livestock account for 67 %, leaving a mere 1 % representing all the remaining terrestrial, vertebrate wildlife (Smil 2011, Population Matters 2021). Such drastic numbers coupled with rapidly declining wildlife populations have caused many governments to deem livestock production and wildlife conservation incompatible, labelling livestock husbandry as ecological enemies (Augustine et al. 2011, Davis 2011, Odadi et al. 2011b). Recent studies have challenged this viewpoint and shown that wildlife-livestock dynamics are rarely as straightforward (Muchiru et al. 2008, Augustine and Springer 2013, Gandiwa et al. 2013, Schieltz and Rubenstein 2016). The interactions usually fluctuate and depend largely upon the environmental factors and cues that influence the savanna biome. Multiple interacting factors, such as climate, hydrology, soil characteristics, fire and herbivory have all been crucial in shaping and maintaining the savanna for millions of years (Bond 2008, Lehmann et al. 2011, Bond and Midgley 2012, Sankaran 2019, Phelps et al. 2020). Therefore, understanding and managing the interplay between wildlife and livestock is also about understanding how all of these intrinsic factors interact on the tropical and subtropical savanna biome.

The Savanna Biome Emerges

Today, the grassy savanna covers approximately one fifth of the land surface on Earth (Beerling and Osborne 2006, Osborne 2012, Fig. 1), and is classified as mixed tree-grass systems, where the landscape is dominated by a continuous grass layer, interspersed with trees, shrubs and thickets (Jeltsch et al. 1998, Petty et al. 2007,

Parr et al. 2012, Lehmann et al. 2014). It is regarded as one of the most spatially and temporally heterogeneous biomes on the entire planet (Lomolino et al. 2017). The development and subsequent spread of the modern savanna biome is generally linked to the expansion of the grasses utilizing the C₄ photosynthetic pathway that occurred around the late Miocene, some 6-8 Mya. At the Miocene-Pliocene boundary, the atmospheric CO₂ concentration was historically low while



temperatures were markedly high, promoting the evolution of this alternate photosynthetic pathway that could reduce photorespiration while raising photosynthetic efficiency (Beerling and Osborne 2006, Lehmann et al. 2011, Bond and Midgley 2012). C₄ photosynthesis is highly effective in areas with low shade, high temperature and generally thrives with low CO₂ levels, and in such climatic settings, the photosynthetic efficiency of the C₄ pathway far exceeds that of the ancestral C₃ pathway (Furbank 2016). Indeed, the C₄ pathway is thought to have evolved more than 50 times, across 19 different plant families and the grasses utilizing this photosynthesis account for approximately 20 % of all carbon fixation on the terrestrial plane (Osborne 2012). Given that the climate today is considerably different than in the Miocene-Pliocene epochs, the modern C₄ grasses only maintain their dominance in open and hot environments with heavy sunlight and little shade. Here, their increased photosynthetic rates and higher water- and nitrogen-use efficiency in this environment allow the grasses to facilitate a more rapid biomass accumulation than those of the C₃ pathway (Von Caemmerer and Furbank 2003, Hopkins and Huner 2009, Furbank 2016). This becomes important when delving deeper into how the savanna biome is then maintained to this day.

Maintaining the Savanna: Fire and Other Abiotic Factors

While climate certainly played a vital part in forming the savanna biome, it is not the defining factor in maintaining it. Tropical forest and savanna can occur under the same climatic conditions at the regional or local scale and as such, there must be something else promoting savanna above forest - or vice versa (Skarpe

1992, Jeltsch et al. 1998, Bond 2008). Around the Miocene, naturally occurring fires were increasing and this was likely the result of the expansion of grass biomass that was happening at the same time (Lehmann et al. 2014). The higher biomass provided ample fuel for the fires raging across the grasslands, thus promoting the higher degree of burning, in what has been described as a positive feedback loop (Van Langevelde et al. 2003, Accatino et al. 2010, Beckage et al. 2011). Grasses, in general, grow a higher part of their biomass below the soil surface and their above-ground meristems are located close to the soil, thus being able to reaccumulate lost biomass even if most of the above-ground tissue has been removed (Blair et al. 2014, Hempson et al. 2015b). C₄ grasses further their advantage with their ability to rapidly regrow the aboveground biomass, and are therefore particularly well-adapted to regular disturbances, such as burning (Bond and Midgley 2012, Bernardi et al. 2019). During the wet season, the heavy rainfall stimulates rapid grass growth, and this accumulated biomass then adds additional fuel for more, severe fires that occur when the dry season hits (Van Langevelde et al. 2003, Beckage et al. 2011, De L. Dantas et al. 2013). The frequent fires then promote C_4 grass growth while simultaneously preventing tree encroachment, as fire generally destroys tree seedlings, thus hampering tree recruitment (Laris and Dembele 2012, Bernardi et al. 2019). The species of tress existing on the savanna are adapted to fire, with thick, insulating, corky bark and a tree crown growing high above the ground (Osborne 2012, Parr et al. 2012). However, the trees still utilize the C₃ photosynthetic pathway and are thus outcompeted by the C_4 grasses, which can rapidly re-establish the newly burned patch at a much faster pace than the young C_3 trees (Charles-Dominique et al. 2018). Therefore, as the grass biomass increases, the tree biomass decreases, furthering the feedback loop, because the loss of forest cover slows evapotranspiration and cloud formation, thereby reducing precipitation in the area (Beerling and Osborne 2006). As such, deforestation can lead to longer dry periods and drought, making the system more susceptible to burning. So, more grass supplies more fuel for fires, which then burns easier and more rapidly under seasonally dry conditions, thus completing the feedback loop of grass-tree-fire interactions (Accatino et al. 2010, Beckage et al. 2011, De L. Dantas et al. 2013). Now, frequent burning does not equate to annual fires. Some savanna systems experience fire every 2-3 years, with a few even burning twice a year, while others only experience large fires every 3-10 years, but the disturbance level is still enough to maintain the grass-dominated savanna (Accatino et al. 2010, Reid 2012). The frequent burning of savanna vegetation not only influences the vegetation but the soil as well. The ashes left by fire can markedly enrich the nutrient content within the soil, re-fertilizing it and providing the vegetation with renewed nutrients for regrowth (Osborne 2012, Donaldson et al. 2018). If the fire intervals are long enough and moisture-levels sufficient, the nutrient-rich soil can even allow closed-community forests to overtake the otherwise grass-dominated patch (De L. Dantas et al. 2013).

So, while fire can influence plant growth, it is generally stimulated mostly by two factors: nutrient availability and water content; where nutrient availability controls the growth rate, water supply controls the duration of the growth period (Skarpe 1992). Nutrient content can also influence the mammal distribution, as

richer soils generate higher-quality grass that can attract a higher number of herbivores reliant on forage quality rather than quantity. It has been found that nutrient-rich savannas can support up to three times the grazing biomass than nutrient-poor savannas (Reid 2012, Bouchenak-Khelladi et al. 2020), and as will be covered in the section below, that can also influence the heterogeneity and vegetation structure of the savanna (Asner et al. 2009, Archibald and Hempson 2016).

Precipitation is a vital part of the savanna ecosystem (Skarpe 1992). Because of the decreased evapotranspiration from low tree cover, savannas are reliant on rainfall generated outside of the system for their hydrological needs (Beerling and Osborne 2006). Savannas are marked by a strong seasonality, with a distinct wet and dry season a year. The savannas of East Africa are even more unique, as these are the only ones with a bimodal rainfall, thereby having two wet seasons and two dry seasons throughout the year instead of one (Reid 2012). This pattern can only occur because of the Intertropical Convergence Zone (ITCZ), which is a belt of rainfall travelling north and then south as a result of the heating of the continent. Thus, the belt passes by the Equator twice on its annual journey, supplying the East African countries with two rainfall periods as opposed to one (Reid 2012, Bartzke et al. 2018). Precipitation is important for shaping the vegetation patterns, not just on the savanna, but across the globe (Ogutu and Owen-Smith 2005). The rainfall patterns on the savanna control the biomass production of plants, with adequate water availability stimulating vegetation growth. It also controls the nutrient availability present in soils, as heavy rainfall becomes run-off water, which does not permeate the soil and instead generates erosion and washes away the nutrients that would otherwise sink into the soil (Coblinski et al. 2019). Precipitation can also influence the fire regimes, as higher rainfall can generate larger fuel loads in relation to a rapid grass biomass accumulation while low rainfall can lead to more extensive and destructive burns as the vegetation will be drier and thus more prone to ignite (Lehmann et al. 2014, Bartzke et al. 2018). Lastly, water availability and rainfall patterns affect both animal and human alike, their distributions and movements are often responses to the oscillations in precipitation levels and this too, plays a major part in shaping and maintaining the savanna (Laris and Dembele 2012, Lankester and Davis 2016).

Maintaining the Savanna: Herbivory

The factors mentioned above all interact to maintain the savanna biome. However, there is one major factor yet to be discussed – one that is vital to the savanna ecosystem. Alongside fire, herbivory is one of the most integral characteristics of savanna vegetation dynamics (Asner et al. 2009, Hempson et al. 2015b). The African savannas host one of the most diverse and impressive array of mammalian herbivores to this day (Cumming 1982, Butt and Turner 2012, Fynn et al. 2016), with body sizes ranging from the small dik-diks (*Madoqua* spp.) weighing 3-4 kilograms, to the large African savanna elephant (*Loxodonta africana*) at 3 tons (Cumming 1982, Osborne 2012). Diversifying mammalian herbivores are thought to be linked to the expansion of the savanna biome as the grasses and trees have evolved traits that act as a defense against herbivory, such as less palatable leaves or spinescence on trees and shrubs. The occurrence of these traits

coincides with the rapid expansion of the C_4 grasslands and can be explained by the diversification of the bovid lineages and megaherbivores, which took place just as the grasslands started expanding and opening up the landscape. Indeed, mammalian herbivory have been shown to be highly capable in generating vast, open landscapes and minimize tree coverage (Charles-Dominique et al. 2018, Soto-Shoender et al. 2018, Bouchenak-Khelladi et al. 2020).

Browsers can be severely damaging to trees. Like fire, tree seedlings and saplings are particularly vulnerable to consumption by herbivores and these two life stages are also the major bottlenecks of tree recruitment on the savanna (Van Langevelde et al. 2003, Augustine et al. 2011, Young et al. 2013, Archibald and Hempson 2016). Medium-sized browsing species (meso-browsers), which are primarily the ones feeding on these tree stages, generally pertain to the more open grazing lawns and not the heavy, woody thickets. This is thought to relate to both the clearer visibility of the seed- and saplings as well as minimizing the depredation, as these smaller-bodied browsers will have a higher predation risk (Sankaran 2019, Voysey et al. 2020). Larger-bodied browsers, such as black rhino (Diceros bicornis), giraffe (Giraffa sp.) and elephant (Loxodonta africana), do not suffer from the same risk of predation (Sinclair et al. 2007, Bhola et al. 2012a) and are known to negatively impact large, fully-grown trees as well (Voysey et al. 2020). It is welldocumented that elephants are important ecosystem engineers and exert major influences on tree survivorship and recruitment. Not only do elephants browse on whole plant materials, but they likewise alter the physical structure of trees by uprooting and topple grown trees (Cumming 1982, Skarpe et al. 2004, Young et al. 2013). Their strong influences on woody vegetation have led to concern that elephants can completely destroy plant diversity, and this concern was even the motivation for effectively culling 16,000 elephants in Kruger National Park, SA, between '67 and 94' (Coverdale et al. 2016). However, Coverdale et al (2016) showed that, despite their negative effects on trees, elephants actually increase overall heterogeneity on the savanna and elevate understory plant biomass. Understory plant species comprise more than 70 % of savanna plant diversity, and by knocking over and uprooting trees, elephants create refuges for these rarer understory species to prevent herbivory, thus contributing massively to the general plant diversity on the savanna landscape (Coverdale et al. 2016). Elephants can likewise influence fire regimes, where the uprooted trees make way for grass growth, thereby providing more potential fuel for the next fire (Skarpe et al. 2004, Hempson et al. 2017).

While browsers have an inherently positive effect on maintaining the open grass plains of the savanna, grazers generally generate the opposite effect (Jeltsch et al. 1998, García Criado et al. 2020). It may seem counterintuitive given their major impact on shaping the savanna ecosystem, but grazers feed primarily on the C_4 grasses, which in turn can reduce the fuel load for fires and provide trees and shrubs the opportunity to establish in recently grazed patches (Jeltsch et al. 1998, Waldram et al. 2008, Waal et al. 2011). Indeed, many studies have found that heavily grazed areas receive less fire and have higher woody cover (Van Langevelde et al. 2003, Archibald and Hempson 2016, Hempson et al. 2017). However, Young et al (2013)

found that grazing will have a more pronounced, cascading effect on the vegetation structure in lowproductivity, and low-rainfall areas compared to high-productivity areas. Intermediate grazing levels on many savannas do aid in maintaining open grassland, increasing biodiversity of both flora and fauna, and further advancing landscape heterogeneity (Skarpe 1992, Hempson et al. 2017). The many grazers are often part of a grazing succession system, facilitating each other's presence. Elephants, or other megafaunal herbivores, open up the landscape and stimulate grass growth. The large quantity of grass biomass lures in the large-bodied grazers, such as Cape buffalo (*Syncerus caffer*), and their consumption of the tall grasses leaves lower, but higher-quality forage for smaller grazers, such as topi (*Damaliscus lunatus jimela*) and blue wildebeest (*Connochaetes taurinus*). An example of this grazing succession is on the plains of the Serengeti in Tanzania, where the presence of buffalo and wildebeest consume the tall, coarse grass and leave behind the smaller grass tufts that are favored by the selective, small grazers such as Thompson's gazelle (*Eudorcas thomsonii*) (Cumming 1982).

The presence of herbivores not only affect the vegetation directly (by consumption or destruction) but also indirectly, as they increase the nutrients within the soil by excretion and defecation, enriching it with higher levels of nitrogen and phosphorus (Augustine et al. 2011, Waal et al. 2011). So, while large herbivores, such as elephant and buffalo, can leave pronounced impacts on the vegetation, smaller herbivores can have major effects too, although these might be more subtle and difficult to detect (Cumming 1982). It is generally stated that the ecological response to herbivory on the savanna seem to be an overall, increased vegetation heterogeneity (Asner et al. 2009). It is abundantly clear that mammalian grazers and browsers share both positive and negative effects on the mechanisms and feedbacks that drive the savanna vegetation, and their complex and multifaceted interactions are vital in shaping and maintain the savanna ecosystem (du Toit et al. 2010, Edwards et al. 2010, Archibald and Hempson 2016).

Competition and facilitation

The many herbivore species present on the savanna influence not only the vegetation, but each other as well (Owen-Smith 2002, Odadi et al. 2011a). Interspecific interactions occur in every ecosystem and on every trophic level in nature (Boer and Prins 1990, Pringle et al. 2019), and the complex interplay between the different African herbivores has been the subject of many studies in the past decades (Odadi et al. 2011a, Kartzinel et al. 2015).

COMPETITION

Competition is a major driver in furthering ecological and evolutionary changes within community structures (Butt and Turner 2012, Martorell and Freckleton 2014, Traba et al. 2017). It can occur between individuals of the same species (intraspecific competition) or between different species (interspecific competition). While intraspecific competition is important in population dynamics, interspecific competition is the primary driver of the complexity found in animal community dynamics, especially those found on the savanna

(Dickman and Woodside 1983, Traba et al. 2017). Interspecific competition commonly arises when multiple species require the same resource, such as habitat or food (Dickman and Woodside 1983, van Beest et al. 2014). For many of the herbivores on the African savanna, competition for proper forage is much higher than that of habitat (Owen-Smith 2002). Many herbivores can co-exist within the same grass patch and their joint presence does not represent a competitive interaction, as forage preference can be vastly different from each other, and absence of a species from an area does not necessarily equal to competitive exclusion (Butt and Turner 2012, Kartzinel et al. 2015, Blanchet et al. 2020). Forage competition, in general, can only occur when three conditions are met: (1) there must be habitat overlap between the species. (2) There must be a dietary overlap between the species, and (3) the dietary resource must be limited (Boer and Prins 1990, Butt and Turner 2012). Niche partitioning is a primary solution to reducing interspecific competition and further interspecific co-existence (Young et al. 2005, Macandza et al. 2012, Pringle et al. 2019).

There are two ways of segregating. The first is habitat partitioning, where the species are spatially or temporally separated. Habitat selection is shaped by a species' preferences of several abiotic and biotic factors, such as foraging, anti-predation and competitive strategies, and this can be altered to avoid competing with other, similar species within a given area (Cozzi et al. 2012, van Beest et al. 2014, Traba et al. 2017). This fine-scale habitat selection can be observed for African herbivores by for example different ungulates segregating by a watering hole or by employing a seasonal migration pattern (Osborne 2012, Kartzinel et al. 2015). For African predators, it can be to alter activity patterns; e.g. cheetah (*Acinonyx jubatus*) and African wild dog (*Lycaon pictus*) are proposed to be diurnal or crepuscular to avoid the stronger competing species such as lion (*Panthera leo*) or spotted hyena (*Crocuta crocuta*) (Cozzi et al. 2012).

The second way of niche segregation is through dietary partitioning. One explanation for the high herbivore diversity found on the African savanna is the various and vastly different feeding ecologies (Odadi et al. 2011a, Kartzinel et al. 2015). African herbivores are separated into three overarching feeding guilds: the pure grazer, the pure browser, and the mixed feeder (Hempson et al. 2015a). Grazers, such as wildebeest, buffalo or topi, feed only on grassy and herbaceous biomass while browsers, such as eland (*Taurotragus oryx*) or giraffe, feed on woody vegetation, such as shrubs and trees. Mixed feeders, such as Thomson's gazelle, elephant or impala (*Aepyceros melampus*), shift between grazing and browsing, often grazing in the wet season where there is plenty of forage and browsing in the dry season when grass biomass becomes scarce (Bhola et al. 2012a, Kartzinel et al. 2015). Especially for the grazing guild, gut morphology, mouth anatomy and body size further subdivide the herbivores (Macandza et al. 2012, Fynn et al. 2016). Herbivores can be separated into ruminants (examples include buffalo and wildebeest) and nonruminants (such as zebra (*Equus* spp.) and elephant), depending upon their gut morphology and thus how they digest their food (Macandza et al. 2012, Hempson et al. 2015a). Ruminants, because of their long digestive system and multiple stomachs, are generally able to ingest and digest low-quality forage, such as tall, low-nutrient grasses and therefore, are often foraging in open, tall-grass areas, compared to the nonruminants that feed on

the smaller grass swards, which contain higher nutrient content (Odadi et al. 2011a, Fynn et al. 2016). Body size likewise influence the dietary partitioning (Valls-fox et al. 2018). Large-bodied herbivores often require a high amount of forage and follow a general 'quantity over quality' approach. These big herbivores primarily feed on bulk biomass and can tolerate a lower quality as long as sufficient quantities are available. The direct opposite exists for the smaller-sized herbivores, where they do not require a large biomass but instead select forage based upon quality (Bhola et al. 2012a, Ogutu et al. 2014). The shape of the mouth determines the herbivore's ability to forage, as narrow-mouthed herbivores can select the high-quality stems while circumventing the low-quality leaf litter and will often select habitats with medium-tall grasses (Murray and Illius 2000, Owen-Smith 2002, Fynn et al. 2016). Wide-mouthed herbivores are unable to select on such a fine scale and as such, feed primarily on open, short grazing lawns (Fynn et al. 2016). The different feeding ecologies and herbivory guilds influencing dietary segregation also manifest in the habitat partitioning, as the herbivores will separate into their preferred niches depending upon their feeding requirements (Cozzi et al. 2012, Fynn et al. 2016).

FACILITATION

While competition is generally considered negative, for either one or multiple of the species involved (Butt and Turner 2012), not all interactions are. Facilitation is the process of one species benefiting from the actions of another and are inherently thought of as positive (Odadi et al. 2011a, Bork et al. 2013). It can occur in multiple forms, like habitat facilitation, where one species can alter the environment in a way that benefits another (Arsenault and Owen-Smith 2002). For African herbivores, an example of this could be elephants uprooting trees and altering the vegetation structure, thereby opening up the landscape for the grazers and smaller browsers (Coverdale et al. 2016). Another type of facilitation is feeding facilitation (Augustine and Springer 2013). As mentioned previously, many African herbivores are part of a grazing succession, which is an example of feeding facilitation taking place (Boer and Prins 1990, Owen-Smith 2002). The grazing on tall grass swards by bulk feeders reduces vegetation height, leaving shorter tufts of nutrient-rich grass for the selective grazers to feed upon (Boer and Prins 1990, Waldram et al. 2008), or heavy grazing stimulates rapid regrowth, providing the next grazers colonizing the grazed patch with fresh, higher-quality forage (Fynn et al. 2016). There are several examples of this on the African savanna: a herd of buffalo, a bulk feeder, consume the tall grasses, leaving behind a grazed lawn for wildebeest, zebra, and Thomson's gazelle to forage on the remaining tufts (Cumming 1982, Boer and Prins 1990). Zebra, although their gut morphology is perfectly adapted to process the poor-quality forage (Macandza et al. 2012, Said et al. 2016), are oftentimes found on open grazing lawns and in close proximity to large herds of wildebeest. This is because the many wildebeest not only provide excellent forage opportunities, but also minimize predation risk (Thaker et al. 2010). Feeding facilitation is to some degree thought to improve overall population performance for a certain species. For instance, Vesey-Fitzgerald (1960) found that elephant

presence could have a positive influence on the medium-sized herbivores in the region of Lake Rukwa. Bell (1970) postulated the same sort of pattern for zebra and wildebeest abundances in the Serengeti, but subsequent data have not supported this idea, thus while facilitation remains an important factor in animal communities, it does not equate to increasing population performance (Arsenault and Owen-Smith 2002, Butt and Turner 2012).

Thus, facilitation and competition constantly interplay on herbivore dynamics on the savanna. More often than not, it is not an 'either-or' situation in most animal communities and might even be seasonally or spatially different (van Beest et al. 2014). While a species facilitates one, it might outcompete or displace another (Arsenault and Owen-Smith 2002). For instance, a high abundance of white rhino (*Ceratotherium simum*) and hippo (*Hippopotamus amphibius*) created short-grass grazing lawns, which in turn decreased the abundance of elephant, buffalo and waterbuck (*Kobus ellipsiprymnus*) in a region in Uganda while a population increase of elephant in Tsavo, Kenya saw a concurrent increase of grazers in the region while browsers subsequently declined (Arsenault and Owen-Smith 2002). These examples only further the complex dynamics that exist between herbivores on the African savanna, ones that are difficult to properly outline and understand. And the complexity only intensifies as the human element is introduced into the system.

Pastoralism and Cattle

Pastoralism: Cattle as Currency

The relationship between pastoralists, their livestock and the wildlife in the rangelands of East Africa has been long-lasting and intricately intertwined (Lankester and Davis 2016). Pastoralism is the most widespread form of land-use across the savannas of the world (Goldman 2007, Western et al. 2020) and has been an integral part of the African landscape for millennia (Lamprey and Reid 2004, Davis 2011, Bhola et al. 2012b). Through grazing and fire manipulation, this way of life have been just as instrumental in maintaining the savanna biome the past few thousand years as herbivory, fire, precipitation, and the other alreadydiscussed factors (Vuorio et al. 2014, Lankester and Davis 2016). For centuries, the pastoralists have adapted to the insecurity of stochastic, fluctuating availability of ecological resources by utilizing a nomadic, mobile lifestyle on the African savanna, in much the same way that the corresponding wildlife populations have. This makes it possible for them to successfully exploit the unpredictive rainfall and heterogeneous soil quality that dominate the landscape (Msoffe et al. 2011, Bedelian and Ogutu 2017, Nkedianye et al. 2020, Western et al. 2020). The predominant livelihood of pastoralism is livestock, such as cattle, sheep, goats, camel and donkeys, often coupled with small-scale agriculture or bushmeat hunting and thus, the majority of land-use for pastoralism is pastures for their livestock to feed on (Thompson and Homewood 2002, Bedelian and Ogutu 2017, Nkedianye et al. 2020). Because livestock can commonly be exchanged for goods and services, the number of especially cattle owned by a household is oftentimes indicative of their wealth and social status within their community. Thus the more livestock you own, the bigger your influence and

respect, prompting livestock owners to always increase their stocking rates of cattle (Bos indicus), shoats (sheep (Ovis aries) and goat (Capra hircus)) and donkeys (Equus asinus) (Lamprey and Reid 2004, Goldman et al. 2010, Løvschal et al. 2018). Interactions between pastoralists and wildlife can be manyfold. Wild herbivores with a high predation risk have been observed close to the settlements or homesteads to deter natural predators, utilizing dams and watersheds for livestock as a water source during drought or even resting in the shade created by the planted trees that act as a living fence (Muchiru et al. 2008, Lankester and Davis 2016, Eustace and Tarimo 2019). The pastoralists, in turn, track the local herbivore movements to find suitable foraging areas for their livestock or use species such as wildebeest to pinpoint rainfall patterns (Goldman 2007). However, living in such close proximity to wildlife generate conflicts as well (Mukeka et al. 2018). Big species, such as elephant and buffalo, can pose a significant threat to human health and safety as well as massive property damage (Western et al. 2020). Smaller, herbivorous species can also damage agricultural products while carnivores can prey upon livestock species or severely injure or even kill family members (Lamprey and Reid 2004, Ogutu et al. 2005a). One of the most significant challenges to the dynamics between humans and wildlife is the introduction and transmission of disease (Lankester and Davis 2016). While local pastoralists have learned how best to avoid transmission of endemic wildlife diseases to their livestock throughout their tenure on the savanna (Goldman 2007, Vuorio et al. 2014), that changed with the introduction of foreign cattle in the 19th century when a massive epidemic of rinderpest swept across East Africa, effectively killing 95 % of all cattle populations while practically decimating Cape buffalo and wildebeest populations in the Serengeti (Wafula and Kariuki 1987, Sinclair et al. 2007, du Toit et al. 2010). The rapid and sudden decrease in livestock, coupled with increased colonial disease outbreaks, also influenced the pastoralist populations where famine and illness ravaged most of the local communities (Reid 2012, Lankester and Davis 2016). This period generated a whole new dynamic in the rangelands and occurred alongside colonial administrators realizing the economic potential of large, diverse wildlife populations to increase foreign capita, thus this new rinderpest-resilient wildlife landscape with sparse human populations became the baseline for which future conservation work was to be built upon (Thompson and Homewood 2002, Reid 2012, Lankester and Davis 2016). As the pastoralist populations recovered and gained more livestock, questions about their possible detrimental influences on wildlife began to fluctuate and increase (Schieltz and Rubenstein 2016).

Livestock and Wildlife: Competition, Facilitation or Somewhere In Between

As livestock numbers in Africa have steadily increased, so too has our need for understanding the interactions that occur between livestock and wildlife (Ogutu et al. 2014, Schieltz and Rubenstein 2016). One of the most common concerns is the competitive effect livestock can have on wild herbivores (Odadi et al. 2011b, Averbeck et al. 2012, Augustine and Springer 2013). Whereas wild herbivores have spent millions of years adapting to and minimizing their possible competitive interactions, livestock is an evolutionally new phenomenon for wildlife to respond to. Most livestock and wild herbivores share a significant food overlap,

so it is not farfetched to assume some degree of dietary competition must occur (Augustine et al. 2011, Augustine and Springer 2013, Valls-fox et al. 2018). Among the most widely distributed livestock species in Africa is cattle (Bedelian and Ogutu 2017, Løvschal et al. 2018). Cattle is primarily a grazer, and competition theory then states that the native herbivores most likely to compete will be other grazers, such as zebra, wildebeest and buffalo (Young et al. 2005, Augustine 2010, Hibert et al. 2010), whereas browsing and mixed feeding species are more likely to remain unaffected by cattle presence (Hibert et al. 2010, Schieltz and Rubenstein 2016). A study by Ogutu et al (2014) found that browsing species, such as giraffe, were evenly distributed between a protected, human-free area and the human-dominated ranches surrounding it, in contrast to the large grazers that seemed to avoid the ranches in favor of the protected area, thus suggesting feeding guilds likely factor into the proposed competitive effects of cattle on wildlife (Ogutu et al. 2014). Indeed, several studies have noted that the species displaying the largest spatial avoidance of cattle on the savanna are the grazing, bulk feeders, like the buffalo. Buffalo is a large ruminant grazer, requiring plenty of bulk forage and as such, is in direct competition with the grazing cattle (Averbeck et al. 2012, Bhola et al. 2012b). Buffalo are indeed known for avoiding cattle on the savanna; however, this large grazer has been observed near cattle herds at vital water points during periods of drought or at the peak of the dry season, suggesting the need for water is greater than whatever competitive influences exist between cattle and buffalo (Valls-fox et al. 2018). Topi or kongoni (Alcelaphus buselaphus) likewise exhibit a preference for medium-tall stalks for forage but also use the tall grasses during calving season to hide their vulnerable offspring from predators. Therefore, these two species generally avoid areas currently or recently grazed by cattle, as the cattle's non-selective grazing form tend to leave behind short grazing lawns, unfavorable to either topi or kongoni (Sitters et al. 2009, Green et al. 2019).

Livestock's ability to reduce forage available to wild herbivores is a major concern (Koetke et al. 2020). Not only does the livestock feed on the forage the herbivores would, but they also have the capacity to remove it by simply moving about the landscape. Cattle congregate in large herds and as they travel the savanna, the vegetation underneath their hooves is trampled. Shrubs, bushes and tree seedlings are often also pushed over or stamped on, thus destroying available forage for smaller browsers as well (Muchiru et al. 2008, Ogutu et al. 2014, Bernardi et al. 2019). Shoats have also been known for their destructive capabilities on vegetation. They are a mixed feeder and can feed on grassy and woody vegetation alike. So, although their size does not trample the vegetation as the much-larger cattle, oftentimes they leave a foraged area devoid of any remnants, having fed on the small grass tufts as well as the bushes, shrubs, and tree seedlings (Løvschal et al. 2018).

Competition for water resources becomes an issue as well, especially during a drought (Ogutu et al. 2014). Most animals on the savanna respond to rainfall and water availability, and especially the waterdependent grazers have been shown to suffer heavy losses during drought and in particular if large, grazing herds of livestock occupy the areas close to watering holes or rivers (Hibert et al. 2010). In parts of northern Kenya, for instance, Grevy's zebra (*Equus grevyi*) have been known to visit water points during the night as livestock utilizes them during the day, suggesting this species increases their predation risk in an effort to avoid the livestock (Ogutu et al. 2014). Competitive effects of livestock on wild herbivores are not the only interaction though. Competition can also work in the reverse, where native herbivores influence livestock (Odadi et al. 2011b). Odadi et al (2011) found that the presence of wild herbivores negatively affected cattle's weight gain but they also found that during the wet season, the interaction shifted, and the cattle and herbivores facilitated each other's intake instead. Thus, competitive effects are more likely to occur during dry seasons and periods of drought, where resources are scarce, and therefore competition is not necessarily constant between livestock and herbivores (Augustine 2010, Schieltz and Rubenstein 2016).

Several studies have found that avoidance behavior of some wild herbivores to livestock consistently occurs during dry periods, and when the wet season hits, they aggregate closer (Valls-fox et al. 2018). This can for instance be observed in the Maasai Mara National Reserve and its surrounding conservancies in Kenya. Here, wild herbivores either gather in the reserve or the human-occupied conservancies, depending upon the season and thus the forage availability (Bhola et al. 2012a, Ogutu et al. 2014). The many cattle herds can graze down the tall grasses, leaving behind the coveted, small-medium, nutrient-rich grasses for other herbivores to feed on, opposed to the tall, nutrient-poor grasses present in the reserve (Fritz et al. 1996, Vuorio et al. 2014, Schieltz and Rubenstein 2016). Indeed, there can be many benefits to livestock presence for wild herbivores. Just like the natural grazing successions of elephant and buffalo opening up the savanna, cattle have been known to do the same, thus facilitating small-medium sized herbivores and the selective feeders that require high-quality forage (Bhola et al. 2012b, Bedelian and Ogutu 2017). Small herbivores, such as Thomson's gazelle, have been observed in close proximity to cattle herds. Not only do the cattle create short grazing lawns filled with nutrient-rich grass but their presence also acts to minimize predation risk (Muchiru et al. 2008, Bhola et al. 2012a). Many small-medium sized herbivores are generally in high risk of predation and will oftentimes gather in open areas with little vegetation cover and congregate in big, interspecific flocks to better spot lurking predators (Bhola et al. 2012b, Reid 2012). The massive cattle herds not only open up the landscape and keep the grass short, but also provide protection with their large body sizes and occasional human herders, who also acts as a predator deterrent (Vuorio et al. 2014). Livestock can facilitate wild herbivores more indirectly as well by affecting the nutrient availability and concentration within the soil (Augustine 2010). Especially cattle are often herded around on the savanna and at night, are kept in bomas (temporary, movable enclosures) to protect them from predators and theft. Abandoned boma settlements have been shown to create grazed glades, which serve as elevated nutrient redistribution that increases the nutrient content heterogeneity. These nutrient hotspots act as a beacon to attract wild herbivores even several years post abandonment for rich biomass and high-quality forage (Augustine et al. 2011, Vuorio et al. 2014, Western et al. 2020).

As has hopefully become clear, determining competitive or facilitative effects of livestock on wild

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herbivores is a complex, interchanging issue that is not clear-cut. Like with competition and facilitation between wild herbivores, the interactions between wild and domestic herbivores are usually not an 'eitheror', and livestock can compete with one species while facilitating another. Indeed, many studies have found negative effects of excessive pastoralism and livestock production on wildlife, yet others have found overwhelming, positive responses (Muchiru et al. 2008, Augustine et al. 2011, Augustine and Springer 2013, Gandiwa et al. 2013, Schieltz and Rubenstein 2016). Mainly, any competitive effects of livestock on wild herbivores seem to be mostly influenced by seasonal fluctuations and limited resource patterns and not by any overarching rule about dietary or habitat overlap (Bhola et al. 2012b, Traba et al. 2017). However, it is important to note that many, if not all, neutral or facilitative effects of livestock on native herbivore populations come from an intermediate stocking rate of livestock and that competition will most likely occur throughout the whole year, regardless of season, if livestock levels are markedly high (Ogutu et al. 2005b, Cingolani et al. 2014).

Savannas of the Anthropocene

Savannas across the world today face many similar challenges as the rest of the world's biomes; namely, the increasing pressure of a modernizing, anthropogenic world (Ceballos et al. 2015). The increasing human population acts as a driver for the overexploitation of natural resources and the current wildlife declines documented worldwide (Ceballos et al. 2015, Green et al. 2019, Zhu et al. 2020). These declines are primarily linked to land degradation, habitat fragmentation, deforestation and erosion that are currently taking place across the savanna ecosystems (Fritz et al. 1996, Gandiwa et al. 2013, Mukeka et al. 2018, Green et al. 2019). The epoch of the Anthropocene is defined by massive human-caused influences and the ongoing mass extinctions of all wildlife on Earth (Smith et al. 2018). However, this sixth mass extinction, as it has been named (Ceballos et al. 2015), was already put into motion some 20,000 years ago during the late Pleistocene and has been linked to the global spread of the modern human (Homo sapiens) (Mosimann et al. 1975, Sandom et al. 2014, Lomolino et al. 2017). As humans migrated from Africa and colonized the other continents a rapid decrease of the mammalian fauna, especially the megafaunal species, followed shortly after. Notably, the megafaunal mammals of Africa remained relatively stable, suggesting that these mammals coevolved with humans and thus adapted to life with this apex hunter (Smith et al. 2018). Interestingly, the perseverance of the many and diverse African herbivores, and their subsequent significant effect on vegetation and fire dynamics, is one of the governing reasons why the savanna is so widespread in Africa but not on the South American or Australian continent, even though the environmental conditions in South America and Australia are similar to the African ones. Both these continents experienced heavy megafaunal losses that restricted the savanna biome occurrence (Lehmann et al. 2011). So, the African savanna and its biodiversity proved resilient during the initial megafaunal extinctions happening across the planet, but as the human population steadily increased, so too did the pressure on the wildlife. All across Africa, wildlife

declines have been reported as a result of human activities (Løvschal et al. 2017). In Kenya alone, wildlife populations have, on average, dropped 68 % since the '50s (Ogutu et al. 2016).

Climate Change

One of the most important global concerns, and this is likewise true for the savanna, is climate change and global warming. There has been some discussion as to how climate change will affect the complex savanna biome (Bartzke et al. 2018, Sankaran 2019, Moehlman et al. 2020, Phelps et al. 2020). Because water is a primary driver in the savanna ecosystem and tightly connected to overall production, the alteration of precipitation regimes and recurrent droughts is a major concern (Blair et al. 2014, Bartzke et al. 2018, Moehlman et al. 2020). Both flora and fauna are adapted to periods of drought and it is not uncommon for the savanna to have multiple and consecutive years where the annual rainfall is below average, and though recovery time might be longer after an intense drought, the system remains resilient (Riginos et al. 2018, Sankaran 2019). However, an increase in the frequency and duration of droughts has been noted for many African savanna systems, although with massive small-scale fluctuations across regions (Blair et al. 2014, Bartzke et al. 2018). Should the severity and length continue to increase, this can disrupt the recovery time and ability for the ecosystem, which can cause a shift in vegetation composition, woody encroachment or even desertification, causing a biome shift (Sankaran 2019, García Criado et al. 2020, Moehlman et al. 2020). It is however important to note that so far, no study has been able to link climate change as the sole driver of these ecosystem changes and it is more likely an interplay of other anthropogenic influences, such as heavy grazing, together with the changing climate (Bond and Midgley 2012, Riginos et al. 2018, García Criado et al. 2020). Savannas as an ecosystem have an overall heterogeneous composition, and as such, are highly adapted to and resilient against major disturbances (Reid 2012, Riginos et al. 2018).

More Livestock, Less Wildlife

More pressing, is the ever-increasing livestock numbers. As humans grow in number, so does the livestock. Today, approximately 60 % of all mammal biomass on land consist of livestock (cattle, shoats, donkey, camel, etc.), humans take up circa 36 % while only 4 % of all terrestrial mammalian biomass is wild animals (Bar-On et al. 2018, Baltazary et al. 2019, A Well Fed World 2021, See Fig. 2). As mentioned in the section above, high stocking rates of livestock can have profound effects on both vegetation and wild herbivores (Gandiwa et al. 2013, Young et al. 2013, Cingolani et al. 2014, Green et al. 2019, Zhu et al. 2020). An overabundance of livestock can lead to overgrazing on the savanna, as is evidenced in many areas of Africa, where livestock dominates the overall wild herbivores (Vega and Montaña 2011, Bouchenak-Khelladi et al. 2020), and domestic ungulates constitute 90 % of total ungulate biomass (Du Toit and Cumming 1999). A lot of cattle in a single area require a large amount of

Diet & Biodiversity Loss: Biomass Distribution of Land Mammals on Earth



Figure 2: Distribution of land mammal biomass. Graphic from awellfedworld.org, based on data from Bar-On et al (2018). Source: https://awellfedworld.org/biodiversity

forage and as such, will graze the grasses to the ground, leaving barely any biomass for regrowth or forage opportunities for small, selective feeders. Goats and sheep can have a more profound effect, as goats in particular have the ability to graze close to the roots and have been known to destroy the meristem tissue that is used for regrowth (Løvschal et al. 2018). As already covered, consistent, recurrent grazing on C_4 grasses can stimulate grass growth. However, without respite or sufficient remnant tissue, the plant is unable to recuperate (Skarpe 1992, Yamane et al. 2011, Archibald and Hempson 2016, Voysey et al. 2020). Loss of grassy biomass allows more water available for trees and bushes, thus enhancing their competitive abilities and subsequent spread. An increase in woody vegetation, shrubs and bush along with a decrease in grass cover will influence the fire feedback mechanisms, reducing fire frequencies on the savanna and indeed heavily grazed areas haven't received proper burns in decades. This alteration is changing fire regimes and are furthering the tree- and shrub encroachment, which has been recognized as a growing problem across various African savanna landscapes (Van Langevelde et al. 2003, Archibald and Hempson 2016, Hempson et al. 2017, Voysey et al. 2020). A high grazing pressure has also been shown to lead to lower nutrient availability within the soil, reduced water uptake and increased run-off (Skarpe 1992, Van Langevelde et al. 2003, Vega and Montaña 2011, Yamane et al. 2011). The high quantities of livestock will compete with grazing species to a much greater extent and leave heavily grazed lawns (Cingolani et al. 2014), unfavorable to even the small, selective feeders and eventually, force most grazing herbivores to find forage elsewhere (Gandiwa et al. 2013). Meso-browsers will likewise be deterred, as the preferred forage of tree seedlings and saplings in the open grassland no longer exists and is only found within closed-canopy forests of the bush and tree encroached savanna, which marginally increase the predation risk (Du Toit and Cumming 1999, Voysey et al. 2020). Populations of larger-bodied browsing species, such as elephant or black rhino, would have the capacity to increase over time, however both these species have exhibited spatial avoidance behavior of livestock and their human shepherds (Hibert et al. 2010, Schieltz and Rubenstein 2016). Thus, most herbivores found on the African savanna will decline in areas with high livestock densities, as has been observed throughout the continent (Young et al. 2013). For example, the high wildlife declines in Kenya have been attributed to rising livestock in the recent decades (Ogutu et al. 2012, 2016).

Livestock as an Ecological Engineer?

With the increasing livestock populations overtaking those of the wild herbivores, the question then becomes whether this will have any effect on the ecosystem as a whole. If we lose the native grazers, does it really matter for the ecosystem and its functions, as long as we have the domestic cattle or donkey as replacement? (Veblen et al. 2016, 2019, Riginos et al. 2018). The overgrazing situation painted above is mainly a concern in very restricted areas, where the animals cannot move onto new pastures and allow the area time to regenerate (Yamane et al. 2011). Most livestock in Africa are, or have been, kept on rotation as part of the nomad, pastoralist life, and compared to the husbandry practices of the modern, Western world, this lifestyle is highly sustainable (Msoffe et al. 2011). Livestock densities today vastly exceeds those of wild herbivores

found before the observed anthropogenic declines or even before the Pleistocene extinctions. As the wild herbivore densities continue to decline, and their ecological roles then left unfulfilled, many then start to speculate whether the large livestock populations are able to replace the native herbivores' ecological functions (Hempson et al. 2017). The three most dominant domestic species in Africa are cattle, sheep and goats. Cattle are predominantly a grazing bulk feeder while sheep primarily graze but have been known to browse and goats are a mixed feeder (Bedelian and Ogutu 2017). Already, there seems to be a distortion of the herbivorous composition, compared to the diverse feeding ecologies found in the native herbivore community (Hempson et al. 2017, Veblen et al. 2019) and indeed communities dominated solely of high rates of livestock have been shown to reduce plant species richness (Isbell and Wilsey 2011). While grazing succession could technically occur, where cattle would forage on the bulk biomass first, followed by donkey and then the smaller shoats, there are many instances where this sort of succession would not be feasible, such as in the Serengeti, or the ones initiated by mega-browsers like the elephant (Du Toit and Cumming 1999). Generally, the diversity of livestock species is markedly lower than that of native herbivore assemblages. Most noticeable within livestock assemblage, is that none of the widespread species is a predominant browser. When shoats do browse, they primarily feed on the foliage of the low, woody plants, such as shrubs and bush (Gabay et al. 2011), and cannot inhibit tree recruitment as bigger browsing species are known to. Said in another way, livestock simply lacks one species that has the same functionality as large browsers, in particular the elephant, thus they cannot provide the same vegetation changes without human interference (Young et al. 2013). Although in some systems, livestock has been found to alter vegetation dynamics in much the same way as native herbivores. In the mountain ecosystems of Argentina, Cingolani et al (2014) showed that low to moderate stocking of livestock helps preserve plant biodiversity in a system that had otherwise lost many of its herbivorous species and thereby their ecosystem functions. This study however is feasible only for landscapes that have completely lost their native herbivore assemblages and only if livestock stocking rates are kept below those of industrial, commercial stocking (Cingolani et al. 2014). For many other ecosystems, livestock populations lack the diverse functionality of native populations. This can be observed in various savanna ecosystems of Africa, where the open grassland is either eroded and almost barren, or encroached by bush, shrubs and woody vegetation (Farnsworth et al. 2002, Young et al. 2013, Archibald and Hempson 2016, Veblen et al. 2019).

Stay, Pastoralist!

The human population on the African savanna has steadily increased in recent decades and along with that, comes urbanization (Mureithi et al. 2019). As the urban areas have spread across the land that leaves less space for the rural areas, which support the remaining pastoralist societies (Mureithi et al. 2019, Weldemichel and Lein 2019). Modernization, growing human populations, and changes in land privatization and tenure has led to a sedentarization of many nomadic pastoralist communities, such as the Maasai in East Africa (Sitters et al. 2009, Msoffe et al. 2011, Løvschal et al. 2017, Weldemichel and Lein 2019, Western et

al. 2020). These sedentary pastoralists have then been forced to alter their livelihoods and many have reverted to agricultural practices or cultivation, which rarely merges well with wildlife coexistence (Davis 2011, Ayiemba et al. 2015, Nkedianye et al. 2020). Those who cannot, still maintain their livestock but instead of rearing them on a rotational grazing system as they historically did, now keep them in fenced pastures on their land (du Toit et al. 2010, Løvschal et al. 2017). This in turn can lead to rapid land degradation that cannot be reversed. Mobile pastoralism can also cause land degradation, but this is generally only temporary, and sufficient time is often provided for the soil and vegetation to regenerate before it is settled again (Sitters et al. 2009, Msoffe et al. 2011). Sedentarization of pastoralists does not give the ecosystem adequate time to recuperate and many areas in Africa are experiencing degradation, erosion and habitat destruction as a cause of this (Tyrrell et al. 2017, Mureithi et al. 2019). This new immobile livelihood has not only led to an increase in poverty for many pastoralist communities (Reid et al. 2016), but also further settlement and fencing, thus increasing habitat fragmentation and destruction for many wildlife species (Msoffe et al. 2011, Ayiemba et al. 2015).

In the Mara region, fencing has markedly risen within the past decades (Løvschal et al. 2017, Weldemichel and Lein 2019). The Maasai Mara Conservancies Association (MMWCA) even published a report showing that fencing in the Mara between October of 2014 and June of 2016 had increased a staggering 354 % (Weldemichel and Lein 2019). Fencing has a major impact on wildlife, as it can prevent animals accessing a vital resource, such as food or water (du Toit et al. 2010, Løvschal et al. 2018, Wilkinson et al. 2021). By restricting movement, herbivorous species can be separated from a high-quality forage opportunity while carnivorous species might be separated from preferred, wild prey and thus resort to depredation of livestock (Said et al. 2016, Pekor et al. 2019). Migrant herbivore species are especially affected by the rising fence densities, as it halts or alters their natural migration routes (Seidler et al. 2015, Løvschal et al. 2018, Weldemichel and Lein 2019). A study by Said et al (2016) found that wildebeest numbers in the Plains of Athi-Kaputiei in Kenya have indeed decreased significantly as a result of habitat fragmentation by fences. This subdivision of habitat has severely reduced several local wildlife populations (Thompson and Homewood 2002), and lower populations have a greater risk of inbreeding and lower genetic variation, which can cause local population extinctions (Seidler et al. 2015, Pekor et al. 2019). The expanding fencing also increases human-wildlife conflicts, such as predator-human conflicts as livestock depredation grows in frequency or elephant-human conflicts, as these large-bodied herbivores regularly destroy the fences on their dispersal routes (Pekor et al. 2019).

The Serengeti-Mara Ecosystem

The Serengeti-Mara Ecosystem (SME) supports some of the most diverse and abundant wildlife populations found anywhere on Earth (Karen Blixen Camp 2019a, May et al. 2019, Western et al. 2020). The massive area has been labeled by UNESCO as a World Heritage Site, because of its vast migratory ungulate populations, high mammal and bird diversity and intact, prehistoric sites (Sinclair et al. 2007). The entire

ecosystem stretches some 30,000 km² across northern Tanzania into the southwestern parts of Kenya. Its core comprises two of the most renowned and ecologically important conservational areas, namely the Serengeti National Park (SNP) in Tanzania, and the Maasai Mara National Reserve (MMNR) in Kenya. In the Tanzanian part of the ecosystem, the national park is surrounded by the Ngorongoro Conservation Area, Loliondo Game Controlled Area, Maswa, Ikorongo and Grumeti Game Reserves, while the Kenyan part includes the Conservancies adjoining the Maasai Mara (Homewood et al. 2001, Green et al. 2019, May et al. 2019). The SME is most widely known for hosting one of the largest mammal migrations on the planet; the infamous Great Migration, where approximately 1.5 million wildebeest, a million gazelles and some thousand zebras, migrate from the Ngorongoro Crater in southern Tanzania to the northernmost part of the ecosystem, the Maasai Mara in Kenya, crossing the world-famous Mara River in the process (Vuorio et al. 2014, Karen Blixen Camp 2019a, Veldhuis et al. 2019). The ecosystem also supports one of the largest freeranging elephant populations in the world, as well as other endangered and threatened species populations along with the richest predator assemblage in all of Africa (Green et al. 2019, Western et al. 2020). Because of this migration, and the overall abundant wildlife, the SME not only holds important ecological value but a socio-economical one as well. In recent years, tourism has become a major revenue for both Tanzania and Kenya, as international tourists flock to the vast savannas of the Serengeti and Maasai Mara (May et al. 2019), leading to raising conflicts and concerns about the coexistence between the local Maasai pastoralists and wildlife tourism (Reid 2012).

Indeed, there are many policy makers and stakeholders within the tourism sector that believe the Maasai do not belong in modern conservation management (Goldman 2007, Davis 2011, Mittal and Fraser 2018)), and as a result, many Maasai communities have in fact been evicted from the homelands that have belonged to their families for decades, such as the recent evictions in the Mau forest of Kenya further north and the ones in Serengeti in the 70s (Mittal and Fraser 2018). However, efforts in both East African countries have been made to correct this viewpoint and several attempts have been made to join the traditional pastoralist lifestyle and wildlife conservation (Walpole et al. 2003, Bedelian and Ogutu 2017, Ogutu et al. 2017, Tyrrell et al. 2017). In the Tanzanian part of the system, the massive SNP is strictly for wildlife and only the surrounding conservancies and game reserves allow Maasai occupation. Most of the tourism in the entire area is on government or state property and thus they receive, regulate and distribute the revenue garnered from the industry (Homewood et al. 2001, Thompson and Homewood 2002). On paper the local Maasai communities stand to receive a fair share of the tourism revenue in exchange for a reduction of their pastures and a higher tolerance of wildlife conflicts. However, in reality, they rarely reap the benefits of living next to a protected area and most receive little to no compensation for economic losses following wildlife conflicts, such as property destruction or livestock depredation. For many of the households, the losses far outweigh the rewards and as a result, the anthropogenic pressure surrounding the Serengeti

ecosystem is steadily rising (Davis 2011, Veldhuis et al. 2019). But on the Kenyan side of the system, conservation efforts tell a slightly different story.

Mara North Conservancy

In the southern regions of Kenya, the aptly named Maasailand saw a pivotal change in land ownership throughout 1970s. When Kenya gained independence from colonial rule, communally owned group ranches were established to maximize production, and it wasn't long after, that Kenya altered its land ownership laws. This meant that these group ranches, belonging to several Maasai communities were now being subdivided into smaller plots with the tenure distributed to individual households instead of groups (Thompson and Homewood 2002, Walpole et al. 2003, Løvschal et al. 2018). Individual households are then free to handle the land plots as they see fit: developing agriculture, selling their land to commercial farming or fencing in their livestock and product. This rapid subdivision serves to further fragment the habitats of wildlife species as well as disrupting vital dispersal and migration corridors (Lamprey and Reid 2004, Ayiemba et al. 2015). In Kenya, more than three fourths of all wildlife is found on the rangelands outside of protected areas, such as the MMNR. Therefore, ensuring suitable habitat conditions and vast, uninterrupted areas alongside pastoralist livelihoods is integral for successful wildlife management and conservation in the country (Georgiadis et al. 2007, Mureithi et al. 2019). As Tanzania has also realized, the local Maasai in Kenya require economic incentive for living in close proximity to wildlife if conservation efforts are to be sustainable (Mureithi et al. 2019). One way is the establishment of community-based conservancies that combine pastoralist life and wildlife conservation that benefits both parties. The Maasai households owning each their own plots sublet their land to tourism camps, that are then allowed to perform wildlife game drives for tourists. The Maasai, in return, receive a fixed monthly lease payment, regardless of how the tourism revenues look for each month. The monthly income provides enough incentive to tolerate the many conflicts of living with wildlife, and a compensation scheme likewise exists for livestock depredation to prevent any retaliation against predators (Thompson and Homewood 2002, Walpole et al. 2003, Reid 2012, Bedelian and Ogutu 2017, Green et al. 2019).

One of the first of these conservancies to be established is the Mara North Conservancy (MNC), situated just north of the MMNR border. It was created in 2009 and currently consists of over 800 Maasai landowners and 13 tourism camps and with its 30,000 hectares, the conservancy is the largest of those comprising the Kenyan conservancies of the SME (Mara North Conservancy 2017, Karen Blixen Camp 2019b). There are a few settlements within MNC that house most of the Maasai community and following the steady monthly income, some pastoralists no longer rely just on livestock husbandry and can pursue other careers, especially within the growing tourism industry (Reid 2012, Nkedianye et al. 2020). Rearing and keeping livestock, however, is still the primary income generator for many households and with the increase in wealth, a lot of Maasai are spending the added money on buying more livestock for their flocks, which increases the overall livestock population within the area and therefore the possible detrimental effects on the

local wildlife (Ayiemba et al. 2015, Løvschal et al. 2018). A solution to counteract this, is the development of the rotational grazing scheme. First off, in MNC, there is a limit to the number of cattle allowed within the conservancy, effectively hampering massive overstocking rates. Secondly, all of the cattle rotate across the savanna throughout the year as part of the grazing scheme. Every one or two months, the few but large groups of cattle move from one specified, agreed upon grazing block to another, to mimic the semi-nomadic movements that the Maasai previously utilized and thus allow the vegetation to recover and minimize livestock effects on flora and fauna (Ayiemba et al. 2015, Løvschal et al. 2018, Green et al. 2019).

This Study

Today, wildlife on the African savanna faces massive challenges because of a growing human population and increasing anthropogenic pressure (Homewood et al. 2001, Asner et al. 2009). Many protected areas and national parks exist throughout the African continent, but these areas only support about one fourth of all wildlife (Osano et al. 2013, Mukeka et al. 2019) while the remainder roam the human-dominated landscapes, such as the rangelands in East Africa. If the diverse and vast savanna ecosystem is to prevail in the future, conservation efforts should focus not just on the protected parks but increasingly more on the rangelands (Georgiadis et al. 2007, Ogutu et al. 2017). Because so much wildlife is found among pastoralists, the governing viewpoint is that these locals have been labelled as 'ecological villains' and that wildlife and pastoralism cannot coexist (Goldman 2007, Davis 2011, Mittal and Fraser 2018). Indeed, overstocking livestock, habitat fragmentation and exponential human population growth are some of the major threats to the floral and faunal biodiversity. But low-medium stocking rates and sustainable pastoralism have been shown to facilitate wildlife, not hinder it (Thompson and Homewood 2002, Green et al. 2019). Given that a vast majority of wildlife found on the savanna today share resources and space with livestock, it is vital to understand the complex dynamics shared between domestic and wild animals (Odadi et al. 2011b). These dynamics are constantly interchanging depending upon seasonal and annual precipitation patterns (Odadi et al. 2011b, Moehlman et al. 2020). Since MNC experienced a drought in 2019 while the following year, 2020, proved to be markedly wet (Reynolds 2019, 2020, Russell 2020), and since similar datasets for both years can now be obtained, this provides a perfect opportunity for quantifying the interactions between the cattle and wild herbivores within the conservancy. Hence, the level of competition and facilitation between livestock and wildlife can be examined under fluctuating rainfall patterns, and as such, we can gain an idea as to stability of the ecosystem and the livestock-wildlife interactions within the implemented management plan.

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Part B

Manuscript for the scientific journal 'Journal of African Ecology'

Domestic Bliss or Trouble in Paradise: Wild Herbivore Responses to Cattle Grazing During Multi-Annual Rainfall Fluctuations in a Rotational Grazing Scheme in the Mara Region, Kenya

Abstract

Today, wildlife on the African savanna faces massive challenges because of a growing human population and increasing anthropogenic pressure. In East Africa, a majority of wildlife populations are found in pastoralist rangelands and as such, conservation efforts should focus on these human- and livestockdominated landscapes. Given how much wildlife shares resources and space with livestock, understanding the complex, interchanging dynamics between wild and domestic animals is increasingly important. Many community-based conservancies in Kenya, such as Mara North Conservancy (MNC), operate on a rotational grazing scheme, where cattle graze in allocated blocks that rotate every month throughout the year and appointed no-grazing zones, where cattle are not allowed to graze. The aim of this study was to determine how livestock influence wild herbivores through competitive and facilitative interactions within this grazing scheme under fluctuating precipitation patterns to further our understanding of livestock-wildlife dynamics and whether these conservancies can in fact be a plausible management design. We estimated densities and biomass of wild and domestic herbivores and analyzed how wild herbivores responded to cattle grazing in this grazing scheme during two different rainfall years (rain and drought). We found high overall densities of livestock (cattle, shoats, donkey) in MNC and livestock biomass constituted almost two thirds of all counted herbivores. Surprisingly, wild herbivores had the highest overall density inside cattle grazing zones compared to no-grazing zones in the wet year, while no difference in wild herbivore density was found for the dry year. Competition and facilitation between cattle and wild herbivores varied depending upon the year for most species, with more instances of facilitation in the wet year and higher levels of negative relations in the dry year. Thus, refugia and forage banks, such as the no-grazing zones or closely located protected areas, becomes increasingly important during periods where resources are scarce, i.e., during a drought. This suggests that a livestock-dominated conservancy can support and facilitate large numbers of wild herbivores when resources are abundant but during scarce resource periods, wildlife refugia become equally important to maintain local wildlife populations. As such, both community-based conservancies and protected areas are vital for Kenyan conservation effort, and one is not sustainable without the other.

Keywords: Africa | Cattle | Wild Herbivores | Rainfall | Conservation

Introduction

Savannas account for approximately 20 % of the Earth's entire land surface and just in Africa, the arid and semi-arid savanna takes up a staggering 50 % (Osborne 2012). The African savanna supports a rich and iconic diversity of mammalian species, unlike any found elsewhere on the planet (Butt and Turner 2012, Fynn et al. 2016). However, in recent decades, the diverse African wildlife populations have been declining at an alarming rate. Just in Kenya, located in East Africa, wildlife populations have dropped on average 68.1 % since the 1950s (Ogutu et al. 2016). These declines are primarily attributed to anthropogenic influences, such as land degradation, habitat fragmentation, deforestation and human-wildlife conflicts, all of which are associated with an increasing human population (Fritz et al. 1996, Homewood et al. 2001, Sitters et al. 2009, Bhola et al. 2012a, Said et al. 2016, Hempson et al. 2017, Bartzke et al. 2018, Mukeka et al. 2018, Green et al. 2019). In particular, these problems are most abundant in the Kenyan rangelands, where humans and wildlife occur in close proximity to each other. The rangelands occupy a large majority of Kenya's land area, and support about 70 % of all of Kenya's wildlife, while the remaining 30 % live inside protected areas and conservancies where human occupancy is either entirely prohibited or considerably restricted (Augustine et al. 2011, Osano et al. 2013, Tyrrell et al. 2017, Mukeka et al. 2019). Therefore, while protected areas certainly play a pivotal role in Kenyan wildlife conservation, the surrounding, unprotected rangelands are perhaps even more important if conservation efforts are to prevail (Georgiadis et al. 2007, Ogutu et al. 2017, Green et al. 2019).

The most dominant livelihood of the resident people in the rangelands is pastoralism, which has been a part of the African savanna for some millennia (Thompson and Homewood 2002, Lamprey and Reid 2004, Hempson et al. 2017). The local Maasai communities inhabiting the Kenyan rangelands were historically nomadic pastoralists, moving their villages and livestock in cyclic patterns in correspondence with the dry and wet seasons of the savanna to maximize the fluctuating resources that such an ecosystem provides (Lankester and Davis 2016). In recent years, the rising human population and expanding wildlife reserves have forced a sedentarization of the Maasai communities, which in turn can increase the adverse effects of land degradation, overgrazing and fragmentation of the landscape that can have disastrous effects for the local wildlife (Msoffe et al. 2011, Riginos et al. 2018, Valls-fox et al. 2018, Green et al. 2019, Nkedianye et al. 2020). Indeed, a considerable portion of the wildlife declines documented in Kenya has been related to increasing livestock numbers (Ogutu et al. 2012, 2016). This can have not only ecological implications for the country's ecosystem, but economic ones as well. The Maasai Mara hosts one of the most diverse ecosystems in the world and as such, attracts a large number of foreign tourists every year (Thompson and Homewood 2002, Walpole et al. 2003). Tourism accounts for almost 14 % of Kenya's entire GDP and constitutes 10 % of the national employment, which means a collapse of the Maasai Mara ecosystem would have considerable consequences for the country as a whole (Ogutu et al. 2016). Therefore, the overall view from many governments and conservationists for a long time have been that pastoralism does not belong in

conservation efforts (Augustine et al. 2011, Davis 2011, Odadi et al. 2011, Butt and Turner 2012) and indeed many studies have found and highlighted the negative influences excessive pastoralism can have on wildlife (Muchiru et al. 2008, Averbeck et al. 2012, Schieltz and Rubenstein 2016).

Perhaps the most common concern is the competitive interaction that can exist between livestock and wild herbivores. Competition between species often occur because of a significant niche overlap (Arsenault and Owen-Smith 2002, Butt and Turner 2012). On the African savanna, cattle primarily feed on the tall grasses, providing plenty of the bulk forage required for their ruminant feeding ecology. This goes in direct competition with the wild, large-bodied, bulk feeders, such as buffalo or elephant. Other tall grass feeders, such as topi or kongoni, may likewise directly compete with the cattle for forage (Sitters et al. 2009, Ogutu et al. 2014, Valls-fox et al. 2018, Green et al. 2019). Indirectly, livestock can also exert negative influences on wildlife by altering the vegetation structure, by either trampling or foraging. This can in turn change the food quality and quantity, cover opportunities for predators and possible nesting sites (Schieltz and Rubenstein 2016, Bernardi et al. 2019).

However, pastoralism has co-existed with wild animals for centuries, before modern globalization, and likewise, many recent studies have identified the positive effects pastoralism can have on wildlife (Thompson and Homewood 2002, Goldman 2007, Muchiru et al. 2008, Bhola et al. 2012b, Butt and Turner 2012). While cattle can have a negative, competitive effect, facilitation of wild herbivore species as a response to livestock grazing has similarly been documented. For instance, a study from 1978 found that the highest concentration of wild ungulates was not in the human-free, protected areas, but rather in areas either currently or recently inhabited by pastoralists (Muchiru et al. 2008). Most small-medium sized herbivores, such as Thomson's gazelle or impala, cannot digest the low-quality, tall grass but require the high-quality, nutrient-rich grass of low-medium height. The sort usually left by a grazing, mobile herd of cattle (Arsenault and Owen-Smith 2002, Ogutu et al. 2005a, 2014, Bhola et al. 2012a). Additionally, the lower grass levels can provide a refuge for the smaller-sized herbivores that allows them to spot lurking predators unable to hide in the low vegetation, thereby decreasing predation risk (Augustine et al. 2011, Bhola et al. 2012b, Fynn et al. 2016). Small-medium sized herbivores, e.g., wildebeest and zebra, are at greater risk of predation than the large-bodied ones, e.g., buffalo and elephant, and as such minimizing predation risk has bigger influence on their habitat selection (Sinclair et al. 2007, Bhola et al. 2012a). Cattle can also facilitate wild herbivores in other ways, as a study found that abandoned bomas (temporary enclosures for housing cattle) create nutrientrich glades that attract many wild herbivore species (Augustine et al. 2011).

Pastoralist livelihoods and conservation efforts in non-protected areas are becoming increasingly more intertwined with each other, and several community-owned conservancies are being established across all of Kenya, with about 178 conservancies existing by the end of 2015 (Walpole et al. 2003, Bedelian and Ogutu 2017, Ogutu et al. 2017, Tyrrell et al. 2017). Most of these conservancies consist of land areas that are owned by local communities or private individuals, who lease their land to either government or tourist

camps for a fixed monthly fee. In return, the pastoralists' livestock can continue grazing within the conservancy. However, the livestock are kept on a rotational grazing scheme and the number of livestock allowed in the entire area are strictly regulated to prevent overgrazing and overexploitation of the available resources whilst giving space to the local wildlife (Reid 2012, Bedelian and Ogutu 2017, Mureithi et al. 2019). The whole premise of these conservancies is to minimize the conflicts between the local pastoralists and the wildlife, by incorporating both into the conservation plan to preserve not only the local culture but also the struggling wildlife populations (Løvschal et al. 2018). The question then becomes whether these conservancies are in fact sustainable management designs and how they affect the wildlife in the area.

This study aims to determine the influence livestock, in particular cattle, can have on wild herbivores within a community-owned conservancy to further our understanding of the dynamics that exist between livestock and wild herbivores and whether community conservancies are in fact plausible alternatives to the conservation effort. The study was conducted within Mara North Conservancy (MNC), a community-based conservancy consisting of 13 tourism camps and over 800 local Maasai landowners. It is situated just north of the Maasai Mara National Reserve (MMNR), and is a vital part of the Maasai Mara ecosystem (Mara North Conservancy 2017, Karen Blixen Camp 2019a). Due to a disappointing wet season, a severe drought dominated the Mara region in 2019 and April proved to be one of the driest with total rainfall for the entire month at 86.8mm (Reynolds 2019). The following year, 2020, proved to be remarkably wet, with total rainfall in April at 182mm. The high precipitation levels started with the short rains at the end of 2019 that did not let up and continued on into the long raining season of April-May (Reynolds 2020, Russell 2020). As such, this provided an opportune moment to examine differences in the observed dynamics of cattle and wild herbivores between a wet and a dry year.

Based upon the theory above, the following hypotheses will be examined:

- Biomass and density of livestock have been found to surpass that of wildlife in many African regions (Du Toit and Cumming 1999, Young et al. 2018), and therefore, biomass and density of livestock species (cattle, shoats and donkey) in MNC are expected to exceed that of wild herbivores.
- Because of a general sensitivity to and avoidance behavior for human disturbance (Hibert et al. 2010, Sørensen et al, unpublished), overall wild herbivore density is expected to be higher in no-grazing zones, where cattle are not allowed to graze, than in the grazing zones, where cattle are allowed to graze.
- 3. The density of the wild herbivores in response to cattle grazing is expected to differ depending on the feeding ecology of the herbivores, specifically:

a) The densities of large-bodied, bulk feeding herbivores are expected to be higher in areas, which have not been grazed by cattle for an extended period of time, as these herbivore types are most likely to compete with cattle.

b) The densities of small-medium sized herbivores are expected to be higher in areas currently or recently grazed by cattle, as these herbivores are more likely to be facilitated by cattle presence.

4. Competition and facilitation between cattle and wild herbivores may alternate depending upon the wet and dry seasons because of fluctuating resource availability (Odadi et al. 2011, Moehlman et al. 2020), and this switch may therefore also apply to wet and dry years. Therefore, the level of competition between cattle and wild herbivores (as inferred by the density responses from 3a and 3b) is expected to be higher in a dry year (2019) than in a wet year (2020).

Materials and Methods

The Study Area

Data collection was conducted within Mara North Conservancy (see Figure 1), located in the south-western parts of Kenya, East Africa, bordering the Maasai Mara National Reserve. It stretches 30,000 hectares, from the Oloololo Escarpment in the south to the Lemek Hills in the north (Karen Blixen Camp 2019b). The conservancy receives an annual rainfall of 650mm to 1300mm, depending upon the topographic relief as well as influence from Lake Victoria past the western border. (Bartzke et al. 2018). MNC is part of the Maasai Mara ecosystem and therefore, consists of a 'dry' season, spanning from July till October, and a 'wet' season, spanning November till June. The wet season however is separated into two major rainfall events, with the short rains pouring from October to November and the long, heavy rain occurring from March until May. Thus, January and February are considered dry months. Average temperatures range from the minimum of 7-8 °C to the maximum of around 28 °C (Lamprey and Reid 2004, Mukeka et al. 2019). The vegetation structure primarily consists of tall and short grassland, with the occasional *Acacia* dominated woodland, interspersed with shrub, thicket and riverine forests (Ogutu et al. 2005a, Mogensen et al. 2011).



Figure 1: Location of Mara North Conservancy, Kenya. Surrounding conservancies and MMNR also illustrated. Source: maranorth.org.

The MNC supports a wide range of wildlife, both mammalian and avian. Common predators within the conservancy include the cheetah (*Acinonyx jubatus*), black-backed jackal (*Canis mesomelas*), spotted hyena (*Crocuta crocuta*), lion (*Panthera leo*), and leopard (*Panthera pardus*), while observed herbivorous species include Defassa waterbuck (*Kobus ellipsiprymnus*), impala (*Aepyceros melampus*), kongoni (also known as Coke's hartebeest, *Alcelphus buselaphus cokii*), topi (*Damaliscus lunatus jimela*), Kirk's dik-dik (*Madoqua kirkii*), Thomson's gazelle (*Eudorcas thomsonii*), Grant's gazelle (*Nanger granti*), Western white-bearded wildebeest (*Connochaetes taurinus mearnsi*), African bush elephant (*Loxodonta africana*), Maasai giraffe (*Giraffa camelopardalis tippelskirchii*), plains zebra (*Equus quagga*), common warthog (*Phacochoerus africanus*), ostrich (*Struthio camelus*), common eland (*Taurotragus oryx*), Cape buffalo (*Syncerus caffer*) and the bohor reedbuck (*Redunca redunca*). The black rhino is known for its aggressive behavior (Boeyens and Van Der Ryst 2014), and while MNC does technically provide suitable habitat for this rhino species, all Mara black rhinos reside within MMNR as they are actively kept out of the conservancy to minimize human-rhino conflicts as well as poaching risk for the rhinos (pers. comm., David Noosaron, Maasai landowner, MNC). Therefore, this herbivore species was not included in this study.

Observed livestock species include cattle (*Bos taurus*), sheep (*Ovis aries*), goat (*Capra hircus*) and donkey (*Equus asinus*). Due to similar appearances and herding practices along with difficulty separating the two species in the field, sheep and goats will henceforth be referred to and jointly analyzed as 'shoats'.

Experimental Design

Data sampling occurred over a period of 2.5 months, stretching across October to December of 2020. Data was collected by car and measured as strip transects. Strip transects are a common approach within ecological studies for estimating densities and abundances within a certain area. This is done by counting individuals along a randomly distributed line that remain of a fixed length and width (Carthy et al. 2005, Coburn et al. 2009). Here, a single transect averaged 0.978km (min.: 0.396km, max.: 1.237km) in length, with a width of 200m from either side of the vehicle, totaling 400m across. The varying lengths are attributable to the interchanging dynamics on the savanna, e.g. dense vegetation structures, rough terrain, waterways or even animal behavior – for instance, one transect was cut short by the occurrence of a hunting leopard, which scattered all wildlife within the rest of the transect.

To determine whether an animal occurred within the 200m boundary, a Range Finder (Nikon Forestry Pro II) was utilized. Within each transect, counting occurred every 200m and each point was logged as a GPS location, using a handheld GPS (Trimble Juno SB), which was loaded directly into ArcMap (v. 10.6.1). This allowed us to accurately determine the full length of each individual transect.

The management plan in Mara North Conservancy divides the area into several grazing blocks, wherein the local Maasai can keep their grazing cattle. Each block pertains to a specific month where the cattle are allowed to graze, and the blocks thus rotate across the year. This allowed us to divide the transects into seven groups:

- 1) 0 months since grazing (currently grazing)
- 2) 1 month since grazing
- 3) 2 months since grazing
- 4) 3 months since grazing
- 5) 4 months since grazing
- 6) 5 months since grazing
- 7) >12 months since grazing (no-grazing zones)

12 transects were sampled within each classification, while for the no-grazing block 20 transects were

sampled, totaling 92 transects in total (see Figure 2).

Data from 2019 for analysis and comparison was obtained and collected in a similar manner from Sørensen et al. (unpublished).

For estimating the respective biomasses and densities for livestock and wildlife in MNC (*hypothesis 1*), an additional dataset was obtained from another master's project, occurring concurrently with this study. This dataset was collected alongside the major settlements within MNC, thereby sampling a large majority of the livestock not participating in the rotational grazing



Figure 2: Outline of sampled transects within MNC. Each color represents a different grazing zone: i.e. months since cattle grazed in the blocks. Note: Not all 92 transects are depicted, as some spatially overlapped during the sampling period.

scheme. It also includes the other livestock species, shoats and donkey, which are not allowed beyond the settlement limits. For detailed data collection, see Ochelka (unpublished).

Statistical Analysis

Density was calculated using the formula below,

$$density_x = \frac{count_x}{area_t}$$

Here, the density of a specific species, x, was equal to the count of the species within the specific transect area, t. Biomass for each individual species in MNC was extrapolated from the counts within each transect and the average species-specific body weight from various literature (see table 1). The visualization of

estimated biomass and densities as well as all analyses described below was done using RStudio (v. 1.2.5033).

Species	Scientific name	Average weight (kg)	Source
Western white-bearded wildebeest	Connochaetes taurinus mearnsi	180	(Lundgren et al. 2020)
Cape buffalo	Syncerus caffer	450	(Augustine 2010)
Plain's zebra	Equus quagga	200	(Augustine 2010)
Thomson's gazelle	Eudorcas thomsonii	20.5	(Lundgren et al. 2020)
Grant's gazelle	Nanger granti	55	(Lundgren et al. 2020)
Impala	Aepyceros melampus	40	(Lundgren et al. 2020)
Торі	Damaliscus lunatus jimela	136	(Lundgren et al. 2020)
Kongoni (Coke's hartebeest)	Alcelaphus buselaphus cokii	171	(Lundgren et al. 2020)
Common eland	Tragelaphus oryx	340	(Augustine 2010)
Bohor's reedbuck	Redunca redunca	44	(Lundgren et al. 2020)
Maasai giraffe	Giraffa camelopardalis tippelskirchi	750	(Augustine 2010)
Ostrich	Struthio camelus massaicus	111	(Lundgren et al. 2020)
African bush elephant	Loxodonta africana	1,725	(Augustine 2010)
Kirk's dik-dik	Madoqua kirkii	5	(Augustine 2010)
Common warthog	Phacochoerus africanus	45	(Augustine 2010)
Defassa waterbuck	Kobus ellipsiprymnus	160	(Augustine 2010)
Cattle	Bos taurus	322	(Augustine 2010)
Shoats (sheep and goat)*	Ovis aries + Capra hircus	27	(Marker et al. 2003)
Donkey	Equus asinus	250	(Lundgren et al. 2020)

Table 1: Average body weight for each herbivore species observed in MNC, in kilograms.

*Sheep and goat have been joined, due to their similarity out in the field. Average biomass has been estimated to be similar for goat and sheep respectively, thereby allowing to merge the biomass of the two livestock species together.

To test whether a significant difference exists between the densities of wild herbivores found in the grazing zones and the no-grazing zones, a Wilcoxon rank-sum test was conducted for 2019 (dry year) and 2020 (wet year) respectively. The counted animals were specified as either wildlife or livestock, where the wild species were extrapolated for the test. The active grazing blocks (months 0-5) were pooled together, labeled 'YES' grazing while grazing block 12 was labeled as 'NO' grazing, as these blocks are restricted throughout the year and thus, do not receive any grazing from domestic herbivores. A p-value below 0.05 was considered significant.

For determining competition and facilitation levels between cattle and wild herbivores in MNC, the lag responses of each individual wild herbivore species to the rotational grazing scheme were modelled. A simple linear regression model was constructed for each species with time since grazing as a categorical variable and species density as a response variable, using the stats, plyr and Rmisc packages in R. This was done to test the effect of the different grazing blocks on the species densities and a model was created separately for each year (2019 and 2020) and for each species to assess the annual, species-specific differences, if any, in the density responses. Density responses were inferred from significant p-values (< 0.05) and their coefficient estimates to determine whether there is any indication of competitive and/or facilitative interactions between wild herbivores and cattle. All plots were generated using the ggplot2 package in R.

Results

Livestock and Wildlife Biomass & Density Estimates

Wild herbivore biomass accounted for 37.81 % of all estimated herbivore biomass in MNC, while livestock accounted for 62.19%. The mean biomass of wild herbivores within MNC was calculated to 2,874.53 kg/km², while the mean biomass for livestock was calculated to 38,303.26 kg/km² (Fig. 3 and 4). The mean density for wild herbivores were 55.21 herbivores/km², while the mean density for livestock was calculated to 534.70 livestock/km² (Fig. 3).



Figure 3: Boxplots illustrating the A) biomass (kg/km²) and b) density (animals(km²) of livestock and wild herbivores respectively. The boxplots display the biomass and density values from each transect and have been log-transformed for proper visual interpretation as few outliers in the dataset skew the boxplots. Mean biomass for livestock was 38,303.26 kg/km² while for wild herbivores it was 2,874.53 kg/km². Mean density for livestock was 534.70 livestock/km² while for wild herbivores it was 55.21 herbivores/km².



Figure 4: Bar plot of total herbivore biomass (kg/km²). Total biomass estimates have been separated into domestic (livestock) and wildlife (wild). For species-specific biomass values see appendix S2.

Effect of Cattle Presence on Wild Herbivore Density

The Wilcoxon rank-sum test was conducted to test for differences in wildlife density in the grazing zone and the no-grazing zone showed that wildlife densities were significantly lower in the no-grazing zone than in the grazing zone for the wet year, 2020 (W = 13558, p = 0.00051, Fig. 5B). For the dry year, 2019, no significant difference was found in wildlife density between the two grazing zones (W = 7927.5, p = 0.888, Fig. 5A).



Figure 5: Boxplots displaying the wild herbivore densities (in animals/km2) in the no grazing zone ('No'), where cattle grazing is prohibited, and the grazing zone ('Yes'), where cattle are allowed to graze during the year. (A) Wildlife densities in the two grazing zones for 2019, and (B) wildlife densities for 2020. '***' indicate a significant p-value below 0.05. The density of wild herbivores in the no grazing zone was significantly lower (p = 0.00051) than in the grazing zone in 2020, while no significant difference (p = 0.888) was found for 2019. The densities have been log-transformed, for better visualization and interpretation.

Competition and Facilitation of Cattle on Wild Herbivores

Significant differences in density as a response to the grazing blocks were found and varied across species and years (Table 2, Fig. 6 and 7). In 2019, during the resource-low drought, densities of many of the wild herbivore species were generally low compared to 2020, with the two species waterbuck and dik-dik only being present in the 2020 dataset. Many more species were observed at higher densities in the no-grazing blocks during the dry year than in the wet year. Even species generally avoiding of cattle (i.e. buffalo) gathered closer to cattle grazing in 2020, when there was ample resources, than in 2019, where the same species was only counted in the no-grazing blocks, farthest away from cattle.

Species	Months				
	Since				
	Cattle				
	Grazing	201	0	20	20
		Estimate Coeff.	<u>ש</u>	20 Estimate	p
				Coeff.	•
Thomson's Gazelle	0	66.184	0.034 *	64.668	0.002 **
	1	59.127	0.166	31.445	0.266
	2	82.069	0.056.	2.050	0.942
	3	-1.936	0.964	8.957	0.751
	4	74.200	0.091.	-6.355	0.822
	5	36.330	0.417	-20.790	0.461
	12	1.188	0.975	-62.293	0.015 **
Zebra	0	15.308	0.246	34.448	0.015 *
	1	-7.872	0.665	-12.518	0.526
	2	4.320	0.812	-8.488	0.667
	3	-3.984	0.820	-14.506	0.462
	4	59.326	0.002 **	29.438	0.138
	5	-8.661	0.650	-12.898	0.513
	12	6.912	0.673	-31.731	0.074 .
Wildebeest	0	122.270	0.004 *	147.970	0.001 *
	1	-51.380	0.365	-128.430	0.035 **
	2	-84.680	0.137	-137.660	0.024 **
	3	-111.460	0.057.	-119.550	0.049 **
	4	-110.320	0.060.	-7.700	0.898
	5	-122.270	0.043 **	-91.510	0.130
	12	-75.410	0.143	-146.490	0.008 **
Buffalo	0	-6.855 * 10 ⁻¹⁷	1.00	0.4697	0.985
	1	8.391 * 10 ⁻¹⁷	1.00	-0.4697	0.989
	2	$3.745 * 10^{-17}$	1.00	45.1857	0.201
	3	6.019 * 10 ⁻¹⁷	1.00	50.3580	0.155
	4	9.162 * 10 ⁻¹⁷	1.00	4.3374	0.902
	5	$1.063 * 10^{-17}$	1.00	12.5599	0.721
	12	1.337 * 10 ⁻¹	0.223	1.7313	0.956
Elephant	0	0.4771	0.246	-1.010 * 10 ⁻¹⁵	1.000
	1	0.4055	0.474	9.967 * 10 ⁻¹⁶	1.000
	2	-0.4771	0.400	1.917	0.266
	3	-0.4771	0.411	6.478 * 10 ⁻¹⁶	1.000
	4	-0.4771	0.411	$-4.578 * 10^{-16}$	1.000
	5	-0.4771	0.424	$1.503 * 10^{-15}$	1.000
	12	-0.2652	0.604	3.092	0.047 *
Dikdik	0	N/A	N/A	$-8.925 * 10^{-16}$	1.000
	1	N/A	N/A	8.306 * 10-16	1.000
	2	N/A	N/A	$1.147 * 10^{-15}$	1.000
	3	N/A	N/A	5.677 * 10 ⁻¹⁶	1.000
	4	N/A	N/A	9.378 * 10 ⁻¹⁶	1.000
	5	N/A	N/A	$1.052 * 10^{-15}$	1.000
	12	N/A	N/A	9.401 * 10 ⁻¹	0.035 *

Species	Months				
	Since				
	Cattle				
	Grazing				
		2019		2020	
		Estimate Coeff.	р	Estimate	р
Fland	0	0.472	0.726	0.852	0.736
	1	0.472	0.720	1.615	0.730
	2	-0.472	0.800	7 684	0.031
	2	3 745	0.000	2 964	0.004
	<u> </u>	-0.472	0.804	1 664	0.400
	5	-0.472	0.810	1.602	0.654
	12	-0.130	0.938	0.603	0.850
Grant's	0	1 657	0.530	3 515	0.376
Gazelle	0	1.057	0.011	5.515	0.570
	1	4.386	0.213	0.036	0.995
	2	3.717	0.291	4.847	0.388
	3	0.236	0.948	12.654	0.026 *
	4	0.275	0.939	-1.151	0.837
	5	-1.657	0.653	10.104	0.074.
	12	3.362	0.290	-2.911	0.562
Impala	0	16.438	0.213	2.603	0.814
	1	-16.000	0.379	6.188	0.692
	2	3.969	0.827	6.529	0.676
	3	-15.719	0.399	16.275	0.299
	4	-15.272	0.412	38.065	0.017 **
	5	-5.312	0.781	9.402	0.547
	12	21.267	0.197	12.817	0.360
Kongoni	0	$-2.042 * 10^{-15}$	1.0000	-2.176 * 10 ⁻¹⁵	1.000
	1	$2.285 * 10^{-15}$	1.0000	1.927 * 10-1	0.877
	2	$1.454 * 10^{-15}$	1.0000	1.84	0.142
	3	$1.616 * 10^{-15}$	1.0000	$2.26 * 10^{-15}$	1.000
	4	$1.281 * 10^{-15}$	1.0000	1.817	0.147
	5	$1.361 * 10^{-15}$	1.0000	8.005 * 10-1	0.521
	12	3.067	0.0299 *	$1.227 * 10^{-15}$	1.000
Waterbuck	0	N/A	N/A	$-4.707 * 10^{-15}$	1.000
	1	N/A	N/A	$4.249 * 10^{-15}$	1.000
	2	N/A	N/A	$1.945 * 10^{-1}$	0.914
	3	N/A	N/A	5.086 * 10-15	1.000
	4	N/A	N/A	1.534	0.396
	5	N/A	N/A	5.412 * 10-15	1.000
	12	N/A	N/A	2.271	0.162
Торі	0	10.633	0.190	4.231	0.743
	1	2.762	0.804	45.123	0.015 *
	2	-0.652	0.953	32.625	0.076.
	3	5.049	0.658	32.889	0.074.
	4	/.9/4	0.485	47.353	0.011 *
	5	-/.056	0.54/	1/.4/8	0.339
	12	30.229	0.004 **	4.401	0.787

Species	Months Since Cattle Grazing				
		2019		2020	
		Estimate Coeff.	р	Estimate Coeff.	р
Warthog	0	N/A	N/A	5.102	0.206
	1	N/A	N/A	11.350	0.048 *
	2	N/A	N/A	7.749	0.175
	3	N/A	N/A	6.162	0.280
	4	N/A	N/A	7.371	0.196
	5	N/A	N/A	2.150	0.705
	12	N/A	N/A	-3.088	0.544
Reedbuck	0	-1.005 * 10-1	⁶ 1.000	0.383	0.038*
	1	-2.442 * 10-1	7 1.000	-0.383	0.140
	2	3.688 * 10-17	1.000	-0.383	0.140
	3	$2.752 * 10^{-17}$	1.000	-0.383	0.140
	4	-8.069 * 10 ⁻¹	7 1.000	-0.383	0.140
	5	-1.702 * 10-1	⁶ 1.000	-0.383	0.140
	12	6.479 * 10 ⁻¹	0.144	-0.102	0.660
Ostrich	0	0.669	0.128	-6.019 * 10 ⁻¹⁶	1.000
	1	-0.450	0.456	7.835 * 10 ⁻¹	0.407
	2	-0.670	0.269	8.864 * 10 ⁻¹⁶	1.000
	3	-0.670	0.280	8.504 * 10-1	0.369
	4	-0.670	0.280	$6.327 * 10^{-16}$	1.000
	5	-0.670	0.293	$3.935 * 10^{-1}$	0.677
-	12	0.217	0.690	1.722	0.044 *
Giraffe	0	1.243 * 10-13	2 1.000	0.845	0.592
	1	$3.804 * 10^{-1}$	0.379	-0.845	0.704
	2	-1.609 * 10-1	⁵ 1.000	-0.650	0.770
	3	$7.075 * 10^{-1}$	0.112	0.228	0.918
	4	-8.194 * 10-1	• 1.000	2.761	0.217
	5	-7.657 * 10-1	• 1.000	1.248	0.575
	12	2.430 * 10-1	0.533	1.360	0.495

Table 2: Coefficients and p-values for the linear models created for each species and for both years. Significant p-values have been marked with '**' and highlighted in bold. P-values close to 0.05 is signified with '.'. N/A values for warthog, waterbuck and dik-dik signifies lack of data. Warthog was not included in the 2019 data, while there were no observations of waterbuck or dik-dik in any transects in 2019, only in 2020. No-grazing blocks were given the arbitrary value of '12'.

Various herbivore species, such as buffalo, topi, impala and kongoni, had high densities in the no-grazing blocks in 2019, when resources were scarce, but during the wetter 2020, when resources became more abundant, the same species congregated closer to cattle as their densities peaked in blocks grazed some 1-4 months ago (Fig. 6 and 7).



Figure 6: Barplots of average density in each grazing block for all wild herbivore species in 2019. Significant differences in density between active grazing blocks ('0') and the other grazing blocks, derived from the linear models, are marked with stars '**'. No grazing blocks are given the arbitrary value of '12'. Note each y-axis has different scales. There were no observations of waterbuck and dik-dik in 2019, and therefore the plots are empty. Warthog was not included in this dataset and thus there is no plot for this species.



Figure 7: Barplots of average density in each grazing block for all wild herbivore species in 2020. Significant differences in density of the grazing blocks, derived from the linear models, are marked with stars '**'. No grazing blocks are given the arbitrary value of '12'. Note each y-axis has different scales. There is the additional barplot of warthog, which is included in the 2020 data but not the 2019 data.

The densities of elephant, ostrich and dik-dik were all significantly higher in the no-grazing blocks in 2020 (Table 2, Fig. 7), but no significance difference was found for either species in 2019 (Table 2, Fig. 6). Dikdik was not observed in any transects in 2019 while in 2020, the species was only observed in the no-grazing blocks. Elephant had the highest density in the no-grazing blocks of 2020 while the complete opposite response was seen in 2019, with high densities of this species in the blocks currently or recently grazed by cattle (Fig. 6 and 7). Ostrich density was generally low for both years. However, in 2020, the highest density was observed in the no-grazing blocks while in 2019, density peaked in both the currently active grazing blocks and the no-grazing blocks (Fig. 6 and 7). Both topi and kongoni had significantly higher densities in the no-grazing blocks in 2019 (Table 2, Fig. 6), but while topi density was highest in both one and four months since cattle grazing, kongoni density peaked two and four months past cattle grazing (Table 2, Fig. 7). Grant's gazelle had the highest density in blocks that had been grazed by cattle three months ago in 2020, while the density response appears more evenly distributed in 2019, where density was higher in blocks last grazed by cattle one or two months ago as well as in the no-grazing blocks (Table 2, Fig. 6 and 7). While a significant peak in density for eland was only detected for 2020, density for this species in both years was highest in blocks grazed two-three months ago (Table 2, Fig. 6 and 7). Impala densities in 2020 showed a significant spike four months after cattle grazing while no significant responses were found for 2019. An opposite response occurred for zebra, where their density peaked four months since cattle grazing in 2019 and likewise in 2020, although there was no significant response (Table 2, Fig. 6 and 7). Warthog responses can only be examined for 2020 as the species was not included in 2019. In 2020, though, the density was highest one month since cattle had grazed (Table 2, Fig. 7). Density of Thomson's gazelle peaked at one month since cattle grazing and generally declined afterwards with markedly lower densities in the no grazing blocks in 2020 (Fig. 7). While no significant difference was found in 2019, density seem to peak at two and four months since cattle grazing (Fig. 6). So, Thomson's gazelle appears to follow cattle regardless of the year but seems to follow more closely in the wet year (2020) than in the dry year (2019). Wildebeest had one of the most pronounced differences, as their densities were significantly low in blocks that had been grazed one, two and three months ago by cattle as well as in the no grazing blocks for 2020 (Fig. 7). In 2019, the only significance was found in blocks last grazed by cattle five months ago (Fig. 6). For both years though, density is higher in the active grazing blocks where the cattle are currently grazing and thus seem to be strongly facilitated by cattle presence. Waterbuck, buffalo, giraffe and reedbuck had no significant differences in density response for either year (Fig. 6 and 7). Reedbuck was primarily counted in the nograzing blocks regardless of the year, while buffalo density was highest in the no-grazing blocks in 2019 but in 2020, buffalo density was highest in blocks grazed two-three months prior. There were no instances of waterbuck for 2019 but in 2020, waterbuck density was higher in the no-grazing blocks as well as the blocks last grazed by cattle four months ago (Fig. 6 and 7). Giraffe, interestingly enough, congregated closer to cattle in the resource-scarce 2019 (Fig. 6) whereas this species had higher densities in blocks that had not been grazed for many months or at all in 2020 (Fig. 7).

Discussion

The aim of this study was to investigate how cattle that are a part of a rotational grazing scheme, affect native wild herbivores within the Mara North Conservancy in Kenya, to determine the feasibility of the implemented community-owned management plan. Furthermore, results cover not just data collected by this study but also those of Sørensen et al (unpublished), which comprises similar data in the same area from a previous year, to investigate how rainfall oscillations affect the tested herbivore responses. This can aid in detecting any discrepancies in the conservancy design and optimizing future management.

Livestock and Wildlife Biomass and Density Estimates

Livestock comprised 62.2 % of all herbivore biomass in MNC, while wild herbivore biomass accounted for the remaining 37.8 %, meaning nearly two thirds of all herbivore biomass in MNC consists of domestic species. Mean density estimate of livestock in MNC was found to be 534.70 animals/km², while mean wild herbivore density was 55.21 herbivores/km². This supports the first hypothesis (*1*), stating that livestock biomass and density in MNC will exceed that of wild herbivores. The estimates here coincide with other studies from the Mara region, where livestock biomass in general exceeds that of wildlife (Young et al. 2013, 2018, Kimuyu et al. 2017, Bernardi et al. 2019). Between 2011 and 2013, livestock biomass was estimated to be 8.1 times greater than that of all wildlife biomass in the region. Just three decades previous, between 1977 and 1980, the livestock biomass was only 3.5 times greater than that of wildlife (Løvschal et al. 2018). It is important to note, however, that the estimates of this analysis only consist of herbivorous species and as such, the contrast between livestock and all mammalian wildlife distributions in MNC might be greater, or smaller. Whether that will be the case or not, similar patterns can still be observed throughout most semi-arid ecosystems in East Africa, where livestock biomass generally exceeds that of wildlife. In all of East Africa, for instance, livestock biomass massively outweighs that of wild ungulates (Muchiru et al. 2008).

In the Mara, the number of shoats has risen markedly in the past decades. While cattle numbers have remained constant, the number of shoats has skyrocketed with 235.6 % (Bedelian and Ogutu 2017). Shoats are generally more drought resistant than cattle and are thus more able to handle the fluctuating periods of drought that have increased in intensity and occurrence in recent years (Ogutu et al. 2016, Green et al. 2019). In the MNC, shoats are also not part of the rotational grazing plan and as such, there is no limitations on or restrictions to the number of shoats a household is allowed to own. However, there are restrictions on where the shoats are allowed to graze, as they are not allowed within the conservancy, only by the settlement borders (Green et al. 2019, William Kipetu, manager in MNC pers. comm.). The high grazing pressure generated by the staggering shoat numbers in the MNC can have detrimental effects on the vegetation and wild herbivores, and indeed the borders surrounding many of the settlement areas in MNC are heavily grazed and growing more barren (pers. observation). If the shoats continue to increase, their effect on the surrounding landscape might have more severe consequences than currently observed (Løvschal et al. 2018). Despite the high biomass of livestock in the system, and despite how some wildlife declines in Kenya have

been attributed to increasing livestock populations (Ogutu et al. 2016, Young et al. 2018), livestock rearing remains a constant in pastoralist lifestyle (Ogutu et al. 2016). The high levels of biodiversity still maintained in the Mara ecosystem (Ogutu et al. 2005b, 2014, Augustine 2010, Reid 2012, Young et al. 2018), and within the MNC itself, must be some sort of evidence that integrating high livestock stocking rates with high biodiversity can be a feasible possibility, if properly managed and controlled.

Effect of Cattle Presence on Wild Herbivore Density

Wild herbivore density was found to be significantly higher in the grazing zones of MNC in 2020, while no significant difference was found in 2019 (Fig. 5). This result then does not support the second hypothesis (2). Interestingly, this result also contradicts the findings of Sørensen et al (unpublished), which found that wild herbivore densities were negatively correlated with cattle grazing (with the sole exception of Thomson's gazelle). In 2019, many of the herbivorous species were observed in the no-grazing zones and the blocks not grazed by cattle for an extended period (e.g., blocks grazed 5 months ago) (David Noosaron, landowner in MNC, pers. comm.), whereas the same category of blocks and zones in 2020 were practically empty (pers. obs.). 2019 has been labelled as a drought year, with only 86.8mm rainfall compared to the previous year where April received 290mm rainfall, and as such, many resource banks had been depleted and many annually appearing waterways failed (Reynolds 2019, Russell 2020). The opposite pattern occurred the following year 2020, with heavy rainfall and April receiving 182mm (Reynolds 2020). Heavy precipitation levels in savanna ecosystems can massively increase productivity (Accatino et al. 2010, Tietjen 2016, Sankaran 2019), and indeed, grass height throughout MNC (except in current or very recently grazed blocks) has been markedly taller and overall grassy biomass much greater than in 2019 (Pers. observation, David Noosaron, landowner in MNC, pers. comm.). Only the large-bodied grazers or bulk feeders favor the tall grass plains, as it provides the quantity needed to satisfy their nutritional requirements and, since they have a low risk of predation because of their larger body size, they do not have to account for possible predators lurking in the high grass. Smaller sized herbivores and selective feeders theoretically favor the shorter grass to account for their higher quality-forage requirements and increased predation risk, creating a niche separation pattern of wild herbivores across the savanna based on body size (Riginos 2015, le Roux et al. 2019). When resources are high and more evenly distributed, as in the wet year of 2020, this pattern seems more pronounced as the overall wild herbivore density in MNC is highest in areas where cattle have grazed or are currently grazing (Fig. 5b). When resources become scarce, or in some areas fail completely, as was the case for 2019, many animals will congregate at forage reserves. These reserves can act as 'grass banks'; a constant, reliable source of forage to retreat to when optimal resources elsewhere decrease or fail, such as during a drought (Ogutu and Owen-Smith 2003, Riginos 2015, Abraham et al. 2019, Staver et al. 2019). As seems to be the case in MNC, the dry year saw limited resources in the form of low grass biomass, slow plant regrowth and fewer waterpoints and as such, the wild herbivores gathered at these forage reserves, which in MNC, were the no-grazing zones, which hadn't been disturbed by cattle throughout the year. As

high precipitation has led to rapid regrowth after cattle grazing and an overall increase in grass biomass along with high water availability, the wild herbivores were able to utilize the intermediate and short-grass lawns with higher nutrient content and thus higher quality forage (Bhola et al. 2012b). Judging by these results, it seems like the no-grazing zones are essential – especially during drought and in dry years when resource-levels are low. Indeed, these marked differences in wild herbivore distributions between cattle and no-cattle zones for the different years highlight an important aspect in the management plan. That is, forage source and sinks are vital in maintaining the ecosystem's diversity and animal populations. During unstable periods of limited or fluctuating resources, such as drought, a reserve such as that can be crucial for the survival of both wildlife and humans (Augustine 2010, Ogutu et al. 2014, Schieltz and Rubenstein 2016, Kimuyu et al. 2017, Abraham et al. 2019). Grazing banks for emergency use are also utilized by pastoralist communities for their livestock (Bedelian and Ogutu 2017) and is one of the reasons why the pastoralist cattle in MNC engage in the rotational grazing scheme; so that resources are always available to both cattle and wildlife when resources are scarce (Green et al. 2019). Protected areas (PAs), such as the MMNR, often act as forage sources in tumultuous periods and can provide refuge for wildlife during droughts and indeed, some studies have found that these habitat refugia were particularly important during droughts for maintaining wild herbivore populations (Bhola et al. 2012a, 2012b, Tyrrell et al. 2017). The results here certainly suggest that resource refugia, here the no-grazing zones, for wild herbivores are particularly important during drought years where water and forage are severely limited.

Competition and Facilitation Between Cattle and Wild Herbivores

Competition and facilitation between cattle and wild herbivores can be inferred from the observed density responses, possible lag times and coefficient estimates of the linear models. The overall levels of competition and/or facilitation between domestic and wild herbivores in MNC seem highly species-specific as well as dependent upon the year (Table 2, Fig. 6 and 7), which overall supports hypotheses (3) and (4). Hypothesis (3a) states that the densities of large-bodied, bulk feeders would increase as time since cattle grazing increased, indicative of competition. Overall, large-bodied bulk feeders such as buffalo and elephant do exhibit higher densities in blocks where cattle do not graze or have recently grazed, lending support to the hypothesis. But other smaller, tall grass feeders, such as topi, kongoni, and zebra exhibit more fluctuating and contradictory patterns, thereby rejecting the hypothesis. Hypothesis (3b) states the opposite, where small-medium sized herbivores will decrease in density as time since cattle grazing increases, indicating facilitation. Species such as Thomson's gazelle and wildebeest do have higher densities in blocks recently or currently grazed by cattle while impala and Grant's gazelle also increase in density after some months of cattle grazing, signifying a positive lag time response (Fig. 7). Marked differences in density responses across species also exists between the dry year (2019) and the wet year (2020), indicating that interactions between domestic and wild herbivores do fluctuate dependent upon the differentiating rainfall patterns between years, thus supporting hypothesis (4). Due to the interchangeable, specific patterns of each wild

herbivore species to cattle grazing and weather patterns, each of them will be discussed individually.

Thomson's gazelle had high densities across all active grazing blocks in 2020, with a significant dip in density in the no-grazing blocks (Table 2, Fig. 7). In 2019, densities remained high throughout all seven grazing blocks with two peaks at two and four months since cattle grazing (Table 2, Fig. 6). For both years, the results does suggest a high facilitation of Thomson' gazelle by cattle presence. This ungulate species is a relatively small, mixed feeder and have been shown to prefer open grazing lawns that have a high-quality forage - those generated by a grazing herd of cattle. They are often found in close proximity to other herbivores, as their small body size increases their predation risk (Muchiru et al. 2008, Vuorio et al. 2014, Fynn et al. 2016). Thus, cattle grazing can act as both a feeding facilitator, generating the favorable short grazing lawns, as well as an effective predator deterrent, since most savanna carnivores, especially lions, tend to avoid cattle in the landscape (Mogensen et al. 2011). The density responses are more sporadic for the drier 2019, which could be explained by the increased wildlife density in the no-grazing blocks for this year (Fig. 5A). Here, more herbivores gathered in the no-grazing blocks as forage and water were most likely limited elsewhere in the conservancy. The increase in wild herbivore presence then increased the grazing pressure which in turn reduced the grass height, thus making the no-grazing blocks more favorable to Thomson's gazelle in 2019, as opposed to 2020, where the no-grazing blocks saw limited herbivore activity and therefore higher grass biomass.

These distinct differences between no-grazing blocks and active grazing blocks in wet and dry years are also highly noticeable for buffalo. In the dry 2019, buffalo was only counted in the no-grazing blocks (Fig. 6), undisturbed by cattle presence, whereas in 2020, most buffalo counts occurred within blocks that had been grazed 2 and 3 months ago respectively (Fig. 7). For both years, none of the density responses are significant, but that has likely to do with the spatial behavior of buffalo. Buffalo generally aggregate in big herds (Korte 2008), and due to the current study design, the herds were only counted during one or two of the transects, thus decreasing the statistical power behind the model for buffalo. As such, it is still possible to infer some level of density responses to cattle. Buffalo are large-bodied bulk feeders and feed primarily on the same tall grass as cattle, and the density responses of buffalo in both 2020 and 2019 are suggestive of a competitive interaction, as there are no counts of the species within close proximity to cattle, and indeed, buffalo have been known to spatially avoid cattle whenever possible (Averbeck et al. 2012, Macandza et al. 2012, Valls-fox et al. 2018). However, the massive rainfall in 2020 seems to have generated plenty of water for rapid grass regrowth so that grass quantity was adequate for buffalo consumption already 2-3 months past cattle grazing in 2020, compared to 2019, where only the no-grazing blocks seem to have enough forage to sustain buffalo.

Another large-bodied, bulk feeder is the elephant, although the density responses of this species seem vastly different from the buffalo. In 2019, the highest densities of elephant were in the currently grazed blocks as well as one month past grazing (Fig. 6), whereas in 2020, elephant density was significantly higher

in the no-grazing blocks (Fig. 7). An explanation for this discrepancy could be interspecific competition – not between elephant and cattle, but between elephant and buffalo. Indeed, a study by de Boer and Prins (1990) found that elephant and buffalo consumption was negatively correlated to each other's presence, and this could explain the pattern observed for 2019 density responses. As buffalo graze in the no-grazing blocks, this pushes elephant to seek food elsewhere (Boer and Prins 1990). What is interesting is that elephant then relocates to blocks with active or recent cattle grazing, as this large species have been shown to spatially avoid human and cattle presence on the savanna (Young et al. 2005, Hibert et al. 2010, Valls-fox et al. 2018). However, while buffalo is primarily a bulk grazer, elephants are first and foremost a browser, feeding on tree seedlings and yearlings (Coverdale et al. 2016). Perhaps forage quality and quantity are at the optimum in the no-grazing blocks, evidenced by the markedly high densities in 2020, but when these areas become unavailable (e.g. buffalo grazing) forage opportunities are highest within the grazing blocks where cattle currently are or recently have been grazing, as observed for 2019. It is, however, important to note that the density for elephant in 2020 is higher than in 2019, and one potential explanation for this could be competitive exclusion of elephant by cattle and buffalo grazing when resource availability becomes low.

Eland, Grant's gazelle and impala all exhibit a lag time response in their densities to cattle grazing, indicative of a feeding facilitation. In 2020, both impala and Grant's gazelle had the highest densities three (Grant's gazelle) or four (impala) months since cattle grazing, while both species had the highest densities in the no-grazing blocks in 2019 (Fig. 7). Both species are small-medium sized mixed feeders, and just like the Thomson's gazelle, generally prefer shorter grass with higher nutrient content (Van der Merwe and Marshal 2014). The shorter vegetation also serves to minimize predation risk, as these antelopes also are a favored prey species to many carnivores because of their smaller body size (Arsenault and Owen-Smith 2002, Tyrrell et al. 2017). Thus, they are likely to congregate in areas with low grass height and in 2019, these areas also included the no-grazing blocks, which received a higher grazing pressure. In 2020, however, the grass height in the no-grazing blocks were markedly higher and as such, unfavorable to these smaller sized selective feeders. Eland exhibited the same density pattern regardless of year, namely highest densities two-three months since cattle grazing, although only 2020 was significant (Fig. 6 and 7). Eland is considered a mixed feeder, although it is mainly a browser, and as such, might not be as sensitive to grazing cattle as the more grazing impala or Grant's gazelle (Bhola et al. 2012a, Kimuyu et al. 2017), which is evidenced in the density responses in both the dry (2019) and the wet (2020) year. However, the density in 2020 is markedly higher than in 2019 (Fig. 6 and 7), and therefore, higher quantity of forage could influence eland distribution and density.

Ostrich densities in 2019 yielded no significant differences, however density seems highest in the nograzing blocks (Fig. 6). The same pattern occurs in 2020, with a significant peak in density in the no-grazing blocks (Fig. 7). Ostrich is a curious case as it is the only avian herbivore included in this study. It is classified as an herbivore but has been known to occasionally feed on invertebrates and sometimes even small rodents (Moehlman et al. 2020). When it does graze, however, ostrich primarily feeds on short, green biomass consisting of grass and forbs and are more likely to compete with short grass feeders. Therefore, ostrich in MNC is more likely to compete with shoats than with cattle (Milton et al. 1994).

Zebra densities for 2020 did not have any significant differences, although there is a peak in density in blocks last grazed by cattle four months ago (Fig. 7). For 2019, a significant peak in density was found in that same grazing block (Fig. 6). Zebra is a non-ruminant grazer that feeds primarily on tall grasses and is therefore a bulk feeder. However, zebra has been known to favor short grass grazing lawns even though their feeding ecology allows them to graze on low-quality forage (Macandza et al. 2012, Said et al. 2016). Given the higher grass biomass availability throughout all of MNC in the wetter 2020, the more evenly distributed densities of zebra across all grazing blocks (except for the markedly low density in the no-grazing blocks) (Fig. 7) can be explained by zebra's ability to forage on both high and low grass biomass levels. For the dry 2019, resource availability would be lower and therefore zebra would exhibit higher selection for optimum quality and quantity forage. Odadi et al (2011) found in their study that competition between zebra and cattle was particularly pronounced during the dry season, and it would be reasonable to assume the same pattern would hold true for a dry year when compared to a wet year. Several other studies have likewise found that because of both dietary and habitat overlap, zebra and cattle can be big competitors (Young et al. 2005, 2018, Odadi et al. 2011). The patterns observed here, though, suggests that competitive interactions are primarily restricted to periods where resources are scarce.

Wildebeest densities for both 2020 and 2019 were highest in the blocks currently grazed by cattle, suggestive of high facilitation by cattle (Fig. 6 and 7). Significant declines in density for 2020 were found in blocks grazed by cattle one, two and three months ago as well as in the no-grazing blocks (Fig. 7). For 2019, only the blocks grazed by cattle five months ago were significantly different, but density did decrease in the same grazing blocks as in 2020 (Fig. 6). Because of their feeding ecology, wildebeest generally feed on short grasses as they require high-quality forage (Gwynne and Bell 1968, Waldram et al. 2008). Indeed, some studies have found that wildebeest follow zebra's grazing, as they feed on the taller grasses and leave the shorter stems preferred by wildebeest (du Toit and Olff 2014). This sort of grazing succession could also explain the sudden spike in density in the blocks grazed by cattle four months ago in 2020, which also saw a high zebra density (Fig. 7). Interestingly, wildebeest observations in the four months since grazing were generally quite low in 2019 (Sørensen et al, unpublished), despite the high zebra density (Fig. 6). Perhaps, because of the low rainfall, the resources within those areas could not support both grazing species and wildebeest was forced to seek forage elsewhere. It has been suggested that wildebeest can be facilitated by cattle, as cattle too leave short grazing lawns and thus take over for zebra (du Toit and Olff 2014, Van der Merwe and Marshal 2014). That can also explain the high densities of wildebeest in the active grazing blocks for both 2020 and 2019. However, some studies have found that wildebeest and cattle compete for forage and/or habitat (Ogutu et al. 2011, 2016, Green et al. 2019) and indeed, Sørensen et al (unpublished) found

that wildebeest densities were influenced by cattle grazing and that the densities of wildebeest were primarily found to increase as the number of months since cattle grazing increased, suggestive of some form of competitive interaction.

No significant values were found for giraffe regardless of the year. The density for 2019 is generally low but peaks in blocks grazed one or three months ago as well as the no-grazing blocks (Fig. 6), while in 2020, density is highest in the no-grazing blocks and blocks grazed four months ago by cattle (Fig. 7). As such, there is no clear discernable pattern, but this could also suggest giraffe is not influenced by cattle and that their distributions are likely more a response to forage opportunities than any avoidance behavior or competitive interactions. Giraffe is a browser, mainly feeding on leaves and stems on tall trees or bushes and therefore, their feeding ecology and habitat requirements rarely overlap with that of cattle (Ciofolo 1995, O'Connor et al. 2015). One study in the Mara region found similar results, where giraffe density was not influenced by cattle or human presence like other herbivores in the study area (Ogutu et al. 2014). It stands to reason then, that giraffe densities in MNC will be highest in areas with quality browsing, regardless of cattle presence or annually fluctuating weather patterns.

Warthog was only included and counted in the 2020 dataset, and therefore comparison between the dry and wet years cannot be conducted for this species. A small lag response between cattle grazing and high warthog density was found, as density was significantly higher one month since cattle grazing and then steadily decreased with the lowest density in the no-grazing blocks (Fig. 7). This can indicate a rapid feeding facilitation to cattle presence, as warthog seem to favor the short grazing lawns left by cattle. Indeed, warthog's body size and feeding ecology is somewhat similar to the small Thomson's gazelle and likewise, is a favored prey species to predators (Girma 2018). However, in contrast to the gazelle, warthog does not seem to linger close to the cattle. One explanation hereof could be the shepherds and dogs often herding the cattle. The dogs are mainly kept as guarding animals, where their job is to warn and ward off any lurking predators, and often becoming feral as they are not fed or cared for. Warthogs ofttimes become hunted prey by these feral dogs and as a consequence, generally avoid both human settlements and herded livestock where dog presence is high (Gandiwa et al. 2013, Girma 2018).

Waterbuck, reedbuck, kongoni and dik-dik generally occurred only a few instances in the field, in both 2019 and 2020. Dik-dik and waterbuck were only counted in the 2020 dataset, and both occurred mainly in the no-grazing blocks (Fig. 7). Reedbuck likewise showed the same pattern. In 2020, there were only three instances of counting of reedbuck in the field. Two of them occurred in the no-grazing blocks, while the third was logged in an active grazing zone, but the two animals in that count were observed fleeing from a cattle herd (pers. observation) that had been allowed temporary access to the adjacent no-grazing block where the reedbucks came from (David Noosaron, landowner in MNC, pers. comm.). All three of these species exhibit a preference for dense vegetation habitats, even though dik-dik is a browser while waterbuck and reedbuck are both classified as grazers (Maloiy et al. 1988, Tsegaye et al. 2015, Girma 2018). The no-grazing blocks

were generally denser (pers. observation) and therefore, theoretically provide suitable habitat for these herbivores. However, all densities for these species were very low, and while dik-dik did have significantly higher density in the no-grazing blocks, overall counts for dik-dik, reedbuck and waterbuck were too low to properly predict or infer much. Kongoni had the same pattern in 2020, where counts of this species were too low to gain any significance. While densities are low for this species, the overall response is highest in blocks grazed either two or four months ago (Fig. 7). This contrasts to 2019, where a significant response is seen for the no-grazing blocks (Fig. 6). Kongoni have been known to favor tall grasses, both for forage as well as hiding their vulnerable calves from predators (Sitters et al. 2009, Hibert et al. 2010), and given their density response for 2019, it seems reasonable to assume some form of competition exists with cattle, especially when resources are scarce. A study by Ogutu et al (2014) found that in drier years when resources were limited, kongoni and cattle competed, but their competitive interactions lessened during wetter years, consistent with the patterns observed here.

The same study found a similar pattern for topi, which exhibits the same preferences as kongoni for tall grasses (Ogutu et al. 2014). Just like kongoni, topi also exhibited the same density response in 2019, where significantly higher density was found in the no-grazing blocks (Fig. 6) and coincides with the results for kongoni in much the same way. Interestingly, the pattern is markedly different for 2020. Here, significantly higher densities were found in blocks grazed by cattle one or four months ago (Fig. 7), suggestive of a facilitative interaction instead of a competitive one. Despite the low counts of kongoni, similar patterns are also observed for this species in 2020 (Fig. 7). This suggests that despite both species' preference for tall grass plains, when resource availability is high, any competition between kongoni and topi and cattle is decidedly lessened and instead become a more facilitative relationship. Although topi does require a general grass height of 3 cm or more (Owen-Smith 2002), this species have been shown to forage on relatively low grass swards that have been grazed by species such as buffalo and zebra (Arsenault and Owen-Smith 2002, Sitters et al. 2009). This could explain the density responses for 2020, where the higher rainfall could have generated more biomass more rapidly than in the drier 2019.

Despite the species-specific density responses, some overall patterns can still be drawn. For the drought year, competition between cattle and wild herbivores seem the most dominant interaction given the high densities of various herbivore species, such as buffalo, topi, impala and kongoni, in the no-grazing blocks (Fig. 6). The same species congregated in blocks more recently grazed by cattle during the wetter 2020 (Fig. 7). This can indicate that amble resource availability can considerably lessen the otherwise high level of competition between cattle and these herbivore species. Some herbivore species (zebra, wildebeest, impala, kongoni and topi) also peak in density at four months since cattle grazing in 2020 (Fig. 7), and given how impala, kongoni and topi had high densities in the no-grazing blocks for 2019 (Fig. 6), it seems likely that these species gather where forage quality is at its optimum. As more rain must have generated more biomass in the grazed blocks in 2020 than in 2019, optimum quality forage for these species was more likely

to be found in blocks grazed by cattle four months ago in the wet year and thus many herbivores gathered here instead of the no-grazing blocks, as they did in 2019. As such, competitive interactions between cattle and herbivores in MNC seems more driven by resource availability and when resources are amply available, many competitive relationships between cattle and herbivores can become facilitative instead.

Mara North Conservancy and the Future

Cattle, and livestock in general, have played a major part in the East African pastoralist livelihood for millennia and it is not unreasonable to assume it will continue to do so in the future (Goldman 2007, Lankester and Davis 2016). However, traditional lifestyles are changing for the local pastoralists in the Mara region (Western et al. 2020). Landownership changes and further land privatization in the area further the conversion of old, pastoralist lands into non-pastoral uses, and newer generations are receiving higher schooling opportunities. When this higher-educated generation inherits the land from their parents they have no interest in cattle rearing and instead, wishing to maximize any economic output, will lease their lands to highest bidder (Nkedianye et al. 2020). This can potentially threaten the future viability of MNC as well as the surrounding conservancies utilizing the same conservation strategy. Given the high percentage of Kenyan wildlife that exists within these community-based conservancies, they are growing ever more important in preserving these dwindling animal populations (Georgiadis et al. 2007, Augustine et al. 2011, Butt and Turner 2012, Osano et al. 2013, Ogutu et al. 2017). If leasing your land to the conservancies is no longer economically feasible then only governmental and privatized protected areas will remain as wildlife habitats. Here, human settlement and pastoralism are not allowed and push the local communities to the edges of these areas, causing the anthropogenic pressure to massively increase around them and many wildlife populations in those isolated areas have been declining as a result of this growing human influence (Homewood et al. 2001, Veldhuis et al. 2019). Conservancies such as the MNC continually prove to be a viable alternative and a way of engaging the local communities to preserve wildlife. The local pastoralists in southern Kenya are still among some of the poorest peoples in all of Africa, but today, revenues from tourism provide many households with additional income while job opportunities within the tourism sector continue to grow alongside the industry (Reid 2012, May et al. 2019, Nkedianye et al. 2020). However, relying on tourism for conservation must be approached with a certain level of caution, as political unrest, terrorism and epidemics can easily minimize tourism revenues and thereby destabilize the whole management scheme (Ferreira 2004, Ayiemba et al. 2015, Škare et al. 2021). Despite of this uncertainty, continuing to include the local people in management planning remain a vital tool in wildlife conservation and, at least for the Mara region, pastoralist livelihoods and a thriving wildlife population do not necessarily exclude one another (Ogutu et al. 2005b, Augustine 2010, Butt and Turner 2012, Green et al. 2019).

Conclusion

This study found that wild herbivore responses to livestock, in particular cattle, are rarely fixed and can depend upon both feeding ecology of the herbivore as well as fluctuating rainfall patterns. The level of

competition and facilitation between cattle and wild herbivores differentiated depending on whether it was a wet or a dry year; the no-grazing zones seemed particularly important in the dry year as these had higher wild herbivore densities, while the same areas had markedly lower densities in the wet year. Overall, MNC supported higher densities and had more counts of most wild herbivore species in the year with high rainfall than the previous year where it was a drought. This suggests that the livestock-dominated conservancy with its rotational grazing scheme can support and facilitate a large number of wild herbivores when resources are copiously available. During droughts and when the same resources are suddenly scarce, wildlife refugia, such as the no-grazing zones within the MNC and nearby protected area of MMNR, become increasingly important to maintain the local wildlife. Therefore, protected areas and community-based conservancies are both vital in Kenyan wildlife conservation and one is not sustainable without the other. The true effect of the management plan implemented in MNC and its viability for maintaining both local culture and wildlife remains unknown as it will require multiple decades worth of data to properly assess population trends. Until such time however, we can at the very least conclude that community-based conservancies, such as MNC, can sustain ample wild herbivore populations and limit competitive interactions with livestock, especially during wetter years with abundant resources. When resources become scarce, like during a drought, the rotational grazing scheme is a vital factor in creating refugia and forage banks (like the no-grazing zones) for the ailing wildlife to persist in the landscape.

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Appendix

S1: Transects Overview

Table showing the number of strip transects conducted within each grazing block. Each block has been assigned 'Yes' or 'No' depending on if it receives cattle grazing at any point during the year.

Time Since Cattle Grazing (months)	Number of Transects	Grazing (Yes/No)	Average Transect Length (km)
0	12	Yes	0.930
1	12	Yes	1.025
2	12	Yes	1.021
3	12	Yes	0.980
4	12	Yes	1.028
5	12	Yes	1.000
>12	20	No	0.907

S2: Herbivore Species Biomass

Bar graph depicting total biomass value of each observed herbivore species in MNC, in descending order by most common (and highest total biomass) to rarest (and lowest total biomass).


S3: Rotational Grazing Scheme Map

Example of active grazing blocks in MNC (courtesy of William Kipetu, Manager at MNC). The map illustrates the active grazing blocks for June and July of 2020 as well as tourist camps, Ranger stations and settlement areas in MNC. Blue color describes the grazing blocks for June and green color describes the grazing bl



