Lion (*Panthera leo melanochaita*) diet in relation to prey preference and density in Meru National Park, Kenya

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ABSTRACT

The African lion (*Panthera leo*) plays a key role in savannah ecosystems by directly and indirectly regulating trophic structure. Their foraging behavior has frequently been described as opportunistic, but often reveals a distinct preference for certain prey species that are energetically more profitable. This research project focussed on the population structure and diet of lions in Kenya's Meru National Park. Data were collected from February until April 2019 and contribute to the PhD research of MSc Luka Narisha. A total of 28 lions were identified during fieldwork, indicating a lion density of 2.2 adult lions per 100 km^2. Transect counts of potential prey species in the park revealed that Kirk's dik-dik (*Madoqua kirkii*) had the highest relative abundance of all prey species (50.89%), while African buffalo (*Syncerus caffer*) contributed the most to the total prey biomass (33.94%). Based on carcass counts and microscopic prey hair analysis from lion scats, African buffalo and plains zebra were found to be the principal prey species of the lions in Meru National Park. Few hairs of livestock were found in the lion scats, which indicates a low level of livestock raiding. Prey preference analysis using Jacobs' Index showed that lions had a high prey preference for African buffalo and plains zebra, but Grevy's zebra appeared to be the most preferred prey species. Lions did not seem to have a significant preference or avoidance for selected prey body mass ranges. Overall, results from this study indicate that Meru National Park hosts a healthy lion population in a relatively undisturbed ecosystem, but further research is needed to eliminate remaining uncertainties and monitor the prey and lion populations in view of climate change.

SUMMARY

The global lion (*Panthera leo*) population is declining rapidly. Loss of habitat and prey, and the resulting conflicts between humans and lions, are increasingly threatening the very survival of the species. This study, which contributes to the PhD research of Luka Narisha, aims to better understand the ecology of the lion population in Meru National Park (Kenya) in order to support local management and conservation efforts. Meru National Park is situated in central Kenya and is largely unfenced, allowing wildlife to move freely between the protected area and the surrounding community lands. Over the course of 3 months, lions were actively tracked to understand their population dynamics and structure, and prey populations were monitored to map prey availability inside the park. By recording carcasses and analysing prey hair found in lion scats, it was possible to assess what prey species the lions generally consumed, and how this might be related to conflicts between lions and humans in neighbouring communities. Overall, African buffalo and plains zebra made up the largest portion of the lions' diet, and only a few remains of livestock were found in their diet. This indicates that the lion population in the park is relatively healthy, since it predominantly predates on large, wild prey species. Ample prey was available inside Meru National Park, and it seems unlikely that the lions would resort to livestock raiding due to a shortage of wild prey. However, with large numbers of livestock congregating just outside the park, and climate change potentially disturbing water and prey availability, the risk of conflict between lions and local people may increase in the future. Continuous research and monitoring of the lion population and their prey is therefore critical in establishing mitigation measures and preventing losses on both sides of the conflict.

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INTRODUCTION

General background

Large carnivores play an important ecological role in regulating and maintaining ecosystem dynamics and integrity (Ripple *et al*., 2014). Through so-called trophic cascades, the direct predation pressure they exert on prey populations trickles down across other trophic levels and may directly and indirectly affect other herbivores, sympatric carnivores and vegetation structures (Ripple *et al*., 2014; Atkins *et al*., 2019). The impact of large carnivores on other predators is not only manifested by altering prey availability, their mere presence leads to avoidance behaviour and intraguild competition, especially when there is dietary overlap (Ripple *et al*., 2014; Vogel *et* al., 2019). Furthermore, in addition to reducing grazing- and browsing intensity by limiting the number of herbivores, predation has the potential of altering the spatial patterns of grazing by imposing 'landscapes of fear', in which prey modify their behaviour to avoid predators (Atkins *et al*., 2019). Predator-prey dynamics are fundamental ecological interactions that ultimately shape biotic communities in an ecosystem, and their nature has the potential to impact the ecosystem services and resources upon which all organisms, including humans, depend (Ripple *et al*., 2014).

Human activities, however, continue to impact ecosystems on multiple scales (Hooper *et al*., 2005). The unsustainable exploitation of natural resources and human-induced global changes in biogeochemical cycles, climate and land-use have resulted in an exceptionally rapid loss of biodiversity during recent decades (Hooper *et al*., 2005, Butchart *et al*., 2010, Ripple *et al*., 2014, Ceballos *et al*., 2015). This also includes most of the world's large carnivores, which are currently undergoing continuing population declines (Riggio *et al.*, 2013; Ripple *et al*., 2014). Our understanding of the crucial ecological role that large carnivores play in complex ecosystems should therefore continue to be improved and applied in specific areas and contexts to facilitate local conservation efforts and prevent the further decline of carnivore populations.

On the African continent, the African lion (*Panthera leo*; Linnaeus, 1758) is the top predator in almost every habitat. Lions once roamed throughout most of Africa, except for the Sahara Desert and the Central-African inner rainforest areas, but they are now restricted to just 17% of their historical African range and are mainly found inside protected areas (Ray *et al.*, 2005; Riggio *et al*., 2013). Outside of these areas, although not exclusively, lions are illegally poached for their bones and body parts and are often involved in conflicts with local people (Bauer *et al*., 2016). Human-lion conflicts are becoming increasingly problematic as a result of the continuing shrinkage of natural habitat and the subsequent depletion of prey populations (Treves & Karanth, 2003). Viable areas of African savannah habitat have shrunk by 75% since the 1960's and the remaining patches are often fragmented, which further threatens the persistence of viable lion populations (Riggio *et al*., 2013). Although lions are relatively adaptable,

they are sensitive to loss of cover and prey (Ray *et al*., 2005). Moreover, the collapse of large prey populations due to the anthropogenic conversion of natural habitats is further amplified by the unsustainable and increasingly commercialized bushmeat trade (Bauer *et al*., 2016; Lindsey *et al*., 2013). A frequently used technique in ungulate poaching is steel wire snaring, an indiscriminate but effective way of trapping game through the use of steel wires and cables (Becker *et al*., 2013). However, the indiscriminate nature of snaring and the tendency of lions to scavenge the carcasses of snared animals often results in the unintentional snaring of lions instead of their prey (Ray *et al*., 2005).
With pastoralism heavily encroaching upon lion habitat, lions are often forced to intrude on community land and predate on livestock, which fuels persecution and retaliatory killings by local people (Woodroffe, 2000; Ogada *et al*., 2003). Persecution of lions by means of shooting and the poisoning of carcasses are just a few of the various outcomes which result from these conflicts (Ray *et al*., 2005). In Kenya, retaliatory killings by humans are so substantial that they have been found to be the main cause of death of lions outside protected areas (Patterson *et al*., 2004; Oriol-Cotterill *et al*., 2015; Tuqa *et al.*, 2015).

Lion taxonomy and conservation status in Africa and Kenya

Because their requirements often overlap and conflict with those of local people, lions are particularly sensitive to human activity and are continuing to decline in numbers worldwide (Woodroffe, 2000; Riggio *et al*., 2013). Currently, the IUCN has listed *Panthera leo* as Vulnerable on the global IUCN Red List (category A2abcd ver 3.1, 2017), and estimates the global number of adult lions between 23,000 and 39,000 individuals (Bauer *et al.,* 2016). Based on recent genetic research, *Panthera leo* is further split into two subspecies (Kitchener *et al*., 2016). *Panthera leo leo* (Linnaeus, 1758) inhabits West and Central Africa and India and is currently undergoing local extinctions even in nominally protected areas (Riggio *et al*., 2013; Bauer *et al*., 2016; Kitchener *et al*., 2016). The other subspecies, *Panthera leo melanochaita* (Hamilton Smith, 1842), populates East and southern Africa (Bauer *et al*., 2016; Kitchener *et al*., 2016). According to a study by Riggio *et al*. (2013), the current extent of free-ranging lion populations is 3.4 million km^2, or about 25% of the total savannah area. More than half of this is hunting zone (Lindsey *et al.*, 2006). Riggio *et al*. (2013) identified 67 lion areas, 10 of which are qualified as strongholds (4 in East-Africa and 6 in Southern Africa). A lion stronghold contains at least 500 individuals, is located within a protected area or a designated hunting zone and the number of lions must be stable or increasing (Riggio *et al*., 2013).

Kenya hosts two of the four East-African lion strongholds in cross-border ecosystems with Tanzania and holds one more potential stronghold in the centre of the country (Riggio *et al.*, 2013). However, it is estimated that Kenya is home to less than 4% of the global lion population (KWS, 2008). National numbers have declined from 7,000 in 1990 to about 3,000 in 2002 and about 2,000 in 2010 (Chardonnet,

2002; KWS, 2008; Riggio *et al.*, 2013). As stated before, habitat loss, prey depletion and indiscriminate killing are the main threats lions presently face. Long-term conservation efforts will therefore only be successful when enough protection and space is ensured and direct conflicts with local communities are mitigated (Ogada *et al*., 2003).

Social structure of the African lion

The African lion is the only large cat species that lives in social units, known as prides, which are characterized by a fission and fusion social structure (Schaller, 1972). Although members can be widely scattered, a lion pride is usually a fairly cohesive social unit composed of a core of related females, their cubs and one or more males (Schaller, 1972). All pride members cooperate in activities such as defending the territory, rearing offspring and hunting (Schaller, 1972; Packer *et al*., 1990).
While lions can be active throughout the 24-hour daily cycle, most activity, including hunting, takes place between sunset and sunrise (Schaller, 1972; Hayward & Kerley, 2005). Hunting is mostly undertaken by lionesses and nomadic males, although pride males sometimes assist in taking down larger prey such as African buffalo (*Syncerus caffer*; Sparrman, 1977) (Schaller, 1972; Bertram, 1979; Packer, 1986; Van Orsdol, 1986). Because of their unique social structure, lions are capable of hunting cooperatively by driving prey into an ambush (Stander, 1992b). Such collaborative hunts are generally more successful, but timing is crucial and requires careful cooperation, with each lion fulfilling a complimentary role (e.g. flanking, driving, ambushing) (Schaller, 1972; Stander, 1992a/b).

Although they are able cover large distances in relatively short periods (12-18 km/day), lions can stay in the same area for weeks (Schaller, 1972). Their movement patterns are spatially and temporally variable and thus particularly unpredictable (Schaller, 1972). This is especially true for young males, which become nomadic and form coalitions with other males after being expelled from their natal pride at about 3 years old (Schaller, 1972). Only by overthrowing the dominant male can they gain residence into another pride (Schaller, 1972; Rudnai, 1974; Packer *et al*., 1991). Females, on the other hand, usually remain in the same pride as the one in which they were born (Schaller, 1972). The size and composition of a pride, as well as the lion density in a given area, depends on various factors such as birth and death rates, emigrations, pride take-overs, season, prey availability and prey abundance (Smuts, 1976; Hayward *et al*., 2007). Lion group size, which is defined as the number of adult lions sighted together during an observation at a certain time and place, also depends on similar ecological factors (Bauer *et al*., 2003).
Accurate estimates about pride structure and group size are intrinsically difficult to make, since lion populations are generally at low densities within relatively large home ranges (Ogutu & Dublin, 2002; Riggio *et al*., 2013). Because lions can only hunt larger prey when they are in large enough groups, areas with higher mean prey body mass and prey densities typically support larger lion group sizes than

disturbed areas where prey densities and prey body mass are low (Caraco & Wolf, 1975; Gittleman, 1989; Bauer *et al*., 2003). Larger groups allow for cooperative hunting, which not only enables larger prey species to be taken, but also optimizes prey capture rate and efficiency (Bailey *et al*., 2012). The risk of injury and the energetic costs are furthermore reduced and the per capita of food is increased, resulting in an overall increase of individual fitness and enhanced reproduction (Bailey *et al*., 2012).

Diet and prey preference

Factors influencing carnivore diet

The feeding strategy of a predator is driven by natural selection and aims to maximize net energy and/or nutritional gain (Hayward & Kerley, 2005). Net energy gain is determined by the energetic cost of hunting versus the energetic uptake after prey ingestion (Griffiths, 1975; Sunquist & Sunquist, 1997). Although prey with larger body masses reflect higher potential energy uptakes, an increase in body size also relates to an added risk of prey capture (Clements *et al.*, 2016). Consequently, a predator is required to carefully estimate the costs and benefits of hunting certain prey in order to maximize hunting success and the resulting energetic profit (Hayward *et al*., 2006b/c). The nature of predator-prey dynamics thus implies that some species are taken more frequently than expected based on their relative abundance in the total pool of available prey animals (Hayward & Kerley, 2005). These species are considered "preferred" prey, while species that are predated on less frequently than expected based on their availability are considered "avoided" prey (Hayward & Kerley, 2005).

The selection of suitable prey species, and the ensuing preferences and avoidances, is highly determined by the balance between predator life attributes (predator size, hunting tactics) and prey-specific characteristics (body mass, habitat choice, anti-predator strategies) (Hayward & Kerley, 2005). Prey species have evolved and adopted strategies to thwart predatory attacks by expressing passive defensive behaviour (e.g. crypsis, herd formation, habitat selection) and active defensive behaviour, often through morphological features (e.g. horns) (Hayward & Kerley, 2005; Clements *et al*., 2016). The expression of anti-predator strategies differs between prey species and is reflected by the species' behavioural and morphological traits (Hayward & Kerley, 2005). For example, the active defence of zebra (*Equus spp.*) is not as effective as that of the larger African buffalo, but zebra are able to outrun lions in 6 seconds and reduce overall catchability by avoiding dense cover at night when predators are active (Elliott *et al*., 1977; Hayward & Kerley, 2005; Fischhoff *et al*., 2007). Habitat selection is a strategy used by many prey species to avoid predation (Hayward & Kerley, 2005). Whereas some species, like zebra and wildebeest (*Connochaetes spp.*), seek refuge on open plains and in large groups (herds) to increase predator detectability, others, such as lesser kudu (*Tragelaphus imberbis*) and bushbuck (*Tragelaphus sylvaticus*), make use of dense vegetation and crypsis to lower their visibility (Hayward *et al*., 2006b).

Dense vegetation may provide prey with cover and decrease their detectability, but predators are also able to use dense vegetation to reduce their prey capturing effort (Hayward *et al*., 2006c). Many predators, like African wild dogs (*Lycaon pictus*), therefore rely on smell and hearing as much as sight to facilitate prey detection in densely vegetated areas (Hayward *et al*., 2006c).

Fuelling the ever-present 'arms race' between predator and prey, predators have evolutionary sought to counteract the existing anti-predator strategies of their prey by employing various hunting techniques (Kruuk, 1975; Packer, 1983; Fanshawe & FitzGibbon, 1993; Caro, 2005). This often includes specializing hunting behaviour according to habitat, prey species and other related aspects (Hayward & Kerley, 2005). For example, leopards (*Panthera pardus*; Linnaeus, 1758) are solitary hunters and they are specialized in capturing small (<50 kg) and medium (50 – 100 kg) sized prey in ambush to minimize risk of injury (Hayward & Kerley, 2005; Hayward *et al*., 2006a). Cheetahs (*Acinonyx jubatus*; Schreber, 1775) and African wild dogs (*Lycaon pictus*; Temminck, 1820) select their prey based on prey body mass and the relative abundances of the available prey species (Hayward *et al*., 2006b/c). Spotted hyaenas (*Crocuta crocuta*; Erxleben, 1777), on the other hand, do not exhibit an outspoken preference for any prey species, which is reflected by their scavenging behaviour and flexible hunting strategies (Hayward, 2006).

Diet and prey preference of the African lion

Lions, being Africa's largest felid and land carnivore species, distinguish themselves from all other predators by their capacity to take down some of the continent's largest herbivores, such as African buffalo and giraffe (*Giraffa camelopardalis*) (Carbone *et* al., 1999; Hayward & Kerley, 2005). Their relatively large size and cooperative hunting technique enable them to predate on larger prey species that provide a higher potential energy gain (Hayward & Kerley, 2005). To sustain their high energetic requirements, male and female lions require a mean daily dietary uptake of 10.4 kg and 7.5 kg of prey meat, respectively, although they can also go up to 4 days without eating (Schaller, 1972; Carbone *et al.*, 1999). They prefer to prey upon larger species that are within a body mass range of 190 to 550 kg, which includes species such as African buffalo and zebra (Hayward & Kerley, 2005). However, they remain limited by the abundance, accessibility and defensive strategies of the available prey species (Hayward & Kerley, 2005). Furthermore, as lions inhabit ecosystems with heterogeneously distributed environmental resources which are exposed to seasonal variations, their choice of prey is often opportunistic and typified by seasonal switches (Schaller, 1972; Hayward & Kerley, 2005; Davidson *et al*., 2013). These switches are usually related to water availability and the associated herbivore distributions, which differ between wet and dry seasons (Tumenta *et al*., 2013; Tuqa *et al*., 2014; Davidson *et al*., 2013). For example, in the semi-arid ecosystem of Hwange National Park (Zimbabwe), lionesses have been observed switching their main prey consumption from browsers (e.g. giraffe) in the early dry season, to grazers (e.g. plains zebra (*Equus quagga*), warthog (*Phacochoerus africanus*)) in

the late dry season (Davidson *et al*., 2013). Although many studies have observed a prevalent preference towards large herbivores, lions are also known for their opportunistic feeding behaviour (Schaller, 1972; Hayward & Kerley, 2005; Joubert, 2006; Sogbohossou *et al*., 2011; Davidson *et al*., 2013). Consequently, lions will not reject livestock in times of prey scarcity, which can potentially cause a peak in human-lion conflicts (Patterson *et al*., 2004; Bagchi & Mishra, 2006; Valeix *et al*., 2012; Tumenta *et al*., 2013; Tuqa, 2015).

Effects of human disturbance

To meet the metabolic demands imposed by their large size and social structure, lions require large prey weighing more than 45% of their own body mass (e.g. African buffalo, plains zebra) and expansive, undisturbed landscapes (Carbone *et al*., 1999; Ripple *et al*., 2014). Such landscapes provide a habitat for larger herbivores and are characterized by a high functional diversity and species richness, thus allowing lions to access a variety of different prey species (Ogutu *et al*., 2014; Ripple *et al.*, 2014). However, throughout large parts of the lion's distribution range, human activity and disturbance are becoming increasingly prominent (Ripple *et al*., 2014). Disturbance factors such as noise pollution, hunting and pastoralism, not only affect prey species composition, but they also impact the behaviour of prey- and lion populations (Ogutu *et al*., 2014; Lesilau *et al*., 2019). Studies have shown that lions generally live in smaller prides and have lower group sizes when they inhabit disturbed environments (Van Orsdol, 1985; Bauer *et al*., 2003; Bauer *et al*., 2008; Packer *et al*., 2013). This, in turn, reduces their chances of successfully taking down larger prey, as they are restricted to hunting solitarily or in pairs (Bauer *et al*., 2003; Packer *et al*., 2013; Tuqa *et al*., 2015). Consequently, the relative contribution of smaller prey species (< 45% of predator's body mass; Carbone *et al*., 1999) to the diet of lions is expected to be higher in disturbed ecosystems than in undisturbed ecosystems (Lesilau, 2019).

Research hypothesis

Research for this project was done in Meru National Park, an open-access protected area part of a larger, relatively healthy and undisturbed ecosystem in Central-Kenya. It was therefore hypothesized that the park's resident lion population is characterized by large pride sizes and large group sizes, and that the lions predominantly incorporate larger prey animals such as African buffalo in their diet (Bauer *et al*., 2008).

RESEARCH OBJECTIVES

The aim of this project was to understand the structure and social dynamics of the lion population in Meru National Park (Kenya), as well as to determine the lions' diet and associated prey preferences. Lions were observed during opportunistic encounters and calling stations, and their diet was assessed using carcass counts and microscopic prey hair analysis from lion scats. Transect counts were done in Meru National Park, Bisanadi National Reserve and the community area around the village of Korbesa to document the composition of the prey populations inside and outside the protected areas.

By better understanding lion ecology in the local context of Meru National Park, in-situ conservation efforts can be more effectively supported with relevant information specifically targeting the lion population in the park.

1. **LION POPULATION SIZE AND STRUCTURE**
   1.1. What is the lion population size and density in Meru National Park?
   1.2. What is the number and composition of the lion prides in Meru National Park?
   1.3. What is the average group size?
   1.4. What is the adult:juvenile ratio?
   1.5. What is the male:female ratio?

2. **PREY POPULATION CHARACTERISTICS**
   2.1. What are the absolute and relative densities and abundances of prey species in Meru National Park, Bisanadi National Reserve and Korbesa community area?
   2.2. What is the biomass distribution of prey species in Meru National Park?
   2.3. What is the abundance of domestic prey species outside Meru National Park?
   2.4. How is the total prey biomass related to the total lion biomass in Meru National Park?

3. **LION DIET AND PREY PREFERENCE**
   3.1. What species contribute to the diet of the lions in Meru National Park?
   3.2. What are the absolute and relative contributions of the different prey species to the lions' diet?
   3.3. What are the contributions of the different prey body mass classes to the diet?
   3.4. What is the contribution of livestock to the diet?
   3.5. What are the prey preferences?
   3.6. What prey-specific traits influence prey preference and avoidance?

METHODS

Site description

The study area covered the Meru Conservation area, a 4,000 km^2 complex of protected areas in Central-Kenya (Sitienei *et al*., 2014; Bundotich *et al*., 2016) (see Figure 1, 2). The Meru Conservation area is the second largest of such complexes in Kenya and encompasses Meru National Park (MNP), Bisanadi National Reserve, Kora National Park and Mwingi National Reserve (Sitienei *et al*., 2014; Bundotich *et al*., 2016). Data during this project were collected from the 5th of February 2019 until the 20th of April 2019 in MNP, the adjacent Bisanadi National Reserve and the buffer zone around Korbesa-village (Figure 1, 2). MNP is approximately 870 km^2 in size and located in the Eastern Province of Kenya, between 0°19′N~0°5′S and 37°59′E~38°26′E. At the base of the Nyambene Hills on the north-western boundary, it reaches an elevation of 850 m above sea level, while the elevation drops to 330 m at the Tana River in the south (Sitienei *et al*., 2014; Bundotich *et al*., 2016) (See Figure 1, 2).

MNP was first established as a game reserve in 1957 by the Meru County Council and gazetted as a National Park on the 18th of December 1966 (Bundotich *et al*., 2016). During the 1970's it was a popular tourist destination, mostly made famous by George and Joy Adamson and their lioness Elsa. However, during the 1980's and 1990's, the area suffered from heavy poaching and political instability (Bundotich *et al*., 2016). The resulting decline in wildlife populations was eventually reversed in 1999, when a successful rehabilitation programme was initiated through the reintroduction of herbivore species, the enhancement of security and infrastructure and the mitigation of human-wildlife conflicts by building fences and instituting community support programs (Bundotich *et al*., 2016).

Currently, the park hosts a wide variety of different wildlife species, including rare species such as Grevy's zebra (*Equus grevyi*; Oustalet, 1882), and it maintains a population of black rhino (*Diceros bicornis*; Linnaeus, 1758) and white rhino (*Ceratotherium simum*; Burchell, 1817) in its rhino sanctuary. MNP has a semi-arid climate with irregular rainfall (Kenya Wildlife Service | Meru National Park, n.d.). Two wet seasons usually occur, the first and longest starts around April and ends in June, and the second starts in November and ends in December (Kenya Wildlife Service | Meru National Park, n.d.). Despite a highly variable but typically low mean annual rainfall of 724 mm, a total of 14 rivers flow through MNP and provide relatively stable water sources for wildlife and vegetation (Bundotich *et al.*, 2016). Vegetation and ecosystem types within MNP mainly consist of thorny *Acacia-Commiphora* bushland in the south, *Acacia* wooded grassland in the north and north-east, *Combretum* wooded grassland in the West and *Acacia* woodland, swamps and riparian forests of *Raffia* palm or *Phoenix reclinata* elsewhere (Bundotich *et al*., 2016).

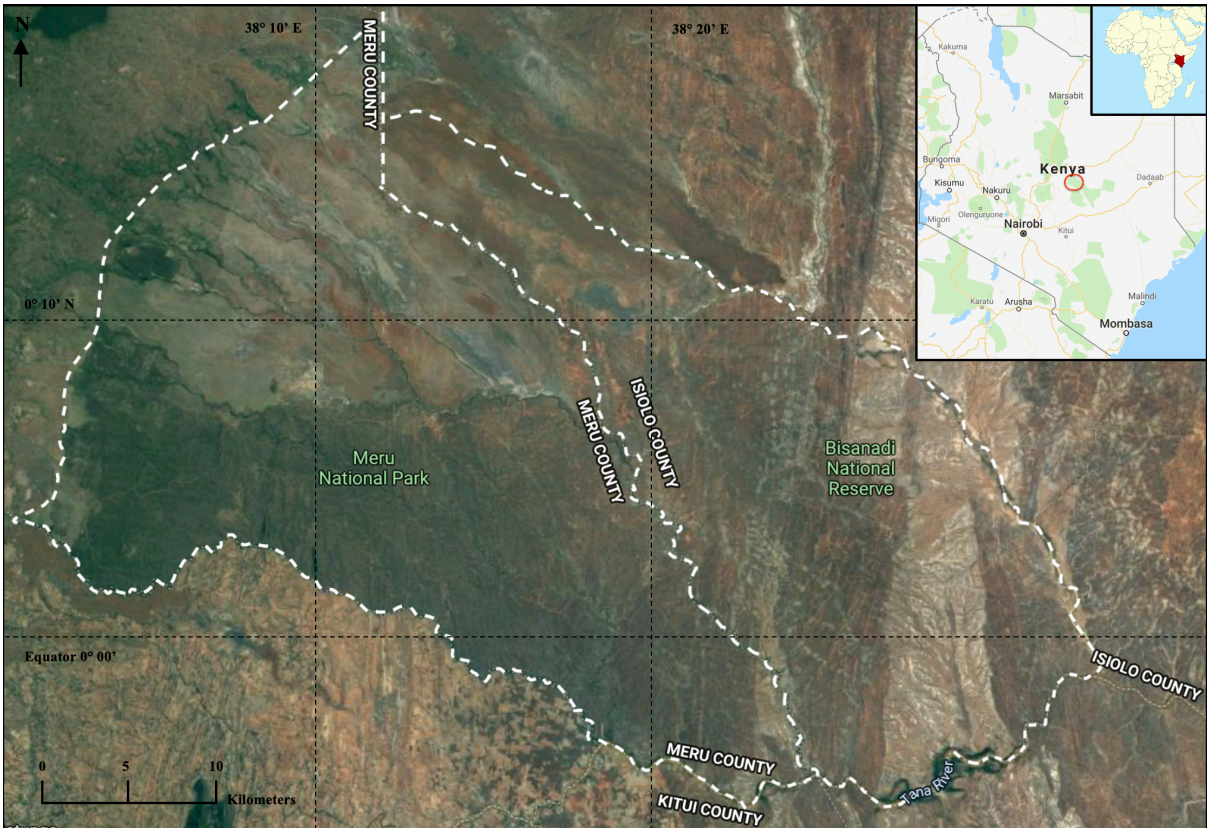


Figure 1. Location of Meru National Park and Bisanadi National Reserve in Kenya, Africa (Source: Google Maps).

The number of lions inhabiting MNP is estimated to be around 40 individuals (Riggio *et al*., 2013), although a 2016 census estimates the number to range between 36 and 79 individuals, with a mean population estimate of 59 individuals (Bundotich *et al.*, 2016). So far, Born Free Kenya has identified 33 individual lions using LINC, the Lion Identification Network of Collaborators ("LINC", n.d.).

MNP has also been the release site for several lion translocations. In fact, over the period of 2012-2018, 13 lions were translocated to MNP by Kenya Wildlife Service (KWS) (Narisha, 2018). Although the main purpose of conservation translocations is to (re)introduce or reinforce populations in the wild, conservation translocations are also often applied as a way of mitigating human-wildlife conflicts and to remove "problem animals" from areas with dense human populations (Davies & Du Toit, 2004). In general, the translocation of "problem lions" is considered a more humane and desirable method of removal than lethal control (Narisha, 2018). However, the overall effectiveness of translocations in reducing conflicts in both the removal and the release site, and their impact on the fitness of the translocated lions, remains poorly documented (Boast *et al.*, 2016). KWS claims to be aware of the potentially adverse effects of translocations but argues that there are currently no better options and that translocations are often essential to appease local communities in conflict situations (Narisha, 2018).

Lion population size and structure

Lion population size and structure were assessed using observational data from opportunistic encounters and calling station surveys (adapted according to Ogutu & Dublin, 1998; Tumenta *et al*., 2013). A total of 7 calling stations were done between late afternoon and midnight, lasting a maximum of 1 hour with 10 minutes of calling and 5 minutes of silence. Four calling stations took place inside MNP, one in Bisanadi National Reserve and two in the buffer zone around Bisanadi National Reserve. For every survey, MP3-played sounds of distress calls of an African buffalo calf and feasting hyaenas were played and amplified with speakers mounted onto the vehicle roof to attract inquisitive predators. Calling stations were done after the sun had set when predators are most active, and a dimmed spotlight was used to check and identify the responding animals. According to Bauer (2004), the maximum estimated response distance is around 2 km and calling stations were therefore always set more than 5 km from each other.

Five lions had been equipped with satellite-GPS/VHF collars (Savannah Tracking ltd) by the Born Free Foundation, and one lion was equipped with an AWT Iridium satellite collar provided by the Leo Foundation. This would have allowed active tracking using a VHF receiver given that the lions were within 5 km (Tuqa *et al*., 2014; Lesilau *et al*., 2019). VHF tracking was attempted on two occasions, but unfortunately proved ineffective. However, throughout the duration of the fieldwork in MNP, lions were also actively searched using the expertise and knowledge of local researchers and guides.
Whenever a (group of) lion(s) was encountered, a number of observational data were documented in a pre-structured form. This included the detailed logging of coordinates, habitat, group composition, presumed pride, sex and age of the lion(s), lion behaviour and their general health conditions. (Smuts *et al.*, 1978; Schaller, 1972). Lions were aged based on teeth colour and wear, facial scarring, nose darkness, mane development and jowl slackness (Miller & Funston, 2016), and subsequently classified as juveniles (< 2 years old) or adults (> 2 years old). Group size was recorded and defined as the number of adult lions observed during an encounter at a given time and place (Smuts *et al*., 1978). All lions were photographed using a Nikon D5100 so that each lion could later be identified based on nose pigmentation, ear notches, scars, whisker spots and other personal traits (Pennycuick & Rudnai, 1970).

Prey population characteristics

Transect counts

In order to determine the prey availability for lions in MNP and the park's surrounding areas, prey counts were conducted using line transects (Thomas *et al*., 2010). A total of 7 transects were selected so that a compromise was achieved in representing the majority of the park's different habitats, as well

as being able to include one line transect just outside Bisanadi Reserve to estimate wildlife and livestock presence in a nearby, unprotected area (Table 1; Figure 2). During an 8-week period throughout the dry season (February - April 2019), all transects were sampled two days a week, twice a day to avoid bias (Visser, 2011). A PF210 rangefinder was used to estimate the distance from the observer to the sighted prey species within 500 m on either side of the transect line. Transects varied from 1.80 to 3.05 km in length. Line transect no. 5, however, crossed thick bushland and visibility was therefore limited. Consequently, species on this transect were only counted within 200 m on either side of the line transect, but for a total length of approximately 6 km in order to cover a similar surface area as the other transects (Table 1). No transect counts were done in the southern part of the park due to time and logistical constraints, but the vegetation in transects no. 4, 5 and 6 was relatively representative for that of the southern part. Prey composition and densities derived from transects no. 4, 5 and 6 were therefore assumed to be comparable to those in the southern part.

The seventh transect covered the community area of Korbesa, an unprotected area just outside Bisanadi National Reserve (Figure 2). Because an additional aim of this study was to assess the presence of livestock in the diet of lions with regard to human-lion conflicts, it was important to have a comprehensive understanding of the abundance of domestic species in the buffer zone near the park boundary. Korbesa proved to be a suitable location for this purpose since the local water well attracted nomadic tribes and their livestock from kilometres away.

Table 1. Transect number, location, covered surface area (in km^2) and distance sampled on each side of the line transect (in m). Main vegetation type per transect based on field observations and a dataset made available by KWS (classified region). Region size based on vegetation dataset (in km^2).

No.	Location	Surface area (km^2)	Distance sampled (m)	Vegetation (field observation)	Vegetation (classified region)	Region size (km^2)
1	Meru National Park	1.80	500	Open *Acacia* woodland-grassland	Open woodland/grassland	243
2	Meru National Park	3.05	500	Open *Acacia* woodland-grassland / Swamp	Open woodland/grassland	243
3	Meru National Park	2.22	500	*Acacia* woodland-grassland	Open woodland/grassland	243
4	Meru National Park	2.14	500	*Acacia* woodland-shrubland	Shrubland/bushland	623
5	Meru National Park	2.22	200	*Acacia-Commiphora* bushland	Shrubland/bushland	623
6	Bisanadi National Reserve	2.43	500	*Acacia* woodland-shrubland	Shrubland/bushland	606
7	Korbesa community area	2.38	500	*Acacia* woodland-shrubland	Shrubland/bushland	2.38

Distance sampling analysis

Prey densities and abundances where calculated using the Distance-package (v0.9.8; Miller *et al*., 2019) in RStudio (v1.1.423; R Core Team, 2016). The DISTANCE-software corrects for visibility bias and allows for the calculation of animal densities using detection functions based on transect length, effort and the number and distance of the observed animals per species per encounter per transect. The maximum distance to which an animal or group of animals was allowed to be counted was set before and during data analysis. The DISTANCE-program incorporates this maximum distance, also referred to as the truncation distance, so that far away objects, which have little influence on the abundance estimate, can be discarded (Buckland *et al*., 2001; Thomas *et al*., 2010). In this study, all herbivores were counted within 500 m on either side of the road, except for transect no. 5, for which the distance was limited to 200 m due to low visibility (see Table 1). Transect effort was calculated by multiplying the length of each transect with 32, which was the total number of times each line transect was visited. Although transect no. 5 was sampled for a longer distance, the resulting higher effort is largely compensated by the lower truncation distance.

To differentiate prey composition between the various habitat types, the study site was stratified into vegetation strata or regions using ArcGIS (Thomas *et al*., 2010; ESRI, 2014) (see Figure 2). The resulting region sizes were then implemented into the DISTANCE-program. A dataset on vegetation cover for Meru National Park was provided by KWS, but these data did not fully correspond with observations in the field (see Table 1). However, because this was the only existing data on local vegetation types, the dataset was used to ultimately divide the whole park into two major vegetation regions ("Open woodland/grassland" & "Shrubland/bushland") based on the denseness of the vegetation (Figure 2). The "Open woodland/grassland"-region is approximately 243 km^2 in size and was widespread near transects no. 1-3 (Table 1). The "Shrubland/bushland"-region predominated more than 623 km^2 of the park and was mostly represented alongside line transects no. 4-7 (Table 1). The sum of these two regions is 866 km^2, which is comparable to the park's estimated total size of 870 km^2. Stratification made it possible to estimate herbivore densities for each of the two regions, specifically based on the results of the line transects relevant to the respective region. These results were then combined for a total prey density and prey abundance estimate. The abundance of each prey species was furthermore multiplied by the species' average body mass to illustrate their proportional significance to the total prey biomass of all prey species combined. Prey species' average body masses were taken from Stuart & Stuart (2009) and were multiplied by 3/4 to account for subadult animals (Hayward & Kerley, 2005) (Appendix I).

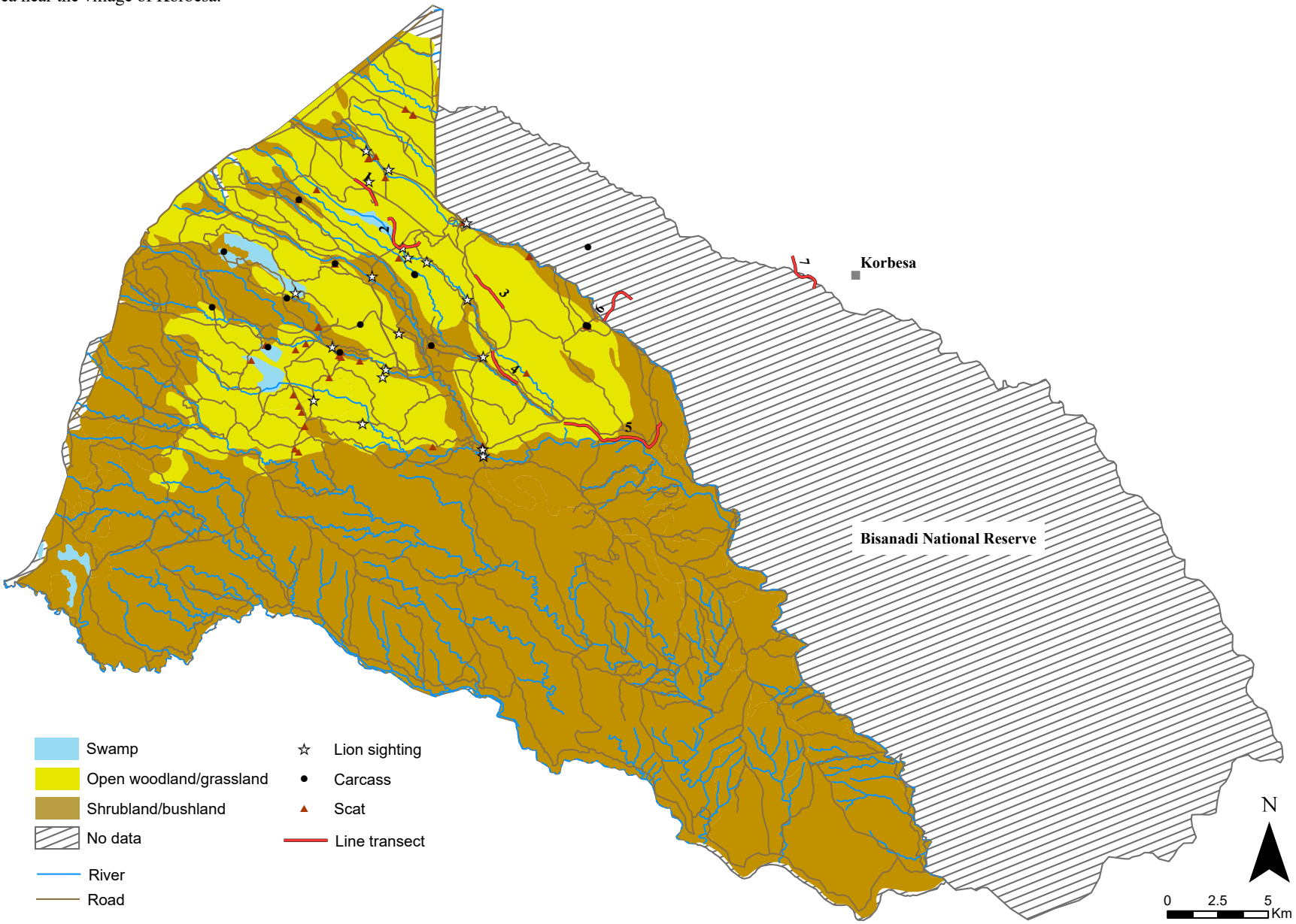
Transect counts were also done in Bisanadi National Reserve and the unprotected community area around Korbesa-village (Figure 2). The size of Bisanadi National reserve is 606 km^2 (Kenya Wildlife

Service | Bisanadi National Reserve, n.d.), but the size of Korbesa is unknown and herbivore densities were therefore only calculated for the area that was covered by the 7th line transect, which is 2.38 km^2. Because this study is focused on the diet of lions in Meru National Park, prey density results from transect no. 6 and 7 were considered irrelevant for the estimation of prey preferences. Furthermore, since pastoralists concentrated around the local water sources near Korbesa and the 7th line transect, density results for domestic species are unreliable as they would overestimate the abundance of livestock around the protected areas. Nevertheless, herbivore counts in Bisanadi National Reserve and Korbesa community area provide highly relevant data to park management because they describe both wild and domestic prey composition and distribution in the direct vicinity of the park.

Prey- and lion biomasses

The total biomasses of prey animals and lions were calculated in order to estimate the amount of prey (in kg body mass) that is theoretically available per kg lion (body mass) per km^2 in MNP. The abundance results for all prey species in MNP were summed to get the total number of prey animals that are believed to inhabit the park. Prey density results were multiplied by each species' respective average body mass (Appendix I) and added up to approximate the total prey biomass per km^2 in MNP.
Lion population size was assessed using data from opportunistic encounters and calling stations (see page 15, "Estimating lion population size and structure"). From this estimated value, lion density in MNP was calculated and multiplied by the average body mass of lions (98 kg; de Iongh *et al.,* 2004), to uncover the total lion biomass per km^2.

Figure 2. Map of Meru National Park and Bisanadi National Reserve, with representation of the two major vegetation regions in the park. Locations given for lion encounters, recorded carcasses, collected scats and line transects. Line transects no. 1-5 crossed Meru National Park, no. 6 crossed Bisanadi National Reserve, and no. 7 crossed the unprotected area near the village of Korbesa.



Lion diet

Carcass counts

Whenever a carcass of a potential prey species was encountered, the location of the carcass (GPS), species, sex, age (adult/juvenile) and condition of the carcass (fresh/old) were recorded on a pre-structured form. Carcasses were included in the dietary analysis when they were confirmed to be the result of a lion kill. A number of features were investigated that would suggest a lion kill, since the presence of lions around a carcass does not necessarily mean they are responsible for the kill. Firstly, only lions are able to take down large prey such as African buffalo, giraffe and elephant (*Loxodonta africana*; Blumenbach, 1797). Secondly, claw and bite marks on the head, neck, throat, body and limbs can further suggest the predator responsible for the kill (Bauer *et al*., 2008; Davidson *et al*., 2013). Lastly, the area was searched for clear evidence of lion presence, such as lion tracks and droppings. Carcass counts are generally biased towards relatively fresh kills, when these signs are still visible and the predator responsible for the kill can still be determined with certainty. If no evidence was found that a lion was responsible for the kill, the carcass count was omitted from counts.

Scat analysis

Over the period of February, March and April 2019, lion scats (faeces) were collected and analysed after Ramakrishnan *et al*. (1999). They were collected routinely along the road and by visiting known lion resting sites, carcasses and water points. The GPS location, habitat type and time and date of collection were recorded for every scat on a pre-structured form.

Scats were identified based on shape, size and colour to confirm they were from a lion (Stuart & Stuart, 1994). Identifications were confirmed by the accompanying research assistant. Afterwards, each confirmed lion scat was brought to MNP research quarters and air dried until fieldwork was terminated in April 2019. All scat samples were then transferred to KWS headquarters in Nairobi for further analysis.

Each scat was put into a nylon stocking and washed for 30 minutes until most of the dirt was washed off and mainly hair, bones and horn fragments remained. Bone- and horn fragments were separated and photographed, since they could later be used as supplementary material for species identification. Next, 5 intact hairs were randomly selected from every scat and their morphological features (colour, thickness, length) were recorded and photographed with a BH2 Olympus Type light microscope (Figure 3). Afterwards, a cuticle imprint of each recovered hair was made (Figure 3). Cuticle slides were prepared from 1.7 g of gelatin by soaking it in 40 ml demi-water for 5 minutes. The solution was then placed on a hot plate (65°C) until the gelatin was completely dissolved. A thin layer of the gelatin solution was then spread on a microscope slide and the 5 hairs were placed on the layer until the gelatin

was completely dry (after 10-30 minutes). When the gelatin was dry, the hairs were carefully removed with forceps so that a clear imprint of the hair scale pattern remained (Figure 3).

The imprint left by each hair was visible with a microscope under 40x magnification. Imprints were then compared to hair imprints of a species reference collection in order to assign each hair to a specific species (Ramakrishnan *et al*., 1999). Morphological features of each individual hair, such as colour and size, had to be compared to an existing hair reference collection in order to differentiate between species that have similar hair scale patterns but different hair features (Ramakrishnan *et al*., 1999) (Figure 3).

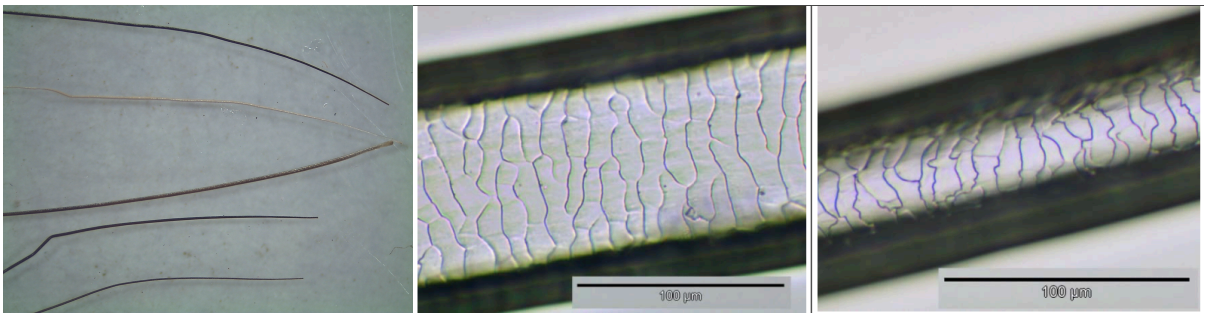


Figure 3. Recuperated hairs were photographed for morphological features and gelatin imprints were taken to visualize scale patterns. Left: 5 hairs, belonging to plains zebra (*Equus quagga*), recovered from one scat; Middle: hair scale pattern (reference) at base of impala (*Aepyceros melampus*) hair; Right: hair scale pattern (reference) along shaft of impala hair.

Prey preference

Prey preferences of lions in MNP were examined using the Jacobs' selectivity index (Jacobs, 1974). There are numerous selection indices that can be used to determine food preferences (e.g. forage ratio and Ivlev's electivity index; Ivlev, 1961), but these often suffer from biases (Jacobs, 1974). The Jacobs Index is believed to minimize most of these biases and is preferred by the majority of ecologists (Krebs, 1989; Hayward and Kerley 2005; Hayward *et al*., 2006b). A species is considered a preferred prey item when it is selected more frequently by a predator than expected based on the species' relative availability (Johnson, 1980; Hayward & Kerley, 2005). Likewise, a species is referred to as an avoided prey item when the predator selects it proportionally less than expected based on the prey's relative availability. The formula for calculating Jacobs' Index (JI) is as follows:

$$JI_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

JI_i standardizes the relationship between r_i, which is the proportional contribution of prey species i to the lions' diet, and p_i, which is the proportional availability of prey species i. The resulting value ranges from -1 to +1, where +1 indicates maximum preference and -1 indicates maximum avoidance (Jacobs, 1974). Transect counts (processed with DISTANCE-software) provided the data necessary to calculate

the relative abundance and availability of each recorded prey species, while the results from the hair analysis, combined with the results from the carcass counts, reflected the proportional contribution of each prey species to the lions' diet. Since no carcasses or scats were found in Bisanadi National Reserve or the adjacent buffer zone near Korbesa, it was not possible to assess prey preferences of lions in these areas.

As mentioned in the introduction, the prey choice of a predator mainly depends on minimizing the energetic investment and risk of injury during prey capture while maximizing the potential energy gain from a successful hunt (Hayward & Kerley, 2005). This potential energy gain is reflected by the body mass of the prey species (Hayward & Kerley, 2005). To examine a possible correlation between JI-values and prey body masses, the $\log_{10}$ value of the average body mass of each observed prey species was plotted against their respective JI-value using Microsoft Excel (v16.34; Microsoft Corporation, 2020). A polynomial trendline was then projected to visualize the average body mass range in which the highest JI-values can be found. Furthermore, each prey species was, based on its average body mass, assigned to a body mass class in order to assess if the JI-values of certain classes significantly deviated from 0 (no preference or avoidance) (Appendix I). The body mass classes included 'Very small' (< 5 kg), 'Small' (5 – 50 kg), 'Medium' (50 – 200 kg) and 'Large' (> 200 kg) prey (Appendix I).

The effects of prey-specific traits on prey preferences were analysed using multiple regression similar to Hayward & Kerley (2005). In the model, JI-values were set as response variable and prey body mass, prey herd size, prey habitat and prey threat were set as explanatory variables. Each explanatory categorical variable was quantified using specific values adopted from Hayward & Kerley (2005) (Appendix I). The average herd size of a prey species determines its ability to detect predators and was given values of 1 (solitary individuals), 2 (exist in pairs), 3 (small family groupings), 4 (small herds; 10–50) and 5 (large herds; >50) (Hayward & Kerley, 2005). Because habitat type may affect detectability and predator-prey encounter rates, the habitat preference of a prey species was also included in the model, with 1 referring to open grasslands, 2 to savannah and 3 to densely vegetated areas (Hayward & Kerley, 2005). Lastly, some species may pose greater threats to a predator due to defensive strategies, so values of 0 (no threat), 1 (minor threat or active defence of young) and 2 (severe threat; known deaths attributed to predators caused by this species) were assigned to each prey species to quantify threat level (Hayward & Kerley, 2005).

Data analysis and statistics

JI results were analysed in RStudio (v1.1.423; R Core Team, 2016) to test whether any of the four body mass classes was significantly preferred or avoided. First, the normality of the JI-values per body mass class was tested using a Shapiro-Wilk test. If a class showed a normal distribution, a one-sample *t*-test

(parametric) was performed against a mean of 0 (JI-value indicating no preference or avoidance) (Hayward & Kerley, 2005). If values did not conform to normality, a non-parametric one-sample Wilcoxon signed rank test was used against a mean of 0 (Hayward & Kerley, 2005).
Furthermore, multiple regression in RStudio (v1.1.423; R Core Team, 2016) was done to test for significant effects of prey-specific characteristics on the JI-values as response variable. Interactions between the four characteristics were tested but omitted from the model when they were not significant.

RESULTS

Lion population size and structure

Population and prides

Lions were observed on 22 different occasions (Figure 2), with 2 observations during two separate calling station surveys. Encounters took place in a variety of habitats, including savannah woodlands, savannah grasslands and riverine forests, but usually in the presence of shade and a nearby water source. Lions were most often seen resting, although territorial, feeding, mating and hunting behaviour were also occasionally observed. The majority of the sighted lions appeared to be in good condition and two females were presumably lactating, which would indicate the existence of newly born cubs. These cubs, however, were not seen during fieldwork.

Lions were identified based on their whisker spot patterns, scars and other traits. This resulted in a total count of 28 individual lions split into 6 different prides, with 1 pride presumably being a male coalition (see Table 2). The Mulika pride was the most numerous of all prides and counted 11 lions in total (4 adult females, 1 adult male, 6 juveniles) (Table 2). Elsa's pride consisted of 6 lions (1 adult male, 2 adult females, 3 juveniles) and Bisanadi pride of 4 lions (2 adult males, 2 adult females) (Table 2). A single adult lioness was sighted once and appeared to be nomadic. However, local researchers suspected her to belong to the G-Coy pride, of which only this one lioness was seen (Table 2). Similarly, local researchers assigned 2 adult lionesses, which were also observed on just one occasion, to the Sanctuary pride. (Table 2). Finally, a (suspected) coalition of 4 related, nomadic adult males, ironically called the Nairobi Girls, was seen (Table 2).

Table 2. Lion (*Panthera leo melanochaita*) prides in MNP. "Members seen" refers to the number of lions that were observed and assumed to belong to a certain pride. Lions were classified as adults (> 2 years) or juveniles (< 2 years). Number of observed males and females per pride includes both adult and juvenile lions. "Times sighted" refers to the number of times that at least one member of that pride was observed during an opportunistic encounter or calling station.

Pride	Members seen (n)	Adults (n)	Juveniles (n)	Males (n)	Females (n)	Times sighted (n)
Bisanadi	4	4	0	2	2	4
Elsa's	6	3	3	3	3	4
G-Coy	1	1	0	0	1	1
Mulika	11	5	6	3	8	7
Nairobi Girls	4	4	0	4	0	5
Sanctuary	2	2	0	0	2	1
TOTAL	28	19	9	12	16	22

Density

Combining the total number of adult and juvenile lions observed during this study (28) and the size of MNP (approx. 870 km^2), lion density in MNP was estimated around 0.032 lions per km^2, or 3.2 lions per 100 km^2. Excluding juvenile lions, the density drops to 0.022 adult lions per km^2, or 2.2 adult lions/100 km^2.

Group size

Lions were most frequently observed in groups of 4 and 11 lions (incl. juveniles) (23%) (Figure 4). Solitary lions were observed on three occasions (14%) (Figure 4). Groups of 7, 8, 10 or more than 11 lions were never sighted (Figure 4). Lion group sizes, however, are typically expressed as the number of adult (> 2 years old) lions observed at a given time and place, thus excluding juvenile lions. Accordingly, lion group size in MNP varied between 1 and 5 lions, with groups of 4 and 5 lions being the most frequently observed (24%) (Figure 4). The weighted average adult lion group size was 3.24 ± 0.31 individuals.

Age and sex ratio

About 69% of the observed lions were adults (> 2 years old), while 31% were juveniles (< 2 years old) (Table 2). All juveniles were presumably under the age of 1. The overall ratio of adults to juveniles was 19:9, or 2.1:1 (Table 2). The overall ratio between males and females was 1:1.33 including juvenile lions, or 1:1.38 excluding juvenile lions (Table 2).

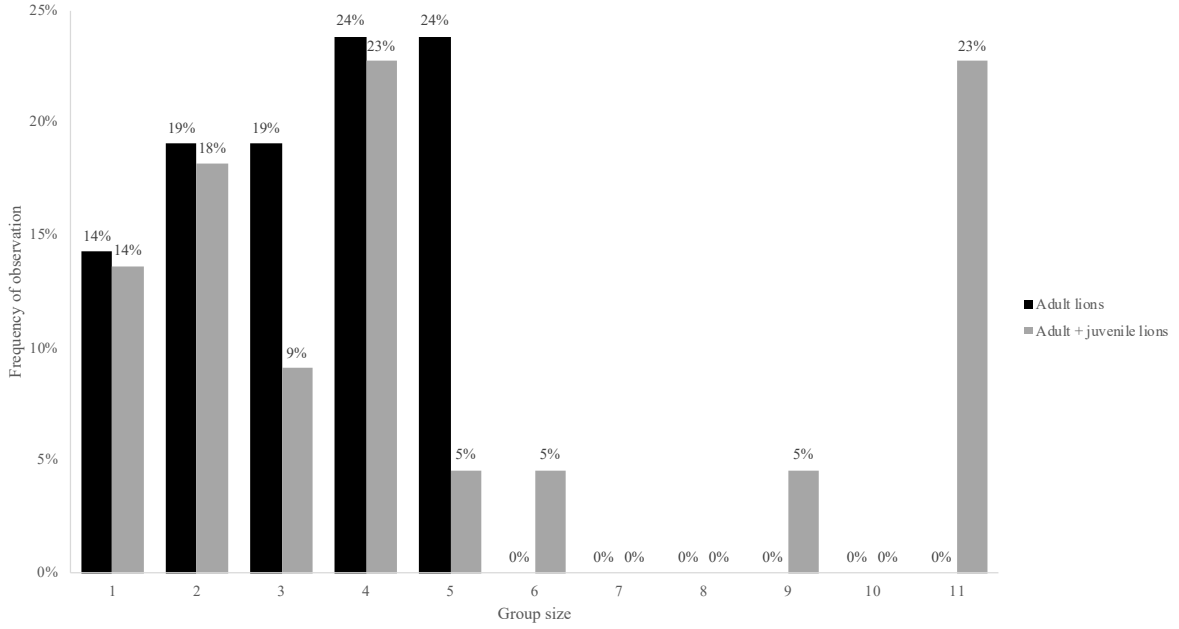


Figure 4. Frequency of observed lion (*Panthera leo melanochaita*) group sizes in Meru National Park as a % of the total number of observations (n=22). Black bars: group size excluding juvenile (< 2 years) lions; grey bars: group size including juvenile lions.

Prey population characteristics

Throughout the 8 weeks of transect counts, a total of 28 wild (herbivore) species were counted as potential prey species for lions, and 4 domestic species were counted outside the protected area (see Table 3, 4; Figure 5). However, some of the wild prey species that were counted had to be omitted from further analyses because there was no information available that would allow the identification of their hairs or feathers if these were recovered from lion scats. This was true for 9 species, most of which were large birds and very small mammals such as the unstriped ground squirrel (*Xerus rutilus*) and dwarf mongoose (*Helogale parvula*). Densities and abundances were calculated for the remaining 19 wild species and 4 domestic species. Results are presented in Table 3 (results for MNP) and Table 4 (results for Bisanadi National Reserve and Korbesa).

Meru National Park

With 244 observations during transect counts, Grant's gazelle was the most commonly observed prey species in MNP, closely followed by Kirk's dik-dik, which was counted on 239 occasions (Table 3). However, because of the higher availability of suitable habitat in MNP for Kirk's dik-dik, this species was projected to be the most abundant prey species when extrapolated to the entire park. Kirk's dik-dik had an estimated density of more than 26 individuals per km^2 and represented more than 50% of

the total number of prey animals in MNP (Table 3; Figure 5). Plains zebra, African buffalo, impala and waterbuck also occurred in relatively high numbers. The lowest density estimate belonged to Grevy's zebra, for which only 17 individuals were estimated to live inside the park (Table 3). Each prey species' abundance estimate was furthermore multiplied by the species' average body mass (Appendix I). African buffalo seemed to account for about 34% of the total prey biomass in MNP, the highest of all prey species (Figure 5). Plains zebra, waterbuck, giraffe and elephant also contributed proportionally more to the total prey biomass compared to their relative abundance results (Figure 5). Contrarily, Kirk's dik-dik was only responsible for about 2% of the total prey biomass, despite the species' high relative abundance (Figure 5).

Bisanadi National Reserve & Korbesa community area

Under the assumption that the vegetation type of Bisanadi National Reserve is reasonably uniform, results from line transect no. 6 were extrapolated to the whole reserve. Kirk's dik-dik was projected to predominate the landscape with an estimated density of about 114 individuals/km^2 (Table 4). Other species, such as lesser kudu, waterbuck and giraffe, were also occasionally observed, albeit considerably less than Kirk's dik-dik (Table 4).

Domestic species were only encountered on transect line no. 7, which covered an unprotected area outside Bisanadi National Reserve, near Korbesa-village (see Figure 2). Shoats, which is the collective name for sheep and goats, occurred in a very high density of about 805 individuals per km^2 (Table 4). Wild prey species were rarely observed, although olive baboon, Kirk's dik-dik, warthog, lesser kudu and gerenuk were occasionally sighted (Table 4).

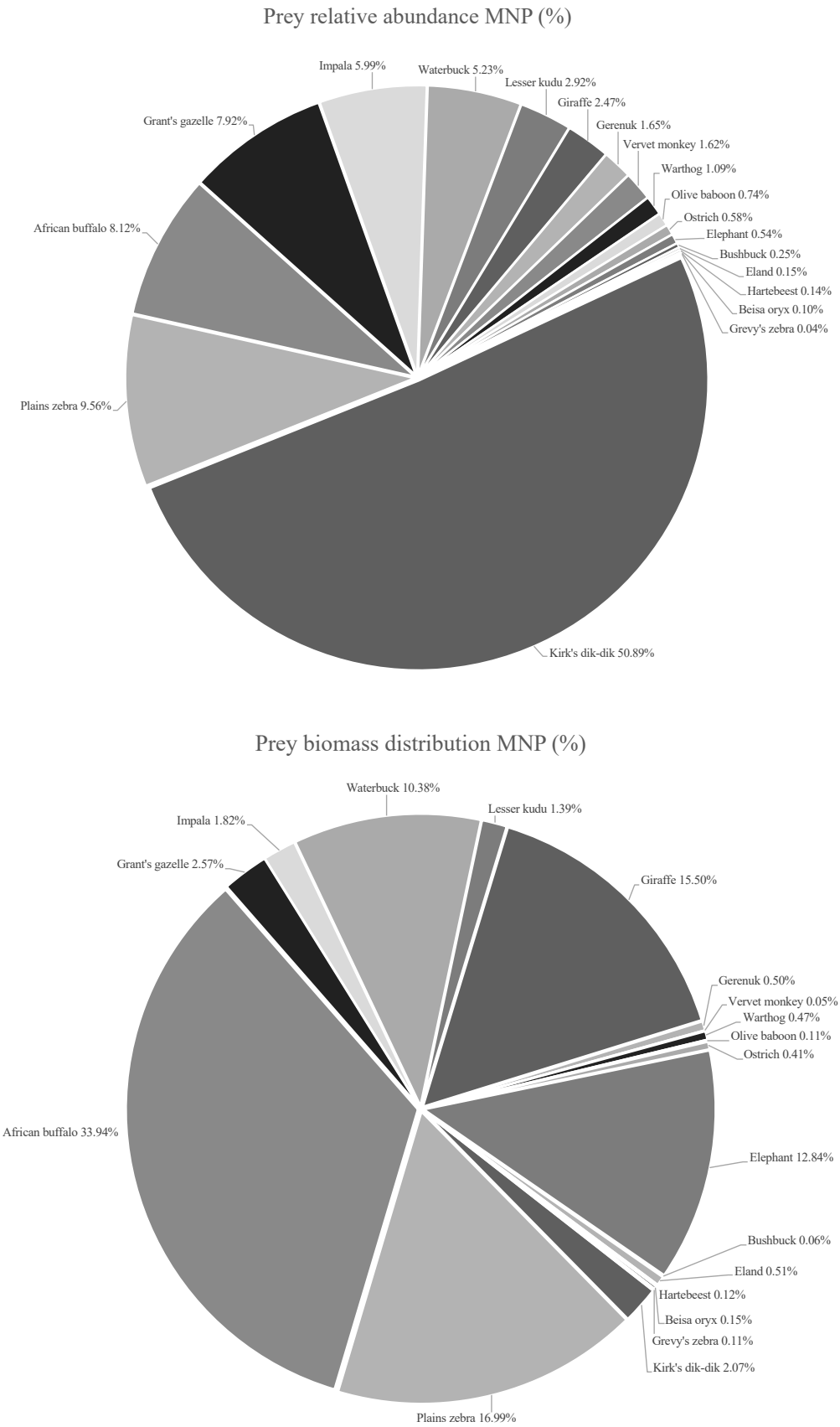


Figure 5. Relative prey species abundances (above) and relative prey species biomasses (below) in MNP, as a % of the total prey abundance and prey biomass, respectively. Results based on transect counts no. 1-5 and mean prey body masses (see Appendix I).

Table 3. Results of transect counts and scat analysis in Meru National Park. "Times observed" refers to the number of times a prey species was observed and counted during line transects no. 1-5. "Density" (individuals per km^2 ± standard error (SE)), "abundance" (± SE) and "relative abundance" (%) per prey species are based on prey counts from line transects no. 1-5. "Prey" refers to the relative contribution of each prey species to the lions' diet based on each species' number of occurrences in scats and carcasses combined. Prey species' relative abundance and relative contribution to the lions' diet ("Prey") were used to calculate Jacobs' Index.

Species	Times observed	Density (ind/km^2) ± SE	Abundance ± SE	Relative abundance (%)	Contribution to diet (n)		Prey (%)	Jacobs' Index
					Carcass	Scat		
African buffalo (*Syncerus caffer*)	113	4.17 ± 2.93	3616 ± 2542	8.12	10	88	32.34	0.69
Beisa oryx (*Beisa oryx*)	14	0.05 ± 0.01	42 ± 8	0.10	0	0	0.00	-1.00
Bushbuck *(Tragelaphus scriptus)*	1	0.13 ± 0.09	115 ± 58	0.25	0	5	1.65	0.74
Eland *(Tragelaphus oryx)*	5	0.08 ± 0.05	66 ± 29	0.15	1	0	0.33	0.38
Elephant *(Loxodonta africana)*	8	0.28 ± 0.20	238 ± 157	0.54	0	0	0.00	-1.00
Gerenuk (*Litocranius walleri*)	25	0.85 ± 0.37	739 ± 323	1.65	0	4	1.32	-0.11
Giraffe (*Giraffa camelopardalis*)	100	1.27 ± 0.36	1101 ± 314	2.47	2	6	2.64	0.04
Grant's gazelle (*Gazella granti*)	244	4.07 ± 1.18	3525 ± 1024	7.92	0	19	6.27	-0.12
Grevy's zebra *(Equus grevyi)*	5	0.02 ± 0.01	17 ± 10	0.04	0	1	0.33	0.79
Hartebeest *(Alcelaphus buselaphus)*	9	0.07 ± 0.05	59 ± 20	0.14	0	3	0.99	0.76
Impala (*Aepyceros melampus*)	39	3.08 ± 0.66	2668 ± 569	5.99	0	18	5.94	0.00
Kirk's dik-dik (*Madoqua kirkii*)	239	26.15 ± 13.27	22672 ± 11509	50.89	0	2	0.66	-0.99
Lesser kudu (*Tragelaphus imberbis*)	49	1.50 ± 0.66	1294 ± 575	2.92	0	11	3.63	0.11
Olive baboon *(Papio anubis)*	5	0.38 ± 0.36	329 ± 190	0.74	0	12	3.96	0.69
Ostrich (*Struthio camelus*)	33	0.30 ± 0.16	260 ± 139	0.58	0	0	0.00	-1.00
Plains zebra (*Equus quagga*)	194	4.91 ± 1.67	4261 ± 1446	9.56	1	74	24.75	0.52
Vervet monkey *(Cercopithecus aethiops)*	1	0.83 ± 1.31	718 ± 1076	1.62	0	6	1.98	0.11
Warthog (*Phacochoerus africanus*)	39	0.56 ± 0.33	484 ± 289	1.09	0	3	0.99	-0.05
Waterbuck (*Kobus ellipsiprymnus*)	135	2.69 ± 1.69	2336 ± 1464	5.23	1	35	11.88	0.42

Table 4. Prey density results (individuals per km^2 ± standard error (SE)) for Bisanadi National Reserve and Korbesa community area. Results based on prey counts from line transects no. 6 and 7, respectively. Times observed refers to the number of times a prey species was observed and counted during line transects no. 6 and 7 combined.

Species	Times observed	Density (ind/km^2) ± SE	
		Bisanadi National Reserve	Korbesa community area
African buffalo (*Syncerus caffer*)	1	0.29 ± 0.15	0
Gerenuk (*Litocranius walleri*)	8	1.51 ± 0.89	0.10 ± 0.22
Giraffe (*Giraffa camelopardalis*)	11	0.71 ± 0.35	0
Impala (*Aepyceros melampus*)	6	1.50 ± 0.87	0
Kirk's dik-dik (*Madoqua kirkii*)	239	114.04 ± 8.00	5.69 ± 1.68
Lesser kudu (*Tragelaphus imberbis*)	16	3.21 ± 1.03	0.23 ± 0.31
Olive baboon (*Papio anubis*)	6	5.94 ± 2.73	6.44 ± 4.54
Plains zebra (*Equus quagga*)	4	1.11 ± 0.30	0
Warthog (*Phacochoerus africanus*)	8	0	4.34 ± 1.59
Waterbuck (*Kobus ellipsiprymnus*)	13	4.25 ± 1.60	0
Camel (*Camelus dromedarius*)	53	0	244.90 ± 50.52
Cow (*Bos taurus*)	32	0	52.42 ± 13.32
Donkey (*Equus asinus*)	55	0	177.69 ± 32.41
Shoat (*Ovis aries/Capra aegagrus hircus*)	51	0	805.26 ± 131.16

Prey- and lion biomasses

After extrapolating the results of transect counts no. 1-5 to the whole park, a total of 44542 individual prey animals are estimated to inhabit MNP (Table 5). Approximately 5075 kg prey per km^2 is projected to be available in MNP (Table 5). The total lion density in MNP (including juvenile lions) was estimated around 0.032 lions per km^2, or 3.2 lions per 100 km^2 (see "Density", page 24). This comes down to about 3.15 kg of lion biomass per km^2 in MNP when averaging the body mass of a lion around 98 kg (Table 5). Altogether combined, there is a theoretical amount of 1609 kg prey available per 1 kg lion per km^2 in MNP (Table 5).

Table 5. The amount of prey (in kg body mass) that is theoretically available for every kg of lion per km^2 in Meru National Park. Total number of prey animals based on prey density calculations from transect counts no. 1-5. Total number of lions based on lion observations in MNP.

Total number of prey animals	Total number of lions	Total prey biomass (kg) per km^2	Total lion biomass (kg) per km^2	Kg prey per 1 kg lion per km^2
44542	28	5075	3.15	1609

Lion diet

Carcass counts

A total of 15 carcasses were encountered and confirmed to be the result of a lion kill. The majority of these were African buffalo (10), but also included giraffe (2), eland (1), waterbuck (1) and plains zebra (1) (Table 2). Eight carcasses were considered fresh, while the other 7 were mainly scattered bones that had persisted in the environment for a long time. Nonetheless, these were still identifiable using the experience and knowledge of the accompanying research assistants. Carcass locations ranged from bushlands and grasslands to riverine forests and swamps.

Scat analysis

In total, 71 scats were collected (see Figure 2) that were identified as lion scat. From these scats, 306 hairs were recovered that yielded imprints of a quality good enough to allow species identification. Microscopic hair analysis revealed that 16 hairs were from lions (presumably ingested after grooming), 2 from donkey, 1 from sheep and 287 from 19 different wild prey species (Figure 6). No bone or skull fragments were found that would indicate the consumption of very small prey species. Overall, African buffalo and plains zebra were the most important contributors to the lions' diet (Figure 6). African buffalos were responsible for 88 out of the 287 wild prey species' hairs, while 74 hairs belonged to plains zebra (Table 2; Figure 6). Combined with carcass count data, African buffalo and plains zebra accounted for about 32% and 25% as prey items in the lions' total diet, respectively (Table 3).

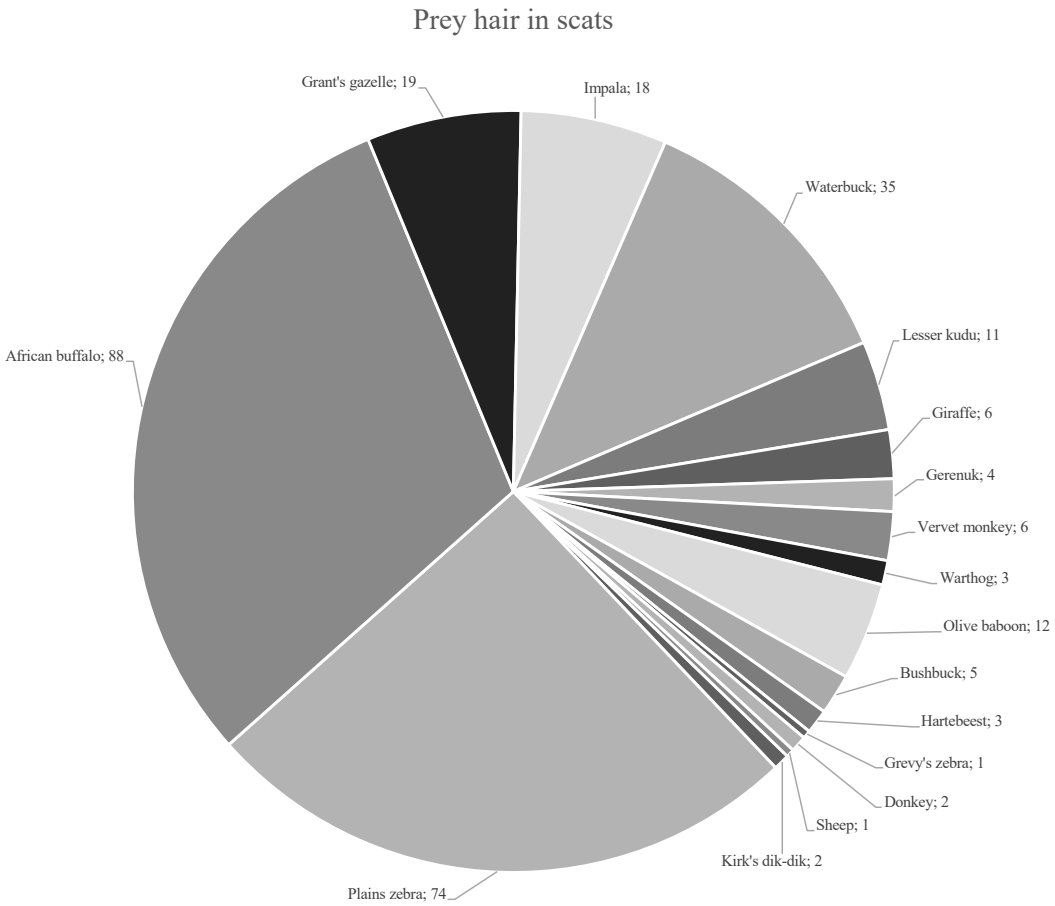


Figure 6. Number of hairs recovered from lion scats per prey species. In total, 71 scats were collected, which yielded 290 identifiable imprints of prey hair.

Prey preference

Jacobs' Index (JI) values were calculated for all 19 wild prey species that were observed during transect counts in MNP and for which reference material was available during scat analysis (Table 3). Lions preferred 11 prey species (JI >0) and avoided 8 (JI<0). The most preferred species were Grevy's zebra, hartebeest, bushbuck, olive baboon and African buffalo, while Kirk's dik-dik, elephant, ostrich, and beisa oryx were nearly completely or completely avoided (Table 3; Figure 7). Giraffe, impala and warthog showed values relatively close to 0 (Table 3; Figure 7), which indicates a situation where lions did not show an outspoken preference or avoidance towards these species.

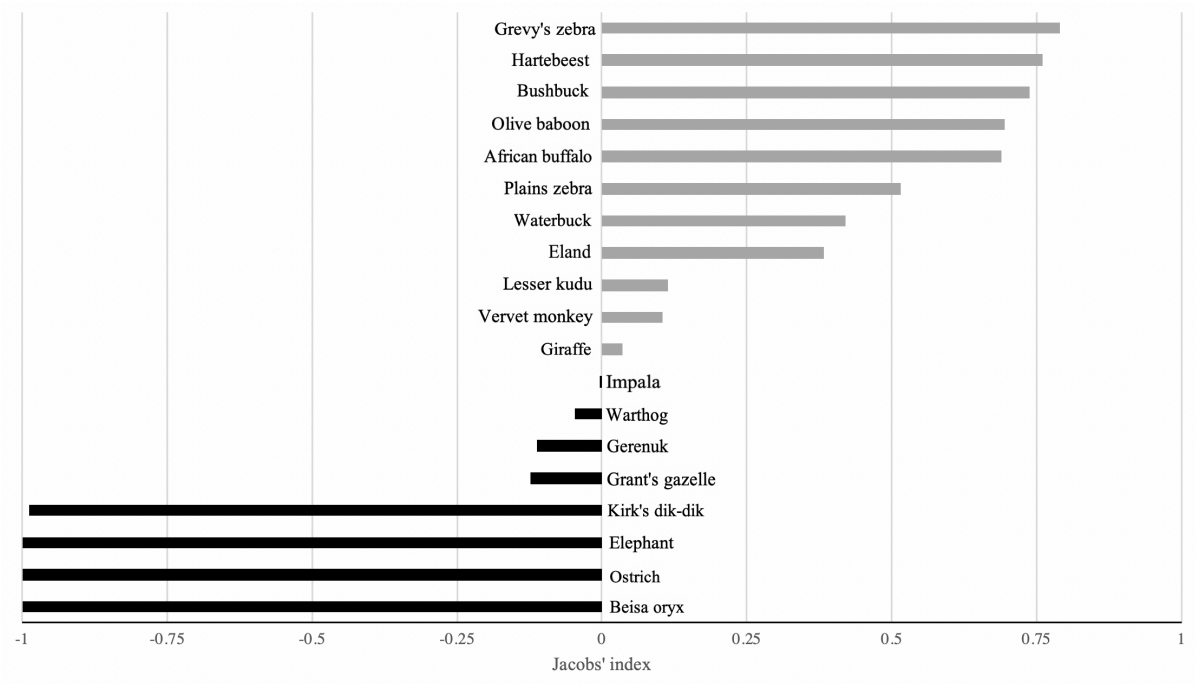


Figure 7. Jacobs' Index values for all 19 potential prey species. Grey bars represent species with a value > 0 and which are thus considered preferred prey; black bars represent species with a value < 0 and which are considered avoided prey.

Knowing the JI-value and average body mass of each prey species (Table 3; Appendix I), the relationship between the two variables was plotted and further visualized using a polynomial trendline. This showed that the JI-values were, on average, highest when prey body mass was around 100 kg (Figure 8).

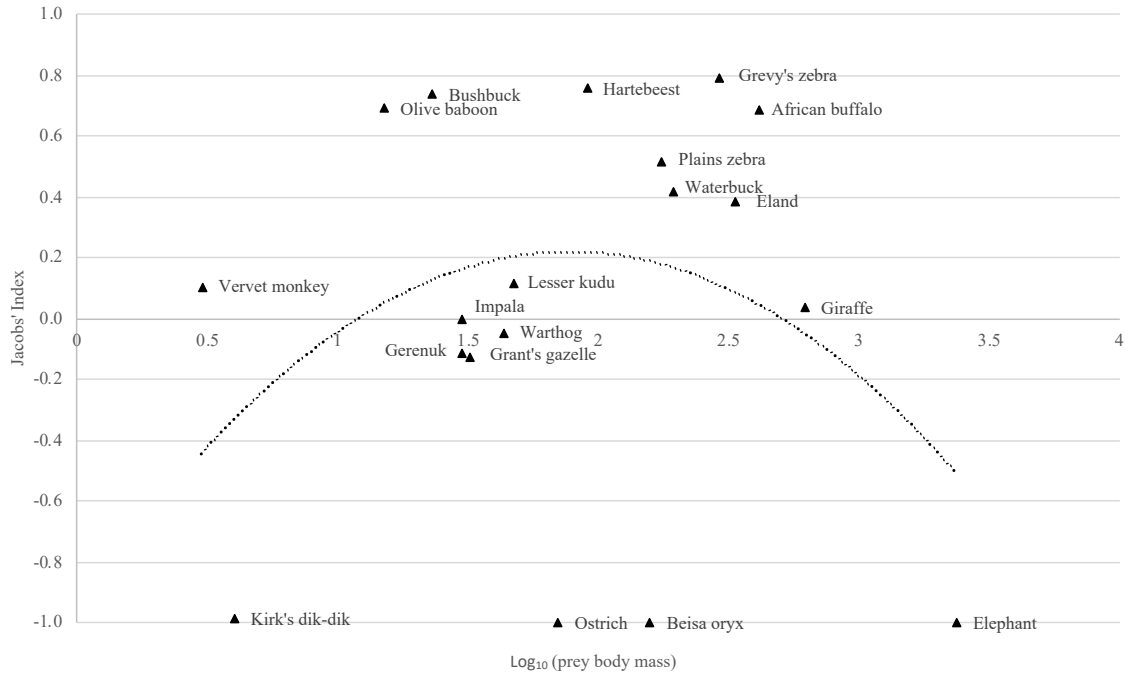


Figure 8. Relationship between lion (*Panthera leo melanochaita*) prey preference (quantified by Jacobs' Index) and the $\log_{10}$ of prey body mass. Each triangle represents a species for which the prey body mass and Jacobs' Index value is known.

Only two species of potential prey observed in MNP had an average body mass of less than 5 kg, and these were grouped in the 'Very small' body mass class (Appendix I). Most recorded prey species (7) had a body mass between 5 kg and 50 kg and these were assigned to the 'Small' body mass class (Appendix I). Another 5 species weighed between 50 kg and 200 kg and were assigned to the 'Medium' body mass class. The remaining 5 prey species had a body mass of over 200 kg and were assigned to the 'Large' body mass class (Appendix I). Figure 9 shows the distribution and the means of the JI values per prey body mass class. Since the 'Very small' body mass class was represented by only two JI-values, it was not possible to test for normality or significant deviation from 0. Shapiro-Wilk tests were done for the other three classes and only the 'Small' body mass class did not follow a normal distribution ('Small': W= 0.76, *p*-value= 0.02; 'Medium': W= 0.79, *p*-value= 0.06; 'Large': W= 0.87, *p*-value= 0.27). Next, a one-sample Wilcoxon signed rank test was done for the 'Small' body mass class, while one-sample *t*-tests were done for the other two classes. None of the classes appeared to significantly deviate from 0 ('Small': V= 17, *p*-value= 0.69; 'Medium': t= -0.16, *p*-value= 0.88; 'Large': t= 0.56, *p*-value= 0.61). Thus, none of the body mass classes are considerably preferred or avoided by lions. Multiple regression analysis, with JI-values as response variable and prey body mass, prey herd size, prey habitat and prey threat as explanatory variables, did not yield any significant results. This means that there are no prey characteristics that have any significant influence on the outcome of JI and consequently the prey preferences of lions.

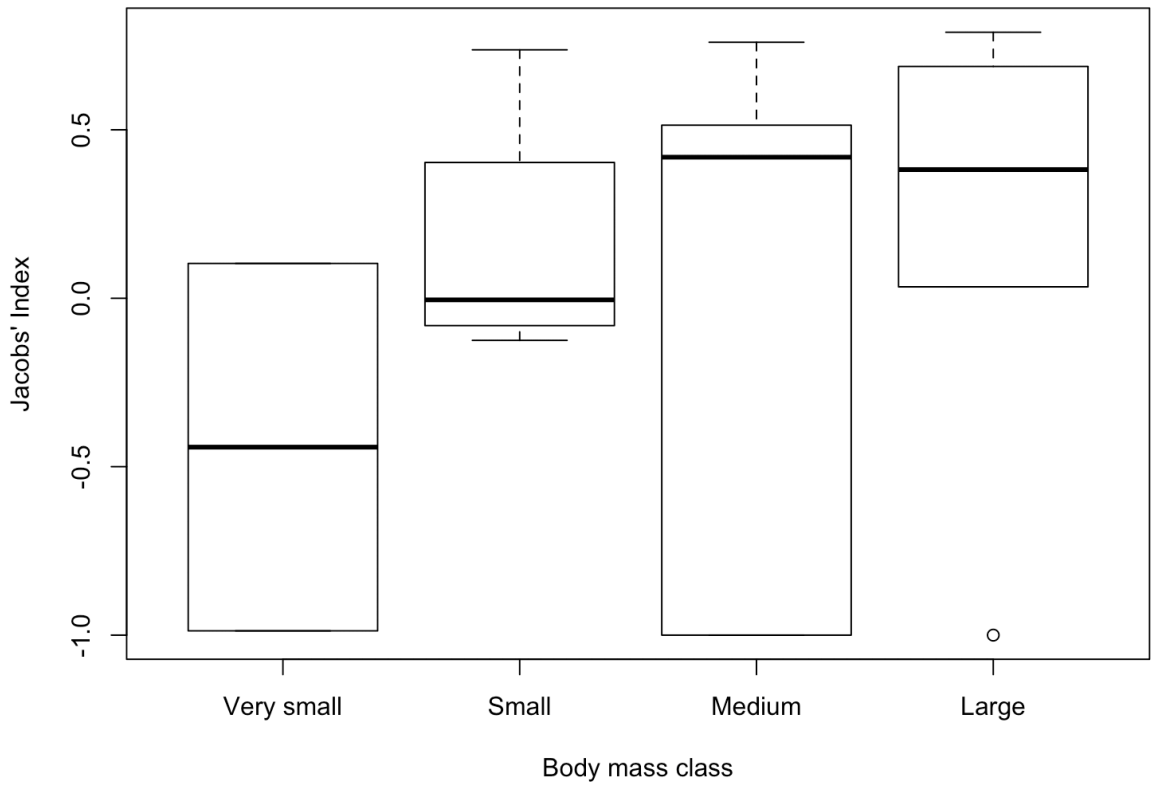


Figure 9. Boxplot representation of Jacobs' Index values per prey body mass class. 'Very small': < 5 kg; 'Small': 5-50 kg; 'Medium': 50-200 kg; 'Large': > 200 kg.

DISCUSSION

Overall, the results of this study support the research hypothesis that MNP is a healthy ecosystem with large lion prides, large lion group sizes and a high contribution of large prey species to the lions' diet.

Lion population size and structure

Population and prides

In total, 28 different lions were identified in MNP during this study. However, this approximation is likely to only reflect the lion population in the open woodland/grassland part of the park. MNP is to a large extent covered by densely vegetated bushland, making encounters with lions in these parts especially rare due to the low visibility and lack of roads that span the area. For similar reasons, searching effort was mostly restricted to the northern part of the park, where it was easier and more common to detect lions in the relatively open landscapes.

Compared to a recent large carnivore census, which estimated 59 lions to inhabit MNP (Bundotich *et al*., 2016), it is clear that not all lions of MNP were observed during this study. The Born Free Foundation also actively monitors lions in the park and has identified 30 adult lions so far ("LINC", n.d.). Of these 30 lions, 15 were also observed during this study and 7 were not. Identification of the remaining 8 lions was unfortunately not possible due to the limited number and quality of photos.

Based on personal observations and the knowledge of park researchers, the identified lions were divided into 5 different prides and 1 nomadic male coalition. However, the social group organization of lions can be very dynamic, and pride members are often widely scattered due to the fission-fusion pattern of lion prides (Schaller, 1972). The classifications made during this study should therefore be interpreted with caution.

The Mulika pride was the largest and most cohesive pride. Every member was usually present during an observation of the pride, although one adult male and one adult female were sighted twice away from the rest of the pride. It was believed that they had temporarily left the pride to mate. However, based on the information made available by the Born Free Foundation on the LINC-database, it appears that these two lions were in fact siblings, which raises serious concerns regarding inbreeding.

The nomadic lions nicknamed "Nairobi Girls" (a coalition of 4 adult males) were also consistently seen together, supporting their classification as a nomadic coalition. Members of the Bisanadi pride also seemed to interact frequently and their classification as a pride is also likely to be correct. In fact, one of the females was supposedly lactating, and mating behaviour between an adult male and lioness from the Bisanadi pride was confirmed during one of the observations. Pride structure was less pronounced in Elsa's pride, since only one out of four sightings recorded all six members.

The classification of the remaining lion groups as a 'pride' depends less on personal observations during this study as it does on the knowledge of Born Free and KWS staff. The lionesses that were believed to belong to the Sanctuary pride were only observed once, but park staff were confident that they belonged to a pride residing in the park's rhino sanctuary. Other lions belonging to the Sanctuary pride were not observed during this study. A similar situation was true for G-Coy pride, for which only one member was observed on one occasion.

Density

Adult lion density in MNP (2.2 lions/100 km^2) was well below the average of 16.2 lions/100 km^2 in East Africa (Woodroffe & Ginsberg, 1998) and was especially low compared to other parks such as Nairobi National Park (Kenya) (25.2 adult lions/100 km^2; Lesilau *et al.*, 2019) and Masai Mara National Park (Kenya) (37 adult lions/100 km^2; Ogutu *et al.*, 2005). In fact, it was more similar to the average lion density of West Africa (1-3 lions/100 km^2; Bauer & van Der Merwe, 2004) and comparable to situation in Pendjari National Park (Benin) (2 lions/100 km^2; Sogbohossou *et al.*, 2011).
As stated before, the number of observed lions during this study does not represent the total lion population of MNP and thus underestimates the expected lion density. The number lions that were observed in the sampled, open savannah area could also not be extrapolated to the entire surface area of MNP because it is not known if lion density and distribution in the open savannah region are equivalent to those found in the densely vegetated areas.

Group sizes

Excluding juvenile lions, the mean lion group size in MNP was 3.24. This is relatively high compared to other areas in Africa. In Nairobi National Park, adult lion group size is estimated around 1.23 lions (Lesilau *et al.*, 2019), in Serengeti National Park (Tanzania) 2.8 lions (Schaller, 1972), in Waza National Park (Cameroon) 1.6 lions (De Iongh *et al.*, 2009) and in Pendjari National Park around 2.7 lions (Sogbohossou *et al.*, 2011). In Amboseli National Park (Kenya) and Kruger National Park (South-Africa), average group sizes are slightly larger, at about 3.7 and 4 individuals, respectively (Funston, 2003; Tuqa *et al.*, 2014). Generally, larger group sizes indicate healthier lion populations which are less exposed to disturbance, experience higher prey availability and have the possibility to hunt cooperatively and predate on larger prey (Van Orsdol, 1985; Bauer *et al.*, 2003; Bauer *et al.*, 2008). The results of this study thus confirm the hypothesized healthy conditions of the Meru ecosystem.

Age and sex ratio

Since aging and age classifications are often subjective, it is not possible to reliably compare age ratio results with other studies. However, the relatively high number of juvenile lions that were seen in the

park, combined with others that were expected to occur in the park based on personal communication with park staff, indicates that MNP is a reasonably healthy environment with a developing lion population.

The sex ratio of adult males to females (1:1.38) was comparable to the ratio found in Nairobi National Park (1:1.56; Lesilau *et al.*, 2019) and Amboseli National Park (1:1.6; Tuqa *et al*., 2014). It has been suggested that the number of females to males increases in small, isolated reserves when young adult males are forced to leave their natal territory and when the immigration of new males is rare (Van Orsdol, 1985). Since MNP has a relatively low lion density, it is expected that males are not required to leave their natal home range and that immigration of new lions is possible.

Prey population characteristics

Abundances and densities of wild prey

With a proportional abundance of 50.89% and a density of around 26 individuals/km^2, Kirk's dik-dik was projected to be the most abundant potential prey species in MNP. Kirk's dik-diks were observed 239 times in MNP, and another 239 times in Bisanadi National Reserve and Korbesa. According to Ogutu *et al*. (2006), precision in abundance estimates increases with increasing sample size, and the results for Kirk's dik-dik can thus be considered relatively reliable.

Kirk's dik-diks are known to inhabit a variety of mainly arid habitats (IUCN SSC Antelope Specialist Group, 2016) and the species is expected to thrive in the dense thorn scrub and bushland that predominate the majority of the park's surface area. Brotherton (2013) found a similar density of 24 individuals/km^2 in Serengeti National Park, but he observed a much higher density of 109 individuals/km^2 in Tsavo East (Kenya) (IUCN SSC Antelope Specialist Group, 2016). The density of Kirk's dik-dik in Tsavo East is comparable to the 114 individuals/km^2 that resulted from the transect counts in Bisanadi National Reserve. Unlike MNP, Bisanadi National Reserve is thought to be entirely covered by the densely vegetated, arid habitat preferred by the species. Kirk's dik-dik are well adapted to such arid regions and require relatively little water to survive (Hoppe, 1977). The expected habitat uniformity in Bisanadi National Reserve might also explain the lower prey species richness in the reserve compared to MNP, which is more diverse in habitat types.

Despite the relatively high abundance of Kirk's dik-dik that was found in MNP, the species' proportional contribution to the total prey biomass in MNP is, at just 2.07%, almost negligible. The African buffalo, on the other hand, accounts for around 34% of all prey biomass in the park, the highest percentage of all prey species (Figure 5). At a density of approximately 4.17 ± 2.93 individuals/km^2, African buffaloes were the third most abundant prey species for lions in MNP, with around 3616 ± 2542 individuals estimated to roam the park. African buffaloes are notoriously difficult prey to hunt and are

known to form large herds as a response to increased predation pressure (Mitchell *et al*., 1965; Tambling *et al*., 2012). A study on the effect of lion reintroduction on African buffalo group dynamics by Tambling *et al*. (2012) showed that African buffalo populations were characterized by smaller herds (< 20 individuals) in the absence of lions, while larger herds were formed after lions were reintroduced. After all, larger herds are more efficient in predator detection and the protection of calves and juveniles (Mitchell *et al*., 1965).

The majority of the sightings of African buffalo in this study (95%) included group sizes of no more than 6 individuals. This could indicate that the population of African buffalo in MNP was, in general, relatively unaffected by lion predation pressure as assumed by Tambling *et al*. (2012). It is, however, important to note that older African buffalo males also often roam around singly or in small bachelor groups after they have been ejected from a larger herd (Hosking & Withers, 2006; Briggs & Van Zandbergen, 2016). Unfortunately, transect counts did not include the registration of sex and age of the observed prey animals and it is therefore not possible to assess whether the aggregation of African buffaloes in small groups mostly involved old bulls.

The number of African buffaloes estimated in this study is comparable to the number of African buffaloes counted during a large herbivore census in MNP (2711) (Ngene *et al*., 2017). However, there remains a relatively high degree of uncertainty to the African buffalo abundance estimated in this study. The high standard error (SE) that is associated with the estimate is most likely due to extrapolation errors and the large variation in observed group sizes. As mentioned earlier, African buffaloes were most frequently observed in small groups of 6 or less individuals, but large herds of about 470 animals were recorded on two separate occasions. This discrepancy in observed group sizes most likely affected the species' abundance and density estimate in MNP. Additionally, the extrapolation of these estimates to the entire park may have further amplified these uncertainties. Similar reasons, combined with a lack of data, can explain the high SE values associated with the density and abundance results of other prey species.

Presence of livestock

Livestock were never observed in MNP or Bisanadi National Reserve during the transect counts of this study, but on some occasions shoats and cattle were seen grazing in Bisanadi National Reserve during other fieldwork activities. Nevertheless, livestock were abundantly present alongside line transect no. 7, which covered an unprotected area just outside the reserve near Korbesa-village (Figure 2). Nomadic tribes, mostly Borana and Somali, would assemble near the village to collect water from the well and let their livestock drink from a small river that flowed just at the border with Bisanadi National Reserve. Because of the attraction of the water well, livestock were assumed to congregate in larger concentrations than what would be representative for the entire region bordering the protected areas. Other studies have observed large aggregations of camels, cows, donkeys and shoats (sheep and goats)

not only in the surrounding areas of MNP and Bisanadi National Reserve, but also inside Bisanadi National Reserve and occasionally inside MNP (Bundotich *et al*., 2016; Ngene *et al*., 2017). Ngene *et al*. (2017) noticed a steep reduction in the overall number of livestock in the Meru Ecosystem since 2014, but they observed a significantly higher concentration of shoats in the protected areas adjacent to MNP (Ngene *et al*., 2017).

The encroachment of husbandry and pastoralism around MNP drastically increases the risk of livestock depredation by large carnivores and might escalate tensions between local people and wildlife (Patterson *et al*., 2004; Van Bommel *et al*., 2007; Tumenta *et al*., 2013). The ensuing intensification of human-carnivore conflicts is often accompanied by the persecution and retaliatory killings of carnivores by local pastoralists that suffered livestock depredation (Ogada *et al*., 2003). Lions in particular are known to incorporate both wild and domestic prey species in their diet when livestock husbandry occurs in close proximity to their home ranges (Hayward & Kerley, 2005; Tuqa *et al*., 2015). Moreover, Lesilau *et al*. (2019) saw that lions would raid livestock irrespective of wild prey availability once it proved to be an efficient hunting strategy.

Prey biomass

It was estimated that approximately 5075 kg of prey biomass was available per km^2 in MNP. Combined with an estimated lion population size of 28 individuals, this came down to a theoretical amount of 1609 kg of prey that is available per 1 kg lion per km^2. However, MNP is also home to an estimated 98 spotted hyenas and a smaller number of other predators (Bundotich *et al*., 2016). Taking into account the abundances and biomasses of spotted hyena and 5 other predators (Bundotich *et al*., 2016), the amount of prey biomass available per kg predator drops to 511 kg/km^2. Although this seems like a substantial reduction in prey availability per lion, it remains relatively high compared to other areas in Africa. For example, an estimated 312 kg of prey meat is available per kg predator per km^2 in the Serengeti National Park, 94 kg of prey is estimated to be available per kg predator per km^2 in Nairobi National Park and 76 kg of prey is estimated to be available per kg predator per km^2 in Waza National Park (De Iongh *et al*., 2004). Supporting the research hypothesis, the relatively high amount of prey biomass available to the lions in MNP indicates thriving prey populations and a healthy environment.

Assessment of methodology – prey population characteristics

Results of the transect count analysis provide a reliable representation of the overall presence of prey animals in MNP, Bisanadi National Reserve and Korbesa community area. However, several limitations in the methodology need to be addressed. Line transects were selected throughout the park in such a way that the majority of habitat types and vegetation structures were represented, but these did not encompass the entire park and could therefore not completely cover every habitat type. Moreover, due

to the limited availability of data on vegetation types, MNP was divided into just two large vegetation regions that were most comparable with observations in the field. This, however, affected the size of the areas to which abundance estimates were extrapolated. Moreover, it reduced the accuracy of the estimates since the detailed habitat and vegetation preferences of prey species were partially overlooked. In retrospect, another shortcoming of the methodology was the apparent underrepresentation of riverine habitats during the transect counts, with only small parts of transects no. 2 and 5 that included riverine habitat. Because data were collected during the dry season (January – April), animals would be expected to concentrate around water sources and avoid dry, open areas that become too hot during the day. Indeed, fewer animals were counted during afternoon drives on transects that covered open plains and wooded grasslands (transects no. 1-3). Animals were also easier to detect on the open grasslands than inside the shrub and bushland (transects no. 4-7). Prey densities for these densely vegetated areas might therefore be considerably higher in reality than estimated based on the transect counts. However, by analyzing the transect data using the DISTANCE-program, detection probability is taken into account, which relaxes the assumption of presuming a complete census of all animals (Buckland *et al*., 2001; Ogutu *et al*., 2006).

Lion diet

Of all prey species, African buffalo consistently appeared as the most important contributor to the diet of the lions in MNP. The species was responsible for the majority of the carcasses and accounted for most of the identified prey hairs (32%). Since African buffaloes were one of the most common larger herbivores in MNP, it is not surprising that the majority of the carcasses belonged to this species. The large number of African buffalo hairs found in the lion scats further displayed their significance as prey item. Plains zebra came in second (25%), although only one carcass of the species was found despite its relatively high abundance.

A different project on the diet of lions in MNP applied eDNA-analysis on faecal samples from the same lion scats that were collected during this study (Verhagen, 2019). This approach allowed for an alternative, perhaps more precise and less biased look into the dietary composition of lions. Verhagen (2019) found that African buffalo made up 74% of the total lion diet, while plains zebra only contributed 10% to the total lion diet. However, it must be noted that the DNA of other, rather unlikely prey species (*Eucyclops agilis*, leopard) was found as well (Verhagen, 2019).

Nonetheless, results from this study and the eDNA-analysis confirm the well-documented fact that African buffalo and plains zebra are two of the principal prey species of the African lion (Hayward & Kerley, 2005; Davidson *et al*., 2013; Lesilau *et al*., 2019). They also indicate the ability of the lions in MNP to successfully predate on larger herbivores, particularly African buffalo. This generally requires a cooperative hunting strategy and thus a sufficiently large group size (Hayward & Kerley, 2005).

Therefore, the results confirm the research hypothesis that MNP is a relatively undisturbed environment that allows these conditions.

Since the foraging strategy of lions is known to be temporally variable (Smuts, 1978), it is important to emphasize that the results of this study remain limited to the dry season. The dietary composition found during this study may well differ from the wet season. For example, drought is known to increase the susceptibility of African buffalo to lion predation, which might explain the species' high contribution to the lion diet (Prins & Iason, 1989). Seasonal variation in prey preference is also highly relevant for the seasonality of human-lion conflicts (Patterson *et al*., 2004). Although only 3 hairs of domesticated species were found, this may not represent the situation during the wet season.

Assessment of methodology – lion diet

The diet of the lions in MNP was assessed by means of carcass counts and the microscopic analysis of prey hair recovered from lion scats. These methods provide a reliable reflection of a carnivore's diet as long as their limitations are taken into consideration. A known limitation of the counting of carcasses is the obvious bias towards larger prey species, since their carcasses are easier to detect and persist in the environment for a longer time (Bauer *et al*., 2008; Tambling *et al*., 2012). Moreover, small prey species are often consumed in their entirety and thus leave no carcasses (Tambling *et al*., 2012).

The analysis of prey hair allowed for a supplementary, less biased look into the diet of the lions, but the method's accuracy and reliability were partially affected by a number of factors. Firstly, it is possible that some scats were misidentified and belonged to species other than lion. However, since every scat was carefully examined and verified by a local researcher to be of a lion, this error is minimised. Secondly, a number of prey hair imprints failed to yield identifiable scale patterns. In some cases, none of the five imprints belonging to a scat were successful, and these scats thus had to be omitted from the record. Yet, this is also unlikely to have significantly affected the outcome of the hair analysis.

There may still be a bias due to the wrong interpretation of prey hair morphology. The morphology and scale patterns of the recovered prey hairs had to be compared to an existing reference collection, which was often limited. A number of species known to inhabit the Meru Ecosystem were not represented in the collection, in particular birds and small mammals. The notion that lions in MNP incorporate proportionally fewer small prey animals in their diet is therefore difficult to assess. Because of the limited reference collection, recovered hairs were often identified and appointed to a prey species based on the similarity, or least dissimilarity, with existing reference hairs rather than with absolute certainty. The similarities between species and the intraspecific variation in hair morphology and scale patterns further complicated reliable identifications of prey species. Nevertheless, the results of this study give at least a fairly reliable and valuable overview of the relative contributions of different prey species to the lions' diet in MNP.

Prey preference

Preferences and avoidances

Of the 19 prey species that were recorded during this study, 11 show JI values greater than 0. By definition, these species are considered preferred prey since they are taken proportionally more than expected based on their relative abundance. Unexpectedly, bushbuck and olive baboon show some of the highest JI-values. This is in sharp contrast to the results of Hayward & Kerley (2005), who found that lions strongly avoided these species. Although it is possible that bushbuck and olive baboon are, together with Grevy's zebra and hartebeest, some of the most preferred prey species in MNP, it can be argued that the results for these four species are unreliable due to a lack of data. Calculating JI requires robust estimates of the relative abundance of a prey species and its proportional contribution to the lions' diet. However, because these four species were rarely observed during transect counts, their abundance and density estimates are particularly uncertain. Additionally, the incorrect identification of prey hair may have a substantial impact on a species' final preference results, especially when the species occurs in low numbers, such as Grevy's zebra.

The preference towards African buffalo, on the other hand, is reasonably reliable and supports the research hypothesis that lions prefer to incorporate large herbivores in their diet. The species was observed on 113 occasions during transect counts and was the most represented prey species in the diet based on carcass counts and hair analysis. In contrast to the abovementioned species, this makes the final results for the African buffalo less vulnerable to extrapolation errors and hair misidentifications.

The same is true for plains zebra and waterbuck. These species were also found to preferred prey, which is consistent with the research hypothesis. Although plains zebras have a lower average body mass and provide a lower potential energy gain compared to African buffalo, they are a less risky prey to hunt (Hayward & Kerley, 2005). Moreover, Hayward & Kerley (2005) attributed the preference of lions for plains zebra to the species' grouping strategy and habitat choice. However, lions remain slightly tempered by the active predator defence and high detection distance of plains zebra (Elliott *et al*., 1977).

Waterbuck was also found to be a preferred prey species. The fact that waterbucks require grassland habitat near water likely increases their encounter rate with lions and might explain the resulting prey preference (Hayward & Kerley, 2005).

A number of species had JI-values close to 0, indicating no clear preferences or avoidances. Giraffes, for example, were only taken slightly more than expected based on their availability. Hayward & Kerley (2005) found a much more pronounced preference towards the species, and Davidson *et al*. (2013) found that lions generally avoided giraffes. This may imply that the preference for giraffe is spatially variable and depends on a lion population's ability to tackle the species' size and active defence (Hayward & Kerley, 2005).

Grant's gazelles were one of the most common herbivores in MNP but were predated on slightly less frequently than expected based on their availability. Although Hayward & Kerley (2005) also observed a negative JI value for Grant's gazelle, they revealed a much more outspoken avoidance for the species. Field observations do not suggest a reduced encounter rate between Grant's gazelle and lions, since both species were frequently spotted in the same areas. The JI-value is also not low enough to indicate active avoidance by lions, as presented by Funston *et al*. (2001). Therefore, it is most likely that lions only take Grants' gazelle opportunistically and will not actively invest energy in hunting the species, probably because of the low potential energetic return and the active vigilance and speed of the Grant's gazelle.

A truly outspoken prey avoidance was found for Kirk's dik-dik, which was abundantly present in MNP but only observed twice in the lions' diet. This result clearly illustrates how the lions in MNP avoid predating on Kirk's dik-dik, probably because of the species' low body mass and evasion tactics. However, stating that lions in MNP disregard small prey and only prefer larger prey species is contradicted by the results for beisa oryx. The extremely low JI-value of beisa oryx is quite surprising, since Hayward & Kerley (2005) found that the highest prey preference of lions was for gemsbok, a species closely related to the beisa oryx. Nevertheless, prey preferences may differ between regions and contexts, and the low number of beisa oryx in MNP probably reduces their encounter rate with lions.

Influence of prey-specific traits

Overall, JI-values, and thus prey preference, seemed to be highest around a prey body mass of 100 kg. This differs from the 190 – 550 kg range observed by Hayward & Kerley (2005), suggesting that the lions in MNP prefer lower prey body masses. However, the preference results of some prey species should be interpreted with caution, since some results are based on a limited dataset with particularly uncertain estimates of abundance and dietary contributions. As previously mentioned, the incorrect identification of prey hair may have a large impact on the final preference results of multiple species, especially when these occur in low numbers. This might also explain why none of the prey-specific traits seemed to significantly influence the outcome of the preference analysis. Moreover, none of the body mass classes was significantly preferred or avoided. Lions are known to be opportunistic hunters, readily taking smaller prey or scavenging the carcasses of large herbivores (Schaller, 1972; Hayward & Kerley, 2005), and the results of this study indicate that this might also be true in MNP. However, the mean JI-values of medium and large sized prey appear higher than those of small and very small sized prey, which might suggest an overall higher prey preference for larger herbivores.

CONCLUSION

The Meru Conservation Area, which encompasses MNP and Bisanadi National Reserve, is often regarded and upheld as one of Kenya's truly unspoilt and undisturbed wilderness areas. Results from this research project cautiously support this statement and confirm the hypothesis that the Meru Conservation Area represents a healthy ecosystem. Lions occurred in relatively large prides and groups and incorporated a substantial amount of larger prey animals into their diet. Furthermore, a remarkably high theoretical amount of prey biomass was available per lion. Taking into consideration the park's low lion density, there is probably a potential for a growing lion population.

However, the presumed healthy conditions in MNP do not guarantee the long-term viability of the park's lion population, nor do they exclude the risk of conflict between lions and local people. Local communities and pastoralists are rapidly encroaching on the buffer zones bordering the protected areas, which will likely intensify livestock depredation and conflicts with large carnivores in the future. As the climate changes and the natural water supply becomes scarcer and less predictable both outside and inside the protected areas, this will likely worsen. In a recent statement, Mr. Bakari Chongwa, senior warden of MNP, explicitly warned about the dramatic rate at which the rivers in MNP are drying (DailyNation, 2019). The loss of natural water sources will not only directly affect the lion population in the park, it will also drastically affect the populations of strictly water-dependent prey species such as African buffalo and waterbuck.

In conclusion, the results of this study further improve our understanding of the characteristics and diet composition of the lion population in MNP. In this way, local conservation efforts can be further supported in their goal to protect the park's lions and mitigate human-lion conflicts.

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APPENDIX

Appendix I. Average prey body masses (Stuart & Stuart, 2009), designated body mass classes ('Very small': < 5 kg; 'Small': 5-50 kg; 'Medium': 50-200 kg; 'Large': >200 kg) and given values quantifying herd size, habitat and threat, after Hayward & Kerley (2005).

Species	Body mass (kg)	Body mass class	Herd size	Habitat	Threat
African buffalo (*Syncerus caffer*)	412	Large	5	2	2
Beisa oryx (*Beisa oryx*)	158	Medium	4	2	1.5
Bushbuck *(Tragelaphus scriptus)*	23	Small	1	3	0
Eland (*Tragelaphus oryx*)	337	Large	5	2	1
Elephant (*Loxodonta africana*)	2363	Large	3	2	2
Gerenuk (*Litocranius walleri*)	30	Small	3	3	0
Giraffe (*Giraffa camelopardalis*)	618	Large	3	2	2
Grant's gazelle (*Gazella granti*)	32	Small	4	1	0
Grevy's Zebra (*Equus grevyi)*	293	Large	3	2	1
Hartebeest (*Alcelaphus buselaphus*)	90	Medium	4	1.5	0.5
Impala (*Aepyceros melampus*)	30	Small	4	2	0
Kirk's dik-dik (*Madoqua kirkii*)	4	Very small	3	3	0
Lesser kudu (*Tragelaphus imberbis*)	47	Small	3	3	0
Olive baboon *(Papio anubis)*	15	Small	5	2	1
Ostrich (*Struthio camelus*)	70	Medium	3	1.5	0
Plains zebra (*Equus quagga*)	175	Medium	3	2	1
Vervet monkey *(Cercopithecus aethiops)*	3	Very small	4	2	0
Warthog (*Phacochoerus africanus*)	43	Small	3	2	0
Waterbuck (*Kobus ellipsiprymnus*)	195	Medium	3.5	2	0.5