The effect of resource abundance and dispersion on the ecology of African lions (*Panthera leo*) in a semi-arid landscape



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Doctor of Philosophy

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“Cecil the lion”



A moment that became a movement

A death that shook the world

A legend, a story to be retold for many generations

A global icon for conservation

A majestic beast, the king of the jungle

Roaming in the Africa savannah

Unbeknown, the fate that will befall him

The change that a death can bring

Awakening a passion in many

And a demand for change

The bright light, shining on the horizon

A new day is dawning

A better tomorrow for all creatures, great and small

Cecil the lion, forever remembered....

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Abstract

In natural ecosystems, resources are often heterogeneously distributed and one of the key challenges in ecology is to understand how environmental heterogeneity influences population dynamics, species distributions, community composition, social structure and individual behaviour. In this study, the spatial and temporal heterogeneity of the Hwange National Park landscape and the ability to measure and quantify the abundance, dispersion and the richness (characterised by herd size and prey size) of prey at the lion home range scale provided us with a unique opportunity to examine the effects of resources on the ecology of a social large carnivore. The abundance, dispersion and richness of prey patches is expected to influence various aspects of the ecology of African lions, including patterns of sociality, ranging behaviour and foraging behaviour. In this study I first assessed the applicability of the spoor count method in estimating relative abundance of herbivores and found it to be a useful index (Chapter 2). I then tested the effect of prey availability on the ranging behaviour (home range size) and the broad-scale social structure (group size) of lions by applying the four main prediction of the Resource Dispersion Hypothesis (RDH) (Chapter 3). Results revealed that all four predictions of the RDH were supported. Indeed home range size increased with increase in the dispersion of prey while lion group size increased with increase in patches richness. I then went on to test the effect of prey availability on the fine-scale social structure (community structure) of lion prides using the social network toolbox and advanced analytical methods (Chapter 4). Results showed that all prides demonstrated strong patterns of within-pride sub-grouping, or 'communities', and that the intensity of sub-grouping behaviour is linked to resource availability. More specifically, communities were more strongly defined as prey dispersion increased and when the body size of available prey decreased. Finally, I applied the optimal foraging and social foraging theories to understand the drivers of lion foraging behaviour (prey preference) (Chapter 5). Results revealed that the richness of prey patches both in terms of prey body size and herd sizes as well as lion hunting group size were important factors in influencing prey preference of lions. The foraging behaviour of this lion population suggested that they seek to maximise energy gain and optimise foraging success. Together the results of this thesis reveal that the dispersion and richness of resource patches are important factors in influencing lion ecology.

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Chapter 1



General Introduction

Preface

Some species such as the European badger (*Meles meles*) and red fox (*Vulpes vulpes*) live in groups but derive no obvious benefits such as cooperative hunting, alloparental care and predator defence from group living (Kruuk, 1978; Kruuk & Parish, 1981; Macdonald, 1981), and to explain group living in such animals, Macdonald (1983) formulated the Resource Dispersion Hypothesis (RDH). The RDH is an hypothetical model that proposes that, the economics of exploiting resources that are patchily distributed over space and/or time, allows several individuals to share resources over a common area, provided that resource needs of all individuals can be met without imposing costs on others (Johnson *et al.*, 2002; Macdonald & Johnson, 2015). It is against this background that this study seeks to understand the meaning of a resource patch for an animal and how the abundance, spatial distribution and richness of these patches influence animal ecology at both the individual level and at the group level.

Role of resources

Patchy distribution of resources occur in most natural habitats, resulting in a heterogeneous landscape that is further divided into patches of different sizes, each characterized by a distinctive resource value for animals (Kotliar & Wiens, 1990). For example, in the Serengeti National Park (Serengeti hereafter), Tanzania, river confluences provide important resources to various animal species and hence, represent high-value landscape features (Hopcraft, Sinclair & Packer, 2005; Mosser *et al.*, 2009). The abundance, distribution and quality of resource patches affect several aspects of animal ecology including the spatial structure and the social organization of animal populations. For example, solitary animals are expected to form spatial groups when heterogeneity of resources is high and competition among residents for those

resources is low (Macdonald, 1983; Carr & Macdonald, 1986). For animals to succeed within heterogeneous environments, they must acquire movement and search behaviours that maximize exposure to limiting resources (Grunbaum, 1998; Valeix *et al.*, 2010). Animals respond to and contribute to these patches and the ability to locate and exploit resource patches is particularly important in poor quality habitats (Leising & Franks, 2000). Resource patches come in various forms and degrees of importance for the different animal species. For example, for all animal species food patches are a critical resource for their fitness and survival. The richness of food patches can have an influence on reproductive success; Michel et al. (2017) found the clutch size of little owls (*Athene noctua*) to be positively correlated with the amount of food-rich habitat. Breeding sites are also an important resource for some animals, for example dens play a significant part in cougar (*Puma concolor*) fitness and kitten survivorship in the Southern Yellowstone ecosystem (Elbroch *et al.*, 2015). While for others, areas of refuges are key resources; as an anti-predator strategy, caribou (*Rangifer tarandus*) select resource patches more strongly in areas richer in refuge land-cover (Mason & Fortin, 2017). And still for some animals, water (e.g. Chamaillé-Jammes, Valeix & Fritz, 2007c) and forage (e.g. Fryxell, 1991) are essential resources.

There is variability in the responses of different animal species to the abundance and distribution of these resources and these can differ even between different species found in the same landscape or the same species found in different landscapes. For example both black kites (*Milvus migrans*) and Egyptian vultures (*Neophron percnopterus*) aggregated around food resources during summer, when food was clumped and patchily distributed, but remained widely and randomly distributed during winter, when resources were widespread (Cortes-Avizanda *et al.*, 2011).

However, during the desert locust outbreaks, the black kites shifted their spatial distribution in a conspicuous way, increasing group sizes significantly, while the spatial distribution of the Egyptian vultures did not change to take advantage of this sudden surge in food availability (Cortes-Avizanda *et al.*, 2011). The degree of flexibility of a species also affects its response to the heterogeneity in resource distribution. For example sea birds have been shown to be especially vulnerable to the reductions in prey availability during the breeding season when spatial constraints limit their capacity to adapt to these changes (Boyd *et al.*, 2017). When foraging conditions are poor and food abundance is low, adult chinstrap penguins (*Pygoscelis antarctica*) may reduce reproductive success rather than increase foraging effort to avoid jeopardizing their own survival and future reproductive success (Croll *et al.*, 2006). Resource distribution can also affect different sexes of the same species differently; spatial distribution of females of most mammal species is determined primarily by resource distribution while spatial patterns of males are influenced by the distribution of females (e.g. Macdonald, 1983; Gehrt & Fritzell, 1998). Response to resource distribution can also vary with reproductive status where an animal sacrifices abundant resources for other factors that can result in increased reproductive success. In southern flying squirrels (*Glaucomys volans*), females moved into areas with an abundance of potential dens and relatively low food resources while rearing young in response to competition for maternal dens and to avoid contact with other squirrels (Fridell & Litvaitis, 1991).

Resource availability can be assessed in terms of the abundance of resource patches, their spatial distribution and richness/quality. All these three measures can have key implications on the ecology of animals, specifically foraging behaviour and

consequently ranging behaviour and sociality (Mosser *et al.*, 2009; Valeix, Loveridge & Macdonald, 2012). The abundance, spatial distribution, and richness of resource patches are also important attributes that can influence the opportunities for social interactions among individuals in a social group (Tanner & Jackson, 2012). The measure of resource patch abundance characterises the amount of patches available to an animal within its home range. When resources are abundant competition between individuals in a group is reduced. The associations between individuals in a group are expected to be stronger and the social structure highly interconnected when resources are abundant (Foster *et al.*, 2012). A measure of resource patch dispersion describes the distance an animal has to travel to encounter a resource patch or the effort involved in searching for the patch. When food is aggregated, animals usually aggregate around these food sources and scatter when food becomes dispersed in the landscape (e.g. Valeix *et al.*, 2010). The advantages of these aggregations include an increased chance of finding a mate (Blanco & Tella, 1999), reduced effort in searching for food (e.g. Bailey & Thompson, 2006) as well as increased and efficient information transfer (Marzluff, Heinrich & Marzluff, 1996). Patch richness represents the quality of the resource patch in terms of the energy or fitness gained from utilizing that resource patch. For predators, patches with large prey species are rich patches as they give a higher energy gain and are also expected to feed several individuals in a predator group (Macdonald, 1983). Access to larger prey can therefore increase the range of group sizes that can satisfy individual feeding requirements (Caraco & Wolf, 1975).

Research in ecology over the last few decades has been focused on understanding the relationship between animals and the abundance and distribution of food resources.

Across different taxa, the relative contribution of food patchiness and predictability, both in space and time has been shown to have some effects on different aspects of animal ecology including foraging efficiencies (Caraco & Wolf, 1975), mate availability (Korpimaki *et al.*, 1996), and reproductive success (Michel *et al.*, 2017). However the majority of the earlier studies around this topic were done in controlled experiments on arthropods, birds and fish (e.g. Werner & Hall, 1974; Krebs *et al.*, 1977) as these taxa are more manageable under experimental manipulation than, for example, wild mammals. Ivlev's (1961) experiments on fish were seminal and he found that the abundance and spatial distribution of food influenced foraging behaviour. As interest in the subject grew, more and more studies began to investigate this in primates and other wild mammals. Some of these studies have assessed and found a relationship between resources (dispersion, abundance and richness) and the broad-scale social structure and ranging behaviour of primates and other mammals (see Hanya & Chapman, 2013; Macdonald & Johnson, 2015 for reviews). Crook (1972) listed food abundance among other factors such as predation pressure, and distribution of waterholes as important determinants of primate group size. The optimization of carnivore group size is often in response to prey availability, in an attempt to maximize the total benefit-to-cost ratio for individual group members (Caraco & Wolf, 1975). Golden jackals (*Canis aureus*) have also been reported to aggregate around clumped food sources resulting in a more cohesive group (Macdonald, 1979).

However several of these studies showing the link between food availability and carnivore ecology are theoretical, and more empirical studies need to be carried out across geographical scale and across different species. The challenge of this study was

to (1) consider what a resource patch is and its attributes for a large carnivore, and (2) study the importance of these resource patches (abundance, dispersion and richness/quality) on several aspects of the ecology of a large mammalian carnivore, specifically its foraging behaviour, ranging behaviour, broad-scale social structure and fine-scale social structure (Figure 1.1). Foraging behaviour has been one of the most explored areas of animal ecology when it comes to trying to understand how resource heterogeneity affects the ecology of animals. However there are still gaps around the issues of how prey availability influence decision rules by a predator and preference and avoidance of certain prey species. Although we now have a better understanding of the effect of resources on the broad-scale animal social structure, the effect of prey abundance, dispersion and richness on the fine-scale patterns of animal social structure has received the least attention. Innovatively, in this study I combined data on prey (herd abundance, dispersion, and characteristics of patch richness such as herd size and prey body size) with information on African lion (*Panthera leo*) ranging behaviour, lion kill sites, and lion social aspects (group size, sub-group size) to understand the effect of resources on the ecology of a social carnivore.

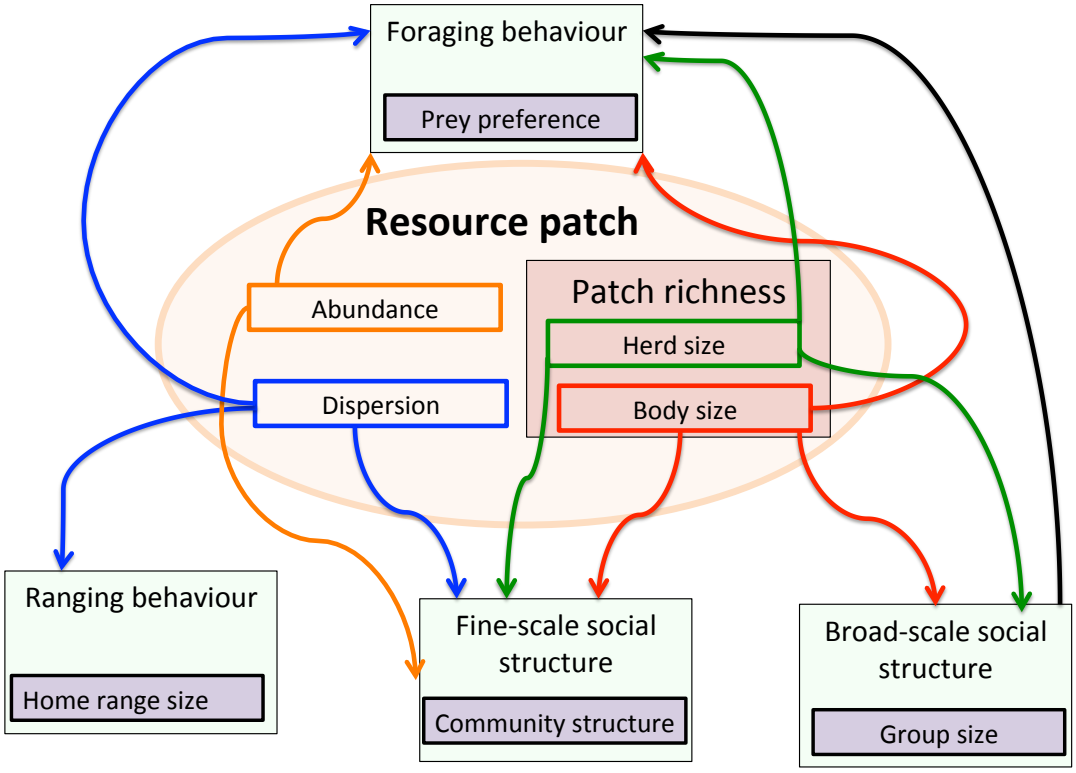


Figure 1.1 The hypothesis tested in this study on the ways in which resource patches specifically their abundance, dispersion and richness (characterised by prey herd size and prey body size) can affect the ecology of a social predator particularly its foraging behaviour, ranging behaviour, broad-scale social structure and fine-scale social structure.

Foraging behaviour

The strategies of a predator are forged by natural selection to maximize nutrient intake while being tempered by a wide range of ecological constraints, such as prey density and habitat, which differ throughout its geographical distribution (Sunquist & Sunquist, 1997). As long as a predator can increase its survival chances or reproductive success by hunting more efficiently, natural selection will favour efficient, optimally foraging predators (Krebs, 1978). Prey characteristics such as

their abundance, temporal and spatial distribution, size of herds and body size of prey together with factors such as their habitat use and defensive behaviour (including vigilance) (Sunquist & Sunquist, 1989; Macdonald, Loveridge & Nowell, 2010a) as well as extrinsic landscape features (Hopcraft *et al.*, 2005) have important implications for predator foraging behaviour. This is because a predator has to search, chase and kill the prey (Elliott, Cowan & Holling, 1977). The predator incurs costs across all these stages in the foraging sequence and would need to maximise energy gain from prey consumption to compensate for these energetic costs (MacArthur & Pianka, 1966; Townsend & Winfield, 1985) and is therefore expected to prefer prey that offer the highest net returns (Emlen, 1966; Krebs, 1977). For large predators the most profitable prey type would be the largest available prey that could be killed safely (Sunquist & Sunquist, 1989). The advantage of large prey is that they are divisible and would provide an opportunity for all group members to feed on the carcass (Caraco & Wolf, 1975). Apart from the prey characteristics, the hunting group size of predators can also have an affect on preference for certain prey species as group size can influence decisions about which size of prey to hunt, with larger groups being more capable of taking down larger prey (Scheel & Packer, 1991; Funston, Mills & Biggs, 2001; Creel & Creel, 2002).

Ranging behaviour

The heterogeneity of a landscape means animals cannot form evenly shaped territories and instead the size and shape of these territories depends on the dispersion of the important resources needed for survival and reproduction (Macdonald & Johnson, 2015). Under the RDH, the dispersion of resource patches is therefore expected to influence the size of territories (Johnson *et al.*, 2002). Bradbury & Vehrencamp's

(1976) study on neotropical bats was one of the seminal studies that helped shape the predictions of the RDH, the territory sizes of these bats were determined by the dispersion of insect swarms over rivers. Seasonal changes in food availability within an area can potentially have an effect on the seasonal home range size of an animal (e.g. Palphramand, Newton-Cross & White, 2007), with the home range size increasing in a season with more dispersed resource patches and shrinking when resource patches become more aggregated. However, the effect of resource dispersion on home range may be obscured in males of any species as their spatial arrangement is often driven by the distribution of females (Emlen & Oring, 1977; Vangen *et al.*, 2001). Some other forms of resources such as water sources and habitats with good cover may indirectly influence the home range size of animals. For example the dispersion of water sources can have important implications on predator home range not because predators use water much, but because these water sources are prey hot spots and increase the predictability with which prey are distributed (Hopcraft *et al.*, 2005; Valeix *et al.*, 2010). In this case, home range will be expected to increase with increases in the dispersion of water sources, as predators would need to expand their home range to encompass enough rich water sources (Valenzuela & Macdonald, 2002; Valeix *et al.*, 2012).

Broad-scale social structure

The patchiness with which resources are distributed is believed to have played an important role in facilitating the formation of social groups in animal societies (Macdonald, 1983; Carr & Macdonald, 1986). Under the RDH, the richness of resource patches, in both space and time, is expected to influence animal group size (Macdonald, 1983). The RDH has also been applicable even to animals that gain clear

benefits from group living (e.g. Mosser, 2008; Valeix *et al.*, 2012), and for such animals resource distribution determines the framework of constraints within which all other benefits of group living may operate (Macdonald, 1983). The richness of patches is expected to set a limit on group size (Valeix *et al.*, 2012) and also allow larger groups to be supported in these rich patches. This may in turn facilitate the development of other group living behaviours such as cooperative hunting and cooperative defense of territories (Krause & Ruxton, 2002), which are important in helping to maintain social ties within a group. However there is a possibility that effects of patch richness on group size may not be clear-cut for animals that live in fission-fusion societies, in which groups often separate into smaller foraging sub-groups. A measure of the fission-fusion dynamics may need to be taken into account when assessing this relationship, as this might mask the effects of patch richness on group size.

Fine-scale social structure

Within a group, each individual can be seen as part of a network of social associations and interactions varying in strength, type, and dynamics (Hinde, 1976). Social structure (at a finer scale) emerges as a result of such individuals making non-random associations. Social interactions among group members can have important implications for the survival and fitness of many group-living species (Alexander, 1974). Although the process by which individuals decide to associate has been examined by various studies (Baker *et al.*, 2000; Kasper & Voelkl, 2009; Pace, Pulcini & Triossi, 2012), an understanding regarding how this decision is made is still unclear. The heterogeneity in the distribution of resources emerged as one of the most important factors that can have an influence on association patterns between

individuals in a group, with an expected weakening of social ties during times of resource scarcity (Belton, Cameron & Dalerum, 2018). These social ties are often weakened by the increased competition among individuals during periods of low resource abundance. For fission-fusion societies, the structure of associations within a network may also have significant consequences for the way information flows among individuals that are often apart and in different sub-groups (Baker *et al.*, 2000). Cohesion within a group of social animals can result in increased cooperation within the group thereby providing the species with significant benefits from living in groups, such as defence of a territory and young (Packer & Pusey, 1997; Mosser & Packer, 2009).

The case of the African lion

Why lions?

The lion is a very suitable study species to study the effect of resource availability on a carnivore. Prey availability is expected to affect various aspects of carnivore ecology and behaviour, including its social dynamics. The African lion is the most social wild felid and is an ideal model for studies of social grouping because they live in fission-fusion social units (Schaller, 1972). Because of the vulnerability of lions to extinction from various anthropogenic factors, there is need for more research across their range on their ecology and behaviour, as this knowledge is important for informing management and conservation strategies.

Current status

Lions were historically distributed across most of Africa and parts of Europe and Asia (Turner & Antón, 1997) but are now only found in a number of isolated areas. The

lion has a broad habitat tolerance they are only absent from tropical rain forest and the interior of the Sahara desert (Nowell & Jackson, 1996). The lion population is currently confined to sub-Saharan Africa and a single population is found in India (Nowell & Jackson, 1996) (Figure 1.2). The African lion population has almost halved in the last three decades and continued declines have led to their classification as Vulnerable on the IUCN Red List (Bauer *et al.*, 2016) and the West African lion listed as critically endangered (Henschel *et al.*, 2015). Population models by Bauer et al. (2015) indicated a 67% chance that lions in West and Central Africa will decline by one-half, and a 37% chance that lions in East Africa will also decline by one-half over two decades. The most recent estimate of lion number is around 20,000 free-ranging lions in 67 lion range areas (Bauer *et al.*, 2016).

The main threats to lions are indiscriminate killing, largely as a result of retaliatory or preventive killing to protect human life and livestock (Bauer *et al.*, 2016) and depletion of lion's principal prey species through an unsustainable and increasingly commercialized bushmeat trade (Lindsey *et al.*, 2013a). Habitat loss and conversion has also contributed to the decline of the lion population by causing a number of subpopulations to become small and isolated (Ripple *et al.*, 2014) and as the human population in Africa continues to grow, the demand for land may continue to increase resulting in more habitat loss. An emerging threat to lions is the trade in bones and other body parts for traditional medicine, both within Africa and in Asia (Williams *et al.*, 2015). Trophy hunting has generally contributed to population declines due to poor regulations and unsustainable off-takes specifically in Botswana, Namibia, Tanzania and Zimbabwe (Lindsey *et al.*, 2013b).

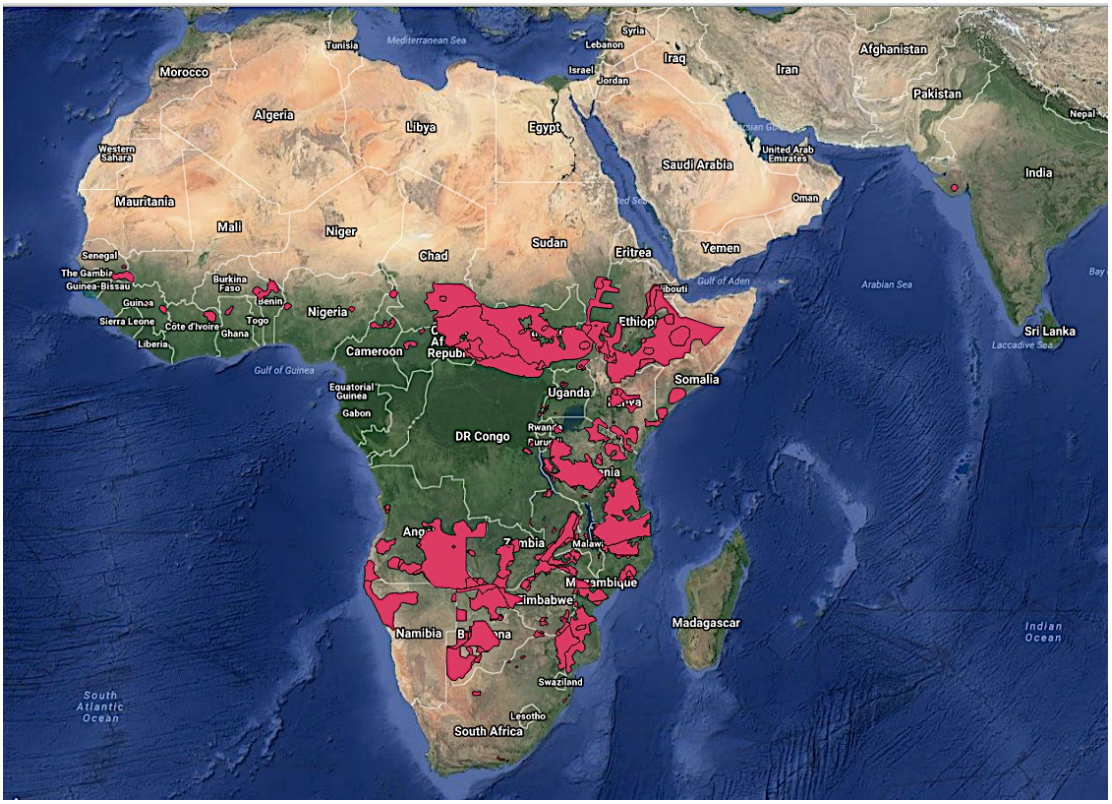


Figure 1.2 The current range of lions (shown in red) found mostly in sub-Saharan Africa and a single population in India. (IUCN 2017). This map is the 'best-case scenario' and may perhaps include some Extant and Possibly Extinct range categories.

Lion social dynamics

A lion pride is comprised of a group of males and females known to each other individually and which routinely hunt, feed, and rest together (Schaller, 1972). The basic unit of the lion pride consists of several related females and their young (Schaller, 1972). In the Serengeti males form separate social units, coalitions of four to nine males composed of close relatives, with coalitions of nonrelatives never growing to larger than three (Packer & Pusey, 1997). There is no social dominance among female lions in the same pride (Schaller, 1972), and female pride mates have equal access to carcasses (Packer & Pusey, 1997). Although lions are widely said to

be the most conspicuously social of felids, pride members are not always together and a process of fission-fusion commonly results in the pride splitting into smaller sub-groups (Schaller, 1972; Packer & Pusey, 1997). In Serengeti, pride lion members usually disperse to hunt and feed alone or in groups of two to eight individuals (Schaller, 1972). Natural selection may have favoured the capacity for social animals such as the African lion to adjust their group size in response to a hierarchy of ecological factors, primarily temporal and spatial patterns of resource availability (Caraco & Wolf, 1975). When preying on large, abundant herbivores, lions have been shown to form groups that are larger than would be predicted by maximum foraging efficiencies (Caraco & Wolf, 1975). It is most probable that sociality in lions is promoted where feeding efficiency is increased by: (1) a co-operative hunting which increases the percentage of successful kills or permits the capture of larger prey (Packer, 1986), or (2) cooperative defence of kills from other predators such as hyaenas (Kruuk, 1972). Actually competition with hyaenas has been observed to reduce the foraging efficiency of smaller lion groups (Caraco & Wolf, 1975).

Pride lionesses, which are in most cases closely related, synchronise their breeding and births tend to coincide, enabling the lionesses to protect and feed one another's cubs (Packer & Pusey, 1997). Schaller (1972) showed that this alloparental care of young resulted in increased chances of cub survival, wherein half of pride cubs survived past 2 years of age. This extremely important selective advantage must therefore strongly favour group living in lions. Indeed pride females were observed to be most gregarious when they had dependent young as it was important to defend themselves and their cubs (Packer & Pusey, 1997). Both male coalitions and pride females defend their preferred hunting grounds, denning sites and waterholes against

other coalitions or females (Packer & Pusey, 1997). In Serengeti, larger prides were found in higher quality habitat and they outcompeted smaller prides for access to those richer habitats (Mosser & Packer, 2009). Although lions engage in a wide variety of group level activities such as cooperative hunting (Scheel & Packer, 1991), mutual defence of kills (Cooper, 1991) and cooperative defence of territory and young (Mosser & Packer, 2009), lion sociality seems to be influenced by resource availability as well (Macdonald, Mosser & Gittleman, 2010b).

Lion hunting and feeding behaviour

Early in their evolutionary history, lions developed and retained specializations for prey capture by concealment, stalk, and a sudden attack and they rarely hunt by pursuit (Kleiman & Eisenberg, 1973; Elliott *et al.*, 1977). Lion hunting behaviour is well documented across different parts of their range. They hunt mostly at night or in cooler daytime periods although they are highly opportunistic and will hunt whenever an opportunity arises (Schaller, 1972). Lions are also able to travel long distances in search of prey (Eloff, 1984) and regularly hunt in groups (Schaller, 1972). Differences in prey selection of lions between different sites reflect differences in prey availability and the vulnerability of prey species (Sunquist & Sunquist, 1989). Hayward and Kerley (2005) carried an analysis of 32 studies over 48 different spatial locations or temporal periods throughout the distribution of the lion range and found that lions preferentially preyed upon species within a weight range of 190–550 kg. The most preferred prey species across lion range included gemsbok (*Oryx gazelle*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*) and zebra (*Equus burchelli*) (Hayward & Kerley, 2005).

Cooperative hunting has been found to facilitate improved foraging or hunting success in open habitats, it is especially advantageous for lions as they are usually more readily detected by prey before being close enough to charge when in open habitats (Elliott *et al.*, 1977; Stander & Albon, 1993). In Kruger National Park, South Africa, hunting success and prey selection by lions increased with increase in group size, with females selecting medium-sized ungulates and males mainly capturing buffalo (Funston *et al.*, 2001). In Serengeti, small lion groups were unable to capture large prey species such as buffalo (Packer, Scheel & Pusey, 1990). Participation during hunts of individual lions in a pride varies, and Scheel and Packer (1991) found that individuals within a pride refrained from participating in a communal hunt if the target prey being pursued was easy to capture but participated for the more difficult to hunt large prey like buffalo and zebra to increase chances of prey capture. Lion foraging behaviour tends to strive to maximise nutrient intake, for example in Kruger National Park male lions in larger coalitions killed more buffalo, a prey that is dangerous to hunt but yields greater reward (Funston *et al.*, 1998). Schaller (1972) observed in Serengeti that the efficiency of prey capture by lions generally increased with increasing group size and that larger groups obtained more multiple kills. These findings were later reinforced by Packer (1986) who found that hunting success increased and distance between kills decreased with increasing group size. In Etosha National Park, Namibia, hunting success increased linearly with lioness group size (Stander & Albon, 1993). Nonetheless, the effectiveness of group hunting among lions is still debatable (Caraco & Wolf, 1975; Packer *et al.*, 1990; Stander, 1992a), but it is highly likely that it may differ between and within populations, between individuals and between ecological circumstances (Macdonald *et al.*, 2010a).

Study area

Hwange National Park (HNP) covers about 15 000 km^2 of semi-arid dystrophic (nutrient-poor soil) savanna on Kalahari sands, in the northern western Zimbabwe (19°00`S, 26°30`E) (Figure 1.3). HNP is bordered to the west by Botswana, to the north by the Matesti and Deka Safari areas, to the South by the Tsholotsho communal land, to the north east by private land owned by the Forestry Commission, and to the south east by agro-pastoralist human settlements. The park is largely flat, the altitude varies between 800 and 1100 m and becoming hillier in the northern parts of the park.

Vegetation and soil

Hwange National Park is characterised by dystrophic savanna with nutrient poor acidic soils. Two thirds of the park is composed of Aeolian Kalahari sands. The remaining one third is on Batoka basalt and Karoo sediments. These sediments form part of the Zambezi drainage basin. The vegetation is primarily woodland and bushland savanna (64%), interspersed with small patches of grassland. Main Camp and Ngamo areas are dominated by open wooded savannahs on Kalahari sands, primarily teak woodland (*Baikiaea plurijuga)* and Combretum/ Terminalia woodlands. Batoka basalt and Karoo sediments in Sinamatella and Robins areas are dominated by *Colophospermum mopane* woodlands on richer basalt soils interspersed with grassland vleis and Shakwanki dominated by scrubland on Kalahari sands (Rogers, 1993b).

Water availability

When Hwange National Park was created in 1930, no surface water was available at the peak of the dry season in dry years (Weir, 1972). The National Parks authority

opted for water management in the dry season by pumping underground water in the waterholes so that wildlife would remain in the park and close to pans during the dry season and not move into neighbouring areas such as Botswana and the Gwayi River. The first pumped waterhole was created in 1935 and a large number of boreholes were drilled in the 1950s (Weir, 1972). Since then, about fifty waterholes have been fitted with pumps. Their distribution across the park is not uniform, most being located in the north-eastern region of the park (Figure 1.3). Pumping usually starts at the beginning of the dry season and is only ceased after the first significant rains. There are also some seasonal rivers that provide water in the northern part of HNP. Waterholes remained consistent in number and were consistently pumped throughout this study; therefore it is highly unlikely that waterhole numbers or pumping regimes could have been a cofounding source of variation in this study.

Seasonality

The long-term mean annual rainfall is 600mm and is highly variable (CV≈25%), generally falling between October and April. Three seasons are present in Hwange National Park: early dry season (March-June), late dry season (July-October) and the wet season (November-February). During the wet season, mean rainfall is around 514 mm and numerous rain-fed pools are available to animals. Water during the wet season is thus unlikely to constrain space use of water dependent herbivores and the browse and graze is likely to be abundant and of high quality. The early dry season (March – June) has a long-term mean rainfall of 111 mm with decreasing forage quality and surface-water availability. The late dry season (July – October) has a long-term mean rainfall of 25 mm and natural surface water is scarce, as only a few pools remain in the river network, and most natural pans dry up. Artificial waterholes

(~ 50) maintain water availability during the dry season. In the late dry season deciduous trees lose their foliage and both browse and grazing is of the lowest quality.

All the data used in this study were from the early dry season and the late dry season and data from the wet season were excluded from our analysis. A comparison between the late dry season and the wet season would presumably have offered much greater variation in resources, both prey and lion distribution in the landscape and thus greater leverage on the hypothesis tested in this study. However the collection of data such as spoor counts, lion group composition and investigation of lion kill sites was not practical during the wet season because most parts of the park were inaccessible due to flooding of roads. At an intuitive level, the Resource Dispersion Hypothesis might well be borne out at this inter-seasonal level, since herbivore distribution is generally more homogeneous in the wet season, when water is abundant and wide spread than in dry season when only permanent water sources and pumped waterholes remain (Davidson *et al.*, 2013). The differences in the distribution of prey in the wet season (homogenous) and in the dry season (heterogeneous) would in turn influence differently lion ranging behavior and movement patterns (Valeix *et al.*, 2010; Valeix *et al.*, 2012)

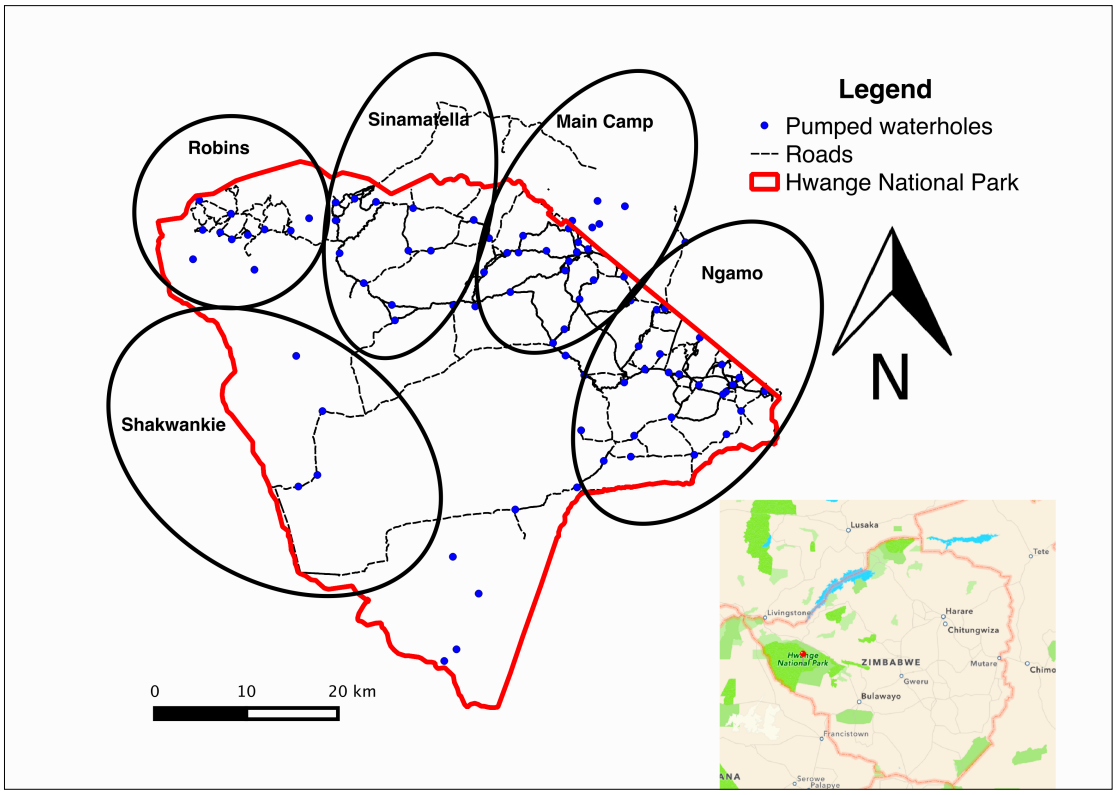


Figure 1.3 The study area Hwange National Park and the five study sites, Robins, Sinamatella, Main Camp, Ngamo and Shakwankie. Also shown on the map are the waterholes, most of which do not retain water in the dry season and are therefore artificially pumped. The insert map shows the location of Hwange National Park in Zimbabwe.

Prey species

The distribution of herbivores in the Hwange National Park landscape is constrained by the distribution of surface water (Valeix *et al.*, 2009a), which is largely influenced by the seasonal and annual rainfall patterns (Chamaillé-Jammes, Fritz & Murindagomo, 2007a). In HNP, changes in local herbivore abundance are likely to arise from the movement of large herbivores that are able to move large distances between the southern sector of HNP where there is nearly no surface water under dry conditions, but where water is widely available in the wet season, and the northern

sector of HNP where artificially supplied waterholes ensure provision of water throughout the year (Tshipa *et al.*, 2017). The Robins area is dominated by medium sized herbivores such as zebra, kudu (*Tragelaphus strepsiceros*), roan antelope (*Hippotragus equinus*) and waterbuck (*Kobus ellipsiprymnus*) while Sinametalla, Main Camp and Ngamo areas are mainly dominated by large herbivores and mega herbivores species such as buffalo, elephant (*Loxodonta africana*) and giraffe. There was a major decline in the abundance of most herbivore species population in Hwange in the early 1990s and this was attributed to being caused by either or both elephant population increase and an extended dry season, nevertheless the population has been stable over the past few years (Valeix *et al.*, 2007; Chamaillé-Jammes *et al.*, 2009). A recent study showed that there is a spatial stability of herbivore community abundance and composition in HNP (Chamaillé-Jammes *et al.*, 2016). Although there has not been any large changes in the spatial and temporal abundance of herbivores during this study, the fine scale spatial and temporal differences in abundance of lion prey species can however have important implications on lion ecology and behavior. Previous studies in HNP have shown that lions prey on a wide range of ungulates including buffalo, giraffe, zebra, roan antelope, kudu, sable (*Hippotragus niger*), warthog (*Phacochoerus aethiopicus*) and impala (*Aepyceros melampus*) (Davidson *et al.*, 2012; Davidson *et al.*, 2013). Lions have also been shown to be opportunistic foragers as they prey on elephants at the height of the dry season, and especially in drought years (Loveridge *et al.*, 2006).

Carnivore community

Hwange National Park has a range of carnivores from very small to large. The main large carnivores are lions, spotted hyaenas (*Crocuta crocuta*), brown hyaenas (*Hyena*

brunnea), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*) and African wild dogs (*Lycaon pictus*). Some of the small carnivores found in HNP include black backed jackal (*Canis mesomelas*), side-striped jackals, caracal, aardwolf (*Proteles cristata*), small spotted genet (*Genetta genetta*), African civet (*Civettictis civetta*) and African wildcat (*Felis silvestris lybica*). There is a strong potential for both exploitation and interference competition between Africa's two largest carnivores, the lion and the spotted hyaena and this can have detrimental effects on populations, resulting in changes in behavior, space and habitat use and population size (Périquet, Fritz & Revilla, 2015). Larger groups of hyaenas have been shown to have a higher chance of displacing lions from kills or retaining their own kills (Cooper, 1991), however competition does not lead to mutual exclusion at the population level. A review by (Périquet *et al.*, 2015) showed that abundance of their prey rather than that of their main competitor mainly drives lion and hyaena densities.

Why Hwange National Park?

The heterogeneity of Hwange National Park provided us with a unique opportunity to examine the effect of prey availability on lions. We also have a rich data set on the lion population in Hwange, with the lion population having been monitored intensively since 1999. Lion density in the study area is currently estimated at 3.5 lions/100km² (Loveridge *et al.*, 2016), a considerable increase from 2007 when the density was estimated at 2.7 lions/100km² (Loveridge *et al.*, 2007). Together this makes HNP an ideal site to carry out this research. Furthermore, the majority of lion studies have come out of the Serengeti National Park, which is a different ecosystem from HNP. In Serengeti, vegetation is mainly grassland and woodland, water is mainly found in rivers, and kopjes (rocky inselbergs) are dispersed throughout the

study area (Mosser *et al.*, 2009). Prey availability in Serengeti is also different from Hwange; there are large herds of migratory wildebeest, zebra and Thomsons gazelle (*Gazella thomsoni*) during the wet season. The annual herbivore migration in Serengeti alter the size and abundance of prey available to lions (Caraco & Wolf, 1975). The resident prey include buffalo, warthog, topi (*Damaliscus korrigum*), kongoni (*Alcelaphus buselaphus*), giraffe, Grants gazelle (*Gazella granti*), impala and reedbuck (*Redunca redunca*) and these are most abundant during the dry season (Mosser *et al.*, 2009). These differences imply that results from studies in Serengeti may not be applicable to HNP.

The increase in lion density in HNP from 2.7 lions/100km² to 3.5 lions/100km² offers the potential for additional variation in variables of interest in the test of the RDH predictions in this study. For example earlier studies in Hwange (Loveridge *et al.*, 2009) found evidence of expansionism (Kruuk & Macdonald, 1985), where pride biomass influenced pride seasonal home range size. Throughout this study adult male lions were removed from the Hwange National Park population by trophy hunting on the border of the park, in hunting concession adjacent to the park. Trophy hunting is one of the dominant causes of mortality in male lions in Hwange National Park and trophy hunting areas act as 'ecological traps' as these areas are used with similar levels of intensity as fully protected areas despite the high risk of mortality (Loveridge *et al.*, 2017). Migrating males fill home ranges made vacant by removal of adult males and this often leads to infanticide by the new males and may also result in changes in the social dynamics of the pride (Loveridge *et al.*, 2007).

Thesis Overview

Chapter 2: **'*Applicability of a spoor based index in estimating the abundance of large herbivore populations: comparison with road abundance kilometric index, road count estimated density and camera trapping rate'***

Spoor counting is a popular and cost-effective method of estimating carnivore abundance, however its applicability for herbivores is still unclear. The spoor counting method was the most practical and cost effective method to use in quantifying the abundance, dispersion and richness of prey patches in my study area. Therefore in this chapter I assess the effectiveness of this spoor-based index (the spoor abundance kilometric index) in estimating the relative abundance of herbivore species. I do this by comparing the spoor abundance kilometric index with other more conventional methods of abundance estimation, namely; the road count estimated density, road abundance kilometric index and camera trapping rate. This chapter has been resubmitted to *Koedoe.*

Chapter 3: '*Applying the Resource Dispersion Hypothesis to a fission-fusion society: A case study of the African lion (Panthera leo)*'

The Resource Dispersion Hypothesis (RDH) describes how groups may form even in the absence of any functional advantage to any individual from the presence of another. The RDH has found support from some empirical tests while others have not, so firm conclusions remain unclear. In this chapter I provide a test of the four general predictions of the RDH that (i) group size and territory size are not correlated, (ii) the dispersion of resources determines territory size, (iii) group size increases with increase in resource heterogeneity, and (iv) group size is determined by the richness

of resource patches. Unlike in other previous studies, I also add the effect of fission-fusion dynamics as it may shed more light on the relationship between patch richness and group size in a fission-fusion species. This chapter is under revisions for resubmission to *PNAS.*

Chapter 4: '*Effect of resource availability on fine scale patterns of social structure in African lions*'

After finding that resource dispersion and patch richness influences the broad-scale structure of lion prides, I go on to investigate the effect of resources on the fine-scale patterns of social structure; that is the association patterns between individuals in a group. This is of great importance as little is known about this subject. In this chapter I take advantage of the effectiveness of the social network analysis toolbox and advances in rigorous analytical methods such as the use of null models and dynamic networks to assess patterns of association and community structure in lion prides across seasonal variations in levels of prey availability. This chapter has been submitted to *Ecology Letters.*

Chapter 5: '*Aspects of optimal resource patch richness drives prey selection of African lions in a heterogeneous landscape'*

The efficient exploitation of available food resources has important implications for the fitness and survival of individuals. There is now a general understanding of predator foraging behaviour, however there is still a gap in our understanding of why certain prey is preferred or avoided. Both the optimal and social foraging theories predict that foraging individuals will seek to maximise their net rate of energy gain. In this chapter I use the optimal and social foraging theories to generate hypotheses of

what would constitute the predicted foraging behaviour of lions. I then test the hypotheses that prey preference is driven by (i) aspects of prey availability, (ii) environmental factors, (iii) aspects of predator group size, and (iv) relative prey size. This chapter is in preparation for submission to *The American Naturalist.*

Chapter 6: *General discussion*

In this chapter I start by highlighting the aims and motivations of this study and then discuss the main findings from this study. I also discuss the application of the results to other large carnivores that utilise the same prey base as lions and exhibit the same social dynamics. I then discuss the possible effects that water distribution and climate change may have on prey availability and hence indirectly have an influence on the ecology of lions. I end by discussing the conservation implications of the results found in this study.

Chapter 2



Applicability of a spoor based index in estimating the abundance of large herbivore populations: comparison with road abundance kilometric index, road count estimated density and camera trapping rate

Resubmitted to *Koedoe* for final decision

Authors: Moreangels M. Mbizah, Marion Valeix, Simon Chamaillé-Jammes, Lovelater Sebele, Hervé Fritz, David W. Macdonald and Andrew J. Loveridge

Abstract

Monitoring the abundance of animal populations is key for understanding animal demography and planning sustainable animal population management and conservation. Spoor counting is a popular and cost-effective method of estimating carnivore abundance, but its applicability to herbivores remains unclear. Here, we used spoor count, road count and camera trapping data collected during the same period to calculate spoor abundance kilometric index (spoor AKI), road abundance kilometric index (road AKI), road count estimated density (road density) and camera trapping rate for eight common large herbivore species in a large African protected area, Hwange National Park, Zimbabwe. We assessed the usefulness of the spoor-based index in estimating relative herbivore abundance in comparison to the three other more traditionally used indices. When comparing relative abundance of different herbivore species, spoor AKI mostly had strong positive correlations with the other abundance indices in the two study sites with sandy substrate, but not in the two study sites on basaltic soils. When focusing on one species and comparing relative abundances between sites and sessions, spoor AKI had moderate to strong positive correlations with road count estimated densities (and often the other abundance indices) for four species (elephant, impala, kudu and warthog), which tend to be the most abundant and widely distributed of the study ecosystem. However, we found weak correlations for low-density species (giraffe), small species (steenbok) and species living in large groups (buffalo). While spoor-based indices can be sufficiently reliable to assess big changes in the relative spatial and temporal differences in herbivore population abundance, rates of changes on a finer scale were not strongly correlated suggesting that this method cannot be used to detect subtle changes. Altogether, our results reveal that spoor-based indices provide an

opportunity for acquiring good information on large changes in herbivore relative abundances (whether at the inter-specific or intra-specific level) while doing carnivore surveys on sandy substrates.

Introduction

Estimating and monitoring the abundance of animal populations is critical for ecological research (e.g. Kurki *et al.*, 1998; Karanth *et al.*, 2004), as well as wildlife management and conservation (e.g. Gerber, DeMaster & Kareiva, 1999; Campbell *et al.*, 2002). Given the importance of estimating the abundance of animal populations, there is a wide range of existing methods ranging from direct counts (observation based) and capture-mark-recapture (CMR) methods to indirect approaches (sign-based) (Wilson & Delahay, 2001). Direct counts involve visually counting the animals, and this can either be total counts of an entire area (Rowcliffe *et al.*, 2008), or sample counts where a subset of an area's population is counted and a statistical estimator used to get an estimate of that area's population size (Buckland *et al.*, 1993). Capture-mark-recapture methods are based on individual identification and long-term monitoring of marked individuals, either through natural markings (e.g. Grange *et al.*, 2015) for Burchell's zebra (*Equus burchelli*) or through artificial marking of the individuals (e.g. Nilsen *et al.*, 2009) for roe deer (*Capreolus capreolus),* which allows demographic analyses (Lebreton *et al.*, 1992) and ultimately estimation of population size (e.g. Holmberg, Norman & Arzoumanian, 2009). Because direct counts and CMR methods based on visual observations may under-detect animals that are difficult to observe, such as rare, nocturnal, cryptic species, or species living in dense vegetation (e.g. Anderson *et al.*, 2013; Fragoso *et al.*, 2016), other techniques such as camera trapping and spoor counting have been developed to

assess population abundance.

The increasing use of camera traps has allowed animal detection and estimation of population abundance for species that are difficult to observe (Carbone *et al.*, 2001), and combining camera trapping and the capture-mark-recapture framework has enabled the calculation of population density of species that can be identified by their spots, stripes and other pelage patterns (e.g. Soisalo & Cavalcanti, 2006). This is particularly the case for large carnivores, such as tiger (*Panthera tigris*) (Karanth & Nichols, 1998), leopard (*Panthera pardus*) (Balme, Hunter & Slotow, 2009) and snow leopards (*Panthera uncia*) (Jackson *et al.*, 2006). Indirect methods, such as spoor or faecal counts have also been used extensively as an alternative (Cavallini, 1994; Funston *et al.*, 2010). These methods assume that the intensity or frequency of animal signs is correlated to population size (Wilson & Delahay, 2001; Engeman, 2005). However, no single best approach exists for animal population abundance estimation and techniques that work well in some situations are impractical in others; in some cases a combination of different methods works best (Gopalaswamy *et al.*, 2012).

Road count estimated density using distance sampling is commonly used to estimate the abundance of herbivore populations over large areas (Karanth & Sunquist, 1992; Varman & Sukumar, 1995). However, distance sampling analyses require a threshold number of observations to generate density estimates, which may sometimes be difficult or impossible to reach (Buckland *et al.*, 1993), especially for species that are cryptic, at low densities or in dense cover (Varman & Sukumar, 1995; Duckworth, 1998). In contrast, indices of abundance such as spoor abundance kilometric index (number of individual spoor encountered per km of road transect) and camera-

trapping rate may detect small, cryptic and nocturnal species, and these methods are generally used to provide relative estimates of abundance between sites in space or over time (Lancia, Nichols & Pollock, 1994; Wilson & Delahay, 2001). Spoor counting has been extensively used for estimating carnivore abundance (Van Dyke, Brocke & Shaw, 1986; Funston *et al.*, 2010), however only a few studies have assessed its reliability in estimating abundance of large herbivores (Silveira, Jacomo & Diniz, 2003; Stephens *et al.*, 2006; Keeping & Pelletier, 2014).

In Hwange National Park, Zimbabwe, road transect counts have been carried out since 1999 to estimate the abundance of large herbivore populations (Chamaillé-Jammes *et al.*, 2009) and spoor transect counts have been carried out since 2004 to estimate the abundance of large carnivore populations (Funston *et al.*, 2010). With limited resources, it would be more efficient and cost-effective to use one method to estimate both herbivore and carnivore population abundance. This example illustrates a problem widely encountered. We investigated the applicability of a spoor-based index (spoor abundance kilometric index) for estimating the relative abundance of herbivore populations. Here, we assessed the relationship between spoor abundance kilometric index and three of the more classically used abundance indices—namely road abundance kilometric index, road count estimated density and camera trapping rate— to ascertain whether spoor abundance kilometric index is a reliable measure of relative herbivore population abundance, and sensitive to changes in relative abundance in space and time.

Methods

Study area

Hwange National Park covers approximately 15 000 km^2 of semi-arid dystrophic savanna, on the north-western border of Zimbabwe. Two thirds of the park is composed of aeolian Kalahari sands. The remaining third is on Batoka basalt and Karoo sediments, which form part of the Zambezi drainage basin (Rogers, 1993a). We focused on five study sites in the park: Main Camp, Ngamo, Sinamatella, Robins and Shakwankie (Figure 2.1). The Main Camp and Ngamo areas are dominated by open wooded savannas on Kalahari sands, primarily teak woodland (*Baikiaea plurijuga)* and *Combretum/Terminalia* woodlands. Sinamatella and Robins areas are dominated by *Colophospermum mopane* woodlands on richer basalt soils interspersed with grassland vleis. Shakwankie is dominated by *Acacia* and *Combretum/Terminalia* scrubland on Kalahari sands (Rogers, 1993a). Three seasons are present in Hwange National Park: early dry season (March - June), late dry season (July - October) and wet season (November - February). The long-term mean annual rainfall is approximately 600mm but is highly variable (CV≈25%). During the wet season numerous waterholes, rivers and pools are rain fed and available to animals, but during the dry season, most water sources dry up and pumped waterholes (about 50) maintain water availability, mainly in the northern sector of the park (Figure 2.1).

Spoor count surveys

Multi-species spoor (animal track) count surveys were conducted from 2013 to 2015 during the early dry season and the late dry season in the five study sites. However, spoor surveys for Shakwankie were carried out in only three out of the six seasons due to logistic constraints. Spoor surveys could not be carried out in the wet season as

some roads became inaccessible because of the rains. Roads or routes, termed transects, were divided into shorter segments, of between 9 and 55 km and these formed the units of the survey. There were instances where more than one transect was driven per day, but this was only done for roads that did not intersect or run parallel to one another at close proximity in order to avoid double counting. Each transect was only surveyed once per season.

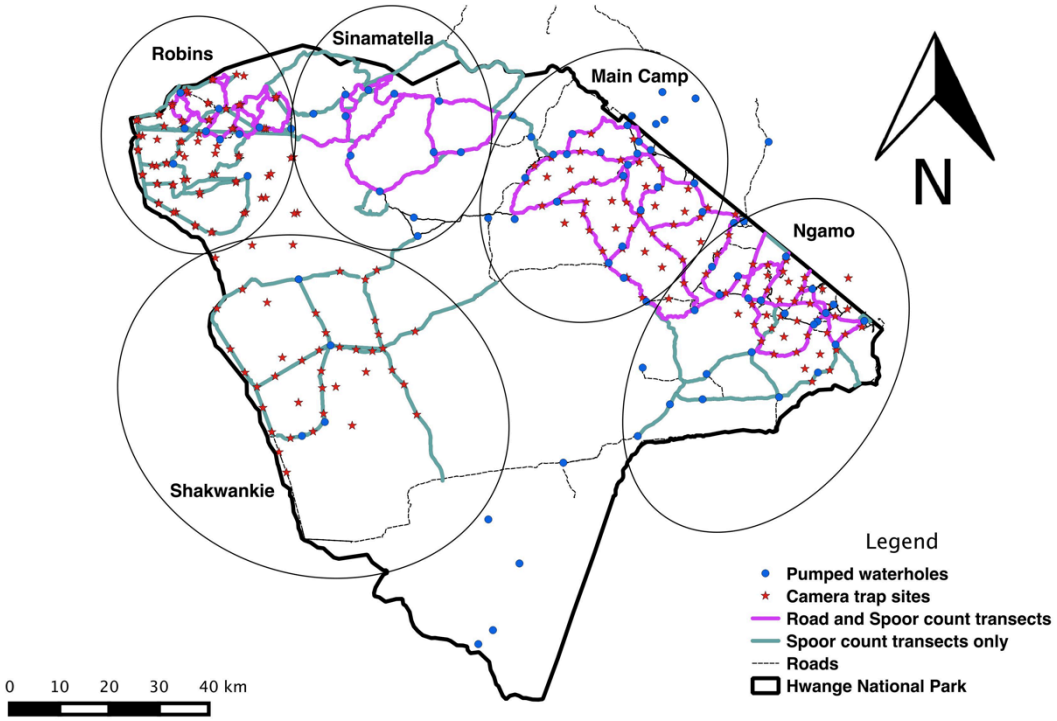


Figure 2.1 Map of Hwange National Park, Zimbabwe, showing the pumped waterholes, camera trap sites, and spoor and road count transects, in each of the five study sites.

Selected transects (Figure 2.1) were driven and spoor were identified with the help of highly skilled and experienced trackers and care was taken to avoid double counting spoor. To guarantee consistency, the same team of trackers carried out all the spoor

surveys. Vehicles driven at an average speed of 10 - 15 $km.h^{-1}$ served as an observation platform during spoor surveys, with a driver, a recorder and a tracker sitting on a customized seat mounted to the front of a vehicle. Roads were not swept before the surveys and surveys were undertaken once per season for each of the five study sites. The sampling intensity, measured by road penetration (calculated as distance sampled (km) as a ratio of the study area (km^2)) (Stander, 1998), did not vary greatly across sites and seasons; it ranged between 0.12 and 0.33 (Appendix 2.1).

Surveys usually began around 0700hrs and ended around 1200hrs. They were only carried out during conducive weather conditions, i.e. when there was no rain or wind and when light was of a good quality and intensity. Transect number, road substrate, date, and time of day were recorded at the beginning of each transect. When fresh spoor (less than 24h old) was encountered, it was assessed for species, group size, age class and sex. Spoor were counted if they crossed transects but subsequent re-crossings were ignored when the trackers judged from the animal's movement patterns that these were apparently made by the same animal. During the surveys, spoor of a range of herbivores and carnivores were identified to the species level, but only spoor from herbivores were used in this analysis. In this study, we focused on the eight most common herbivore species: Burchell's zebra, giraffe (*Giraffa camelopardalis)*, greater kudu (*Tragelaphus strepsiceros)*, impala (*Aepyceros melampus)*, warthog (*Phacochoerus aethiopicus)*, steenbok (*Raphicerus campestris)*, African elephant (*Loxodonta africana)*, and buffalo (*Syncerus caffer)*. In this study, the spoor abundance kilometric index (spoor AKI) is expressed as the number of individual spoor encountered per 100 km of road driven. We calculated spoor AKI for each season, year, and site and for each species.

Road count surveys

During the same period (between 2013 and 2015), road count surveys were conducted in four sites in the park: Main Camp, Ngamo, Robins and Sinamatella. No road count surveys were carried out in Shakwankie. Road count surveys were carried out in the late dry season in all four sites, and in the early dry season in some of the sites (Main Camp was consistently monitored but other sites were not surveyed because of logistical difficulties). Most of the available roads were used as transects (see Figure 2.1) and these were driven at least twice per season at different times of the day. We distinguished 3 periods of the day: early morning (0600hrs-1000hrs), hot hours of the days (1000hrs-1500hrs) and late afternoon (1500hrs-1800hrs). If a transect was surveyed once in the early morning, the subsequent time it was surveyed either in the hot hours of the day or the late afternoon. Vehicles were driven at an average speed of 10 - 15 $km.h^{-1}$ and animals were spotted by the driver and two observers positioned on car seats at the back of the vehicle. All large mammals detected were recorded. The censuses followed the line transect method and perpendicular distances were calculated using the angle and the direct distance as measured by a rangefinder between the vehicle and the animals at first detection.

The animal counts and associated distance data were later used to model visual detection probabilities as a decreasing function of distance from the transect line. This modelling and the subsequent estimation of herbivore densities and their variances were accomplished by using the estimation algorithms implemented in computer software DISTANCE (Thomas *et al.*, 2010). As recommended by Buckland et al. (2001), (i) we discarded observations corresponding to the 10% largest distances. A further truncation was performed when felt necessary from the observation of the

detection function; (ii) as bigger groups are more likely to be detected, we used predicted group size from size bias regression if the regression was significant (at $P < 0.1$). If not, the mean group size was used; (iii) we studied the four key-function models for the detection function (half-normal, uniform, hazard-rate and negative exponential) with cosine series expansion term; (iv) we selected the model with the smallest Akaike Information Criterion (AIC – Burnham & Anderson 2002). Exceptions were made when it was the negative exponential, known to have a low accuracy, while at least another model had a $\Delta AIC < 2$. The following most likely model was selected in such cases; (v) we checked that the selected detection function fit the data reasonably well, i.e. the goodness of fit chi-square test was non-significant ($P < 0.05$) (see also Chamaillé-Jammes *et al.* (2009). We defined road abundance kilometric index (road AKI) as the number of individual animals encountered per 100 km of road driven. We calculated road count estimated density (number of individuals per km^2) (road density) and road AKI for each season, year, site and for each species. The sampling intensity measured by road penetration did not vary greatly across sites and seasons; it ranged between 0.16 and 0.51 (Appendix 2.1). Sampling effort and road penetration for both the spoor count surveys and road count surveys are provided for the five study sites (Appendix 2.1).

Camera trap surveys

Camera trap surveys were carried out in Shakwankie in the late dry season 2013, in Robins in the late dry season 2013, in Ngamo in the late dry season 2014, and in Main Camp in the early dry season 2015. The camera trap surveys were carried out during the same period as the spoor surveys and road count surveys were being carried out to allow comparability. Because camera traps were initially set for the monitoring of

large carnivore populations, camera trap sites were first selected on the Hwange National Park map by taking into account locations were carnivore scats had been previously picked up. These coordinates were used as a guide to choose the final locations on the ground. Each camera trap station consisted of two independently operating cameras, approximately six metres apart, to serve as a back-up in the event of one camera failing during the survey period. The cameras were attached mostly to metal fencing standards hammered into the ground, but where a suitable tree or stump was available they were strapped to it, all at approximately 60cm above ground level.

The camera traps used in the surveys were the Cuddeback Capture Model 1125 and Cuddeback Model 1149 (Cuddeback. Non-Typical Inc., Wisconsin, USA). Cameras were set to a high firing rate that could take five photos during a single capture event. The camera trap survey was primarily intended for capturing carnivores and the camera traps were placed approximately 4 - 5 km apart, as this is optimal for effective detection of large and medium sized carnivores (Brassine & Parker, 2015). For comparability between surveys and other studies, each survey was run for at least 40 days after setting up all camera traps, which is consistent with other studies that use 10 - 90 days (Rowcliffe *et al.*, 2008; Rovero & Marshall, 2009; Cusack *et al.*, 2015). Consecutive photographs of the same species at the same site were deemed independent when there was at least 1 hour interval between them (following Bowkett, Rovero & Marshall, 2008). Instances where the same camera captured the same species more than once within 1 hour were excluded from camera trapping rate calculation. We calculated survey effort as the total number of camera trap days (number of 24 hour periods during which either one or both cameras were operating) and camera trapping rate was defined as the ratio of independent photographs to the

survey effort (Rovero & Marshall, 2009). Camera trap effort varied across the four study sites (Appendix 2.2).

Statistical analyses

We first tested whether substrate type influenced spoor detection and pooled all data across sites, species, seasons and years for linear regression analyses to test the effect of substrate on the relationship between spoor AKI and road AKI and between spoor AKI and road density. We then assessed whether spoor counts could detect changes in the relative abundance between different herbivore species and tested the correlation (Pearson and Spearman's rank) between spoor AKI and the other three indices of abundance (road AKI, road density and camera trapping rate) for each site and study session and across species. We used both the Pearson's correlation and Spearman's rank correlation tests because of the small sample size in some of our data. We also assessed whether for a given species, spoor counts could detect changes between the different survey sessions and between the study sites. We used the Pearson's correlation and Spearman's rank correlation to test the relationship between spoor AKI and the other three indices of abundance for each herbivore species across sites, seasons and years. Results for these correlations are presented according to the three feeding types, grazers (herbivores that feed on grass), browsers (herbivores that feed on trees and shrubs) and mixed feeders (herbivores that feed on both vegetation types). For the herbivore species for which there was a positive correlation between spoor AKI and road estimated density, we went on to assess whether changes in relative abundance between survey sessions were similar between spoor AKI and the other 2 methods (road AKI and road density). We calculated the rate of change (estimated abundance at t (survey session) divided by estimated abundance at t-1) to

test whether spoor AKI rate of change is correlated with rate of change of the other 2 methods. Because of the low sample size, we were not able to perform this approach for the relationship between spoor AKI and camera-trapping rate. All analyses were performed in R software (R Development Core Team, 2018).

Results

Overall, 21 herbivore species were detected during the surveys but we only focused on the eight most frequently detected herbivore species in this study. Information on herbivore feeding type is provided in Table 2.2 as feeding type correlates with habitat use and spatial distribution (Fritz & Loison, 2006).

Effect of substrate

The relationship between the log-transformed spoor AKI and road AKI was not significantly influenced by substrate type (estimate ± SE = -0.060 ± 0.122; P = 0.625). Road AKI significantly increased with increase in spoor AKI ($F_{3, 138}$ = 35.19; P < 0.001; R^2 = 0.42) (Figure 2.2a). The relationship between log-transformed spoor AKI and density estimates from road counts was not significantly influenced by substrate type (estimate ± SE = 0.163 ± 0.113; P = 0.154). Density significantly increased with increase in spoor AKI ($F_{3, 89}$ = 23.95; P < 0.001; R^2 = 0.43) (Figure 2.2b).

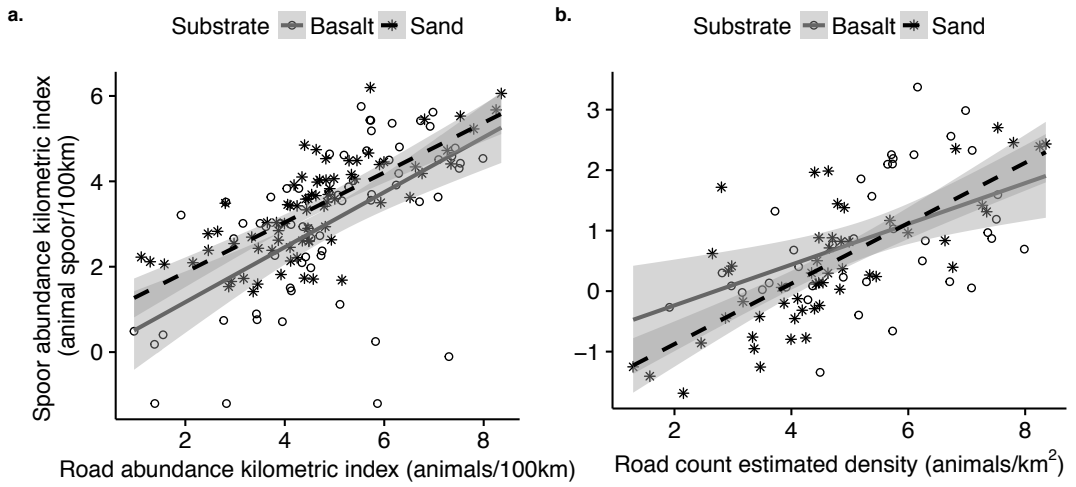


Figure 2.2 Relationship between spoor abundance kilometric index and the interaction of (a) road abundance kilometric index and (b) road count estimated density with substrate type, in Hwange National Park, Zimbabwe, for Main Camp, Ngamo, Robins, Shakwankie and Sinamatella from 2013 to 2015. Note the logarithmic scale for both the x and y-axis.

Analyses at the ungulate community level

For Main Camp and Ngamo study sites, the relationship between spoor AKI and road AKI and the relationship between spoor AKI and road density were generally strong ($r \geq 0.7$) positive correlations (for both the Pearson's and the Spearman's rank correlations)(Table 2.1; Figure 2.3). The substrate at both sites is Kalahari sandy soils (Appendix 2.1) and the combined mean ± SD correlation was strongly positive for both the relationship between spoor AKI and road AKI ($r = 0.79 \pm 0.26$ for Pearson's and $r = 0.77 \pm 0.16$ for Spearman's) and the relationship between spoor AKI and road density ($r = 0.79 \pm 0.24$ for Pearson's and $r = 0.71 \pm 0.22$ for Spearman's). However, for Sinamatella and Robins (basaltic soils), the correlations were generally weak ($r < 0.5$), particularly for the Pearson's correlation (Table 2.1). The combined mean ± SD

correlation for these two sites was weak for both the relationship between spoor AKI and road AKI ($r = 0.38 \pm 0.22$ for Pearson's and $r = 0.58 \pm 0.27$ for Spearman's) and the relationship between spoor AKI and road density ($r = 0.15 \pm 0.24$ for Pearson's and $r = 0.42 \pm 0.28$ for Spearman's). For the relationship between spoor AKI and camera trap rate, we only had enough data to do a correlation for two sessions (Table 2.1).

Table 2.1 Correlation coefficients between the abundance indices for the different herbivore species for (i) the relationship between spoor abundance kilometric index (spoor AKI) and road abundance kilometric index (road AKI), (ii) the relationship between spoor AKI and road count estimated density (road density), and (iii) the relationship between spoor AKI and camera-trapping rate (camera TR) for each study site and study session in Hwange National Park, Zimbabwe.

			Pearson's correlation coefficient			*Spearman's rank correlation coefficient*		
Site	**Year**	**Season**	**Spoor AKI and Road AKI**	**Spoor AKI and Road density**	**Spoor AKI and Camera TR**	**Spoor AKI and Road AKI**	**Spoor AKI and Road density**	**Spoor AKI and Camera TR**
Maincamp	***2013***	***Early dry***	**0.50**	**0.61**		**0.71**	**0.71**	
Maincamp	***2013***	***Late dry***	**0.99**	**0.96**		**0.95**	**0.89**	
Maincamp	***2014***	***Early dry***	**0.94**	**0.99**		**0.48**	**0.86**	
Maincamp	***2014***	***Late dry***	**0.93**	**0.81**		**0.53**	**0.36**	
Maincamp	***2015***	***Early dry***	**0.85**	**0.51**	**0.98**	**0.81**	**0.68**	**0.10**
Maincamp	***2015***	***Late dry***	**0.96**	**0.99**		**0.95**	**0.86**	
Ngamo	***2013***	***Early dry***	**0.24**	**0.99**		**0.93**	**1**	
Ngamo	***2013***	***Late dry***	**0.98**	**0.93**		**0.81**	**0.40**	
Ngamo	***2014***	***Early dry***	**0.53**	**0.30**		**0.83**	**0.50**	
Ngamo	***2015***	***Late dry***	**0.94**	**0.77**		**0.74**	**0.80**	
Sinamatella	***2013***	***Late dry***	**0.60**	**0.47**		**0.88**	**0.60**	
Sinamatella	***2014***	***Early dry***	**0.49**	**0.13**		**0.58**	**0.40**	
Sinamatella	***2014***	***Late dry***	**0.23**	**0.46**		**0.17**	**0.66**	
Sinamatella	***2015***	***Early dry***	**0.59**	**-**		**0.76**	**-**	
Sinamatella	***2015***	***Late dry***	**0.41**	**0.18**		**0.81**	**0.60**	
Robins	***2013***	***Late dry***	**-0.11**	**-0.12**	**0.97**	**0.31**	**0.20**	**0.62**
Robins	***2014***	***Early dry***	**0.52**	**-**		**0.54**	**-**	
Robins	***2014***	***Late dry***	**0.37**	**0.03**		**0.32**	**0.60**	
Robins	***2015***	***Late dry***	**0.29**	**-0.10**		**0.86**	**-0.10**	

Correlation coefficients between two abundance indices are moderate positive correlations when ($0.5 \leq r < 0.7$) and strong positive correlations when ($r \geq 0.7$).

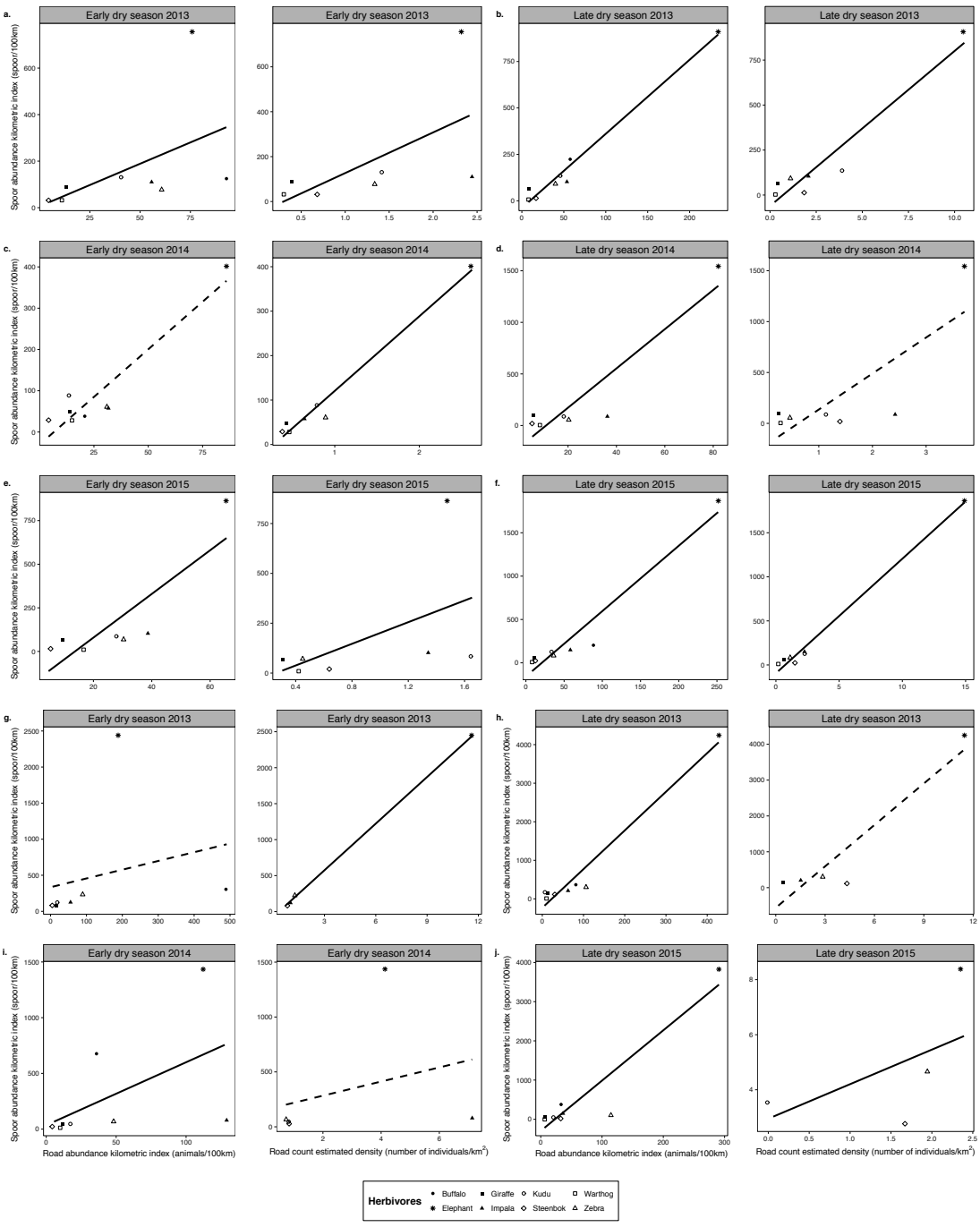


Figure 2.3 Correlations between spoor abundance kilometric index and (i) road abundance kilometric index, and (ii) road count estimated density in Hwange National Park, Zimbabwe, for Main Camp (a - f) and Ngamo (g - j) from 2013 to 2015. Solid trend lines represent relationships where both the Pearson's correlation coefficient and Spearman's rank correlation coefficient were > 0.5 and dashed trend lines for the cases where only one correlation coefficient was > 0.5.

Analyses at the species level

When we compared spoor AKI and road AKI, we found moderate ($0.5 \leq r < 0.7$) and strong ($r \geq 0.7$) positive correlations in four out of eight herbivore species for the Pearson's correlation and in four out of eight herbivore species for the Spearman's rank correlation (Table 2.2; Figure. 4). Elephant, impala and steenbok had moderate to strong positive correlations for both the Pearson's correlation and Spearman's rank correlation (Table 2.2; Figure. 4). For the relationship between spoor AKI and road density, we found moderate ($0.5 \leq r < 0.7$) and strong ($r \geq 0.7$) positive correlations for both correlation coefficients in four (elephant, impala, warthog, kudu) out of seven herbivore species for which reliable density estimates could be calculated (Table 2.2; Figure. 4). For the relationship between spoor AKI and camera trapping rate, we found moderate ($0.5 \leq r < 0.7$) and strong ($r \geq 0.7$) positive correlations in five out of eight herbivore species for the Pearson's correlation and in six out of eight herbivore species for the Spearman's rank correlation (Table 2.2). The mixed feeders (elephant and impala) and the grazers (warthog, buffalo and zebra) had moderate to strong positive correlations ($r \geq 0.5$) for both correlation coefficients (Table 2.2).

Table 2.2 Correlation coefficients for (i) the relationship between spoor abundance kilometric index (spoor AKI) and road abundance kilometric index (road AKI), (ii) the relationship between spoor AKI and road count estimated density (road density), and (iii) the relationship between spoor AKI and camera-trapping rate (camera TR) for the eight most common herbivore species in Hwange National Park, Zimbabwe.

		Pearson's correlation coefficient			*Spearman's rank correlation coefficient*		
Herbivore diet	Herbivore species	Spoor AKI and Road AKI	Spoor AKI and Road density	Spoor AKI and Camera TR	Spoor AKI and Road AKI	Spoor AKI and Road density	Spoor AKI and Camera TR
Mixed feeders	Elephant	0.74	0.50	0.63	0.64	0.57	0.80
Mixed feeders	Impala	0.78	0.73	0.81	0.78	0.81	0.60
Browsers	Kudu	0.39	0.64	0.32	0.30	0.75	0.80
Browsers	Giraffe	0.52	-0.62	-0.24	0.43	-0.62	-0.40
Browsers	Steenbok	0.50	0.26	0.37	0.56	-0.27	0.20
Grazers	Warthog	0.49	0.52	1.00	0.65	0.68	1.00
Grazers	Buffalo	-0.11	-	0.58	0.15	-	0.80
Grazers	Zebra	0.26	0.49	1.00	0.32	0.49	1.00

Correlation coefficients between two abundance indices are moderate positive correlations when ($0.5 \leq r < 0.7$) and strong positive correlations when ($r \geq 0.7$). Road count estimated densities could not be calculated for buffalo because of low number of observations.

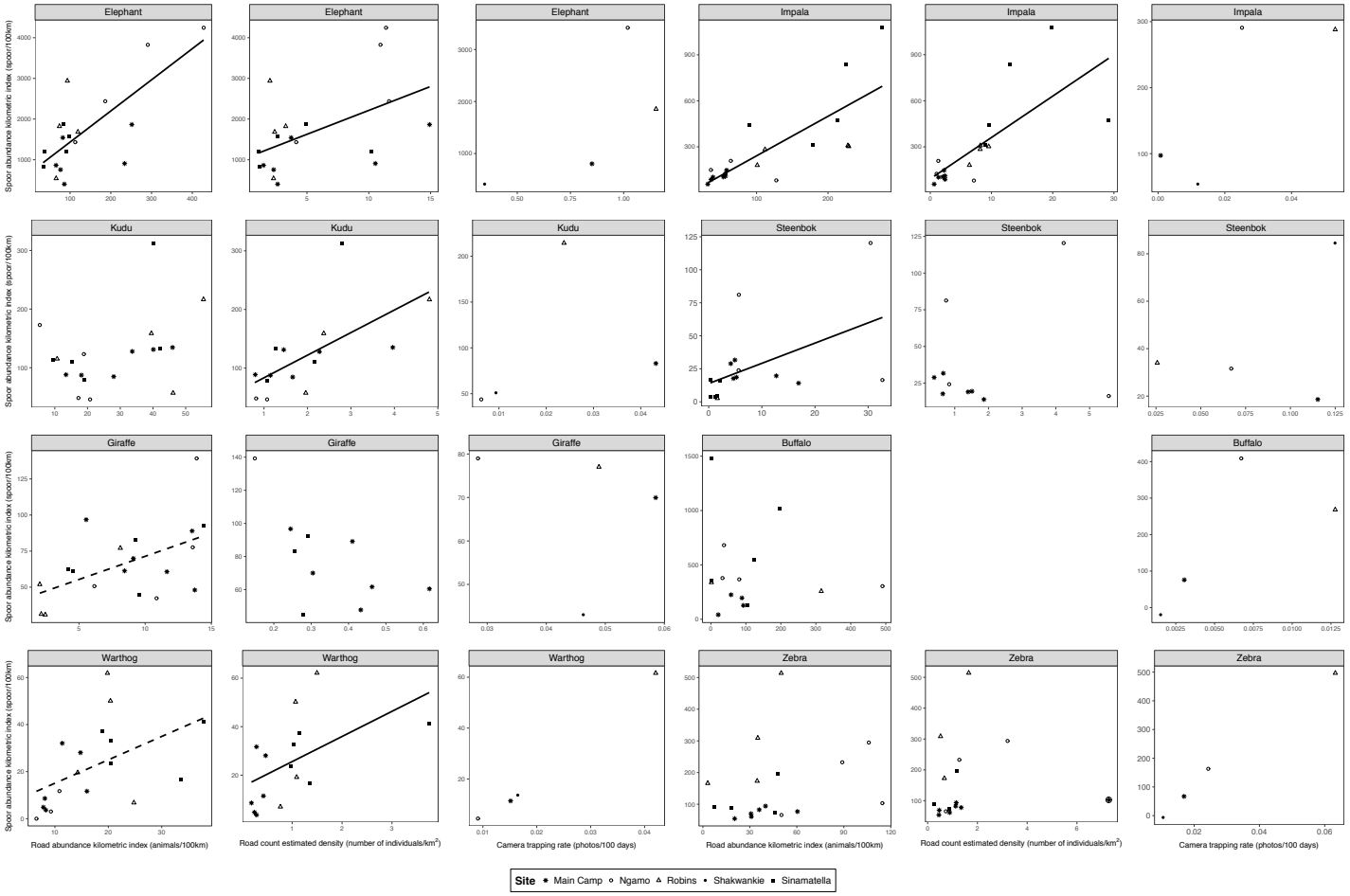


Figure 2.4 Correlations between spoor abundance kilometric index and (i) road abundance kilometric index (ii), road count estimated density,

and (iii) camera trapping rate for the mixed feeders (elephant and impala); the browsers (kudu, steenbok and giraffe), and the grazers (warthog, buffalo and zebra) in Hwange National Park, Zimbabwe, for Main Camp, Ngamo, Robins, Shakwankie and Sinamatella from 2013 to 2015. Solid trend lines are for the relationships where both the Pearson's correlation coefficient and Spearman's rank correlation coefficient were > 0.5 and dashed trend lines for the cases where only one correlation coefficient was > 0.5. An exploratory scatter plot analysis of the relationship between spoor abundance kilometric index and road count estimated density revealed an outlier in the zebra data (crossed circle) and so this point was excluded from the analyses.

Rates of change

For the relationship between spoor AKI and road AKI, we found a strong positive correlation ($r \geq 0.7$) in the rates of change of the abundance estimates of impala for the Pearson's correlation (Table 2.3), and a moderate positive correlation ($0.5 \leq r < 0.7$) in the rates of change of the abundance estimates of both impala and elephant for the Spearman's rank correlation (Table 2.3). For the relationship between spoor AKI and road density, we found strong ($r \geq 0.7$) positive correlations in the rates of change of the abundance estimates of warthog for both the Pearson's correlation and Spearman's rank correlation (Table 2.3) and a moderate ($0.5 \leq r < 0.7$) positive correlation in the rates of change of the abundance estimates of elephant and kudu for the Spearman's rank correlation (Table 2.3).

Table 2.3 Correlations of the rate of change (RC) between spoor abundance kilometric index (spoor AKI) and road abundance kilometric index (road AKI) and between spoor AKI and road count estimated density (road density) in Hwange National Park, Zimbabwe, from 2013 – 2015.

		Spoor AKI and Road AKI		Spoor AKI and Road density	
Herbivore diet	Herbivore species	RC Pearson's correlation	RC Spearman's correlation	RC Pearson's correlation	RC Spearman's correlation
Mixed feeders	Elephant	0.43	0.6	0.16	0.54
Mixed feeders	Impala	0.93	0.52	0.24	0.45
Browsers	Kudu	0.1	0.06	0.36	0.51
Grazers	Warthog	0.46	0.45	0.79	0.71

Correlation coefficients between two abundance indices are moderate positive correlations when ($0.5 \leq r < 0.7$) and strong positive correlations when ($r \geq 0.7$).

Discussion

The type of soil substrate did not influence the relationship between the spoor abundance index and the other abundance estimation methods. However, at the ungulate community level, results from our study revealed that, in sites with sandy soils (Main Camp and Ngamo), the spoor count method was able to detect differences in the relative abundance of the herbivore species. We also found that ranking of species abundance was somewhat consistent across methods. This was not the case in sites with basaltic soils (Sinamatella and Robins), which corroborated previous findings on the importance of substrate for spoor counting (Funston *et al.*, 2010). At the species level, spoor AKI had moderate to strong positive correlations with at least one of the other abundance indices from other more traditional abundance estimate methods for all the study herbivore species. However, because road count surveys using distance sampling is recognized as the most robust method for herbivore population abundance estimation, and this methodology is widely used around the world (Anderson *et al.*, 1979; Burnham, Anderson & Laake, 1980; Duckworth, 1998; Plumptre, 2000), including previous studies in Hwange National Park (Chamaillé-Jammes *et al.*, 2009), our findings suggest that spoor counts can be reliable when spoor AKI correlate with road count density estimates.

In this study, the relationship between spoor AKI and road count estimated density was positively correlated, with moderate to strong positive correlations, in four (elephants, impalas, kudus and warthogs) out of the seven herbivore species for which density estimates could be calculated. Density could not be calculated for the low abundance and large group forming species (buffalo), because we failed to collect the threshold number of observations required to generate a density estimate (Buckland *et*

al., 1993). Spoor counting appeared to be reliable for elephant and impala, which are abundant mixed-feeders and hence habitat generalists likely to be widespread in the landscape, and abundance estimates for these two species produced positive correlations (moderate to strong) when comparing spoor AKI with the other three indices. We found no relationship, or weaker relationships between spoor AKI and other methods, for the low abundance (giraffe) and small cryptic browser species (steenbok). Interestingly, for the most common browser, kudu, the correlation was strong (for Spearman's correlation) with the road density estimates, which take into account probability of detection. Unexpectedly, spoor counting appeared to work quite well for warthog, while for other grazers (buffalo and zebra), our results revealed strong correlations between spoor AKI and camera trapping rate, but no correlation between spoor AKI and either road AKI or road density estimates, suggesting that for low encounter rate species that occur in large groups such as the buffalo and to a lesser extent zebra, abundance could not be estimated accurately by some of the methods used. This illustrates the importance of considering the abundance, ecology and behaviour of the target species when selecting animal abundance estimation methods (Wilson & Delahay, 2001) since different methods have different strengths for different animal species. Movement ecology of the target species should also be considered, as herbivores that move more will be more likely to be detected through spoor counts or by camera traps. The spoor count method relies upon the systematic identification of spoor and consequently results are potentially variable depending on the capabilities and experience of the trackers (Stander, 1998), but also on the spoor detectability, which might explain why steenbok relative abundance is not well estimated by spoor counting.

Spoor AKI and the traditional line transect method are carried out along roads and concerns have arisen about potential biases linked to this sampling along roads (Buckland *et al.*, 2001) as roads have been shown to influence the ecology of some species (e.g. Varman & Sukumar, 1995). Yet, in many ecosystems, roads are the only practical way to sample animal abundance. Although we had a small sample size, results from this study confirm that sampling along roads does not introduce a bias to abundance estimates since where there was a high camera-trapping rate (less road dependent); there was also a high spoor abundance. However, the use of camera trapping rate as an index of abundance has been criticised as it requires describing and calibrating the relationship between capture rate and true density (Jennelle, Runge & MacKenzie, 2002). Foster and Harmsen (2012), pointed out that in some cases capture rate can vary independently of density and that when using capture rate only, it is often difficult to distinguish between many individuals with few recaptures versus few individuals with many recaptures. However, if animals move randomly with respect to the camera trap locations then camera trap rates should on average be correlated with animal abundance (Carbone *et al.*, 2002). O'Brien, Kinnaird and Wibisono (2003) for tigers and their prey and also Balme, Slotow and Hunter (2010) for leopards and their prey, found that relative abundance indices calculated from camera trap surveys were directly related to their true densities calculated from the capture-recapture method and the line transect sampling method. These studies and indeed ours, highlight the potential of using the camera trapping method as a survey or monitoring tool for herbivores. Several studies have encouraged the use of methods such as capture-mark-recapture since they provide estimates of density with a much greater level of precision (Gopalaswamy *et al.*, 2012; Broekhuis & Gopalaswamy, 2016). The capture-mark-recapture method relies on individual recognition; most of

the herbivore species assessed in our study (except zebras and giraffes) could not be individually identified.

The correlations for the rate of change were mostly low, revealing that while spoor counting is reliable for detecting large changes in abundance, it is not reliable to estimate short-term (e.g. year-to-year, or session-to-session) temporal changes in abundance, except for impala and warthog for which spoor AKI changed at more or less the same rate when compared to other more traditional methods. The accuracy of the spoor count method can be increased by repeatedly sampling each transect, during each survey (Stander, 1998; Funston *et al.*, 2010). This was not possible during this study and is clearly one limitation of this work but it was not achievable in terms of cost and time to monitor such large areas. In light of the above, we conclude that in Hwange National Park the spoor count method works well in sandy soils but counting spoor may be much harder in other soil substrates. The spoor count method is reliable to detect large changes in relative abundance either between species or for one species between different periods. The spoor count method performs well for species that are often encountered. It works well for mixed feeders (elephants and impalas), which are abundant and are habitat generalists, as well as for kudu, an abundant browser that is encountered at relatively high rates in Hwange because it is a wooded savannah. The spoor count method also performed well for warthog, whose abundance estimates using the spoor count method changed at the same rate as the road density estimates. We recommend using the spoor count method for comparing between or within-site, if of the same substrate. Further studies should investigate whether increasing the sampling effort within sessions is worthwhile to improve census reliability and increase the spectrum of species surveyed. The spoor-based index should be used to

estimate herbivore relative abundance when a high level of tracking expertise is available, when exact densities are not important, and when the abundance estimates are to be used for carnivore studies since it is most cost- and time-effective to carry out herbivore and carnivore spoor counts simultaneously.

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Appendix

Appendix 2.1 Summary of the study sites, size, substrate types and sampling efforts and road penetration (Road P) for both the road count and spoor count surveys in Hwange National Park, Zimbabwe, from 2013 to 2015.

Study site	Substrate	Season	Year	Road sampling effort	Road P	Spoor sampling effort	Road P
Main Camp (1266 km²)	Kalahari sands	Early dry	2013	650	0.51	246	0.19
		Early dry	2014	581	0.46	242	0.19
		Early dry	2015	625	0.49	248	0.20
		Late dry	2013	650	0.51	247	0.20
		Late dry	2014	650	0.51	247	0.20
		Late dry	2015	567	0.45	244	0.19
Ngamo (1628 km²)	Kalahari sands	Early dry	2013	265	0.16	265	0.16
		Early dry	2014	275	0.17	239	0.15
		Early dry	2015	0	0	269	0.17
		Late dry	2013	260	0.16	263	0.16
		Late dry	2014	0	0	261	0.16
		Late dry	2015	260	0.16	273	0.17
Robins (1026 km²)	Basalt soils	Early dry	2013	0	0	295	0.29
		Early dry	2014	196	0.19	250	0.24
		Early dry	2015	0	0	226	0.22
		Late dry	2013	222	0.22	294	0.29
		Late dry	2014	234	0.23	265	0.26
		Late dry	2015	245	0.24	266	0.26
Sinamatella (1060 km²)	Basalt soils	Early dry	2013	0	0	346	0.33
		Early dry	2014	333	0.31	325	0.31
		Early dry	2015	333	0.31	337	0.32
		Late dry	2013	333	0.31	344	0.32
		Late dry	2014	333	0.31	327	0.31
		Late dry	2015	333	0.31	318	0.30
Shakwankie (2129 km²)	Kalahari sands	Early dry	2013	0	0	269	0.13
		Early dry	2014	0	0	261	0.12
		Late dry	2013	0	0	252	0.12

Appendix 2.2 Camera trapping effort (in days) and number of independent photographic events for the eight most common herbivore species captured in Main Camp (early dry season 2015), Robins (late dry season 2013), Shakwankie (late dry season 2013) and Ngamo (late dry season 2014) in Hwange National Park, Zimbabwe.

	Main Camp	Robins	Shakwankie	Ngamo
Effort (days)	2325	1638	1647	2136
Number of independent photographic events				
Buffalo	8	21	3	13
Elephant	1973	1885	639	2080
Giraffe	138	80	76	62
Impala	7	85	21	61
Kudu	101	38	16	11
Steenbok	274	42	205	141
Warthog	33	68	29	21
Zebra	41	98	14	58

Chapter 3



Applying the Resource Dispersion Hypothesis to a fission-fusion society: A case study of the African lion (*Panthera leo*)

Under Revision for resubmission to *Proceedings of the National Academy of Sciences of the United States of America* (PNAS)

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Abstract

The relationship between spatial and temporal distribution of resources and patterns of sociality is widely discussed. The Resource Dispersion Hypothesis (RDH) was formulated to explain why animals sometimes live in groups from which they derive no obvious sociological benefits. While some empirical tests have supported the RDH, others have not, so firm conclusions remain equivocal. Here, we test four predictions of the RDH in an African lion population in the context of their fission-fusion society. We analysed data on group composition of GPS-collared female lions and prey availability. First, in accord with the RDH, lion group size was not correlated with home range size. Second, and also in accord with the RDH, home range size increased with distance between encounters with prey herds. Third, and also in accord with the RDH, total pride size increased with increase in coefficient of variation of mean prey herd size. Fourth, and also in accord with the RDH, pride size increased with increase in mean prey herd size. Our study is the first to show that fission-fusion dynamics plays an important role in the relationship between sociality and prey availability, which explains why the relationship between patch richness and group size is complex and was not revealed easily before. In the complicated reality of nature, observational tests of hypotheses are seldom clear-cut, so it is striking that four predictions of the RDH appear to be upheld in this lion population. To the continuing explorations of the RDH, we add an adaptation to account for the dynamics of fission-fusion society.

Introduction

The selective advantage of group living is, in many social animals, readily attributed to the direct benefits of cooperation, such as cooperative hunting, alloparental care, defense of kills and territorial defense (Krause & Ruxton, 2002). However, some species such as European badgers (*Meles meles*) (Kruuk, 1978), giant otters (*Pteronura brasiliensis*) (Groenendijk *et al.*, 2015), red foxes (*Vulpes vulpe*s) (Macdonald, 1981), and brown hyaenas (*Hyaena brunnea*) (Mills, 1982) live in groups but they often travel and hunt alone and show no obvious sociological benefits of group living. In 1983, Macdonald crystalized an idea that linked ecological factors, such as spatio-temporal patterns in the richness and dispersion with which resources become available, with sociological characteristics such as the size of social groups and the extent of their territories (Macdonald, 1983). The quest for an ecological explanation (not invoking cooperation) for group-living (Kruuk, 1978), and the link between the richness of ephemeral resource patches and group size (Bradbury & Vehrencamp, 1976) had been taking shape, and Macdonald codified it as the Resource Dispersion Hypothesis (RDH) (Macdonald, 1983), which has stimulated much research, and some support (Macdonald & Johnson, 2015).

The RDH is an hypothetical model that predicts that where resources are heterogeneously distributed in space and time, individuals have to defend a large enough territory to guarantee that there are always sufficient resource patches available and this allows several individuals to share the same resources without imposing intolerable, if any, costs on each other (Macdonald, 1983; Carr & Macdonald, 1986; Johnson *et al.*, 2002). The RDH describes how groups may form even in the absence of any functional advantage to any individual from the presence

of another (Carr & Macdonald, 1986; Bacon, Ball & Blackwell, 1991). The RDH can be adapted to specific circumstances (a flexibility that some consider a criticism), but here we focus on four of its general predictions: (i) group size and territory size (referred to as home range size in this study) are not correlated, (ii) the dispersion of resources determines territory size, (iii) group size increases with increase in resource heterogeneity, and (iv) group size is determined by the richness of resource patches (Macdonald, 1983; Carr & Macdonald, 1986; Macdonald & Johnson, 2015).

While the RDH is widely recognized as a potential explanation for grouping behavior in animals, there has nonetheless been particular debate around the prediction of the RDH that patch richness is positively related to group size: some studies garner support for this prediction (e.g. Kruuk & Parish, 1982) for European badgers and (Verdolin, 2009) for Gunnison's prairie dog (*Cynomys gunnisoni*)) while others report no evidence for it (e.g. Revilla & Palomares, 2002) also for European badgers (see Macdonald & Johnson, 2015 for a review). In a study that was seminal to the RDH, Bradbury and Vehrencamp (1976) reported that territory sizes of neotropical bats were determined by the dispersion of insect swarms over rivers, and the richness of these swarms determined bats flock size. With respect to African lions (*Panthera leo*), water sources might be a critical resource for lions not because lions drink there, but because their prey aggregate there to access water (Redfern *et al.*, 2003; Valeix *et al.*, 2009b), and indeed waterholes in Hwange National Park, Zimbabwe, and river confluences in the Serengeti National Park, Tanzania, have emerged as RDH-style patches (and Mosser *et al.*, 2009 respectively; see Valeix *et al.*, 2012). Valeix *et al.* (2012) offered particular insight through their discovery that prey biomass visiting a particular waterhole, which they interpreted as a proxy for patch richness, appeared to

limit the group size of lions hunting there. Mosser, Kosmala and Packer (2015) went on to explore the interaction of landscape structure, population density and behaviour in influencing group territoriality in Serengeti lions. Their study found resource heterogeneity to be a prerequisite to the evolution of group territoriality and that at lower resource quality social groups exclude solitary individuals from richer patches. Our study now seeks to build on this growing body of knowledge, which explores the role of the interaction of ecology and behaviour in the evolution of sociality. Our approach differs from its predecessors by measuring prey distribution directly and by taking into account for the first time the role of fission-fusion dynamics, which is characteristic of lion sociality.

Lions live in social groups of between two to eighteen related females, their dependent offspring, and a coalition of adult males; there is no social hierarchy among pride lionesses (Packer & Pusey, 1982). Although lions are widely said to be the most conspicuously social of felids, pride members are often not together and a process of fission-fusion commonly results in the pride splitting into smaller sub-groups (Schaller, 1972; Packer & Pusey, 1997). Schaller (1972) speculated that the spatial and temporal variability of resources in heterogeneous landscapes caused these fission-fusion dynamics. However, the probability of a pride splitting is higher in larger lion prides than in smaller prides (VanderWaal, Mosser & Packer, 2009). The evolution of fission-fusion social organization in both the spider monkey (*Ateles paniscus chamek*) and chimpanzee (*Pan troglodytes*) has been linked to the high-level of feeding competition between females within a group, caused by the spatial and temporal patchiness in food dispersion and abundance (Symington, 1990). Sueur *et al.* (2011) attributes fission-fusion dynamics in avian systems to the variation in the

environment across seasonal diel and tidal cycles. Black kites (*Milvus migrans*) and Egyptian Vultures (*Neophron percnopterus*) are migratory scavengers, which aggregate when food resources are scarce in Europe, but rarely do so in the Sahel where carcasses are widely available (Silk *et al.*, 2014). Given that both patterns of sociality and resource distribution have an effect on fission-fusion dynamics, it is therefore important to understand how the fission-fusion dynamics can subsequently influence the relationship between prey availability and sociality.

Here, we test the four predictions of the RDH and the effect of fission-fusion on the relationship between prey availability and sociality based on field data collected on lions in Hwange National Park. Such field tests are few because the data necessary are not readily gathered (Johnson *et al.*, 2002). In the case of lions, waterholes have been useful surrogates for prey hotspots in Hwange National Park (Valeix *et al.*, 2010) and most lion kills occur there (Davidson *et al.*, 2013). Nonetheless, lions also make kills in other parts of their home ranges, so we have sought to measure prey availability directly and at the home range scale. We considered a herd of prey to represent a resource patch that is available to lions and the different characteristics of the herd such as herd size and prey body size to characterize the richness of the patch. All three dimensions of prey (prey dispersion, mean prey herd size and mean prey body size) have key implications to lion foraging and consequently ranging behaviour and sociality (Mosser *et al.*, 2009; Valeix *et al.*, 2012).

The strongest tests of the RDH occur when changes in resource distribution and richness can be experimentally manipulated and then test the predicted changes in the animals' territory or group size at each stage (Macdonald *et al.*, 2010b). The spatial

heterogeneity in prey abundance and dispersion in Hwange National Park provided us with a valuable opportunity to examine the effects of prey availability on lion sociality. The heterogeneity of this landscape and the ability to measure and quantify the abundance and distribution of prey at the home range scale facilitated our test of the four main predictions from the RDH, specifically (i) home range size and group size are not correlated, (ii) home range size increases with increase in prey dispersion, (iii) group size increases as resource heterogeneity increases, and (iv) group size increases with increase in patch richness. We further assessed the role of fission-fusion dynamics in the relationship between prey availability and sociality. We expected the frequency of pride fission to have an important effect by interacting with patch richness to influence group size.

Methods

Study area

Hwange National Park is a semi-arid dystrophic savannah on Kalahari sands, on the north-western border of Zimbabwe and it covers approximately 15 000 km^2. The east and southern parts of the park are dominated by open wooded savannas on Kalahari sands, primarily teak woodland (*Baikiaea plurijuga)* and *Combretum/Terminalia* woodlands. Batoka basalt and Karoo sediments in the north and north-west of the park are dominated by *Colophospermum mopane* woodlands interspersed with grassland vleis. Three seasons characterise Hwange National Park: early dry season (March - June), late dry season (July - October) and the wet season (November - February). During the wet season, water becomes available in waterholes, rivers and pools. Some of these sources of drinking water dry up during the dry season and only pumped waterholes (~ 50), mostly in the North of the park, maintain water

availability during the dry season. These differences in vegetation and water distribution across the park result in differences in the distribution of herbivores in terms of both assemblages and abundance (Chamaillé-Jammes *et al.*, 2016).

Lion data

We used data from 12 female lions, all from different prides across the park, equipped with GPS radio-collars between 2013 and 2015. The lions' locations were available every two hours, day and night. Positional data from the GPS radio-collars were downloaded regularly and for this study we used lion location data for the early dry season and late dry season only (which corresponds to periods when prey data were available). Some of the collared female lions were studied for more than one season resulting in a total of 17 samples. Lions were located and observed at least five times a month to record the size and composition of their groups at those times. For each lion sighting, we recorded the number of individuals, identity, age and sex of the individuals in the group. We looked at two aspects of lion group size: (1) total pride size (total number of adult females, sub-adults and cubs in the pride) and (2) mean sub-group size (mean number of adult females, sub-adults and cubs observed in sub-groups). We also calculated for each pride the frequency of pride fission, calculated as the number of times the pride was seen in sub-groups as a percentage of the total number of pride and sub-group sightings. We defined home ranges as the 90% probability contour of location distribution using the fixed kernel density estimator (Powell, 2000) and the reference smoothing factor href (Hemson *et al.*, 2005). Only animals whose GPS receiver was operational during a whole season were included in the analyses. Home range analyses were undertaken using the AdehabitatHR package in the statistical software R (Calenge, 2006). An earlier analysis by Loveridge *et al.*

(2009) in Hwange National Park revealed that lionesses from the same pride stayed together most of the time (89.2 ± 7.4% of the time), we therefore assumed in this study that individual home ranges generally represent pride ranges.

Prey data

We conducted multi-species spoor surveys in Hwange National Park from 2013 to 2015 during the early dry season and the late dry season. Selected sections along roads or routes were driven and we identified and counted spoor in different sectors of the park. When fresh spoor (less than 24hrs old) was encountered, it was assessed for species, group size, age and sex (when possible). During the surveys, spoor of a range of herbivores and carnivores were identified to species, but only spoor from common lion prey species in the area was used in this analysis. Prey species included in the analysis were: Burchell's zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and juvenile African elephant (*Loxodonta africana*) (frequently recorded as prey during drought years in Hwange; Loveridge *et al.*, 2006).

The spoor survey data were overlaid on lion home ranges in QGIS (Quantum GIS Development Team, 2017) and the spoor transects that fell within each lion home range were clipped. For each home range and each season we assessed five measures of prey availability: one index of prey dispersion (number of km/prey herd), two indices of resource heterogeneity (coefficient of variation of mean prey herd size and

coefficient of variation of mean prey body size) and three indices of patch richness (mean prey herd size, mean prey body size (kg) and total prey biomass). Prey body size was calculated using the average adult female body mass of individuals in a population obtained from Cumming and Cumming (2003). These measures of prey availability describe the important prey attributes for lions. A measure of prey dispersion describes the distance lions have to travel to encounter prey or the effort involved in searching for prey. A measure of resource heterogeneity describes the variability in which lions encounter patches of different levels of richness. The mean prey herd size (a measure of patch richness) is significant to lions as larger herds provide more than one lion with an opportunity to make a kill (Schaller, 1972) and larger prey herds also provide a higher chance of lions finding a vulnerable individual within the herd. The mean prey body size (also a measure of patch richness) represents the quality of the food resource in terms of the energy gained from consumption of that prey species and larger prey are rich patches as they can feed several lions (Carr & Macdonald, 1986). The total prey biomass (another measure of patch richness) is the mean prey body size multiplied by the mean herd size and it represents the total energy to be gained from each patch (i.e. each prey herd). For each lion home range, we also calculated an index of waterhole dispersion, calculated by averaging the distance between two neighbouring waterholes over all waterholes encompassed within the home range.

Statistical Analyses

Data were first tested for normality and mean prey body size was subjected to a logarithmic transformation to reach normality requirement. We preliminarily tested the correlations between all measures of prey availability and we found that total prey

biomass was strongly correlated with both the mean prey body size and the mean prey herd size and we therefore dropped total prey biomass from the analysis as the other two were better measures (as defined above). We used linear mixed-effects regression, lmer, with the lme4 package in R (Bates *et al.*, 2015) to test our four RDH predictions and lion identity was included as a random factor. We tested the first RDH prediction that there is no correlation between home range size and group size. We then tested the second RDH prediction that the dispersion of resources (mean distance between two neighbouring waterholes and mean distance between encounters with prey herds) determines territory size. In this test, we included both measures of resource dispersion in an attempt to disentangle effects of prey dispersion from that of waterhole dispersion. We later tested the third RDH prediction that group size increases with increase in resource heterogeneity and the fourth RDH prediction that group size is determined by the richness of resource patches. For the fourth RDH prediction, we first did a preliminary analysis to assess the relationship between frequency of pride fission and total pride size and the relationship between coefficient of variation of sub-group size and total pride size. To test the effect of the frequency of pride fission on the relationship between patch richness and group size, we examined separately for each measure of lion group size (total pride size and the mean sub-group size) its associations with the two indices of patch richness (mean prey herd size and mean prey body size (kg)) and the interaction of the two indices of patch richness with frequency of pride fission. For a set of candidate models, the model with the lowest AICc (Akaike Information Criterion corrected for small sample size) was considered the most plausible model and models with ΔAICc values of < 2 were also considered as plausible models (Burnham & Anderson, 2002). Information-theoretic weights (w) were calculated from the ΔAICc values. When more than one

model was plausible, we performed model averaging and calculated the coefficient estimates of the averaged variables (Burnham & Anderson, 2002). We also calculated the confidence intervals of the coefficient estimates and if zero was lying within that confidence interval, then there was a possibility that the mean of that variable was not different from zero.

Results

1. Relationship between home range size and group size

Total pride size did not correlate with home range size (estimate ± SE = -6.37 ± 16.35; t (2.6) = -0.39; p = 0.73) (Figure 3.1a). The outliers for home range size were as a result of the very large home ranges of lions in the Shakwankie area (see Figure 2.1). We also found no correlation between mean sub-group size and home range size (estimate ± SE = 34.08 ± 52.22; t (11) = 0.65; p = 0.53) (Figure 3.1b).

2. Relationship between home range size and prey dispersion

The best model explaining home range size included a positive effect of the mean distance between encounters with prey herds, an index of prey dispersion, and a positive effect of mean distance between two neighbouring waterholes, an index of waterhole dispersion (Table 3.1). Home range size increased with increase in the mean distance between encounters with prey herds (estimate ± SE = 2063 ± 993; 95% CI = [117, 4010]) (Figure. 3.1c). However, the coefficient estimate of mean distance between two neighbouring waterholes had a confidence interval that included zero (estimate ± SE = 106 ± 70; 95% CI = [-32, 245].

Table 3.1. Predictor variables, Akaike Information Criterion with the small-sample bias adjustment (AICc), delta AICc (ΔAICc), and Akaike weights (*w*) of candidate models for the relationship between lion home range size and resource dispersion (prey dispersion (mean distance between encounters with prey herds) and waterhole dispersion (mean distance between two neighbouring waterholes)) for lion prides in Hwange National Park, Zimbabwe, between 2013 and 2015. Bold indicates the most plausible models (ΔAICc < 2).

	Home range size		
Models	AICc	ΔAICc	*w*
Null	216.5	24.21	0.00
Prey dispersion	200.2	7.91	0.02
Waterhole dispersion	207.1	14.81	0.00
Prey dispersion, Waterhole dispersion	**192.3**	**0.00**	**0.98**

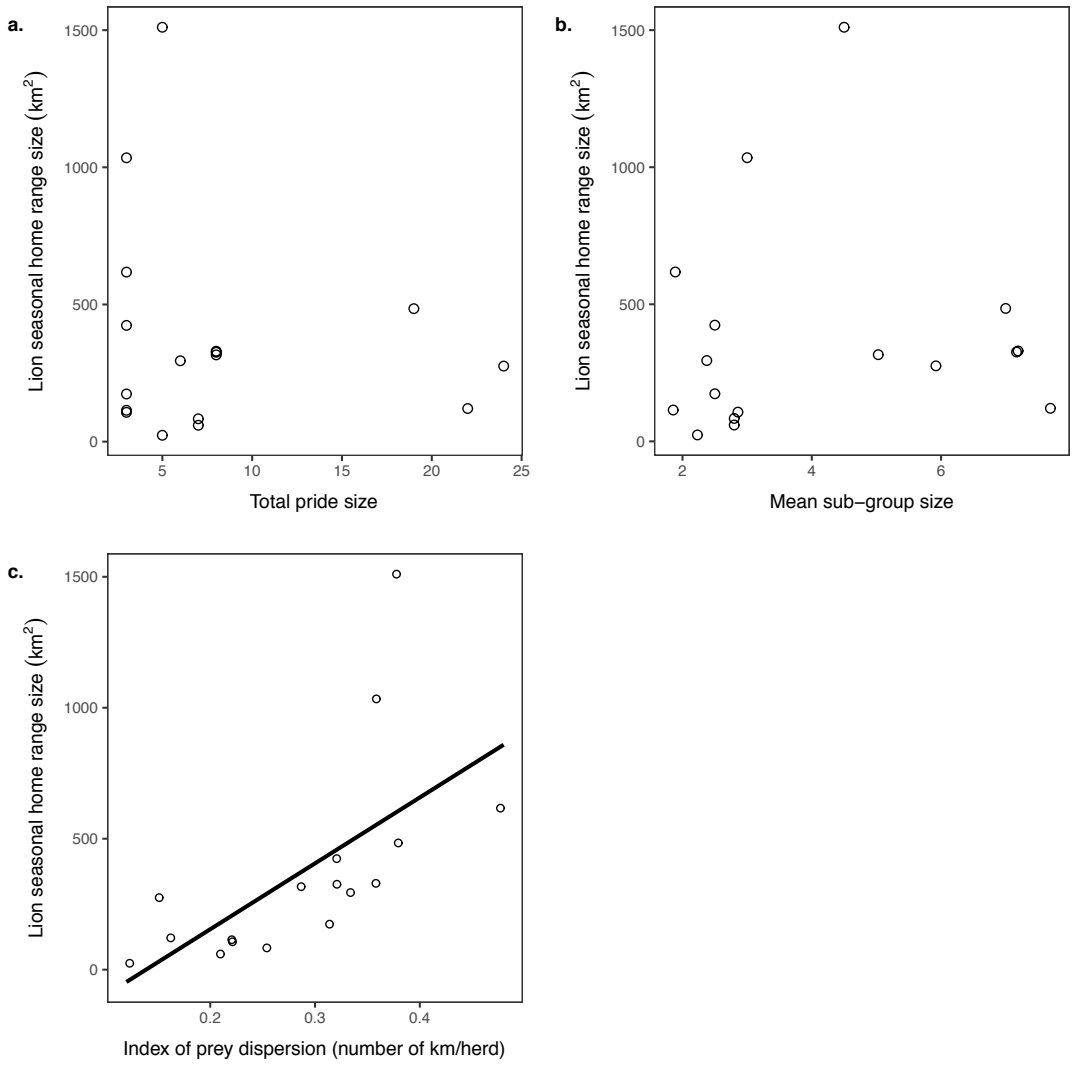


Figure 3.1 Relationship between female lion seasonal home range size and a) total pride size, b) mean sub-group size and c) the index of prey dispersion (number of km/prey herd) in Hwange National Park, Zimbabwe, between 2013 and 2015.

3. Relationship between group size and resource heterogeneity

The best model explaining total pride size included a positive effect of the coefficient of variation of mean prey herd size, an index of resource heterogeneity (Table 3.2). The model that included positive effects of both the coefficient of variation of mean prey herd size and the coefficient of variation of mean prey body size, also an index of resource heterogeneity, was also plausible (ΔAICc < 2, Table 3.2) and hence

included in the model averaging. Total pride size increased with increase in the coefficient of variation of mean prey herd size (estimate ± SE = 0.92 ± 0.20; 95% CI = [0.53, 1.31]) (Figure 3.2a). However, the confidence interval of the coefficient estimate of the coefficient of variation of mean prey body size included zero (estimate ± SE = 1.94 ± 1.82; 95% CI = [-1.63, 5.51]). When the best model for the relationship between total pride size and resource heterogeneity was controlled for patch richness, variation in heterogeneity independently influenced pride size. The best model for mean sub-group size included a positive effect of the coefficient of variation of mean prey body size (Table 3.2). The null model was the second best model also plausible (ΔAICc < 2; Table 3.2) and hence included in the model averaging. However, the confidence interval of the coefficient estimate of the coefficient of variation of mean prey body size included zero (estimate ± SE = 1.49 ± 1.22; 95% CI = [-0.91, 3.88]).

Table 3.2 Predictor variables, Akaike Information Criterion with the small-sample bias adjustment (AICc), delta AICc (ΔAICc), and Akaike weights (*w*) of candidate models for the relationship between group size (total pride size and mean sub-group size) and resource heterogeneity (coefficient of variation of mean prey herd size (CV Herd size) and coefficient of variation of mean prey body size (CV Body size)) for lion prides in Hwange National Park, Zimbabwe, between 2013 and 2015. Bold indicates the most plausible models (ΔAICc < 2).

	Total pride size			Mean sub-group size		
Models	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
Null	94.6	7.14	0.01	74.3	**0.29**	**0.38**
CV Herd size	87.5	**0.00**	**0.46**	77.0	3.03	0.10
CV Body size	90.5	3.04	0.10	74.0	**0.00**	**0.44**
CV Herd size, CV Body size	87.7	**0.16**	**0.43**	77.2	3.23	0.09

4. Relationship between group size and patch richness

The best model for total pride size included a positive effect of mean prey herd size and a positive effect of mean prey body size (Table 3.3). The model that included a positive effect of mean prey herd size was also a plausible model (ΔAICc < 2; Table 3.3) and hence included in the model averaging. Total pride size increased with increase in mean prey herd size (estimate ± SE = 0.71 ± 0.17; 95% CI = [0.38, 1.01]) (Figure 3.2b). Nonetheless, the confidence interval of the coefficient estimate of mean prey body size included zero (estimate ± SE = -2.33 ± 1.52; 95% CI = [-5.30, 0.64]). The outliers for total pride size were caused by the very large lion prides in the Ngamo area (see Figure 2.1). The best model for mean sub-group size included a positive effect of mean prey body size (Table 3.3); the null model was the second best model and also plausible (ΔAICc < 2; Table 3.3) and hence included in the model averaging. However, the model averaged coefficient estimate of mean prey body size had a confidence interval that included zero (estimate ± SE = 2.28 ± 3.11; 95% CI = [-3.82, 8.38].

Table 3.3 Predictor variables, Akaike Information Criterion with the small-sample bias adjustment (AICc), ΔAICc, and Akaike weights (*w*) of candidate models for the relationship between group size (total pride size and mean sub-group size) and patch richness (mean prey herd size (Herd size) and mean prey body size (Body size)) for lion prides in Hwange National Park, Zimbabwe, between 2013 and 2015. Bold indicates the most plausible models (ΔAICc < 2).

	Total pride size			Mean sub-group size		
Models	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
Null	94.6	4.84	0.05	74.3	**1.06**	**0.33**
Herd size	90.7	**0.87**	**0.34**	78.3	5.15	0.04
Body size	93.1	3.29	0.10	73.2	**0.00**	**0.56**
Herd size, Body size	89.8	**0.00**	**0.52**	77.4	4.23	0.07

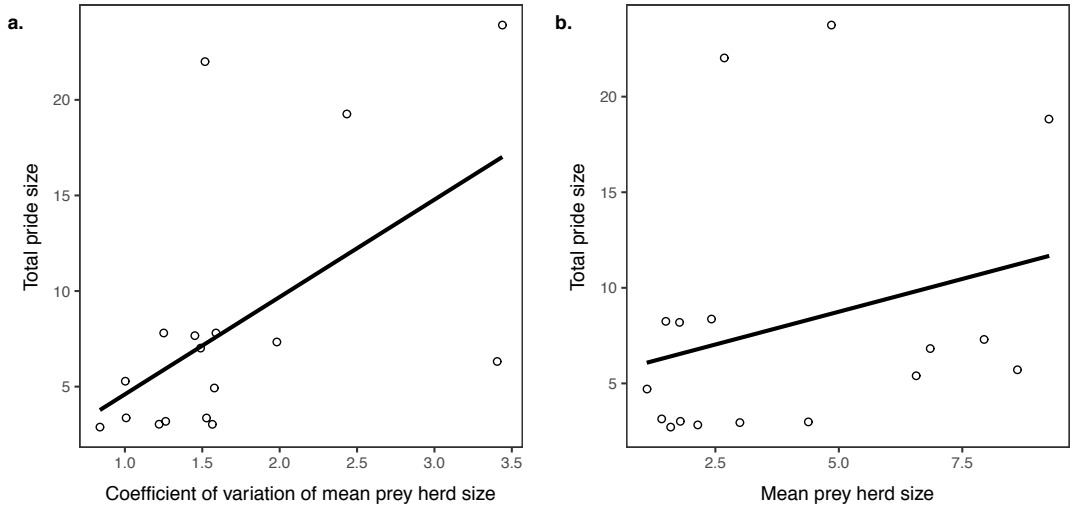


Figure 3.2 The relationship between a) an index of resource heterogeneity (coefficient of variation of mean prey herd size) and total pride size and b) an index of patch richness (mean prey herd size) and total pride size in Hwange National Park, Zimbabwe between 2013 and 2015

5. Influence of fission-fusion dynamics on the relationship between group size and patch richness

Total pride size significantly influenced frequency of pride fission (estimate ± SE = 0.035 ± 0.008; t (15) = 4.64; $p < 0.001$), with frequency of pride fission increasing with increase in total pride size (Figure 3.3a). Total pride size also significantly influenced the coefficient of variation of mean sub-group size (a measure of variability in sub-group size), with variability in sub-group size increasing with increase in total pride size (estimate ± SE = 0.036 ± 0.007; t (15) = 5.26; $p < 0.001$) (Figure 3.3b).

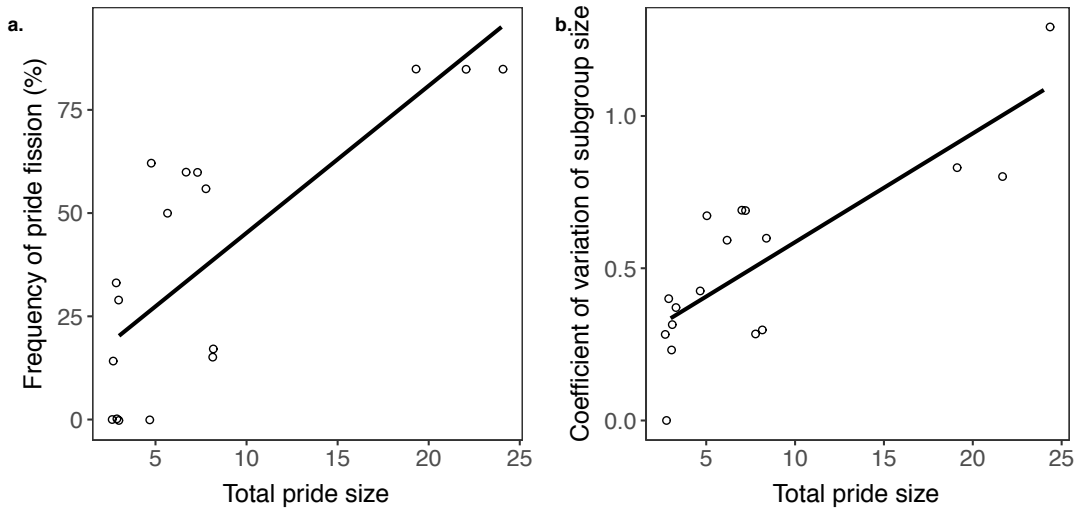


Figure 3.3 The relationship between a) total pride size and the frequency of pride fission (the number of times the pride was in sub-groups as a proportion of the total number of whole pride and sub-group sightings) and b) total pride size and the coefficient of variation of lion sub-group size (a measure of variability in sub-group size) in Hwange National Park, Zimbabwe between 2013 and 2015.

When the frequency of pride fission was included as an interaction to the relationship between group size and patch richness we found that the best model to explain total pride size included a positive effect of mean prey body size (estimate ± SE = 1.02 ± 1.12; 95% CI = [-0.70, 2.72]), a positive effect of frequency of pride fission (estimate ± SE = 118.12 ± 15.78; 95% CI = [93.87, 142.07]) and a negative effect of the interaction between mean prey body size and frequency of pride fission (estimate ± SE = -19.11 ± 2.55; 95% CI = [-22.98, -15.19]) (Table 3.4). The relationship between total pride size and mean prey body size becomes more negative at higher frequencies of pride fission (Figure 3.4). The best model to explain mean sub-group size included, a positive effect of mean prey body size, a negative effect of frequency of pride fission and a positive effect of the interaction of mean prey body size with frequency of pride fission (Table 3.4). A model that included a positive effect of mean prey body size was also plausible (ΔAICc < 2; Table 3.4) and hence included in model averaging. However, model averaged coefficient estimates of all the variables had confidence intervals that included zero; mean prey body size (estimate ± SE = 1.63 ± 3.03; 95% CI = [-4.31, 7.56]); frequency of pride fission (estimate ± SE = -74.82 ± 46.03; 95% CI = [-165.03, 15.40]) and interaction between mean prey body size and frequency of pride fission (estimate ± SE = 11.60 ± 7.46; 95% CI = [-3.02, 26.22]).

Table 3.4 Predictor variables, Akaike Information Criterion with the small-sample bias adjustment (AICc), delta AICc (ΔAICc), and Akaike weights (*w*) of candidate models for the relationship between group size (lion pride size, and mean sub-group size) and patch richness (mean prey herd size (Herd size) and mean prey body size (Body size)), frequency of pride fission (Fission) (the number of times the pride was in sub-groups as a proportion of the total number of whole pride and sub-group sightings) and their interaction for lion prides in Hwange National Park, Zimbabwe, between 2013 and 2015. Bold indicates the most plausible models (ΔAICc < 2).

	Total pride size			Mean sub-group size		
Models	AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
Null	94.6	11.01	0.00	74.3	2.48	0.15
Herd size	90.7	7.03	0.02	78.3	6.57	0.02
Body size	93.1	9.46	0.01	73.2	**1.42**	**0.26**
Herd size, Body size	89.8	6.16	0.03	77.4	5.65	0.03
Herd size*Fission	86.1	2.50	0.21	79.9	8.08	0.01
Body size*Fission	83.6	**0.00**	**0.73**	71.8	**0.00**	**0.53**

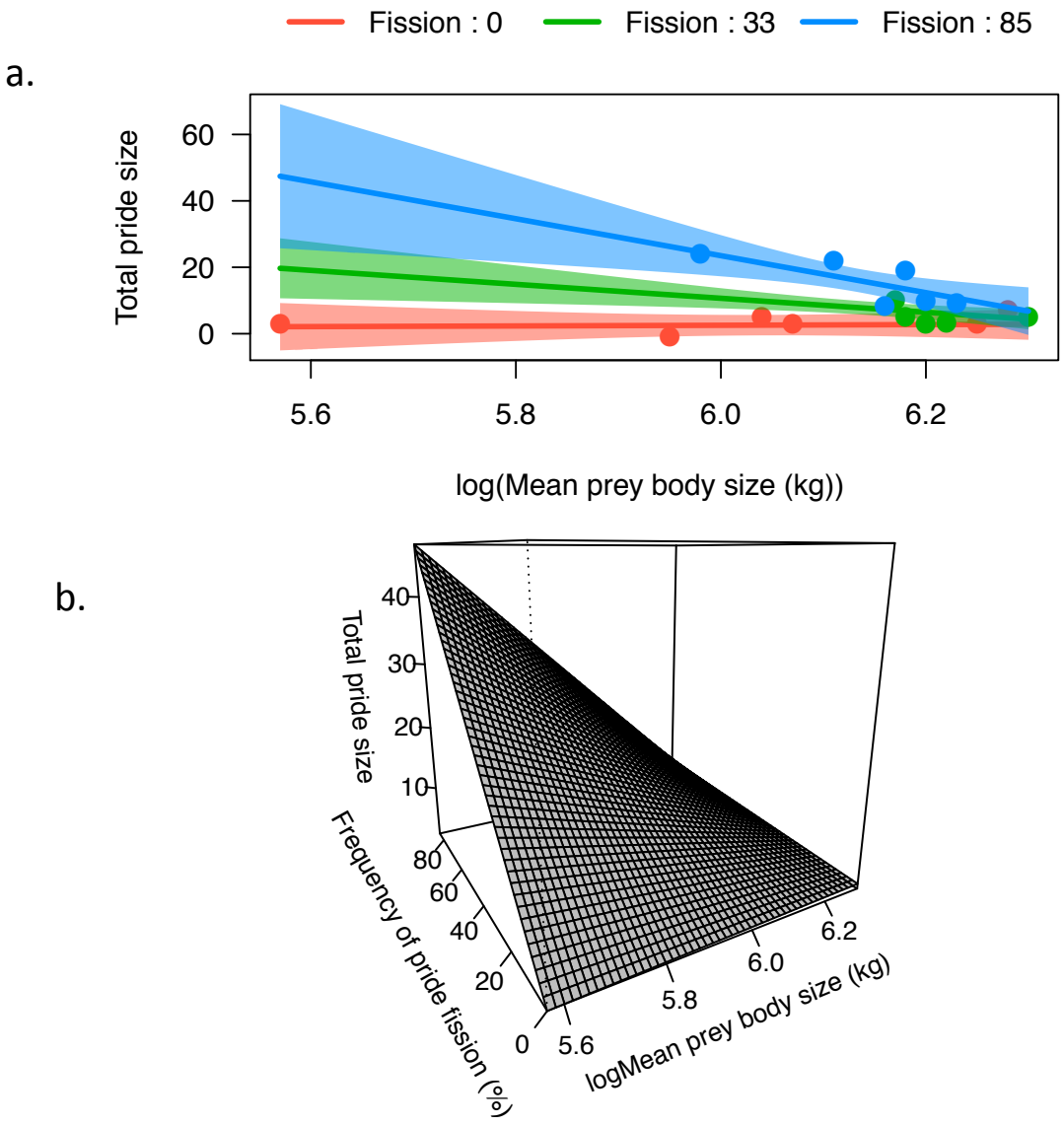


Figure 3.4 The best model for the relationship between total pride size and the interaction between mean prey body size and frequency of pride fission (the number of times the pride was in sub-groups as a proportion of the total number of whole pride and sub-group sightings) across lion prides in Hwange National Park between 2013 and 2015. In a) frequency of pride fission increases from 0% (red) through 33% (green) to 85% (blue) and in b) the same graph in two-dimensional showing a continuous increase in frequency of pride fission. Mean prey body size was subjected to a logarithmic transformation.

Discussion

The four general predictions of the RDH we tested gained support from our study of lions. First neither pride size nor sub-group size correlated with home range size (prediction i). In a null hypothesis, as might be expected in an homogeneous landscape (as depicted in the earliest renditions of the RDH, Macdonald, 1981) one might expect that territory would expand to meet the increased metabolic requirements of larger groups (Johnson *et al.*, 2001) (see Kruuk & Macdonald, 1985 for a discussion of this mechanism, known as "expansionism" within the RDH). However, we found no such correlation between lion home range size and group size, similarly to previous studies on European badgers (Kruuk & Parish, 1982). According to prediction ii, home range size increased with prey dispersion as measured by how herds of prey were spread out through the landscape. In this study, both the dispersion of prey herds and dispersion of waterholes were important factors in shaping lion home range size, nonetheless prey dispersion showed the strongest effect. Our results therefore corroborate earlier finding that dispersion of waterholes was a strong determinant of lion home range size (Valeix *et al.*, 2012). Our study builds on this earlier work by disentangling effects of prey dispersion from that of waterholes by showing that dispersion of prey herds is a more important determinant of lion home range size than waterhole dispersion, which is not unexpected as waterholes are prey hotspots and hence good proxies of herbivore distribution in the landscape but do not capture the whole variability of prey herd distribution.

Patch richness is expected to limit lion group size (Valeix *et al.*, 2012). Lion prey species examined in this study are gregarious, and each prey herd represents a patch available to lions with a larger herd size (richer patch) providing an opportunity for

more than one lion to make a kill. Certainly, we found that total pride size increased with increase in mean prey herd size. We interpret this as evidence that lion group size increases with patch richness (prediction iv). Group size has sociological fitness benefits for lionesses, such that their reproductive success depends on the number of female companions (Packer, 1986) while the individual fitness of males increases with increase in coalition size (Packer *et al.*, 1991). Our results support and considerably extend those for lions in Hwange National Park by Valeix *et al.* (2012), who used waterholes as a surrogate for prey availability. Their measures, using coarse scale data, did not detect a correlation between measures of patch richness and lion group size, but did show that the number of herbivore herds using a waterhole, also interpreted as an index of patch richness, sets a maximum ceiling on lion group size. Our findings resonate with those from the Serengeti where, despite being a different ecosystem, dry-season surface water is also restricted, in that case to river confluences (Wolanski & Gereta, 2001), which are prey hot spots (rich patches under the RDH) and valuable hunting locations (Hopcraft *et al.*, 2005). In the Serengeti National Park, larger prides were found in higher quality habitat and they also outcompeted smaller prides for access to those richer habitats (Mosser & Packer, 2009). Similar results were obtained in a study on Dark-bellied Brent Geese (*Branta bernicla bernicla)*, for which flock size increased as primary productivity increased during the spring season, with the benefit of improved grazing efficiency when foraging in larger groups (Bos, van de Koppel & Weissing, 2004).

We found that pride size increased with increase in the index of resource heterogeneity (prediction iii), meaning that larger prides are found in areas with a higher variability in the richness of patches. Although fission-fusion dynamics are

often associated with ecological factors such as food competition, there is also evidence that demographic factors like group size can also influence fission-fusion patterns (Lehmann & Boesch, 2004; Smith *et al.*, 2008). Our study has shown that larger prides have a higher frequency of fission than smaller prides; members of larger prides were rarely all found together and the same was observed in Serengeti lions (Schaller, 1972). However this does not mean that the pride members become different prides in a process of fission but rather they remain in the same group over the long term. The frequency of fission in chimpanzees has also been attributed to the size and composition of their communities with larger communities showing an increased fluidity in the fission-fusion system (Lehmann & Boesch, 2004). We also found a greater variability in the sub-group size of these larger prides, simply put, large prides fission more frequently into smaller sub-groups of varying sizes, which can range from very small (1-3 individuals) to very large (≥10 individuals)). Group living inevitably leads to competition between group members for access to limiting resources. Given this, the above results combine to reveal that perhaps fission-fusion in larger prides is a potential mechanism for coping more efficiently with the spatial and temporal variability in food sources (Lehmann, Korstjens & Dunbar, 2007). This is a typical case of demographic variables interacting with ecological parameters to play an important role in the social organisation of lion prides. Perhaps the decision about which sub-group size large prides fission into is determined by the size of the available prey herds, that is the richness of the patches. Observations of hyaena hunting methods by Kruuk (1972) indicated that hyaena hunting formation and sub-group size influenced the type of prey species they would hunt, with larger groups almost always hunting larger prey even when smaller prey are the most easily accessible.

As highlighted earlier, some previous RDH studies failed to find a clear relationship between patch richness and group size and hence support for this RDH prediction. Although our study found support for this prediction, the relationship between pride size and mean prey herd size (an index of patch richness) was weak while that of pride size and mean prey body size (another index of patch richness) was not supported in the model averaging. An obvious expectation would be for a positive correlation between prey body size and group size (Kruuk, 1972; Schaller, 1972) on the grounds that each large prey can feed several predators. Both the individual large prey, and the herds into which they aggregate, potentially constitute rich patches in terms of the RDH (Carr & Macdonald, 1986), raising the question of at which scale patchiness operates. Shedding light on this puzzle, we found that when fission-fusion is taken into account, the model including the interaction of the frequency of pride fission and mean prey body size receives the strongest support in explaining the variability in lion pride size. The relationship between pride size and mean prey body size became more negative with increase in the frequency of pride fission. This is likely to be because where large prides predominantly hunt large prey they operate as an intact cooperative unit (Packer & Pusey, 1997), the size of which is adapted to the large meal size provided by a large prey (Packer *et al.*, 1990). Whereas where they eat predominantly small prey, each prey item provides an inadequate meal for the whole pride, they tend to fission into smaller hunting parties and, perhaps paradoxically, this leads to a larger total pride size comprised of a greater number of smaller hunting parties. The overall outcome is that when the prey size is smaller and the pride size larger, then there is an increasing tendency to fission, itself a reflection of these smaller prey existing as many patches each of which is most likely to yield a relatively small meal. In this respect the fission-fusion dynamics is hypothetically an

adaptive mechanism for reducing competition within the group (Lehmann & Boesch, 2004), thus allowing larger prides to be supported even when patches become provisionally poor. Like lions, hyaenas also live in fission-fusion societies and adjust grouping patterns to match seasonal variation in local prey abundance and energy available at food sources (Smith *et al.*, 2008). They have been shown to join clan mates at ephemeral kills with the number joining being correlated with the energetic value to be gained from the prey (Smith *et al.*, 2008).

It is important to mention here that our results have revealed that the home range size outliers were in areas with few waterholes, while the total pride size outliers were in areas with many waterholes. In other words the home range outliers were not the same outliers as the total pride size outliers and this is in contrast with intuition but fits very well with the RDH predictions. Our results illustrate the importance of resource distribution as it determines the framework of constraints within which all other benefits of group living operate. It is the richness of patches that allows larger groups to be supported in these areas and this facilitates the development of other group living behaviours such as cooperative hunting and cooperative defense of territories, which in turn helps maintain social ties within the group. We also highlight the importance of taking into account the fission-fusion dynamics of a species when seeking to understand the relationship between sociality and prey availability. We demonstrate that fission-fusion is conceivably a mechanism for coping with the heterogeneous distribution of resources as well as allowing for the balance between the costs and benefits of group living in fission-fusion social groups.

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Chapter 4



Effect of resource availability on fine-scale patterns of social structure in African lions

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Abstract

Resource abundance and distribution influence the broad-scale structure of animal societies. However, there are still gaps in our knowledge on how resource availability affects the fine-scale patterns of association among individuals in animal societies. We used dynamic network analysis to assess patterns of association among individuals in lion prides across temporal and spatial variations in prey availability. All prides demonstrated strong patterns of within-pride sub-grouping, or 'communities', and these communities were more strongly delineated as prey dispersion increased and when the body size of available prey decreased. A strongly delineated social structure implies that individuals were observed in consistent sub-groups, which we captured as high modularity resulting from the network community assignment This study demonstrates the importance of the dispersion and richness of resource patches in shaping animal community structure, and this can have important implications on the structure of animal societies.

Introduction

One of the primary goals in animal ecology is to understand the relationship between environmental factors and animal population abundance, spatial distribution, and social structure (Macdonald, 1983). Studies across different taxa have demonstrated that resource availability is an important determinant of the broad-scale structure of animal societies, with most of these studies showing that animal group size is generally larger when food resources are more abundant and of a higher quality (see Hanya & Chapman, 2013; Macdonald & Johnson, 2015 for reviews). In group living animals, individuals or subgroups of individuals within a group often establish a network of social relationships (Hinde, 1956; Macdonald, Yamaguchi & Kerby, 2000b; Krause & Ruxton, 2002). The nature, number, and strength of these relationships are complex and can mediate the benefits, such as food sharing, that individuals accrue from living in groups, particularly in times of need (Carter, Farine & Wilkinson, 2017). Earlier attempts at understanding the interactions among individuals in a carnivore social structure, using the example of farm cats (*felis catus*), although analytically unsophisticated, offered early insights into patterns of social structure of group living carnivores (see Macdonald *et al.*, 1987; Kerby & Macdonald, 1988; Macdonald *et al.*, 2000a). Research in ecology and evolution is now increasingly focused on understanding the patterns of animal social structure at a finer level of social organization (e.g. Tanner & Jackson, 2012; Farine *et al.*, 2015), including in carnivores (e.g. Ellwood *et al.*, 2017). However, there is still only preliminary understanding of how ecological variables shape these fine-scale patterns of animal social structure, and the implications of these on the overall group social structure and stability.

Studies of structure in animal societies have been enabled by social network analysis (SNA). At its base, SNA quantifies the strength of associations or interactions (called edges) among each pair of individuals (called nodes) in a social group (Whitehead, 2009). It then provides a powerful toolbox for understanding complex social and ecological interactions in animal communities (Croft, James & Krause, 2008; Farine & Whitehead, 2015). Some pioneering studies have used social network analysis to unravel details of the relationship between food availability and patterns of animal social structure. For example, Tanner and Jackson (2012) found that European shore crab (*Carcius meana*) individuals aggregated into cohesive stable subgroups when resources were clumped. Additionally, Foster *et al.* (2012) showed that when prey was abundant, the killer whale (*Orcinus orca*) population was characterized by a highly interconnected social network. Nevertheless, the relationship between food availability and the nature and strength of association of individuals within and between subgroups remains poorly understood.

A useful tool in network analysis is community detection (Newman, 2006), which identifies and divides the nodes (i.e. the individuals) in the network into communities whose members are more tightly-connected to each other than they are to others. Community detection can be performed using optimal modularity, which has proven to be one of the best methods for detecting communities within networks (Danon *et al.*, 2005). The calculated modularity value is a numerical index of how good a particular division is (Newman, 2004) by comparing the level of community structure (within-cluster vs. between-cluster connections) in an empirical network compared to a random network with the same fundamental properties (Shizuka & Farine, 2016). Network modularity is useful for measuring the degree of heterogeneity of a social

system and, being quantitative, makes it easier to compare between different groups or to relate group heterogeneity to other social or ecological variables (Kasper & Voelkl, 2009). Network measures, such as communities, can also be quantified for different points in time, which is known as dynamic network analysis (Farine, 2018). When repeatedly measured in the same groups across time, and combined with external data, dynamic community analysis is a powerful tool for studying the social dynamics of the whole group, for example how fragmented the group is into variously cohesive subgroups across different ecological conditions.

One species that has been widely reported as regularly forming subgroups (i.e. exhibiting fission-fusion dynamics) is the African lion (*Panthera leo*) (Schaller 1972). Although lions engage in a wide variety of group level activities such as cooperative hunting (Scheel & Packer, 1991), mutual defence of kills (Cooper, 1991) and cooperative defence of territory and young (Mosser & Packer, 2009), lion sociality has also been reported to be influenced by resource availability (Macdonald *et al.*, 2010b). Habitat quality was suggested as a major driver of lion social organisation in the Serengeti National Park, Tanzania (Mosser *et al.*, 2009). By contrast, the number of prey herds visiting a waterhole determines maximum lion group size in Hwange National Park, Zimbabwe (Valeix *et al.*, 2012), where a more recent study further showed that prey herd size influenced lion group size (Mbizah *et al.*, *submitted*). These studies provide evidence that the overall structure of lion populations (i.e. group size) is linked to resource availability. However, the interactions between individuals within a group are also likely to vary under different conditions. There has been, however, no attempt to relate the finer-scale patterns of associations between individuals in a pride to the distribution and abundance of resources.

In this study, we combine data on the fine-scale patterns of association between individuals across multiple prides of African lions with data on the prey herds available for these prides across Hwange National Park, Zimbabwe. We consider a herd of prey to represent a resource patch available to lions (Carr & Macdonald, 1986), and the abundance, dispersion, and richness of these patches as important attributes that can influence the opportunities for social interactions (Tanner & Jackson, 2012). By applying community detection to dynamic networks generated by observations of lions together, we test the hypothesis that prey abundance, dispersion, and richness impact the within-pride structure as a result of the relative value of grouping under the different conditions. Here, we show that the dispersion of resource patches in the landscape and the richness of these patches has a bearing on fine-scale association patterns and the strength of community structure of this lion population.

Methods

Study area

Hwange National Park covers approximately 15 000 km^2 of semi-arid dystrophic savanna on Kalahari sands, on the north-western border of Zimbabwe. Three seasons occur in Hwange National Park: the early dry season (March - June), the late dry season (July - October) and the wet season (November - February). During the wet season, various waterholes, rivers and pools are rain fed and are available to animals, but many become dry during the dry season. Pumped waterholes (about 50) maintain water availability during the dry season. Lion density is estimated at around 3.5 lions/100 km^2 in the study area (Loveridge *et al.*, 2016) and there is a heterogeneous distribution of prey, both spatially and temporally (Chamaillé-Jammes *et al.*, 2016).

Lion pride observations

In this study we used data from seven GPS-collared lions from four different prides for the study period 2013-2015. The GPS collars recorded locations every two hours day and night, and we regularly downloaded this positional data to estimate lion home range. Lion prides were located and observed at least five times a month to record the size and composition of their group at that time. When a group was observed, we recorded the name of the pride, the identity of the individuals present, as well as their age and sex. All lion individuals are recognizable by whisker patterns that are unique to each individual and natural markings such as scars, muzzle spots and tooth irregularities (Pennycuick & Rudnai, 1970). We used the gambit of the group method to collect data on sub-group membership. This method involves observing animal groups across time and all individuals present together are recorded as being connected (Franks, Ruxton & James, 2010). In the gambit of the group method, the assumption is that animals are likely to interact at a similar rate to which they associate (Whitehead & Dufault, 1999; Farine, 2015) (see also Macdonald *et al.*, 1987).

Prey abundance and distribution

To measure the abundance and distribution of prey, we conducted multi-species spoor surveys from 2013 to 2015 during the early dry season and the late dry season. We drove along selected sections of roads and we identified and counted spoor in most parts of the study ecosystem. When fresh spoor (less than 24hrs old) was encountered, it was assessed for species, group size, age and sex. During the surveys, spoor of a range of herbivores and carnivores were identified to species, but only spoor from common lion prey species in the area was used in this analysis. Prey species included

in the analysis were: Burchell's zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and juvenile African elephant (*Loxodonta Africana*) (frequently recorded as prey during drought years in Hwange; Loveridge *et al.*, 2006).

Information on the abundance and distribution of prey was extracted for each lion home range in each season. Lion home ranges were defined as the 90% probability contour of location distribution using the fixed kernel density estimator (Powell, 2000) and the reference smoothing factor href (Hemson *et al.*, 2005). Home range analyses was undertaken using the AdehabitatHR package in the statistical software R (Calenge, 2006). We used data from only one GPS collared lion per pride for each of the lion pride seasons. Prey abundance and distribution data from spoor counts were overlaid on lion home ranges in QGIS (Quantum GIS Development Team, 2017) and the road transects that fell within each lion home range were clipped. For each home range and each season, we calculated four measures of prey availability, comprising of an index of prey abundance (number of prey herds/km), an index of prey dispersion (nearest neighbour index of prey herds), and two indices of patch richness (mean prey herd size and mean prey body size). The nearest neighbour index was calculated in QGIS (Quantum GIS Development Team, 2017) by measuring the distance between each prey herd and its nearest neighbour and then averaging all these nearest neighbour distances. Prey body sizes were obtained from Cumming and Cumming (2003). The measure of prey abundance characterises the amount of food patches

available to lions within their home range. The measure of prey dispersion describes how dispersed prey is in the landscape and how much searching effort the lions may have to invest to access the prey. Regarding measures of patch richness; mean herd size represents an opportunity for more than one lion to make a kill and mean prey body size represents the quality of the food resource in terms of the energy gained from consumption of that prey.

Social networks construction

We used lion pride observational data to construct a social network for each pride and for each season. In this study, each social network represents a cumulative pattern of pride associations over a four-month period in the early dry season and the late dry season from 2013 to 2015. The social networks contained all of the individuals in one pride as nodes and pairwise association indices as edge weights. Because we did not have complete data on observations of all groups simultaneously, we had to convert the number of associations into an association rate (the propensity for individuals to be seen together). To calculate these edge weights, we used the Simple Ratio Index (SRI) (Cairns & Schwager, 1987), which ranges from 0 for two individuals never seen in the same sub-group and 1 for two individuals always seen in the same sub-group. A recent study by Hoppitt and Farine (2017) recommended the use of SRI in the absence of calibration data, as it is a better measure compared to other association indices and can accurately estimate the relative strengths of social bonds.

Social network analysis

We used modularity optimization to assign individuals to social communities (indivisible sub-graphs) in a way that maximizes the within community rates of

association or interactions (Newman, 2004; Newman, 2006). Modularity describes the separation of networks into clusters and the degree to which the nodes (individuals) in those clusters are connected (Girvan & Newman, 2002). In all the study networks, we used the community detection algorithm by Clauset, Newman and Moore (2004) and implemented in the 'fastgreedy.community' function in igraph v1.0.0 (Csardi & Nepusz, 2006) to detect communities. The function assigned each node to a cluster or community and the modularity value Q measured as the proportion of edge weights occurring within communities relative to the expected proportion in an equivalent network if edges were randomly distributed (Newman, 2006). The modularity coefficient Q ranges from 0 to 1, with a Q close to 1 indicating a network with a strong clustered structure in which interactions of individuals belonging to different clusters do not occur (Newman, 2006). The modularity coefficient of the undivided network is zero, this is when the fraction of within-community edges is no different from what would be expected from a randomized network (Clauset *et al.*, 2004). We represented the resulting community assignments by giving different colours of nodes to each community within a pride (Figure 4.1).

After assigning individuals to network communities, it was also important to assess how robust these community assignments were to sampling uncertainty. We used a method by Shizuka and Farine (2016) that combines bootstrapping with a coefficient of assortative mixing to generate a single metric called 'community assortativity' (r_{com}). This process generates the statistic r_{com}, which represents the proportion of community co-membership in bootstrap replicates occurring between individual lions assigned to the same observed community (Shizuka & Farine, 2016). The value of r_{com} ranges between -1 and 1. Negative values are very unlikely, while values near 0

suggest that community assignments in bootstrap replicates are random with respect to the original communities. Values of r_{com} approaching 1 suggest that all bootstrap replicates result in exactly the same community assignments as the observed network and that this assignment is robust (Shizuka *et al.*, 2014; Shizuka & Farine, 2016). Once the division of prides into communities was detected and characterized, we assessed the effect of resource availability on the strength of the level of community structures within these prides.

Null models

Social data are typically non-independent (Croft *et al.*, 2011), in order for one individual to have a connection (edge), it requires another to do so as well. We used null models (permutation tests) to estimate the significance in the relationships between prey availability and community structure. Null models also allow us to account for confounding non-social factors that affect the co-occurrence of individuals so that only the signal of social factors that shapes the social network are evaluated when estimating significance (Farine & Whitehead, 2015; Farine, 2017). We first did a pre-network permutation test in the R package 'asnipe' (Farine, 2013) to compare modularity of the study network to that of a random network. We ran 10 000 permutations for each network and this works by sequentially swapping observations of pairs of individuals between groups to increasingly randomize the observed data (Bejder, Fletcher & Brager, 1998). After each swap, the associations between all individuals are recalculated and the modularity recalculated for each random network. The P-value for each network was calculated as the number of modularity values from the randomised networks that were greater than or equal to the modularity of the observed network, divided by the number of random networks

generated. Because we were using two-tailed tests, we considered our effects to be significant at P = 0.05 if fewer than 2.5% of the modularity values of the randomised networks were larger or equal to that of the observed network (Farine, 2017).

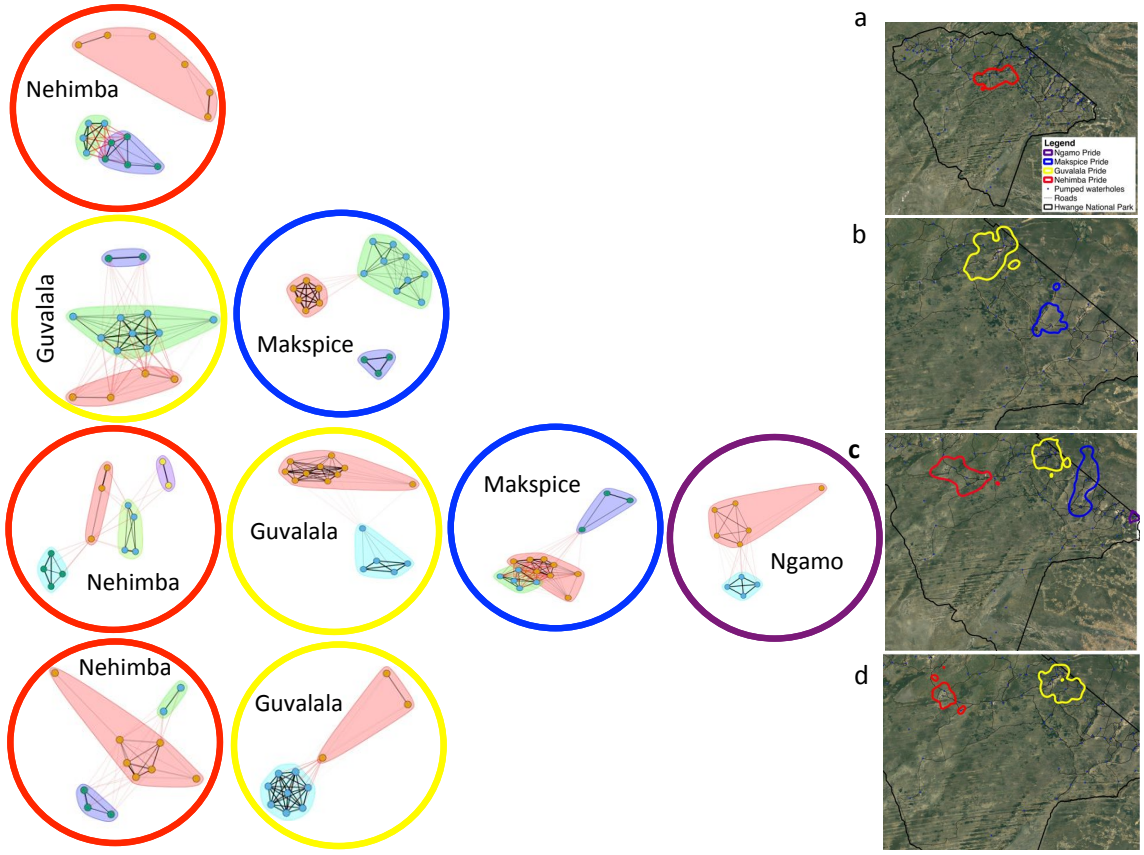


Figure 4.1 Social communities or sub-groups within lion prides for each pride season across Hwange National Park for a) late dry season 2013, b) late dry season 2014, c) early dry season 2015, and d) late dry season 2015. Each node, representing an individual lion, is assigned to a social community, which is denoted by node colour and coloured bubbles. Edge weights are proportional to the association index. The social community structure represents the partitioning of the pride into clusters of individuals that associate more often with each other than expected. The lion seasonal home ranges of each pride are overlaid on the Hwange National Park map.

Hypothesis testing

We then performed a linear mixed effect regression analysis of the relationship

between modularity of each network and each of the four measures of prey availability; number of prey herds/km, nearest neighbour index of prey herds, mean prey herd size and mean prey body size in the corresponding season. The modularity was the response variable while the measures of prey availability were the fixed effects; with lion pride ID as the random effect. Using the null model procedure described above, we also generated 10 000 randomised version of each network, and ran the same regression with each of these networks. We then calculated P-values for each fixed effect by calculating the number of coefficients of the regression slopes from the randomised networks that were greater than or equal to the corresponding coefficient of the regression slopes using the observed network, divided by the number of random networks generated and corrected for a two-tailed test as described above. All analysis were done in R statistical package (R Development Core Team, 2018).

Results

Network structure

The seasonal home range size of the lion prides ranged between 28 and 499 km^2 (mean ± SD = 295 ± 170 km^2). This wide range in home range size was because of the differences in prey and waterhole dispersion across the study area (see Chapter 3). The assignment of individuals to communities was generally robust to sampling error and the coefficient of assortativity (r_{com}) was largely high, ranging between 0.64 and 1 (Table 4.1). All were above the threshold of 0.5, which Shizuka and Farine (2016) found as a threshold suggesting robust community assignment. This means that pairs of individuals in the same community in the observed network were generally in the same communities in bootstrap replicate network, while individuals assigned to

different communities in the observed network were rarely in the same community in bootstrap networks (Appendix 4.1). In this study, networks could be partitioned into two, three and four main social communities (Table 4.1, Figure 4.1).

Table 4.1 The number of pride observations (Number of obs), number of individuals in a pride (Number of indiv), number of communities (number of comm), the modularity and the coefficient of assortativity (r_{com}) for each pride, per season, per year in Hwange National Park, Zimbabwe between 2013 and 2015.

Pride	Year	Season	Number of obs	Number of indiv	Number of comm	Modularity	r_{com}
Guvalala	2015	Early dry	66	9	2	0.36	0.92
Guvalala	2015	Late dry	45	9	2	0.04	0.65
Makspice	2015	Early dry	29	13	3	0.14	0.71
Nehimba	2015	Early dry	16	5	4	0.52	0.76
Nehimba	2015	Late dry	23	7	3	0.30	0.77
Ngamo	2015	Early dry	23	7	2	0.37	1.00
Guvalala	2014	Late dry	31	11	3	0.10	0.64
Makspice	2014	Late dry	23	8	3	0.56	1.00
Nehimba	2013	Late dry	26	8	3	0.18	0.66

Community structure

The modularity coefficient, that is the level of community structure varied considerably, from 0.04 to 0.56 (Table 4.1). Makspice pride in the late dry season of 2014 showed the strongest level of community structure, the pride had the highest modularity (Q = 0.56) and the most robust data based on r_{com} (Table 4.1). Guvalala pride in the late dry season of 2015 had the lowest modularity (Q = 0.04), suggesting

that individuals in this pride had a tendency to associate randomly with multiple sub-groups or communities. A modularity value above 0.3 is usually a good indicator of significant community structure in a network (Clauset *et al.*, 2004), where associations are stronger within communities than between communities and this was the case in five out of the nine networks (Table 4.1). Observed network modularity for each of the indices of resource availability was generally higher than the random modularity and, in most cases, it was higher than the 0.975 quartile of the random modularity (Figure 4.2).

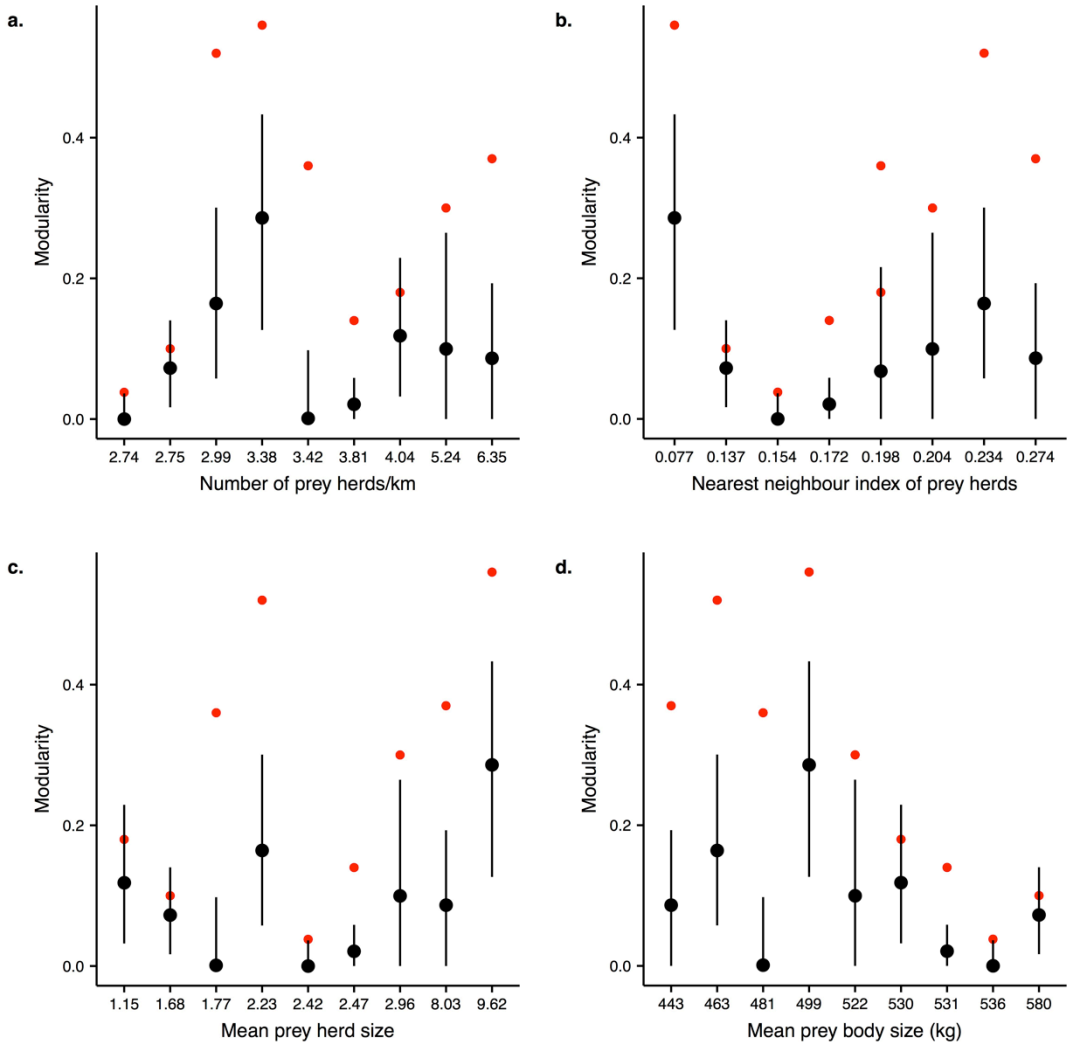


Figure 4.2 The distribution of the random modularity (at 0.025, 0.5 and 0.975 quartile) from the 10 000 permutated networks (black line and dot) and the observed modularity (red dot) for each of the four measures of prey availability a) number of prey herds/km (index of prey abundance), b) nearest neighbour index of prey herds (index of prey dispersion), c) mean prey herd size (index of patch richness) and d) mean prey body size (index of patch richness) for four lion pride networks from 2013 to 2015 in Hwange National Park, Zimbabwe. Observed network modularity was generally higher than the random modularity.

Effect of resource availability on community structure

Prey abundance had no significant effect on community structure as 2.82 % (P = 0.056) of the coefficients of the regression slope of the random networks (range = -0.124 to 0.058; mean ± SD = -0.005 ± 0.019) were greater than the coefficient of the regression slope of the observed network (0.028) (Figure 4.3a.i). Prides in both low and high prey abundance areas showed similar patterns of within and between community associations (Figure 4.3a.ii). Prey dispersion had a significant effect on community structure, only 0.63 % (P = 0.013) of the coefficients of the regression slope of the random networks (range = -2.891 to 0.733; mean ± SD = -0.921 ± 0.504) were greater than the coefficient of the regression slope of the observed network (0.295) (Figure 4.3b.i). Removing outliers from this analysis increased the coefficient of the regression slope of the observed network; it became more positive (3.017) and also larger than expected by chance (P = 0.0006), (range = -1.323 to 3.150; mean ± SD = 0.465 ± 0.483) (Figure 4.3b.i). An increase in prey dispersion resulted in an increase in community structure (Figure 4.3b.ii). This result implies that more dispersed prey leads to structured, within-pride, communities with clearer and more consistent sub-groups. Mean prey herd size (index of patch richness) had no significant effect on community structure, 12.83 % (P = 0.257) of the coefficients of the regression slope of the random networks, (range = -0.005 to 0.061; mean ± SD = 0.024 ± 0.010) were greater than the coefficient of the regression slope of the observed network (0.036) (Figure 4.3c.i). Prides in both areas with small and large prey herds showed similar patterns of within and between community associations (Figure 4.3c.ii). Finally, the analysis of the effect of mean prey body size (index of patch richness) on community structure revealed that the coefficient of the regression slope of the observed network was more negative (-0.003) than expected by chance (P

= 0.0004), (range = -0.003 to 0.001; mean ± SD = -0.0005 ± 0.0004) (Figure 4.3d.i). Community structure decreased with increase in mean prey body size (Figure 4.3d.ii), as prey in a pride's home range becomes larger (i.e. resource patch becomes richer), the community structure becomes weaker, i.e. individuals within the pride tend to associate more evenly.

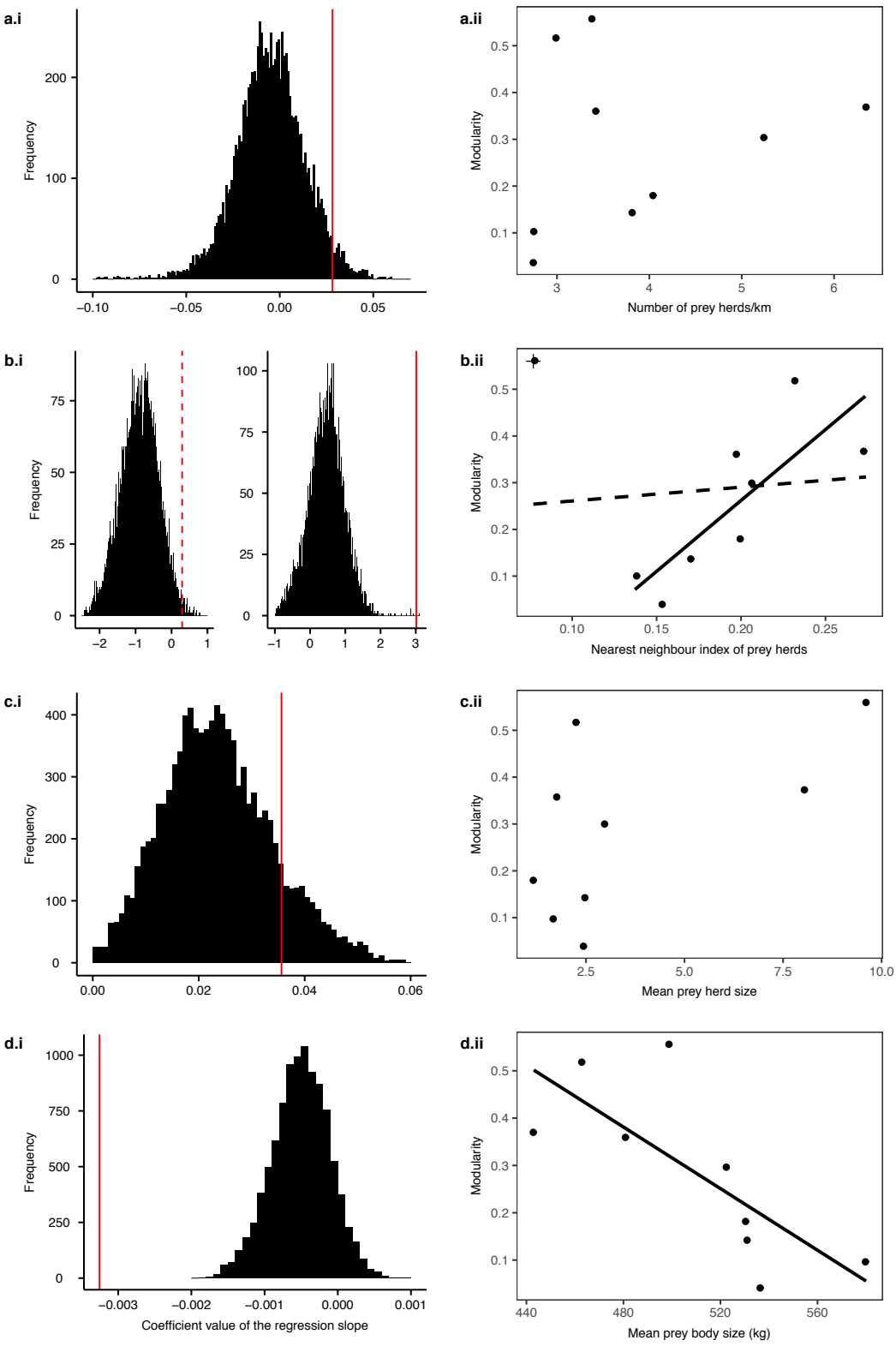


Figure 4.3 The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line) for each of the four measures of prey availability ai) number of prey herds/km (index of prey abundance),

bi) nearest neighbour index of prey herds (index of prey dispersion), ci) mean prey herd size (index of patch richness) and di) mean prey body size (index of patch richness). On the right are the regression plots of the relationship between each of the four measures of prey availability and modularity (aii to dii). A circle and a cross denote the outlier in 3a; the coefficient of the observed network and the regression line before the outlier is removed is shown as dashed lines then shown as solid lines after removing the outlier.

Discussion

This study demonstrates that resource availability is an important determinant of not only broad population structure, but also the patterns of association among individuals within groups. More specifically, our study reveals that increasing prey dispersion and decreasing patch richness resulted in more delineated social structure within lion prides. A strongly delineated social structure implies that individuals were observed in consistent sub-groups, which we captured as high modularity resulting from the network community assignment. A strength of our study is that we conducted our analyses across different seasons in the same prides (using dynamic network analysis) to identify the links between resource availability and within-pride social structure. Given the well-known importance of interactions among members of lion prides, where individuals are highly dependent on their pride mates for survival and reproduction (Packer, Pusey & Eberly, 2001), changes in resource availability is likely to have strong implications for lion populations.

When resource patches are more aggregated, for example clustering of prey herds in patches of specific habitats or around waterholes, lion prides tend to use these

resource patches intensively (Valeix *et al.*, 2010). This aggregation of prey resulted in more regular associations among pride members. These frequent interactions and associations around prey patches resulted in highly connected pride members with little sub-grouping within prides. Large prey species (rich patches), such as buffalo, zebra, giraffe or juvenile elephant feed several lions. Consequently, competition for prey within the pride is likely to be minimal and individuals can associate frequently outside of their close connections. Essentially, all individuals in the pride can come together (fusion), and this might allow them to cooperatively hunt the large sized prey (Scheel & Packer, 1991) and increase success of prey capture (but see Caraco & Wolf, 1975; Packer *et al.*, 1990). Similarly, Kruuk (1972), and later Smith *et al.* (2008), showed that when prey is abundant and energy per resource patch is high, hyaenas (*Crocuta crocuta*) tend to congregate at such food patches and spend relatively more time with conspecifics than alone. Golden jackals (*Canis aureus*) have also been reported to aggregate around clumped food sources resulting in a larger and more cohesive group (Macdonald, 1979). Increased pride-level cohesion may also provide a number of other benefits to pride members, including increased chances of communal defence of cubs (Packer & Pusey, 1983) and territorial defence (Grinnell, 2002; Mosser & Packer, 2009), which may be particularly important in periods of high prey abundance.

The dispersion of resources potentially increases searching behaviour (Sogard & Olla, 1997; Valeix *et al.*, 2010), thus limiting the opportunity for social interactions between individuals (Tanner & Jackson, 2012). We found that this leads to prides that are socially fragmented, with few connections between sub-groups of strong associates. Cooperation in animals often occurs among more strongly affiliated

individuals (Clutton-Brock *et al.*, 2001), and stronger connections, here captured by individuals being in the same community, has previously been predicted to promote cooperation when prey are dispersed (Marcoux & Lusseau, 2013). Such cooperation is likely to be important for locating the dispersed prey, as previous studies have shown that well-connected individuals are more likely to acquire information about the location of dispersed food sources (Aplin *et al.*, 2012).

We further found that prides had a more distinct community sub-structure when prey size was small (poor quality patches). This pattern could also be linked to an increased tendency to cooperate among hunting lions of the same sub-group, which could be critical for increasing chances of capturing prey as shown by Stander (1992a) and minimizing energetic costs, since energy invested in prey capture may not be well compensated because of the small size of the available prey (Carbone, Teacher & Rowcliffe, 2007). Cooperation and coordination during hunts is important especially in landscapes where there is little cover and less opportunities for stalking (Stander, 1992c). Cooperation is particularly essential in areas where there are higher densities of hyaenas as lions might need to defend their kills from hyaenas (Cooper, 1991). The weaker connections between communities in prides living in areas with small sized prey is perhaps a mechanism for reducing feeding competition (Kummer, 1971), as the small sized prey may not be divisible among several communities (Packer *et al.*, 1990). However, a strong separation between communities within a pride reduces encounter rates and contacts between individuals of different communities thus affecting mate choice and other social behaviours, which can have important repercussions on the fitness of individuals (Banks *et al.*, 2007; Krause, Lusseau & James, 2009). The weaker associations between communities can also lead

to pride fragmentation and reduced social benefits such as alloparental care (Pusey & Packer, 1994).

Our results also indicated that the abundance of prey and the mean prey herd size had no effect on association patterns and community structure of lion prides. This is contrary to what Foster *et al.* (2012) discovered for killer whales for which the associations between individuals in a group were stronger and the network highly interconnected when food was abundant. In bottlenose dolphins (*Tursiops truncates*), when resources are limiting, individuals spread out into smaller sub-groups to reduce intraspecific competition for food and then aggregate into larger groups when food is abundant (Connor *et al.*, 2000). We were therefore expecting both the abundance and size of prey herds to have a strong influence on the dynamics of social interactions in the lion prides. Yet the null model approach demonstrated that the associations and community structure in the lion network could not be explained by patterns of either prey abundance or mean prey herd size alone. This result shows that perhaps the number of prey herds, which represents overall abundance, is not as important as their dispersion, which may ultimately affect prey accessibility in terms of searching effort, or their richness in terms of prey body size, which denotes the energy gained from consumption. For Serengeti lions, prey accessibility was more important than prey abundance, as lions selected areas where prey was easier to catch, rather than areas where prey densities were highest (Hopcraft *et al.*, 2005).

In this study, modularity could reliably detect the transition from random associations in networks (modularity closer to 0) to more structured associations (modularity above 0.3). The assortativity coefficient we calculated for the community assignments

was consistently higher than the recommended threshold (> 0.5) for a high quality network (Shizuka & Farine, 2016) thus giving us confidence in the community assignments and modularity values calculated in this study. Further, our study is relatively unusual in being able to draw comparisons both within and across different social networks. Comparisons across networks have been previously reported as particularly challenging (Croft *et al.*, 2008). We were able to achieve this by combining standardised observation methods across prides with null models based on permutation tests for hypothesis testing. The latter was particularly important as it allowed us to account for potential biases in our observation data that may be caused by factors that impact association strength such as sub-group and pride sizes (influencing detectability), and differences in relatedness within prides, age and sex structure, and overall sampling effort (Farine & Whitehead, 2015; Farine, 2017). This is achieved by comparing the observed network data to data that could have been generated if individuals were behaving in exactly the same way (and with the same pride size, relatedness, age, sex, and sampling effort) but where individuals were associating with others at random.

Our findings enrich understanding of lion social structure and dynamics. We demonstrate the potential of using a social network approach to explore the relationship between ecological factors and social dynamics at multiple scales (within and between prides and across seasons). We hope to stimulate further discussions and more research on how resource availability influences the fine-scale patterns of animal social structure. Results from our study have shown the importance of the dispersion of resource patches in the landscape and the richness of these patches in influencing the association patterns and hence strength of the level of community

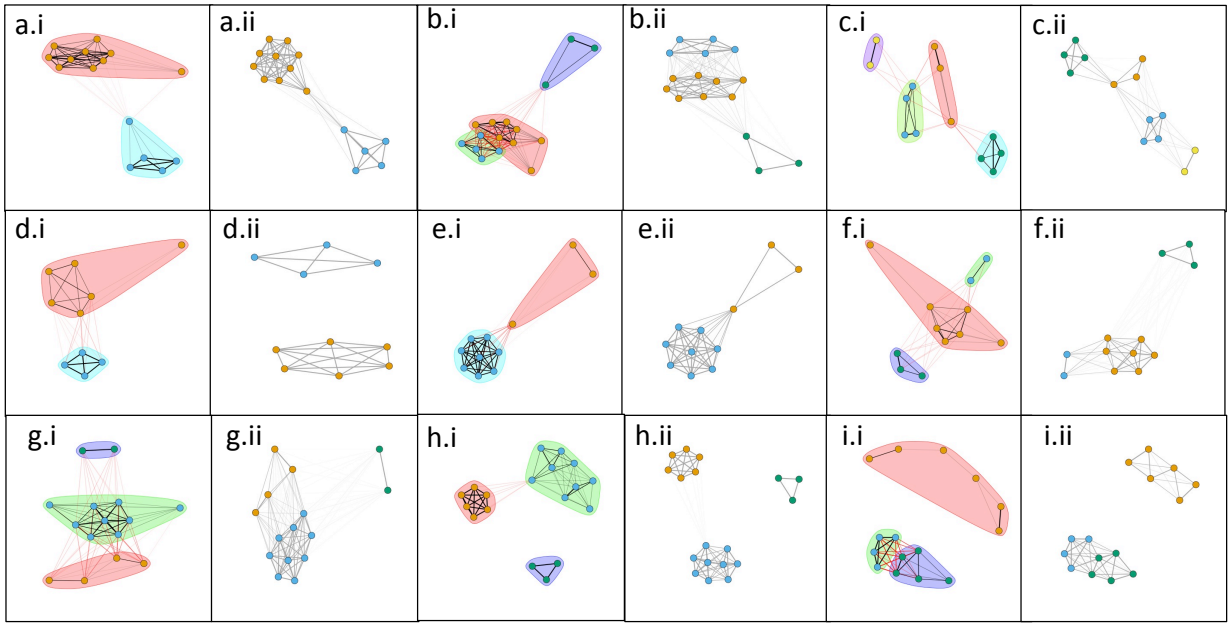
structure within lion prides. These results are possibly applicable to other species that live in social groups including primates, birds, and other carnivores, whose ecology and social structure is influenced by the distribution of resources. Many studies in animal ecology and conservation have already started to benefit from the social network analysis tool (for example a long running study on European badgers (*Meles meles*) in Wytham Woods, U.K (see Ellwood *et al.*, 2017)), as it can be used to inform about important changes in animal social structures that might be too subtle to detect by other conventional methods (Snijders *et al.*, 2017). The information obtained from this study is particularly important for informing lion conservation and management since the stronger clustering and division of the prides into communities due to dispersed or poor resource has the danger of leading to fragmentation of the pride and possibly permanent division of the pride. Conservation measures such as increasing the number of large prey species (patch richness) and increasing number of waterholes (facilitating prey aggregations) can help increase the association among individual lions and as a result avoid pride fragmentation.

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Appendix



Appendix 4.1 Social network of the observed networks (networks i) where edge widths represent the pairwise association index and node colours represent assignments into social communities versus the social network of bootstrap replicate networks (networks ii) in which nodes represent the same individuals and edges represent the number of times a pair of nodes was assigned to the same community in bootstrap replicate networks using the same community detection algorithm.

Chapter 5



Optimal resource patch richness drives prey preference by African lions (*Panthera leo*) in a heterogeneous landscape

In preparation for submission to *The American Naturalist*

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Abstract

The efficient exploitation of available food resources is a fundamental requirement for the fitness and survival of individuals. Although great strides have been made in understanding predator foraging behaviour, understanding of why prey is preferred or avoided is still incomplete. Here, we evaluate prey preference of African lions by combining simultaneous data on lion diet, prey availability and lion pride size and composition. We used optimal and social foraging theories to generate hypotheses of what would constitute the predicted foraging behaviour of lions. We tested the hypotheses that prey preference is driven by (i) aspects of prey availability, (ii) environmental factors, (iii) aspects of predator group size, and (iv) relative prey size. In accord with optimal foraging theory, prey body size, an index of patch richness, was the main driver of lion prey preference and this relationship followed a bell-shaped curve. The profitable medium-sized and large prey species were preferred while the less profitable small prey and potentially dangerous megaherbivores were avoided. Our results also showed that prey herd size, a potential index of patch richness, influenced lion prey preference, with lions preferring species forming larger herds. In accord with the social foraging theory, lion prey preference was also influenced by predator group size: preference for large prey species increased with increase in lion hunting group size (and pride size) but preference for medium-sized prey species decreased with increase in lion hunting group size (and pride size). Findings from this study suggest that lions are sensitive to variation in prey profitability and that prey preference might be driven by the need to maximise energy gain and optimise foraging success.

Introduction

Diet is the most direct link between predators and their environment (Macdonald *et al.*, 2010a), and the evolutionary fitness of a predator is determined by the quality and the quantity of its diet (Sunquist & Sunquist, 1989). When foraging, a predator incurs some costs (energy and time) in searching for, chasing, subduing and killing prey and from risk of injury, but will also gain energy from prey consumption (Griffiths, 1980). Optimal foraging theory predicts that foraging individuals will seek to balance such costs and benefits to maximise their net rate of energy gain (MacArthur & Pianka, 1966). Some of the pioneering efforts at understanding optimal foraging behaviour have been from controlled experiments on arthropods, birds and fish (e.g. Werner & Hall, 1974; Krebs *et al.*, 1977); taxa more tractible under experimental manipulation than, for example, wild mammals. Early studies on large mammalian carnivore feeding behaviour were largely descriptive but nonetheless insightfully revealed relationships between predators, their prey and the environment (Hamilton, 1935; Estes & Goddard, 1967; Hornocker, 1970; Kruuk, 1972; Schaller, 1972; Macdonald, 1977; Richards, 1977). Research into the fundamental reasons for predatory behaviour observed across various carnivore species is gaining momentum and optimal foraging and social foraging theories have provided a framework for interpretation. For example, amongst the earliest attempts to quantify carnivore foraging decisions was Macdonald's (1980) application of optimal foraging theory to red fox (Vulpes vulpes) predation on earthworms (Lumbricus terrestris). Four decades of scholarship have refined the predictions of optimal foraging theory, specifically clarifying what foragers might seek to maximise under different circumstances (e.g. Parker & Smith, 1990; Stephens *et al.*, 2008; Watanabe, Ito & Takahashi, 2014; Frank

& Linsenmair, 2017; St Juliana *et al.*, 2017) and the economic interaction between the actions of individuals and those of other foragers (Giraldeau & Caraco, 2000).

An optimally efficient predator is expected to be able to rank the available food types in terms of profitability (energy obtained per unit of foraging effort) (Krebs, 1977; Krebs, 1978). However the variance of profitability can also affect prey preference in cases where the predator seeks to minimise the risk of starvation (Stephens & Charnov, 1982). Following the optimal foraging theory, a predator would be expected to choose a patch containing the most profitable prey item (Scheel, 1993), but any random fluctuation in foraging success may cause them to leave that patch (Ward, Austin & Macdonald, 2000). To maximise rates of energy gain, many predators forage selectively, instead of consuming prey items in proportion to their availability, they prey selectively on a particular prey. This preference for certain prey species can be influenced by various facets of the relative availability and vulnerability of prey such as their abundance, body size, group size, age, taste, habitat use, temporal and spatial distribution, defensive behaviour (Macdonald, 1977; Sunquist & Sunquist, 1989; Scheel, 1993; Macdonald *et al.*, 2010a; Petrunenko *et al.*, 2016) as well as extrinsic landscape features that increase the probability of a successful hunt (Hopcraft *et al.*, 2005). For some carnivore species, such as the jaguar (*Panthera onca*), prey preference is primarily based on socio-ecological and prey behavioural traits (prey abundance and prey herd size) rather than morphological prey characteristics (prey body size) (Hayward *et al.*, 2016). Although it was more profitable to kill moose (*Alces alces*) than roe deer (*Capreolus capreolus*), Sand *et al.* (2016) found that the risk of injury from moose was likely an important factor for the decision of wolves (*Canis lupus lupus*) to select roe deer when present at sufficiently

high densities. For African wild dogs (*Lycaon pictus*), the diet predicted when it is assumed that they maximise their rate of food intake was similar to the observed diet, suggesting that hunting decisions by wild dogs take profitability and encounter rates into account (Creel & Creel, 2002).

The size of prey is one of the most conspicuous features that a predator could use to discriminate prey quality, in terms of the quantity and quality of biomass that it provides. It would consequently be more profitable to eat large prey (Krebs, 1978), provided the prey is not too difficult to catch and not so large as to cause an injury during prey capture (Sunquist & Sunquist, 1989). Indirect measures of fitness (e.g. net energy gain) are sometimes assumed to be directly proportional to a given foraging strategy (Parker & Smith, 1990), for example the net energy gain is expected to increase with increase in prey body size. However this is not always the case as this relationship can be non-linear; for example the optimal prey body size may occur when the ratio between energy gain and the cost of prey capture is maximal (Parker & Smith, 1990). Given such a scenario, the relationship between predator prey preference and prey body size is expected to follow a non-linear shape; an increase in preference with increase in prey body size until an optimal prey body size beyond which further increase in prey body size results in a decrease in prey preference (e.g. Hayward & Kerley, 2005). The same can also be said for the prey herd size, where preference increases with prey herd size, as larger herds are more visible to a predator, may provide an opportunity for more than one predator to make a kill (in the case of a social predator) and increases chances of finding a vulnerable prey. However, further increase in herd size may result in prey becoming more difficult to catch because of increased predator detection or collective defense (Powell, 1974;

Pays *et al.*, 2013).

Giraldeau and Dubois (2008) formulated the social foraging theory to deal more effectively with cases where foraging animals interact and affect each other's rate of net energy gain. Therefore the social foraging theory might be more applicable than optimal foraging theory when examining the foraging behaviour of a social predator as it offers a method to investigate questions of the size and dispersion of groups, foraging cooperation and the complications of prey selection under competitive conditions (Giraldeau & Dubois, 2008). Group size may influence two aspects of predator foraging: (i) hunting success and (ii) decisions about the prey sizes to hunt. Predator group hunting has been perceived as a strategy to increase hunting success, especially when hunting large prey species (Schaller, 1972; Creel & Creel, 2002; MacNulty *et al.*, 2014), however this has been refuted by other studies (Packer *et al.*, 1990; Stander, 1992b). Shedding some light to this debate Creel and Creel (1995) and later Creel and Creel (2002) noted that analyses of optimal hunting group size are strongly dependent on the currency of foraging success that is used. The hunting group size has also been shown to influence the prey that predators attempt to hunt, with large prey being pursued only when in large groups (e.g. Holekamp *et al.*, 1997; Creel & Creel, 2002), which reduces costs that can be accrued from failed hunts. The prey that predators seek to hunt can also be influenced by the demand for food, and this would mean that large groups (in terms of biomass) would need to hunt larger prey to meet energetic requirements of individuals within a group. Additionally, environmental conditions such as surface water distribution and snow depth may also have an influence on predator foraging behaviour by influencing the searching effort

involved for the predator to encounter prey animals, and also the vulnerability of prey (Hopcraft *et al.*, 2005; Valeix *et al.*, 2010; Gervasi *et al.*, 2013).

In this work, we tested hypotheses from optimal foraging theory and social foraging frameworks for African lion (*Panthera le*o) foraging behaviour. Despite there being a sizeable number of studies on lion diet and foraging behaviour, there are very few that have quantitatively applied foraging models to understand lion foraging behaviour. Hayward and Kerley (2005) carried out an analysis of 32 studies throughout the distribution of the lion and found that prey preference was mainly driven by the morphological characteristics (body size) of prey, however their analysis did not include the effect of lion group size. In the Serengeti National Park, Tanzania, lions preferred close prey over distant prey, frequently hunted young individuals and adjusted foraging behaviours according to their group size. These foraging strategies suggest sensitivity to prey profitability (Scheel, 1993).

The spatial heterogeneity in prey abundance and dispersion in Hwange National Park, Zimbabwe, the fission-fusion dynamics of lion prides and the investigation of lion kills provided us with a valuable opportunity to examine the factors influencing prey preference in lions. We considered a herd of prey to represent a resource patch that is available to lions and the different characteristics of the herd, such as prey body size and herd size, to characterize the richness of the patch. All four dimensions of prey that denote availability: abundance, dispersion, herd size and body size have key implications to lion foraging. We used optimal and social foraging theories to generate hypotheses of what would constitute the ideal foraging behaviour of lions. In this work, we investigated how (i) prey availability, (ii) environmental factors, (iii)

predator group size, and (iv) relative prey size (which is the prey to predator aggregated body weight) drive prey preference by African lions. We postulate that for such a large predator and in accord with optimal foraging and social foraging theories, prey preference would be influenced by the need to maximise the rate of energy gain and optimising foraging success.

Methods

Study area

Hwange National Park is a semi-arid dystrophic savanna on Kalahari sands, on the north-western border of Zimbabwe and it covers approximately 15 000 km^2 (Figure 5.1). The long term mean annual rainfall is ~600 mm. Open wooded savannas on Kalahari sands, primarily teak woodland (*Baikiaea plurijuga)* and *Combretum/Terminalia* woodlands dominate the east and southern parts of the park. Batoka basalt and Karoo sediments in the north and north-west of the park are dominated by *Colophospermum mopane* woodlands interspersed with grassland vleis, while the western part of the park is dominated by scrubland on Kalahari sands (Rogers, 1993a). Three seasons characterise Hwange National Park: early dry season (March - June), late dry season (July - October) and the wet season (November - February). During the wet season, water becomes available in waterholes, rivers and pools. Most of these sources of drinking water dry up during the dry season and only pumped waterholes (about 50), mostly in the North of the park, maintain water availability during the dry season (Figure 5.1). This difference in vegetation and water distribution across the park resulted in differences in the distribution of herbivores in terms of both assemblages and abundance (Chamaillé-Jammes et al. 2016). Three

contrasted study areas were monitored in this work: Robins, Main Camp and Ngamo (Figure 5.1).

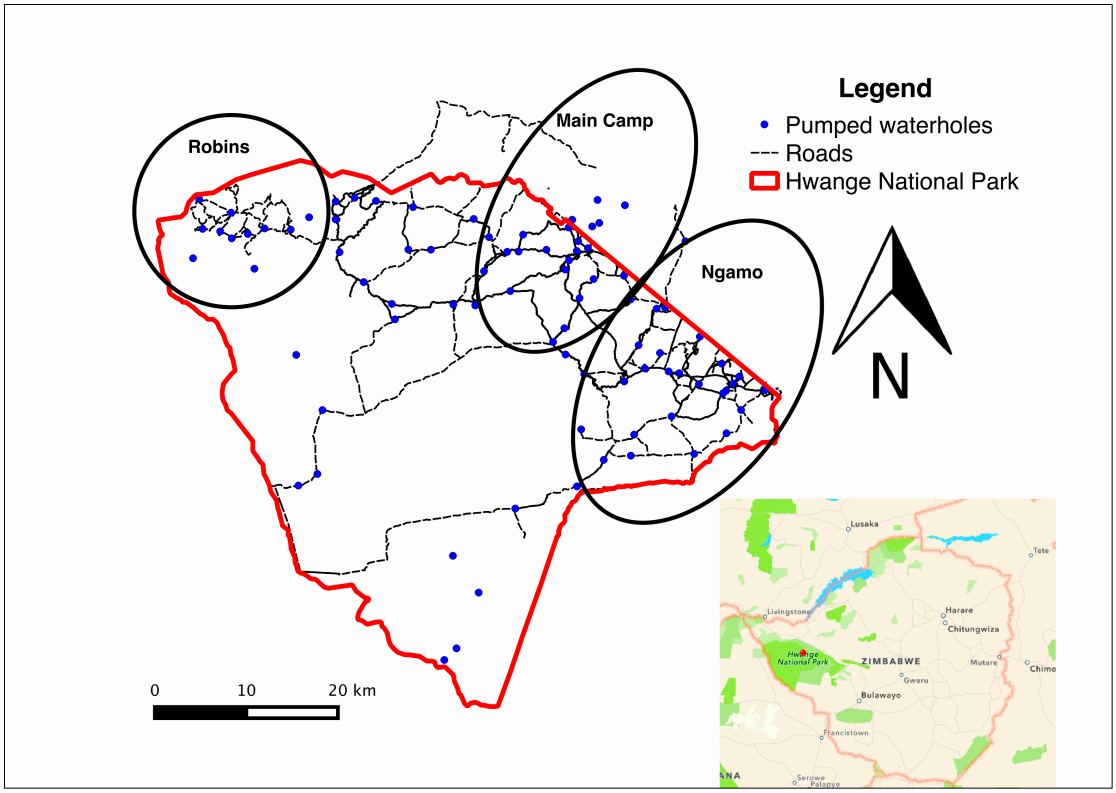


Figure 5.1 Hwange National Park map showing the three study areas; Robins, Main Camp and Ngamo. Also shown on the map are the waterholes, most of which do not retain water in the dry season and are therefore artificially pumped. The insert map shows the location of Hwange National Park in Zimbabwe.

Lion data

Lions have been monitored in Hwange National Park since 1999 and in this study we used data from 12 female and 15 male lions, from different prides across the park, equipped with GPS radio-collars between 2014 and 2015. Collars were set to record GPS coordinates once every two hours day and night. Positional data from the GPS radio-collars were downloaded regularly and for this study we used lion location data

for the early dry season and late dry season only (which corresponds to periods when prey availability data was available). We defined seasonal home ranges as the 90% probability contour of location distribution using the fixed kernel density estimator (Powell, 2000) and the reference smoothing factor href (Hemson *et al.*, 2005). Home-range analyses were undertaken using the AdehabitatHR package in the statistical software R (Calenge, 2006). Lion pride members are not always together and a process of fission-fusion normally results in the pride splitting into smaller sub-groups (Schaller, 1972; Packer & Pusey, 1997). Lions were therefore located and observed at least five times a month to record the size and composition of their sub-groups at those times. For each lion sighting, we recorded the number of individuals, identity, age and sex of the individuals in the group, and calculated the hunting group size (total number of adults and sub-adults in the sub-group), and the total biomass of the sub-group from the composition and body mass of each age class (adults, sub-adults and cubs). Therefore, for each study lion and each study season, we calculated the pride size (total number of adults and sub-adults in the pride), the mean hunting group size , the total pride biomass (biomass of all adults, sub-adults and cubs) and the mean sub-group biomass .

Kill data

We used the downloaded lion positional data to attain potential lion kill sites by identifying clusters of coordinates that had more than 4 hours of sequential locations within a defined proximity (150 m) (Davidson *et al.*, 2012; Davidson *et al.*, 2013). These sites were then investigated on foot to determine the activity at each GPS cluster (see also (Tambling *et al.*, 2010; Tambling *et al.*, 2012). Clusters were investigated as soon as possible, and generally within 30 days after lions occupied the

clusters to reduce chances of disturbance occurring at the sites and before scavengers eliminated all signs of feeding sites. Investigated clusters were searched for carcasses in a 50-m diameter around the GPS point, identified as the start of the cluster. A total of 970 potential kill sites were investigated during the study period and remains of kills were found at 210 sites. We identified kills by the presence of stomach contents and in most cases we also found carcass remains (bones, hair, horns, hooves, skin or teeth) at the sites. In this study, we only used data from lion kills and not from scavenging events. These were confirmed using several supporting indicators including: lion tracks, hair and scats, indications of a struggle visible in broken and trampled vegetation, the positioning of the carcass remains and the condition of any remaining hide bearing claw and bite marks typical of lion predation. Carcasses found at clusters were classified to species, age and sex based on the presence of identifiable material, such as horns, jaws, bones, hair and teeth wear.

Prey data

We conducted multi-species spoor surveys in the three study areas within Hwange National Park from 2013 to 2015 during the early dry season and the late dry season. Selected sections along roads or routes were driven and we identified and counted spoor in different sectors of the park. When fresh spoor (less than 24hrs old) was encountered, it was assessed for species, group size, age and sex (when possible). During the surveys, spoor of a range of herbivores and carnivores were identified to species, but only spoor from common lion prey species in the area was used in this analysis. Prey species included in the analysis were: Burchell's zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), waterbuck (*Kobus*

ellipsiprymnus), wildebeest (*Connochaetes taurinus*), steenbok (*Raphicerus campestris*), reedbuck (*Redunca arundinum)*, sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and juvenile African elephant (*Loxodonta Africana*) (frequently recorded as prey during drought years in Hwange; Loveridge *et al.*, 2006). Prey body size was estimated as three-quarters of adult female body mass to account for juveniles and sub-adult prey killed (Schaller, 1972) and the adult female body mass was obtained from Cumming and Cumming (2003). A previous study in Hwange divided prey into eight different prey size categories; 2275 kg for elephant, 828 kg for giraffe, 513 kg for buffalo, 302 kg for zebra, 273 kg for the class ‘‘medium Bovidae’’ (roan, sable, eland, wildebeest, tsessebe, waterbuck and reedbuck), 157 kg for kudu, 56 kg for the class ‘‘Suidae’’ (warthog and bush pig), and 11 kg for ‘‘small antelopes’’ (impala, common duiker, bushbuck and steenbok) (Davidson *et al.*, 2013). To understand the effect of different prey size categories on the relationship between prey preference and lion hunting group size we divided prey species into five prey size categories: megaherbivores ≥ 500 kg (elephant and giraffe), large herbivores ≥ 300 < 500 kg (buffalo, zebra and eland), medium-sized herbivores ≥ 100 < 300 kg (sable, kudu, waterbuck, wildebeest and roan antelope), small herbivores ≥ 20 < 100 kg (impala, warthog and reedbuck) and very small herbivores < 20 kg (steenbok).

The spoor survey data were overlaid on lion home ranges in QGIS (Quantum GIS Development Team, 2017) and the spoor transects that fell within each lion home range were clipped (Figure 5.1). For each home range and each season we assessed four measures of prey availability: one index of prey abundance or encounter rate (number of prey herds/km), one index of prey dispersion (nearest neighbour index of

prey herds), and two indices of patch richness (mean prey body size and mean prey herd size). The nearest neighbour index was calculated in QGIS (Quantum GIS Development Team, 2017) by measuring the distance between each prey herd and its nearest neighbour and then averaging all these nearest neighbour distances. If the average distance is less than the average for a hypothetical random distribution, the distribution of the prey herds is considered clustered, and if the average distance is greater than a hypothetical random distribution it is considered dispersed (five outlier points for the nearest neighbour index were removed from the analysis). These measures of prey availability describe the important prey attributes for lions and they are a gauge of the quantity, dispersion and quality of food resource patches available to lions. A measure of prey abundance describes the amount of food resource available to lions in their home range. A measure of prey dispersion describes the distance lions have to travel to encounter prey or the effort involved in searching for prey. The mean prey body size (a measure of patch richness) represents the quality of the food resource in terms of the energy gained from consumption of that prey species. The average prey herd size (a candidate measure of patch richness) is significant to lions as larger herds provide an opportunity for more than one lion to make a kill, and increase the probability of encountering vulnerable prey. For each prey herd, we also measured its distance to the nearest waterhole and averaged the distances in each lion home range for each prey category. This was taken as a measure of the predictability with which prey is distributed in the landscape, as waterholes are prey hotspots in Hwange National Park (Valeix *et al.*, 2012).

Statistical analyses

We used the Jacobs' (1974) index to determine prey preference by lions. We calculated a Jacobs' index for each prey body size category and for each lion pride and season. Jacobs' index values range between -1 and 1 with positive values indicating preference while negative values indicate avoidance (see Jacobs, 1974). We calculated prey preference for the late dry season 2014 and both early and late dry season 2015 to match the prey availability data. We found no significant difference in prey preference between male and female lions (estimate ± SE = -0.23 ± 0.20; t = -1.19; P = 0.24), as a result both data were analysed together. We preliminarily looked at the spatial distribution across the study areas of the proportion of lion kills of each prey body size category and of prey preference.

We first performed a generalized linear regression analysis with a Gaussian distribution and an identity link function to test the role of each of the various measures of (i) prey availability, (ii) environmental factors, (iii) predator group size, and (iv) relative prey size in influencing prey preference of lions. Regarding the role of prey availability, we specifically tested the following hypotheses: (a) lions prefer the most abundant prey in their home range, (b) lions prefer the most aggregated prey in their home range, (c) lions prefer richer resource patches (larger prey body size and larger prey herd size), and (d) lions prefer intermediate patch richness (medium to large-sized prey and medium to large herd size). Regarding the role of environmental factors, we specifically tested that (e) lions prefer prey encountered in the vicinity of waterholes as this increases the predictability with which lions can find them. Regarding the role of predator group size, we specifically tested the following hypotheses: (f) larger hunting group sizes prefer larger prey, and (g) larger prides

prefer larger prey species. We further tested non-linear relationship between (h) hunting group size and prey preference and (i) pride size and prey preference for the different prey body size categories as an optimal hunting group size or pride size may exist for each prey size category. Finally, regarding the role of relative prey size, we tested the hypothesis that (j) lions prefer prey that maximises the ratio of the biomass of the prey by the sub-group/pride biomass. Of the above significant hypotheses (four candidate models), we went on to further use a model selection approach to investigate the best model to explain prey preference of this African lion population. The model with the lowest AICc (Akaike Information Criterion corrected for small sample size) was considered the most plausible model and models with ΔAICc values of < 2 were also considered as plausible models (Burnham & Anderson, 2002). Information-theoretic weights (w) were calculated from the ΔAICc values.

Results

Spatial heterogeneity

From the investigation of lion kill sites, we found 14 herbivore species in the diet of lions, ranging in size from steenbok to giraffe and elephant (Table 5.1). The spatial distribution of lion kills revealed that medium-sized herbivores made up the highest proportion of lion diet in Main Camp and Robins while large herbivores made up the highest proportion of lion diet in Ngamo (Table 5.1, Figure 5.2). When the relative abundance of prey herds was accounted for to assess prey preference, large and medium-sized herbivores were the preferred prey body size categories in Main Camp, while in Robins medium-sized prey species were taken according to their availability and small-sized prey were preferred (Figure 5.2). In Ngamo lions preferred large, and to a lesser extent medium-sized and small prey species (Figure 5.2). There was a

general avoidance of megaherbivore and very small sized prey species across the study areas (Figure 5.2).

Table 5.1 Lion prey species found at the 210 kill sites in Hwange national Park, Zimbabwe, between 2014 and 2015, and their respective prey body size categories (megaherbivores, large, medium, small, and very small sized herbivores) and proportions for each of the study areas (Main Camp, Ngamo and Robins).

				Proportion of kills (%)			
Common name	Scientific name	Prey size category	Number of kills	Total	Main Camp	Ngamo	Robins
Elephant	*Loxodonta africana*	Mega	12	6	9	4	0
Giraffe	*Giraffa camelopardalis*	Mega	15	7	10	5	5
Cape Buffalo	*Syncerus caffer*	Large	49	23	18	30	10
Burchell's Zebra	*Equus quagga*	Large	30	14	7	21	15
Eland	*Taurotragus oryx*	Large	2	1	1	1	0
Greater Kudu	*Tragelaphus strepsiceros*	Medium	50	24	39	11	25
Roan	*Hippotragus equinus*	Medium	4	2	3	0	5
Sable Antelope	*Hippotragus niger*	Medium	4	2	2	2	0
Waterbuck	*Kobus ellipsiprymnus*	Medium	7	3	2	2	15
Wildebeest	*Connochaetes taurinus*	Medium	18	9	2	16	0
Warthog	*Phacochoerus africanus*	Small	6	3	5	1	5
Impala	*Aepyceros melampus*	Small	11	5	1	7	15
Reedbuck	*Redunca arundinum*	Small	1	0	0	0	5
Steenbok	*Raphicerus campestris*	Very Small	1	0	0	1	0
Total number of kills			210	210	88	102	20

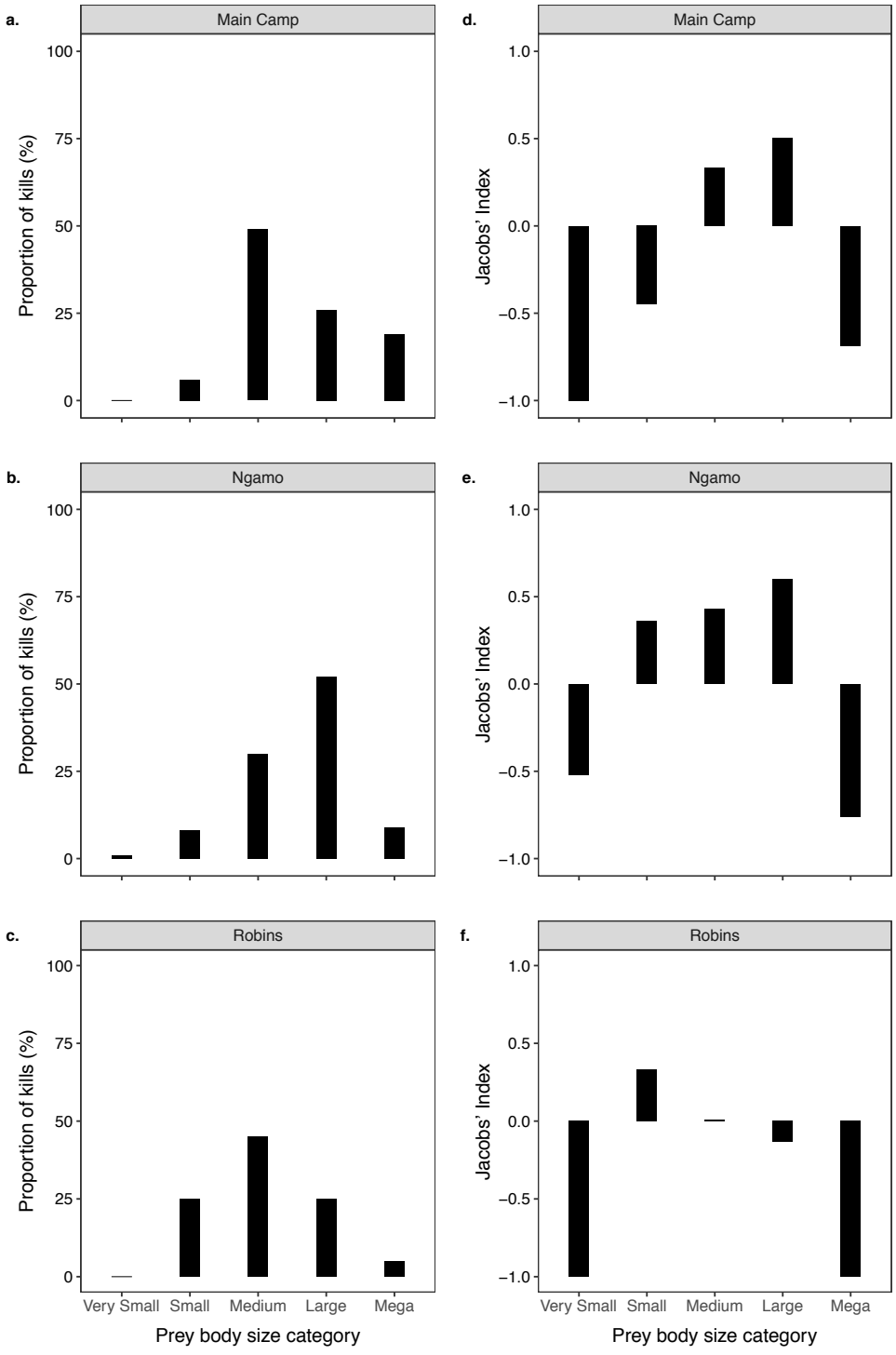


Figure 5.2 The proportion of kills of each prey body size category made across the three areas Main Camp, Ngamo and Robins (a - c) and the prey preference (measured by the Jacobs' index) of each prey body size category across the three areas (d - f) , from very small sized herbivores to megaherbivores in Hwange National Park, Zimbabwe, between 2014 and 2015.

1. Effect of prey availability on prey preference

Our results revealed an unexpected negative relationship between prey preference and the number of prey herds/km, an index of prey abundance, which was caused by megaherbivores, especially elephants, which are particularly abundant in the study ecosystem. However, prey abundance did not significantly influence prey preference (estimate ± SE = -0.19 ± 0.13; t = -1.45; P = 0.15), even when megaherbivores were excluded from the analyses and the relationship became positive (estimate ± SE = 0.78 ± 0.38; t = 2.06; P = 0.05). The nearest neighbour index of prey herds, an index of prey dispersion, did not significantly influence prey preference (estimate ± SE = 0.21 ± 0.27; t = 0.77; P = 0.44). The quadratic model for the relationship between prey preference and mean prey body size, an index of prey patch richness, had a better fit (AICc = 97.53) than the linear model (AICc = 126.43), and thus we only report results of the quadratic model (Figure 5.3a). The constant terms for the quadratic relationship were significant (a: estimate ± SE = $-1.57 \times 10^{-5} \pm 2.49 \times 10^{-6}$; t = -6.31; P < 0.001; b: estimate ± SE = 293.30 ± 11.96; t = 24.52; P < 0.001; and c: estimate ± SE = 0.43 ± 0.14; t = 3.14; P = 0.003). Prey preference increased with increase in mean prey body size up until 350 kg after which point prey preference started to decrease with increase in mean prey body size (Figure 5.3a). The linear model for the relationship between prey preference and mean prey herd size, a candidate index of prey patch richness, had a better fit (AICc = 118.38) than the quadratic model (AICc = 120.55), and thus we only report results of the linear model (Figure 5.3b). Prey preference significantly increased with increase in mean prey herd size (estimate ± SE = 0.04 ± 0.01; t = 2.92; P = 0.005) (Figure 5.3b).

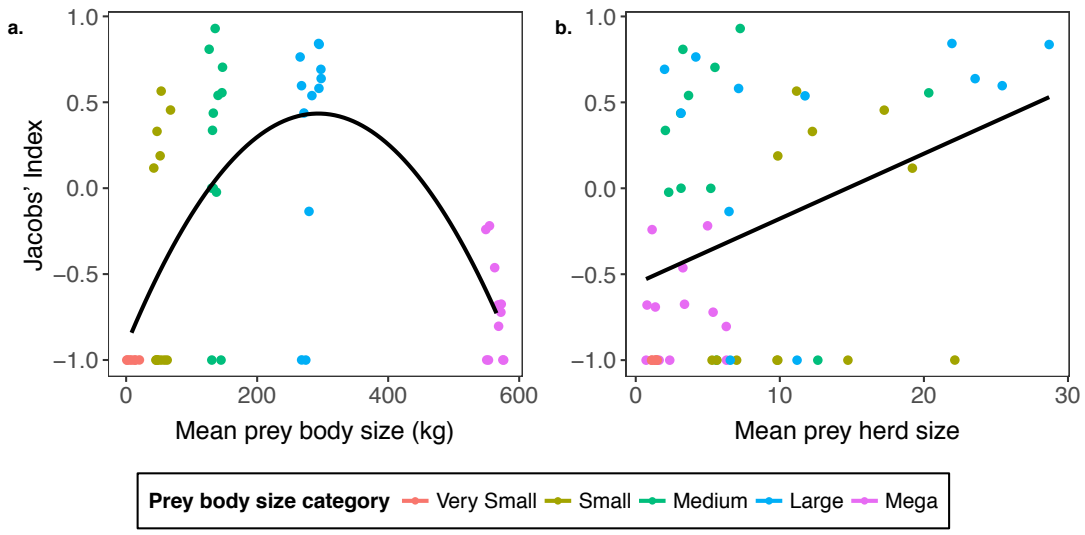


Figure 5.3: Plots of the relationship between lion prey preference (using the Jacobs' index) and a) mean prey body size (kg), an index of patch richness and b) mean prey herd size, also a candidate index of patch richness, from very small sized herbivores to megaherbivores in Hwange National Park, Zimbabwe, between 2014 and 2015.

2. Effect of environmental factors on prey preference

The distance to nearest waterhole did not significantly influence prey preference (estimate ± SE = -1.91 × 10^{-4} ± 1.53 × 10^{-4}; t = -1.25; P = 0.22). There was no difference in the preference of prey that were closer or further away from the waterholes.

3. Effect of predator group size on prey preference

The linear model for the relationship between prey preference and the interaction of hunting group size with prey body size category was a better fit (AICc = 108.3) than the quadratic model (AICc = 122.0), and thus we only report results of the linear model. The slope of the relationship between prey preference and hunting group size for large prey species was significantly different from the slope for medium-sized

prey species (estimate ± SE = 0.21 ± 0.09; t = 2.33; P = 0.02). For large-sized prey, preference increased with increase in hunting group size (Figure 5.4a). For medium-sized prey, preference decreased with increase in hunting group size (Figure 5.4a). Preference for very small, small and megaherbivores did not change with increase in hunting group size (Figure 5.4a). The linear model for the relationship between prey preference and the interaction of pride size with prey body size category was a better fit (AICc = 104.8) than the quadratic model (AICc = 116.7), and thus we only report results of the linear model. The slope of the relationship between prey preference and pride size for large prey species was significantly different from the slope for medium-sized prey species (estimate ± SE = 0.13 ± 0.04; t = 2.97; P = 0.005). For large-sized prey, preference increased with increase in pride size (Figure 5.4b). For medium-sized prey, preference decreased with increase in pride size (Figure 5.4b). Preference for very small, small and megaherbivores did not change with increase in pride size (Figure 5.4b).

4. Effect of relative prey size on prey preference

The ratio of the biomass of the prey by the sub-group biomass did not significantly influence prey preference (estimate ± SE = -0.11 ± 0.25; t = -0.43; P = 0.67). The ratio of the biomass of the prey by the pride biomass did not significantly influence prey preference (estimate ± SE = -0.28 ± 0.45; t = -0.62; P = 0.54). There was no preference for prey that maximises the ratio of prey biomass to sub-group/pride biomass.

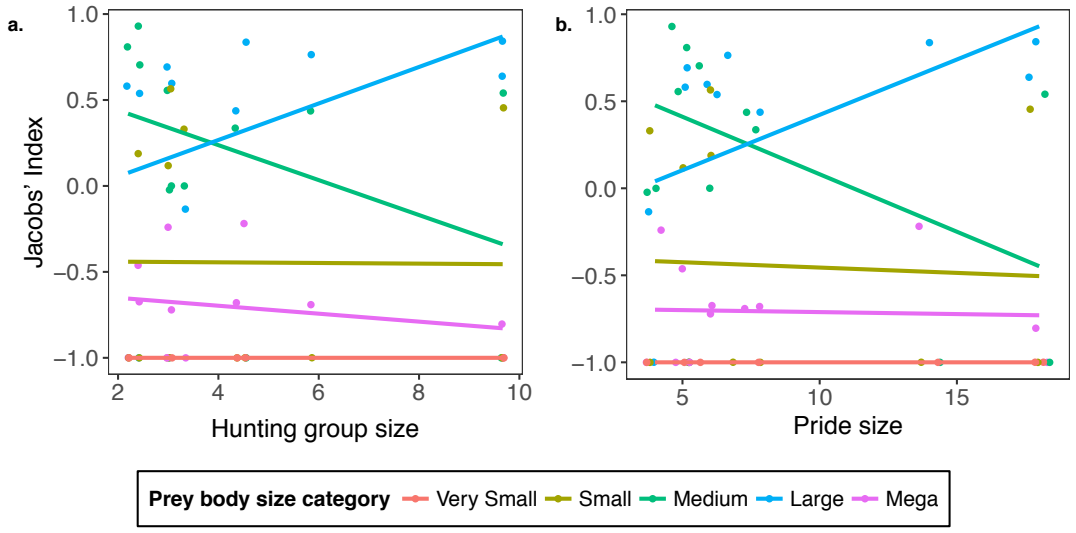


Figure 5.4 Plots of the relationship between lion prey preference (using the Jacobs' index) and a) lion hunting group size (number of sub-group adults and sub-adults) and b) lion pride size (number of pride adults and sub-adults) from very small sized herbivores to megaherbivores for lions in Hwange National Park, Zimbabwe, between 2014 and 2015.

Drivers of prey preference

Model selection of the drivers of prey preference by lions showed that the quadratic relationship between prey preference and mean prey body size was the most supported model to explain prey preference by lions (Table 5.2). Prey preference increased with increase in prey body size until about 350 kg, after which point preference started to decrease with increase in mean prey body size (Figure 5.3a).

Table 5.2 Biological hypotheses, predictor variables of candidate models, Akaike Information Criterion with the small sample bias adjustment (AICc), delta AICc (ΔAICc) and Akaike weights (*w*) of candidate models. Linear and nonlinear quadratic models for the relationship between prey preference (measured by the Jacobs' index) and aspects of (i) prey availability: mean prey body size and mean prey herd size, (ii) predator group size: hunting group size (i.e. sub-group size) and pride size and interaction with prey body size category ("Prey size category") for lion prides in Hwange National Park, Zimbabwe, between 2014 and 2015.

Candidate models	Model type	AICc	ΔAICc	*w*
Null				
Null model	Linear	124.3	26.81	0.000
(i) Prey availability				
a. Optimal prey patch richness				
Mean prey body size	Quadratic	97.5	**0.00**	**0.970**
b. Prey patch richness				
Mean prey herd size	Linear	118.4	20.85	0.000
(ii) Predator group size				
c. Hunting group size				
Hunting group size*Prey size category	Linear	108.3	10.74	0.005
d. Pride size				
Pride size*Prey size category	Linear	104.8	7.25	0.026

Discussion

In accord with predictions of optimal foraging theory, we found that prey preference in this lion population is largely driven by prey body size. Prey preference increased with increase in prey body size, as lions preferred the more profitable medium-sized and large prey species and avoided the less profitable small prey species and more dangerous (to the hunter) megaherbivores. We also found that prey preference increased with increase in mean prey herd size. The preference for larger prey herds was perhaps because they provide more than one lion with a chance to make a kill and possibly increases the probability of encountering a vulnerable individual within a herd. Our findings also indicated that prey preference was influenced by predator group size; prey preference increased with increase in hunting group size for large prey species but decreased with increase in hunting group size for medium prey species. This strategy suggests an optimisation of foraging success by both large and small lion groups. Although lions are generally thought to sometimes hunt opportunistically (Schaller, 1972; Packer *et al.*, 1990), the fact that they prefer large prey herds and medium and large-sized prey and that they adjust the size of their target prey species depending on hunting group size may suggest that the different prey species and herd sizes are not treated as equally profitable. Lions may be sensitive to variation in prey profitability (Scheel, 1993), including seasonal shifts in profitability (Davidson *et al.*, 2013) and shifts in profitability due to unforeseen environmental conditions such as rainfall condition, which affects prey vulnerability (Owen-Smith, 2008). In this lion population prey preference appears to be influenced by the need to maximise energy gain and optimise foraging success.

Lion diet ranged in size from steenbok to giraffe and elephant, in accord with previous findings for lion diet in Hwange (Loveridge *et al.*, 2006; Davidson *et al.*, 2013). The spatial distribution of the proportion of kills in the study areas showed some differences in the prey categories making the highest contribution in lion diet. This was at least partly attributable to the differences in the spatial distribution of prey assemblages across the study area (Chamaillé-Jammes *et al.*, 2016) and the associated lion pride sizes and lion fission-fusion dynamics in these contrasting areas (Mbizah *et al.*, *submitted*). Macdonald (1981) also discovered that foxes living in neighbouring territories showed some distinctions in their diet composition, as Sidorovich *et al.* (2001) also found for both American mink (*Neovision vison*) and European mink (*Mustela lutreola*). In our study, large- and medium-sized prey species were the most preferred prey size categories in two out of the three study areas. This is in line with previous studies in Hwange (Loveridge *et al.*, 2006; Davidson *et al.*, 2013) and also an analysis by (Hayward & Kerley, 2005), which revealed the generalisation that the most preferred weight range of lions is 190 - 550 kg.

Prey body size, an index of patch richness was the main driver of prey preference and this can be interpreted within the framework of optimal foraging theory (Pulliam, 1974; Pyke, Pulliam & Charnov, 1977). Prey preference increased with increase in prey body size and the relationship followed a bell curve. Lions would avoid small prey species, as they are not profitable and likely harder to catch (Elliott *et al.*, 1977) and favour the medium-sized and large prey species, as these would provide a higher net energy gain. However, lions would also avoid the very large prey species (megaherbivores), as they are too risky to hunt safely (Makacha & Schaller, 1969; Elliott *et al.*, 1977). These megaherbivores are therefore often considered invulnerable

to predation (Sinclair et al. 2003) even though they happen to be hunted under specific circumstances in Hwange (Loveridge *et al.*, 2006; Fritz *et al.*, 2011). Large prey species such as buffalo may be dangerous to hunt (Mangani, 1962) but they are preferred by lions in most habitats (Makacha & Schaller, 1969; Funston *et al.*, 1998; Davidson *et al.*, 2013) because of the high returns in energy investment which makes the risk rewarding.

In this study prey preference increased with increase in prey herd size, another plausible index of prey patch richness. Larger herds potentially provides a chance for several predators within a group to make a kill or for more than one individual to be killed from the herd (e.g. Schaller, 1972; Creel & Creel, 2002). Although we did not have evidence of multiple kills in this study, lions were however observed attempting to hunt more than one buffalo from the same herd or continued to hunt even after making a kill. If these herds are large-sized prey (e.g. buffalo herds) then large herds translate to a higher overall amount of potential energy to be gained. Our results match results by (Hayward & Kerley, 2005), who also found that prey preference increased with increase in prey herd size. Creel and Creel (1995) observed that larger wild dog packs often chased several prey animals from a single herd and these simultaneous chases often resulted in simultaneous kills of up to six wildebeest and seven impala. We expected the relationship between prey preference and prey herd size to follow a bell curve. We anticipated prey preference to increase with increase in prey herd size and then start decreasing after an optimal herd size because of the increased group vigilance by very large herds (Hamilton, 1971; Kenward, 1978). However this was not the case, it seems that what lions can gain from larger herds is more important than the risk of being detected by the prey. Several studies have

assessed anti-predator benefits of group living (e.g. Lima & Zollner, 1996; Uetz *et al.*, 2002) but only a few have examined the effect of prey group size on predator foraging decisions and hunting success (e.g Krause & Godin, 1995; Creel & Creel, 2002). A more rigorous test of this particular hypothesis in future carnivore foraging studies would shed more light on predator foraging behaviour.

As predicted by the social foraging theory predator group size had an effect on prey preference. The effect of hunting group size on prey preference was significantly different for medium and large prey species. This may suggest that hunting group size may affect the decision about which prey size to hunt. Lion preference for medium-sized prey species decreased with increase in hunting group size. This is in line with the optimal foraging theory where preference for a species decreases when the per capita energy gain starts to decrease (MacArthur & Pianka, 1966). On the contrary, preference for large prey species increased with increase in hunting group size. Larger herbivores such as buffalo and zebra are more profitable but they may be difficult to hunt, especially buffalos which have been known to mob predators and kill lions (Mangani, 1962; Estes, 1991). Consequently a larger pride or hunting group size may allow lions to hunt such large prey as a larger group is better suited to coordinate their hunt and to chase, overpower and subdue the large prey (Stander, 1992c). Hunting large prey may not necessarily increase food intake, however larger prey would allow a range of lion group sizes including larger groups to meet their physiological requirements (Caraco & Wolf, 1975). When hyaenas set out to hunt larger prey species they often leave the den in a large group size than when they set out to hunt smaller prey species and they often pass on smaller prey even when encountered (Kruuk, 1972), indicating that preferential predation is probably initiated early in the

predatory behavioural sequence (Creel & Creel, 2002; Hayward *et al.*, 2011). In a heterogenous landscape such as Hwange, lions are bound to encounter different prey species and decisions can then be made about which prey size to hunt. Hayward *et al.* (2011) found that lions hunted preferred species more frequently than expected based on their encounter rate, and hunted avoided prey far less frequently than expected, implying that lions actively and cognitively decide what to hunt.

The relative prey size, which is the ratio of prey biomass to pride biomass, had no effect on prey preference. We would have expected this ratio to have an influence on prey preference, as pride biomass 'mouths to feed' would affect decisions about which prey size to hunt. Prides with a larger biomass would need to hunt a larger prey to meet the daily requirements of individuals within the group. Therefore this result raises questions about the mismatch between prey size and the ultimate yardstick of energetic gain. Perhaps this result was caused by the crudeness of our analysis, as our data was inadequate for an in-depth exploration and this could have masked any real effects even if present. Such an analysis could be improved by using a more comprehensive measure of energy gain per individual such as the mean edible prey weight per individual. This measure takes into account the interaction of various factors such as energetic expenditure per hunt, edible biomass for each prey type, kill rate, palatability, predator group size and loss to scavengers (specially for small predator groups) (Caraco & Wolf, 1975; Hubel *et al.*, 2016). This again is another hypothesis that future studies can examine rigorously to get a better understanding of energetics of group foraging and the foraging efficiencies of various predator group sizes, all within the framework of the social foraging theory.

Our study has contributed to an understanding of the dynamics of lion foraging behaviour and also aspects of the evolution of lion social behavior as well as predator-prey relationships. We have shown that the richness of prey patches both in terms of the body size of prey and the size of prey herds as well as lion hunting group size are important factors that influence prey preference in lions. The foraging behaviour of this lion population can be interpreted within the framework of the optimal foraging and the social foraging theories; lions preferred larger prey, larger herds and preferred larger prey when in larger group sizes, suggesting that they seek to maximise energy gain and optimise foraging success.

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Chapter 6



General Discussion

Aims and motivations

The aim of this thesis was to investigate how availability of resources such as prey, and particularly the (i) abundance, (ii) dispersion and (iii) richness of prey patches (measured as prey herd size and prey body size), influences the ecology of lions, specifically their (a) foraging behaviour, (b) ranging behaviour, (c) broad-scale social structure and (d) fine-scale social structure. This work was motivated by an emerging body of literature suggesting that the abundance and distribution of prey plays an important role underpinning sociality and foraging behaviour in animals (Macdonald, 1983; Sunquist & Sunquist, 1989; Johnson *et al.*, 2002; Macdonald *et al.*, 2010b). However, the majority of the studies that looked at the relationship between lions and their prey used habitat characteristics and water sources (waterholes and river confluences) as surrogates for prey availability (e.g. Mosser *et al.*, 2009; Valeix *et al.*, 2012). It was therefore important in this study to measure prey availability directly by counting the available prey within each lion home range, as this is a better portrayal of what is actually available to lions. In this study, I used the spoor count method to estimate relative abundance of prey within lion home ranges and the spoor-based index was sufficiently reliable to assess big changes in the relative spatial and temporal differences in herbivore population abundance (Chapter 2). Furthermore, the majority of studies on lion social behaviour and feeding ecology are from Serengeti National Park, Tanzania, and results from this landscape are often not applicable to other ecosystems particularly in Southern Africa where water distribution is managed and water is supplemented with pumped waterholes in the dry seasons and the vegetation also differs. For example, in Hwange National Park, there is no evidence of seasonal shift in diet of male lions (Davidson *et al.*, 2013) unlike in the Serengeti

ecosystems where seasonal shift in diet can be caused by variation in prey abundance over shorter time scales (Campbell & Borner, 1995).

It is often difficult to test hypotheses on animals in the wild, especially on large carnivores as they are wide-ranging, often nocturnal and elusive, and consequently difficult to track and observe and the different predicator variables difficult to measure and manipulate. However, the heterogeneity of Hwange National Park and the long-term study of GPS-collared lions provided us with a unique opportunity to examine the effect of prey availability on lions. In this thesis, I first examined the Resource Dispersion Hypothesis as various studies across several species supported its predictions, while others could not. Besides testing predictions of the RDH, it was also important for this study to investigate the effect of fission-fusion dynamics as it was something that had not been examined before but that could potentially explain why the relationship between group size and patch richness in fission-fusion societies may not be so apparent (Chapter 3). After I had shown that prey availability had an influence on the broad-scale of lion social structure that is the lion group size (Chapter 3), I innovatively evaluated the influence of prey availability on a finer-scale of lion social structure (Chapter 4). I took advantage of the social network toolbox and the recent advances in social network analysis, such as the use of the null models and dynamic social networks, to facilitate the exploration of lion social network structure and understand how prey availability influences association patterns between individuals in a pride and pride community structure. Despite there being a sizeable number of studies on lion diet and foraging behaviour, there are very few that have quantitatively applied foraging models in understanding lion foraging behaviour, so in Chapter 5 I applied the optimal foraging and social foraging theories to better

understand lion foraging behaviour. I also wanted to go beyond the usual descriptive approach of dietary studies to a predictive approach so that results from this study could be used to predict the range of foraging behaviours of lions at other sites.

Key findings

I have shown in Chapter 2 the potential usefulness of the spoor count method in estimating the relative abundance of herbivores. The spoor count method has the advantage that spoor counts can be carried out simultaneously with carnivore counts thereby saving on costs. While it was already known that prey are vital for lions this thesis in Chapters 3 – 5 highlights the greater importance of patch richness in playing an integral role in the ecology of lion prides. This thesis has also shown in Chapters 3 & 4 that prey availability with regard to dispersion of prey patches also plays an important role in lion ecology. Among the four measures of resource patch, only the abundance of prey patches seemed not to play any role in lion ecology (Figure 6.1).

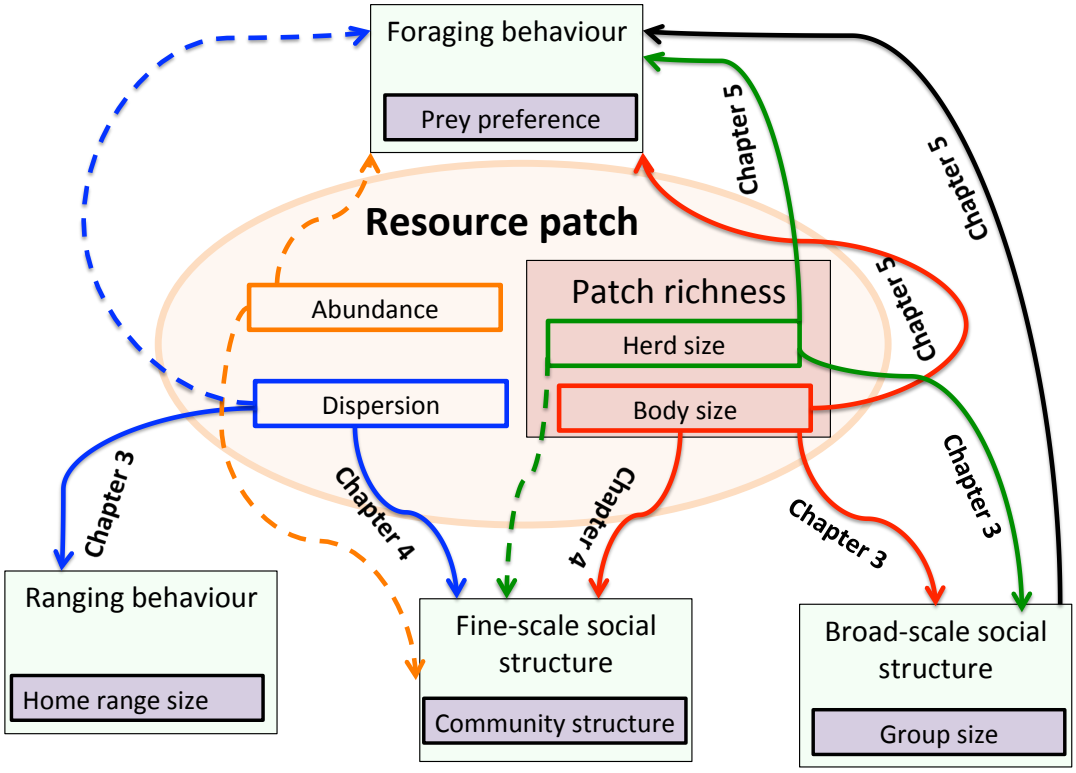


Figure 6.1 The hypothesis tested in this study on the ways in which resource patches, specifically their abundance, dispersion and richness (characterised by prey herd size and prey body size) can affect the ecology of a social predator particularly its foraging behaviour, ranging behaviour, broad-scale social structure, and fine-scale social structure. The dashed arrows show the hypotheses that we not supported in this study and the bold arrows the hypotheses that received support.

Body size

Although prey body size on its own had no significant effect on lion group size, our results revealed an interactive effect of prey body size and the frequency of pride fission on lion group size with the relationship between lion group size and prey body size becoming more negative with increase in frequency of pride fission (Chapter 3). This is likely to be because where large prides predominantly hunt large prey they

operate as an intact cooperative unit (Packer & Pusey, 1997), the size of which is adapted to the large meal size provided by a large prey (Packer *et al.*, 1990), whereas where they eat predominantly small prey, each prey item provides an inadequate meal for the whole pride, so they tend to fission into smaller hunting parties and perhaps this leads to a larger total pride size comprised of a greater number of smaller hunting parties. Prey body size had an effect on the association patterns between individuals in a pride and the community structure of lion prides (Chapter 4). As prey body size increased, the associations between individuals in a pride became more random, resulting in highly connected pride members with little sub-grouping within prides. This may provide a number of benefits to pride members including increased chances of mating (Croft *et al.*, 2008), alloparental care (Pusey & Packer, 1994) and territorial defence (Mosser & Packer, 2009). Within its home range or territory, a predator might have to make choices about where to forage and which food items to eat (Krebs, 1977). This study has revealed that prey body size is the main driver of prey preference in lions (Chapter 5). Prey preference increased with increase in prey body size and this relationship followed a bell-shaped curve. Lions preferred the more profitable medium-sized and large prey species and avoided the non-profitable small prey species and risky to hunt mega herbivores. These results suggested that lions are possibly sensitive to variation in prey profitability (Scheel, 1993), and that in Hwange lions prey preference appeared to be driven by the need to maximise energy gain.

Herd size

Prey herd size (a plausible index of patch richness) had an influence on lion group size (Chapter 3). As predicted by the Resource Dispersion Hypothesis, lion group size increased with increase in mean herd size. This result suggests that it is the richness of

patches that allows larger groups to be supported in these rich areas and this facilitates the development of other group living behaviours such as cooperative hunting and cooperative defense of territories (Grinnell, 2002; Mosser & Packer, 2009), which in turn helps maintain social ties within the group. Prey herd size also had an influence on lion foraging behaviour (Chapter 5). As predicted by the optimal foraging theory, lion prey preference increased with increase in mean prey herd size as larger herds provide more than one lion with an opportunity to make a kill. Larger herds are more visible to lions and also increases the probability of finding a vulnerable individual within a herd and this increases chances of prey capture. If these large herds are composed of large prey such as buffalo then this can also translate to maximized energy gain.

Dispersion

As predicted by the Resource Dispersion Hypothesis, the dispersion of prey patches had an influence on lion home range size (Chapter 3). When prey is dispersed lions have to defend a larger home range to incorporate the dispersed prey patches and this might mean energy that could otherwise be invested in activities such as reproduction might need to be spent in patrolling and defending the large home range. The dispersion of prey patches also had an influence on the association patterns between individuals in a lion pride (Chapter 4). When prey was more dispersed there were stronger within community and weaker between community associations, resulting in a more structured community with individuals associating more with individuals from their own sub-group and rarely associating with individuals from other sub-groups. This has the effect of limiting the opportunity for social interactions between individuals (Tanner & Jackson, 2012), leading to prides that are socially fragmented,

with little contact between sub-groups and this has a risk of reduced social benefits such as alloparental care.

Often foraging studies of social predators neglect to take into account predator group size when studying their foraging behaviour. I have shown in Chapter 5, the importance of group size in influencing lion prey preference. In accord with the social foraging theory, preference for large prey increased with increase in hunting group (and pride size) and the preference for medium sized prey decreased with increase in hunting group size (and pride size). Larger prey species are more profitable but they may be difficult to hunt, especially buffalos (Mangani, 1962; Estes, 1991), consequently a large hunting group size may allow lions to hunt such large prey by coordinating in chasing, overpowering and subduing the large prey (Stander, 1992c). This study has highlighted that the continued persistence of the lion population in Hwange National Park, may as well among other things depend upon the preservation of adequate supplies of food.

Application to African large carnivores

Results of this study may be widely applicable across the Carnivora especially the large social carnivores, such as spotted hyaenas (*Crocuta crocuta*) and African wild dogs (*Lycaon pictus*) that utilise the same prey base as lions and exhibit the same social dynamics. Next to lions, spotted hyaenas are the second largest social carnivore in Africa and wild dogs although much smaller are one of the most social canids. It has been shown among the Carnivora that societies reflect their ecological environments (Macdonald, 1983; Gittleman, 1989) and previous studies have indicated that intraspecific variation in carnivore grouping patterns is related to the

availability and distribution of food resources (Kruuk, 1975; Bertram, 1979; Macdonald, 1983; Kruuk & Macdonald, 1985; Tilson & Henschel, 1986).

Size relationships are central in structuring trophic linkages within food webs and there is a differing selection shown by carnivores for specific size ranges of prey (Owen-Smith & Mills, 2008). The chances of successful capture and subduing of large prey sets the upper size limit to the prey consumed, while the lower size limit depends upon how frequently smaller prey can be found and eaten (Owen-Smith & Mills, 2008). Judging from the large volume of literature on the relationship between prey body size and predator foraging and social behaviour, it is clear that prey body size is perhaps the most important prey characteristic for large predators. In this study, prey body size was the main driver of prey preference in lions (Chapter 5). In a previous study in HNP, buffalo a large prey species emerged as the primary prey species for lions (for both males and females) with a high contribution to lion diet throughout the year, and a strong selection by lions in all seasons (Davidson *et al.*, 2013). A review of lion prey preference by Hayward and Kerley (2005) showed that there was a general preference for medium to large sized prey across lion range. Hayward (2006) reviewed prey preference in hyaenas and found that in stark contrast to the rest of Africa's large predator guild, the hyaenas did not show any particular preference for any prey body size, but however seemed to avoid the large prey. This was however in contrast to a study in Niokolo Koba National Park, Senegal, where hyaenas preferred the large and medium-sized prey species, such as buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus buselaphus*) and warthog (*Phacochoerus africanus*) (Di Silvestre, Novelli & Bogliani, 2000). Hyaenas are conceivably the most successful of Africa's large predators and one of the reasons for this success being the

flexibility in their diet. On the contrary, a review on African wild dog prey preference revealed that they mainly prefer small and medium sized prey (Hayward *et al.*, 2006). However, wild dogs have also been recorded preying on prey as large as juvenile buffalo and eland (*Taurotragus oryx*) (Creel & Creel, 2002).

Foraging group size in carnivores is often linked directly to food acquisition in terms of locating, pursuing and killing the prey (Gittleman, 1989). Early studies on lions, hyaenas and wild dogs found that these species often hunted in groups and as a result increased chances of finding and catching prey and also increased the diversity and size of prey captured (Estes & Goddard, 1967; Kruuk, 1972; Schaller, 1972; Caraco & Wolf, 1975; Kruuk, 1975). The difficulty in subduing prey and risk of injury (to the hunter) should rise with prey size; therefore a large hunting group would be required to successfully subdue a large and dangerous prey species (Funston *et al.*, 2001; Creel & Creel, 2002). Where there is large prey, predators are therefore expected to form large groups because (i) large groups would increase chances of prey capture and therefore maximise energy gain (Chapter 5) and (ii) under the RDH, large prey are rich patches and can therefore support large group sizes (Chapter 3). Results from this study (Chapter 5) revealed that the preference for large prey species increased with increase in lion hunting group size and this was as we had expected from the social foraging theory that a predator would aim to maximise foraging success (Giraldeau & Caraco, 2000). Kruuk (1972) indicated that hunting success by hyaenas hunting blue wildebeest calves in the Serengeti increased with increase in hyaena group size. Observations of hyaena hunting methods by Kruuk (1972) also indicated that when hyaenas set out to hunt, the prey type they hunt would depend on their group size, with larger groups almost always hunting larger prey even when smaller prey were

the most easily accessible. In Masai Mara National Reserve, hyaena hunting success was influenced by group size and only zebra were usually hunted in groups (Holekamp *et al.*, 1997).

African wild dogs are possibly the most efficient group hunting large carnivore, the pack functions primarily as a hunting unit, cooperating closely in killing and in mutual defence of prey, prioritising group activity to individual and having strong discipline during the chase (Estes & Goddard, 1967). Communal hunting in African wild dogs resulted in increased chances of capturing large prey whose capture required long, energetically costly runs and/or cooperation of multiple individuals to subdue them but provided greater returns per individual than the smaller prey (Estes & Goddard, 1967; Creel & Creel, 1995; Creel & Creel, 2002). In the Serengeti larger packs of wild dogs were more successful than smaller ones in hunting medium-sized prey like adult wildebeest and hunting in groups also reduced interspecific competition from spotted through improved defence of carcasses (Fanshawe & Fitzgibbon, 1993). The positive relationship between group size and prey size or hunting success has been widely used to argue that group hunting favours sociality. However, there is still need for more in-depth analysis on the net energy gain from such group hunts as sharing of prey in larger groups can lead to a decrease in daily per capita food intake even when hunting success of large prey increases (Schaller, 1972; Packer *et al.*, 1990; Caro, 1994). Such studies will doubtless need to be carried out across the range of these carnivores as energetic returns might differ substantially between populations, owing to variations in prey size and hunting effort.

Although we were not able to show that rich patches in terms of prey body size support larger groups (Chapter 3), we however revealed that this could be because of the fission-fusion dynamics of lion prides, where they adjust their sub-group size according to the size of the available prey species. In this case, large prides would be able to be supported in poor patches by splitting into small sub-groups when they encounter small prey. As in lions, group living in African wild dogs has many advantages, such as defence of kills, communal rearing of pups and defence of pups from predation and this could be critical for its survival (Malcolm & Marten, 1982; Creel & Creel, 1996; Gorman *et al.*, 1998). Where interspecific competition with lions (primarily via direct killing) and spotted hyaenas (primarily via food loss) is high, this exerts a strong selective pressure in favour of large packs as well as for close cooperation at kills (Estes & Goddard, 1967). We would therefore expect the richness of resource patches to facilitate sociality and group size in wild dogs. The size of hyaena clans are complex, fission–fusion societies in which individual members travel, rest and forage in sub-groups that frequently change composition (Smith *et al.*, 2008). We would therefore expect hyaena clans to adjust their sub-groups according to the size of available prey and their group size to be influenced by the richness of resource patches in that regard.

The availability of food plays an important role in the life of a social carnivore, by influencing its relationships with conspecifics. This study (Chapter 4) has shown that prey body size plays an important role in the association patterns and community structure of lion prides. At present, no study has yet attempted to examine the effect of prey availability on association patterns between individuals in hyaenas or wild dogs. But Creel and Creel (2015) showed that wild dogs are cooperative hunters with

highly cohesive packs within which there is communal rearing of cubs. Wild dogs have been observed to greet and engage in a pre-movement ‘rally' behaviour and this was suggested to be a behaviour that promote pack cohesion before hunting (Creel & Creel, 2002). As wild dogs packs are highly cohesive it will be potentially difficult to tease apart the effect of resource availability on their association patterns and community structure. Unlike lions and wild dogs, there appears to be little cooperative breeding in hyaenas, this has been attributed to the low relatedness and hence absence of kin selection pressure to favour helping rear young (Kruuk, 1972; Mills, 1985). But Knight, Jaarsveld and Mills (1992) recorded some rare displays of allo-suckling in Kalahari hyaenas and they proposed that the stressful ecological conditions and the high cub mortality resulting from it may have been one of the factors to cause such a behaviour. This may suggest that the interactions and associations between individuals within hyaena clans may potentially be influenced by variations in prey availability. It will therefore be important and quite revealing for future studies to examine the effects of prey availability on association patterns and community structure of hyaena clans and wild dog packs.

An animal's home range is often considered to be mediated by the abundance of resources, as well as by their dispersion, and the predictability with which they are available (Macdonald & Carr, 1989). When prey is dispersed, this implies higher costs to the carnivore in terms of energy spent during travelling, as well as energy ‘‘not gained’’ due to time spent travelling instead of foraging. We showed in Chapter 3 that when prey is more dispersed, lions increase their home range and this is a strategy to increase the amount of food available within the home range. A previous study in Hwange also showed that female lion home range was influenced by the

dispersion of prey in the landscape (Loveridge *et al.*, 2009). Valeix *et al.* (2012) also found that the dispersion of waterholes, which are prey hotspots in Hwange, influenced lion home range, with large home ranges found in areas with more dispersed waterholes. In the late dry season, buffalo and young elephant in Hwange can be predictably found near waterholes and thus lions configure their ranges to ensure access to these areas (Loveridge *et al.*, 2009). In the central Namib desert, hyaena clans were observed to utilise large home ranges and this was described as an adjustment to a dispersed poor prey assemblage and to the limited availability of water (Tilson & Henschel, 1986). In this arid landscape, the distribution of available water was also a key resource that dictated where a hyaena clan's core area was located (Tilson & Henschel, 1986). The ranging behaviour of wild dogs has often been linked to denning, with a contraction in home range during the denning season (Pomilia, McNutt & Jordan, 2015). However, there have not been any studies investigating the effect of resource dispersion on home range size of wild dogs and this is a hypothesis that future wild dog studies can explore.

Effect of water management

Water availability is a crucial limiting factor in arid and semiarid environments (Redfern *et al.*, 2003). Several studies have shown that the distribution of surface water has an influence on herbivore distribution patterns in arid and semi-arid ecosystems (e.g. Bergström & Skarpe, 1999; Fensham & Fairfax, 2008), as many herbivores depend on drinking water to fulfil their daily water requirements. This is especially so in the dry season where the locations of water sources might impose a landscape-scale constraint on herbivore distributions (Redfern *et al.*, 2003). One of the most important and widely applied management option to promote herbivore

viability in arid and semi-arid regions is the provisioning of artificial waterholes (Owen-Smith, 1996), but this often comes with unintended consequences. Water provisioning has attracted a lot of debate, especially in Kruger National Park, where it has been associated with changes in herbivore distribution as well influencing the density and distribution of elephants (see Chamaillé-Jammes, Valeix & Fritz, 2007b; Smit, Grant & Whyte, 2007a; Smit, Grant & Whyte, 2007b). Nonetheless, water provisioning has been indeed a necessity in some parts of semi-arid to arid Africa where only seasonal rainfall is available to animals (e.g. Redfern *et al.*, 2003). In Hwange National Park, water provisioning is an important management option available to ensure the survival of herbivores during the dry season as well as to manipulate the densities and distribution patterns of certain herbivores (Chamaillé-Jammes *et al.*, 2007c). As the dry season progresses in HNP, most rain-fed water sources start to dry up, forcing most animals to concentrate in the immediate vicinity of the few remaining permanent sources of drinking water, which are artificially pumped during the dry season (Chamaillé-Jammes *et al.*, 2007c; Valeix, 2011).

Herbivore species are usually not distributed randomly over an area (Redfern *et al.*, 2003), water dependant herbivore species such as waterbuck (*Kobus ellipsiprymnus)*) would need a constant supply of water and therefore usually occur close to a permanent source of water in the dry season (Smit, 2011; Valeix, 2011), thus water dependency is one of the traits that determine the spatial distribution of prey species for carnivores. Water also attracts prey species that are often closely linked to dense vegetation, around riverine areas and waterholes (Van Orsdol, 1984; Hopcraft *et al.*, 2005). Waterholes have been shown to be important in the ecology and foraging behaviour of large carnivores such as lions as prey are predictability found there and

are more vulnerable (Valeix *et al.*, 2010) and easier to stalk because of increased cover around these water sources (Hopcraft *et al.*, 2005). Hopcraft *et al.* (2005) showed that Serengeti lions selected erosion embankments, view-sheds from rocky outcrops, woody vegetation, and access to free water and thus fed in these areas of high prey catchability. In Hwange, Davidson *et al.* (2013) indicated that lions preferred to kill within 2km of a waterhole, suggesting that surface-water resources form passive traps and contribute to the structuring of lion foraging behaviour.

The pumping of waterholes in HNP is financed by several charities such as Friends of Hwange, and in the event that funds for the pumping of these boreholes have seized, then that would affect both the herbivore and carnivore populations in the park. Given the economic instability in Zimbabwe, this scenario is quite likely. Browsers such as giraffe and kudu are less water dependant, while common generalist grazers (zebra, wildebeest and buffalo), although water dependant are more flexible in their habitat and forage requirements than the more selectively grazing rare antelope (roan, sable and tsessebe) (Skinner & Smithers, 1990). Therefore, if some waterholes are closed down there is a higher possibility that in the short term the browsers and the generalist grazers will be more readily able to adjust their distribution, without necessarily compromising their forage or habitat requirements significantly. However, in the long term even these herbivores will succumb to the effects of water shortage as they will be forced to travel greater distances to reach surface water (Smit & Grant, 2009) and this will impact on the lions as we have shown in Chapter 5, that the large prey species (zebra and buffalo) are the most important in lion diet and drive prey preference and in Chapter 4 that when prey is large, pride members associate frequently outside of their close connections resulting in increased pride-level

cohesion. Therefore, the management of waterholes can potentially have an effect on the dispersion and richness of prey patches and therefore exert an indirect effect on the ecology of the lion population in Hwange.

Effect of climate change

Climate change is bound to induce habitat change and have an effect on the availability of water and forage and consequently the distribution and assemblages of prey as well as the vulnerability of prey to a predator. Arid and semi-arid tropical environments have always been characterised by a high climatic variability, consequently climate change induced drought cycles (prolonged rainfall shortage) in arid and semi-arid savanna are expected to become more frequent and severe in the future (Prins & Iason, 1989; Sithole & Murewi, 2009). This will have consequences on water distribution and herbivore abundance and composition as well as reducing the carrying capacity of a system (Prins & Iason, 1989). In HNP, the year 2003 was a drought year having received very little rainfall, during this period there was an increased use of waterholes and the level of aggregation of herbivores at waterholes was significantly higher (Valeix, 2011). Drought has also been shown to increase the susceptibility of water dependent species such as buffalo to lion predation (Prins & Iason, 1989). During droughts in Hwange, buffalos and elephants have to travel long distances between waterholes and are mostly killed by lions close to waterholes where they will come in large numbers to drink, but because of the long travel and days without water the young and the old would be vulnerable to lions (Loveridge *et al.*, 2006; Chamaillé-Jammes *et al.*, 2016). This will be advantageous for lions over the short-term as they would not have to invest much energy in hunting for prey, but in the long run, droughts across a period of consecutive years can have an impact on

prey dispersion and richness of prey patches, especially of water dependent prey and the grazers and this can have an impact on lion ecology as shown in this thesis in Chapters 3 to 5.

Conservation implications

Results from this study indicated that the most important prey characteristics affecting lion broad-scale social structure (Chapter 3), fine-scale social structure of lion prides (Chapter 4) and foraging behaviour (Chapter 5) is the dispersion of prey (Chapter 3 & 4) and the richness of prey patches, both in terms of the size of prey herds (Chapter 3 & 5) and the prey body size (Chapter 3 to 5). Thus, if it is desired to maintain a healthy lion population then large herd forming and larger prey species should be maintained in the park. The aggregation of prey should also be facilitated; this can be done through pumping more waterholes in the dry season as prey has been shown to aggregate around waterholes. Perhaps species such as the buffalo is in this regard the most important prey species for lions in Hwange National Park as it fits all the prey characteristics that are important for lions. Buffalos are large prey species (450 kg adult female body weight), they are often in large herds and they usually aggregate around waterholes especially in the dry season. Indeed, it has been suggested in a previous study in Hwange that buffalo are likely to have a crucial influence on the spatial and behavioural ecology of lions in all seasons (Davidson et al., 2013). In Hwange National Park and many other similar sites, tourism demands often interact with ecological goals, therefore the management options that promote a healthy lion population (stated above) or the aggregations of lions around waterholes (making it easier for tourists to find and see lions) may need to be implemented so as to promote tourism. It is also important to note here that manipulations intended to

benefit lions could nevertheless have an impact on the demography and ecology of the smaller members of the guild such as wild dogs, hyaenas and cheetah as well as other rare or low-density prey species such as sable. The impact of lions on theses species can be complex and risky for example an increase in lion density in Savé Valley Conservancy, Zimbabwe resulted in increased lion induced pup mortality and a lower pup to adult ratio and hence a lower adult recruitment (Groom, Lannas & Jackson, 2017). In Hwange National Park, the long-term risk of predation by lions appeared to influence the distribution of all browsers across the landscape (Valeix *et al.*, 2009b). Lions are being reintroduced in some parts of Africa especially in South Africa (e.g Hunter *et al.*, 2007) and results from this study could potentially shed some light on some of the important prey characteristics to consider when reintroducing lions. For semi-arid and arid ecosystems such as the Hwange National Park, successful management of the ecosystem and conservation of large herbivores and carnivores will require an understanding of the relationship between surface water, herbivore populations and carnivore ecology and behaviour.

General Conclusions

This study reiterates the importance of resource dispersion in among other things laying the foundations for the evolution of lion sociality. We have shown that ecology (prey availability) strongly influences the behaviour and social structure of a social carnivore. However it is somewhat complex and challenging to disentangle the effects caused by ecological constraints from those caused by social constraints. It may as well be that social species that do not glean benefits of group living (e.g. badgers) continue to need the RDH to explain their large groups, while in contrast for social species that do glean benefits of group living (e.g. lions) the RDH may not be a

sufficient explanation, although it may have been a crucial one in their past and an on-going contributory one today, especially in explaining constraints on social organisation. It will be imperative for future studies to build on the results of this thesis and attempt to understand the extent to which social constraints (social ties and social behaviour) of social carnivores rather than ecological constraints causes them to partition space and groups. It is probable that this might cause them to sometimes socially organize against the grain of the prevailing ecology, for example female lions staying in large groups so as to protect their young against infanticidal males, even when in areas with small prey species (poor quality patches). There is no doubt that social and ecological constraints are not mutually exclusive and results from this study provide new insights (that can be explored further) by considering the fission-fusion dynamics of social animals and the fine scale association patterns among individuals within groups and between subgroups.

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