The Spatial Ecology of Lion (*Panthera leo*) and Spotted Hyaena (*Crocuta crocuta*) in Hluhluwe-iMfolozi Park: Implications for the African wild dog (*Lycaon Pictus*)

by

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As the candidate's supervisor I have approved this thesis for submission.

Signed: Name: Rob Slotow Date: 12 Apr 2010

Abstract

The ecological role of apex predators in ecosystems is increasingly recognized not only as a result of their affects on prey species, but also on the numbers and behaviour of other predator species within their guilds. In an African context, dominant apex predators such as lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) have been implicated in limiting endangered intraguild species such as wild dogs (*Lycaon pictus*) via direct intraguild interactions, such as interference and predation. As a result of this it has been predicted that spatial and temporal refugia are critical for wild dogs to co-exist with lions and spotted hyaenas. Whether such refugia are actually present within small protected areas, such as Hluhluwe iMfolozi Park (HiP), within which these three species co-exist, has been questioned.

For wild dogs, interference or predation refugia may be equated to areas or periods which contain a relatively low level of encounter probability with spotted hyaenas and lions respectively. By combining well established field research techniques, such as radio telemetry and audio playbacks, with novel geographic information system tools, I investigated the two key drivers of the probability of encounter with spotted hyaenas and lions, namely density and utilization intensity.

Results from the analyses showed that substantial spatial and temporal variation existed in the utilization intensity of lions, as well as the density of both lions and spotted hyaenas, at short and intermediate time scales, in HiP. The spatial scale across which these patterns resolved appear to be well suited to the movement capabilities of wild dogs. This indicated that wild dogs may be able to exploit such areas of temporary lower density and/or utilization intensity, suggesting the dynamic nature of refugia involved in the interactions within these two species-pairs. Results from the lion analyses further suggest that groups rather than individuals are the basic units around which intraguild interactions of social predator and prey species should be investigated, and that social grouping in combination with predator territoriality may stabilize intraguild interactions. An important prediction emerging from this work is that wild dogs, or other subordinate African large predator species, may be forced to trade-off safety from hyaena interference vs. safety from lion predation.

Preface

The work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, under the supervision of Prof. Rob Slotow and co-supervision of Dr. Michael Somers (University of Pretoria).

This study represents original work by the author and has not otherwise been submitted in any form for any degree to any tertiary institution. Where use has been made of the work of others, it is duly acknowledged in the text.

____________________	12 December 2008
J. A. Graf	Date

Declaration 1 - Plagiarism

I, Jan Andreas Graf, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

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Declaration 2 - Publications

Details of contribution to publications that form part and/or include research presented in this thesis:

Publication 1: **Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park.** J.A. Graf, M.J. Somers, M. Szykman & R. Slotow. *(submitted).*

The logistics and organization of hyaena call-ups were done by myself. I attended all call-ups, which were conducted with help from other researchers (including M. Szykman). Collation of the data into a database, data analysis, and writing the manuscript was done by myself. The manuscript was reviewed and received inputs once each from M. Szykman and three anonymous reviewers at the South African Journal of Wildlife Research, and twice each from my supervisors, R. Slotow and M. J. Somers.

Publication 2: **Lion spatial ecology generates potential predation refugia in Hluhluwe-iMfolozi Park.** J.A. Graf, M.J. Somers, M. Szykman, L. Turelli, C. Packer & R. Slotow. *(in prep.).*

Lion data collection occurred over a five and a half year period and many people (including M.J. Somers) contributed to this. I collected data, together with other researchers (including L. Turelli and M. Szykman), during the last three years of the project. Lions were collared by KZN Wildlife conservation managers, section rangers, and veterinarians working in Hluhluwe iMfolozi Park (L. Turelli, M. Szykman and myself assisted at the majority of these events). Collation of the data into a database was done by a number of people (including L. Turelli, M. Szykman and myself). Data analysis and writing of the manuscript was done by myself. The manuscript was reviewed twice each by my supervisors, R. Slotow and M. J. Somers.

Signed: ____________________

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Han Olff from the Community and Conservation Ecology Group, at the University of Groningen in the Netherlands, gave me office space, a computer, and all the amenities normally reserved for PhD students. Thank you very much not only for this, but also your interest in my work over the years. Thanks go also to all the many other people in the group for friendship and support.

To the friends all over South Africa who provided beds and food during the travels and study periods associated with this work – Michael and Michele in Mthatha, Lorette and the Engelbrecht family in Johannesburg, Alida and Graham in Durban, Pieter and Mazzi and the Lottering and Somers families in Pretoria, and the Howison and Aitchison families in Pietermaritzburg – I appreciate it very much.

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I have made extraordinary and wonderful new friends during my six years in the park, with managers, rangers, researchers, trails officers, game drivers, staff and non-staff alike. All of you have made a special contribution to this work in some way or other. On account of the great number of you involved, I hope you will forgive me for not writing out your names here. Know

though, that I am immensely grateful to all of you, and that your friendship means the world to me.

Aan Don Juan en Jane, Santa Maria della Salute, Boontjie en Pampoen, Phiva en al die ander honde: mag julle soos ou Koos Doep julle tente rustig in die melkweg pitch. Die regop bobbejaan in die wit geraas-boks is julle ewig dankbaar vir die wonderbaarlike veropenbarings in hierdie been van sy pad.

All the members (in flesh, *and* spirit) of my Swiss, South African, and later also English and Greek families, provided food, financial support, retreats, encouragement, guidance, and huge amounts of love. Baie dankie vir alles! Danke viel, viel mal für alles! Thank you for everything! To my mother and father for your love, never failing support, and endless belief in me, I am deeply indebted.

In the very end, when I should have been long finished with this thesis, there came along a small being who turned my world upside down: your gurgle and smile lights the world.

Most importantly, to Cleo, my Gozzi, for friendship, caring, sharing, compassion, laughter, patience, and above all, Love: Thank you Beautiful, with all of my being!

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If you haven’t tasted
Tamalina Mdluli’s *unqushu*,
you haven’t lived yet!

Chapter 1
General introduction

1.1 Background

Apex predators from a guild perspective

Terrestrial apex predators (mostly mammalian) are increasingly recognized as important multi-trophic ecological agents (Terborgh *et al.* 1999; Terborgh *et al.* 2001; Terborgh 2005), even though their trophic position intrinsically dictates their occurrence at relatively low densities (Farlow 1993; Spencer 2000). Several species significantly impact on the population dynamics of their prey via predation (Messier 1994; Sinclair & Arcese 1995; Sinclair 2003; Sinclair *et al.* 2003; White & Garrott 2005; Owen-Smith & Mills 2008). However, predation is not the only mechanism through which apex predators may significantly affect their prey populations. Trait mechanisms, risk effects, or indirect effects (not to be confused with indirect effects outlined below), as they have been variously called, involve behavioural or morphological responses of prey species to reduce the risk of predation (Luttbeg & Kerby 2005). These mechanisms, while reducing the rate of predation, most often carry fitness costs (Preisser *et al.* 2005; Preisser & Bolnick 2008), and consequently may have equal or even larger impacts on prey populations than predation (Luttbeg & Kerby 2005; Preisser *et al.* 2005; Creel & Christianson 2008; Pecharsky *et al.* 2008; Preisser & Bolnick 2008).

Both predation and risk effects within intermediate trophic levels (primary or secondary consumers) may be transmitted to species at lower trophic levels (primary producers or primary consumers), often titled indirect effects or trophic cascades (Crooks & Soulé 1999; Schmitz *et al.* 2000; Terborgh *et al.* 2001; Werner & Peacor 2003; Ripple & Beschta 2004a; Schmitz *et al.* 2004; Beschta 2005; Croll *et al.* 2005). In the Greater Yellowstone ecosystem for instance, elk (*Cervus elaphus*) responses in foraging behaviour to predation risk by wolves (*Canis lupus*) (i.e. risk effect), significantly influenced the structure and recruitment of various tree species (Ripple *et al.* 2001; Ripple & Beschta 2004a, b; Ripple 2006). Alternately, moose (*Alces alces*) population responses to wolf and grizzly bear (*Ursus arctos*) predation in the same and adjoining ecosystems, similarly influenced certain tree species, with further knock-on effects for avian species dependent on the habitats created by these trees (Berger *et al.* 2001).

In many ecosystems apex predators often occur as guilds (Dalerum *et al.* 2008a), composed of varying numbers of co-existing species competing for similar and potentially limiting resources

(Polis *et al.* 1989; Simberloff & Dayan 1991). Apart from directly increasing species diversity (Dalerum *et al.* 2008a), species rich predator guilds may also enhance the functional diversity of predation and its risk effects (Sih *et al.* 1998; Blackburn *et al.* 2005; Dalerum *et al.* 2008a; Dalerum *et al.* 2008b), and potentially affect ecosystem functioning (Terborgh *et al.* 1999; Terborgh *et al.* 2001; Finke & Denno 2004, 2005; Terborgh 2005; Snyder *et al.* 2006). However, species-rich predator guilds may inherently threaten their own diversity, not only via the indirect interaction of exploitation competition but also via direct intraguild interactions. In this context, the body size difference between two guild members is a key determinant in the probability of an asymmetric outcome for such direct intraguild interactions (Donadio & Buskirk 2006). The consequences of these asymmetric interactions frequently influence the behaviour, abundance, and distribution of the smaller species involved, sometimes even leading to the local exclusion of a guild member (Linnell & Strand 2000; Donadio & Buskirk 2006). Additionally, these interactions may also result in character displacement of the smaller species (Donadio & Buskirk 2006).

Direct intraguild interactions have been recorded for a diverse range of guilds in various ecosystems across the world (Polis *et al.* 1989; Palomares & Caro 1999; Linnell & Strand 2000; Caro & Stoner 2003), and can generally be classified into either interference competition or intraguild predation (IGP) (although IGP is often included under interference competition in the literature, here, for the sake of clarity, IGP is treated as a distinct lethal form of direct interaction, whereas interference competition includes non-lethal forms of direct interaction only). Interference competition occurs when an “interfering species” gains a resource by directly interfering with a competing species, which would have or was in the process of utilizing the contested resource (Case & Gilpin 1974). For instance, as a result of aggressive encounters red foxes (*Vulpes vulpes*) may induce arctic foxes (*Alopex lagopus*) to abandon their denning sites (Linnell *et al.* 1999; Tannerfeldt *et al.* 2002), and spotted hyaenas (*Crocuta crocuta*) may displace cheetahs (*Acinonyx jubatus*) from their kills (Hunter *et al.* 2007a, 2007b). Both these interactions free up a shared resource for potential use by the interfering species (Case & Gilpin 1974). Depending on the reaction of each species during such encounters they may be alternately classified as the behaviourally dominant or “winning” species and the subordinate or “losing” species (although roles may also be reversed for some species pairs) (Whitehead & Walde 1993; Fedriani *et al.* 2000). Since the process of obtaining a resource may carry a substantial energetic cost (Gorman *et al.* 1998), the subordinate species may respond to a perceived risk of interference by spatially or temporally displacing their utilization of this resource in order to reduce the probability of losing the resource (Case & Gilpin 1974; Durant 1998, 2000a, 2000b).

Direct interactions between competitors may also entail situations where the dominant species kills the subordinate species, and this combination of competition and predation results in a distinct interaction termed IGP (Polis *et al.* 1989; Holt & Polis 1997). For example, in areas where coyotes (*Canis latrans*) and wolves co-exist, these species often share similar resources, and the former may even trail the latter with the prospect of obtaining food from wolf kills (Paquet 1992; Wilmers *et al.* 2003a; Wilmers *et al.* 2003b). However, wolves often kill coyotes independent of the presence of prey kills (Paquet 1992; Thurber *et al.* 1992; Arjo & Pletscher 1999; Switalski 2003). Similar to the behavioural responses of the subordinate species in the context of interference competition, guild members predated on may also respond by attempting to reduce their predation risk via changes in their spatial or temporal utilization patterns as originally documented in classic predator-prey interactions (Lima & Dill 1990; Brown *et al.* 1999).

In order for spatial or temporal avoidance mechanisms aimed at reducing the risk of interference or predation to function, variation across space and/or time in the utilization intensity or numerical density of the dominant species needs to exist. Simply put, an area in space or period in time, which contains a relatively low intensity of utilization or density of individuals, consequently contains a relatively *reduced* risk of interference or predation by a dominant guild member. If a subordinate guild member has the ability to enter such an area or shift its activity into such a period of *reduced* risk, and this risk is sufficiently low, both the area or period may be considered a dynamic or probabilistic refuge for this species (Hochberg & Holt 1995; Berryman *et al.* 2006). Providing that the subordinate guild member can successfully trade-off the benefits of using or entering such refugia vs. forfeited gains from other important fitness related behaviours, such as territorial maintenance, foraging, or mating, dynamic refugia may contribute towards the co-existence of a pair of asymmetrically interacting guild members (Case & Gilpin 1974; Durant 1998; Brown *et al.* 1999).

Utilization by subordinate guild members of areas, or periods, with lower density or reduced utilization intensity by dominant guild members, has been documented for a number of apex predator guilds (see Linnell & Strand (2000) for review). In south-western Spain, the Iberian lynx (*Felis pardina*) is the largest member of a small to medium sized predator guild, also including red fox, common genet (*Genetta genetta*), European badger (*Meles meles*), and

Egyptian mongoose (*Herpestes ichneumon*) (Palomares *et al.* 1996). During direct intraguild interactions with foxes, genets, and mongooses, lynx are clearly dominant, sometimes resulting in the death of the subordinate species (Palomares *et al.* 1996; Fedriani *et al.* 1999). Consequently, all three subordinate species preferentially used areas with low levels of lynx utilization and lynx densities, even though these areas contained comparable or lower densities of their favourite prey species and similar availability of resting sites compared to areas used by lynx (Palomares *et al.* 1996; Fedriani *et al.* 1999). The above highlights the importance of the spatial aspects of variation in population density and utilization intensity for the co-existence of asymmetrically interacting guild members.

Most of the above scenarios of interference competition and predation only consider species pairs; however, as noted above, an apex predator guild may include several more species. In such cases, a species may be subordinate to several species within the guild, one may be dominant over more than one species, or several other arrangements may also be possible. This strongly suggests that studies of interspecific interactions embedded within species-rich predator guilds should ideally investigate the relationships within all potential pairs, and also whether the nature of interactions of one pair influences the intensity or outcome of interactions of other pairs.

The African large predator guild from a conservation management perspective: the South African scenario

Land-use change, habitat fragmentation, and direct persecution led to the local extinction of most co-existing large predator species in South Africa (SA), with massive concomitant range reductions for all species (Pringle 1977; Skead 1980; Stuart 1981; Skead 1987; Friedman & Daly 2004; Skinner & Chimimba 2005). This guild includes spotted hyaena (hereafter referred to as “hyaena”, except where distinction from brown hyaena (*Parahyaena brunnea*) is necessary), leopard (*Panthera pardus*), lion (*Panthera leo*), cheetah, and African wild dog (*Lycaon pictus*). Successful re-introduction efforts for all these species, motivated by ecological restoration, single species conservation, or ecotourism reasons, resulted in many places in the intended or co-incidental reestablishment of complete or near complete large predator guilds (Rowe-Rowe 1992; Hunter 1998; Hayward *et al.* 2007a; Hayward *et al.* 2007b). However, with the absence of large protected areas outside the Kruger National Park (National Park hereafter abbreviated by “NP”) and the Kgalagadi Transfrontier Park in SA, all of these reintroductions have taken place in small protected areas (<1000 km^2) (Rowe-Rowe 1992; Hayward *et al.* 2007a; Gusset *et al.* 2008b; Slotow & Hunter *in press*).

Because of the typical expansive space requirements of large predators and the constraints on space in these small reserves, most of the reintroductions have only resulted in the creation of small, unviable populations (Rowe-Rowe 1992; Hayward *et al.* 2007a; Hayward *et al.* 2007b; Gusset *et al.* 2008b; Slotow & Hunter *in press*). Lions are a particularly good example in this regard with at least 37 small and isolated protected areas reintroducing lions since 1991 and only one of these containing a population above 40 individuals in 2007 (Slotow & Hunter *in press*). The great majority of these lion reintroductions, as well as those of the other species, have been successful (at least in the sense of re-establishing the species), since the technical aspects involved are well understood and controlled during all the phases involved in these re-introductions (Hayward *et al.* 2007b; Gusset *et al.* 2008b; Slotow & Hunter *in press*). However, in the absence of natural migration and/or reserve expansion, most of these predator populations will need continual active management in order to offset detrimental demographic and genetic processes (Mills *et al.* 1998; Hunter *et al.* 2007c; Slotow & Hunter *in press*). For some species such as the wild dog, isolated populations have been managed from the outset according to a national meta-population framework (Mills *et al.* 1998), whereas others such as lion still lack a coherent national conservation management strategy (Slotow & Hunter *in press*).

Notwithstanding the success of the above-mentioned re-establishment efforts, most members of the African large predator guild are still classified as threatened in SA (Friedman & Daly 2004). Since edge effects (Woodroffe & Ginsberg 1998) are probably substantially less in South African than in other African protected areas as a result of effective fencing and rigorous protection via game guards (Hayward *et al.* 2007a; Woodroffe *et al.* 2007; Gusset *et al.* 2008b), mortality rates of competitively dominant guild members such as lions are exceptionally low, and their populations seem to be mainly food limited (Kettles & Slotow; Hayward *et al.* 2007c; Hunter *et al.* 2007c). In contrast to this, the main agent of natural mortality of subordinate guild members such as wild dog, are lions (Woodroffe *et al.* 2007; Slotow & Hunter *in press*), although Allee effects may still impose a significant constraint on wild dog population growth at these low numbers as well (Courchamp *et al.* 2000; Courchamp & Macdonald 2001; Somers *et al.* 2008).

The arising scenario of multiple threatened large predator species, mostly co-occurring in small isolated non-viable populations, while also threatening each others co-existence, inherently creates complex situations for conservation management. Enhancing the understanding of large predator ecology from a multi-species guild perspective would consequently contribute significantly towards informing conservation management approaches and actions (Creel *et al.* 2001), specifically in terms of re-introduction reserve selection, the ideal local predator community assemblage, and subsequent individual species population management. This guild perspective strongly relates to the recent paradigm shift in conservation biology from a single-species practice to a more community orientated approach (Simberloff 2004).

Apart from conservation management concerns, most of the African large predator guild members are highly charismatic species, sightings of which are very desirable (Lindsey *et al.* 2005b; Gusset *et al.* 2008a) within the large ecotourism industry of South Africa (Van Der Merwe & Saayman 2003). With the proliferation of reserves offering sightings of the "Big Five", following numerous reintroductions of these species (Garaï *et al.* 2007; Slotow & Hunter *in press*), an emerging market niche exists in additionally offering or alternatively specialising in sightings of the less well known species such as wild dog (Lindsey *et al.* 2007). Thus, having diverse and complete large predator guilds within protected areas, may complement both the biodiversity aims of conservation management, as well as the economic goals of the ecotourism industry (Lindsey *et al.* 2007).

1.2 Thesis context and aims

Within the African large predator guild, hyaenas and lions are generally behaviourally dominant during direct intraguild interactions with other guild members, especially in relation to wild dogs and cheetahs (Estes & Goddard 1967; Kruuk & Turner 1967; Kruuk 1972; Schaller 1972). These interactions may result in direct predation (Creel & Creel 1996; Mills & Gorman 1997; Woodroffe & Ginsberg 1999; Woodroffe *et al.* 2007), direct food loss (Fanshawe & FitzGibbon 1993; Mills & Biggs 1993; Carbone *et al.* 1997; Durant 2000a; Carbone *et al.* 2005; Hunter *et al.* 2007b), or behavioural displacement into sub-optimal habitats (Mills & Gorman 1997; Durant 1998; Creel & Creel 2002). As a result of the substantial asymmetry of these interactions, it has been argued that hyaenas and lions are responsible for the significant negative relationship between the densities of these dominant guild members and those of the subordinate species (wild dog and cheetah) across several African ecosystems (Laurenson 1995; Creel & Creel 1996, 2002).

Interference competition between hyaenas and wild dogs, in the form of kleptoparasitism of wild dog kills (i.e. direct food loss), is highly variable across ecosystems, ranging from 2% to 60% (Fanshawe & FitzGibbon 1993; Creel & Creel 1998, 2002). Although this has not been quantified, Creel and Creel (Creel & Creel 1996; Creel 2001; Creel & Creel 2002) suggested that vegetation cover might be an important factor mediating the rate at which the above-mentioned kleptoparasitism occurs, with woodland significantly reducing this. Hunting carries exceptionally high energetic costs for wild dogs, and the loss of food may require physiologically unfeasible additional foraging efforts from wild dogs in order to meet their daily energetic requirements (Gorman *et al.* 1998). Conversely, lions have been identified as a significant source of known-cause adult and juvenile wild dog mortality for several ecosystems (Mills & Gorman 1997; Creel & Creel 2002; Woodroffe *et al.* 2007; Slotow & Hunter *in press*). Various population viability modelling exercises have indicated either or both these demographic variables as vital factors for wild dog population persistence (Woodroffe *et al.* 1997; Vucetich & Creel 1999; Cross & Beissinger 2001; Creel *et al.* 2004). Largely similar results, in terms of the above interactions, have been found for the relationships between cheetah, and respectively, hyaena and lion (Caro & Laurenson 1994; Laurenson 1994, 1995; Durant 1998; Kelly *et al.* 1998; Durant 2000a, 2000b; Kelly & Durant 2000; Durant *et al.* 2004; Hunter *et al.* 2007b).

Because of the high energetic demands of their hunting strategy (Gorman *et al.* 1998), wild dogs are expected to be behaviourally sensitive to variation in the risk of losing their kills to hyaenas, as documented for cheetahs (Durant 2000a). Similarly, since lion predation represents such a major mortality agent in some wild dog populations, it can be expected that wild dogs should display sensitivity to variation in the risk of lion predation, as also documented for cheetah (Durant 2000a). Predation incorporates the outcome of multiple sequential processes (MacNulty *et al.* 2007). However, the risk of predation can be decomposed into the following basic components: first the probability of encountering a predator, second the frequency of attack once encountered, and third the rate of predation once an attack has been launched (Creel & Creel 2002). Since the interaction of interference represents a similar sequence of behaviours, involving subordinate and dominant guild members, the risk of interference can be similarly decomposed into the above components, namely, encounter probability, frequency of interference attempts once encountered, and rate of successful interference once attacked.

Subordinate guild members sensitive to variation in the risk of interference or predation may employ anti-predator or avoidance behaviours (Lima & Dill 1990; Brown 1999), in order to influence the outcome of each of these components. For instance, to decrease their chances of losing a kill to hyaenas, wild dog packs may attempt to maximize their hunting group size in order to alter the outcomes of both the second and third component (Fanshawe & FitzGibbon

1993; Carbone *et al.* 1997; Carbone *et al.* 2005). Alternatively, wild dogs may reduce the risk of predation by lions by employing behaviours which may reduce the probability of the first component. For example, in the Kruger NP wild dogs paradoxically occur at their lowest densities where the biomass of their principal prey species is most abundant (Mills & Gorman 1997). That study simultaneously found a significant negative correlation between the ranked habitat preferences of wild dog and lion, and thus the above apparently contradictory situation is thought to have resulted from wild dogs avoiding habitats favoured by lions (or the lions within these habitats) (Mills & Gorman 1997). In other words, wild dogs appeared to minimize their risk of predation by lions, by reducing their probability of encountering lions, and at the same time were behaviourally displaced into sub-optimal habitats.

Independent of the behaviour of the subordinate guild member, the probability that it will encounter a dominant guild member at any position in space or time, is shaped by the density and utilization intensity exhibited by dominant guild members at this position. Over time at a given location, or across space for a point in time, the densities and utilization intensity of dominant guild-members may show variation, leading to a constantly altering probability of encounter surface across the landscape. Such spatial and temporal variation in density and utilization intensity has been well documented for lion and hyaena in a number of ecosystems, at various spatial and temporal scales (Kruuk 1972; Schaller 1972; Van Orsdol *et al.* 1985; Mills 1990; Hofer & East 1993a, 1993b, 1993c; Cooper *et al.* 1999; Höner *et al.* 2002; Hemson 2003; Trinkel *et al.* 2004; Höner *et al.* 2005; Mosser 2008). The majority of studies interested in this variation have primarily been undertaken from the perspective of these two species themselves, and have mainly attempted to elucidate the potential ecological drivers, such as prey biomass and dispersion, causing this variation (Van Orsdol *et al.* 1985; Scheel & Packer 1995; Höner *et al.* 2002; Boydston *et al.* 2003b; Hemson 2003; Höner *et al.* 2005; Kolowski 2007). In contrast to this, little attention has been paid to the effects of this variation within the context of direct intraguild interactions (Mills & Gorman 1997; Durant 1998; Creel & Creel 2002; Höner *et al.* 2002).

The protected area within which this study was carried out, namely the Hluhluwe iMfolozi Park (HiP), contained the complete African large predator guild (Whateley & Brooks 1985; see Chapter 2). For at least two decades before the commencement of this study as well as during the study period, the resident wild dog population occurred at substantially lower densities in comparison to those of lion and hyaena (Anderson 1980; Whateley & Brooks 1985; Maddock *et al.* 1996; Maddock 1999; Somers *et al.* 2008; KZNW 2007, unpubl. data; Chapter 3). Studies during the mid 1990’s indicated that the resident wild dog population (in effect only one pack) was not limited by space, habitat, or prey requirements, and recommended the addition of more packs to the population (Andreka 1996; Kruger 1996; Andreka *et al.* 1999; Krüger *et al.* 1999; Maddock 1999). At the same time, in light of the fact that the already small wild dog population in HiP had recently declined considerably (Andreka 1996; Maddock 1999), as well as the results of the above-mentioned wild dog intraguild interaction studies elsewhere, a larger project was initiated in HiP to examine the relationships between hyaenas and lions on one hand and wild dogs on the other. Both lion predation on wild dogs and kleptoparasitism of wild dog kills by hyaenas had been recorded (MJ Somers 2001, pers. comm.), and indicated that wild dogs did indeed have to contend with these intraguild interactions in HiP.

During the course of this project, additional packs were translocated into the population as recommended by the earlier studies (Graf *et al.* 2006; Gusset *et al.* 2006a; Gusset *et al.* 2006b; Somers *et al.* 2008). These artificial increases in the local wild dog population appeared to shift this population over a pack formation threshold (Somers *et al.* 2008), and by the end of the project (end 2004) the population had, even considering the translocations, increased substantially in number of packs and individuals (Somers *et al.* 2008). Somers *et al.* (2008) further found that wild dog population size, number of juveniles surviving to one-year, and annual survival rates (for juvenile, yearling, and adult wild dogs) was not correlated to number of hyaenas or lions over a 25 year period. This consequently raised the question as to what mechanisms (passive or active) have allowed wild dogs to adequately reduce the frequency of interference and predation interactions with hyaenas and lions in order for these not to affect the above wild dog demographic parameters in HiP.

The study comprising this thesis formed part of this larger project and aimed to address one aspect of the above question in terms of the spatial relationships between the dominant guild members, hyaenas and lions, and wild dogs. More specifically, the study had the following aims:

- To document the magnitude and scale of potential spatial variation in hyaena density across HiP, in order to map variation in hyaena encounter probability across the landscape.
- To document the magnitude and scale of potential spatial and temporal variation in density and utilization intensity of lion across the lion study area in HiP, in order to map variation in lion encounter probability across the landscape.

Hyaenas were substantially more numerous than lions in HiP, and this as well as other logistical constraints necessitated a landscape scale approach for this species. The methods involved in this allowed the mapping of the distribution of hyaena density across the whole park for short periods, but not the investigation of variation in utilization intensity. For lions on the other hand, a more local, but longer and spatially finer scale approach was afforded through the use of radio-telemetry location data, which allowed investigation of both the variation in density and utilization intensity for different temporal and spatial scales. The results were then interpreted in terms of the potential existence and nature of dynamic hyaena interference and lion predation refugia for wild dogs in HiP. Subsequent studies may use the patterns in hyaena and lion probability of encounter across HiP, as elucidated in this study, to investigate the potential influence of this parameter on variation in the risk of interference by hyaenas, and predation by lions, experienced by wild dogs, and thus to test the predictions made in terms of dynamic refugia.

The results are largely discussed within the context of the behavioural-ecology of wild dogs, however the conclusions are also broadly applicable to other asymmetrical predator intraguild relationships as well as classical predator-prey relationships where space and time represent important dimensions for the concerned interactions. The results are also considered from an autecological perspective of the two study species. Furthermore, considering their conservation status in South Africa, the results also have implications for the conservation management of each species, especially that of hyaenas in HiP and the surrounding region.

1.3 Thesis layout

Following from the above outlined aims, the thesis is divided into the following chapters:

- Chapter 1 is represented by the above introduction to the subject, and the context and aims of the study.

- Chapter 2 first describes the current ecological status of the study site in terms of its major abiotic and biotic features. This is followed by a brief description of the human role in the ecological history of HiP and it’s implications for the large predator guild. Subsequently, an overview of the social and ecological behavioural patterns of the two study species is presented, highlighting pertinent behaviours where these are relevant to the density and/or utilization intensity patterns of these species.

- Chapter 3 investigates and describes hyaena spatial density distribution at the landscape scale for two short periods. The results are primarily discussed with regards to potential mechanisms creating heterogeneity in hyaena density, the co-existence of hyaenas with other large predators, and the relevance of scale when evaluating potentially competitive, interspecific spatial relationships involving hyaenas. An estimate of total hyaena population size for HiP is also presented, and aspects of their existences in the landscape surrounding HiP are considered in light of the conservation status of this species in South Africa.

- Chapter 4 quantifies and describes lion spatial utilization at various temporal and spatial scales in the context of lion sociality and territoriality. The results are discussed in terms of their potential to create dynamic refugia and what strategies wild dogs could potentially employ to benefit from variation in probability of encounter.

- Chapter 5 is formed by a concluding discussion of the results of this study in relation to wild dog co-existence within the African large predator guild and the conservation management implications of this. Some general implications of the results pertaining to the conservation and management of these two species in HiP and the surrounding area are also discussed.

Note to readers

Both chapters 3 and 4, containing original data, were written as potentially publishable manuscripts, and consequently were written from the perspective of a multiple author publication. For the same reason, there is a degree of repetition across the chapters of this thesis.

Chapter 2

Study site and species

2.1 Study site

The abiotic and biotic environment

The Hluhluwe-iMfolozi Park (HiP; previously Hluhluwe-Umfolozi Park) is situated in the north east of KwaZulu-Natal Province (KZN), South Africa (Fig. 2.1). The park covers an area of approximately 900 km^2 and is located within the Latitudes 28°00′ and 28°26′ South and Longitudes 31°41′ and 32°09′ East (WGS 1984). HiP occupies the foothills of the escarpment rising above the Southeast African coastal plain, with altitudes ranging from 40 to 590 m above sea level. The topography varies from rugged, steep-sided hills surrounding the Hluhluwe River and its tributaries in the north-east, through rolling hills in the central area, to the low and broad river basins of the Black and White Mfolozi Rivers in the south-west. These three rivers mostly stop flowing for some months of the year, but ample water remains in regularly occurring natural pools along their courses. A conspicuous feature of the landscape is the large number of ephemeral pans and wallows, which may carry water for several months following good rains.

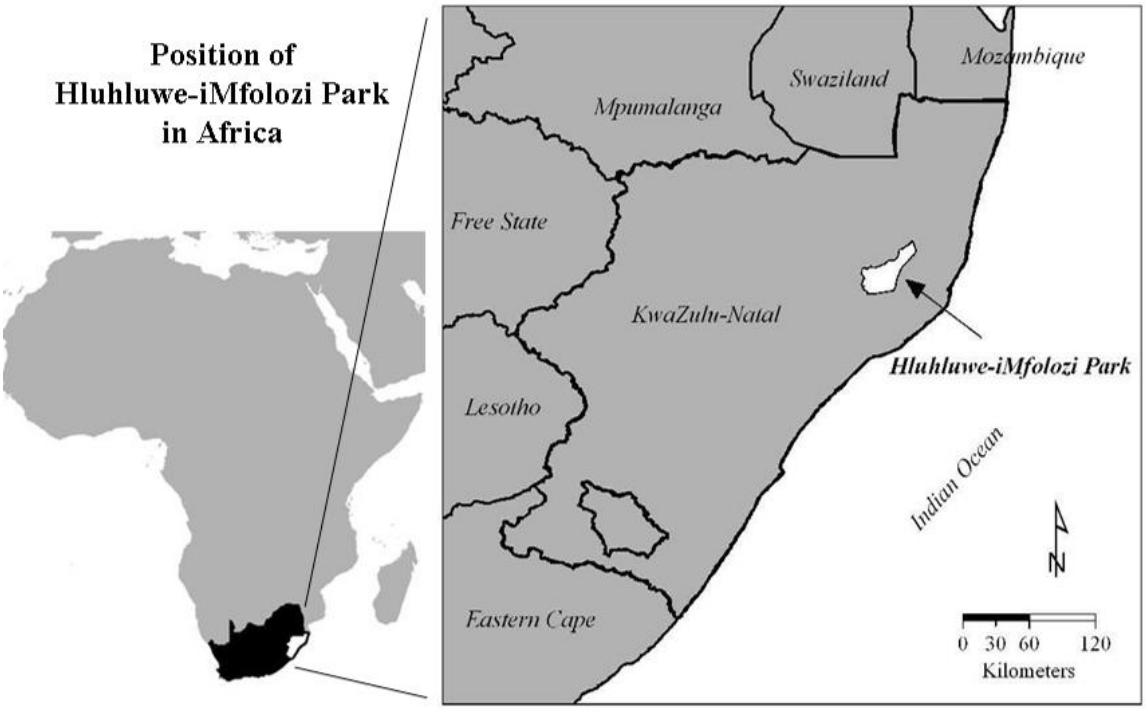

Fig. 2.1. Map indicating the relative position of Hluhluwe-iMfolozi Park in KwaZulu-Natal province, South Africa, within the continent of Africa.

HiP is typified by a highly diverse geology, with the majority of the main rock series of KZN being represented in the park (King 1970; Downing 1980). Shales and sandstones form the most common sedimentary rocks, whereas dolerite intrusions, mainly in the form of sills, are the dominant igneous rock (King 1970; Downing 1980). Lesser areas of Dwyka tillite, granite, basalt, and rhyolite are also represented, with more recent deposition of alluvium along the larger drainage lines (King 1970; Downing 1980). Intense faulting associated with vertical and lateral rock movements have further altered local geological patterns (King 1970; Downing 1980). Due to the above-mentioned geological patterns and processes, a large number of soil types, mainly associated with their parent geologies and topographical locations, are present in HiP (King 1970; Downing 1980; Barrow 1986).

The close proximity of the Indian Ocean results in a coastally modified subtropical climate, with hot humid summers (October to March) and dry moderate winters (April-September). Within HiP, rainfall is strongly modulated by elevation, and mean annual rainfall varies from 990 mm (range: 670-1594 mm) on the higher hills of the north-eastern parts to 635 mm (range: 333-1127 mm) in the lower lying west (Pattenden 1988; Balfour & Howison 2002). Medium term fluctuations in mean annual rainfall result in alternating dry and wet phases ranging from four to ten years in duration (Balfour & Howison 2002). Summer and winter temperatures average 33ºC (range 15-42ºC) and 18ºC (range 4.9 -29.2 º C) , respectively (Waldram 2005).

Most probably as a result of the highly heterogeneous spatial and temporal abiotic environment, HiP contains a varied range of woody vegetation types. The largest part of the park is covered by several types, or mixtures, of fine-leaved (thorn) and broad-leaved woodland or savannah. In the fine-leaved communities, various *Acacia* species predominate (Whateley & Porter 1983; Bond *et al.* 2001), whereas the broad-leaved communities are dominated by tambotie (*Spirostachys africana*) and bushwillow species (*Combretum* spp.) (Whateley & Porter 1983). Fine- and broad-leaved scrub or thicket communities also cover extensive areas, with fine-leaved thicket alternately dominated by sweet thorn (*Acacia karroo*), hook thorn (*Acacia caffra*), and sicklebush (*Dichrostachys cinerea*), and broad-leaved communities dominated by various guarri species (*Euclea* spp.) (Whateley & Porter 1983). Semi-deciduous Scarp forest, dominated by white stinkwood (*Celtis africana*) and Natal milkplum (*Englerophytum natalensis*) in the canopy and mid-stratum respectively, covers the higher hills and south facing slopes in the north east of the park (Whateley & Porter 1983). Riverine gallery forest fringes the major rivers and streams and is dominated by weeping boerbean (*Schotia brachypetala*), tambotie, splendid thorn (*Acacia robusta*), and sycamore fig (*Ficus sycamorus*) (Whateley &

Porter 1983). For further descriptions of the woody vegetation of HiP see Henkel (1937), Downing (1972), King (1987), Graham (1992), West (1996; 1999), and Mucina *et al.* (2007).

Although pure grasslands are rare within the park, all of the above-mentioned communities, especially the woodlands and thickets, contain varying degrees of grass cover. These grass communities occur in spatially heterogeneous mosaics of tall, bunch grass associations and shorter, stoloniferous lawn grass associations. As in most savannahs, the bunch grass communities in HiP, dominated by red grass (*Themeda triandra*), catstail dropseed (*Sporobolis pyramidalis*), and weeping love grass (*Eragrostis curvula*), are particularly prone to frequent fires (Henkel 1937; Balfour & Howison 2002; Archibald *et al.* 2005). The lawn grass communities are highly palatable to grazers and are locally dominated by bushveld signal grass (*Urochloa mosambicensis*), false couch grass (*Digitaria longiflora*), curly-leaved dropseed (*Sporobolis nitens*), small buffalo grass (*Panicum coloratum*), and LM grass (*Dactyloctenium australe*) (Waldram 2005; Cromsigt 2006).

HiP is currently home to a highly productive and diverse fauna with one of the highest biomass densities amongst African savannah ecosystems (Waldram 2005; Cromsigt 2006). A total of 22 different ungulate species are present in the park, ranging from the blue duiker (*Philantomba monticola*) to the African elephant (*Loxodonta africana*). Eland (*Tragelaphus oryx*), oribi (*Ourebia ourebi),* and klipspringer (*Oreotragus oreotragus*) have gone locally extinct, and steenbok (*Raphicerus campestris*), mountain reedbuck (*Redunca fulvorufula*), and common reedbuck (*Redunca arundinum*) are present at precariously low numbers (Bourquin *et al.* 1971; Brooks & Macdonald 1983; Rowe-Rowe 1994). Mammalian carnivore species are equally well represented (Bourquin *et al.* 1971; Whateley & Brooks 1985), and amongst the historically recorded large carnivore species only the brown hyaena (*Parahyaena brunnea*) is currently absent from the park (see below for carnivore history and reintroductions). More than 400 bird species have been recorded in HiP, with a large number of small mammal, reptile, and amphibian species present as well (Bourquin *et al.* 1971; MacDonald & Birkenstock 1980; Howells 1987; Skowno & Bond 2003). Invertebrate diversity is high, with a few species endemic to the park (Doube 1983; Rivers-Moore & Samways 1996; Samways & Kreuzinger 2001; Hamer & Slotow 2002).

Human land-use and management history

The original Hluhluwe and iMfolozi reserves of HiP, along with the nearby St. Lucia reserve (within the formerly Greater St. Lucia Wetlands Park, now Isimangaliso Wetland Park), constitute the oldest colonially protected landscapes in Africa. However, human (*Homo sapiens*) interaction with the landscape and its associated biota, before and after this proclamation, has played a significant role in shaping the ecosystem of which HiP forms a part (Hall 1979, 1981; Brooks & Macdonald 1983; Hall 1984). Zulu people, practicing pastoralism and agriculture, still inhabited the central area of HiP (termed the Corridor) up to 1944 before they were removed (for history of removals see Brooks (2005)), while various management regimes during the past century have had a similarly large influence (Brooks & Macdonald 1983), as is detailed below.

The KwaZulu-Natal province, within which HiP is located, has a long history of human inhabitation, stretching back to at least the early Stone Age at *ca.* 1.6 million years before present (Mazel 1989). Iron-age people started arriving *ca.* 1700 years ago and from these the Zulu kingdom emerged during the early 19th century (Maggs 1989). The primary economic activities of these people, namely pastoralism, agriculture, and metallurgy, most probably had a significant ecological impact on the structure and composition of the floral and faunal communities in the area now covered by HiP (Hall 1979; Feely 1980; Hall 1981, 1984; West 1999).

Early colonial trade via Delagoa Bay between the Portuguese and late Iron Age people, as well as the subsequent arrival in Zululand of Boer and British farmers, traders, and hunters during the 19th and early 20th century had a significant impoverishing effect on the local biota (Vincent 1970). Following the proclamation of the Hluhluwe and iMfolozi reserves in 1895, early conservation management practices in HiP, as in other African protected areas, included the persecution of carnivores through shooting and poisoning (Kirby 1916; Bourquin *et al.* 1971). As a result of these various human activities several large mammalian species went extinct in the area covered by HiP during the end of the 19th and beginning of the 20th centuries, including elephant, hippopotamus (*Hippopotamus amphibius*), eland, lion (*Panthera leo*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*) (Bourquin *et al.* 1971; Pringle 1977; Rowe-Rowe 1992, 1994).

During the anti-nagana/tsetse fly (*Glossina* spp.) campaign from the 1920's to mid 1950's, the iMfolozi reserve and surrounding areas underwent massive herbivore culls (excluding white (*Ceratotherium simum*) and black rhinos (*Diceros bicornis*)) overseen by the Division of Veterinary Services of the South African Department of Agriculture (Brooks & Macdonald 1983). Only aerial spraying of DDT and BHC brought the tsetse fly under control in 1952

(Brooks & Macdonald 1983; Brown 2008). Two further large scale culling regimes were also undertaken during the subsequent three decades by the managing conservation authority (Ezemvelo KZN Wildlife – from here on KZNW – formerly Natal Parks Board and KwaZulu Department of Nature Conservation)(Brooks & Macdonald 1983).

HiP has seen several planned introductions of exotic and African savannah herbivore species not historically recorded in the park (Brooks & Macdonald 1983). Impala (*Aepyceros melampus*), were introduced into Hluhluwe from Mkhuze Game Reserve ("Game Reserve" hereafter abbreviated by "GR") during the 1930's by the first conservator stationed in the park, Captain H.B. Potter (Potter 1934). Giraffe (*Giraffa camelopardalis*) were introduced into the park in the 1960's from Kruger NP (Bourquin *et al.* 1971; Brooks & Macdonald 1983; Rowe-Rowe 1994), although recent evidence indicates that giraffe may have occurred historically within the area (Cramer & Mazel 2007). Reintroductions of hippopotamus and elephant have been successful, whereas that of eland has failed (Bourquin *et al.* 1971; Brooks & Macdonald 1983; Rowe-Rowe 1994; Slotow *et al.* 2005). Translocations and internal movements of other large herbivore species have also occurred sporadically to augment local populations (Brooks & Macdonald 1983; Maddock *et al.* 1996).

Reintroductions and translocations of the above-mentioned locally extinct large carnivores have mostly been successful in re-establishing these species. After an absence of three decades a single male lion appeared in iMfolozi in 1958 (Steele 1970). Following an unsuccessful translocation in 1963, two adult females and three cubs (2 females, 1 male), from a game ranch in the Mpumalanga lowveld, were unofficially released into the park in 1965 (Anderson 1980). Although large numbers of sub-adult males and females were culled in the 1970's and 80's, to reduce lion dispersal and associated stock killing outside the park, the population increased steadily and peaked at *ca.* 140 animals in 1987 (Anderson 1980; Maddock *et al.* 1996). Subsequently, the population declined and started showing indications of inbreeding depression during the 1990's (Maddock *et al.* 1996; Stein 1999). In order to address this situation 16 further lions were translocated into HiP in four phases from 1999 to 2002 (Trinkel *et al.* 2008).

Early records on spotted and brown hyaenas in HiP from the 1920's indicate that the former were rare in iMfolozi, with the latter being more numerous (Roberts 1954). In Hluhluwe, however, spotted hyaenas were initially considered "plentiful" (Potter 1934), but were subsequently reduced through large scale poisoning inside and outside the reserve (Potter 1941). Breeding by brown hyaenas was last recorded in the 1950's in iMfolozi (Player & Steele 1997), and the last sighting in 1961 (Bourquin *et al.* 1971; Pringle 1977; Whateley & Brooks 1985). Persecution of spotted hyaenas was stopped in 1952, and by the beginning of the 1960's spotted hyaenas were considered common across the whole of HiP (Deane 1962). Simultaneously, brown hyaenas disappeared and probably went locally extinct as a combined result of increasing spotted hyaena densities associated with the increase of large mammalian herbivores within the park (see also Mills & Gorman (1997)), as well as persecution outside. Reestablishment was unsuccessfully attempted via the re-introduction of four individuals into HiP in the late 1970's, however various complications resulted in the termination of this project (Whateley & Brooks 1985; Rowe-Rowe 1992).

African wild dogs were originally common in Zululand with successful reproduction recorded through the 1910's and large packs sighted up to 1933 (Kirby 1916; Potter 1934; Pringle 1977; Rautenbach *et al.* 1980). Although it was originally speculated that an unknown disease lead to their local extinction, intensive persecution was the most likely cause (Pringle 1977). Between 1913 and 1915, a total of 89 wild dogs (17 within reserves, rest outside) are recorded to have been killed by the resident Game Conservator, F.V. Kirby, and his staff alone (Kirby 1916). In 1980 and 1981, 22 wild dogs were re-introduced into HiP in four separate releases (Whateley & Brooks 1985; Maddock 1995, 1999). At least one pack persisted until 1997, from whence the population became part of the South African Wild dog meta-population with regular translocations to the park (Gusset *et al.* 2006a; Somers *et al.* 2008). At the end of 2004, the population was composed of six packs with a total of 31 adults and yearlings (Somers *et al.* 2008). Cheetahs apparently disappeared from HiP slightly before wild dogs in the 1920's. Following this, sixty-four individuals were re-introduced into HiP from 1966 to 1969 (Bourquin *et al.* 1971; Pringle 1977; Whateley & Brooks 1985; Rowe-Rowe 1992). Further translocations to augment the population took place during 1995 from Namibia (Marker-Kraus (1996) in Hunter (1998)), and currently the population stands at ca. 25-40 individuals (Friedman & Daly 2004).

Rudimentary fencing of the original Hluhluwe and iMfolozi reserves began in 1939 and 1952, respectively (Brooks & Macdonald 1983; Brooks 2005). However game-proof fencing of the whole park was only completed in the mid 1970's (Brooks & Macdonald 1983). Currently, HiP is still completely surrounded by community owned, semi-subsistence, agricultural land with high human and livestock densities (Infield 1988). Controlled utilization of natural resources within the park occurs in the form of periodic wood, and seasonal thatch grass and reed collection by these communities. Further use occurs via the capture and translocation, or culling of large herbivores by KZNW (Scriven & Eloff 2003), illegal hunting of these species (mostly with domestic dogs and spears), as well as illegal medicinal plant collection (bark removal, etc.). Ecotourism as an alternative form of utilization has occurred in the park since the early 1930’s (Potter 1949; Aylward 2003; Brooks 2005). A public road, tarred during 2002 to 2004, bisects the park.

2.2 Study species

Spotted hyaena (Crocuta crocuta)

Spotted hyaenas form highly social groups of individuals termed clans (Kruuk 1966, 1972; Mills 1990). The social behaviour of this species is the most complex amongst terrestrial carnivores and is considered similar to that of cercopithecine primates (Holekamp *et al.* 2007). Clans of three to ninety individuals consist of one to several matrilines of adult females and their offspring plus one or more immigrant adult males (Kruuk 1972; Frank 1986a; Mills 1990). Nearly all males disperse from their natal clan by the age of three, whereas females are philopatric (Frank 1986a; Mills 1990; Smale *et al.* 1997; East & Hofer 2001).

Clan members of both sexes cooperatively maintain and defend a group territory against neighbouring clans (Kruuk 1972; Mills 1990; Henschel & Skinner 1991; Hofer & East 1993a; Boydston *et al.* 2001). However, both males and females are significantly more likely to attack intruding individuals of the same sex than the opposite sex (Boydston *et al.* 2001). Clan members also cooperate in defending carcasses against kleptoparasitism by neighbouring clans or lions (Kruuk 1972; Mills 1990; Henschel & Skinner 1991; Boydston *et al.* 2001), and may cooperate in hunting prey and stealing carcasses from other predators (Kruuk 1972; Mills 1985, 1990; Cooper 1991; Holekamp *et al.* 1997). However, clan members do not cooperate in defending and rearing juveniles (Mills 1985).

A conspicuous feature of this species is its use of a communal den where all den dependent cubs of a clan are kept together, and which forms the centre of social activity of the clan (Kruuk 1972; Mills 1990). A hyaena clan functions as a fission-fusion society with members mostly foraging on their own or in small groups (Kruuk 1972; Mills 1990; Smith *et al.* 2008). Clan members only congregate in large numbers at the communal den, around large kills, or when rallying together to defend their group territory (Kruuk 1972; Tilson & Hamilton 1984; Frank 1986a; Mills 1990; Hofer & East 1993a).

Fig. 2.1. Hyaena cub approximately two-three months old at Isivivaneni, Hluhluwe.

Clan females are socially structured according to strict linear, matrilineal dominance hierarchies (Frank 1986b; Smale *et al.* 1993). Dominance rank is maternally inherited with younger non-littermate siblings dominating older siblings within a matriline (Holekamp & Smale 1993; Smale *et al.* 1993), and all natal individuals outrank all immigrant males within a clan (Frank 1986b; Mills 1990). Dominance rank translates directly into priority of access to food (Tilson & Hamilton 1984; Frank 1986b; Mills 1990), and via this mediator has a significant influence on the reproductive success of adult females (Holekamp *et al.* 1996). High ranking females experience significantly shorter birth intervals and higher offspring survival compared to low ranking females (Frank *et al.* 1995; Holekamp *et al.* 1996). Rank further influences the ranging behaviour of females without den bound cubs, with high ranking females having significantly smaller home ranges, and being spaced farther from the territorial boundary, and closer to the communal den, than low ranking females (Boydston *et al.* 2003a).

Sexual maturity is reached at two to three years of age with females slightly older than males (Matthews 1939). Gestation is approximately 110 days and litter size ranges from one to three with a median of two (Kruuk 1972). A degree of seasonality in the conception/birth of hyaena cubs has been recorded in several populations (Kruuk 1972; Lindeque & Skinner 1982; Frank 1986a; Mills 1990; Holekamp *et al.* 1999). Litters may be born at the communal den or at a natal den from where they are moved to the communal den between one and five weeks of age (Kruuk 1972; East *et al.* 1989; Mills 1990; Boydston *et al.* 2006). Clans may often relocate to new communal dens, however, occupation length may vary substantially between different ecosystems ranging from a few days to more than a year (Mills 1990; Boydston *et al.* 2006). Communal dens are often located close to sources of water (Mills 1990; Boydston *et al.* 2006).

Females with denning cubs have significantly smaller home ranges, are spaced farther from the territorial boundary and closer to the communal den than females without denning cubs (Boydston *et al.* 2003a). Cubs mostly remain at the communal den for their first eight to twelve months (Mills 1990; Hofer & East 1993c; Holekamp & Smale 1998; Boydston *et al.* 2005; Boydston *et al.* 2006). Subsequent to leaving the communal den, meat forms a continually increasing proportion of a cub’s diet, and suckling progressively declines until complete weaning occurs at 10 to 18 months (Mills 1990; Hofer & East 1993c; Holekamp & Smale 1998).

The exclusive use of a territory by its owners and related territorial behaviour is to a certain degree flexible within and across populations (Kruuk 1972). Generally, within ecosystems with resident, stable, and relatively homogenously distributed herbivore populations, territory use is to a large degree exclusive with only little intrusion by hyaenas from neighbouring clans (Kruuk 1972). However, short-term and spatially small-scale but still significant herbivore density fluctuations across territories, may force inhabitants (especially low ranking individuals) in these systems to temporarily engage in extra-territorial foraging when prey densities become low in their own (Kruuk 1972; Cooper 1990; Höner *et al.* 2005). With large-scale herbivore migrations, as in the Serengeti ecosystem, where extensive local fluctuations in migratory herbivore density are coupled with very low resident herbivore densities within territories, clans whose territories are not covered by any migratory herds are necessitated to “commute” to the nearest wildebeest herds well outside their own territories (Hofer & East 1993a, 1993b, 1993c).

The above is considered in the context of stable territorial boundaries, however, a large number of phenomena may influence the spatial extent of and/or spatial relationship between clan territories. Territorial boundaries between neighbouring clans may be vague in low density areas, or alternately hard (apart from those imposed by landscape features) in high density areas (Kruuk 1972; Mills 1990). Populations in less productive ecosystems frequently exhibit large unused gaps between adjacent territories (Tilson & Henschel 1986; Mills 1990; Trinkel *et al.* 2004). The gaps in these ecosystems may then allow seasonal or annual territorial expansion and shrinking in response to prey dispersion (Mills 1990; Trinkel *et al.* 2004). Permanent shifts of territorial boundaries at the cost of a neighbouring territory (Kruuk 1972), or the complete shift of a territory into a new previously unoccupied area, have also been documented (Höner *et al.* 2005). Clans may also undergo fission, after which the two new territories are created via the division of the original territory (and thus no spatial emigration takes place), or one of the new territories may be established at a distance from the original territory (resulting in the spatial emigration of the moving individuals) (Mills 1990; Höner *et al.* 2005).

The hyaena is the most numerous species within the African large predator guild, and consequently is globally classified as "least concern" (Höner *et al.* 2008) on the IUCN Red list of threatened species. However, within South Africa its conservation status is less secure and it is classified as "vulnerable" (Friedman & Daly 2004).

African lion (*Panthera leo*)

In contrast to all other felid species, the socio-biology of African lions is typified by social groups of individuals termed prides (Packer 1986). A pride consists of two or more related adult females, plus their juvenile (0-2 years) and sub-adult (2-4 years) offspring (Schaller 1972; Packer 1986; Pusey & Packer 1987). Adult pride females cooperatively defend a matrilocal group territory against other prides (Schaller 1972; Packer 1986; Heinsohn & Packer 1995). Pride members may also cooperate during hunting, however the degree to which individuals contribute varies significantly (Scheel & Packer 1991; Stander 1991a). Single or cooperative coalitions of adult males, originating from elsewhere, temporarily gain and defend mating access (tenure) to a pride, or sometimes two or more prides simultaneously (Packer & Pusey 1982). A small percentage of most populations live as non-territorial nomads predominantly composed of non-territorial sub-adult and adult males (Schaller 1972; Mills 1978; Bygott *et al.* 1979; Pusey & Packer 1987; Grinnell *et al.* 1995; Funston *et al.* 2003).

A coalition generally establishes tenure, or mating access, over a pride by eviction of the resident breeding/territorial male/s (Packer & Pusey 1983b). However, tenure may also be gained opportunistically when a pride is not attended by territorial male/s (Pusey & Packer 1987; Funston *et al.* 2003). During male take-over events, the new males either kill or cause the death of most cubs, while eviction of sexually immature females and all surviving males takes place at the same time (Pusey & Packer 1987).

Fig. 2.2. Adult lioness of the Magangeni pride at Magangeni, Hluhluwe. Note identification brand and radio-collar.

The mortality and/or eviction of the pride offspring following a male take-over generally results in the synchronization of oestrous amongst the adult females, which on average conceive four-and-a-half months following the take-over (Packer & Pusey 1983a; Packer & Pusey 1983b; Pusey & Packer 1987). The median time to conception following loss of cubs under other circumstances is 24 days (Packer & Pusey 1983b). Time from parturition to conception with successful recruitment of cubs is on average 18.6 months (Packer & Pusey 1983b). Parturition follows approximately 110 days after conception and litter size ranges from one to four (Packer *et al.* 1988).

Litters are initially hidden in a den and only join the rest of the pride at one to two months of age (Estes 1991). Litters from several females are typically pooled into cohorts – if these are born within one year of each other – and reared communally, including non-offspring suckling and cooperative defence against other prides and infanticidal males (Packer *et al.* 1990; Pusey & Packer 1994; Grinnell & McComb 1996). Sub-adult females reach sexual maturity at three to four years of age, by which time the majority is recruited into their natal pride (Pusey & Packer 1987). Approximately a third of sub-adult females are not recruited, and either disperse to attempt establishment of an independent territory with other females from their natal pride, or alternatively disappear (Hanby & Bygott 1987; Pusey & Packer 1987). Emigrating females often wander over large areas before establishing new territories (Pusey & Packer 1987).

Although female prides may spatially maintain territories for many generations, new pride establishment via dispersal or pride fission may occur frequently (Schaller 1972). In the event of pride fission, where the adult females split into two, or sometimes three groups, the original territory is generally sub-divided (Pusey & Packer 1987; Spong 2002). Territory establishment by dispersing sub-adult females, however, results in three potential configurations of the new territory: completely within, partially overlapping, or directly adjacent to the natal territory (Pusey & Packer 1987). Alternatively, when a pride dies out, its territory is occupied by adjacent prides (Pusey & Packer 1987). Although pride females show pronounced territorial behaviour (Schaller 1972; Pusey & Packer 1987; Heinsohn 1997), territorial exclusivity may be highly variable within and across ecosystems (Schaller 1972; Spong 2002). In this sense, it is probably more appropriate to refer to the complete area used by a pride as a “pride area” or pride range (Schaller 1972).

The age of natal male dispersal, either through eviction or by own volition, varies substantially according to ecosystem, however, most have emigrated by 48 months of age (Pusey & Packer 1987; Funston *et al.* 2003). Dispersing males generally become nomadic before gaining tenure over a pride (if they ever do so), however, delayed dispersal followed by immediate establishment of tenure in an adjacent pride has been recorded as well (Pusey & Packer 1987; Funston *et al.* 2003). The majority of males disperse in coalitions of two or more males, often originating from the same cub cohort (Pusey & Packer 1987). During this nomadic period, coalitions of two or less males frequently form larger coalitions with other unrelated/unfamiliar males up to a total of three males (Pusey & Packer 1987). Male coalitions may eventually gain tenure and breed in prides adjacent to their natal pride, or move further before attaining tenure (Pusey & Packer 1987; Spong & Creel 2001; Funston *et al.* 2003). The average tenure length is between two and three years (Pusey & Packer 1987; Stander 1991b), with forceful evictions by a new coalition significantly shortening this period in comparison to voluntary secondary dispersal (Pusey & Packer 1987). Voluntary departure always involves the acquisition of a new pride or situations where a coalition already held tenure over two or more prides (Pusey & Packer 1987; Funston *et al.* 2003).

Systematic comparison of sex differences in range size, as documented for large felid species such as leopard, puma (*Puma concolor*), jaguar (*Panthera onca*), and tiger (*Panthera tigris*)

(Nowell & Jackson 1996; Skinner & Chimimba 2005), is still lacking for lions. The males of these solitary species generally have larger ranges than females, and a few lion studies have also indicated the same pattern for this species (Schaller 1972; Stander 1991b; Hemson 2003). Substantial variation in the degree of association between pride females and coalition males between populations (Funston *et al.* 1998), further predicts the potential for sexual differentiation in ranging behaviour. In open systems, territorial coalitions are more often encountered with pride females, whereas in more wooded areas males associate less with females (Pusey & Packer 1987). Other ranging parameters such as utilization distribution, may be affected by pride size, in that larger prides often exhibit fission-fusion behaviour by splitting into sub-groups, which range apart for variable lengths of time (Schaller 1972; Packer 1986). Considering the above outlined sex differences in dispersal, reproduction, and male-female association patterns for lion, it is clear that substantial sex differences in range size and utilization distribution can be expected for this species.

The African lion has recently undergone a substantial species population reduction, and is globally classified as vulnerable on the IUCN Red list of threatened species (Bauer *et al.* 2008). Although the number of lions within South Africa has recently increased as a result of numerous local reintroductions (Slotow & Hunter *in press*), its conservation status within the country is still “vulnerable” (Friedman & Daly 2004).

Chapter 3

Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park

3.1 Summary

Animal population sizes and trends as well as their distributions are essential information to the understanding and conservation of ecosystems. During this study in Hluhluwe-iMfolozi Park, South Africa, a spotted hyaena (*Crocuta crocuta*) population was surveyed by attracting individuals with pre-recorded sounds. The hyaena population (excluding cubs) was substantially larger (321 individuals) than the previous estimate of 200, and this population is the second largest protected population in South Africa. Average hyaena density at 0.36 individuals/km^2 is relatively high compared to other southern African conservation areas, and ranged from zero to 1.25 individuals/km^2 across sampling areas. For short periods, spatial heterogeneity in density was substantial at small and large spatial scales, but decreased when averaged over time. This heterogeneity, by creating potential dynamic interference refugia through variation in encounter probability across space and time, may be important in promoting the coexistence of other large and mobile predators in Hluhluwe-iMfolozi Park. Furthermore, heterogeneity of hyaena density at smaller scales should influence studies investigating the avoidance of hyaenas by competitively subordinate predators, or prey species.

3.2 Introduction

Animal population sizes and trends as well as their distributions, are essential information to the understanding and conservation of ecosystems. This is particularly relevant to predators, which generally occur at low densities, but which may impact on the coexistence of other predators (Palomares & Caro 1999), the population dynamics of their prey (Sinclair 2003; Sinclair *et al.* 2003; White & Garrott 2005; Owen-Smith & Mills 2008), and even species at lower trophic levels (Crooks & Soulé 1999; Schmitz *et al.* 2000; Ripple *et al.* 2001; Terborgh *et al.* 2001; Schmitz *et al.* 2004; Beschta 2005; Croll *et al.* 2005).

Spotted hyaenas (*Crocuta crocuta*) (Hyaenidae) are large African carnivores, and are generally the most numerous within the African large predator guild. Previous studies from various ecosystems have shown spotted hyaenas as important interference competitors and/or predators of sympatric large predators such as cheetahs (*Acinonyx jubatus*) (Laurenson 1995; Durant

1998; Kelly *et al.* 1998; Durant 2000a, 2000b; Kelly & Durant 2000; Hunter *et al.* 2007b), lions (*Panthera leo*) (Cooper 1991), brown hyaenas (*Hyaena brunnea*) (Mills 1990), and African wild dogs (*Lycaon pictus*) (Estes & Goddard 1967; Kruuk & Turner 1967; Fanshawe & FitzGibbon 1993; Carbone *et al.* 1997; Carbone *et al.* 2005). For example, it has been argued that such an interference relationship is partly responsible for the negative correlation between spotted hyaena and wild dog densities across several African ecosystems (Creel & Creel 1996, 2002). According to the 2004 Red Data Book of the Mammals of South Africa, all of the above-mentioned predator species are classified as either “endangered”, “vulnerable”, or “near threatened” (Friedman & Daly 2004). Consequently, the combination of the ecological role of spotted hyaenas within the African large predator guild, as well as its own conservation status and that of the other guild members (excluding leopard (*Panthera pardus*)), poses a multifaceted challenge to the management of large predator diversity within South African protected areas.

An example of one such protected area is the Hluhluwe-iMfolozi Park (HiP), in KwaZulu-Natal Province, South Africa. Reintroductions of locally extinct large carnivores including wild dog, cheetah and brown hyaena have been undertaken in HiP, of which only the former two have resulted in persisting, small populations (Whateley & Brooks 1985; Rowe-Rowe 1992; Maddock 1999; Somers *et al.* 2008). The population and feeding ecology of spotted hyaenas (hereafter referred to as “hyaenas”) in HiP has been studied in the late 1970’s, but there have been no investigations into the potential interference interactions amongst hyaenas and the above-mentioned predators. A determining component of the rate at which interference interactions may occur is the probability of encounter, of which density distribution is a major driver. Consequently, for predator species locked into such interactions spatial and temporal heterogeneity in density, may be an important factor for their continued co-existence via the creation of dynamic refugia (Durant 1998; Saleni *et al.* 2007). Durant (1998) further argued that the distribution of a species averaged over long periods might exhibit very little spatial heterogeneity, but at any given moment may show significant heterogeneity in distribution, with areas of low density or utilization representing such dynamic refugia. Thus, in light of the small size of the re-introduced and threatened large predator populations (principally wild dogs) in HiP, we investigated whether any short term spatial and temporal variation of hyaena density existed, in order to determine the presence (or absence) of any short term dynamic interference refugia from hyaenas in HiP. This density mapping was done by combining a well-established density estimation method, the audio playback, with geographic information system interpolation techniques.

The first objective of this study was to provide an updated estimate of total population size of hyaenas for HiP. The second objective was to determine the mean hyaena density across HiP and the magnitude of heterogeneity in hyaena density. The third objective was to produce a map of hyaena density across the surface of the park for the relevant sampling periods. The results are discussed with regards to previous studies using the same census technique, earlier hyaena population estimates for HiP, potential mechanisms creating heterogeneity in hyaena density, the co-existence of hyaenas with other large predators, and the relevance of scale when evaluating potentially competitive, interspecific spatial relationships involving hyaenas. Finally, we consider aspects of the hyaena's existence in and around HiP, and it's bearing on the conservation status of this species in South Africa.

3.3 Methods

Study site

This survey was conducted in Hluhluwe-iMfolozi Park (HiP; previously Hluhluwe-Umfolozi Park) (28°00′–28°26′S, 31°41′–32°09′E), KwaZulu-Natal Province, South Africa. This completely fenced reserve covers an area of approximately 900 km^2, with altitudes ranging from 40–590 m above sea level. The landscape is broken by numerous valleys and hills, especially in the north-eastern part of the park. HiP is completely surrounded by community owned, subsistence agricultural land with high human and livestock densities (Infield 1988).

HiP comprises a diverse range of habitats and lies within the Zululand thornveld subcategory of coastal tropical forest types and the lowveld subcategory of tropical bush and savannah types (Acocks 1988). All species of the African large predator guild, including wild dogs, cheetahs, lions, and leopards are present. A wide range of ungulate species with mostly sedentary or non-migratory habits is present (Bourquin *et al.* 1971; Brooks & Macdonald 1983).

Response distance and probability

To census the hyaena population in HiP we used the broadcasting of pre-recorded sounds (i.e. "playbacks", "call-ups", or "call-ins") since it is an inexpensive and rapid technique and has been extensively used for this species in various conservation areas across Africa (Kruuk 1972; Whateley & Brooks 1978; Whateley 1981; Sillero Zubiri & Gottelli 1992b; Creel & Creel 1996; Ogutu & Dublin 1998; Mills *et al.* 2001; Maddox 2003; Salnicki 2004; Leigh 2005; Ogutu *et al.* 2005; Kiffner *et al.* 2007). Independent trials were conducted to determine the maximum response distance (RD) and the response probability, in order to calibrate the observed results with these parameters, which then allows the calculation of the hyaena density and population size (Ogutu & Dublin 1998; Mills *et al.* 2001; Maddox 2003; Ogutu *et al.* 2005).

Locating stationary hyaenas in HiP in order to conduct these response trials proved to be problematic for several reasons. Although hyaenas were regularly seen, these animals were mostly moving, and searching for hyaenas was restricted to the tourist road and management track network. This was further complicated by limited visibility away from roads and tracks due to the dense vegetation of HiP. In order to circumvent this problem, hyaenas were called to a station by playback where identification footage was taken by video of as many as possible of the responding hyaenas. Following this, a subsequent playback was done at a set distance away. This method was conducted at six different distances across a range of locations spread over HiP (Table 3.1, p. 31). In this regard, a positive response was defined as when any of the previously identified animals arrived within view of the second playback location. From the RD, a circular census area around each playback station was calculated. The response probability was determined by the ratio of responding identified hyaenas to total identified hyaenas within the RD. RD testing was also conducted following the Mills *et al.* (2001) method on a single radio-collared adult female hyaena (with her two *ca.* 11 month old cubs) after she was located by radio telemetry.

Playbacks

Playback procedures in the field mainly followed Mills *et al.* (2001) and Creel & Creel (1996). Playbacks were conducted between the hours of 18:00 (starting range 18:00–18:43h) and 02:00 (finishing range 22:00–01:54h), depending on the number of playback stations (hereafter referred to as "stations") visited per night. Response calibration trials indicated a RD of 2.8 km. Thus, adjacent stations were located at least 5.6 km apart, although the majority were substantially further apart. Given this minimum distance of 5.6 km between stations, positions for stations were located on roads and management tracks from a GIS road map of HiP. To obtain maximum visibility as open an area as possible was selected for each station, and these were either on or within 50 m from a road or management track. A median of four stations (range 3–5) were visited per night, each night covering a different and non-overlapping area, and driving between stations taking on average 26 min (range 15–40 min; excluding a single non-standard event of 62 min).

Upon arrival at a station, an audiotape (obtained from M.G.L. Mills) containing sounds known to have a relatively high probability of attracting hyaenas at night (Creel & Creel 1996; Mills *et al.* 2001; Maddox 2003; Ogutu *et al.* 2005), was played through a mobile 12 V amplifier and cassette tape player attached to two, 12 Ω, horn speakers. The sounds contained on the tape had been successfully used before for the censusing of several hyaena populations across Africa (Creel & Creel 1996; Mills *et al.* 2001; Maddox 2003; Ogutu *et al.* 2005), and included recordings of whooping hyaenas, hyaenas fighting over a kill, an inter-clan fight between hyaenas, and hyaenas mobbing lions. The speakers were mounted on the roof of a small truck and faced in opposite directions. The tape was played for six min, with the speakers turned 90° after three min, followed by five min of silence. This playing procedure was repeated three times at each station. The tape was played a fourth time if hyaenas were heard in the vicinity of the station during the first three repeats, but did not come into view.

Two observers with spotlights stood on the open back of the truck, and scanned the vicinity occasionally. A third observer recorded identification footage of hyaenas with a digital video camera. A fourth person recorded all data, and if present, a fifth observer equipped with a pair of 10x42 binoculars recorded detailed observations. A fixed core of the same two observers was present at all playbacks conducted, in order to reduce observer bias. So as to prevent double counting at stations, all hyaenas that appeared were carefully observed (spot patterns, or other individually characteristic features were noted where possible). The data recorded included the number of hyaenas, age class, and geographical coordinates of the station. The three age classes used, cub (<12 months), sub-adult (12–24 months) and adult (>24 months) were estimated from body size.

Two series were conducted, the first comprising five nights on 13, 14, 15, 21 and 22 October 2003, and the second six nights on 27, 30 and 31 August and 13, 14 and 15 September 2004. As recommended by others (Ogutu & Dublin 1998; Mills *et al.* 2001), the effects of habituation on response were minimized through the lapse of 10 months between the two series. The numbers of stations visited during the two series were 20 and 24, respectively. The second series included a re-sampling of 19 stations of the first series. An additional five stations were added during the 2004 series to sample the south-western area of HiP (see Fig. 3.1, p. 33). The 2003 and 2004 series, respectively, covered 46.3% and 53.3% of the total area of the park.

Data analysis

All spatial analyses and calculations were conducted in the program ArcMap 8.3 (ESRI 2003). Data layers of the station locations and the HiP boundary were created. Another data layer containing circular response areas with radius equal to the RD (2.8 km) for each playback station was created. As some stations had response areas overlapping with the HiP boundary, these external areas were removed to yield adjusted response areas. A single station with response area overlapping the boundary was excluded from this procedure for the following reasons: approximately two-thirds of this station's response area lay outside the park boundary, and during both series hyaenas with snares were recorded at this station indicating that these hyaenas probably had been foraging outside the park, as snaring inside the park is effectively absent. This behaviour was only apparent in the clan adjacent to this single area.

The sizes of all the response areas (unchanged and adjusted) were calculated in km^2. Assuming equivalent response probability across stations as argued by Mills *et al.* (2001), the numbers of observed hyaenas at each station were adjusted with the response probability (in our instance 0.6) to derive expected numbers for each station (Ogutu & Dublin 1998; Mills *et al.* 2001). Hyaena densities (individuals/km^2) were then calculated for each station by dividing the expected number of hyaenas by the size of the unchanged or adjusted response area. Means and confidence intervals for the expected number and density of hyaenas per station for the 2003 and 2004 series were calculated following Ogutu *et al.* (2005) using the non-parametric bootstrap method based on 10 000 replications with replacement, in the program R 2.5.0 (R Development Core Team 2007). Population size (adults and sub-adults) was estimated by multiplying density estimates (mean ± 95% bootstrap confidence limits) with the area size of HiP. The percentage of cubs responding to playbacks was very small as also noted by Mills *et al.* (2001), and thus this was not incorporated into density and population size estimates, i.e. the estimates excluded individuals < 12 months of age. All statistical analysis other than bootstrapping was performed in STATISTICA 6.1 (Statistica 2003).

Spatial interpolation through the inverse distance weighted method was performed on the individual station densities in order to produce a continuous hyaena density map of HiP for the periods covered by both series. For this procedure, power was set at *2*, search radius type as *variable*, number of points set at *n-1* (*n* = number of stations), and output cell size at *100 m*. A composite density distribution map was calculated representing the average of the two maps for the 2003 and 2004 series. All layers were projected with UTM 36S and WGS84 map datum.

3.4 Results

Response distance and probability

We tested seven different RDs for 17 identified hyaenas of which only one test produced a positive response (Table 3.1). No hyaenas responded beyond a distance of 2.8 km. The absence of hyaena response above 2.8 km between testing stations underscored our confidence that the resampling of individuals (at least within one night's playbacks) was highly unlikely during the actual survey. The ratio of responding hyaenas to total hyaenas for the three trials within the RD of 2.8 km yielded a response probability of 0.60.

Table 3.1. The number of adult and sub-adult hyaenas of which identification footage was taken at the first playback station and the number of these individuals subsequently responding at a second station for various distances between playback stations during response calibration testing in HiP.

Distance between stations (km)	**Identified hyaenas**	**Responding hyaenas**
2.2	1	0
2.5	1[1]	0
2.8	3	3
2.9	2	0
3.4	2	0
4.3	5	0
4.4	3	0

[1] represents radio-collared adult female

Hyaena numbers, density and distribution

Hyaenas were seen at 19 of 20 (95.0%) and 22 of 24 (91.7%) stations for the 2003 and 2004 series, respectively. Both sexes and all age classes were recorded, but only 2.7% of the total number of aged individuals were judged to be < 12 months old. Four hyaenas with wire or cable snares around their neck or head were recorded at three stations during the two series. Lions were recorded at five of 44 stations, with hyaenas being present on four (80%) of these occasions. There was no evidence that lion presence influenced hyaena response (Fischer exact test, $p = 0.31$).

Observed numbers of hyaenas per station ranged from 0 – 12 individuals for both series (Table 3.2). There was no significant difference between the number of observed hyaenas responding per station for the 2003 and the 2004 series ($F=0.02$, $p=0.88$). Thus, these estimates were combined to give a mean density of 0.357 hyaenas/km^2 (lower: 0.259, upper: 0.481, range: 0.000 – 1.250) and a mean adult and sub-adult population estimate of 321 hyaenas (lower: 233, upper: 433) (Table 3.2).

Spatial interpolation of the station densities for the 2003 and the 2004 series revealed several prominent low density and high density patches across the park (Fig. 3.1a, b). Visual interpretation suggested that three low density and two high density patches roughly remained in the same area if the two series are compared, however the majority of these patches were not in the same location across series. Integrating the results from both series resulted in homogenisation of density across the landscape, although density variation was still maintained to a certain degree (Fig. 3.1c).

Table 3.2. The total number of hyaenas responding (*n*), estimates of the mean and the associated 95% bootstrap confidence limits (lower, upper) for, the expected number of individuals within the response range of a station, the population density (numbers/km^2), and the population size (number) for the 2003 and 2004 playback series in HiP.

	Playback	**Area**		**Expected number**			**Density**			**Size**		
Year	**stations**	**(km^2)**	***n***	**Mean**	**Lower**	**Upper**	**Mean**	**Lower**	**Upper**	**Mean**	**Lower**	**Upper**
2003	20	417.3	92	7.670	5.750	9.830	0.350	0.268	0.438	315.0	241.2	394.2
2004	24	480.4	107	7.421	5.347	9.583	0.363	0.259	0.481	326.7	233.1	432.9

3.5 Discussion

Previous hyaena playback studies across several African ecosystems found a range of RDs from 2.5 km in Serengeti NP (Maddox 2003), 3.0 km in Ngorongoro Crater and Lower Zambezi NP (Kruuk 1972; Leigh 2005), 3.2 km in Kruger NP (Mills *et al.* 2001), 3.7 km in Selous GR (Creel & Creel 1996), to 4 km in Masai Mara National Reserve (Ogutu *et al.* 2005). Some of the above studies also quantified response probability, and results of 0.61 (Mills *et al.* 2001), 0.88 (Maddox 2003), and 0.583 were determined (Ogutu *et al.* 2005). Our response parameters are very similar to those found in the Kruger NP, which amongst the above-mentioned reserves probably contains habitats most similar to those in HiP, with the slightly shorter RD most probably as a result of the pronounced hilly topography of our study site. Thus, despite the fact that they were based on a small sample size, we believe that these response parameters represent realistic estimates. Nonetheless, we strongly recommend that further response testing should be conducted in HiP in order to increase the robustness of the population size and density estimates. In conjunction with this, the current population size and density estimates should be interpreted with caution. Conversely, the statistical similarity between the two series in our survey in the number of hyaenas responding per station, would indicate the precision of this survey technique. We suggest that surveys within HiP are continued at regular intervals (every 3-4 years) to monitor population trends.

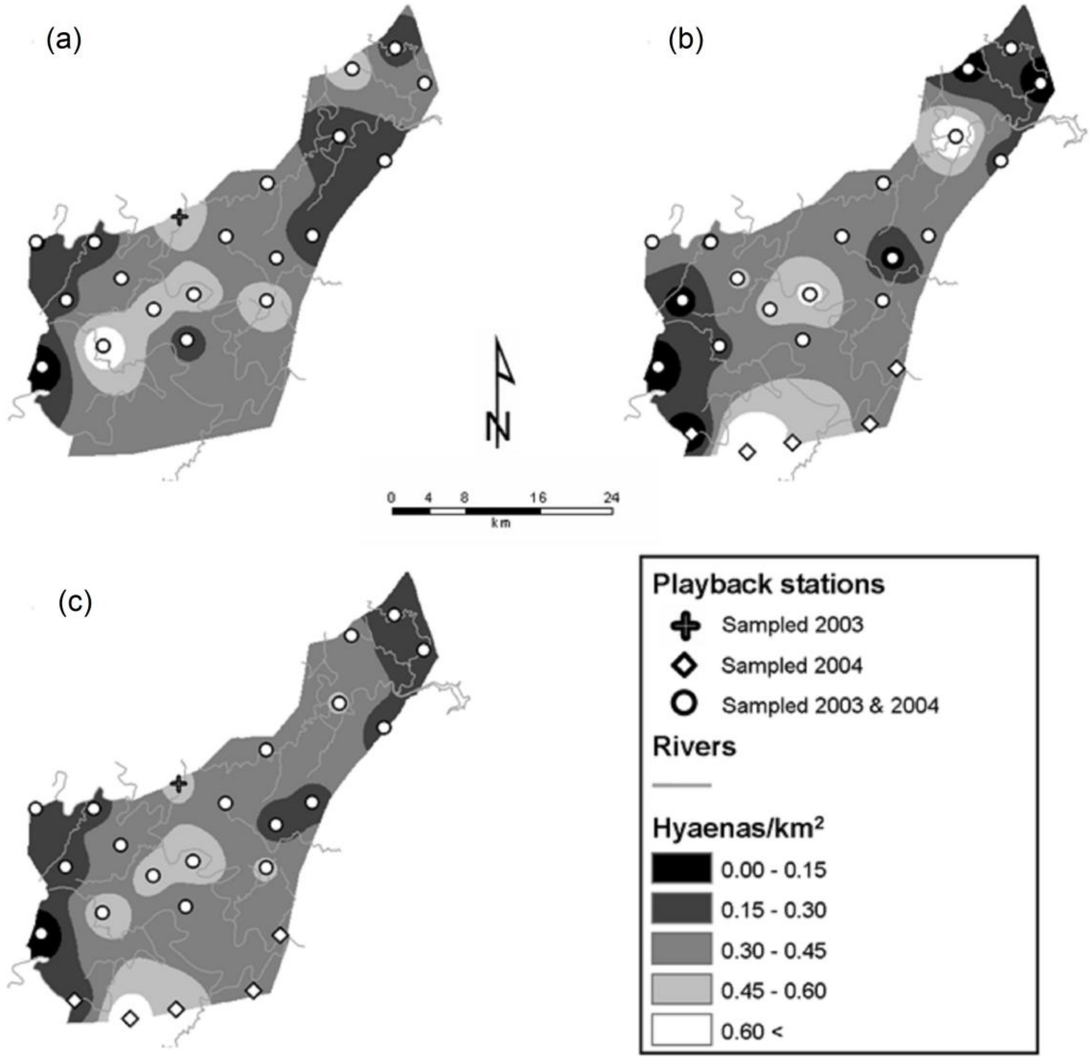

Fig. 3.1. Density (hyaenas/km^2) distribution maps of hyaenas in HiP, illustrating the spatial heterogeneity in hyaena density, and consequently encounter probability, across the park for: (a) the 2003 series, (b) the 2004 series, and (c) the average of the 2003 and 2004 series.

The first detailed population study on hyaenas in HiP from 1975 to 1981, where playbacks were combined with the Lincoln Index, indicated densities of 0.46 and 0.36 hyaenas/km^2 (adult and sub-adult) for the respective study areas in Hluhluwe and iMfolozi (Whateley & Brooks 1978; Whateley 1981). In Hluhluwe, the total study area from which the density was derived, included the minimum territory sizes of the three study clans plus peripheral areas between these territories and the HiP and study area boundary. Subsequently, a forested area representing one quarter of the total study area was subtracted as it was thought to be "little-used", although two of the study clan territories included tracts of forest (Whateley & Brooks 1978). In iMfolozi the minimum territory size of the single study clan was used without the addition of peripheral areas (Whateley 1981). Potentially both, but most probably the Hluhluwe calculation, resulted in the overestimation of hyaena densities with later extrapolations across HiP resulting in the probable overestimation of total population size (350 adults and sub-adults - Whateley & Brooks 1985).

If we adjust the original Hluhluwe density (Whateley & Brooks 1978) to include the forested area they excluded, estimated density becomes 0.35 individuals/km^2. This adjusted estimate as well as the original estimate for iMfolozi is very similar to the estimates of our survey. This may indicate that the population as a whole has remained fairly constant over the intervening period. However, this interpretation should be treated with caution, as preliminary results indicate that hyaena clan size obtained through individual identification has significantly increased in the same area studied by Whateley & Brooks (1978) in Hluhluwe (J.A. Graf, L. Turelli & M. Szykman, 2004, unpubl. data).

Relative to other surveyed southern African conservation areas, the average hyaena density in HiP is high, but intermediate if compared to East African areas (see Table 3.3). Comparing densities on an Africa-wide scale reveals variation of over three orders of magnitude (Table 3.3). This variability is extended on a smaller scale within an ecosystem such as the Kruger NP, South Africa, where substantial spatial heterogeneity in density has been recorded across different habitats (Mills *et al.* 2001). Moreover, large temporal changes in hyaena density across seasons have been illustrated for the highly dynamic Serengeti ecosystem of Tanzania, as a result of large scale ungulate migration and the resultant commuting system of hyaena (Kruuk 1972; Hofer & East 1993a). Significant fluctuations in hyaena density have also been found at longer time scales as documented in the Ngorongoro Crater, Tanzania (Höner *et al.* 2005).

Our data, expand on the above-mentioned understanding of spatial and temporal variation in hyaena density at larger scales, and, as can be expected in a highly heterogeneous environment such as HiP, may demonstrate that hyaena density can be highly variable at small spatial scales (i.e. between the response areas of two stations) if measured over short periods (i.e. within one night, or the length of each series). Although there is a high similarity in the spatial density trends across the two series (both are highly heterogeneous, as opposed to one being heterogeneous and the other homogenous), the above conclusion is based on the results of only two independent sampling events, and should be interpreted with caution. The spatial shifting of low and high density patches across series further indicated that density heterogeneity may be dynamic, even though HiP only contains sedentary or non-migratory herbivores. Spatial heterogeneity in density was still maintained if the density maps were averaged over time (i.e. integrating 2003 and 2004 series), although the magnitude of density gradients across space appeared to decrease. This homogenisation appeared to be stronger at the smaller (between stations) than at the larger (park wide) scale. If more surveys from consecutive time periods were integrated, this would probably result in a more homogeneous spatial distribution of hyaena density, i.e. density would become more homogenous with increasing temporal scale (Durant 1998). As above, the results of this map also represent a first estimate of the average hyaena density distribution across the park, and in future should be improved by adding further sampling series to this average-density spatial calculation. Furthermore, hyaena density estimation was only done for two seasons, and ideally should be examined for multiple seasons in order to improve the average density map, and to see whether the spatial density trends observed so far also hold for the other seasons. In terms of such increased sampling intensity, the sensitivity of these playbacks to hyaena habituation should be kept in mind (Ogutu & Dublin 1998; Mills *et al.* 2001), which may prevent a large number of repeats within a season or even a year.

The mechanisms driving small scale variation in hyaena density at our study site are probably linked to various factors including prey distribution and communal den-site location. Within ecosystems with large resident herbivore populations similar to HiP, hyaena distribution has been correlated with small scale variations in prey density even within relatively small clan territories (Boydston *et al.* 2003b; Höner *et al.* 2005; Kolowski 2007). For the same seasonal period (August-October) as our survey, significant spatial heterogeneity in the densities of four of the main prey species of hyaena in HiP occurred at an even smaller scale (2.5 x 2.5 km grid) than our survey (Cromsigt 2006). This may explain the short term spatial variation in hyaena density found during our survey, however, this needs to be investigated.

Communal den-site location may be another factor driving small scale variation in hyaena density. Adult female hyaenas with cubs need to regularly return to the communal den to feed their cubs until these leave the den between 8 and 12 months of age (Kruuk 1972; Boydston *et al.* 2003a; Boydston *et al.* 2005). Other clan members also congregate at the communal den which forms the centre of social activity within a clan (Kruuk 1972; Mills 1990). Several authors have hypothesized that these behavioural patterns should influence the spatial distribution of hyaenas within their territory, and have in fact shown that the space-use of all hyaena clan members is clumped around these communal den-sites (Boydston *et al.* 2003a;

Kolowski 2007). Communal den-sites are often relocated within a clan's territory (Kruuk 1972; Mills 1990; Boydston *et al.* 2006), and this could lead to variation in hyaena density distribution correlated to the time-scale of these den moves.

Table 3.3. Densities of hyaenas in various East and southern African conservation areas.

Conservation area	**Hyaenas/ km^2**	**Region of Africa**	**Data source**
Selous	0.32	E. Africa	Creel & Creel 1996
Masai-Mara	0.404	E. Africa	Ogutu *et al.* 2005
Serengeti (source)	0.6	E. Africa	Hofer & East 1995
Aberdare	1.3	E. Africa	Sillero Zubiri & Gottelli 1992b
Ngorongoro	1.33	E. Africa	Höner *et al.* 2005
Southern Kalahari	0.008	s. Africa	Mills 1990
Etosha	0.05	s. Africa	Gasaway *et al.* 1991
Hwange	0.07-0.18	s. Africa	Hofer & Mills 1998; Salnicki 2004
Kruger	0.03-0.2	s. Africa	Mills *et al.* 2001
Timbavati	< 0.4	s. Africa	Bearder 1977
Savuti	< 0.4	s. Africa	Cooper 1989
iMfolozi (western)	0.36	s. Africa	Whateley 1981
Hluhluwe (n.-eastern)	0.46	s. Africa	Whateley & Brooks 1978
HiP	0.357	s. Africa	This study

The importance of spatial and temporal heterogeneity in the co-existence of competing species is a well-established concept within community ecology (Holt & Polis 1997; Prins & Olff 1998; Mills & Funston 2003; Owen-Smith 2004). The temporal and spatial heterogeneity in hyaena density demonstrated in this study may promote the co-existence of other large predators with hyaenas in HiP, by creating potential dynamic interference refugia through variation in encounter probability across space and time. Several medium-sized low-density areas were evident for both series in our study and these could function as such refugia. Competitively subordinate large predators (in an interference competition sense) with high mobility, such as wild dogs, may be able to exploit these dynamic refugia as they shift over time, as already demonstrated for cheetah (Durant 1998). Furthermore, this heterogeneity in density at small spatial and temporal scales also has implications for research into the avoidance of hyaenas by subordinate predators. Interpretation of our results suggest that measuring and testing for such interactions at several scales (especially at local or small scale) may be important in order to establish the occurrence of this phenomenon. Previous studies in Kruger NP, South Africa, and Selous GR, Tanzania, have found contrasting results regarding the avoidance of hyaena high density areas by wild dogs (Mills & Gorman 1997; Creel & Creel 2002). In Kruger NP, there was a negative but non-significant correlation between the ranked habitat preferences of hyaenas (based on hyaena response to playbacks) and wild dogs (based on location data) (Mills & Gorman 1997). However, in Selous GR there was a significant positive spatial correlation between hyaena density (based on hyaena response to playbacks) and wild dog space use (based on location data) (Creel & Creel 2002).

Both above-mentioned studies employed wild dog location data grouped over long time periods (several years), and density/distribution relationships between species were necessarily only tested at large spatial scales (habitat scale in Kruger NP and large grid size [9.26 x 9.26 km] in Selous GR), as a result of sparse hyaena data (Mills & Gorman 1997; Creel & Creel 2002). Using a different species combination and method in the much more open landscape of the Serengeti plains, Durant (1998) found a significantly negative relationship between cheetah presence and hyaena density during the wet season at a small scale (1-3 km). Furthermore, cheetah avoidance of hyaenas was found at the local scale as well in a subsequent experimental study where cheetahs were exposed to recorded vocalizations of hyaenas (Durant 2000a). A number of other ecological variables such as prey density, as well as lion density, which has been shown to be negatively correlated to wild dog space use in Kruger NP and Selous GR (Mills & Gorman 1997; Creel & Creel 2002), may complicate the examination of this interaction (Creel & Creel 2002).

The HiP hyaena population is substantially larger (ca. 50%) than the last estimate of 200 individuals (Hofer & Mills 1998), and is the second largest protected population in South Africa following Kruger NP. In the surrounding Zululand and Maputaland area, small populations exist in the Ophathe, Ntshondwe (formerly iThala), and the uMkhuze GRs, and the Isimangaliso Wetland Park (Pringle 1977; Rowe-Rowe 1992; Skinner *et al.* 1992; Hofer & Mills 1998). Hyaenas are reportedly also present on private game reserves and commercial ranches between these formal reserves (Hunter 1998), which may be either resident or dispersing individuals. Long distance male dispersal as noted in HiP by Whateley (1980) may allow hyaenas to emigrate to these local populations, and we believe that the HiP population is probably contiguous with these small populations in a natural meta-population sense. This extended hyaena population currently constitutes a key population for the conservation of this vulnerable species in South Africa (Friedman & Daly 2004), and this recognition should be taken into account in the regional land-use planning and conservation management of this species.

Chapter 4

Lion spatial ecology generates potential predation refugia in Hluhluwe-iMfolozi Park

4.1 Summary

Refugia are critical features for the co-existence of many species locked in predator-prey interactions, even within apex predator guilds. Using a five-year demography and location data-set for two female prides and one male coalition, we investigated the potential for lion density and ranging patterns to create dynamic predation refugia via spatial and temporal variation in the probability of encounter. Variation in encounter probability between pride-ranges was substantial, and influenced by pride size, pride range size, absence or presence of territorial coalitions, and coalition size. Pride differences in range size and proportional range overlap, for seasonal and annual scales, resulted in variably sized low encounter probability areas within different long-term pride ranges. Pride range shifts across years were larger than across seasons, indicating that low encounter probability areas within long-term ranges were more stable at the seasonal than annual time scale. Utilization intensity was not evenly distributed over space, and low encounter probability areas mostly occurred at the edges of long-term ranges. Conversely, the magnitude of variation in utilization intensity over time was slightly biased towards long-term-cores, but also occurred outside of cores at the edge of long-term ranges. Similar to recent predator–prey interaction work, our work suggests that groups rather than individuals are the basic units around which intraguild interactions of social predator and prey species should be modelled. Our work additionally suggests that sociality in combination with predator territoriality may also stabilize such intraguild interactions.

4.2 Introduction

The importance of refugia for the co-existence of many species locked in classical predator-prey interactions is a long-standing concept in ecology (Murdoch & Oaten 1975; Walls 1995), and their use to avoid predation, has been documented for a wide range of taxa in both aquatic and terrestrial ecosystems (Winnie Jr & Creel 2007). The significance of refugia has also been established for many species-pairs, which are not only locked into predator-prey interactions, but which also compete (Durant 1998; Sergio *et al.* 2003; Young *et al.* 2006; Sergio *et al.* 2007).

An example of such an interaction has been demonstrated for badgers (*Meles meles*) and hedgehogs (*Erinaceus europaeus*) in England (Young *et al.* 2006). In this interaction, suburban habitats, which were less used by badgers than the surrounding pasture fields of rural areas, provided spatial refugia for hedgehogs from the effects of badger predation. This mechanism ultimately allowed co-existence of these two competing species at the landscape scale (Young *et al.* 2006). Such a combination of competition and predation between different species within a guild is apparently more frequent than previously recognized, and has been termed intraguild predation (IGP) (Polis *et al.* 1989). IGP has the potential to affect the distribution and abundance of the species involved (Polis *et al.* 1989; Holt & Polis 1997), and has been predicted to play a large role in the trophic structuring of communities (Arim & Marquet 2004).

The African lion (*Panthera leo*) and the African wild dog (*Lycaon pictus*) is a species pair which has received considerable interest in terms of IGP (Mills & Biggs 1993; Van Heerden *et al.* 1995; Creel & Creel 1996; Mills & Gorman 1997; Creel & Creel 1998; Vucetich & Creel 1999; Woodroffe & Ginsberg 1999; Pole 2000; Creel 2001; Creel *et al.* 2001; Creel & Creel 2002; Van Dyk & Slotow 2003; Leigh 2005; Saleni *et al.* 2007), especially in light of the endangered status of wild dogs (Woodroffe *et al.* 2004). A significant negative relationship between the densities of these two species has been found across ecosystems (Creel & Creel 2002), and depending on ecosystem, lion predation may be responsible for a major share of adult and juvenile wild dog mortality (Creel & Creel 1996; Woodroffe & Ginsberg 1999; Woodroffe *et al.* 2007). Furthermore, modelling of wild dog population dynamics predicted that wild dog population extinction risk is particularly sensitive to lion density (Vucetich & Creel 1999). As a result of the above, it has been hypothesized that wild dogs should avoid lions and/or use refugia to reduce their predation risk in order to co-exist with lions in the same ecosystem (Mills & Gorman 1997; Creel & Creel 2002; Van Dyk & Slotow 2003).

In South Africa, the conservation strategy followed for wild dogs has lead to the establishment of a managed wild dog meta-population composed of a number of sub-populations within several small protected areas (Mills *et al.* 1998), the largest of these being the Hluhluwe-iMfolozi Park (HiP) at 900 km^2. Lindsey *et al.* (2004), however, pointed out that the potential for spatial niche differentiation between lions and wild dogs is reduced in small reserves. This raises the question whether wild dog packs within such reserves indeed have access to sufficient areas of reduced predation risk.

Predation risk is a composite of several interacting factors, but can be defined as a function of the probability of encounter, frequency of attack once encountered, and capture probability when attacked (Creel & Creel 2002). Independent of prey ranging, encounter probability is shaped by the density and spatial distribution of the predator. Over time, the densities of lions, as well as their spatial distributions, may show natural variation (Van Orsdol *et al.* 1985; Packer *et al.* 2005), leading to a constantly altering probability of encounter surface across the landscape. This variation in lion density and distribution patterns has mostly been studied in the context of its ecological drivers, such as prey biomass and dispersion (Van Orsdol *et al.* 1985; Scheel & Packer 1995; Hemson 2003), while it has received relatively less attention within the context of IGP (Mills & Gorman 1997; Creel & Creel 2002).

We focus on the probability of encounter aspect of predation risk, and particularly the dynamics of this, as influenced by the variation in lion densities and ranging patterns over time. We examined encounter probability at two spatial scales, an intermediate (across pride-range effects) and a smaller scale (within pride-range effects). In addition to varying the spatial scale of assessment, we varied the temporal scale, assessing refugia over six months (wet or dry season), over a calendar year (continuous wet-dry cycle), and over five years (across wet-dry cycles). In the context of a small fenced protected area, our objectives were, first, to examine the inter pride-range variation in probability of encounter. Second, to determine what proportion of annual and long-term pride ranges are potentially constituted by low encounter probability areas for shorter time scales. Third, to quantify range overlap between prides for different time scales. Fourth, to establish the stability of low encounter probability areas within long-term pride ranges for different time scales as affected by range shift. Fifth, to map both the distribution of utilization intensity as well as the distribution of variation in utilization intensity over time for each lion group, and assess its influence on encounter probability. The results are discussed in terms of their potential to create dynamic predation refugia, and what strategies wild dogs could potentially employ to benefit from such variation in probability of encounter.

4.3 Methods

Study site and subjects

Data were gathered from groups of lions in the north-eastern part of HiP, South Africa. The park (28°00′–28°26′S, 31°41′–32°09′E) occupies the foothills of the first escarpment rising above the Southeast African coastal plain and has a varied topography with altitudes ranging from 40 to 590 m.a.s.l.. Annual average rainfall ranges from 979 mm on the higher hills of the north-eastern parts of HiP to 630 mm in the western parts (Pattenden 1988; Balfour & Howison 2002). The predominant vegetation is Acacia-dominated woodland, with forest, grassland, broad-leaved woodland, and thicket communities also present (Whateley & Porter 1983). HiP is completely enclosed by an electrified fence, which is generally effective in containing lions within HiP, with breakouts occurring only sporadically at temporary weak points.

A wide range of ungulates are present in HiP, ranging from the blue duiker (*Philantomba monticola)* to the African elephant (*Loxodonta africana*) (Bourquin *et al.* 1971; Brooks & Macdonald 1983). Major prey species in the diet of HiP lions include, in declining order of frequency: African buffalo (*Syncerus caffer*), nyala (*Tragelaphus angasii*), Burchell’s zebra (*Equus burchelli*), blue wildebeest (*Connochaetes taurinus*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), and common waterbuck (*Kobus ellipsiprymnus ellipsiprymnus*) (Maddock *et al.* 1996). Besides lion and wild dog, other members of the African large predator guild present in HiP include spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), and cheetah (*Acinonyx jubatus*) (Whateley & Brooks 1985). A wild dog pack has been present within the boundaries of our study area since 1980/1, when wild dogs were re-introduced into HiP (Maddock 1999). The minimum complex polygon range (including outliers) of this pack was estimated at 242 km^2 for the period 1993 to 1994, at which time it covered approximately 81% of our study area (Andreka *et al.* 1999).

The HiP lion population arose from a founder group of six individuals in the 1960s and peaked at ca. 140 animals in 1987 (Steele 1970; Anderson 1980; Maddock *et al.* 1996). Subsequently, the population declined and started showing indications of inbreeding depression during the 1990’s (Maddock *et al.* 1996; Stein 1999). In order to address this situation 16 lions were translocated into the existing population in four phases from August 1999 to January 2002 (Trinkel *et al.* 2008).

We used location data from two female prides (Magangeni and Maphumulo prides) and one territorial male coalition (Pilanesberg coalition), which formed part of this translocation. A female pride here denotes a territorial single female or group of females plus offspring (including sub-adult males that have not dispersed), and will from here on be referred to as a pride regardless of composition, i.e. territorial coalition males are not included. Following translocation to HiP, the original members of the above-mentioned three groups were held together for a period, and subsequently released as a single group in August 1999 into the north-eastern part of our study area (Trinkel *et al.* 2008). This area was essentially lion free at that stage, and the intention was that these lions should form a single pride with attendant three-male coalition (Trinkel *et al.* 2008).

The three males split into two groups within a week of release, whereas the two females ranged mostly together for the first six months. The females then split into two single-female prides (Magangeni and Maphumulo prides), which ranged and raised offspring separately until the end of the study in December 2004 (see Table 4.1). The single male (Madikwe male) initially associated with the two females, but ranged with the Maphumulo pride female after the females split up. The remaining two-male group (Pilanesberg coalition) ranged on their own for the first six months after release, before starting to associate with the female of the Magangeni pride. Both coalitions subsequently left these prides and gained tenure in new prides where they had evicted resident male coalitions (Table 4.1). In August 2003, a new three male coalition (Isivivaneni coalition) established tenure over the Magangeni pride which they maintained until the end of the study. During early to mid 2004, the Pilanesberg coalition again started ranging beyond the range of their “second” pride (Nqumeni pride), apparently looking to acquire another pride (which they achieved after the study period; KZNW 2007, unpubl. data).

Field methods

At least one individual in each of the three study groups was collared with a VHF radio collar (Africa Wildlife Tracking) throughout the study period (except for a three month period in 2002 when the Magangeni pride collar was malfunctioning). For fitting or replacing of radio-collars, individuals were captured using a variation of a previously described capture technique (Smuts *et al.* 1977). Lions were located with irregular sampling intervals by conventional radio tracking techniques using Telonics TR-3 receivers and 2-element yagi antennae from a vehicle. Tracking intensity varied among collared individuals and across years but on average an attempt was made to locate each collared individual at least once per week. This was for the most part achieved, except for three periods (ranging from one to three months) when either no field researchers were present or as a result of a malfunctioning collar. A few locations were also collected opportunistically when lions were encountered outside tracking sessions.

Table 4.1. The composition and social status of the Magangeni and Maphumulo prides through consecutive six-month periods from 1999 to 2004 in HiP, illustrating the fluctuation in lion numbers present within ranges over time.

Period	**Magangeni pride**			**Maphumulo pride**		
	# Adults & sub-adults[1]	# Cubs[2]	Coalition presence	# Adults & sub-adults[1]	# Cubs[2]	Coalition presence
Oct 99 – Mar 00	2[3]	0	3 males	n.a.[3]	n.a.[3]	n.a.[3]
Apr 00 – Sep 00	1	0	2 males	1	0	1 male
Oct 00 – Mar 01	1	0	2 males[4]	1	0	1 male[5]
Apr 01 – Sep 01	1	2	0	1	2	0
Oct 01 – Mar 02	1	2	0	1	2	0
Apr 02 – Sep 02	1	2	0	1	2	0
Oct 02 – Mar 03	1	2	0	1	2	0
Apr 03 – Sep 03	3	0	3 males[6]	3	0	0
Oct 03 – Mar 04	3	0	3 males	1	3	0
Apr 04 – Sep 04	2	0	3 males	1	3	0

[1] denotes adult females plus sub-adults of both sexes between two and four years old,

[2] denotes lions between two months and two years old

[3] Maphumulo pride female still ranging with Magangeni pride

[4] Pilanesberg coalition abandoned tenure over pride during second half of January 2001, moved southwest and established tenure over the Nqumeni pride (range: 6-9 adults & sub-adults), which was not included in this analysis since a female in this pride was only collared in February 2004.

[5] The Madikwe male was closely associated with the Maphumulo pride until he abandoned tenure over this pride in April 2001, moving out of our study area, and is not analysed separately.

[6] During July 2003 the Maphumulo pride female and her two sub-adult male offspring briefly associated with the Magangeni pride when one of these females came into oestrus. Subsequently, the Isivivaneni coalition established tenure over the Magangeni pride in August 2003. None of these coalition males were collared and thus could not be analysed separately.

When an individual was visually encountered, a geographical location was determined with a handheld Geographical Positioning System (Garmin). When individuals remained out of view, locations were determined from 1:50000 topographical maps of the park by triangulation with at least 3 different bearings, as well as taking into account the topography of the terrain and the boundary of the park. Individuals were never further away than 3 km from such triangulation positions (as dictated by the road and management track coverage and boundary of this part of HiP). Number of individuals, composition, and reproductive status were recorded when groups were seen during tracking, capture attempts, and opportunistic sightings. Estimates of the proportion of time that prides were accompanied by coalition members during their tenure period over the pride, were derived from triangulations and sightings of individuals. These association estimates (%) were calculated by dividing the total number of times that a pride was located by the number of times that a coalition member was with the pride.

Spatial analysis

A total of 361, 436, and 343 locations, for the Magangeni, Maphumulo and Pilanesberg groups, respectively, which spanned the period from October 1999 to the end of September 2004, were used in the spatial analyses. All these spatial analyses outlined below were conducted within ArcGIS 9.1. Ranges and cores were calculated with the Abode tool via kernel density estimation (KDE) (Laver 2005), which gives a probabilistic estimation of the utilization distribution of an individual within its range (Worton 1989). For the KDE, a biweight kernel function with fixed smoothing parameter (*h*) was used. The 50% and 95% volume contours generated from each KDE calculation were operationally defined to contain the "core" and the "range", respectively, although we do not necessarily imply that these actually represent true home ranges or cores. In order to reduce spatial autocorrelation, locations used in the analysis were separated by at least one complete movement period (i.e. one night) (Spong 2002).

Mean daily displacement distance (MDDD) as an alternative to least-squares cross validation (LSCV) was used to calculate *h* (Laver 2005), where daily displacement distance represents the Euclidean distance between two consecutive locations separated by one day. Recent work had indicated several problems with LSCV (Hemson *et al.* 2005), and the MDDD method had independently been proposed to be a useful and biologically relevant substitute for LSCV (Laver 2005). Initial examination of our data also revealed that MDDD performed better than LSCV at producing representative ranges for the lion groups. Since irregular sampling intervals were used during the study, a limited number of daily displacement distances could be calculated each year. In order to increase sample sizes and to enable cross season and year comparison, a single *h* was calculated from the complete dataset of each lion group. These *h* values of 1731 for the Magangeni pride, 1984 for the Maphumulo pride, and 2087 m for the Pilanesberg coalition were then used to calculate all cores and ranges for the respective groups.

Firstly, for each group we calculated six-month cores and ranges for the wet (October – March) and the dry (April – September) seasons separately for each year. Then, we calculated annual cores and ranges for each group for a continuous wet and dry period, i.e. one year starting in October and ending in September of the next calendar year. Finally, we calculated five-year cores and ranges for each group using the complete datasets. As some cores and ranges overlapped with the HiP boundary these external areas were removed (by clipping) to yield areas contained within HiP (none of the radio-collared lions were ever located, or reported to be, outside the HiP boundary fence).

We examined the variation in range size and corresponding lion density within and between prides over time. For each group, we calculated mean and standard error for range and core sizes for the annual and six-month periods, but only one range and core size was available for the five-year period. These, and all following descriptive statistics, were performed in STATISTICA 6.1 (Statistica 2003). For each of the six-month periods we also knew the number of lions present within both pride ranges. Using these, we calculated densities of lions within each six-month range for both prides by dividing the total number of adult and sub-adult females as well as coalition males present within the pride ranges by the corresponding range sizes.

Any area within a long-term group range, that is unused for a particular period by that group, potentially constitutes a low encounter probability area, and could function as a temporary dynamic refuge from lions, if it is also unused by other lions. To determine the magnitude of such potential refugia at the six-month (seasonal) scale as created by the ranging characteristics of each group, we defined what percentage of an annual group range was unused by the corresponding group during the dry or wet season. We divided each wet and dry season range by its corresponding annual range. A mean from these two values was then calculated for each annual period, and an overall mean from all the annual means was then derived. To determine relative unused range at the annual scale, we divided the mean annual range sizes by the size of the overall five-year ranges of the three groups.

Range overlap between neighbouring prides has been shown for some ecosystems, and could influence the amount of low encounter probability space within the long-term range of a pride during any shorter seasonal or annual period. Accordingly, for each separate six-month, annual, and five-year period we calculated the size of the area overlapped by the ranges of both prides. Mean size of overlap was calculated from all values for the six-month and annual scales (including zero values for no overlap), whereas the five-year ranges yielded a single value. The percentage of each pride range covered by the overlapping area from the corresponding period was calculated by dividing the overlap size by the range size for that period for each pride. The mean percentage of each pride range covered by an overlapping area was calculated from the above percentages of range overlap for each pride for the six-month and annual scales (including zero values for no overlap), whereas the five-year ranges yielded a single value.

We assessed the spatial stability of potential low encounter probability areas within group ranges, which may be affected as a result of range shifts between periods, at two different time scales. We calculated the size of the section of the first period range remaining unused during the consecutive period range for each consecutive six-month range pair, and similarly for consecutive annual range pairs. These emerging unused, or low encounter probability areas, were then divided by the total area of the first period range to yield percentage of the first range becoming unused during the consecutive period. The means of these percentages were then calculated for the six-month and annual scales (larger percentages indicate greater range shift, and thus increased spatial instability of low encounter probability areas within a long-term group range across time).

The above calculations give an idea of the potential size of dynamic refugia for various time-scales. Additionally we attempted to characterize locations which could potentially function as dynamic refugia within long-term pride ranges in terms of long-term utilization intensity as well as variation in utilization intensity over time. To represent long-term utilization intensity across space for each group, we generated five-year utilisation distribution maps for each group. Here we used the KDE methodology, as for the range and core calculations above, to generate 10, 30, 50, 70, 90, and 95% (volume) utilization distribution contours (Laver 2005). Ideally here, the utilization distribution patterns of all lion groups should be integrated into a single surface, however, systematic radio-tracking location data were not available for two lion groups which also used the study area during the study, and consequently, we calculated utilization distribution patterns for each group individually. Given that lions may alter their utilization distribution over time, in order to investigate the variation in utilization intensity over time, we calculated the Standard deviation in utilization intensity for each grid cell (grid cell size: 100 x 100 m) from the annual utilization distribution rasters for each group. These annual utilization distribution rasters were also created with the Abode tool (Laver 2005). Standard deviation was calculated with the Cell Statistics function in ArcCatalog 9.1, and was simply used as an index of variation over time at a given location, which consequently allowed us to map the spatial fluctuation in the magnitude of the variation of utilization intensity.

4.4 Results

During his tenure period, the Madikwe male was with the Maphumulo female most of the time when she was located (92.8%). The association calculation for the collared Pilanesberg male and Magangeni pride female was 50% (sighting and triangulation locations combined; association percentage for sightings was only 2.4% less than for triangulations). For the uncollared Pilanesberg male, who fathered the 1st set of cubs of the Magangeni female, this value was 69.7% (sighting locations only).

The combined five-year ranges of all three groups nearly completely covered our study area in the north-eastern part of HiP (Fig. 4.1). The Magangeni pride had substantially smaller ranges than the Maphumulo pride at all time scales, and this was especially pronounced at the five-year scale (Table 4.2). We found a similar pattern between the cores of the two prides. The large core and range size differences between the prides at the five-year scale is probably the result of the Maphumulo pride having access to a largely lion free space allowing them to adjust their ranging patterns over time. Contrary to this, the range of the Magangeni pride was surrounded by fences on three sides and by the range of the Maphumulo pride on the fourth. However, the Maphumulo pride still had substantially larger annual ranges, which may indicate that the smaller Magangeni pride ranges covered an area of higher lean season prey biomass as predicted by earlier studies (Van Orsdol *et al.* 1985; Hemson 2003). Both prides showed considerable variation in range size as reflected by the standard error; however, this variation was larger for the Maphumulo pride. To generalise, one pride tended to range over relatively large, but more variably sized areas, and the other over relatively small and less variable areas.

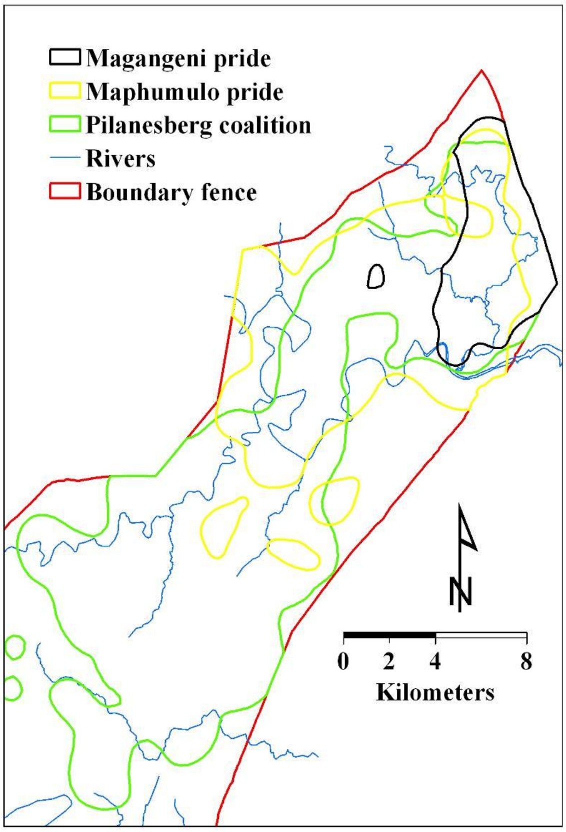

Fig. 4.1. Area used by the three lion study groups in the north-eastern part of HiP over the five-year study period. We display the five-year ranges (95% volume contours). Note the small size of areas unused by lions in this part of HiP. The south-western part of the Pilanesberg coalition's range was also used by a separate pride (Nqumeni pride) under their tenure (not analysed in this study).

Table 4.2. The mean (±SE) fixed Kernel density estimation range and core sizes (95% and 50% volume contours) for six-month, annual and five-year scales for the Magangeni and Maphumulo prides and the Pilanesberg coalition in HiP. Note the variation within and between these time scales as well as between the groups.

	Prides				**Coalition**	
Time scale	**Magangeni**		**Maphumulo**		**Pilanesberg**	
	95% Range (km^2)	50% Core (km^2)	95% Range (km^2)	50% Core (km^2)	95% Range (km^2)	50% Core (km^2)
Mean (±SE) six-month	23.9±2.3	6.1±0.5	43.8±6.8	10.9±2.9	61.6±7.9	17.3±2.6
Mean (±SE) annual[1]	29.1±4.3	6.7±0.8	57.9±7.9	12.7±2.6	96.9±11.4	26.4±4.2
Five-year	34.9	7.2	117.8[2]	23.7	223.8	55.1

[1] includes consecutive wet & dry seasons starting in October and ending in September of the next year

[2] only from February 2000 (post female split up)

The coalition cores and ranges were substantially larger than those of the prides at all time scales (Table 4.2). Variation in range and core size of the coalition for six-month and annual periods (except for six-month core) was also larger than those of the prides (Table 4.2). At both the annual and five-year scale, pride cores were mostly continuous, whereas the coalition had multi-modal cores separated in space. The larger range size and multi-modal core of the coalition at the five-year scale, compared to the prides, is clearly related to their repeated acquisition and desertion of tenure over prides, as found elsewhere (Schaller 1972; Pusey & Packer 1987; Funston *et al.* 2003).

Densities of lions within the respective six-month pride ranges varied substantially over time and between prides (see Table 4.3). Although the number of adults and sub-adults in one pride equalled the number in the other pride for most of the time (seven of the nine six-month periods after the females had split up), variable coalition attendance led to differences in the amount of animals present within the respective six-month pride ranges (Table 4.1). This pattern, in combination with the smaller ranges of the Magangeni pride, lead to substantially higher densities within the ranges of this pride (Table 4.3). The differences in lion density between the six-month ranges of the two prides may have been slightly less than calculated here, as the Pilanesberg coalition did use parts of the Maphumulo pride six-month ranges during two out of nine seasons (post Maphumulo pride split-off). Also, the Isivivaneni coalition traversed the Maphumulo pride range to reach the Magangeni pride range before gaining tenure over the latter pride. However, these temporary range overlaps were not to the extent where they would significantly influence the above density patterns.

Table 4.3. Mean (±SE) lion density (including adult and sub-adult, male and female) within the six-month pride-ranges of the Magangeni and Maphumulo pride. This illustrates the variation in the potential probability of encounter within ranges over time and across ranges for a given period.

	Density (lions/100 km^2)	
Period	**Magangeni**	**Maphumulo**
Oct 99 – Mar 00	23.0	–[1]
Apr 00 – Sep 00	14.5	3.9
Oct 00 – Mar 01	18.1	2.6
Apr 01 – Sep 01	5.4	3.3
Oct 01 – Mar 02	–[2]	3.2
Apr 02 – Sep 02	4.4	2.8
Oct 02 – Mar 03	4.7	2.4
Apr 03 – Sep 03	21.8	4.0
Oct 03 – Mar 04	23.1	4.6
Apr 04 – Sep 04	12.4	3.4
Mean (±SE)	14.2±2.6	3.4±0.2

[1] Maphumulo pride female still ranging with Magangeni pride
[2] insufficient spatial data as a result of malfunctioning collar

Increase in range size with increasing time scale occurred for both prides and the coalition; however, this was much more pronounced for the Maphumulo pride and the coalition (Table 4.2). Proportionately similar amounts of low encounter probability space remained available within the annual ranges of both prides at the six-month scale (Table 4.4). The proportion of low encounter probability space remaining available within the five-year range at the year scale differed substantially between the two prides. Compared to the six-month vs. annual range ratio, the proportion doubled for the Maphumulo pride, but remained approximately the same for the Magangeni pride (Table 4.4). The coalition used proportionately less of the mean annual range at the six-month scale compared to the prides, with the proportion of range represented by low encounter probability areas nearly double that of the pride mean (Table 4.4). A similar pattern was obtained for the coalition when comparing the mean annual range to the five-year range (Table 4.4). Since the above three groups had largely divergent range sizes at all time scales (Table 4.2), all the above proportions necessarily translated into different sizes of potential low encounter probability areas.

Table 4.4. The mean percentage of the annual ranges of the three lion groups remaining unused by the corresponding group at the six-month scale, and the mean percentage of the five-year ranges of the three lion groups remaining unused by the corresponding group at the year scale. This indicates the proportional size of potential dynamic refugia (percent of range unused) at six-month and annual time scales.

	Unused Range (95% KDE) (% of the longer period unused during shorter period)			
	Prides			**Coalition**
Ratio	**Magangeni**	**Maphumulo**	**Pride mean**	**Pilanesberg**
Annual to six-month	17%	22%	19.5%	36%
Five-year to annual	17%	51%	34%	57%

Range overlap patterns between the two prides showed increasing overlap size with increasing time-scale (Table 4.5). However, since the two prides had largely divergent range sizes at all time-scales, these overlaps represented substantially different proportions of each pride range on average. The Magangeni pride shared more than double the percentage of its ranges at the six-month and annual scale, and more than three times at the five-year scale, with the Maphumulo pride (Table 4.5). The different levels of overlap indicate that the potential size of low encounter probability areas within the Magangeni pride range is substantially reduced, whereas this reduction occurs only to a smaller degree within the Maphumulo pride range.

Table 4.5. The mean (±SE) size of the overlapping area between the ranges of the Magangeni and Maphumulo pride, and the mean percentage that this represents of the corresponding ranges of each pride for the six-month, annual, and five-year scales (single value for five-year), indicating the increasing overlap size with increasing time-scale.

		Mean percentage of pride range	
Time scale	**Mean size (km^2)**	**Magangeni**	**Maphumulo**
Six-month	6.2±2.7	27%	11%
Annual	9.5±5.2	33%	14%
Five-year	25.1	72%	21%

All three groups showed varying degrees of range shift from one six-month period to the next (Table 4.6), as also partly predicted by range size increases from the six-month to year scale. Seasonal range shifts by the Magangeni pride resulted in an average of 22% of a current six-month range not being used during the following six-month period (Table 4.6). For the Maphumulo pride this percentage approximately doubled as a result of large seasonal range shifts (Table 4.6). In comparison to the pride mean, the Pilanesberg coalition showed a further increase in this percentage, as a result of even larger seasonal range shifts (Table 4.6). For both prides, the average percentage of an annual range not being covered by the range of the following year increased in comparison to that of the six-month ranges (Table 4.6). The

Pilanesberg coalition showed an opposite trend in this regard, although their average percentage for the year scale was still larger than the pride mean (Table 4.6).

The utilization distribution maps for all three groups showed similar patterns to the range and core, as well as range shift results (Fig. 4.2, p. 53). The Magangeni pride had a near uni-modal pattern of space-use (except for a single free standing area from the main range), with intense utilization at the centre of the range (Fig. 4.2a), whereas the Maphumulo pride (Fig. 4.2b) and Pilanesberg coalition (Fig. 4.2c) showed clear multi-modal space use over larger areas.

Table 4.6. The mean percentage of a current range which fell outside the range of the following period as a result of range shifts for the three lion groups between consecutive six-month ranges as well as between consecutive annual ranges within HiP. This indicates potential newly available dynamic refugia as a result of range shifts, at different temporal scales.

	Mean % of current range which fell outside the range of the subsequent period			
	Prides			**Coalition**
Time scale	**Magangeni**	**Maphumulo**	**Pride mean**	**Pilanesberg**
Six-month	22%	47%	34.5%	56%
Annual	29%	50%	39.5%	46%

The Maphumulo pride and Pilanesberg coalition also had considerably larger magnitudes of variation in the utilization intensity (Fig. 4.3b, c, p. 54), compared to the Magangeni pride (Fig. 4.3a). These patterns agree with the large annual range shifts of the first two groups compared to the more stable annual ranges of the third group. The magnitude of the variation in annual utilization intensity also fluctuated spatially (Fig. 4.3). For all three groups, five-year cores tended to be associated with higher levels of variation in annual utilization intensity (Fig. 4.3). However, high levels of variation were not restricted to the cores and were also found outside of these, at the edges of ranges. In other words, the level of variation in utilization intensity over time also varied spatially, and higher variation was not strictly correlated to the higher or lower utilization distribution contours of the five-year ranges.

4.5 Discussion

The combined five-year ranges of all three lion groups nearly completely covered our study area, indicating that over longer periods only a few small areas could function as spatially stable or absolute refugia within which wild dogs, or other species, could always find a nearly zero likelihood of encountering lions. Such small lion free areas, as also found within other fenced small protected areas (Van Dyk & Slotow 2003), are not adequately sized to support a single wild dog pack (Lindsey *et al.* 2004). This may necessitate wild dogs to continually search out areas with low probabilities of encounter within long-term lion ranges, suggesting that predation refugia might be present within such areas, but that these refugia probably have more of a dynamic spatio-temporal nature, and less of a static habitat-based nature (Mills & Gorman 1997; Creel & Creel 2002).

At the short time-scale, lion density, and thus encounter probability, within neighbouring pride ranges may differ substantially from each other, and fluctuate independently over time as shown by our results. Such density variations appear to be driven by both independent seasonal range size fluctuations and decoupled local demographic processes, including variable coalition attendance/absence (Funston *et al.* 2003), as well as within-pride breeding synchrony in combination with aseasonal reproduction of the population as a whole (Bertram 1975; Packer & Pusey 1983b).

However, increased density within a pride range, resulting from coalition attendance, may not necessarily increase the probability of encounter. This probability will only increase over that of an unattended pride range at similar density if the coalition to some extent moves separately from the female(s) (i.e. at any given point in time there may be two locations instead of only one where lions could be encountered within the range). This was the case when the two-male Pilanesberg coalition held tenure over the Magangeni pride, as indicated by their association percentages. The Maphumulo pride, however, was mostly accompanied by the Madikwe male during his tenure.

The above pattern may imply that coalition size could influence territorial male-female association; however, more data are needed to test this relationship. Funston *et al.* (1998) investigated the relationship between male-female association and a range of variables (excluding coalition size) across several African ecosystems, and found that this association was strongly influenced by vegetation structure. In open systems, territorial coalitions were more likely to be encountered with pride females, whereas in more wooded areas males associated less with females (Funston *et al.* 1998). Inter-pride variation in the probability of encounter as a result of density effects may thus be further altered via the effect of vegetation structure and coalition size on coalition association with prides.

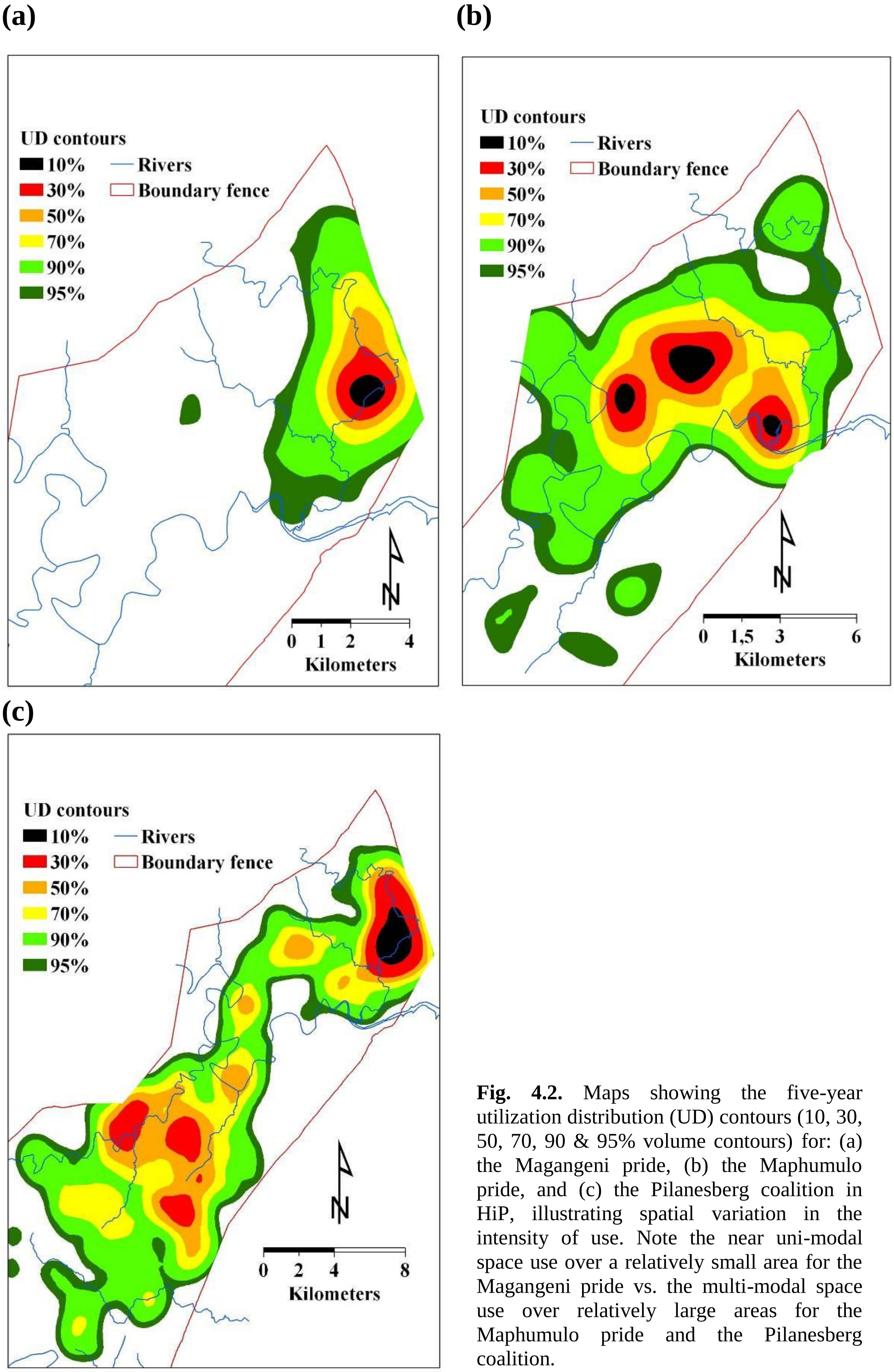

Fig. 4.2. Maps showing the five-year utilization distribution (UD) contours (10, 30, 50, 70, 90 & 95% volume contours) for: (a) the Magangeni pride, (b) the Maphumulo pride, and (c) the Pilanesberg coalition in HiP, illustrating spatial variation in the intensity of use. Note the near uni-modal space use over a relatively small area for the Magangeni pride vs. the multi-modal space use over relatively large areas for the Maphumulo pride and the Pilanesberg coalition.

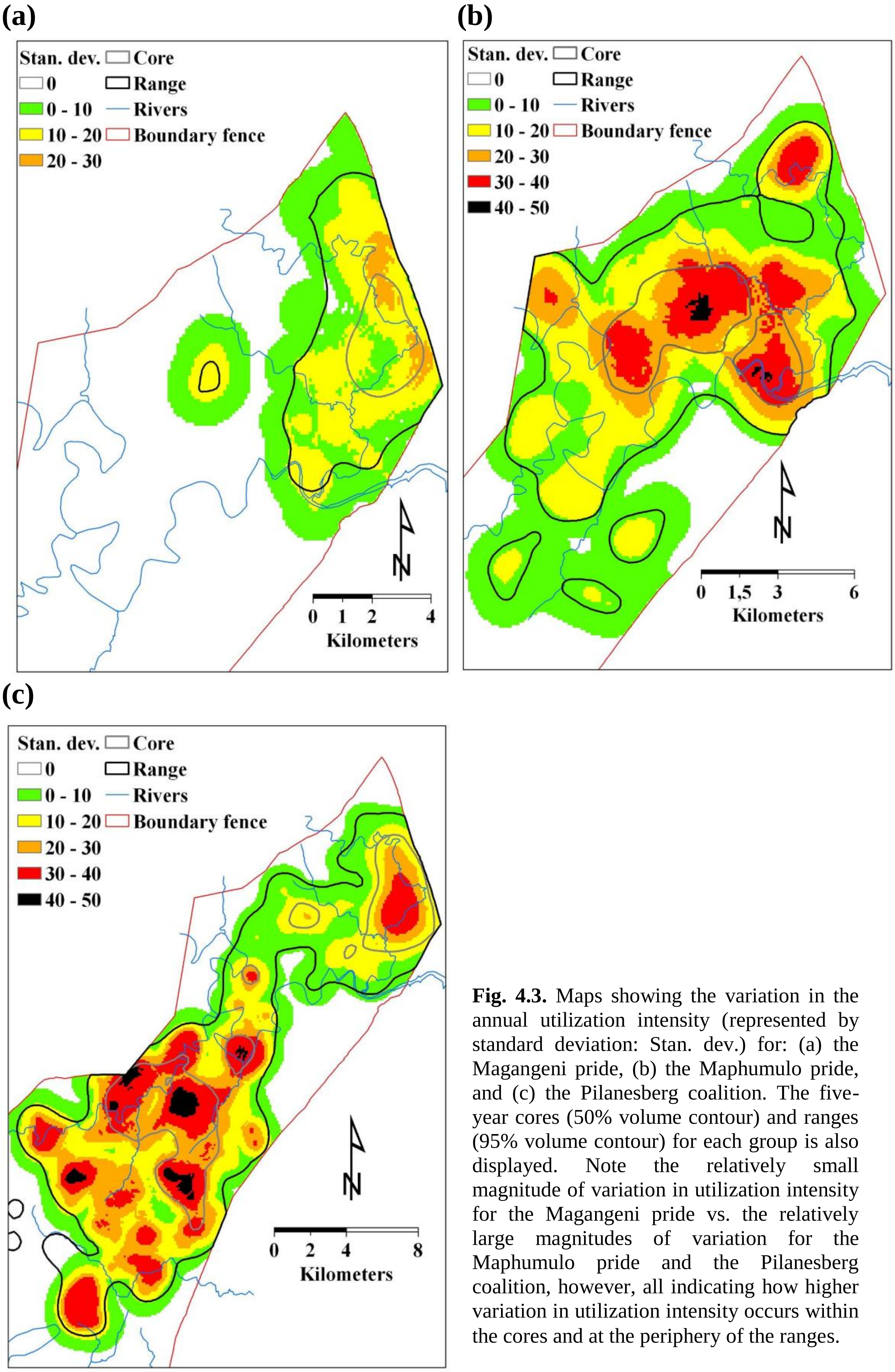

Fig. 4.3. Maps showing the variation in the annual utilization intensity (represented by standard deviation: Stan. dev.) for: (a) the Magangeni pride, (b) the Maphumulo pride, and (c) the Pilanesberg coalition. The five-year cores (50% volume contour) and ranges (95% volume contour) for each group is also displayed. Note the relatively small magnitude of variation in utilization intensity for the Magangeni pride vs. the relatively large magnitudes of variation for the Maphumulo pride and the Pilanesberg coalition, however, all indicating how higher variation in utilization intensity occurs within the cores and at the periphery of the ranges.

Analogous to the above consideration, at equal densities, pride ranges containing larger prides will only show increased probability of encounter above those of smaller prides, if individuals or sub-groups range separately. Larger lion prides do in fact exhibit “fission-fusion” behaviour, where members may range apart for varying lengths of time (Schaller 1972; Pusey & Packer 1987; Spong 2002). Although not represented in this study, at equal densities, the ranges of larger prides should be avoided in response to this fission-fusion ranging behaviour, which should increase the probability of encounter within such a range.

From the above multiple neighbouring prides perspective, territoriality in lions in effect creates a mosaic of pride ranges across the landscape, which may remain relatively stable over long periods (Pusey & Packer 1987; Funston *et al.* 2003). The approximate resolution of this mosaic within any ecosystem will be roughly equal to the average pride range size in a system. This spatial structuring of a lion population into a mosaic of pride ranges, in combination with the above-outlined variation in encounter probability across pride ranges, may contribute towards the co-existence of wild dogs and lions. Since wild dog pack ranges are significantly larger than matching lion pride ranges within most ecosystems where they co-exist (Skinner & Chimimba 2005), wild dog pack ranges will generally overlap several neighbouring pride ranges or parts thereof. As a result of their high mobility (large daily movements) and large ranges (Creel & Creel 2002), wild dog packs could exploit this inter-pride variation by switching between these ranges as their probabilities of encounter change. Although following a habitat centred instead of pride-range centred approach, Mills and Gorman (1997) showed that wild dogs in Kruger NP indeed occurred at their highest density in habitats least favoured by lions, even though these contained low densities of wild dog prey. Further, wild dogs in Pilanesberg NP adjusted their ranging area in response to changes in the lion population (Van Dyk & Slotow 2003).

At a smaller spatial scale within long-term pride ranges, variation in encounter probability across space for short or intermediate time scales, will depend on what proportion of their range lions use at these scales. Given the mean daily displacement distance found for the two prides in this study, these prides could easily cover their five-year ranges within a few days or weeks. However, daily displacement did not translate into rapid range size increases with time in this study. After six months, areas within the annual range still remained unused, and especially so relative to the five-year ranges. This effect varied between the prides, where the pride with a relatively small five-year range did not show much range size increase beyond the year scale. In the wider-ranging pride, however, the large unused areas within the annual and five-year ranges could function as short or intermediate term dynamic refugia (Hochberg & Holt 1995; Berryman *et al.* 2006), with lower probabilities of encounter.

These “unused” areas within the long-term ranges of prides may, however, be used by neighbouring prides. In our study, the two prides did show range overlap at all three time scales, but the patterns were largely divergent for both prides. The level of range overlap for the smaller-ranging pride, at the short and intermediate time-scale, would probably significantly reduce the amount of unused space within its long-term range. Opposed to this, the small level of range overlap, at the short and intermediate time-scale, would have little effect on unused space within the long-term range of the wider-ranging pride. This pattern further reinforces the above prediction that the unused areas within the long-term range of the wider-ranging pride could function as dynamic refugia.

The stability of the above-mentioned short- and intermediate-term dynamic refugia within the long-term range will depend on the amount of range shift undergone by the pride between periods and at what time scale this shift is most pronounced. Here, the wide-ranging pride showed substantial and constant range shift compared to the pride with smaller range, especially at the annual scale. This indicates that the above dynamic refugia within the long-term range of the wide-ranging pride, and to a lesser degree in the other pride range, are spatially more stable at the seasonal than annual scale. The large difference in range shifts between the two prides is probably related to the fact that the wide-ranging pride had access to a large area unoccupied by other prides. This potentially allowed the pride to continually adapt to changing prey distributions in order to enhance their foraging success. However, some of the range shifts of the wide-ranging pride coincided with certain life history and social events, such as the birth of cubs and the arrival of a new coalition (Isivivaneni coalition) in the area. Thus, it appears that in conjunction to having access to this larger pride-free space, some range shifts seem to be driven by socio-biological factors rather than by ecological factors.

If the probability of encountering a lion is considered in terms of the utilization distribution within pride ranges, wild dogs should select areas with low utilization intensity more often, i.e. areas which may be seen as equal to either less selected habitats (Mills & Gorman 1997; Creel & Creel 2002) or dynamic refugia (i.e. temporally “unused areas”). Alternatively, in terms of utilization distribution, wild dogs should avoid pride core areas (highly selected habitats) with a higher probability of encounter (Mills & Gorman 1997; Creel & Creel 2002). However, we further predict that over time wild dogs should more often utilize sections with low levels of variation in utilization intensity within the above-mentioned low utilization intensity areas, i.e. areas which across time are consistently used at a low level. In the Selous GR, although wild dogs selected for habitats less preferred by lions, completely remaining within such areas would have lead to unsustainable increases in foraging effort as a result of reduced prey encounter rates within this habitat (Creel & Creel 2002). Thus, in order to meet their high energy demands (Gorman *et al.* 1998), wild dogs may from time to time have to use areas within the highly utilized parts of lion ranges as well (Creel & Creel 2002). In our study, even within the long-term core of the smaller-ranging pride, there were high levels of variation in utilization intensity over time, and thus temporal variation in probability of encounter within the long-term core. Although such areas probably could not be considered dynamic refugia, they could be intermittently utilized by wild dogs to potentially increase their prey encounter rates (Creel & Creel 2002).

Wild dogs may have access to various types of lion information, which they could use to reduce their risk of encountering lions. Lions reveal their approximate locations nightly by roaring and their recent locations by scent marking (Schaller 1972; Grinnell & McComb 2001). The use of interspecific scent identification, as a cue to reduce interference interactions experienced by a subordinate guild member, has been demonstrated for mammalian predators (Erlinge & Sandell 1988). If wild dogs further possess the numerical assessment of roaring which lions do (McComb *et al.* 1994; Grinnell & McComb 1996), as is likely for a highly social species such as wild dogs, they may even obtain information on lion group size. Furthermore, wild dogs potentially could also identify the sex of a roaring lion, as lions in fact do (Grinnell & McComb 1996, 2001). If wild dogs have an understanding of the numerical and social composition of several local lion groups, which fall within their range, they could use such cues in a hierarchical manner in order to ideally respond to the information they contain. Firstly, over time the location and social information may reveal the rough membership and range of a pride to wild dogs. Secondly, the numerical and social information may reveal which pride ranges currently contain a higher probability of encounter. Thirdly, within a range, location information may become more important in finding areas with the lowest probability of encounter, or at least avoiding areas with the highest probability of encounter.

We have demonstrated with data on density patterns and different types of group ranging behaviour, that variation in these parameters at different spatial and temporal scales may lead to the creation of dynamic refugia (Hochberg & Holt 1995; Berryman *et al.* 2006). We interpreted these data in terms of encounter probability in the context of intraguild predation on endangered wild dog, and illustrated that there are variably sized areas with different levels and variation of predation risk. First, potential absolute refugia existed outside of lion long-term ranges, which were fairly small but temporally and spatially highly stable. Second, relatively larger, low encounter probability areas occurred within the long-term range of the wider ranging pride. Such areas could in fact function as dynamic refugia. These dynamic refugia should be available to other subordinate predators, as well as to prey species that can spatially shift their ranges over the short and medium term. The extent to which a group or individual of any species could use such spatial and temporal variation to its own advantage, will be constrained by its own ability to move over larger distances, and how fast it can do so.

We recommend that our analyses be extended to shorter periods (week, month, and three month periods) via the use of high volume location data from satellite telemetry devices. Our preliminary results should be tested in other potentially more complex systems, and that the responses of the other species be integrated against lion density and ranging patterns to understand if such potential dynamic refugia are actually used as we predict. The ideas emerging from this study are similar to those indicated by recent predator-prey work, which suggests that groups, rather than individuals, are the basic units around which predator–prey interactions of social species should be modelled (Fryxell *et al.* 2007). Our work further adds to this concept, in that not only group formation of intraguild predator and prey may lend stability to such interactions, but the spatial spacing mechanisms of predator populations, such as territoriality, as well.

Chapter 5

Conclusion and Management recommendations

5.1 Synthesis

Recent empirical work and meta-analyses have addressed several evolutionary and ecological aspects related to co-existence within species-rich predator guilds, including character displacement and niche segregation (McDonald 2002), interspecific body size-ratios and intraguild predation (Palomares & Caro 1999; Donadio & Buskirk 2006), and intraguild spatial and temporal relationships (Durant 1998). Seminal work by Polis and Holt (Polis *et al.* 1989; Polis & Holt 1992; Holt & Polis 1997) and recently others (see special feature in *Ecology* volume 88, issue 11) has also provided a firm theoretical framework for the population biology of species-pairs involved in competition and predation interactions. Nonetheless, in the context of wild dog, lion and hyaena co-existence, questions still remain regarding the relationship between certain aspects of wild dog behavioural and population ecology, and direct intraguild interactions with lion and hyaena (Creel & Creel 2002; Woodroffe *et al.* 2007). Similarly, in the context of HiP the question remains as to what mechanisms have resulted in the adequate reduction in the frequency of hyaena interference and lion predation experienced by wild dogs, in order for these interactions not to affect wild dog demographic parameters in HiP. This thesis has in part described one aspect, which needs consideration within the above question. This aspect is the spatial and temporal variation in probability of encounter, and its main drivers, namely density and utilization intensity.

The results of chapter 3-+ demonstrate substantial spatial variation in hyaena density at a relatively small scale for short periods of time. The hyaena density maps for both the 2003 and 2004 series revealed several low density and high density patches. Some of these patches overlapped across the two series; however, most were differently aligned in space, indicating the dynamic nature of hyaena probability of encounter across the landscape. Owing to their ability for large daily movements (Creel & Creel 2002) and the size of these patches in relation to these movements, wild dog packs may easily and completely inadvertently move into either high or low density patches. By purely reacting to the amount of interference interactions they experience at any location, wild dog packs may use this variation in probability of encounter adaptively to their benefit. Two potential mechanisms could be used in this regard: the continuation of long distance daily movements when interference is experienced at kills (until interference decreases), or alternatively by reducing the distance moved and remaining in the same area when minimally interfered with.

Other mechanisms may also have lead to a natural lowering of wild dog-hyaena encounter frequency in HiP. Several authors have compellingly argued for a reduction in interference interactions at kills made in wooded habitats in comparison to open ones (Creel & Creel 1996; Creel 2001; Creel *et al.* 2001; Dominguez-Rodrigo 2001; Creel & Creel 2002; however see Hunter *et al.* 2007a). This is mainly driven by the significantly increased distance across which visual information is available to a recipient in open and flat environments (open savannah, grasslands, deserts, etc.) compared to heavily wooded and/or topographically varied environments (woodlands, forests, mountains, etc.). For a wild dog pack on a kill this means that with increasing "information distance" an exponentially increasing "information area" is created (the surface of a circle increases exponentially with increase in radius). The "information distance" will of course have a limit correlated with the distance limit of the average hyaena's visual perception. Within this limit however, an exponentially increasing "information area" will on average contain an exponentially increasing number of hyaenas,. Thus increasing "information distance" has two main effects. First, the average probability that the wild dog kill will be detected will increase exponentially with distance, since the number of hyaena eyes has increased exponentially. Second, the total potential number of hyaenas which may be drawn into the kill following detection will on average increase exponentially with distance as well. Both these factors may lead to an exponentially increasing number of hyaenas being drawn in to the kill. This in turn could lead to a rapid increase in the hyaena to wild dog ratio at a kill, beyond a threshold which wild dogs can defend, and may result in the loss of their kill (Fanshawe & FitzGibbon 1993).

Two factors may, however, alter the costs or benefits experienced in either type of environment. First, for open environments, visual information is theoretically also available over the same area for wild dogs, assuming equal visual abilities for both species. Wild dogs are usually highly alert at kills (Creel & Creel 2002), and any advance information may be useful in reacting to a possible interference threat from hyaenas. Kruuk (1972; also pers. obs.) noted hyaenas often use the element of surprise in order to run into a feeding pack of wild dogs and steal a kill (or part thereof) from the pack. If however, a hyaena is noticed by the wild dogs before running in, the element of surprise is lost, with potential benefits for the dogs. Second, except for extreme situations, audial information distance for wild dogs is probably less reduced in woodland in comparison to visual information distance. Wild dogs often utter typical vocalizations just before making a kill and during feeding (Kühme 1965; Robbins 2000). This noise may attract hyaenas in wooded environments, which otherwise would not have detected the wild dogs and their kill visually (pers. obs.; also observed for lions), and in turn could negatively offset the benefits of wooded environments in terms of reduced visual information. Hyaena-wild dog fighting at carcasses also sometimes attracts lions (pers. obs.), indicating how audial information generated by interference interactions can escalate a potential energetic loss into a mortality risk.

The results of chapter 4 demonstrated substantial spatial and temporal variation in lion density and utilization intensity, and thus lion encounter probability, across and within lion ranges. Both prides only partially used their long-term ranges at shorter time scales, and so inadvertently generated low encounter probability areas, especially at the seasonal scale. This effect was partly reduced by range overlap, particularly for the pride with smaller ranges. In addition, the levels of utilization intensity as well as variation in utilization intensity were not evenly distributed within long-term pride ranges. Analogous to the spatial shifts in hyaena low density patches across time, the two prides also displayed range shifts across seasons and years, and temporal variation in utilization intensity. As for hyaena low density patches, wild dogs may attempt to reduce their lion predation risk by using such low encounter probability areas, and adjust this use as these areas change over time.

However, if wild dogs do indeed have the capability of functionally “eaves-dropping” on lion communication as suggested in chapter 4, wild dogs may in fact pro-actively respond to lion predation risk, instead of reactively as hypothesized for hyaena interference risk. Opposed to reactive hyaena interference risk reduction, pro-active lion predation avoidance may be more feasible for two reasons. Firstly, lion density is generally lower than hyaena density, including within HiP (Creel & Creel 2002). Secondly, since hyaena clans on average are substantially larger than lion prides, and hyaena foraging group size is similar or smaller than lion (sub-)group size, at least for HiP (Whateley & Brooks 1978; Whateley 1981; Whateley & Brooks 1985; Skinner *et al.* 1992; Trinkel *et al.* 2007; chapter 4), the number of independently ranging hyaena sub-groups (foraging groups) within a clan territory, should be higher than the number of lion sub-groups within a pride territory. At a fixed spatial scale, this may lead to a higher clustering of lions vs. hyaenas in space (see also Creel & Creel (1996; 2002)).

Consequently, even though hyaenas may also partially indicate their numbers and locations via vocalisations (Kruuk 1972; Mills 1990), it should be easier for wild dogs to spatially predict lion predation risk as opposed to hyaena interference risk. Nonetheless, the above suggests that the idea emerging from chapter 4, as recently indicated by predator-herbivore interaction work (Fryxell *et al.* 2007), which proposes that groups are the basic units around which direct intraguild interactions of social guild species should be investigated, may also apply to hyaena-wild dog interactions. This however, would only be applicable to ecosystems where average hyaena foraging group size is two or more. Similarly, the potential for lion territoriality to stabilize lion-wild dog interactions, could also emerge from hyaena territoriality, in that wild dog packs may also switch between hyaena territories covered by their ranges, as the densities of hyaenas (or hyaena foraging groups) fluctuate between these territories over time.

A reduction of hyaena and lion encounter probability may of course also be facilitated by temporal niche segregation on a daily scale (Rautenbach & Nel 1978; Mills & Biggs 1993). Although based on small sample size, Saleni et al. (2007) indicated a significant separation in the daily activity patterns of wild dogs and hyaena, as well as wild dogs and lions, occupying overlapping ranges in HiP. A recent meta-analysis of the daily activity patterns of all African large predator guild members across East and southern Africa, presented further evidence for temporal niche segregation at this time scale, between wild dogs and hyaenas, and wild dogs and lions, driven by direct intraguild interactions (Hayward & Slotow in review).

In terms of hyaena interference, it consequently appears that three potential mechanisms may have facilitated a relative encounter probability reduction in HiP, namely spatial variation in encounter probability, reduced visual information in wooded and hilly environments, and daily temporal separation. For lion predation encounter probability on the other hand, most probably spatial variation in encounter probability, daily temporal separation, as well as significantly lower overall lion densities (compared to hyaenas) may have functioned as frequency reducing mechanisms. These mechanisms may of course take place simultaneously and are not mutually exclusive, and all of them may have contributed towards a relative lowering of encounter probability. This in turn may have reduced hyaena interference and lion predation risks, and so facilitated the co-existence of wild dogs with hyaenas and lions in HiP.

In the context of a multiple-species predator guild, an important feature to consider at this point is that very often refugia are species-pair specific (Hochberg & Holt 1995; Berryman *et al.* 2006). In other words, a refuge for species A from species B is not necessarily a refuge for species A from species C (and equally a refuge for species A from species B is not necessarily a refuge for species D from species B). Consequently, unless hyaena interference refugia overlap spatially and/or temporally with lion predation refugia, wild dogs or other subordinate predator species may be forced to trade-off safety from interference vs. safety from predation (a similar scenario may also be applicable to herbivore species preyed upon by both predators). Temporal refugia from lion and hyaena, on a daily scale at least, do overlap substantially (Saleni *et al.* 2007; Hayward & Slotow *in review*), indicating that a trade-off between predation risk and interference risk may not be necessary in this niche dimension.

However, since there is still a partial temporal overlap in the activity patterns of lions and wild dogs, as well as hyaenas and wild dogs, a trade-off between predation risk and interference risk in space may still be necessary. The level of overlap between hyaena low-density patches and lion low encounter probability areas was not quantified in this study. However, other larger scale studies using different methodologies have indicated that this may not necessarily be the case (Mills & Gorman 1997; Durant 1998; Creel & Creel 2002). Consequently, which risk is primarily avoided in space may depend on different contexts, such as pack size, or the presence/absence or age of pups. Larger packs may be better able to defend their kills against hyaenas (Fanshawe & FitzGibbon 1993) and thus may choose to primarily reduce predation risk, limiting the need for a trade-off. In this context, smaller packs however may be forced to make this trade-off, indicating a further mechanism via which Allee effects could impact on small pack size (Courchamp *et al.* 2000; Courchamp & Macdonald 2001; Somers *et al.* 2008). Alternatively, wild dog pups appear to be highly susceptible to mortality by lions in some ecosystems (Mills & Gorman 1997; Creel & Creel 2002), and thus packs with young pups should attempt to reduce lion encounters. Conversely, the adult members of a wild dog pack also face additional energetic challenges when feeding pups and babysitters during the denning season (Gorman *et al.* 1998; Courchamp *et al.* 2002), and consequently any losses to hyaenas could also have serious consequences for the persistence of the pack (Rasmussen *et al.* 2008).

Thus, it appears that wild dogs have to make a trade-off in this situation with pups. However, since wild dogs pups are kept at a densite for *ca.* three months following birth and only start joining adults on hunts after this period (Malcolm & Marten 1982; Creel & Creel 2002), the location at which pup predation risk should be minimized and the location at which interference risk should be minimized are spatially displaced from each other during this period. This could allow wild dogs to avoid this potentially limiting trade-off between predation risk and interference risk during the denning season via the following mechanism. Since it should be easier to change foraging sites daily than denning location, a wild dog pack should first select a densite at which lion predation risk is maximally reduced over a longer period, i.e. denning season (e.g. see van Dyk & Slotow (2003)). Subsequently, for daily foraging trips during the denning season, wild dog packs should attempt to reselect areas within which low interference by hyaenas was experienced, and vice versa for areas with high interference rates. During the non-denning season, this spatial displacement of interference and predation risk is not available since pups increasingly join the pack during their daily movements, however, increased pup mobility may allow for this to be offset.

By breaking interference and predation risk into several components and addressing the probability of encounter component specifically, this thesis described the drivers of encounter probability, namely density and utilization intensity. It now remains to be seen whether wild dogs indeed use this variation in encounter probability across the landscape of HiP, and elsewhere. Furthermore, interference and predation risk is composed of additional components outside probability of encounter, as outlined in the introduction. Some of these components have been investigated as applicable to wild dogs, such as the probability of losing a kill to hyaenas once encountered by them (Carbone *et al.* 1997; Carbone *et al.* 2005). However, to date a systematic approach addressing all components simultaneously has been strikingly absent in predator intraguild interaction studies, and even most predator–prey studies (Creel & Creel 2002). Each of these components presents the outcome of an interaction between the behaviours of both predator and prey (i.e. vigilance, grouping behaviour, territoriality, etc.) (Liley & Creel 2008), as well as the effects of the local and surrounding environment (i.e. escape substrate and route, visibility, proximity of refugia, etc.) (Hopcraft *et al.* 2005; Bergman *et al.* 2006; Shrader *et al.* 2008). Future studies should attempt to investigate the relative influence of each of these components on predation and interference risk, and subsequently integrate these in addressing how subordinate guild members may and do react to predation and interference risk in a multi-species guild context.

In terms of the aims of this study, several methodological shortcomings should be addressed in the future when investigating variation in lion and hyaena encounter probability. Hyaena density estimation was only done for one time scale (i.e. the duration of each survey) and two seasons, and ideally should be examined for longer time scales and multiple seasons. The sensitivity of hyaena call-ups to hyaena habituation, however, prevents a large number of repeats within a season or even a year (Ogutu & Dublin 1998; Mills *et al.* 2001). The investigation of utilization intensity at a smaller spatial scale via the use of telemetry collars may be an alternative here. However, the majority of hyaenas within a clan would need collaring, requiring large financial and logistical inputs, and potentially entailing substantial disturbances to the clan. This would still only allow variation in the probability of encounter to be investigated at a local instead of landscape scale, which may then limit spatial comparison to wide ranging wild dog packs.

In terms of lions, the study analysed the density and ranging patterns of only two small prides and one coalition, all three of which were translocated into the study area just before the study. Although our study population exhibited behavioural patterns similar to other populations, analyses should be extended to include more and larger groups within settled populations, in order to interpret the generality of results presented here. Although a relatively large number of location data points were used in this study, analyses of ranging patterns for shorter time scales (3 months, 1 month, or 1 week) were limited by the number of data points. Larger volumes of location data would be provided by satellite collars and should allow the investigation of lion utilization intensity variation at shorter time scales.

Finally, the simultaneous investigation of the proximate drivers (distribution of prey, vegetation, water, etc.) of variation in lion and hyaena density and utilization intensity, *and* how these effects may in turn be transmitted to subordinate guild members, could further provide valuable contributions in terms of broadening the understanding of multi-trophic indirect interactions.

5.2 Conservation management implications and recommendations

Recent research has indicated that no urgent management of dominant large predators is necessary in HiP, at least from a wild dog perspective (Gusset 2007; Gusset *et al.* 2008b; Somers *et al.* 2008). This, however, may not hold for other threatened guild members such as cheetah, and could also change in the future for wild dogs. The local lion population appears to be expanding, especially in the iMfolozi section of the park (KZNW 2007, unpubl. data). Consequently, the continuation of lion and wild dog population monitoring, and initiation of cheetah population monitoring, is strongly recommended. The HiP hyaena population on the other hand appears to be stable, and monitoring at the medium-term (every 3-4 years) may be adequate. All the above-mentioned monitoring of population trends should enable the detection of any emerging threats to wild dog (and cheetah) persistence, and allow timely management responses to such threats. Since wild dog reintroductions are relatively expensive conservation actions (Lindsey *et al.* 2005a), prevention may be better than cure in this situation as well.

If the HiP lion population increases substantially (for instance as a result of a recovering buffalo population), and there is an indication of a negative effect on wild dogs, the results of this thesis suggest several population management options for lions. First, the removal of whole large prides should create an immediate lion low-density zone across the previous pride range. Subsequent acquisition of this range by neighbouring prides (Pusey & Packer 1987), should lead to a lowering of lion encounter probability (as a result of increasing range size) in these neighbouring pride ranges, which may remain stable over the medium term (a rough estimate would be two to five years). Second, the removal of an independently ranging sub-group from a large pride, or, third, the reduction in size of large male coalitions (Van Dyk & Slotow 2003). These last two actions should decrease the number of independently ranging sub-groups within a pride range and consequently reduce encounter probability within the pride range.

However, in the case of the first option, such vacuum areas could also temporarily draw in young dispersing male coalitions, or potentially result in pride-fission and occupation of this range, if any of the neighbouring prides are relatively large and contain a big cohort of sexually mature sub-adult females (Packer *et al.* 2005). For the second option, detailed behavioural data would be needed to identify a clear sub-group, which may not be available. The third option may result in the lowering of the genetic diversity of offspring produced by a pride, since these will be sired by fewer males. In the context of the small population size of HiP lions, this may have detrimental genetic consequences (Packer *et al.* 1991; Stein 1999; Trinkel *et al.* 2008). Furthermore, a reduction in lion densities may also have beneficial consequences for the hyaena population, which may result in hyaena population size increase (Watts & Holekamp 2008). Altogether, this indicates that such management options are framed by potentially complex contexts, and may result in unanticipated and unwanted outcomes. Conservation scientists and managers should take account of the above, and remain aware that they may have to make tough choices according to the individual management policies and priorities of different protected areas.

The guidelines for the management of the South African wild dog meta-population in terms of the selection of suitable wild dog re-introduction areas have included, among other criteria, low competitor density, specifically those of lions and hyaenas (Mills *et al.* 1998; WAG-SA 2005). In the context of the current expansion and consolidation of protected areas in South Africa as well as from an ecotourism perspective, lion reintroductions into such areas will most likely continue in the future. However, as the HiP situation, as well as that of many other meta-population reserves have illustrated, wild dogs can successfully co-exist with lions in most of these protected areas with appropriate levels of wild dog meta-population management. Most often, local prey population trends (or the subjective perceptions of these trends) and/or genetic considerations, drive lion management decisions within these reserves, before such decisions may become necessary in terms of wild dogs (Hayward *et al.* 2007c; Slotow & Hunter *in press*; Kettles & Slotow *in press*). Hyaenas on the other hand, are not as much in demand from an ecotourism perspective. And thus, although from an ecological and biodiversity point of view this species ideally should be re-established in communities within which it formerly occurred, from a subordinate and threatened guild member conservation viewpoint it should not necessarily be re-introduced everywhere. This may benefit not only wild dogs but also other threatened large carnivore species, such as cheetah and brown hyaena.

Green *et al.* (1984) determined a mean food consumption rate of 3.79 ±1.24 kg/day for individual hyaenas in HiP, which would translate to an average yearly consumption (excluding consumption by juveniles) of *ca.* 43 2574 kg of biomass by HiP hyaenas. Excluding elephant, white and black rhino, and ungulates smaller than impala, which contribute minimally to the diet of HiP hyaenas (Skinner *et al.* 1992), this figure is nearly 6% of the total ungulate biomass of HiP (Waldram 2005), a substantially larger proportion than that of any other large predator in the park. This recognition should be taken into account when assessing predator-prey interactions in HiP, especially in conjunction with the predation effects of the other large predator species (Sih *et al.* 1998). Any large scale management actions involving ungulates in HiP may potentially destabilize the current competitive relationships within the large predator guild to the detriment of the more specialized and subordinate species such as wild dogs and cheetahs. The reduction of common and important prey species (such as impala and nyala) may also lead to prey switching in the diets of these predators (Holt & Lawton 1994), with potentially negative population consequences for rare and decreasing herbivore species such as waterbuck, mountain and common reedbuck, blue duiker, and steenbok.

As in other areas of South Africa, there is a trend towards game farming as well as the formation of conservancies and larger formal conservation areas, such as the Greater St. Lucia Wetlands Park, in the Zululand and Maputaland regions. The extensive hyaena population throughout the protected areas within these regions may consequently still increase as prey numbers increase. Previous studies have shown that in some areas of iMfolozi small numbers of hyaenas forage outside the park, as indicated by the infrequent occurrence of cattle (2.5%) and goat (1.9%) in the diet of hyaenas from this area of HiP (Perrin & Whateley 1986; Skinner *et al.* 1992). The presence of snares on several hyaenas at call-up sites (in Mbhuzane and Makhamisa sections) during both 2003 and 2004 confirm these studies. Most of the formal and private protected areas in the above regions are surrounded by communal land with high livestock densities, and thus problems regarding hyaena livestock predation may increase in the future. The movement of hyaenas in and out of HiP, may also has implications for the potential transfer of human, wildlife and domestic stock diseases between the park and the surrounding area.

Gusset *et al.* (2008a) have shown largely negative attitudes towards large predators amongst the rural population surrounding HiP, with livestock losses being blamed mainly on hyaenas. Future research should focus on the potential movement of hyaenas in and out of HiP, as well as the existence of potential resident hyaena populations outside of HiP. The degree of impact on rural livestock populations should be established, and potential mitigating practices should be encouraged in order to alleviate potential human-wildlife conflicts (Woodroffe & Frank 2005; Woodroffe *et al.* 2005; Gusset *et al.* 2008a). The findings of such research should be incorporated into local predator conservation education initiatives, since negative attitudes towards hyaenas may potentially affect general attitudes to other large predators as well. This may be especially pertinent to the current proposal to establish a potentially natural wild dog meta-population in the greater Zululand and Maputaland regions with wild dogs dispersing between several KZNW, community, and private protected areas.

In terms of the conservation status of hyaenas in South Africa, the current size of the HiP hyaena population, its continued existence since at least the beginning of the 1900's (Potter 1934; Roberts 1954), as well as the potential for immigration and emigration would indicate that the population is viable. This is despite systematic persecution of hyaenas within HiP during the first half of the 20th century (Kirby 1916; Potter 1941; Bourquin *et al.* 1971), as well as massive culling of game in iMfolozi during the anti-Nagana/tsetse fly campaign of the same period (Brooks & Macdonald 1983). The persistence of the HiP hyaena population, with the additional components of a natural meta-population in the region, should be taken into account in regional land-use planning (e.g. transformation of savannah into agricultural land across potential dispersal corridors). Considering the above, we suggest that surveys are extended to the surrounding game reserves (formal and private) and communal land in order to determine the status and extent of this natural meta-population.

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