Changes in adult female white rhino seasonal home ranges in relation to variation in food quality and availability

By

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DECLARATION

I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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ABSTRACT

As the dry season progresses across southern Africa, the availability and quality of food declines for large herbivores. Female white rhinos compensate for these declines by expanding and/or shifting their home ranges. These changes may be to incorporate habitat types that contain high quality food or quite simply more food. To determine the factors that drive these seasonal changes in home ranges, I focused on dry season changes in the availability and quality of grass in habitats utilised by white rhinos in the Ithala Game Reserve, South Africa. I expected that if food quality was the main driver, white rhinos would follow optimal foraging principles and incorporate habitat types with the highest nutritional quality into their dry season home ranges. Alternatively, due to their large body size (>1000 kg) and thus ability to survive on low quality food, they may rather incorporate habitat types with high food availability. In contrast to previous studies, I found that during the dry season female white rhinos did not increase the size of their home ranges, but rather shifted their home range boundaries. This resulted in individuals increasing the amount of Bushveld and decreasing the amount of Wooded Grasslands within their dry season home ranges. When I explored the different factors that could explain these patterns, I found that changes in the crude protein content of grass was the key factor driving the incorporation and exclusion of habitat types in the home ranges. During the dry season, white rhinos incorporated the habitat that had the smallest seasonal reduction in crude protein content, while excluding the one with the largest decrease in crude protein. As a result, my results suggest that the search for high quality best explains the seasonal home range shifts of female white rhinos in the Ithala Game Reserve.

I dedicate this thesis to my parents for their constant encouragement and support.

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Contents

List of Tables

List of Figures

Chapter 1: Literature Review

Herbivore foraging

Grazing animals live in an environment where food availability and quality varies both spatially and temporally across the landscape (O'Reagain 2001). Ultimately, this variation determines the distribution of quality forage available to herbivores and governs their foraging patterns, movements and thus their space use (Bailey *et al.* 1996). Animals select areas of the landscape according to factors such as forage availability and/or quality, predation risk and thermal stress (Bailey *et al.* 1996, O'Reagain 2001, Kinahan *et al.* 2007, Kotler *et al.* 1994). To meet their nutritional needs, herbivores can selectively consume plant parts and species, and forage preferentially in particular vegetation types across landscapes (Senft *et al.* 1987, Bailey *et al.* 1996, Owen-Smith 2002).

Large herbivores encounter resources spatially at four ecological levels: 1) micro-patches (plant part, plant, and feeding stations), 2) plant communities (habitats), 3) landscapes and 4) regions (Senft 1989). This ecological hierarchy explains how fine scale decisions made by herbivores at a plant, plant part and/or feeding station levels can translate into larger levels of selection at community and landscape levels (Shipley 2007). Thus, both spatial and temporal (e.g. seasons) variation in nutritional quality and availability of food across these levels can influence a herbivore's food selection. This happens because food resources differ in nutritional quality, size and accessibility (Owen-Smith 2002). For herbivores with small mouths (e.g. impala (*Aepyceros melampus*) and goats (*Capra hircus*)), selection at the plant part scale is important (Shipley *et al.* 1999). In contrast, herbivores with wide mouths (e.g. wildebeest (*Connochaetes taurinus*) and white rhinos (*Ceratotherium simum*)) are generally unable to select specific plant parts and thus the smallest scale they can select at is plant species (Shipley *et al*, 1999; Shrader 2003). However, despite their morphological and body size differences, both herbivore types are able to cope with fine and

1

large scale spatial variability in food quality and availability by making a combination of both small and large-scale foraging decisions (Senft 1989, Bailey *et al.* 1996, O'Reagain 2001).

Small-scale selection is influenced mainly by forage depletion at a micro-patch level (e.g. plant parts, plants or feeding stations) forcing animals to move to new micro-patches (Senft 1989, Bailey *et al.* 1996, O'Reagain 2001). The time that it takes to deplete food in a micro-patch governs how long a herbivore can stay within that micro-patch before needing to move. Over time, these small scale decisions compound, leading to large scale selection patterns (Shipley 2007).

Plant species vary in structural and nutritional characteristics. Thus, these characteristics influence bite size and intake rates and therefore influence herbivore food selection (Bailey *et al.* 1996, O'Reagain 2001). Animals respond to spatial and temporal variability of plants by selecting for certain species and avoiding others (O'Reagain 1996, Illius & O'Connor 2000). Leaf quality and the rate at which an animal can harvest plant material determine a grazer's acceptability of a grass plant. For example, cattle prefer grasses that provide many leaves of high quality and low tensile strength (O'Reagain & Mentis 1989).

For herbivores, habitat types can be defined by the plant communities that they contain and thus the degree of use by the herbivores (Owen-Smith 2002). Herbivores generally select the most preferred habitat types within a landscape but seldom forage exclusively within these habitats (Bailey *et al.* 1996). For example, non-migratory herbivores (e.g. buffalo, *Syncerus caffer*) in Serengeti National Park, Tanzania move between upland short grass areas in the wet season and taller low-lying grasslands in the dry season (Bell 1970). White rhino in the Hluhluwe-iMfolozi Park, South Africa follow similar patterns, moving from short grass grasslands in the wet season to taller grasslands that offer a larger forage biomass in the dry season (Owen-Smith 1988, Shrader 2003). Ultimately, this selection is driven by preference for the different grassland types and not for particular

species within these grasslands (Owen-Smith 1988). Naidoo *et al.* (2012) found similar patterns for buffalo. During the wet season, the buffalo depleted the grass biomass on high lying areas leaving little dry season forage. As a result, they shifted and restricted their dry season ranges to low lying grasslands that provided them with larger amounts of food (Naidoo *et al.* 2012).

Selection for plant species can ultimately drive selection at a community level (Shipley 2007). When herbivores begin to select areas according to the plant species that they offer, they begin to select at a larger scale. Thus herbivores end up choosing communities that offer nutritious plants that enable them to meet their nutritional needs (Shrader *et al.* 2012). Large herbivores tend to select plant communities or habitats according the different species available within them (Senft *et al.* 1987, O'Reagain 2001). Not surprising, herbivores will generally feed more intensively in communities that offer high nutritional value compared to communities with low quality vegetation (McNaughton 1988).

In contrast to small-scale selection, large-scale selection is influenced essentially by long-term variability of resources (Senft 1989). At this larger scale, landscapes consist of a collection of habitats (Owen-Smith 2002). Thus, for herbivores the availability of preferred habitats ultimately drives landscape-scale resource selection (Senft *et al.* 1987, O'Reagain 2001). These habitats vary in vegetation structure, species composition, soil fertility, slope and/or rockiness (Senft *et al.* 1987).

In addition, water availability and physical accessibility determine whether portions of a landscape are available to herbivores. For example, water-dependant herbivores need to remain close to water sources during the dry season (Western 1975), while elephants tend to avoid steep terrain (Wall *et al.* 2006). Landscape selection depends on large-scale patterns of forage quality and availability (McNaughton 1978, Senft *et al.* 1987). The ability of a herbivore to trade off availability and quality determines how they select habitats within

landscapes. These factors, combined with the physical factors such as topography and water availability play vital roles in determining the accessibility of food (Kinahan *et al.* 2007).

In addition to spatial changes, large and small-scale selection is driven by temporal variability in the availability and quality of resources (O'Reagain 2001). Seasonal variation in rainfall and temperature drive the patterns of patch quality and food quantity (Anderson & Talbot 1965, Owen-Smith 2002, Shrader & Perrin 2006). These patterns are important as selection for food differs in the wet and the dry seasons. As the dry season progresses, the nutritional quality and availability of plant material both decrease (Dove 1996). As plant senesce, the proportion of green leaves available within grass swards decreases. In response, grazers with small mouths can become more selective and feed on the remaining nutritional plant parts within habitats (Bell 1970, Jarman 1974, Demment & Van Soest 1985). In contrast, large herbivores may have to shift and forage in habitats that provide them with enough food to maintain an adequate nutritional intake (Owen-Smith 1988). Furthermore, both large and small herbivores may expand their diet breadths and include previously avoided species or habitats in order to meet their nutritional needs (Owen-Smith 1988, 2002). For example, Kerley *et al.* (2010) showed that grysbok (*Raphicerus melanotis)* broadened their diet when their important food items became scarce. In addition, Ryan *et al.* (2006) showed that buffalo range farther in the dry season to find high quality food.

Optimal foraging theory

Optimal foraging theory provides a functional approach with which to help understand the foraging behaviours of animals including forage selection, patch selection and movement (Pyke 1981). Optimal foraging models are based on the principal that animals forage to maximise their long-term nutritional intake of energy or a limiting nutrient (Belovsky 1978, Stevens & Krebs 1986, Owen-Smith 1997). Large herbivores must cope with a wide range of

environmental fluctuations and physiological limits by adjusting their foraging behaviour appropriately. Moreover, temporal and spatial variability makes optimal foraging models subject to various constraints (Owen-Smith 1997). Temporal and spatial variability influences basic physiological constraints such as thermal stress, digestive processing capacity, predation risk, and the requirements for specific nutrients are faced periodically (Owen-Smith 1997). Seasonal variation in resources is important because if individuals are unable to meet their nutritional requirements within a particular area when the quality of resources decreases, they will then need to move in search of required nutrients (Owen-Smith 1997), or sacrifice body condition/rely on fat reserves (Shrader *et al.* 2006). When herbivores broaden their diets as the availability of their preferred food source decreases, it leads to the inclusion of less preferred foods (O'Reagain & Grau 1995, Kerley *et al.* 2010). For example, as their favoured species declined over the seasonal cycle, kudu expanded their diet breadth to include food previously avoided during the wet season (Owen-Smith 1997).

Although optimal foraging theory predicts that herbivores aim to maximise energy intake, it does not suggest that herbivores forage optimally (Krebs *et al.* 1983). Rather, it attempts to explain foraging dynamics by providing explanations for foraging patterns of herbivores (Krebs *et al.* 1983). Furthermore, optimal foraging theory may provide a framework with which to provide understanding as to why larger scale patterns such as why herbivores seasonally alter their home ranges.

Body Size theory

Ultimately, nutritional requirements are not consistent for animals of different body sizes. Mass-specific metabolic rates decrease with increasing body mass to the power of three-quarters (i.e. $M^{0.75}$) (Bell 1970, Jarman 1974). In contrast, gut capacity increases linearly with body size (Demment & Van Soest 1985). Ultimately, because of this relationship between

metabolic rate and body mass, smaller herbivores require high quality food and thus should be more selective than large herbivores (Jarman 1974). In contrast, the lower mass-specific metabolic requirements of large herbivores allow them to exploit poorer quality habitats than smaller herbivores (Fritz *et al.* 2002). Moreover, large herbivores are more efficient at digesting fibre compared to smaller herbivores (Clauss and Hummel 2005). As a result, large herbivores should be able to tolerate forage of lower nutritional quality than small herbivores (Bell 1970, Jarman 1974) and be able to survive on poor quality forage (Bell 1971, Owen-Smith 1988, Fritz *et al.* 2002). Over a broad spatial scale, Fritz *et al.* (2002) showed that megaherbivores were largely unaffected by soil nutrient status, which directly influences plant nutritional quality, and thus they utilized a much greater range of plant communities compared to smaller herbivores.

In addition, large herbivores have larger bite dimensions and therefore generally have a higher intake than smaller animals over time (Illius & Gordon 1987). The benefits of their large body size allows them to tolerate low quality food (Demment & Van Soest 1985). Provided non-ruminant large herbivores are able to have a high forage intake, they are generally able to meet their nutritional requirements by ingesting lower quality forage than ruminants (Illius & Gordon 1992). However, just because they are able to tolerate low quality food does not mean that they preferentially select it. In addition, due to their size, large bodied herbivores likely are unable to detect fine-scale food patches and thus should make foraging decisions at large spatial scales (Richie & Olff 1999).

Seasonally, differences in body size can influence how different sized herbivores utilise space. For example, Bell (1970) recorded that as the dry season progressed, large-bodied herbivores (e.g. buffalo and zebra (*Equus quagga)*) left upland feeding sites and shifted their foraging to lower elevations before smaller-bodied herbivores (e.g. topi (*Damaliscus korrigum*) and Thompson gazelle (*Eudorcas thomsonii*)). Bell (1970) suggested

that this was the process of facilitation with the large herbivores moving to the lowlands to eat the readily available tall grass. Smaller herbivores, then followed when access to lower quality food was created by these larger bulk feeders.

However, a number of authors have questioned this interpretation (Illius & Gordon 1987, de Boer & Prins 1990, Prins & Olff 1998, Arsenault & Owen-Smith 2002). A more likely explanation is that the movement of these large-bodied herbivores was due to a reduction in food intake caused by lower grass height (Illius & Gordon 1987). Ultimately, these herbivores were unable to obtain an adequate dry matter intake and thus needed to move into areas with greater food availability. In contrast, smaller herbivores were likely able to remain in the uplands as they could meet their nutritional and dry matter intake on the shorter remaining grass (Illius & Gordon 1987).Thus, the movements of the herbivores were more likely driven by changes in food availability for large herbivores rather than changes in food quality for small herbivores.

Home Range

In response to both spatial and temporal changes, animals move in order to access resources that they need to survive and they do this within their home range (Burt 1943, Jewell 1984). These resources not only include food but also water, shelter from weather and refuges against predation (Jewell 1984). Within a home range, individuals generally become familiar with the distribution and availability of resources. Thus, habitats that provide the most nutritional forage are those generally centred within home ranges (Senft 1989). Large herbivores tend to have larger home ranges than small herbivores. Initially, home range size was thought to be based on the energetic requirements of an animal (McNab 1963). However, after considering metabolic mass ($M^{0.75}$) it was shown that larger animals have proportionally larger home ranges (du Toit 1990). Ultimately, home range size represents a compromise

between individual metabolic requirements and social pressures (Owen-Smith 1988). Physiological constraints of home range size may include thermal stress, cost of moving over the landscape to search for food and the efficiency with which individuals are able to digest food and find mates (Swihart *et al.* 1988).

Home ranges, however, are not static and thus their size and shape may vary over time (Lindstead *et al.* 1986). Fluctuations in home range area and shape occur over seasons and years in response to a number of factors. Seasonal and annual rainfall patterns govern the quality and quantity of food and the availability of surface water over time (Scholes *et al.* 2003). The combination of these factors can greatly affect seasonal home range sizes. When conditions are favourable and food and water resources readily available, an animal may restrict its movements to a small portion of the home range termed the core (Owen-Smith 1973, Grund *et al.* 2002). For example, white-tailed deer (*Odocoileus virgianus*) tend to have larger home ranges during winter when food is scarce, compared to during summer when food is abundant (Grund *et al.* 2002). When conditions become worse, through seasonal depletion of resources, an animal can then shift and utilise a larger extent or different parts of its total home range (Adams & Davis 1967, Owen-Smith 1975).

Seasonal changes in plant nutritional quality, and thus seasonal shifts in home range use, are caused mainly by climatic effects on plant production and fluctuating grazing pressure which affects forage availability (Jones *et al.* 2006). For example, during the dry season, grass stops growing, and leaves senesce as energetic reserves move below ground into the grasses root system (Imbahale *et al.* 2008). As a result, nutrient availability is lower during the dry season compared to the wet season (Wilmshurst *et al.* 1999). In contrast, the nutritional value of grasses can also decrease steadily during the wet season as grasses age (Georgiadis & McNaughton 1990). The primary factor responsible for this is the build-up of cell wall components and fibre (Georgiadis & McNaughton 1990). This results in a negative

correlation between crude protein content and the amount of fibre in the leaves of a plant (Georgiadis & McNaughton 1990). For free-ranging wild grazers, crude protein is thought to be the most limiting nutrient (Bell 1971, Sinclair 1985, 1977).

Nitrogen, the key component of crude protein, plays an important role in metabolic processes and is important for the growth of all organisms (Mattson 1980). The highest content of nitrogen occurs in young plant tissues. However, as a plant ages leaves senesce and the nitrogen content reduces to approximately 20% of the concentration in growing leaves (Mattson 1980). The nutritional value of grasses also depends on the soil type. Species growing in soils high in nitrogen may maintain their nutritional value for longer into the dry season, making these areas more nutritious to foraging herbivores (Georgiadis & McNaughton 1990).

Spatially, home range use is a landscape-scale response. Herbivores generally establish their home ranges such that they incorporate the best foraging habitat types and watering areas (Senft *et al.* 1987). Herbivores that have stable home ranges tend to have localised areas of nutritional sufficiency where they are able to access sufficient nutrients (Georgiadis & McNaughton 1990). These areas act as central points for grazing activity and may make up the core grazing area (Georgiadis & McNaughton 1990). However, throughout the year an animal may adjust its home range in response to seasonal changes in resource availability (Owen-Smith 1975, Fryxell 1991). Ultimately, this can increase an animal's ability to exploit available resources and thus increase their foraging efficiency (White *et al.* 2007).

Such seasonal changes in resource selection have been found for a number of herbivores including kudu (*Tragelaphus strepsiceros*) and wildebeest. For example, Owen-Smith (1997) found that during the dry season, when food quality declined, kudu responded by increasing their intake of lower quality plants. In Serengeti, wildebeest seasonally migrate

across the landscape so as to maximise their intake of high quality forage (Wilmshurst *et al.* 1999, Holdos *et al.* 2009).

Water availability

Abiotic factors such as soil type, topography and water can affect the availability of food and may limit the way grazers forage and utilise space (Bailey *et al.* 1996). Ultimately, the distribution of these resources influences the distribution and movement of herbivores. A key factor that influences home range use is water availability (Thrash and Derry 1999, Gaylard *et al.* 2003). During the wet season, surface water is generally available across the landscape in pans, streams and rivers. As the dry season progresses, temporary pans and streams dry up and the availability of surface water declines. These seasonal changes can influence the way that herbivores utilise and move across the landscape (Hobbs 1996). How herbivores respond to these changes depends on how often they need to drink. Ultimately, water distribution and availability governs the distribution and dispersal of water dependent, obligate drinkers (Western 1975).

Water-dependent large herbivores are those whose movements are bound by water availability and they include buffalo, zebra, elephants (*Loxodonta africana*), and wildebeest (Western 1975, Whyte *et al.* 1998, Macadanza *et al.* 2004). In the Serengeti, Wilmhurst *et al.* (1999) found that although wildebeest moved in search of high quality grazing, water availability strongly influenced their migratory patterns. For elephants, seasonal ranges are governed by the availability of water (Western 1975, Whyte *et al.* 1998). Specifically, during the dry season, elephants contract their home ranges around permanent water sources so that they have daily access to water (Whyte *et al.* 1998, Bradshaw 2008). In addition, black-tailed deer (*Odocoileus hemionus*) select habitats close to streams during the summer (Bowyer *et al.* 1998) so that they can maximise their food intake. Similarly, white-tailed deer have smaller

summer home ranges than in winter as they contract around streams where food is readily available (Grund *et al.* 2002).

In contrast to water-dependant herbivores, water-independent herbivores do not need daily access to water (Western 1975). These species include white rhinos, eland (*Tragelaphus oryx*) and giraffe (*Giraffa camelopardalis*). Ultimately, the distribution and availability of water does not govern how these herbivores utilise the landscape (Western 1975). As a result, their landscape distribution is generally random with respect to the availability of water. Thus, water-independent herbivores tend to show little shift from their wet season ranges and remain within the same areas year round (Western 1975).

However, what may influence seasonal shifts in these herbivores are seasonal changes is the spatial distribution of food (Western 1975, Owen-Smith 1988). For example, Western (1975) found that white rhino space use was unaffected by seasonal variation in water availability. In addition, Owen-Smith (1988) found that during summer white rhinos drink daily, but during the dry season some individuals drank only every four days. These drinking patterns, however, do not explain the seasonal shifts in adult female home ranges (Owen-Smith 1988, White *et al.* 2007). Rather it seems that the quality and/or availability of food are the main drivers behind these seasonal shifts (Owen-Smith 1973). However, if they are unable to meet their water requirements from the food that they eat during the dry season, white rhinos may temporarily leave their home range and make excursions to drink (Owen-Smith 1988).

White rhino foraging and movement

White rhinos are the largest extant pure grass feeder and the second largest terrestrial land mammal in Africa (Shrader 1998, Skinner & Chimimba 2005). Males weigh approximately 2300 kg, while females can weigh up to 1600 kg (Owen-Smith 1988). White rhinos are large-

bodied non-ruminants that require large amounts of food (Owen-Smith 1988). Because of their size and the effects they have on the ecosystem (e.g. generation and maintenance of grazing lawns), they can act as a keystone species (Waldram *et al.* 2008).

White rhino are suited to short grass areas due to their wide mouths and low-slung head. Furthermore, their wide lips enable them to crop high quality short grass close to the ground when it is available (Owen-Smith 1988, Shrader 2003). However, white rhinos are restricted in their food intake because of the slow rate of passage of food through the gut (Owen-Smith 1988). These limitations mean that even though white rhinos have low metabolic requirements per unit body mass, they still require good quality food to meet their nutritional requirements (Owen-Smith 1988). As a result, food quality likely plays a key role in driving white rhino feeding patterns.

The use of space across the landscape by white rhinos differs between the sexes. Males establish territories that they defend aggressively against other males, demarcating with scent marking and defensive behaviours (Owen-Smith 1971, Rachlow *et al.* 1999). These mutually exclusive territories can range between 0.75 km^2 and 2.6 km^2 (Owen-Smith 1984). In contrast, females occupy home ranges that are undefended and overlap with the home ranges of other females and the territories of a number of males (Owen-Smith 1988). Within these two areas, both males and females seasonally shift between habitats so as to feed on the best available food (Owen-Smith 1984, 1988).

During the wet season, white rhinos primarily feed on short grasslands (Owen-Smith 1973, Owen-Smith 1988, Shrader 1998, Shrader 2003). These areas provide the most nutritious grasses. Included in these short grass areas, but not limited to, are grazing lawns. Vesey-Fitzgerald (1965) termed grazing lawns as grass communities maintained in a state where they are nutritious as grasses remain in a juvenile state because of repeated heavy grazing (Vesey-Fitzgerald 1965, McNaughton 1984, Fryxell 1991). As the dry season

progresses, white rhinos may need to compensate for a reduction in the quality and quantity of forage. One way that they might do this is to alter their foraging and movement patterns so that they include additional habitats that provide forage that is not available in their summer grazing areas (Shrader *et al.* 2006). Short grasslands may not provide enough food during the dry season, as both the quality and quantity are lower (Fryxell 1991, Verweij *et al.* 2006).

Owen-Smith (1988) found that white rhinos in the Hluhluwe-iMfolozi Park selected for grassland type and not for particular species. He described four broad grassland types used by white rhino 1) short grasslands dominated by *Digitaria argyrograpta, Panicum coloratum, Urochloa mossambicensis* and *Sporobolus nitens*, 2) Woodland grasslands dominated by *Panicum maximum*, 3) *Themeda* grasslands that were easily accessible, and 4) remote *Themeda* grasslands on hill slopes (Owen-Smith 1973, Owen-Smith 1988).

During the wet season, white rhinos prefer feeding in short grasslands (Owen-Smith 1973, Owen-Smith 1988). As the dry season progresses and the availability and quality of short grass declines, white rhinos shift and fed within woodlands (Owen-Smith 1973, 1988, Shrader *et al.* 2006). Woodland grasses (e.g. *Panicum maximum*) grow in shady areas under trees where they maintain greenness later into the dry season (Shrader *et al.* 2006). As a result, white rhinos favour these grasslands in the early dry season. As the dry season progresses further, the quality and availability of grasslands decline in these woodlands. As a result, white rhinos once again shift their foraging to easily accessible medium to tall *Themeda triandra* grasslands (Owen-Smith 1973, 1988, Shrader *et al.* 2006). In drought years or extended dry seasons, when these *Themeda* grasslands are heavily utilised, white rhinos will then move onto less accessible *Themeda triandra* dominated hill slopes. These areas provided grass further into the dry season and provided individuals with a large quantity of low quality food (Owen-Smith 1973, 1988). During a high rainfall year, Shrader (2003) found that white rhino did not extensively forage in *Themeda triandra* grasslands during the

dry season, but rather preferred the available short grasslands throughout the year. The only time they foraged in the *Themeda* grasslands, was in the early wet season when there was an initial green flush after burning.

Within these grassland types, grass height is an important factor that determines food selection. This is likely because it determines bite mass (Hodgson 1985, Shrader 2003). Shrader (2003) found that white rhinos grazed mainly in intermediate height grasslands. This suggests that they were using habitats that supplied them with nutrients and sufficient volumes of forage and that they were not only selecting for forage volume (Fryxell 1991). An underling factor driving habitat selection is soil type (Georgiadis & McNaughton 1990). Higher soil nutrient status results in better nutritional quality of vegetation growing on these soils (Georgiadis & McNaughton 1990). For white rhinos, individuals prefer feeding in grasslands found on shale- or dolerite-derived soils (Owen-Smith 1988).

White Rhino Home Ranges

As with other species (Bowyer *et al.* 1998, Grund *et al.* 2002, Kinahan *et al.* 2007), the home ranges of female white rhinos are not stable, but rather expand and contract as resource availability changes. When green grass and water are both available, female white rhinos are able to meet their nutritional needs within a core home range area (3 to 6 km^2) (Shrader 2003). When the quality of food declines, however, white rhinos may use the full extent of their home range (10 to 15 km^2) (Owen-Smith 1988). Seasonally, the home ranges of adult females can stay the same, expand or shift (Owen-Smith 1988, Shrader 2003, White *et al.* 2007). For example, Owen-Smith (1988) found that white rhino females expanded their home ranges during the dry season. In contrast, White *et al.* (2007) found that white rhino home ranges shifted to include new habitats during the dry season. Despite making these

observations, neither study determined what drove these changes, but both suggested that the rhinos were looking to increase access to either greater food quantity or quality.

Food quality and availability has a direct effect on the movement of a herbivore as individuals need to meet intake and nutritional requirements (Searle & Shipley 2008). By selecting habitats that provide lots of good food, white rhinos limit the need to increase their intake of poor quality food during the dry season. For example, Owen-Smith (1973, 1988) observed white rhinos limited their feeding to specific grassland habitats during the wet and dry seasons. Shrader (2003) found that white rhinos selected for both individual grass species and habitats within their home ranges. However, neither study was able to quantify whether nutritional changes in the habitat types used by white rhinos governed their habitat and seasonal home range selection.

The study and its expectations

As white rhinos are water independent and thus do not contract their home ranges around water during the dry season (Owen-Smith 1973, Western 1975). As a result, I have focused my study on how food influences the seasonal home ranges of female white rhinos. Owen-Smith (1988) recorded that white rhino females expanded their home ranges during the dry season. He suggested that they did this in order to encompass vegetation types and habitats that contained high quality food during the dry season. However, he did not measure changes in nutritional quality. White *et al.* (2007) found that female home range size did not change but that there was shift in the home range boundaries. They suggested that this was likely due to changes in the pattern of habitat use. To answer the question of what factors influence the expansion and/or shifting of female white rhinos' home ranges, I have focused my study on white rhinos with in the Ithala Game Reserve, South Africa.

The broad aim of my study was to determine how changes in food quality and quantity affect female white rhino seasonal home range size/shape and habitat composition. I approached the study with the objectives to determine: 1) if changes in food quality and/or availability lead to dry season expansion/shift of female white rhino home ranges, 2) how habitat composition of female white rhino home ranges varies seasonally and, 3) if habitats incorporated into dry season home ranges are nutritionally superior to the habitats left out of the dry season home ranges.

By using optimal foraging theory and comparing the alternative drivers of food quality and body size theory (i.e. food availability) I can make predictions on the factors that drive changes/shifts in female white rhino home ranges during the dry season. If the search for a higher availability of food (i.e. benefit of a large body size) is the main driver behind the seasonal changes in the home ranges of white rhinos, then I predict that individuals will incorporate habitats with high forage availability into their dry season home ranges. Larger food quantities will allow greater dry matter intake, and thus the rhinos can meet their nutritional intake requirements. In contrast, despite their large body size white rhinos still need to retain an intake of high quality food during the dry season (Owen-Smith 1988). Thus, I predict that white rhinos should incorporate habitats that provide food with the highest nutritional quality during the dry season. This would suggest that the rhinos are selecting habitats to maximise their intake of nutritionally superior forage during the dry season. Finally, if it is a combination of the two factors, then I would expect that white rhinos would expand their home ranges to incorporate habitats that have the greatest availability of high quality food.

Chapter 2: METHODS

Ithala Game Reserve

The Ithala Game Reserve (29513 ha) is situated in northern KwaZulu-Natal near Louwsburg (Figure 1) (27° 24' S and 27° 35' S, 31° 11' E and 31° 24' E). Within the reserve, there is a 1000 m difference between the highest and lowest points. The many plateaus, valleys and valley bottoms accommodate 23 different vegetation types (Van Rooyen & Van Rooyen 2008) (Table 1). Most of the short grass areas within the reserve are old lands dominated by *Hyparrhenia hirta* and *Hyperthelia dissoluta* (Bonnet, O., University of KwaZulu-Natal, unpublished data). However, grazing lawns (another key short grass area), are present, but they only comprise a very small area of the reserve (i.e. 42 ha, 0.14% of the reserve). The wet season runs from November to February, while the dry season is from May through August. Shallow rocky mispah soils are widespread in the reserve, especially in the northern valleys and central plateaux (Van Rooyen & Van Rooyen 2008). The soils in the higher areas tend to be leached while soils in lower areas are fertile with high clay contents (Van Rooyen & Van Rooyen 2008). Granitic sandy acidic soils are found in the eastern part of the reserve (Van Rooyen & Van Rooyen 2008).

The reserve falls in the Bivane and Pongola River catchment areas with water available in small perennial rivers and streams. In addition, throughout the reserve there are a number of small springs that contain water year round. Finally, the Pongola River forms the northern boundary of the reserve and as it is not fenced.

Vegetation types that occur in the reserve are Northern Zululand Mistbelt Grassland (Gs 1), Ithala Quartzite Grassland (Gs 2), Swaziland Sour Bushveld (SVl 14), Northern Zululand Sourveld (SVl22) and Zululand Bushveld (SVl 23) (Mucina & Rutherford, 2006).

According to Rutherford & Westfall (1994), Ithala Game Reserve comprises portions of both the Grassland and Savanna Biomes.

Figure 1: Ithala Game Reserve is located in northern KwaZulu-Natal near the town Louwsburg, South Africa.

Table 1: The 23 vegetation types and their area in the Ithala Game Reserve, as described by Van Rooyen and Van Rooyen (2008). *No. refers to the number assigned to the vegetation type by Van Rooyen and Van Rooyen (2008).

No.*	Vegetation Type	Area (ha)
9.1	*Combretum apiculatum – Euclea schimperi* rocky Bushveld	4698.8
5.2	*Trachypogon spicatus – Tristachya leucothrix* rocky wooded grassland	4197.9
9.2	*Combretum apiculatum – Diospyro slycioides* subsp. *nitens* rocky Bushveld	3139.1
10.2	*Acacia nilotica - Acacia ataxacantha* dense Bushveld	2426.9
13.2	*Breonadia salicina – Ficus sycomorus* riparian vegetation	2305.1
9.3	*Acacia nigrescens – Combretum apiculatum* rocky Bushveld and woodland	2239.2
6	*Faurea saligna – Searsia harveyi – Cymbopogon excavatus* open woodland	1520.4
4.2.3	*Hyparrhenia hirta – Sporobolus africanus* old field grassland	1152.7
8	*Ficus glumosa - Euphorbia cooperi* wooded rocky outcrops	1001.6
5.1	*Trachypogon spicatus – Themeda triandra – Euclea crispa* rocky wooded grassland	993.3
9.4	*Combretum apiculatum - Bauhinia galpinii* open to dense Bushveld	968
10.1	*Olea europaea* subsp. *africana – Euclea schimperi* dense Bushveld	889.2
12	*Ficussur – Trimeria grandifolia* forests	670.5
4.1	*Hyparrhenia hirta - Acacia tortilis* old field grassland	660.4
3.1	*Englerophytum magalismontanum – Loudetia simplex* rocky wooded grassland and open Bushveld	489.8
4.2.2	*Hyparrhenia hirta – Dichrostachys cinerea* old field grassland	485.2
3.2	*Pterocarpus angolensis – Tetraselago natalensis* rocky wooded grassland and open Bushveld	468.2
1	*Cliffortia nitidula* rocky montane grassland	324.8
2.2	*Greyia sutherlandii* wooded grasslands of sandstone cliffs and scarps	232.4
13.1	*Imperata cylindrica* wetlands	195
4.2.1	*Hyparrhenia hirta – Acacia karroo* old field grassland	174.4
7	*Senecio microglossus – Bewsia biflora* grassland	121.4
2.1	*Leucosidea sericea* thickets and Bushveld of dolerite cliffs and scarps	106
4.2	*Hyparrhenia hirta – Acacia nilotica* old field grassland	43.9
11	*Dichrostachys cinerea – Solanum incanum* open disturbed patches	9.2
	Total area	**29513.4**

For the purpose of this study, I combined the above vegetation types into seven habitat types based on the structure of the grass layer of the vegetation types and their importance with regard to white rhino foraging (Owen-Smith 1988, Shrader *et al.* 2006, White *et al.* 2007) (Table 2). This is similar to Owen-Smith (1973, 1988) and Shrader *et al.* (2006) who used broad habitat classifications in the Hluhluwe-Umfolozi Park (now Hluhluwe-iMfolozi Park). In this park, short grass grasslands are important wet season grazing areas for white rhino (Owen-Smith 1988, Shrader *et al.* 2006).

For my study, the combined habitat types included:

1. Wooded Grasslands (Vegetation types: 3.1, 3.2, 5.1, 5.2, 6)

   These are grasslands with a tree layer dominated by microphyllous or macrophyllous tree species and a sparse shrub layer dominated by broad-leaved species. Wooded Grasslands occur on all soil types, at all altitudes and on all gradients. The grass layer is dominated by *Hyperthelia dissolute, Loudetia simplex,* and *Tristachya leucothrix* and, in some areas, *Cymbopogon excavatus.*

2. Grassland (Vegetation type: 7)

   These grasslands are diverse areas with well-developed grass and herb communities that have not been cultivated. *Eragrostis curvula, Eragrostis racemosa, Hyperthelia dissoluta, Setaria sphacelata* and *Themeda triandra* are the dominant species in this habitat. Most of these grasslands occur at high altitudes and are not easily accessible by many of the larger herbivores such as white rhino.

3. Forest (Vegetation type: 12)

   Small areas of forest are scattered throughout the reserve occurring mainly along mountain streams. Broadleaved species dominate the forests that have a poorly developed grass layer dominated by *Eragrostis curvula, Panicum maximum* and *Panicum deustum.*

4. Old Land Grasslands (Vegetation types: 4.1, 4.2, 4.2.1, 4.2.2, 4.2.3)

   Previously cultivated areas that have re-established as grasslands consisting primarily of tall, tufted species that become unpalatable when mature (Georgiadis & McNaughton 1990). Dominant species of this vegetation class are *Cynodon dactylon, C. excavatus, E. curvula, Hyparrhenia hirta*, *H. dissoluta* and *Sporobolus africanus.* Old land grasslands dominate the flat sections of the reserve.

5. Bushveld (Vegetation types: 9.1, 9.2, 9.3, 9.4, 10.1, 10.2)

   These are areas of open to dense mixture of broadleaved and microphyllous trees and shrubs, with a poor to moderately-developed grass layer dominated by *Aristida congesta, E. curvula, Heteropogon contortus, P. maximum* and *Themeda triandra.* This vegetation type occurs mainly on rocky hillsides and valley bottoms, where the topography is steep and soils are shallow.

6. Wooded Outcrops (Vegetation type: 8)

   Rocky dolerite outcrops only occur in the East of the reserve. They have a sparse tree layer dominated by broadleaved tree species and dense grass layer dominated by palatable grass species, including *Eragrostis superba, P. maximum, Sporobolis africanus* and *T. triandra.*

7. Wetland (Vegetation types: 13.1, 13.2)

   Wetland and riparian vegetation occurs along the banks of all the rivers and streams in the reserve. *Imperata cylindrica* dominates the wetland areas, whereas tall broadleaved trees, mainly *Ficus* spp. dominate small groves along riverbanks.

8. Unused vegetation types (Vegetation types: 1, 2.1, 2.2, 11,14)

   These areas are inaccessible or offer no food for white rhinos. Montane grassland, cliffs and scarps are too steep for white rhino. Degraded areas are bare open patches and have very little or no grass cover and built up areas (e.g. Camps, offices) are fenced off to rhino.

Table 2: Areas (km^2) of the seven habitat types key for white rhinos found in the Ithala Game Reserve. Habitats not important for white rhinos are combined into the 'Other' category.

	Total (km^2)
Bushveld	142.9
Wooded Grassland	61.1
Old Land Grassland	25.0
Wetland	21.8
Rocky Outcrop	10.0
Forest	6.6
Grassland	1.2
Other	26.5

Rainfall and temperature

The long-term mean annual rainfall for the Ithala Game Reserve is 785 mm, varying from 384 mm in dry years to 1239 mm in wet years (Van Rooyen & Van Rooyen 2008). Using rainfall data collected in the reserve from 2001 to 2009, I defined the wet season as November to February where mean monthly rainfall was 114 ± 12 mm (Figure 2). During this time, approximately 85% (~455 mm/year) of the annual rainfall takes place. I defined the dry season as May to August with each month experiencing a mean rainfall of 12 ± 3 mm. In contrast to the wet season, less than 10% (~47 mm/year) of the annual rain falls during the dry season (Figure 2). Transitional periods between the wet and dry seasons have a steady increase (end of dry to the beginning of the wet season) or decrease (end of wet to the beginning of dry season) in monthly rainfall.

The mean annual temperature in the reserve is 20° C, although the temperature differs across the reserve with altitude. Summer temperatures range between 15° C and 27° C, while winter temperatures range between 4° C and 20° C (Van Rooyen & Van Rooyen 2008).
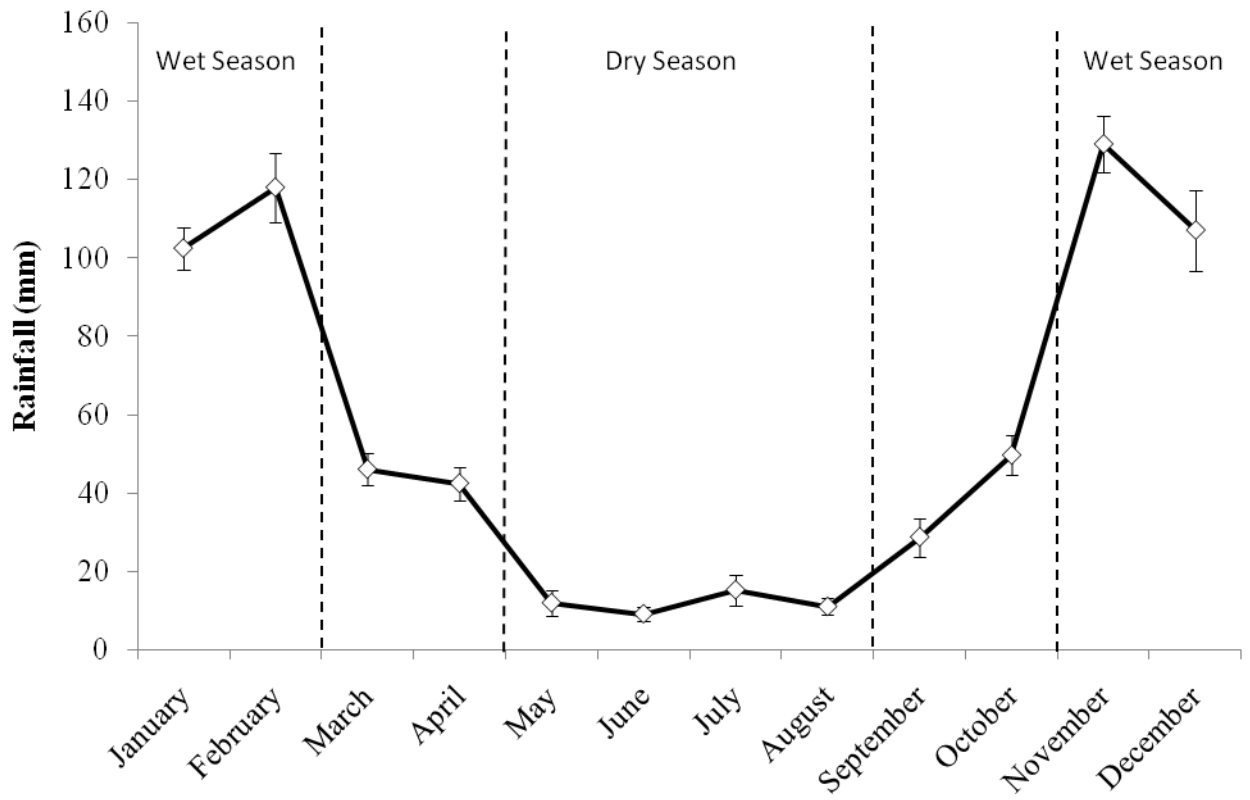
Figure 2: Mean (± SD) monthly rainfall for the years 2000 to 2008 at Ithala Game Reserve, KwaZulu-Natal. Wet and dry seasons are indicated with transitional periods found between them (data provided by Ithala Game Reserve).

23

Data Collection

Home ranges

I used an adaptive kernel estimator with least squares cross-validation of the smoothing parameter (Worton 1989) to generate home ranges. Data points consisted of positional sightings collected by reserve staff over nine years (2001 to 2009) (see below for how years were classified). Unfortunately, these sightings were not recorded using GPS positions, but rather placed into 1 km^2 grid square positions. Each grid square position has a precision of approximately 1000 m and thus the rhino position could fall anywhere within the assigned grid. Generally, management staff assign the position to the midpoint of the grid. Instead of using the midpoint for the different sightings, I assigned each position a random position in decimal degrees within each grid square. I did this by generating a Monte Carlo simulation to generate 1000 random positions. I then calculated an average from these and used that position as the sighting point.

For each adult female (N = 21), I had more than 30 independent locations per season (i.e. 32 to 59 sightings per individual) over the nine year period. Generally there were three sightings per month (range 1-7) for each individual. I only used multiple sightings from a month when these sightings were at least one day (i.e. 24 hours) apart. This reduced the autocorrelation between the different sightings (Swihart & Slade 1985).

Adaptive kernel estimators require a minimum of 30 independent sightings to determine accurate home ranges (Worton 1989, 1995). By exceeding the required minimum number of sightings, I was able to avoid overestimating home range size and thus report more accurate ranges (Aebischer 1993, Girard *et al.* 2002). I used a 95% contour to define a home range. I did not generate home range cores, because of the poor precision (1000 m) of the points generated within each grid square. All home ranges were calculated using the Geospatial Modelling Environment (Beyer 2012). Area calculations and habitat use

24

extraction was done in Arcmap 10 (ESRI, ©1999-2012) with the projected coordinate system "WGS 1984 UTM Zone 36S" using the Intersect tool.

Defining female home ranges

In order to account for the variability in rainfall between the different years over which the positional data were collected, I first separated the data into average years, wet years and dry years. Average years were defined as years where the rainfall was within ± 250 mm of the mean annual rainfall (758 mm) (i.e. 508 mm to 1008 mm). Wet years had rainfall of greater than 1008 mm and dry years were ones with less than 508 mm of rainfall.

My first intention was to generate separate seasonal home ranges in each of the three year categories (dry, average, wet). Unfortunately, the number of positions in the different seasons (i.e. wet, dry) within each of the three categories was less than the required minimum of 30 positions needed to generate accurate home ranges (Worton 1989). In order to meet the required minimum of 30 points, I combined data from the average and wet rainfall years. I did this as a number of studies have shown that during wet years, animals generally do not alter their home ranges as they are able to access the necessary resources within their normal home ranges. For example, Loarie *et al.* (2009) found that, for elephants, seasonal home ranges only changed during dry years (i.e. they became smaller) and did not differ between normal and wet years. In addition, Owen-Smith (1975) found that during wet years overall food quality is generally higher and thus the female white rhinos did not need to alter their home ranges. Moreover, the rhinos tended to remain within the core of their home ranges where food was abundant (Owen-Smith 1975, 1988).

However, despite the support from these studies, I wanted to ensure that the wet year positions were spatially similar to the positions in the average rainfall years. To do this, I first generated home ranges for each adult female using the limited points recorded in the average

rainfall years. Although these home ranges were likely not accurate due to the limited number of points, it gave some indication of spatial distribution of each female. I then overlaid the wet season locations onto the average year home ranges (see example in Figure 3) to determine whether these data fell within the 95% average year home range boundary, and whether the points were similar spatially.

For all 21 females, the wet season points fell within the average year home ranges and the points extensively overlapped (e.g. Figure 3). As a result, I felt confident to combine the data from the average and wet years. Having done that, I then generated new seasonal home ranges using the combined average and wet year data. This provided me with enough data to meet the minimum requirement of 30 independent locations in each season for 16 of the 21 females.

To estimate seasonal shifts in the home ranges, I overlaid the wet and dry season ranges in Arcmap 10 (ESRI, ©1999-2012). I then generated shape files of the non-overlapping areas in the two seasons to calculate seasonal shift (km^2) of the home ranges of each female white rhino. Due to the initial error generated by using 1 km^2 grids for the rhino positions as opposed to GPS positions, I only considered home range shifts of >5 km^2 as true shifts in home ranges and thus potentially habitat use. I used shifts of >5 km^2 as these represented the smallest shifts that the females in Ithala made that would likely not be affected by the initial error and thus provide reliable results.

Searching for high quality food, can result in changes in an individual's home range size and/or position (White *et al.* 2007). Unfortunately, I was unable to generate separate home ranges from positions recorded in dry years. However, in an attempt to determine whether white rhinos altered their home ranges during dry years, I added the dry year positions to the average and wet year data. Even though the low sample size of dry years positions for the different females (mean N = 5 ± 3) does not allow for definitive results, the

addition of the positions enabled me to indirectly see whether the addition of these dry year positions altered the size, position and/or habitat use patterns of the white rhino average home ranges.

Habitat quality

I sampled grass quality and quantity seasonally for each habitat during the dry and wet seasons of 2009, which fell within the variance for average rainfall years (i.e. 919 mm). As a result, I have considered these data sufficient to describe the seasonal variation (wet vs. dry) in habitat quality during the combined average and wet rainfall years. Sample sites were selected in 10 patches (i.e. foraging areas; see Owen-Smith 2002) of each of the seven key habitat types. Sampling took place along a 100 m East to West transect within each area during the wet (January and February) and dry (June, July) seasons. In each area, I collected 10 samples, each separated by 10 m.

Grass greenness and height

As a simple estimate of grass quality, I measured grass greenness in the different seasons in 2009 as the proportion of green grass using Walker's eight point scale (Walker 1976). Specifically, I utilised the grass greenness categories of: 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99% and 100%. I did this within ten 0.25 m^2 quadrats within each foraging area. The specific foraging areas sampled of the different habitat types were predetermined by selecting 10 foraging areas of each habitat type throughout the reserve. This ensured that I collected a representative sample of each habitat type. Within each foraging area, I placed the 10 quadrats 10 m apart along an East-West transect starting at a random point within each foraging area. I repeated this procedure in each habitat type in both the wet and dry seasons.

Figure 3: Dry season home ranges for two adult females generated using the limited positions data from average rainfall years (filled circles). Wet year positions (filled triangles) were overlaid to determine whether these data fell within the 95% average year home range boundary. As they did, I used the combined average and wet year data to generate the home ranges for all 21 of the adult female white rhinos in the Ithala Game Reserve.

This resulted in N = 100 quadrats per habitat type per season.

      The second measure of grass quality was estimated using Near-infrared spectrometry (NIRS) (Andueza *et al.* 2011). To determine seasonal changes in grass quality, I analysed samples (approximately 15 g) collected at each site through a 6500 near-infrared spectrometer in reflectance mode recording visible and near infrared (400 – 2500 nm) spectra. Prior to analyses, the grass samples were dried for 3 days at 70° C and milled to 0.1 cm. This ensured that the samples had a correct consistency for the analysis. I collected reflectance spectra for each sample at UKZN and then sent these to the Département Productions et Filières, Libramont, Belgium. Nutritional values of each sample were determined in Belgium using their reference library of South African grass species. This reference library was generated by first conducting chemical analysis and comparing these values with the reflective spectra patterns (Brown & Moore, 1987; Corson *et al,* 1999). From the spectra, I obtained the percentages of dry matter, ash, nitrogen, crude protein, neutral detergent fibre (NDF), acid detergent fibre (ADF), cellulose and Acid detergent lignin (ADL). I limited my analysis to crude protein and neutral detergent fibre (NDF) to describe the nutritional quality of the grass. This is because for herbivores, crude protein provides an index of food quality, and NDF is an index of cellulose, hemicellulose and lignin, and thus fibre content indicating digestibility (Van Soest 1994). Moreover, crude protein is limiting in herbivores, for example ruminants will avoid forage with crude protein levels below six percent as they will be unable to meet their nutritional requirements (Van Soest 1994). In contrast, hindgut fermenters can tolerate lower levels due to their greater ability to digest fibre (Clauss & Hummel 2005). Furthermore, fibre is an important indicator of potential digestibility (Demment & Van Soest 1985), and NDF provides a more accurate representation of cell wall and fibre components of the plant compared to ADF (Van Soest 1963).

Finally, to estimate grass availability, I measured average grass height (mm) within each of the 200 quadrats (i.e. 100 quadrats/season). I generated a mean grass height value for each quadrat by measuring height in the centre and four corners of the quadrat using a tape measure. I then used the mean heights of the quadrats to calculate mean grass height at each site.

Data analysis

Home range and habitat use

I first tested for differences in wet and dry season home range area using a student t-test. I then used Multi-Response Blocked Procedures (MRBP) (White & Garrot 1990), with Euclidean distances (α was set at 0.01) (Kernohan *et al.* 1998), using PC-ORD (McCune & Mefford 1999) to establish whether there was a significant difference in the proportional habitat use between the seasonal home ranges during wet and dry seasons. I used this test as the data was multivariate and the MRBD does not require distributional assumptions. The blocked procedure using Euclidean distances identifies numerical differences between individuals (Zimmerman *et al.* 1985)

I calculated proportional habitat use as the area of each habitat type found within the home range divided by the total area of the home range. Significance values associated with each seasonal comparison denote the probability that the utilisation distribution (UD) was different between the wet and dry seasons for at least two vegetation classes (Zimmerman *et al.* 1985).

Greenness and height

I tested for differences in grass height between wet and dry seasons using a Student's t-test. I then went on to test whether changes in grass greenness and height would explain the

changes in the habitat types that had a difference in seasonal use. In order to determine whether the greenness and/or height of grass influenced the use of the two key habitats (i.e. Bushveld, Wooded grasslands), I examined trends in the change of area used and the greenness and grass height of the habitats added (or excluded) using regression analysis. I tested the data for normality using a Shapiro-wilk test. Data were normally distributed for all variables, thus no transformations were necessary. I used linear regression to determine whether changes in grass greenness (%) and grass height (cm) influenced changes in the seasonal areas of key habitats within the home ranges (km^2).

Nutritional Quality

To determine whether changes in nutritional value influenced habitat use within the home ranges, I determined how crude protein content and NDF varied between seasons (wet and dry) and habitat (bushveld, forest, grassland, old lands, wetland, wooded grassland, rocky outcrop). I used a general linear model (GLM) with a reciprocal link function adapted for data with a gamma distribution to account for the binomial distribution of the data between the wet and dry seasons (Crawley 2007). I then contrasted each variable with every other variable (i.e. Habitat) for *post hoc* tests to determine differences between habitats during the wet and dry seasons.

Density

Density of white rhinos was calculated as the number of individuals per km^2.

Chapter 3: RESULTS

The density of white rhino females in the reserve was 0.14 rhino / km^2. The home ranges of these females (N= 21), overlapped extensively with a number of the other adult females' home ranges within the reserve (9 ± 4 home ranges overlap; max= 15 and min= 3 home ranges that overlapped). These overlaps occurred in both the wet and dry seasons.

Seasonal home ranges

During the combined average plus wet rainfall years, I found no difference between the wet and dry seasonal home range areas (t_{24}= 1.11, P = 0.278). This indicates that individuals did not expand or contract their seasonal home ranges during these years. The mean wet season home range was 32 ± 17 km^2 and the mean dry season home range was 27 ± 10 km^2. Although seasonal home range area of the rhinos did not change, I did record a shift in the seasonal positions of many of the home ranges that indicated that during these years there is a seasonal change in habitat use (Table 3). In total, only 10 adult females had shifts of > 5 km^2. Thus, these 10 individuals were used to determine seasonal changes in habitat use.

Table 3: Seasonal shift in the white rhino home ranges (km^2). * indicates shifts of > 5 km^2 and thus those females used in the analysis (N= 10).

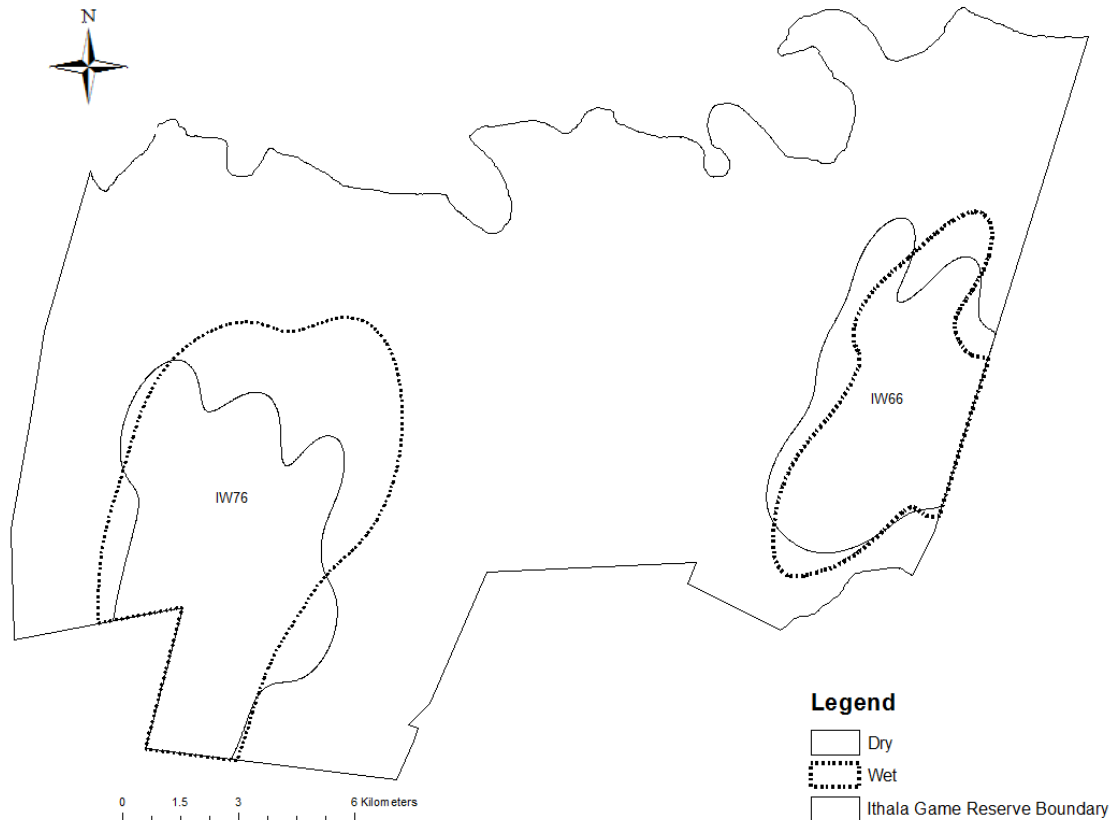|	Seasonal shift (km^2)
IW04	9*
IW102	0
IW104	6*
IW 124	13*
IW 126	18*
IW 13	3
IW 30	37*
IW 32	3
IW 36	10*
IW 44	11*
IW 46	11*
IW 64	3
IW 66	2
IW 70	2
IW 74	8*
IW 76	15*

Figure 4: Map showing examples of the seasonal shift in home range position but similarity in size of wet (broken lines) and dry (solid lines) season home ranges for two adult female white rhinos (IW66 and IW76) in the Ithala Game Reserve.

Habitat use

The multi-response blocked permutation showed that for combined average and high rainfall years the seasonal shift in home ranges resulted in individuals changing their habitat use during the dry season (T = -2.136, P = 0.026). Two habitat types showed marked seasonal changes, namely Bushveld (T= 0.35, df=15, P<0.001) and Wooded Grasslands (T= 0.98, df=15, P=0.003). Individuals significantly increased their proportional use of Bushveld from 43 ± 13% in the wet season to 48 ± 13% in the dry season. In contrast, the females' use of Wooded Grasslands declined significantly from 27 ± 16% during the wet season to 20 ± 13% during the dry season (Figure 5).
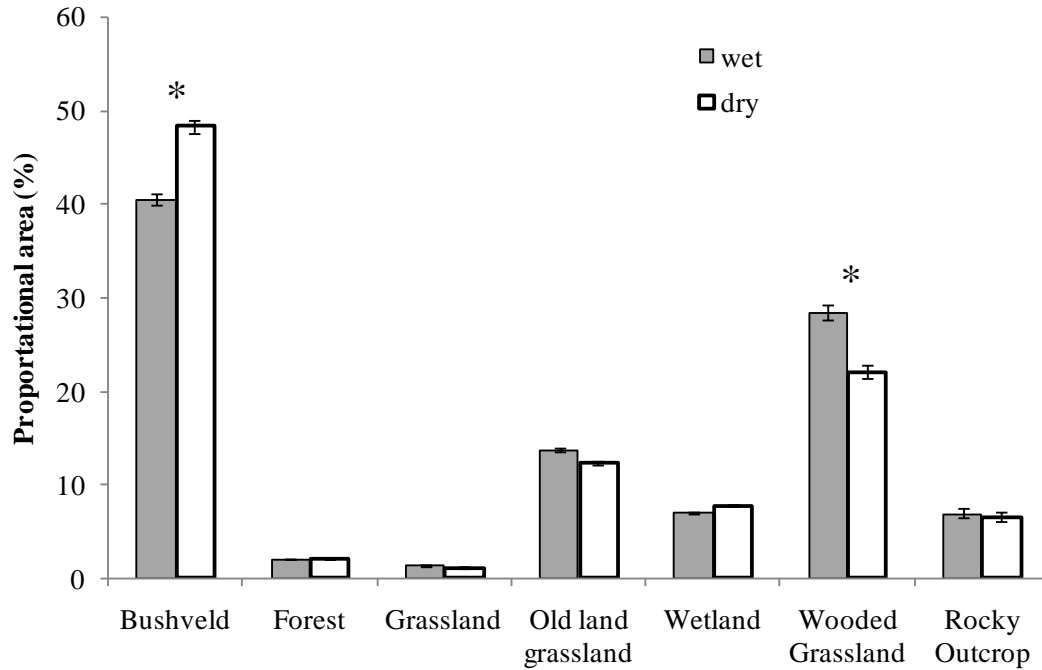
Figure 5: Mean (± SE) proportional wet and dry season habitat use during average rainfall years. * indicates significant (P<0.05) difference between the wet and dry seasons.

Greenness and height

Grass throughout the reserve was taller and greener in the wet season compared to the dry season (wet season height = 23 ±14 cm, dry season height 15 ± 12 cm, $T_{14} = 13.45$, P < 0.0001) (wet season greenness = 76 − 90%, dry season greenness = 51 − 75%, $T_{14} = 4.39$, P < 0.0001). However, seasonal changes in grass greenness and height did not explain the differences in seasonal habitat use of the two key habitats Bushveld and Wooded Grassland by the white rhinos (Table 4).

Table 4: Regression results for height and greenness relative to proportional (%) habitat area from each female white rhino for average rainfall years (* identifies significant value i.e. p < 0.05).

	Height				Greenness				Height*Greenness			
	R^2	P	df	F	R^2	P	df	F	R^2	P	df	F
Bushveld	0.06	0.704	14	0.1501	0.034	0.486	14	0.0352	0.18	0.867	12	0.6326
Wooded Grassland	0.07	0.79	14	0.07312	0.033	0.482	14	0.5116	0.07	0.608	12	0.2394

Nutritional data

Crude protein content of the grass was higher in the wet season than the dry season (t_{138}=5.267, P < 0.001, Table 5, Figure 6). Across all habitats, there was a significant drop in crude protein of around 5% from the wet (11 ± 6% S.D. of Dry Matter) to the dry season (6± 2% S.D. of Dry Matter) (t_{138}= -8.164, P < 0.001, Figure 6). In contrast, NDF increased significantly by approximately 4% across all habitats in the dry season with dry season levels reaching 78 ± 5% of Dry Matter up from 74 ± 4% of Dry Matter during the wet season (F_6=34.24, P<0.00, Figure 7).

Table 5: Seasonal changes in crude protein across the seven habitat types in the Ithala Game Reserve.

Habitat	Wet Season	Dry season	Seasonal Change
Bushveld	11.5	6.1	5.4
Forest	14.6	5.9	8.7
Grassland	10.2	5.7	4.4
Old Land Grassland	10.7	6.1	4.6
Wetland	10.6	5.6	5.0
Wooded Grassland	10.7	5.7	5.1
Rocky Outcrop	10.3	7.2	3.1

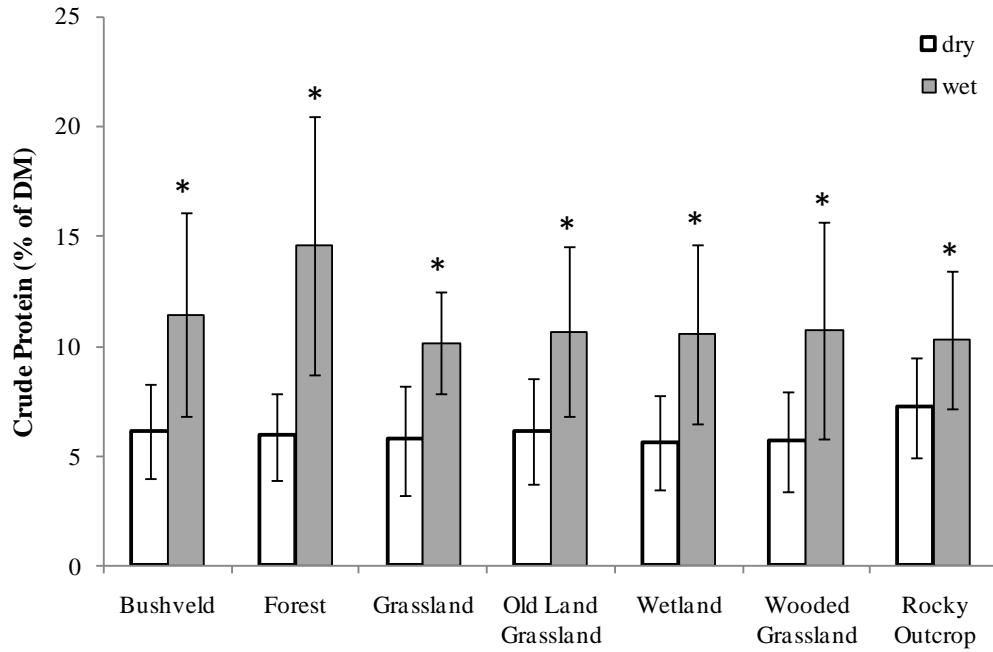Figure 6: Mean crude protein (±SD) as a percentage of dry matter (DM) for the different grassland habitat types found in the Ithala Game Reserve. * Indicates a significant seasonal increase (P<0.05) in crude protein.
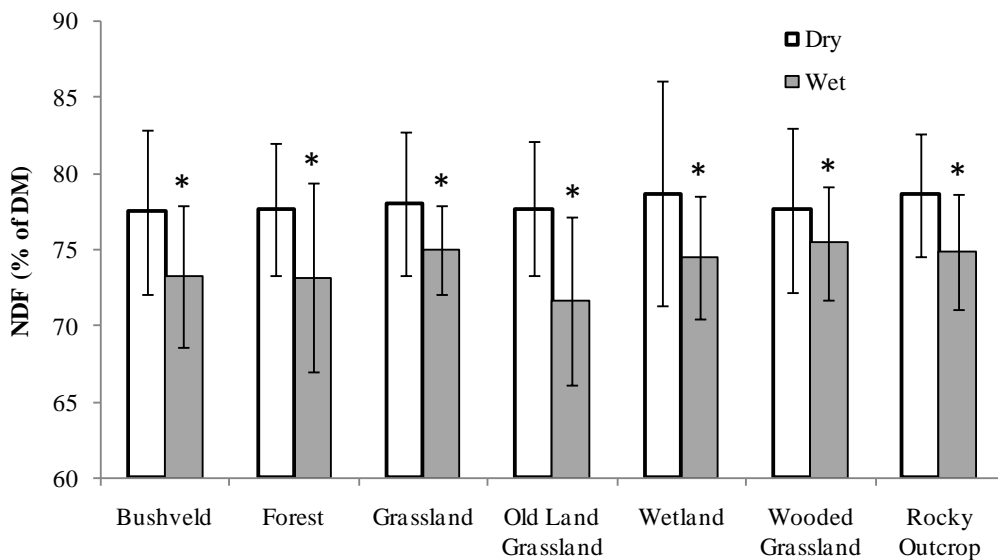

Figure 7: Mean neutral detergent fibre (NDF) (± SD) as a percentage of dry matter (DM) for habitats in Ithala Game Reserve. * Indicates a significant seasonal decline (P<0.05) in NDF.

The average seasonal crude protein decrease across the habitats during the dry season was 40% of the wet season content. Crude protein content of both Bushveld and Wooded grasslands dropped approximately 5% in the dry season compared to the wet season (Bushveld: wet season = 11.5 ± 4.7%, dry season = 6.7 ± 2.4% (F_7= 6.08, P < 0.001); Wooded grasslands: wet season = 10.42 ± 4.4%, dry season = 5.6 ± 2.3% (F_7= 6.3, P < 0.001)). Although the decrease in crude protein was similar for both habitats, Wooded Grasslands had the lowest dry season crude protein content (5.6 ± 2.3 %) of all the habitats in the reserve (Forest= 6.9 %, Wetland= 5.7%, Grassland= 6.0%, Old Land Grassland= 6.2%, Rocky outcrop= 8.4%). In contrast, Bushveld had the smallest seasonal decrease in crude protein.

Effect of low rainfall years on home range size and habitat use

After adding in the data from the dry years to the combined average and wet years, I once again found that the wet and dry season home range sizes did not differ ($F_{2, 20}$ = 0.94, P = 0.34). Mean wet season home range was 32 ± 18 km^2 and the mean dry season home range was 30 ± 10 km^2. Although there was no change in home range area (t_{20}= 1.48, P= 0.19), the shift in home ranges and habitat use was consistent with years that received average rainfall.

As during the combined average and wet years, the proportional area of Bushveld utilised by white rhino females increased during the dry season, while the proportional use of Wooded Grasslands decreased (T = 4.63, P = 0.029) (Figure 8). The addition of the dry years resulted in a decrease in the use of Wooded Grasslands by 1 ± 0.5% in the dry season and an increase use of Bushveld 3 ± 0.3%. The MRBP showed the same habitat pattern as in the average years, but the degree of separation between the seasonal use of these two habitats increased with dry year data added to the analysis ($T_{average\ rainfall\ years}$ = -2.71, P= 0.021;

$T_{\text{Average rainfall years with dry years}} = 4.71$, P= 0.023). This tends to suggest that during dry years, white rhino females show the same seasonal changes in habitat use as in the average and wet years, but the degree of change was larger.
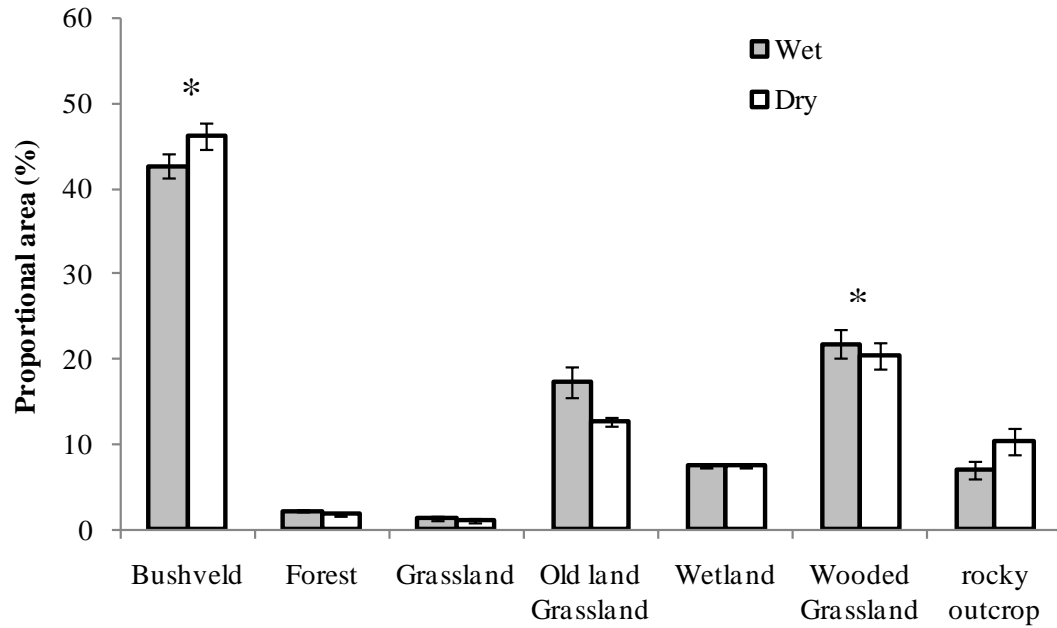

Figure 8: Mean (± SE) proportional habitat use (% of total home range area) for female white rhinos in the wet and dry seasons for all years. * indicates significant (P<0.05) change between the wet and dry seasons.

Chapter 4: DISCUSSION

During the dry season, adult female white rhinos have been found to either expand (Owen-Smith 1988) or alter (White *et al.* 2007) their home ranges. It has been suggested, that these changes could be due to these females either trying to incorporate habitats that contained either higher quality food, or those with greater food availability (Owen-Smith 1988, White *et al.* 2007). The findings of my study indicate that in the combined average and wet rainfall years, white rhino females in the Ithala Game Reserve altered their dry season home ranges to incorporate the habitat that provided the best quality food (i.e. Bushveld). When I then added the dry rainfall years to gain insight into what may happen during dry periods, I found that as with the combined average and wet years, female white rhinos showed an even greater preference for the Bushveld habitat. These results suggest that in average and wet rainfall years, seasonal home range expansion is driven by the search for increased intake of higher quality food. The inclusion of the data from dry years suggests that this may also be true in dry years. However, as I had limited data for these dry years, it may also be possible that adult females take advantage of their tolerance of low quality food (Owen-Smith 1988, Fritz *et al.* 2002). As a result, this requires further exploration before a definitive answer can be given.

Data from average, wet and dry rainfall years shows that female white rhino in the Ithala Game Reserve have larger home ranges (34 ± 18 km^2) compared to other parks. For example, in Hluhluwe-iMfolozi Park, Owen-Smith (1975) found home ranges to range between 8 and 15 km^2, similarly Shrader (2003) recorded home ranges between 10 and 15 km^2, while White *et al.* (2007) estimated home ranges to be approximately 20 km^2. In Kruger National Park, Pienaar *et al.* (1993) estimated white rhino home ranges to be between 12 and 23 km^2. Finally, Rachlow *et al.* (1999) found home ranges in Matobo National Park,

Zimbabwe, to be between 19 and 59 km^2, but attributed this wide spread to smaller home ranges in areas with high rhino density (i.e. conservation areas) and the larger homes ranges in areas with a lower white rhino density (i.e. communal lands).

Home range size represents a compromise between individual metabolic requirements and social pressure in relation to landscape quality (Owen-Smith 1988). Thus, larger home ranges in Ithala may be due to the lower white rhino density (0.16 rhino/km^2) compared to Hluhluwe-iMfolozi (5.3 rhino/km^2) and Kruger National Park (0.5 rhino/km^2) as female home ranges are constricted at higher densities (Rachlow *et al.* 1999). At lower densities, there is less competition for resources between individuals. Moreover, if there are lower social pressures, individuals can spread out and use a larger area as they will have greater accessibility to resources (Burt 1943).

The broad aim of my study was to determine whether female white rhinos adjusted their seasonal home ranges to access better quality food or a larger quantity of food. Owen-Smith (1975) found that home ranges expanded during the dry season as individuals shifted between different grassland types. Thus, he suggested that white rhinos expanded their home ranges in order to maintain their intake of high quality food. In contrast, Pienaar *et al.* (1993) found that white rhinos in Kruger National Park contracted their home ranges during the dry season and attributed this seasonal contraction to a decrease in water availability during the dry season. In a divergence from both these studies, White *et al.* (2007) found that female white rhino home range size did not vary between the wet and dry seasons. Rather, females altered the shape of their home ranges during the dry season. As with Owen-Smith (1975), White *et al.* (2007) suggested that these shifts were to incorporate better quality habitats. In line with the findings of White *et al.* (2007), I found that the wet and dry season home range sizes did not differ in the Ithala Game Reserve. Furthermore, the data from the combined

average and wet rainfall years indicated that the female white rhinos altered the shape of their home ranges in the dry season rather than expand them.

One potential explanation for the lack of seasonal home range expansion in my study may be the extreme topography found in Ithala, particularly in the eastern part of the reserve. Very steep and rocky areas are generally not accessible to megaherbivores such as white rhinos (Owen-Smith 1988) and elephants (Wall *et al.* 2006), but are common in Ithala. Thus it may be possible that opportunities for white rhinos to expand their home ranges seasonally are more limited in Ithala compared to white rhinos living in the Hluhluwe-iMfolozi Park. If this is the case, then it may be possible that limitations on expansion might lead to movement up and down altitudinal gradients within the white rhino home ranges. Unfortunately, the poor resolution of the positional data (1 km) did not allow for this analysis. Due to the degree of error associated with using random positions within the 1 km^2 grid system, altitudinal changes would need to be accompanied by very large positional shifts for the analysis to produce reliable results. This, however, was not the case in this study.

Altitudinal movement is well documented in northern hemisphere herbivores. For example, white- and black tailed deer, bison (*Bison bison*) and elk (*Cervus Canadensis*) move up and down the catena as snow makes forage inaccessible (Bowyer *et al*. 1998, Grund *et al.* 2002). In Africa, buffalo in the Serengeti move onto higher lying grasslands in the dry season to access habitats that provide more food during the drier winter months (Campbell & Borner 1995), similar patterns of movement have also been observed for small sedentary herds of springbok (*Antidorcas marsupialis*) (McNaughton 1978). As a result, it might be that the seasonal home range shifts of white rhinos that I recorded incorporate an unseen altitudinal aspect. If this is the case, then white rhinos may be shifting attitudinally within their home ranges to access unused resources and thus reduce their need to expand home range boundaries. Unfortunately, I did not collect data on altitudinal movements of the rhinos, thus

determining whether rhinos make these sorts of movements is beyond the scope of this study. However, this would be an interesting focus for future research, especially as it would be a unique example of a megaherbivore making these sorts of seasonal movements.

Despite not expanding their home ranges during the dry season, I did find that 10 of the females shifted the shapes of their home ranges by more than 5 km^2. This resulted in these females seasonally changing the proportion of the different habitats within their home ranges. Specifically, this shift resulted in female white rhinos increasing the proportion of the high quality Bushveld and decreasing the proportion of low quality Wooded Grasslands in their dry season home ranges. As a result, this supports the prediction that white rhinos should select habitats that will provide them with nutritionally superior food, so that they can maximise their nutritional intake.

A seasonal selection of higher quality habitats is not unique. For example, kudus seasonally move between habitats that provide high quality food and select species with the lowest chemical defences (Owen-Smith & Novellie 1982). In addition, moose (*Alces alces*) in North American tall grass rangelands selected home ranges containing the highest quality browse available and only made use of poorer species and poorer habitats when the nutritionally best species were depleted (van Beest *et al.* 2010). Georgiadis & McNaughton (1990) found that in the Serengeti, herbivores tend to aggregate in grazing areas where the grasses contain high levels of nutrients. Additionally, Ben-Shahar & Coe (1992) found that seasonal habitat selection of wildebeest and zebra in the Serengeti was influenced by the levels of P and N levels in grasses. These herbivores favoured grass communities that had a high proportion of species that retained high nutritional value for longer into the dry season (Ben-Shahar & Coe 1992).

A key difference between these herbivores and white rhinos are that white rhinos are much larger and thus should be able to remain in poor quality areas longer than smaller

herbivores due to their lower mass specific metabolic requirements. However, my results tend to suggest that white rhinos, like these smaller herbivores seek out high quality food throughout the year. For example, during the dry season the average decrease in crude protein was 40% of the wet season content. This decrease, however, was not consistent over all habitat types (Table 5). Bushveld retained a high crude protein content into the dry season (6.4% of dry matter) compared to other habitats (6 ± 2% S.D. of Dry Matter), while Wooded Grasslands had the lowest crude protein content of all the habitats during the dry season (5.3 % of dry matter). Thus, not surprisingly individuals incorporated more Bushveld into their dry season home ranges and decreased the use of Wooded Grasslands.

With regard to my alternative hypotheses of whether food quality (grass greenness, crude protein) or food quantity (grass height) was the driving factors behind the adjustment of the female white rhinos' home ranges, the findings tend to agree with Owen-Smith's (1988) suggestion that the white rhinos' relatively slow passage rate of food (due to their large body size) forces them to seek out high quality food. Thus, it would seem that the incorporation of the Wooded Grasslands into the dry season home range was an attempt by the rhinos to increase the availability high quality food in their home ranges.

As large herbivores, white rhinos are unlikely to select for particular forage species as they need to maintain sufficient intake to meet their metabolic requirements and therefore select food at larger spatial scales (Senft 1989, Bailey *et al.* 1996; O'Reagain 2001). For example, elephants (another megaherbivore) in Ithala Game Reserve select habitats initially and then the species within those habitats (Shrader *et al.* 2012). With regard to white rhinos, Shrader (2003) found that individuals also selected more for habitats rather than particular grass species. In contrast to my study, Shrader (2003) found that white rhinos favoured shorter grasslands during the dry season, but as the study was conducted during above average rainfall years, these grasslands retained higher than average forage availability.

Ultimately, the dominant plant species within habitats play a role in determining habitat quality and thus influence habitat selection (Shrader 2003, Shrader *et al.* 2012). In my study, the dominant plant species in Bushveld were similar to the species that white rhinos in the Hluhluwe-iMfolozi Park preferred. Specifically, the Bushveld habitat in the Ithala Game Reserve is dominated by *Eragrstis curvula, Heteropogon contortus, Panicum maximum* and *Themeda triandra*. In contrast, the grass layer in Wooded Grasslands is dominated by *Hyperthelia dissolute, Loudetia simplex*, and *Tristachya leucothrix* and, in some areas, *Cymbopogon excavates*. In contrast to the species found in the Bushveld habitat, these species are generally not eaten by white rhinos (Shrader 2003).

One surprising result of my study was that the white rhinos were not found extensively in the Grassland habitat type of Ithala. This is surprising as grasslands are widely considered to be the most important habitat type for white rhino foraging (Owen-Smith 1988, Shrader *et al.* 2006). For example, White *et al.* (2007) found that female white rhinos preferred grasslands, in Hluhluwe-iMfolozi Park, utilising them more than expected relative to availability. Of the different types of grasslands, one key type for many grazers is grazing lawns (McNaughton 1984, Fryxell 1991). Grazing lawns are present in Ithala Game Reserve, but they are generally small, widely scattered, and not very abundant (Bonnet, O., University of KwaZulu-Natal, unpublished data). Furthermore, they comprise *Cynodon dactylon* patches that have established in historic kraaling areas (Valls-Fox *et al.*in review).

In contrast to body size theory, the results of my study indicate that the food availability was not the driving factor behind the shifting of the adult female white rhinos' home ranges. I collected field data during a year that fell within the range of average rainfall years. However, it was at the upper end of these years. As a result, my data may provide an elevated measure of nutritional value. However, as plant nutritional quality is not likely to differ greatly between average and wet years (Georgiadis & McNaughton 1990), I am

confident that my data provide a good measure of the seasonal changes in the nutritional quality of the habitats during these combined years. Unfortunately, as I did not collect nutrition and availability data of food during the dry years, I am unable to determine how these changes during this period could affect seasonal habitat use. However, as suggested by Shrader *et al*. (2006) it is likely that in very dry years when high quality food is limited, that white rhinos will take advantage of the benefits of their large body size by ingesting low quality food, and utilising fat reserves to survive.

In addition to not recording food quality data during the dry season, I did not have enough positions to generate home ranges in dry years. However, by adding the available dry season data to the combined average and wet year data, I was able to gain some, if maybe only limited, insight into how dry years influence white rhino home ranges. Interestingly, the addition of the dry year data did not alter the white rhinos' dry season habitat selection patterns. As with the combined average and wet years, white rhinos selected the nutritionally superior Bushveld habitat, and avoided the poorer Wooded Grasslands. The only difference was that the strength of the selection of the Bushveld habitat increased suggesting a greater utilisation in dry years. As a result, this leaves an interesting question that could be explored in future studies.

In conclusion, the results of my study indicate that for white rhinos living in the Ithala Game Reserve, food quality plays an important role in influencing seasonal changes in home range shape/location. This is in line with the idea that despite their large body size, their slow passage rate requires them to eat a high quality food (Owen-Smith 1988). Thus, unlike other large mammals that have the ability to tolerate low quality food, but choose to eat high quality food, white rhinos seem to have to select high quality food and thus adjust their large-scale movements to obtain it.

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APPENDIX I: Home Ranges of female white rhinos in Ithala Game Reserve

This appendix is made up of the wet and dry season home range maps for the 16 adult female white rhinos in Ithala Game Reserve.
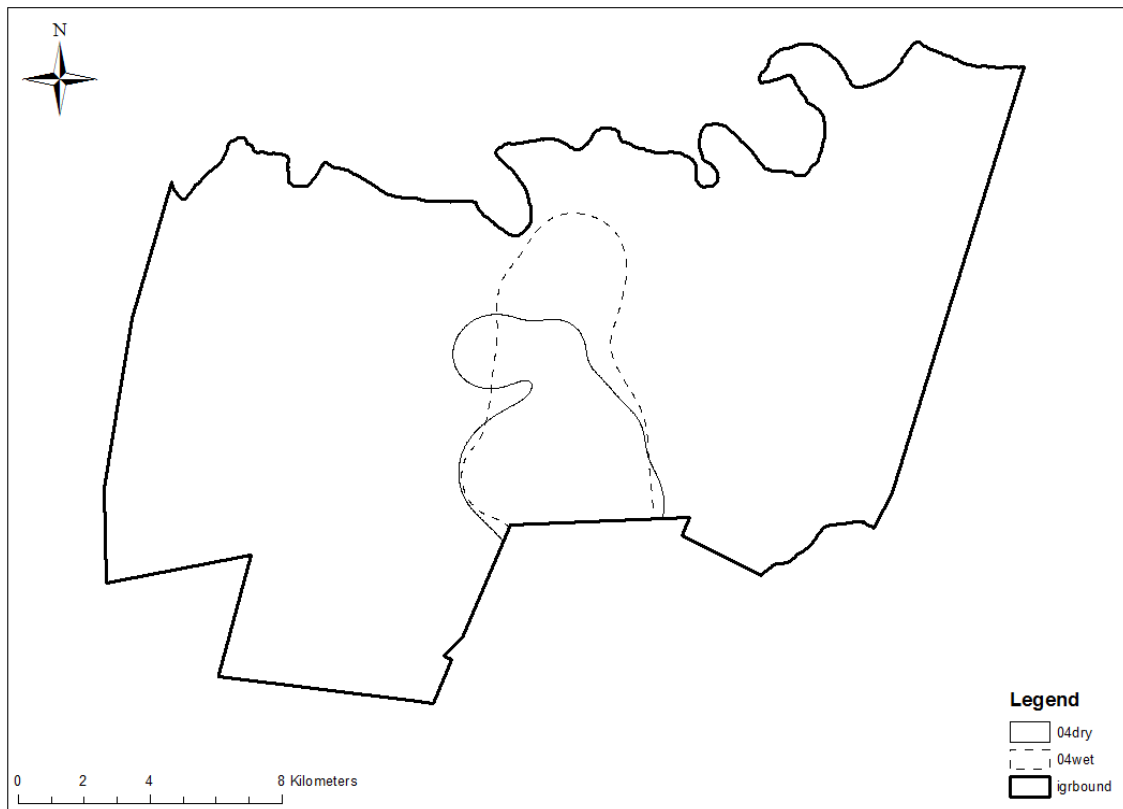
Figure 9: Wet (34 km^2) and dry (26 km^2) season home ranges for female IW04 at the Ithala Game Reserve.
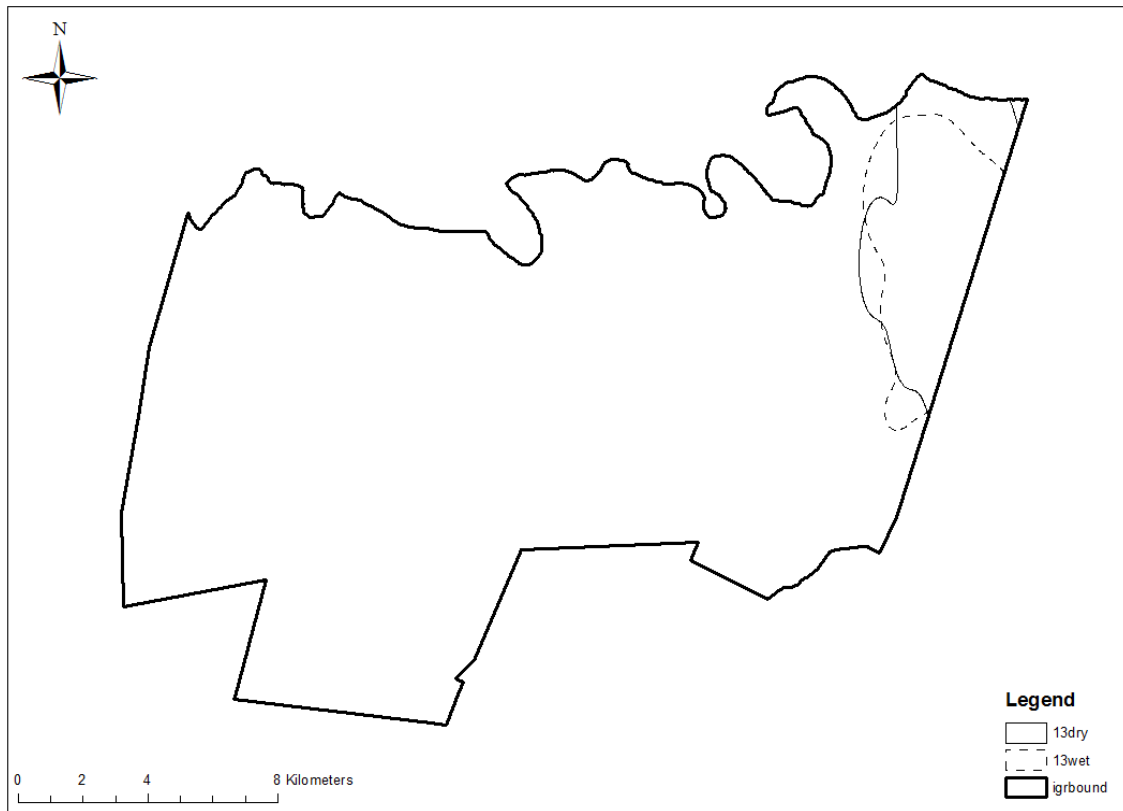
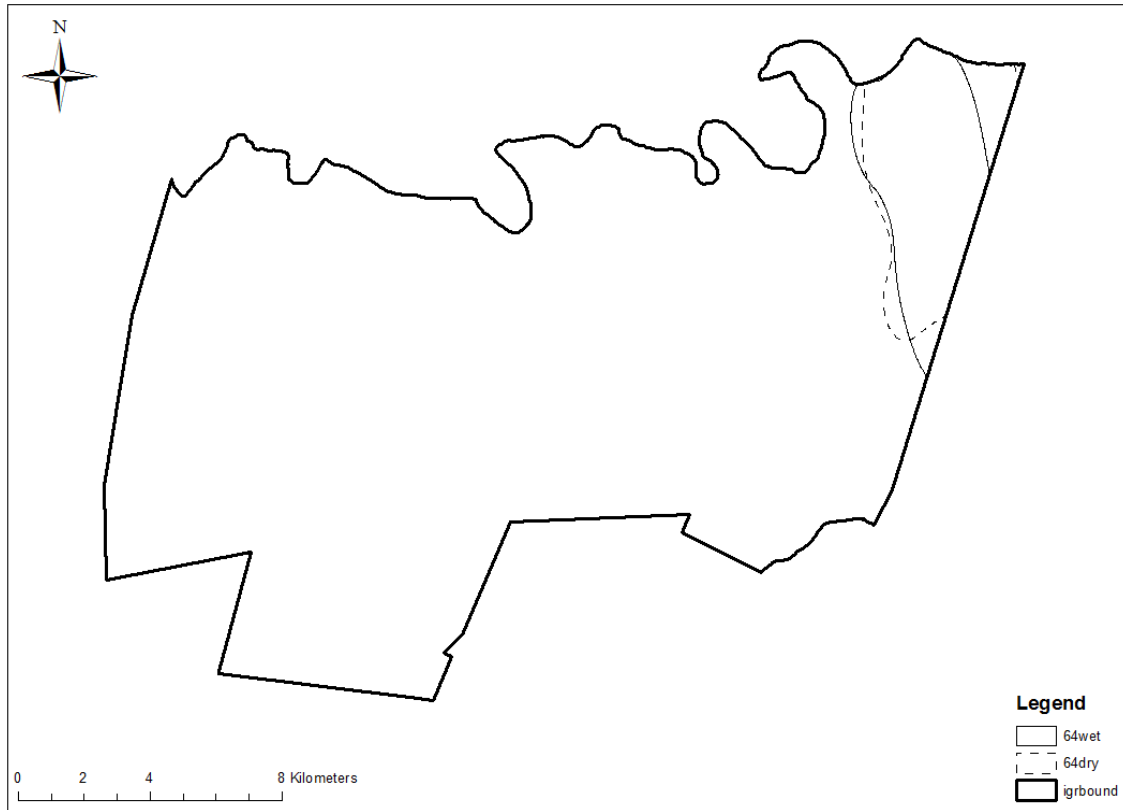Figure 10: Wet (22 km^2) and dry (25 km^2) season home ranges for female IW13 at the Ithala Game Reserve.
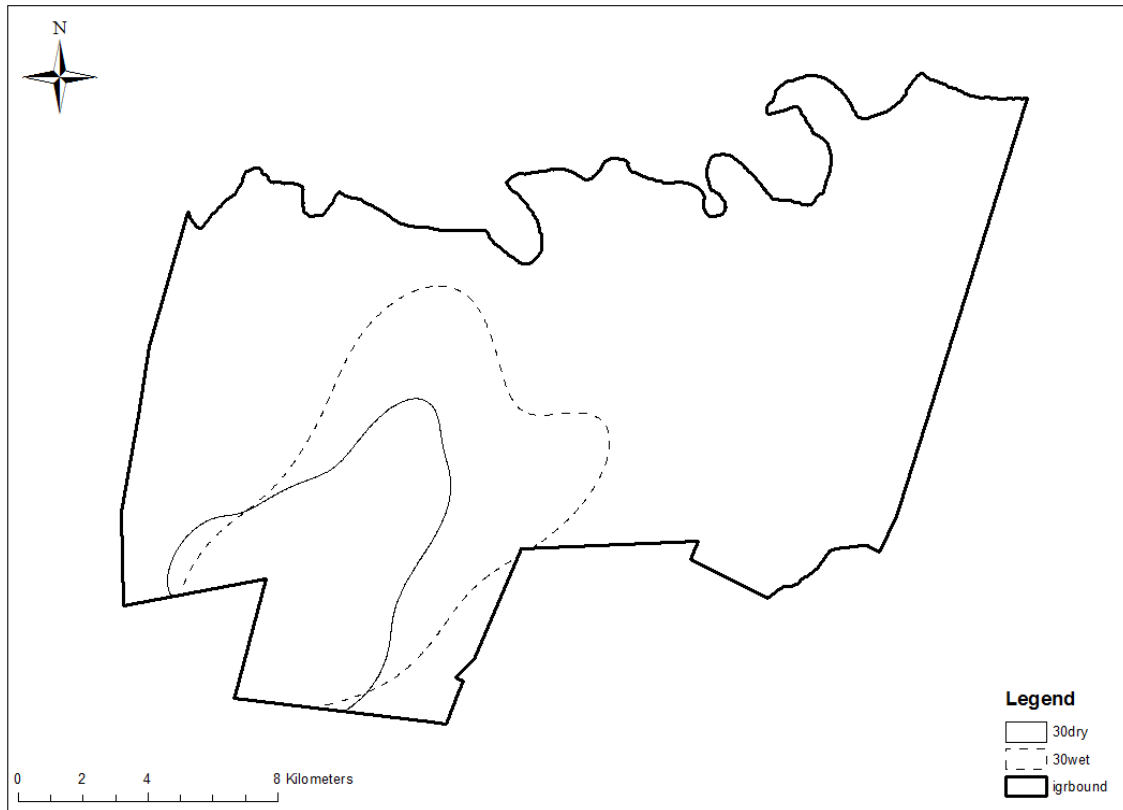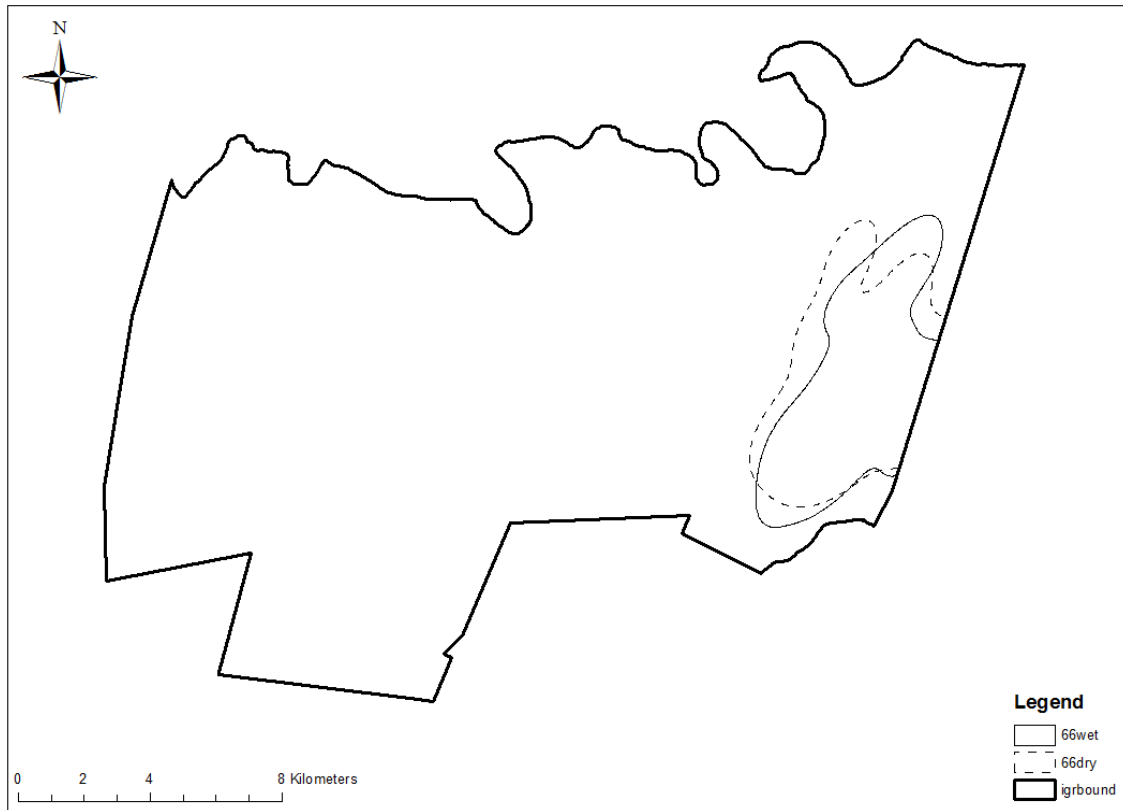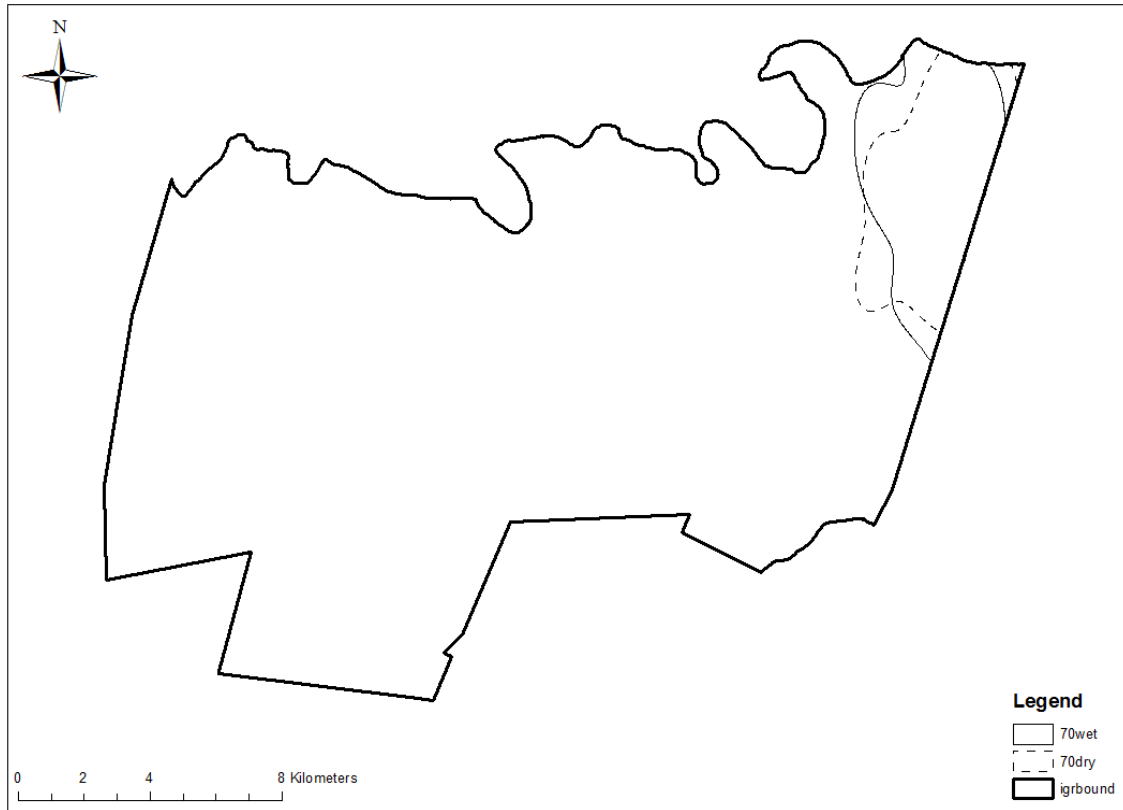
Figure 11: Wet (76 km^2) and dry (39 km^2) season home ranges for female IW30 at the Ithala Game Reserve.
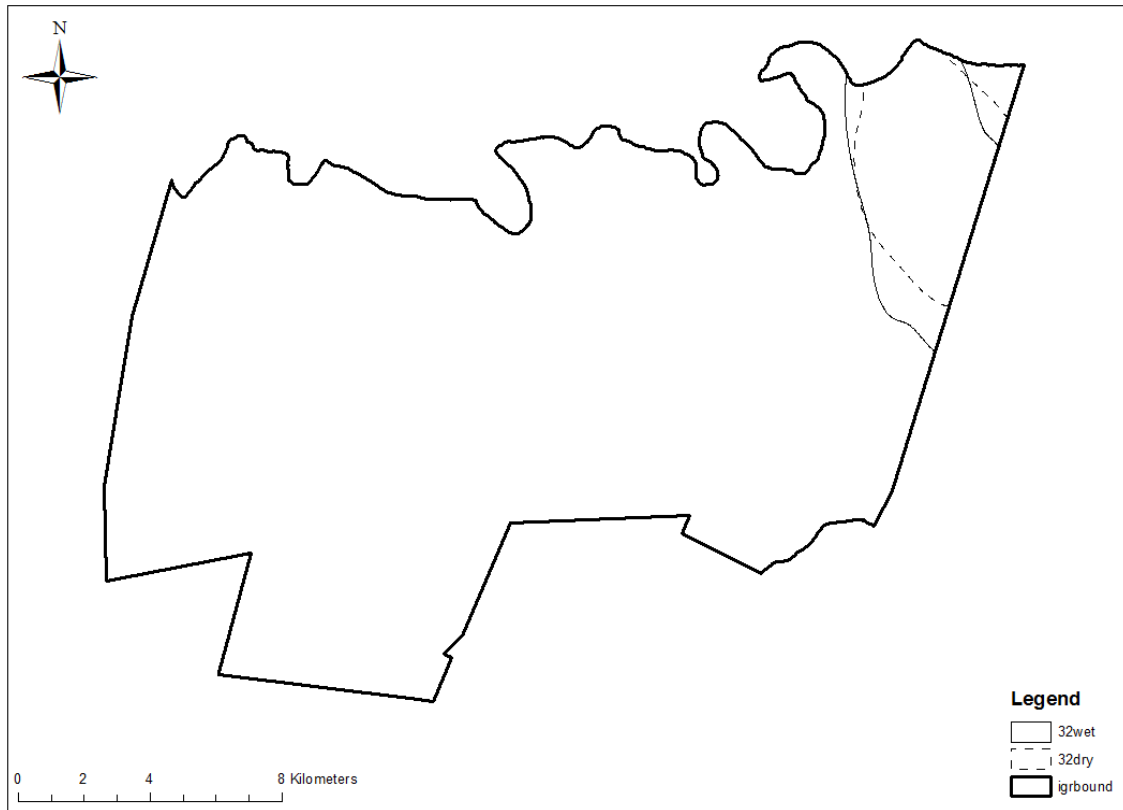
Figure 12: Wet (24 km^2) and dry (21 km^2) season home ranges for female IW32 at the Ithala Game Reserve.
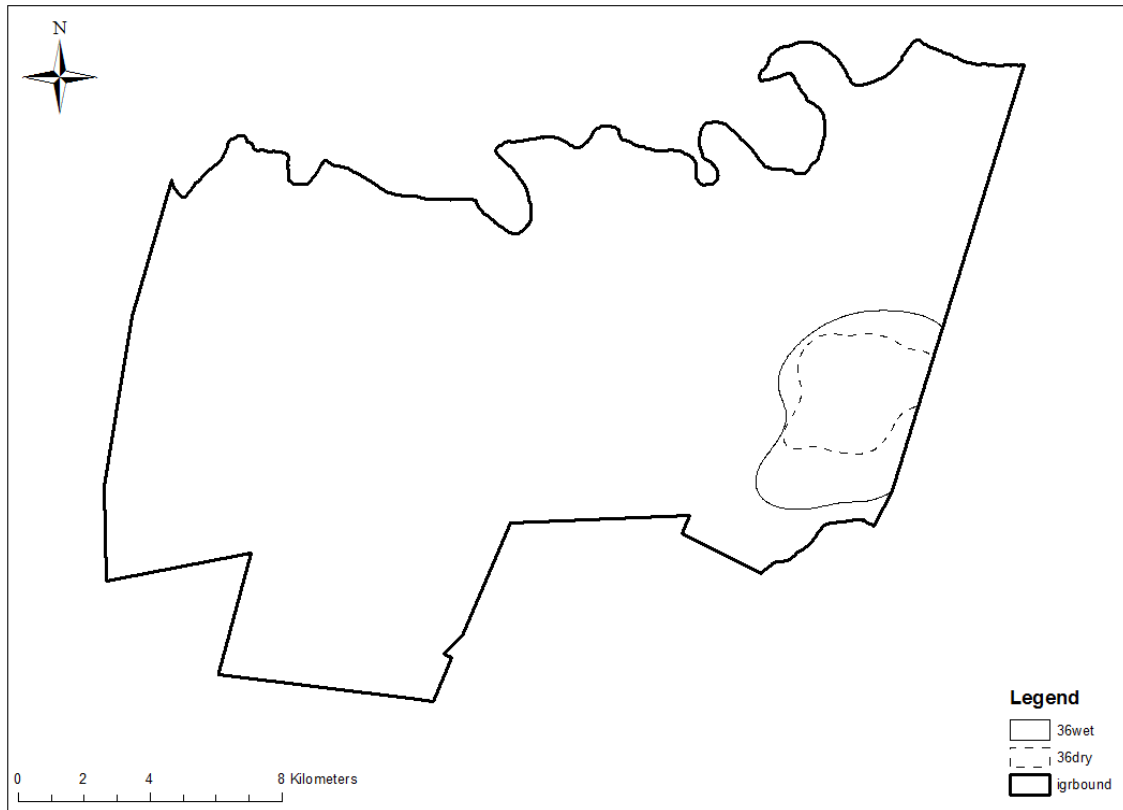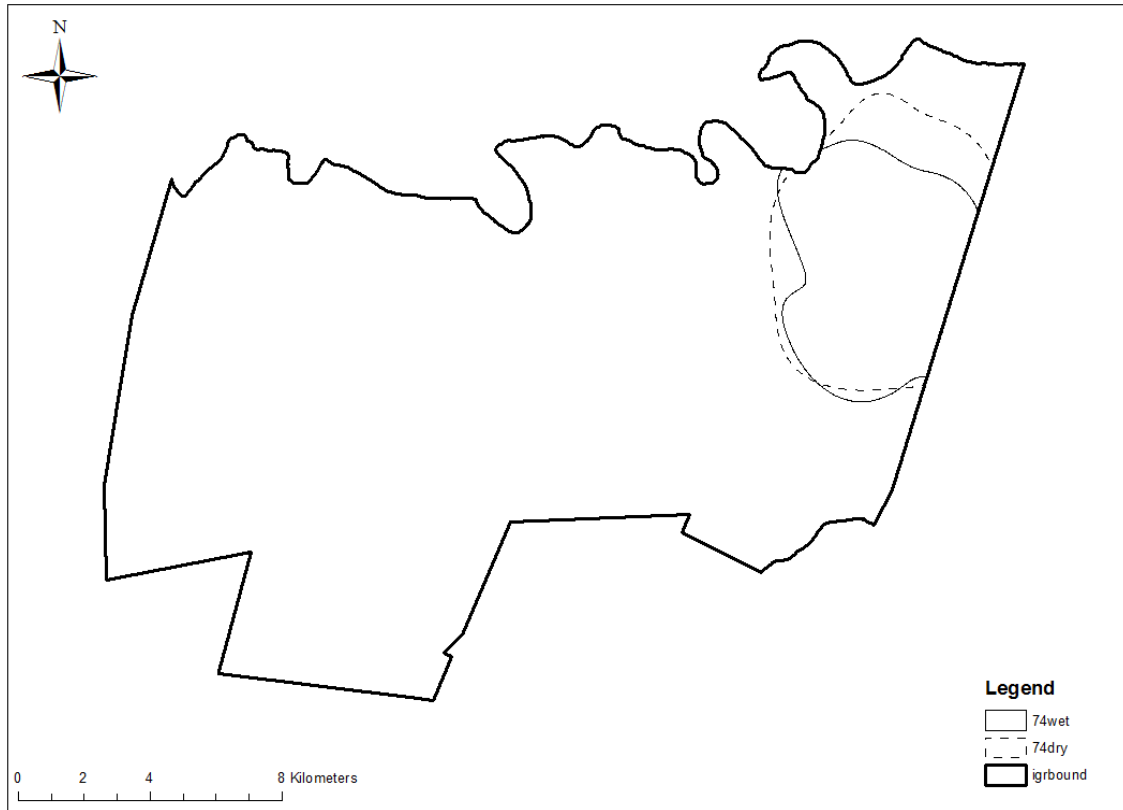
Figure 13: Wet (21 km^2) and dry (11 km^2) season home ranges for female IW36 at the Ithala Game Reserve.
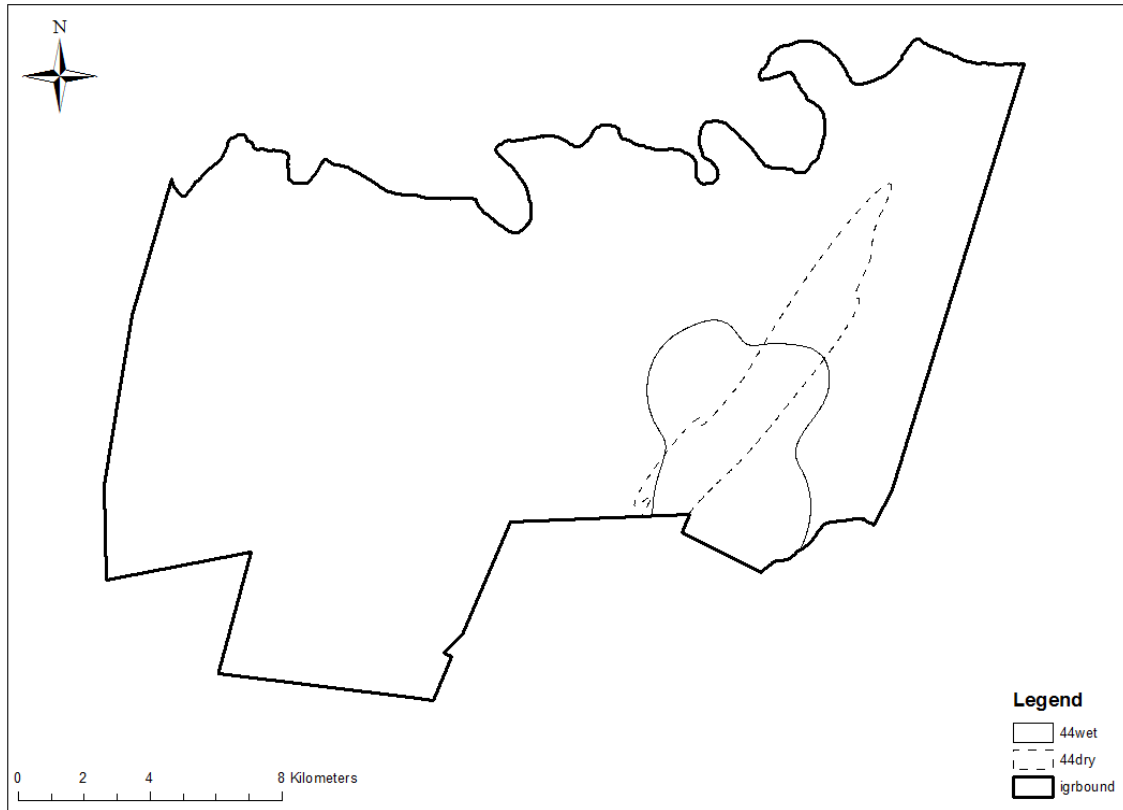
Figure 14: Wet (27 km^2) and dry (16 km^2) season home ranges for female IW44 at Ithala Game Reserve.
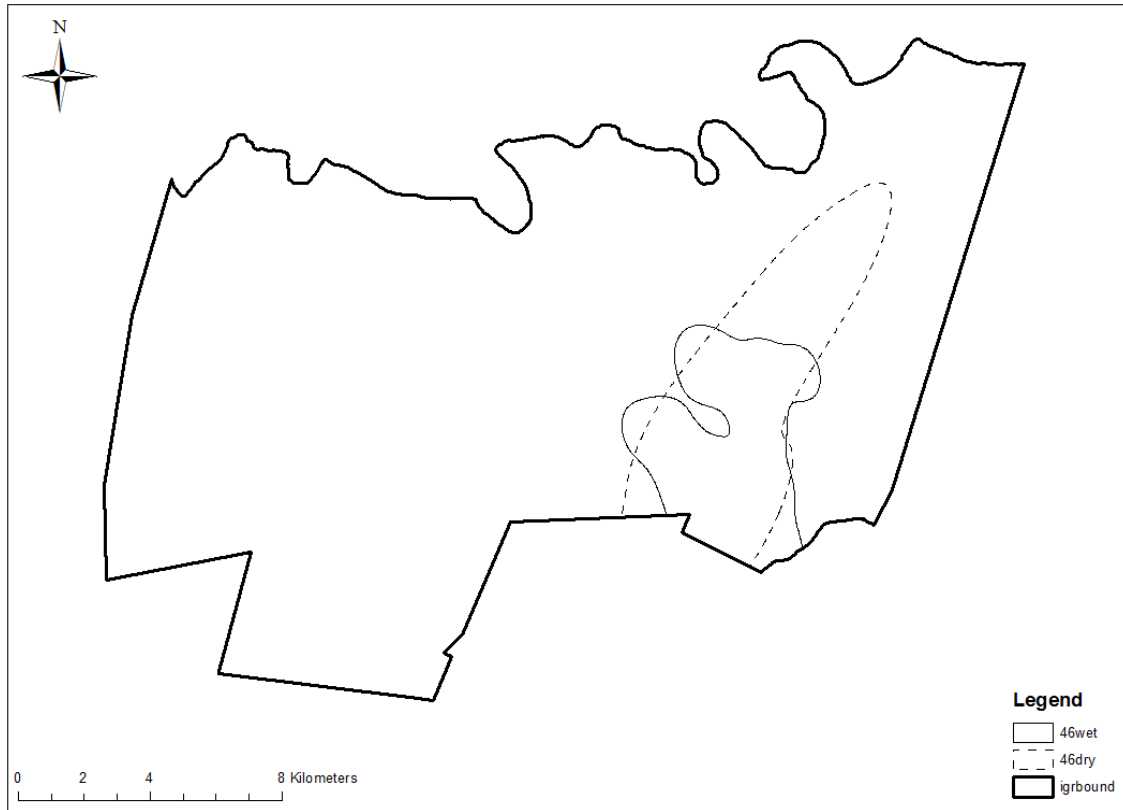
Figure 15: Wet (24 km^2) and dry (35 km^2) season home ranges for female IW46 at the Ithala
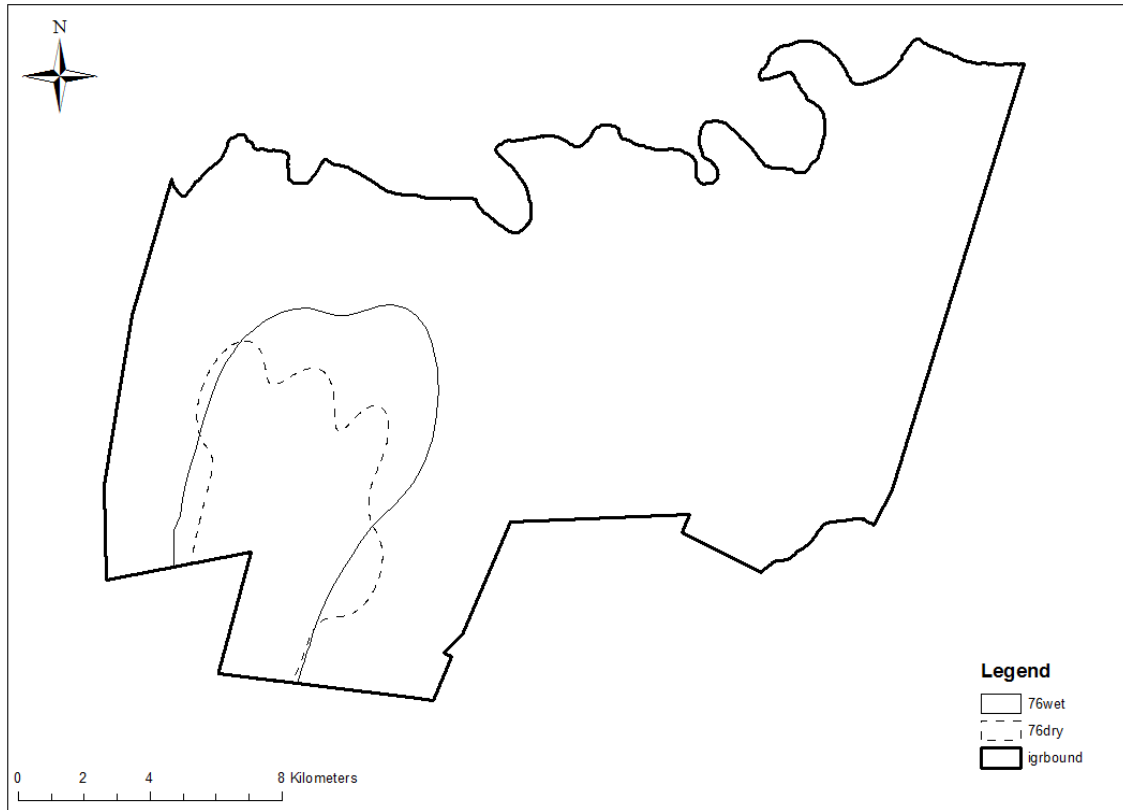Game Reserve.

Figure 16: Wet (22 km^2) and dry (24 km^2) season home ranges for female IW64 at the Ithala Game Reserve.

Figure 17: Wet (24 km^2) and dry (27 km^2) season home ranges for female IW66 at the Ithala Game Reserve.

Figure 18: Wet (24 km^2) and dry (22 km^2) season home ranges for female IW70 at the Ithala Game Reserve.

Figure 19: Wet (31 km^2) and dry (39 km^2) season home ranges for female IW74 at the Ithala Game Reserve.

Figure 20: Wet (51 km^2) and dry (40 km^2) season home ranges for female IW76 at the Ithala Game Reserve.
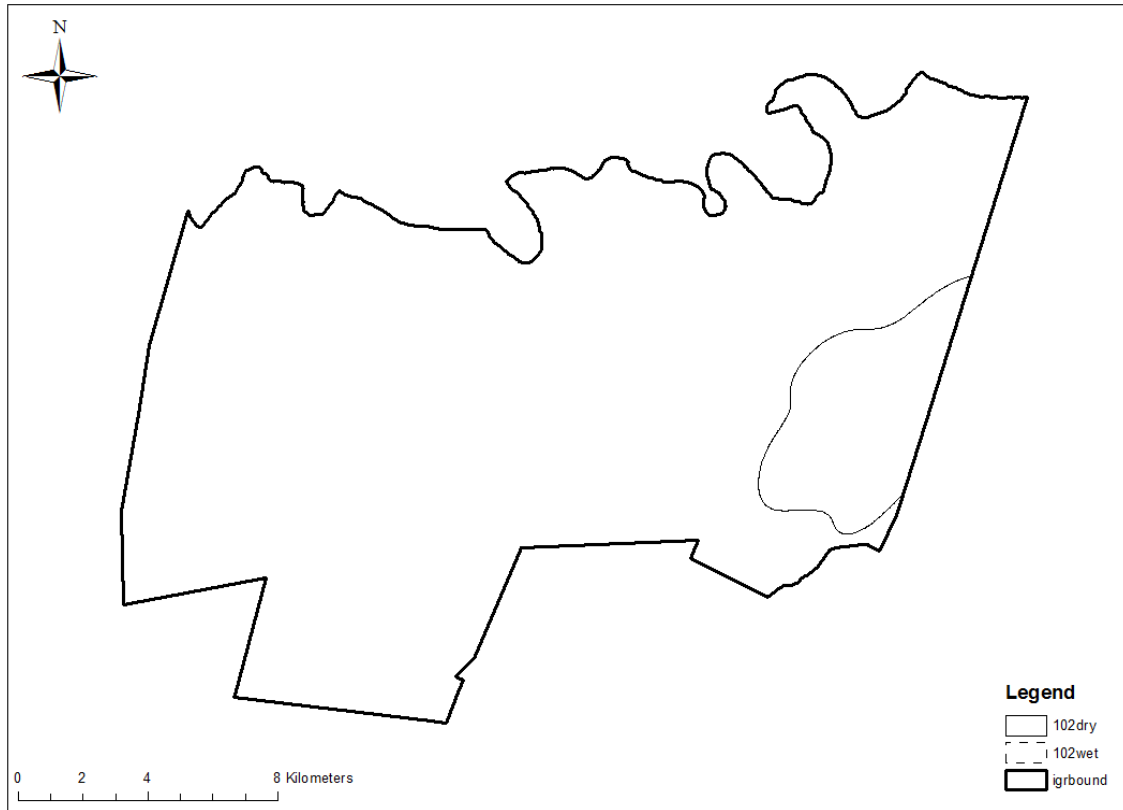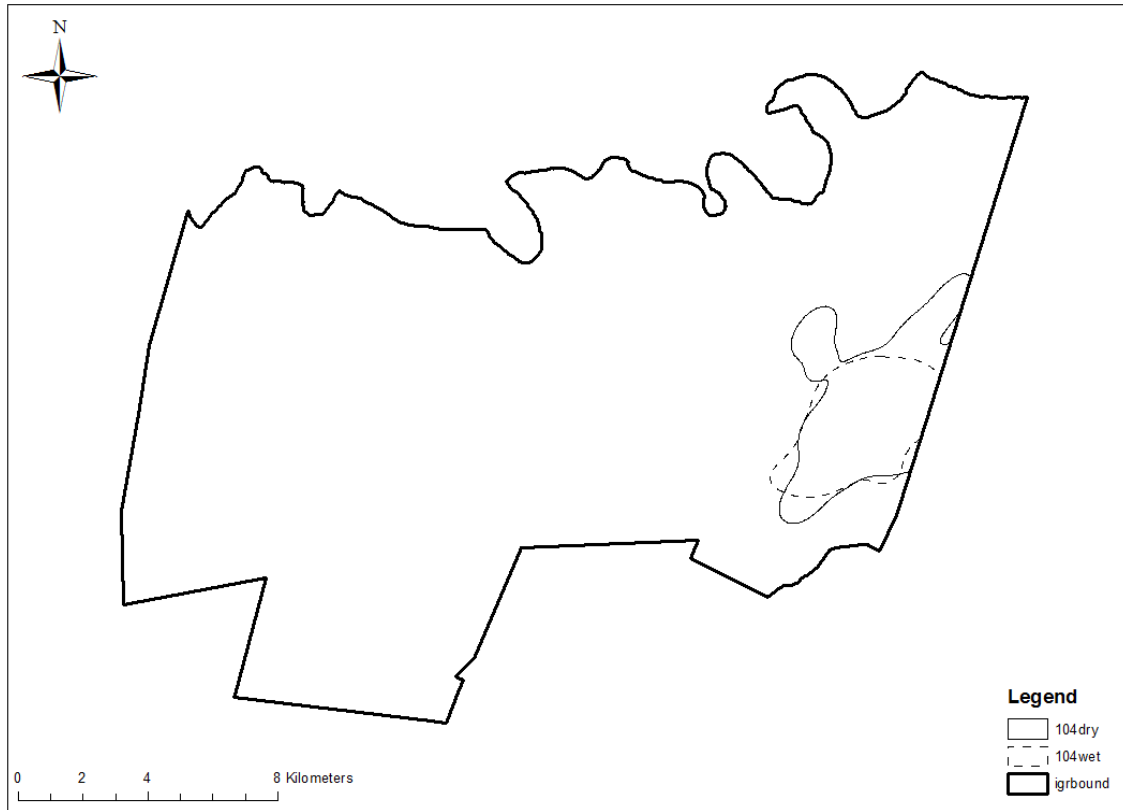
Figure 21: Wet (24 km^2) and dry (24 km^2) season home ranges for female IW102 at the Ithala Game Reserve.

Figure 22: Wet (13 km^2) and dry (19 km^2) season home ranges for female IW104 at the Ithala Game Reserve.
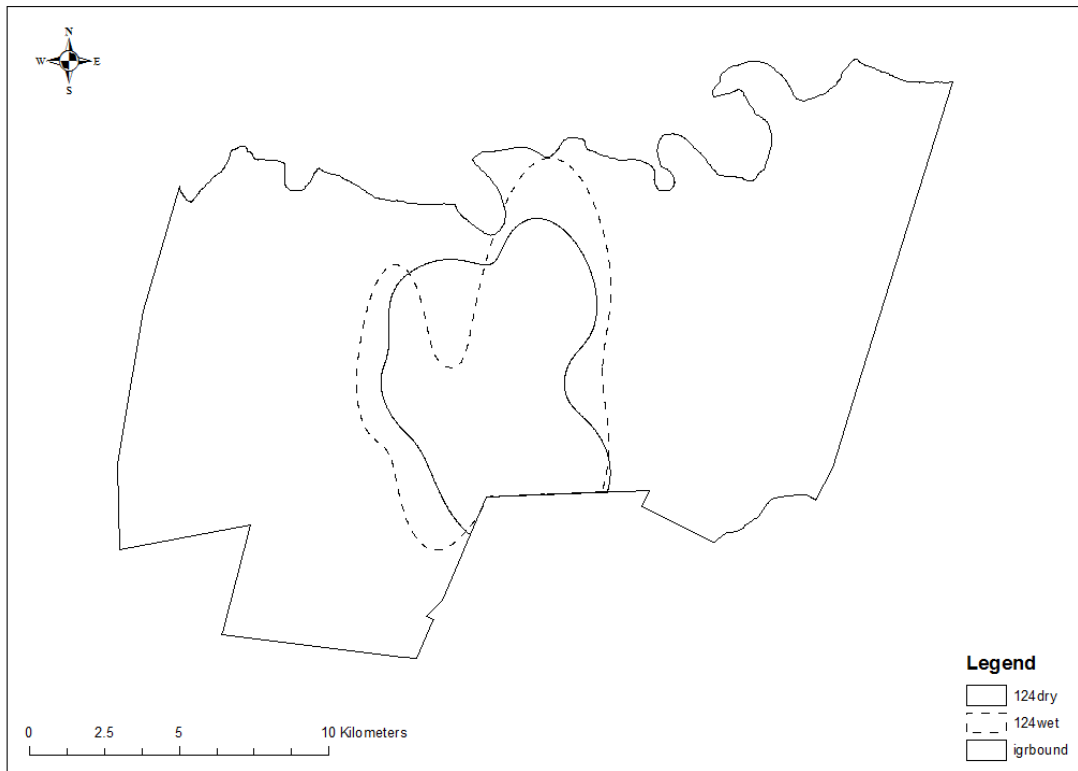
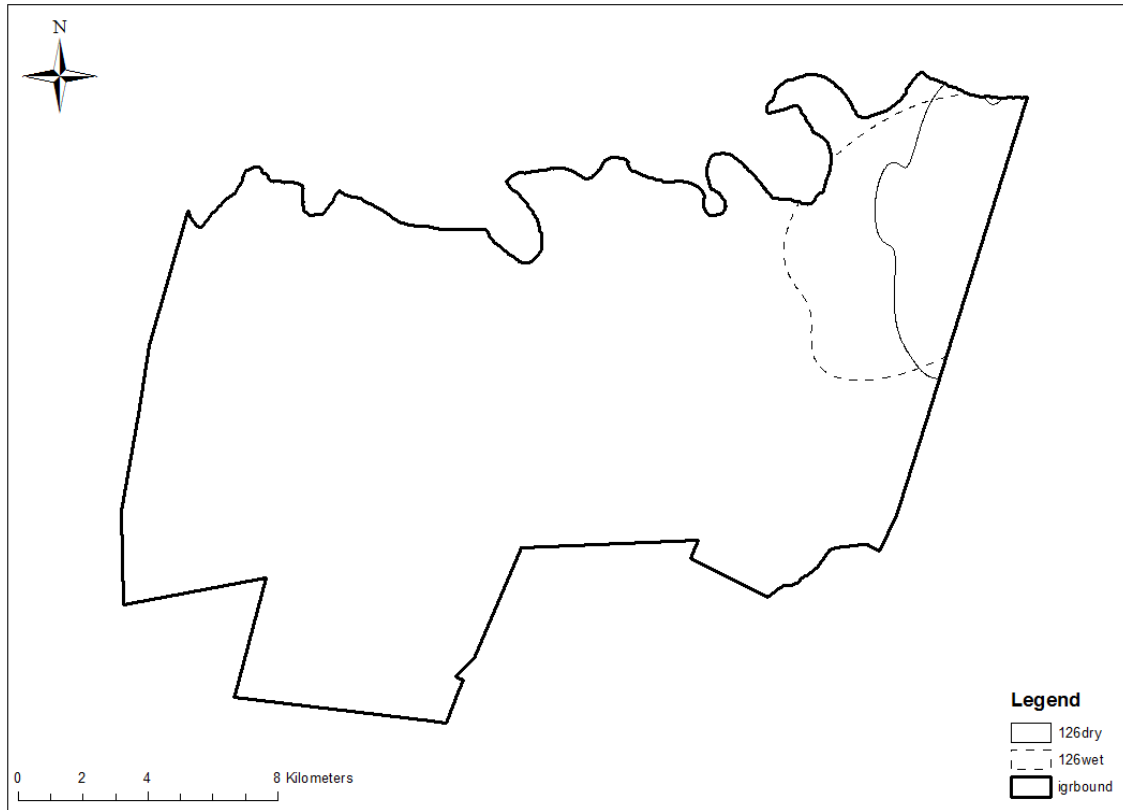Figure 23: Wet (60 km^2) and dry (47 km^2) season home ranges for female IW124 at the Ithala Game Reserve.

Figure 24: Wet (38 km^2) and dry (20 km^2) season home ranges for female IW126 at the Ithala Game Reserve.

APPENDIX II: Nutritional Data for habitats in Ithala Game Reserve

Table 6: Wet season nutritional data (using Near Infrared Spectrometry; NIRS) for the most abundant grass species in each habitat type in the Ithala Game Reserve.

Habitat	Dry Matter	Ashes	Crude protein base 1	Crude Protein base 2	Cellulose	NDF	ADF	ADL
Bushveld	94.5	8.7	11.5	7.6	35.9	73.3	40.5	4.6
Degraded area	93.7	8.4	13.4	8.6	35.5	73.2	38.8	4.6
Forest	93.8	10.0	14.6	9.9	34.5	73.2	39.6	4.4
Grassland	94.8	7.9	10.2	6.4	36.8	75.0	41.0	4.2
Grazing lawn	94.3	10.6	12.7	8.6	34.7	71.6	42.0	5.3
Old Land grassland	94.5	8.7	10.7	7.0	36.6	74.5	41.7	5.2
Rocky outcrop	94.6	8.2	10.3	7.1	36.1	74.4	40.5	4.2
Wetland	94.4	8.6	10.6	6.3	37.5	75.5	43.2	5.6
Wooded grassland	94.6	8.3	10.7	6.6	36.7	74.9	41.8	5.0

Table 7: Dry season nutritional data (using Near Infrared Spectrometry; NIRS) for the most abundant grass species in each habitat type in the Ithala Game Reserve.

Habitat	Dry Matter	Ashes	Crude protein base 1	Crude protein base 2	Cellulose	NDF	ADF	ADL
Bushveld	95.0	10.5	6.1	1.0	40.3	77.5	50.2	8.5
Degraded area	94.2	9.1	5.5	0.3	41.4	80.5	52.8	8.9
Forest	95.3	9.8	5.9	1.5	40.0	77.7	49.6	8.1
Grassland	95.5	10.2	5.7	1.1	40.5	78.1	50.2	8.0
Old Land grassland	95.4	10.5	6.1	1.4	39.4	77.7	49.2	7.8
Rocky outcrop	94.7	10.0	7.2	2.2	40.1	78.6	49.5	8.5
Wetland	94.8	10.5	5.6	0.2	41.5	78.7	52.0	9.1
Wooded grassland	95.2	10.1	5.7	0.7	40.3	77.6	50.3	8.3