Cape mountain zebra (*Equus zebra zebra*) habitat use and diet in the Bontebok National Park, South Africa

by

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DECLARATION

I, Taniia Strauss (student number 20106975), hereby declare that the thesis for Degree of Masters of Technology to be awarded is my own work, and has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

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ABSTRACT

Cape mountain zebra habitat utilization and diet in the dystrophic fynbos habitat of the Bontebok National Park was found to be highly selective. Mountain zebra concentrated in specific sectors and habitat types in the park on a seasonal basis, preferring recently burnt habitat with a veld age younger than one year in all seasons, except during the warm, dry summer. Proteoid Fynbos with a veld age between one and five years was preferred in the cool winter, while Drainage Lines and the fringes of Inland Pans were preferred during summer. Asteraceous Fynbos was avoided, irrespective of veld age, as well as all other habitats with a veld age greater than five years. Within habitat types with a veld age greater than one year, specific sites were selected and avoided on a seasonal basis, which were found to differ in terms of habitat suitability, based on the availability of dietary plant species. The annual diet consisted of 72.6% grass, 11.8% restio, 5.9% sedge, 8.8% geophyte and less than 1% forb and shrub species. Three grass species formed the bulk of the annual diet, *Themeda triandra, Cymbopogon marginatus* and *Eragrostis curvula*, for which leaf use was greater than stem use. *Themeda trianda* was preferred throughout the year, but contributed to the diet in greatest proportion in the warm, dry summer, when it was available at greatest leaf height and diameter. *Cymbopogon marginatus* was preferred during the cool winter, when diet composition and greenness was also greater than in other seasons. Preference of *Cymbopogon marginatus* decreased as leaf height and diameter increased. *Eragrostis curvula* was preferred in the warm autumn, when it composed the largest proportion of the diet, and selection of this species at feeding sites was based on both greenness and volume. In summer mountain zebra also preferred grass stems and inflorescences of *Aristida diffusa*, *Stipagrostis zeyheri* and *Briza maxima*. During the cool spring the diet included stems and inflorescences of sedges and restios, primarily *Ischyrolepis capensis*, and in autumn, dry bulbs of the geophyte *Moraea collina* were utilized. Habitat utilization, as well as grass height and greenness surveys in the Recently Burnt Area, and the nutritional status of mountain zebra was found to be in line with the Summer Nutritional Stress Hypothesis. The hypothesis proposes that the harsh climatic conditions of the area during summer are linked to the low availability of C4 grass, on which grazers would depend in summer. This is supported by the avoidance of the Recently Burnt Area in summer, and the preference of species like *Themeda triandra* during summer despite low greenness levels. Faecal nitrogen and phosphorus for mountain zebra in Bontebok National Park and De Hoop Nature Reserve were at minimum levels during the warm seasons. Faecal nitrogen was below the threshold for dietary deficiency in all seasons except spring, and faecal phosphorus was above the threshold for deficiency during two seasons only. The findings of this study are in line with other recent work on mountain zebra in the Baviaanskloof suggesting that, due to a high required rate of forage intake, mountain zebra are limited by both poor resource quantity and quality in dystrophic fynbos ecosystems.

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To my dad, David J. Strauss
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CHAPTER 1: INTRODUCTION

1.1. BACKGROUND

The lack of suitable habitat to conserve large herbivores is a challenge in conservation today (Cowling *et al.*, 1999a; Kerley *et al.*, 2003). In the case of species like the Cape mountain zebra (*Equus zebra zebra*), habitats need to be suitable and large enough to sustain viable populations (Cowling *et al.*, 2003; Watson *et al.*, 2005; Watson and Chadwick, 2007). Historically, mountain zebra distribution extended from the south-western Cape coast northwards to the Kamiesberg in the Northern Cape, but the current documented distribution of mountain zebra is limited to national parks, reserves and private game farms in the Western and Eastern Cape provinces of South Africa (Novellie *et al.*, 2002; Skead *et al.*, 2007). Despite dedicated conservation efforts in recent years, the shortage of protected areas of sufficient size and with adequate quality habitat still threatens the survival of the Cape mountain zebra (Kerley *et al.*, 2003; Hrabar and Kerley, 2009). Since Cape mountain zebra utilize both mountainous and lowland habitats seasonally (Boshoff *et al.*, 2001), targets for habitat conservation in the Cape Floristic Region (CFR) need to include the full range of habitats required by this species (Boshoff and Kerley, 2001; Kerley *et al.*, 2003; Rouget *et al.*, 2003).

None of the existing reserves in the CFR are of adequate size and habitat configuration to sustain viable populations of all herbivorous and carnivorous mammals that occupied the CFR in pre-European times (Kerley *et al.*, 2003; Rouget *et al.*, 2003). The Bontebok National Park (BNP) is the smallest national park in South Africa (Kraaij, 2011; Kraaij *et al.*, 2011), but protects critically endangered lowland fynbos-renosterveld habitat types in which Cape mountain zebra historically occurred (Boshoff and Kerley, 2001). However, the ecological dynamics of herbivorous mammals in dystrophic ecosystems (such as fynbos) is poorly understood and thus pose management challenges. Zebra species are considered to survive in marginal habitat and during periods of drought better than ruminants, as their digestive system and feeding strategies allow them to utilize coarse plant material (Owaga, 1975; Janis, 1976; Hofmann, 1989; Stevens and Hume, 1996;

Radloff, 2008; Cromsigt *et al.*, 2009). However, other work in this field suggests that zebra also need good quality habitat and forage (Duncan *et al.*, 1990; Illius and Gordon, 1992). Thus in dystrophic ecosystems, such as fynbos, where nutrient availability is low (Van Wilgen and Le Maitre, 1981; Cowling, 1992; Van Wilgen *et al.*, 1992; Richards *et al.*, 1997), the species composition of mountain zebra diet and the ecological mechanisms that drive utilization of less suitable habitat warrant investigation, and are of great conservation value, since these populations (Kammanassie Nature Reserve, Gamka Mountain Nature Reserve, Baviaanskloof Nature Reserve, De Hoop Nature Reserve and the Bontebok National Park) represent genetic material from all three relic populations (Watson *et al.*, 2005; Watson and Chadwick, 2007; Smith *et al.*, 2011; Watson *et al.*, 2011). Since the BNP represents such a dystrophic ecosystem, this study had the following objectives: (a) to determine seasonal variation in area use and habitat preference of mountain zebra in the light of habitat suitability; (b) to determine annual and seasonal trends in diet composition and preference of mountain zebra; (c) to determine the factors that influence grass selection by mountain zebra, and evaluate the role of these factors in relation to seasonal changes in the reserve; and (d) to determine the seasonal nutritional status of mountain zebra in the reserve, through analysis of faecal nitrogen and phosphorus.

1.2. MOUNTAIN ZEBRA TAXONOMY AND CONSERVATION STATUS

Genetic work on the species *Equus zebra* concluded that the Cape mountain zebra (*Equus zebra zebra*) and Hartman’s mountain zebra (*Equus zebra hartmannea*) are closely related subspecies (Moodley and Harley, 2005). This study focuses on the Cape mountain zebra (*Equus zebra zebra*) of the BNP, hereafter referred to as mountain zebra (unless specified otherwise). Historically mountain zebra occurred in the mountainous regions of the southern districts of South Africa. By the 1930’s extensive hunting and habitat destruction had reduced the subspecies to three relict populations – that of the Mountain Zebra National Park (MZNP), the Gamka Mountain Nature Reserve (GMNR) and the Kammanassie Nature Reserve (KNR), the total population numbering less than 80 individuals (Novellie *et al.*, 1996; Novellie *et al.*, 2002; Skead *et al.*, 2007; Hrabar and Kerley, 2009). Conservation efforts have gradually increased mountain zebra numbers, but mainly within the MZNP, and thus low population growth and poor genetic diversity within the subspecies is still of great concern (Novellie *et al.*, 2002; Moodley and Harley, 2005; Watson *et al.*, 2005; Sasidharan, 2006; Sasidharan *et al.*, 2011), and the species is currently listed as Vulnerable (Friedmann and Daly, 2004; Hrabar and Kerley, 2009; IUCN, 2011).

The mountain zebra population of the MZNP has thrived since proclamation of the park, which was established for the purpose of conserving the subspecies, and by the 1980's the population increased sufficiently to allow introduction of mountain zebra into 25 other protected areas and game ranches, including the BNP (Novellie *et al.*, 2002). Positive population growth was also found in the Karoo National Park, as well as eight of the provincial nature reserves (three reserves in the Western Cape, four in Eastern Cape Nature and one in the Free State), with an increase of as much as 25% per year between 1990 and 1995 in the Commado Drift Nature Reserve (Lloyd and Rasa, 1989; Novellie *et al.*, 2002; Hrabar and Kerley, 2013). However, the other two relict populations, in the Gamka and Kammanassie mountains have shown poor population growth, which has been linked to poor habitat quality in these areas (Watson *et al.*, 2005; Watson and Chadwick, 2007).

Twelve mountain zebra from MZNP were introduced into BNP, three from MZNP in 1986 and nine from Karoo National Park in 1990, further introductions were made in 1994 (Watson *et al.*, 2011). Since their introduction into the BNP however, the performance of mountain zebra has been poor, with slow population growth, low genetic diversity, and high incidence of sarcoid tumours (Sasidharan, 2004; Sasidharan *et al.*, 2011; Watson *et al.*, 2011). The BNP population decreased from 24 to 17 between 1995 and 1998 (Novellie *et al.*, 2002), and showed increase only when the bontebok population was reduced (Watson *et al.*, 2011). Since the high incidence of sarcoid in the population, culling and translocation was recently implemented and the population was reduced from 49 in 2009 (Watson *et al.*, 2011) to less than 10 healthy individuals in 2012 (SANParks, 2014).

The poor performance of mountain zebra in fynbos has been linked to limited extent of suitable habitat (Novellie *et al.*, 2002; Watson *et al.*, 2005; Watson and Chadwick, 2007; Faith, 2011; Watson *et al.*, 2011; Weel *et al.*, 2015). In theory, non-ruminant performance on poor quality grazing should be better than ruminants (Bell, 1971;

Janis, 1976; Owen-Smith, 1982; Menard *et al.*, 2002), but due to the high required intake rate and digestive strategy of equids, poor quality habitat may be a limiting factor (Duncan *et al.*, 1990; Illius and Gordon, 1992; Weel *et al.*, 2015). This would explain the poor population growth in other protected areas with nutrient-poor soils in the former range of mountain zebra, such as the Baviaanskloof Wilderness Area and the Zuurberg section of the Addo Elephant National Park (Novellie *et al.*, 2002; Weel *et al.*, 2015). Similarly, in GMNR and KNR the mountain zebra population growth is dependent on fire, and limited by sufficient suitable habitat (Watson *et al.*, 2005; Watson and Chadwick, 2007). In De Hoop Nature Reserve (DHNR) a small proportion of the park is suitable to large herbivores, and the lack of sufficient C4 grass during the drier summer period is specifically challenging to large grazers such as zebra in fynbos (Radloff, 2008; Smith *et al.*, 2011). The impact of grazers on the unique vegetation of the CFR also requires continuous monitoring (Novellie, 1987; Radloff, 2008; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010). This study aims to provide data on mountain zebra resource utilization in the fynbos biome, as recommended by other research (Boshoff *et al.*, 2001; Faith, 2011; Watson *et al.*, 2011).

Hrabar and Kerley (2009) suggest that the high incidence of sarcoid tumours within the populations of BNP and Gariep could be linked to the high level of inbreeding in these small “island” populations, and work by Sasidharan (2006) and Marais *et al.* (2007) support this. Although the relationship between the incidence of sarcoid tumours and habitat suitability for zebra specifically is unclear, Sasidharan (2004) and Sasidharan (2006) presented evidence of inbreeding depression being more severe in environments with irregular rainfall patterns, erratic or extreme temperatures, and limited food resources for raising offspring. The small size of BNP may also be predisposing animals with sarcoid tumours to immune suppression when environmental conditions deteriorate (Van Dyk *et al.*, 2009). The BNP population originates from MZNP only (given that animals from Karoo National Park also originate from MZNP), representing only one third of the genetic diversity of the meta-population (Moodley and Harley, 2005). Limited genetic heterozygosity within the BNP population may thus also have contributed to the poor population growth (Novellie *et al.*, 1996; Novellie *et al.*, 2002). For the genetic diversity of this population to increase, genes from the other two relict populations (GMNR and KNR) need to be introduced (Novellie *et al.*, 2002; Watson *et al.*, 2005; Watson and Chadwick, 2007).

The introduction of mountain zebra to the BNP in the 1980's was supported by the notion that mountain zebra did occur in the Swellendam area historically (Boshoff and Kerley, 2001; Kraaij *et al.*, 2011). However, since population growth in the BNP has been poor, the current presence of mountain zebra in the park provides an opportunity to investigate the diet and habitat use of mountain zebra in a dystrophic system specifically.

1.3. LITERATURE REVIEW

1.3.1. HABITAT USE

In the ecology of grazing and browsing mammals, it is evident that large mammalian herbivores are distributed unevenly across the landscape (Jarman and Sinclair, 1979; McNaughton and Georgiadis, 1986). Senft *et al.* (1987) evaluated the ecological hierarchy of large herbivore dispersal with particular attention to resource availability, at the regional, landscape and community scale. This is in line with the levels of habitat selection of others, namely the regional, home range scale, habitat or camp and feeding site (Johnson, 1980; Bailey *et al.*, 1996). These sources concur that the factors determining habitat selection by large grazers include: (a) the seasonal availability of preferred grasses and soil-derived nutrition; (b) predation; (c) abiotic factors such as geology, aspect, altitude, shelter, thermoregulation and proximity to drinking water; (d) inter-specific competition; and (e) fire; (Lamprey, 1963; Leuthold, 1977; Leuthold, 1978; Sinclair, 1979; Sinclair, 1985; McNaughton and Georgiadis, 1986; Senft *et al.*, 1987; Bailey *et al.*, 1996; Dekker *et al.*, 1996; Hopcraft *et al.*, 2010; Owen-Smith *et al.*, 2010). An evaluation of the role of these factors on habitat selection in an ecosystem informs management decisions regarding fire regime, sustainable stocking densities and translocation (Petrides, 1975; Novellie, 1987; Ben-Shahar and Coe, 1992; Dekker *et al.*, 1996; Dekker, 1997; Owen-Smith, 2003; Luyt, 2005; Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010).

The area that a mammalian herbivore occupies must be of adequate size and quality to ensure survival. The range of a herbivore is defined my its movement patterns, and home range represents the broad scale level at which herbivore dispersal and migration occurs (Bailey *et al.*, 1996). Herbivores will adapt their area use in terms of locality and size on a monthly, seasonal or annual basis (Senft *et al.*, 1987; Bailey *et al.*, 1996). The area used increases with body size and metabolic demands (Harestad and Bunnel, 1979; Mace and Harvey, 1983; Swihart *et al.*, 1988).

In herbivore ecology both “bottom-up” and “top-down” forces determine large mammalian herbivore movement and habitat selection (Power, 1992; Grange and Duncan, 2006; Burkepile *et al.*, 2013; Wigley, 2013). From the “bottom-up” perspective, herbivores will select habitat types that provide for their needs in terms of food, water, nutrition, and protection from the elements. In this respect, diet is regarded as the most important factor driving herbivore moment (McNaughton, 1987; Owen-Smith, 1988). The suitability of the habitat is thus one of the most important determining factors in the location and size of the area used. Consequently habitat selection is the process by which herbivores utilise sites that provide essential resources for survival (Leuthold, 1978; Hutto, 1985; Melton, 1987b; Orians and Wittenberger, 1991; Hopcraft *et al.*, 2010). According to the “bottom-up” view of trophic interaction, resource distribution is a more powerful driving force in herbivore distribution patterns than predation, since resource distribution is more stable over time than predation (Sinclair, 1985; Power, 1992; Lima, 1998; Grange and Duncan, 2006; Thaker *et al.*, 2011; Burkepile *et al.*, 2013). Since natural habitats are heterogeneous, herbivores are continuously faced with alternatives in terms of resource selection (Stephens and Krebs, 1986; Senft *et al.*, 1987; Dekker *et al.*, 1996).

Predation influences herbivore feeding success (Barnier *et al.*, 2014), and cause grouping behaviour in open habitat by herbivores, to avoid predation (Thaker *et al.*, 2010). Similarly day-night habitat use in game like plains zebra (*Equus burchelli*) has been linked to predator avoidance (Fischhoff *et al.*, 2007). This represents the “top-down” driving force paradigm, illustrated by work in systems such as the Kruger National Park (KNP) and the Serengeti (Janis, 1976; Illius and Gordon, 1992; Power, 1992; Grange and Duncan, 2006; Burkepile *et al.*, 2013). In the Serengeti, plains zebra are predator limited as opposed to habitat limited (Grange *et al.*, 2004). Research in this regard suggests that the movement of ungulates is limited by predation instead of resource availability (Laundré *et al.*, 2010), where ungulates learn to associate certain landscapes with high risk of predation.

According the “top-down” perspective, avoidance of predators is the stronger driver, often resulting in seasonal migrations (Jarman and Sinclair, 1979; Maddock, 1979; Sinclair, 1985; McNaughton and Georgiadis, 1986; Power, 1992; Lima, 1998; Grange and Duncan, 2006; Fischhoff *et al.*, 2007; Thaker *et al.*, 2010; Thaker *et al.*, 2011; Burkepile *et al.*, 2013; Barnier *et al.*, 2014). Close proximity to lion, for instance, constrained the ability of plains zebra in a dystrophic system in Zimbabwe to consume adequate quantities of forage, where forage quality was already compromised due to the nutrient-poor habitat (Barnier *et al.*, 2014). This is supported by other work in savanna systems where lion (*Panthera leo*) have been found to influence the distribution of zebra (Grange and Duncan, 2006; Fischhoff *et al.*, 2007).

Mountain zebra are also hypothesized to avoid thicket areas in the BNP, representing “landscapes of fear”, linked to possible ambush by predators (Laundré *et al.*, 2010; Weel *et al.*, 2015). However, large ungulates may aggregate even when predation is a low risk (Skarpe and Hester, 2008), based on the benefit from modifying vegetation when feeding in groups (McNaughton, 1984). The role of predation in controlling mountain zebra movement thus needs to be evaluated in combination with forage factors, supported by the high quality and quantity forage requirement by non-ruminants (Illius and Gordon, 1987; Illius and Gordon, 1992; Gordon and Illius, 1996), which is a challenge in poor quality habitat (Watson *et al.*, 2005; Watson and Chadwick, 2007; Smith *et al.*, 2011; Weel *et al.*, 2015). However, leopard (*Panthera pardus*) is the only potential large predator in the BNP region, and not considered resident in the park (Balme *et al.*, 2007; Hayward and Kerley, 2009). In their review, Hayward *et al.* (2006) found that mountain zebra are also not a preferred prey species for leopard, since (a) mountain zebra body mass is greater than the preferred prey mass of leopard; (b) there is a high risk of injury during capture; and (c) the habitat preference of mountain zebra is unfavourable for ambush by leopard. Thus predation by leopard in the BNP is unlikely, and predators appear not to be an important factor in determining mountain zebra distribution in this reserve.

Abiotic factors like surface water availability are important drivers of habitat selection, especially in arid to semi-arid biomes (Western, 1975; McNaughton and Georgiadis, 1986; Fryxell and Sinclair, 1988; Redfern *et al.*, 2003), and less important in climates with higher rainfall, or in areas with short distance to water (Shannon, 2005; Kraaij and Novellie, 2010). Other factors such as geology and associated soils determine plant community structure (Cowling and Holmes, 1992) and the availability of nutritional plants (McNaughton and Chapin, 1985; McNaughton, 1987; Augustine *et al.*, 2003; Anderson *et al.*, 2006). Habitat selection thus incorporate abiotic factors since habitat types are based on geology, soils and associated plant community structure (Lambrechts, 1979; Venter *et al.*, 2003). During the current study, the role of geology and associated soils is not investigated independently, but noted in terms of the indirect influence of these factors on the habitat.

Ungulates optimize their feeding behaviour to get the best nutrient mix from the available area (Westoby, 1974). Historically *Equus burchelli* seasonally migrated between eutrophic and dystrophic habitat types in the Serengeti (Frank *et al.*, 1998). Grass communities with a high proportion of nutritious species primarily determine seasonal movements between habitat types by zebra and wildebeest: sites with highly nutritious grass are selected rather than particular nutritious species at the feeding site (Ben-Shahar and Coe, 1992). This concurs with the notion that herbivores choose feeding sites that maximise their forage and nutritional intake (Bell, 1970; Bell, 1971; Bell, 1982; Owen-Smith and Novellie, 1982; Winkler, 1992; Searle and Shipley, 2008). This is particularly relevant to larger non-ruminant bulk feeders that rely on a large intake of fibrous material (Duncan *et al.*, 1990; Illius and Gordon, 1992; Stevens and Hume, 1996). A more fibrous and abrasive grass diet requires a greater intake and degree of mastication, which grazers are physiologically adapted to, in terms of jaw, jaw muscle and muzzle structure (Janis, 2008; Searle and Shipley, 2008). Thus when grazers are ingesting adequate biomass in nutrient-poor areas, they may be subjected to seasonal nutrient deficiencies obtained from the available fodder (Owen-Smith, 1982).

Theoretically there is an inter-specific rank order between species competing for the same resource base, for example roan and sable moving away from feeding sites where wildebeest dominate (Owen-Smith, 1982). Competition may influence habitat utilization when a species reduces a shared food resource below a level that can be used by another species (Illius and Gordon, 1987; Murray and Illius, 2000; Arsenault and Owen-Smith, 2002). Theoretically herbivore species could thrive in shared habitat through niche differentiation (Bell, 1970). This is supported by work in other ecosystems, where differentiation in feeding strategies exists between ruminants and non-ruminants (Owaga, 1975; Grunow, 1980; Cromsigt and Olff, 2006). In the MZNP, mountain zebra as well as red hartebeest (*Alcelaphus caama*) preferred good condition veld with taller Decreaser grasses, whereas black wildebeest (*Connochaetes gnou*) favoured poor condition veld with shorter Increaser grasses (Novellie, 1990). Arsenault and Owen-Smith (2002) reviewed evidence of feeding facilitation versus competition between grazers sharing habitat, and concluded that a seasonal exchange between facilitation and competition exists: Feeding facilitation occurs mainly during the growing season, as large grazers stimulate re-growth and temporarily improve forage quality for other species in the absence of fire, whereas in the dormant season the total amount of available forage is reduced as species share habitat, and exploitative competition prevails (Arsenault and Owen-Smith, 2002; Arsenault and Owen-Smith, 2008). This phenomenon is based on a broad spectrum of studies in savanna ecosystems and includes studies on browsers (Gwynne and Bell, 1968; Bell, 1970; Bell, 1971; Owen-Smith, 1994; Owen-Smith, 2002; Arsenault and Owen-Smith, 2008). In this regard, it has been suggested that mountain zebra should feed at a higher grass sward level than bontebok (*Damaliscus pygargus pygargus*) in the BNP (Novellie, 1987; Novellie and Kraaij, 2010). However, work by Kraaij and Novellie (2010) and Watson *et al.* (2011) emphasize the importance of fire in grass height utilization, and suggest that mountain zebra and other grazers in the BNP are competing for recently burnt areas with shorter grass. However, if grass is particularly short, intake rate can be reduced to the degree that feeding becomes unprofitable, and the short grass is avoided (Arnold, 1987).

The high intake rate of bulk grazers like equids is thus an important factor in the benefit of choosing feeding sites with inadequate forage quantity (Searle and

Shipley, 2008). Inter-specific competition between bontebok and mountain zebra has been suggested, in that the numbers of mountain zebra in the park increased after bontebok numbers were reduced in 2004 (Watson *et al.*, 2011). These findings are in line with recent work suggesting that when resources are scarce, ruminant and non-ruminant species compete, due to the similarity between the feeding niches (Illius and Gordon, 1992). The assessment by Kraaij and Novellie (2010) of the utilization of the various habitat types and veld age units by large herbivores in the BNP also showed an overlap in habitat use, instead of the anticipated grazing facilitation / niche differentiation (Owaga, 1975; Grunow, 1980; Novellie, 1987; Cromsigt and Olff, 2006). The current study does not test inter-specific competition between species in terms of feeding height specifically, but the volume of grass available to mountain zebra would be influenced by grazers with which zebra share habitat in the BNP.

Fire is one of the most important driving factors in habitat selection by herbivores in a variety of biomes and habitat types (Archibald and Bond, 2004; Archibald *et al.*, 2005; Archibald, 2008; Wagner, 2008; Venter *et al.*, 2014). Fire increases the nutrient load in the soil (Boerner, 1982; Stock and Lewis, 1986; Van de Vijver *et al.*, 1999; Wan *et al.*, 2001), and grasses are of the first species to flush after fire (Mentis and Tainton, 1984), resulting in it being a crucial grazing management tool, particularly in dystrophic ecosystems (Booysen and Tainton, 1984; Cowling, 1992). Fire also plays a critical role in plant-animal interactions in fynbos ecosystems specifically, with herbivores favouring recently burnt young fynbos (Novellie, 1987; Watson *et al.*, 2005; Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Watson *et al.*, 2011). During a period in the BNP when the fire rotation was at four year intervals, the most intensive utilization by grazers was in the first year after fire, with a sharp decline thereafter (Novellie, 1987). Seasonal influences could not yet be tested in the BNP, and studies in the BNP emphasize the necessity for further work on habitat preference by grazers (Watson *et al.*, 2011). The objectives of the introduction of mountain zebra to the BNP were: (a) to open up the grass sward for bontebok; (b) to even out the grazing pressure on the vegetation; and (c) to allow park management to lengthen the then four-year fire rotation (Novellie and Strydom, 1987; Kraaij and Novellie, 2010; Kraaij *et al.*, 2011). Ultimately the fire rotation needed to be brought in line with fynbos and renosterveld management objectives (Novellie, 1987; Kraaij and Novellie, 2010). In 2004 the fire management regime for

BNP was changed from a four year interval to an eight to 16 year interval, to favour of the preservation of endangered lowland fynbos vegetation occurring in the park (Kraaij, 2004; Kraaij, 2010). A run-away fire during February 2012, which burnt 11% of the park shortly before the onset of the study, allowed for the investigation of the role of fire in mountain zebra utilization.

1.3.2. DIET COMPOSITION AND PREFERENCE

Throughout the resource selection process, herbivores make decisions with regard to the feeding location, feeding time, forage species selection and feeding duration (Schoener, 1971; Stephens and Krebs, 1986). At the local scale of the feeding site after Bailey *et al.* (1996), individual plants and plant parts are specifically selected and preferred to others (Senft *et al.*, 1987). Feeding herbivores generally shift between feeding sites every 1 to 30 minutes, and between foraging areas every 1 to 4 hours, primarily based on forage abundance and quality (Bailey *et al.*, 1996; Owen-Smith, 2002; Owen-Smith *et al.*, 2010). Herbivore diet studies investigate the choices the herbivore makes in obtaining food resources from the available habitat (Grunow, 1980; Owen-Smith and Novellie, 1982; Winkler, 1992; Watson and Owen-Smith, 2000). The available food resource is classified into plant growth forms, such as graminoids, geophytes, forbs and shrubs; plant species; and plant parts such as leaves, stems, and inflorescences (Owen-Smith, 1982). Diet composition primarily focuses on the intensity with which a herbivore is feeding on taxonomically unique food species at the feeding station, each bite taken by the animal representing a decision about which plant species to eat (Senft *et al.*, 1987; Bailey *et al.*, 1996).

Mountain zebras are primarily grazers, and similar to other equids, only take browse occasionally (Penzhorn, 1975). Grazing is a recent specialization in ungulate evolution, and based on their evolutionary adaptations, equids are believed to have evolved from mixed feeders into specialised grazers (Janis, 2008). Eurasian horses that were specialist browsers (subfamily Anchtheriinae, genera *Hypohippus* and *Megahippus*) were extinct by the end of the Miocene era (Janis, 2008). For mountain zebra specifically, diet studies in the MZNP support this, showing that the diet of mountain zebra consisted mainly of grass species (Grobler, 1983; Novellie *et al.*, 1988). Mountain zebra avoid shrub-dominated vegetation communities and select communities with high grass cover (Winkler, 1992; Winkler and Owen-Smith, 1995), but forbs and shrubs could form up to 9% of the monthly diet (Winkler, 1992). In De Hoop Nature Reserve, another dystrophic ecosystem, grass species constituted the largest proportion of diet for mountain zebra throughout the year, but there was a proportional increase in browse taken during the dry season, when grass quality was poor (Smith *et al.*, 2011). Work by Novellie *et al.* (1988) suggests that mountain zebra tend to take browse when graze quality and quantity declines. When browse is utilized, Cape mountain zebra limit their browsing behaviour to small shrubs (Penzhorn, 1975; Winkler, 1992). The hypothesis is that the higher protein levels in other growth forms may substitute seasonally lower levels in grass (Penzhorn, 1982b).

Grass selection by herbivores occurs at the feeding site when a plant is either accepted or rejected (Westoby, 1974; Johnson, 1980). In the assessment of herbivore feeding ecology, it is thus important to distinguish between principal food species – species occurring in greatest quantity in the diet; and preferred food species – species more frequent in the diet than in the accessible environment (Petrides, 1975; Grunow, 1980; Johnson, 1980; Owen-Smith and Cooper, 1987). Management of the ecosystem needs to incorporate the differentiation in selection strategies by herbivores like mountain zebra, as known preferred species may be recorded in the habitat, but may not be available at suitable levels.

Preference indices estimate the probability with which herbivores consume plant species in relation to their availability in the environment (Jacobs, 1974; Petrides, 1975; Papageorgiou, 1978; Johnson, 1980; Hobbs and Bowden, 1982; Lechowicz, 1982; Owen-Smith and Cooper, 1987). A widely accepted index used for the assessment of diet preference is the acceptability index of Owen-Smith and Cooper (1987). While diet composition illustrates which species formed the greatest contribution to the diet, in other words principal species, preference indices (such as the acceptability index) assess the preference of the dietary species based on how frequently it is encountered.

Preferred species are only principal species if available in large quantities (Petrides, 1975). For example, Grobler (1983) found *Themeda triandra* to be both a preferred and principal species in the diet of mountain zebra, whereas *Eragrostis curvula*, though a very prevalent species, was not as preferred as expected, and utilization was seasonal. In Baviaanskloof Nature Reserve (BNR), *T. triandra* proved to be a principal and seasonally preferred species, while there was seasonal variation in the diet composition and preference of *E. curvula*, as it was preferred in winter and moderately preferred in early summer, and not utilized in the later summer (Weel *et al.*, 2015). It is thus apparent that seasonality plays an important role in diet preference (Grobler, 1983; Boyers, 2011; Smith *et al.*, 2011; Weel *et al.*, 2015).

1.3.3. FACTORS INFLUENCING FORAGE SELECTION

The rate of intake for ungulates is directly related to body size (Gordon, 2003; Janis, 2008). The larger the body weight, the larger the gut capacity (Bell, 1970; Bell, 1971; Owen-Smith, 1982; Owen-Smith and Novellie, 1982; Demment and Van Soest, 1985). This illustrates the need for adequate quantity forage for bulk grazers. Fibre content in the diet increases with body size, and non-ruminants being of large to very large body size, the hindgut fermentation digestive strategy necessitates high quantity forage (Parra, 1978; Demment and Van Soest, 1985).

This differentiation between the digestion of ruminants and non-ruminants has led to the widely accepted notion that non-ruminants feed non-selectively, even in poor quality habitat (Bell, 1971; Janis, 1976). More recent work however, suggests that based on retention time in the digestive tract, besides the high quantity requirement, non-ruminants including equids also benefit from better quality grazing (Duncan *et al.*, 1990; Illius and Gordon, 1992). Thus the best diet selection strategy for non-ruminant grazers would be to ingest the maximum quantity of the most essential nutrient over a wider range of dietary qualities (Illius and Gordon, 1992). Bulk grazers thus not only need adequate quantity forage, but are dependent on adequate quality over time. The need for adequate nutrition is a strong driving factor in forage selection for all herbivores (Bell, 1970; Bell, 1971; Owen-Smith, 1982; McNaughton, 1985; Owen-Smith, 1988).

Early research in the field of factors influencing plant selection focused particularly on the nutritional composition of grass species, showing how fluctuations in nutrients like protein, fat, carbohydrate, calcium, phosphates influence grass selection (Irvines, 1955; Leigh, 1961; Heady, 1964; Cook, 1972; Field, 1976; Owen-Smith and Novellie, 1982; Grobler, 1983). From these studies it became evident that nutritional characteristics were not the only important factors in forage selection (Heady, 1964; Westoby, 1974; Field, 1976). Physical plant attributes such as growth form, plant species, plant part, phenological state and plant volume also determine acceptance at the feeding site (Grunow, 1980; Owen-Smith, 1982; McNaughton and Georgiadis, 1986).

Plant part selection can play in important role in ungulate forage selection (Winkler, 1992; Macandza *et al.*, 2004; Venter, 2006; Magome *et al.*, 2008). Grazers generally prefer leaves to stem (Bell, 1970; Bell, 1971; Janis, 1976; Owen-Smith, 1982; Owen-Smith and Novellie, 1982; Wright *et al.*, 2004). This is attributed to the digestibility of stems being lower than for leaves. Stems have a higher fibre content (Murray and Illius, 1996), while leaves have a higher nutrient to fibre ratio (Owen-Smith and Novellie, 1982; Grobler, 1983). However, in studies that measure leaf and stem use by various ungulates sharing habitat, plains zebra have also been found to use stem more readily than other species (Bell, 1971; Janis, 1976). Mountain zebra still preferred plants with a high leaf-to-stalk ratio, and generally avoided species with high stem volume or moribund material in the MZNP, and stem and inflorescence use was also recorded (Winkler, 1992). Winkler (1992) measured the grass species utilization in terms of the proportion of above-ground leafiness, using the eight-point Walker scale (Walker, 1976). The findings indicate a high acceptability of couch grasses (*Cynodon* spp.), in this case *Cynodon incompletus*, which was linked to its high level of accessible leaf material, but the correlation analysis showed a weak positive correlation between plant acceptance and leafiness. Moderate or low use of stoloniferous grasses can be supported by the hypothesis that stoloniferous growth in grasses (such as *Cynodon* spp.) is an evolutionary escape mechanism (Skarpe and Hester, 2008). Not all grass species offering high leafiness were favoured by mountain zebra, including *Merxmuella disticha*, of which the tough leaf structure could explain the moderate usage (Winkler, 1992). Other grasses with low leafiness but high inflorescence or seed-head availability such as *Digitaria eriantha*, *Panicum* *stapfianum* and *Sporobolus fimbriatus* were consistently favoured by mountain zebra (Winkler, 1992). Based on these findings, the argument is that feeding ecology studies which showed a high stem proportion in zebra diets using faecal analysis, such as that of Owaga (1975), may have been due to the accidental ingestion of stems when targeting grass inflorescences (Winkler, 1992). This is further supported by evidence of inflorescence use recorded for mountain zebra by Penzhorn (1982b).

Environmental conditions may also influence the preference of leaf and stem. Though grass leaves seem to be generally preferred, stem use may be utilized more readily depending on season. Gwynne and Bell (1968) found plains zebra to utilize equal proportions of stem and leaf plus sheath during the dry seasons. Mountain zebra also fed on stems and inflorescences of *Eragrostis curvula* in the dry winter months, May to July, in the MZNP (Grobler, 1983). In dystrophic ecosystems such as the BNP, the utilization of plant parts like seed heads may represent a valuable food resource to mountain zebra in dry seasons or older veld, as suggested by a pilot study in the dystrophic GMNR (De Villiers, 1999).

Plant phenology plays an important role in forage selection by ungulates (Illius and Gordon, 1987; Owen-Smith and Cooper, 1987; Winkler, 1992; Sinclair *et al.*, 2000; Watson and Owen-Smith, 2002; Kuntz *et al.*, 2006; Venter, 2006). Other grazer species such as sable (*Hippotragus niger niger*), blue wildebeest (*Gorgon taurinus*) and buffalo (*Syncerus caffer caffer*) also target species with a high level of above-ground green material (Grobler, 1981; Magome, 1991; Parrini, 2006). Magome (1991) also noted a preference for species that stayed green longer than others, such as *Panicum maximum*. Owen-Smith and Cooper (1987) and Watson and Owen-Smith (2002) recognised the importance of classifying food species according to seasonal acceptability at the various growth stages. In other words, a species may be preferred in a particular season and avoided in another, due to its phenological growth stage. Preference for a particular growth stage may also differ among growth forms, as graminoids and forbs flush sooner after rain than other growth forms, (Coe *et al.*, 1976; Joubert and Stindt, 1979; Owen-Smith, 1982; East, 1984; Kraaij and Milton, 2006). Grass phenology also needs to be considered, in terms of how the growth seasons for utilized grass species are influenced by both the fire season and rainfall (Novellie, 1986; Novellie, 1987; Novellie and Bezuidenhout, 1994; Archibald, 2008; Kraaij and Novellie, 2010). Fire increases the available amount of green material, since it stimulates abundant new growth (Kruger and Bigalke, 1984; Van Wilgen *et al.*, 1994; Parrini, 2006; Kraaij and Novellie, 2010; Wessels *et al.*, 2011). This is significant both in terms of how herbivores respond to flushing plants after fire, and how plants respond to varying degrees of utilization at different stages following fire (Kruger, 1983; Kruger and Bigalke, 1984; Mentis and Tainton, 1984; De Ronde, 1990; Wan *et al.*, 2001; Bond *et al.*, 2003; Watson *et al.*, 2005; Archibald, 2008; Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010). Veld age thus needs to be considered in the assessment of the phenological stage of selected food plants, based on the time interval since the fire. This is particularly important in dystrophic ecosystems, where fire plays an important role in ungulate utilization of the habitat (Novellie, 1987; Watson *et al.*, 2005; Watson and Chadwick, 2007; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Watson *et al.*, 2011). Phenology may be measured in terms of the degree of greenness, research in this field showing a strong positive correlation between grass acceptance by *Equus* species and the degree of greenness (Winkler, 1992; Wilsey, 1996; Boyers, 2011).

Seasonal utilization of graminoids at varying height is another factor that influences forage selection (Bell, 1970; Bell, 1971; Novellie, 1987). Variation in seasonal utilization of grass at various heights was found to occur between species sharing habitat in the Serengeti, namely plains zebra, topi (*Damaliscus korrigum*), Thomson's gazelle (*Gazella thomsonii*) blue wildebeest and buffalo (Bell, 1970; Bell, 1971). In the wet season good quality short grass was preferred, while in the dry season grazers moved into areas with poorer quality, medium to tall grass, in order of species body size. Along with buffalo, zebra’s greater body size was linked to the ability to utilize taller grass. Bulk grazers generally tend to select taller grasses in order to obtain adequate quantity forage, but acceptance of preferred taller grass species declines in the dry season, when the availability of green, nutritious material is lower (Heady, 1964; Grunow, 1980; Macandza *et al.*, 2004). Smaller grazers tend to find greater benefit from shorter grass (Bell, 1970; Demment and Van Soest, 1985). In the MZNP mountain zebra fed at a higher level than the other grazers, feeding at a height of 40 to 80 mm, and rarely below 30 mm, and sweet grasses up to 200 mm (Winkler, 1992). When selecting seed heads of *E. curvula* in the dry season, feeding occurred between 310 and 480 mm (Grobler, 1983). As the largest herbivore in the BNP, mountain zebra was expected to differentiate from other grazers in height preference by utilizing taller grasses, though studies since their introduction suggest that they are competing with other grazers for recently burnt areas and grazing lawns with short, nutritious grass instead (Kraaij and Novellie, 2010; Watson *et al.*, 2011). Other work suggests that if the population of other grazers preferring low-level grass was allowed to increase to the extent that the mean grass height of preferred food species were kept below that of the mean zebra feeding height, it would impact negatively on the zebra population over time (Grobler, 1983).

In relation to feeding technique, plant height can also be an important determining factor (Owen-Smith, 1982; Owen-Smith and Novellie, 1982; Arsenault and Owen-Smith, 2002). Zebra grip grass clumps between the front teeth and pluck the grass with a side motion of the whole head, which is less efficient than the ruminant strategy in utilizing short grass (Owen-Smith, 1982). In DHNR Cape mountain zebra preferred grassy areas despite grass height being below the preferred 40 to 80 mm for half of the year (Smith *et al.*, 2008; Smith *et al.*, 2011). Prior to the introduction of mountain zebra into the BNP, the relationship between grass height and degree of defoliation by grazers after fire was investigated (Novellie, 1987). The findings suggest that grass species responded differently to utilization after fire, in that taller-growing grasses which allowed larger bite sizes were initially favoured. Once the shorter-growing grass height increased, utilization of these grasses increased, since the taller growing grasses had become coarser and less nutritious. Based on the complex interaction of plant part selection, percentage greenness, and plant volume (leaf height and diameter) in forage selection, especially for bulk grazers in nutrient poor environments, the diet of mountain zebra in the BNP is of particular research interest.

1.3.4. NUTRITIONAL STATUS

Ungulate nutritional status plays an important role in ecosystem management, as nutrient availability will determine ungulate movement, as well as game health (Grant *et al.*, 1995; Wrench *et al.*, 1996; Grant *et al.*, 2000; Grange and Duncan, 2006; Codron *et al.*, 2009; Fuggle *et al.*, 2009). In the MZNP for example, seasonal movements between habitat types by mountain zebra corresponded with the fluctuation in nutritional value and biomass availability of preferred foods (Penzhorn, 1982b; Grobler, 1983; Novellie *et al.*, 1988; Winkler, 1992; Novellie and Bezuidenhout, 1994; Winkler and Owen-Smith, 1995).

Due to the large required intake rate of non-ruminant grazers, the nutrient matrix in the ingested forage is important, and would influence ungulate nutritional status (Bell, 1971; Parra, 1978; Demment and Van Soest, 1985; Owen-Smith, 1988; Duncan *et al.*, 1990; Illius and Gordon, 1992; Duncan and Poppi, 2008). In areas where resources are limited, ruminants should cope better, as they can extract the same amount of energy from 20% less forage than non-ruminants (Illius and Gordon, 1992). This is particularly relevant to dystrophic ecosystems, where soil and vegetation nutrient concentrations are low (Cowling and Holmes, 1992; Johnson, 1992; Van Wilgen *et al.*, 1992; Richards *et al.*, 1997), and provides a possible explanation for the poor performance of mountain zebra in the BNP to date, compared to the ruminant grazers in the park (Kraaij *et al.*, 2011; Watson *et al.*, 2011). The seasonal abundance of bontebok and eland dung groups in DHNR were significantly affected by the soil type (Radloff, 2008). Dung groups were positively associated with the more nutrient rich Bokkeveld Shales and Waenhuiskrans limestone substrates, as opposed to Table Mountain sandstone and Strandveld formations. Management objectives in these areas may thus include: (a) maintaining diversity in the landscape in order to provide adequate forage types for ungulates to utilize; and (b) monitoring ungulate nutrient status (Novellie, 1994; Grant *et al.*, 1995; Wrench *et al.*, 1996; Wrench *et al.*, 1997; Grant *et al.*, 2000).

Disturbances like fire will also influence ungulate nutrient status, as fire increases the availability of nutrients in the system and boosts the grass component, creating favourable conditions for grazers (Boerner, 1982; Kruger, 1983; Mentis and Tainton, 1984; Trabaud and deChanterac, 1985; Novellie, 1987; De Ronde, 1990; Van Wilgen *et al.*, 1994; Bond and Wilgen, 1996; De Klerk *et al.*, 2001; Wan *et al.*, 2001; Bond *et al.*, 2003; Archibald and Bond, 2004; Archibald, 2008; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Ligavha-Mbelengwa and Bhat, 2013). Again this is particularly important in fynbos ecosystems such as the BNP, where fire is a crucial tool in the management of the vegetation and herbivore populations (Kraaij, 2004;

Watson *et al.*, 2005; Watson and Chadwick, 2007; Kraaij *et al.*, 2008; Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Watson *et al.*, 2011).

Seasonal changes in nutrient availability also needs careful consideration, as nutrient levels fluctuate with the phenological state of plants, in response to climatic conditions (Schaefer, 1973; Nahal, 1981; Novellie and Bezuidenhout, 1994; Cowling and Lombard, 2002; Bond *et al.*, 2003; Wright *et al.*, 2004). In arid environments, equids may survive in severe drought more efficiently than ruminants, as long as they have adequate access to water (Bell 1970; Owaga 1975; Stevens & Hume 1996). However, in the southern Cape fynbos context, there is evidence of nutritional stress in ungulates, specifically linked to seasonal drought (Radloff, 2008).

In natural ecosystems, game health can be monitored through determining faecal nitrogen and phosphorus (Moir, 1960; Moir, 1966; Bell, 1982; Holechek *et al.*, 1982a; East, 1984; Mitchell *et al.*, 1984; Ben-Shahar and Coe, 1992; Grant *et al.*, 1995; Wrench *et al.*, 1996; Wrench *et al.*, 1997; Grant *et al.*, 2000). Particularly for grazers in dystrophic ecosystems, obtaining enough nitrogen and phosphorus from the available food resource is a challenge, as levels of these nutrients are particularly low in fynbos (Specht and Moll, 1983; Specht *et al.*, 1983; Campbell, 1986; Stock and Lewis, 1986; Radloff, 2008). This is supported by the postulation that fynbos ecosystems cannot sustain large numbers of large ungulate herbivores per unit area (Boshoff and Kerley, 2001; Boshoff *et al.*, 2002; Coetzee, 2002; Radloff, 2008). Monitoring faecal nutrient levels of mountain zebra in fynbos thus serve as an important management tool, to establish whether the population is thriving in the dystrophic ecosystem or not, and adapt fire rotation and animal numbers in the system accordingly.

CHAPTER 2: STUDY SITE

2.1. LOCATION AND TOPOGRAPHY

The Bontebok National Park (BNP; 34°02'S, 20°25'E) falls within the Cape Floristic Kingdom, an internationally recognised hotspot of biodiversity and priority for conservation (Goldblatt and Manning, 2002; Cowling *et al.*, 2003; Rouget *et al.*, 2004; Rebelo *et al.*, 2006; Jacobs and Jangle, 2008). The park is situated 7 km from Swellendam, in the Western Cape Province, and at 34.35 km^2, it is the smallest National Park in South Africa (Kraaij, 2011; Kraaij *et al.*, 2011). The vegetation of the BNP is diverse (Kraaij, 2011) and the BNP currently conserves a small remnant of a unique fynbos type, classified as Swellendam Silcrete Fynbos (Rebelo *et al.*, 2006). Figure 2.1 displays the extent of the BNP in relation to the Breede River, which flows along the southern boundary of the park. A system of tributaries, streams and drainage lines draining into the Breede River, including the Furrow River (also known as the Bontebok River) are present in the park (Russell, 2001; Vlok and De Villiers, 2007; Kraaij *et al.*, 2011). The BNP lies on a coastal plateau between the Indian Ocean and the Langeberg mountain range, between 60 and 198 m above sea level (Grobler and Marais, 1967; Theron, 1967; Robinson *et al.*, 1981).

Topographically the BNP consists of four distinct terraces connected by a network of steep, south-west sloping hills and drainage lines (Theron, 1967; Chief Director of Surveys and Land Information, 1984; Vlok and De Villiers, 2007; Kraaij *et al.*, 2011). The four terraces are: (a) a higher level greater than 122 m above sea level (masl); (b) a level between 77 and 122 masl; (c) a level between 77 and 85 masl on the edge of the river; and (d) a level between 60 and 77 masl, which includes the Breede River flood plain and the area where the terrain levels out in the south-eastern region of the park (Grobler and Marais, 1967; Theron, 1967; Robinson *et al.*, 1981; Kraaij *et al.*, 2011).

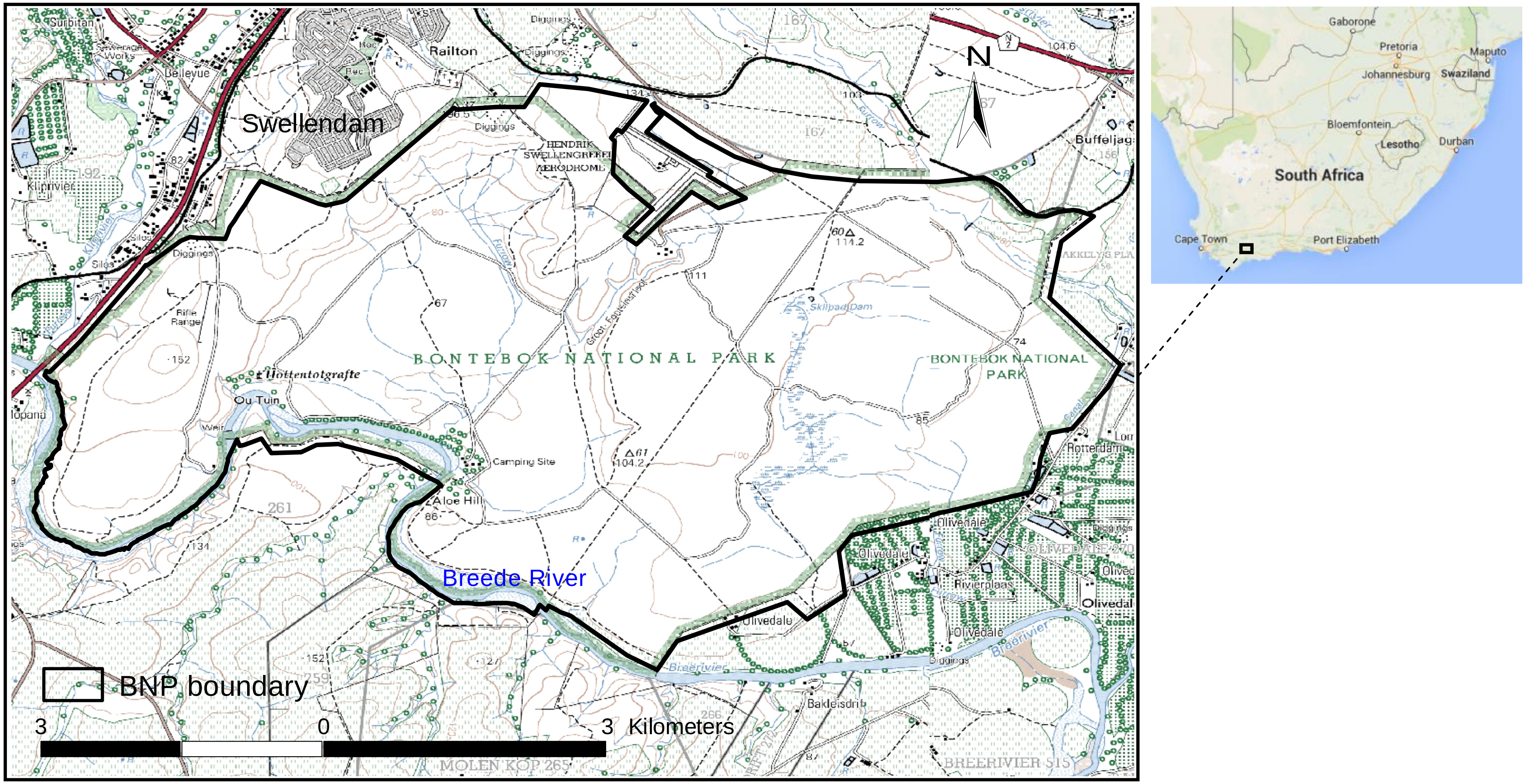


Figure 2.1: The location of the Bontebok National Park depicted on the national 1:250 000 topographical land type series (Chief Director of Surveys and Land Information, 1984).

2.2. GEOLOGY

The geological terraces present in the Overberg district and the BNP are characteristic of wave action between 7 and 20 million years ago (Robinson *et al.*, 1981; Norman and Whitfield, 2006). The geology in the BNP is mainly of the Bokkeveld group, with formations of the Uitenhage group, Enon Conglomerate, in the north and central region of the park, and Witteberg formations present in the southern interior (ARC, 2014). This is supported by DWAF (2004) and Norman and Whitfield (2006), who note the Enon Conglomerates of the Uitenhage group as being prevalent in the lower Breede River domain. The geological formations present in the Lower Breede River and Overberg are Quartzitic Table Mountain Sandtone, Witteberg Sandstone, Bokkeveld and Malmesbury Shales, Enon Conglomerate, Coastal Deposits, Limestone and Marine Sands (DWAF, 2011).

The geology of BNP itself consists of 90% alluvial plains and gravel terraces, and portions of consolidated rock along the Breede River (Theron, 1967). Three age classes can be distinguished in the gravel terraces, consisting of quartz and sandstone roll-stones and sandy gravel (Theron, 1967; Chief Director of Surveys and Land Information, 1993). Silcrete and ferricrete occur in the northern and central parts, and alluvial and sandy loam in the south-western plateau (Theron, 1967).

The highest terrace (> 122 masl) is in the north-western region of the park, and consists of a sandy ferricrete gravel fused with white quartzite pebbles, and thin bands of silcrete (Theron, 1967). The texture of the younger second level (between 77 and 122 masl) is also mainly a white and brown quartzite gravel, but small pieces of shale are more prevalent in this sandy gravel, and the pebbles are well rounded (Theron, 1967). The level between 77 and 85 masl consists mainly of light brown to white river sand with white quartzite/sandstone pebbles scattered throughout (Theron, 1967). In the south-western part of the park a sandy alluvial plain is postulated to be a remnant of a meander in the Breede River, which was gradually filled in with sand as the river bed shifted south (Theron, 1967; Whittingham, 1975; DWAF, 2004).

The area in the west known as “Die Stroom” forms part of the geological formations that extend south- and westward from the park, and is underlain by Bokkeveld Shale and Siltstone (Theron, 1967; Robinson *et al.*, 1981; Chief Director of Surveys and Land Information, 1993; Norman and Whitfield, 2006; Kraaij *et al.*, 2011).

Exposed sandstone outcrops of the Witteberg series are restricted to areas near the Breede River and consistently south-east facing (Theron, 1967; Norman and Whitfield, 2006). This consolidated rock consists of mica-rich, grey to light brown, medium to fine grained sandstone (Theron, 1967). Theron (1967) notes that silt stone and shale also occur in this area.

2.3. SOILS

The soils of the Swellendam and BNP region are leptosols of limited pedological development, usually shallow and on hard or weathering rock (ARC, 2014). More specifically, the soils associated with the Uitenhage formation in the central, northern and eastern region of the BNP are described as poorly drained, strong texture contrast soils. This comprises podzols, young brown earth, prismacutanic and pedocutanic horizons and gravel (Theron, 1967; Chief Director of Surveys and Land Information, 1984; ARC, 2014). Alluvial sand in the central to southern region of the park give way to shallow lithosols in the vicinity of the Breede River, which are of limited pedological development, often on hard or weathering rock (Theron, 1967; ARC, 2014). Some lime of the Glenrosa and Mispah forms is present in the south and at “Die Stroom” (Theron, 1967; Chief Director of Surveys and Land Information, 1984; Fey, 2010; Kraaij *et al.*, 2011; ARC, 2014).

Soils depth for the BNP area is generally less than 450 mm; soils are sandy with a very low clay content (mean clay content for the area: 15%); and at the broad scale, soil pH for the area is between 5.5 and 6.4 in the north-eastern section of the park, and 6.5 and 7.4 in the south-west (ARC, 2014).

Due to leaching in sandstone-associated fynbos, the nutrient status for the Cape lowland soils is generally low, particularly in nitrogen and phosphorus, though the presence of silcrete and alluvium in the landscape, with reduced leaching in some areas may cause a marginal increase in local soil fertility (Specht and Moll, 1983; Campbell, 1986; Low and Rebelo, 1996; Mucina *et al.*, 2006; Rebelo *et al.*, 2006; Radloff, 2008). Lambrechts (1979) mapped the soils between Swellendam and the Breede River as heavy textured, moderate to poorly leached soils. The soils of the BNP are well leached in the north, and moderately leached in the central interior (Specht and Moll, 1983; ARC, 2014). Soil nutrient status for specific elements is below average: soil selenium < 0.45 $mg.kg^{-1}$; soil cobalt < 2.0 $mg.kg^{-1}$; soil copper < 2.0 $mg.kg^{-1}$; soil iodine < 0.64$mg.kg^{-1}$, and soil zinc as < 1.0 $mg.kg^{-1}$ (ARC, 2014). Soils derived from Bokkeveld Shale such as the area known as “Die Stroom”, would be much higher in nutrients, especially potassium (Lambrechts, 1979).

2.4. CLIMATE

The climate of the Cape Coastal Lowlands varies from typically Mediterranean in the south-west to year-round rainfall region in the north-east (Fuggle and Ashton, 1979; Nahal, 1981; Cowling, 1992; Raitt, 2005). The locality of the BNP is in a transition area between a moderate winter rainfall and a non-seasonal rainfall seasonality regime (Cowling and Heijnis, 2001).

The mean annual rainfall in the BNP is 528 mm (1961-2005), 59% falling in winter from April to October, with a markedly low rainfall in December and January (Novellie, 1986; Kraaij *et al.*, 2011). Two rainfall peaks are noted for the BNP, one in April-May and the other in August (Novellie, 1986; Kraaij *et al.*, 2011). Low rainfall coincides with high temperatures in summer, causing a summer drought, which plays an important role in vegetation structure (Kruger, 1979; Nahal, 1981; Specht and Moll, 1983; Cowling *et al.*, 1997; Raitt, 2005; Rebelo *et al.*, 2006). Summer mist and fog precipitation are characteristic features of the climate of the Cape Coastal Lowland region (Schulze, 1997). Temperatures range between a summer maximum of 40°C and a winter minimum of 0°C, average temperatures varying between 6°C and 32°C (Figure 2.2) annually (Grobler and Marais, 1967; Novellie, 1987; Goldblatt and Manning, 2002). The prevailing winter winds are south-westerly, and prevailing summer winds are south-easterly, with strong east-west winds in spring and hot berg winds in autumn (Fuggle and Ashton, 1979; Schulze, 1980).

For this study, data are grouped into four seasons, based on rainfall data for BNP from 1991 to 2010 (SANParks, Unpublished) and climatic patterns for the region (Cowling and Lombard, 2002; Born *et al.*, 2007). The winter and spring seasons are characterised by cool temperatures, and the summer and autumn seasons by warm temperatures (Fuggle and Ashton, 1979; Pierce, 1984; Pierce and Cowling, 1984) and were grouped accordingly, into the cool winter, cool spring, warm summer and warm autumn seasons. The long-term mean monthly rainfall for the winter season is 44 mm; for the spring season 43 mm; for the summer season 33 mm; and for the autumn season 48 mm (SANParks, Unpublished). The mean monthly rainfall during the study period for the cool winter season was 45 mm; for the cool spring season 47 mm; for the warm summer season 37 mm; and for the warm autumn season 48 mm (SANParks, Unpublished).

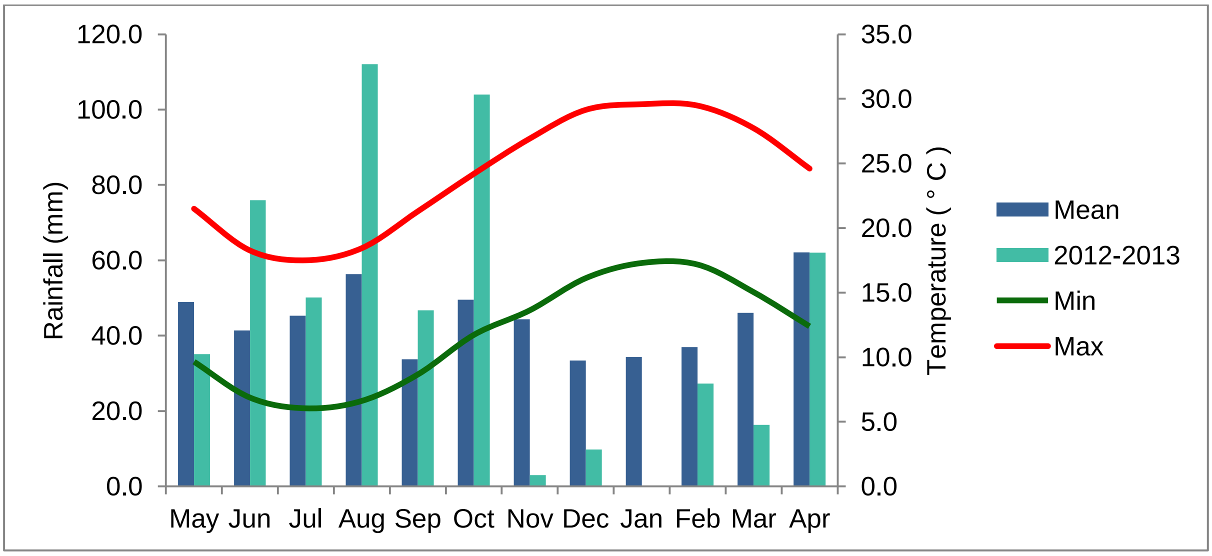


Figure 2.2: Climate of the Bontebok National Park: Long-term minimum and maximum temperatures and rainfall, compared with rainfall during the study period (SANParks, Unpublished).

2.5. WATER SOURCES

Access to water can limit game distribution within a protected area, and even exclude some favourable habitats from utilization in arid areas (Western, 1975; McNaughton and Georgiadis, 1986; Fryxell and Sinclair, 1988; Gaylard *et al.*, 2003). Seasonal surface water availability can limit the distribution of animals, especially during the dry season (Redfern *et al.*, 2003). Though the BNP is not in an arid biome, seasonal drought conditions have been suggested to prevail in the area (Kruger, 1979; Raitt, 2005; Radloff, 2008). However, in the BNP due to the prevalence of surface water access points, water is not seen as a limiting factor. This constitutes over 12 km of river frontage, as well as pans, dams, watering points and seasonally wet drainage lines (Kraaij and Novellie, 2010; Kraaij *et al.*, 2011). Kraaij and Novellie (2010) calculated the maximum distance to water from any point in the park as 2 km.

2.6. VEGETATION

Due to its small size and the presence of over 650 plant species, the BNP is the national park with the highest plant species richness per unit area in South Africa (Kraaij 2011). Of the 650 plant species in the BNP, 250 are endemic to the Cape Floristic Region, and 52 are of conservation concern, falling in IUCN Red Data categories Critically Endangered, Endangered and Vulnerable (Goldblatt and Manning, 2002; Raimondo *et al.*, 2009; Kraaij, 2011). Of all BNP species 23% are geophytes, 20% dwarf shrubs, 16% herbs, 15% graminoids, 13% shrubs, 8% succulents, 3% trees, 2% climbers and 40 are alien plant species (Kraaij, 2011). Three plant species are endemic to the BNP: *Aspalathus burchelliana*, *Diosma fallax*, and *Erica filamentosa* (Kraaij, 2011).

2.6.1. HABITAT TYPES

The vegetation of the BNP has been included in various national and regional vegetation classification systems. At a national scale, it is classified as Coastal Renosterbosveld (Acocks, 1953; Kruger, 1979). In more recent and fine scale work, the majority of the BNP comprises Swellendam Silcrete Fynbos, an intermediate fynbos type between shale and sandstone fynbos, exhibiting floristic features of both fynbos and renosterveld (Mucina *et al.*, 2006; Rebelo *et al.*, 2006). Along the southern boundary of the park Rebelo *et al.* (2006) defined the vegetation as Eastern Rûens Shale Renosterveld. Other vegetation classifications recognised the following vegetation types: South Coast Renosterveld (Moll *et al.*, 1984), South and South-West Coast Renosterveld (Low and Rebelo, 1996), Overberg and Riversdale Coast

Renosterveld Fynbos/Renosterveld Mosaic (Cowling *et al.*, 1999b; Cowling and Heijnis, 2001), the critically endangered Cape Lowland Alluvial Vegetation and Cape Lowlands Renosterveld (Von Hase *et al.*, 2003; Rouget *et al.*, 2004; Mucina *et al.*, 2006).

Swellendam Silcrete Fynbos is also recognised as an endangered vegetation type, with a conservation target of 30%, over 43% currently transformed and 4% protected in the BNP (Rouget *et al.*, 2004; Rebelo *et al.*, 2006; Jacobs and Jangle, 2008; Kraaij, 2011).

According to Rebelo *et al.* (2006) Swellendam Silcrete Fynbos is mainly Asteraceous, and graminoid at higher altitudes and on northern slopes when disturbed. This vegetation type is particularly susceptible to overgrazing pressure, burning and liming are among the farming practices commonly used in the area to stimulate grazing, and the extent of grassy areas have been artificially increased by farming (Rebelo *et al.*, 2006). Rebelo *et al.* (2006) and Kraaij (2011) note that Swellendam Silcrete Fynbos is poorly understood, and assuming it has the characteristics or carrying capacity of “true” Renosterveld would be unfounded.

At the regional scale, Vlok and De Villiers (2007) identified five vegetation or habitat types within the boundaries of the BNP, as part of the Riversdale domain: Asteraceous Fynbos, Proteoid Enon Conglomerate Fynbos, Inland Pans, Drainage Lines, and River & Floodplain. The predominant types are Asteraceous and Proteoid fynbos, supported by the classification of Rebelo *et al.* (2006), which notes that silcrete fynbos is dominated by mesotrophic Asteraceous and Proteoid fynbos.

Kraaij and Novellie (2010) and Watson *et al.* (2011) combined the habitat types of Vlok and De Villiers (2007) with veld age and fire history to assess herbivore distribution in the BNP. They further recognised several transformed areas in the park, often dominated by *Cynodon dactylon* due to historical livestock kraaling, now frequently grazed by bontebok (Luyt, 2005; Watson *et al.*, 2011; Novellie and Gaylard, 2013). These areas were differentiated by Watson *et al.* (2011) as the Kraal Lawn vegetation. In other work, 13 vegetation communities were defined by Grobler and Marais (1967) for the 1967 extent of the BNP, and Luyt (2005) refined and extrapolated these communities in a Geographic Information System (GIS), using satellite imagery and roadside observations as part of a habitat assessment.

For the current study, the vegetation map of Vlok and De Villiers (2007) was used in combination with categorisation similar to that of Kraaij and Novellie (2010) and Watson *et al.* (2011) to delineate vegetation communities / habitat types, with an additional type, the Recently Burnt Area included, based on the boundaries of the fire in February 2012 as mapped by park staff (SANParks, 2013). During the course of the study, the boundaries of the communities were refined in a Geographic Information System (GIS) using 1:10 000 orthophotos, topographical maps, 5 m contour data, soil maps, expert input and ground truthing (Chief Director of Surveys and Land Information, 1984; Chief Director of Surveys and Land Information, 2000; Chief Director of Surveys and Land Information, 2010; Vlok, 2014 *pers. comm.*). Figure 2.3 displays the habitat types delineated for this study, also distinguishing between young (between one and five year old veld) and old (greater than 5 years in veld age) habitat types, and displaying an area of 100 ha which is classified as unsighted ground for analysis in the research Chapters of this study.

(a) The **Proteoid Fynbos** forms 36% of the park area, and includes *Leucadendron salignum*, *Leucospermum calligerum*, *Protea decurrens*, *Protea piscina*, *Protea repens*, *Serruria acrocarp*a and *Cliffortia ruscifolia* (Rosaceae), while *Dicerothamnus rhinocerotis* is present but not dominant (Grobler and Marais, 1967; Vlok and De Villiers, 2007). Dominant grass species in this habitat type are *Brachiaria serrata, Cymbopogon marginatus, Cynodon dactylon, Digitaria eriantha, Eragrostis capensis, Eragrostis curvula, Eragrostis obtusa, Eustachys paspaloides, Harpochloa falx, Sporobolus fimbriatus, Themeda triandra* and *Tribolium uniolae* (Grobler and Marais, 1967; Vlok and De Villiers, 2007).

(b) The **Asteraceous Fynbos** forms 36% of the park area, and is characterised by a number of Asteraceous species: renosterbos (*Dicerothamnus rhinocerotis*), *Eriocephalus africanus*, *Metalasia* spp., *Oedera capensis*, *Stoebe* spp. (Grobler and Marais, 1967; Vlok and De Villiers, 2007), and Asteraceous geophytes of the genus *Corymbium*, which is prominent after fire (Vlok and De Villiers, 2007). Widespread graminoids include *Restio triticeus, Ischyrolepis capensis*, *C. dactylon, D. eriantha*, *Ehrharta capensis*, *Eragrostis* spp., and *Themeda triandra* (Vlok and De Villiers, 2007). This type is represented by the renosterbos vegetation communities of (Grobler and Marais, 1967). Another important bunch grass in this habitat type is *Merxmuellera stricta*, formerly *Danthonia stricta* (Grobler and Marais, 1967) .

(c) The **Recently Burnt Area** constitutes 11% of the park area in the north, and north-eastern region of the park, burnt by a runaway fire during late February 2012, two months before the onset of the sampling period for this study (SANParks, 2013). Recently Burnt Area was regarded a distinct habitat type, irrespective of the vegetation type as mapped by (Vlok and De Villiers, 2007). This meant that for the 12 months of sampling, 3 distinct age classes could be identified in the park, namely areas with a veld age of: (a) less than 1 year (“recently burnt”), (b) between 1 and 5 years (“young”), and (c) more than 5 years (“old”). The cut-off between old and young veld was based on the work of Kraaij and Novellie (2010), which showed a distinct decline in count data for mountain zebra in veld older than 5 years. During the last month of sampling a block burn was also initiated by park management, but no grazers were observed in the Recently Burnt Area during the sampling days of that month. This area consists of 96% Proteoid Fynbos and 4% Drainage Lines habitat. A significant proportion of the Recently Burnt Area (approximately 33% of the Proteoid Fynbos) comprises old farmlands, which was historically subjected to transformation such as heavy grazing and ploughing (Kraaij, 2011; Kraaij *et al.*, 2011).

(d) **Drainage Lines** cover 10% of the park area, and represents the same areas as the Drainage Lines habitat of Watson *et al.* (2011). Grobler and Marais (1967) did not specifically separate this habitat type in their description of the vegetation of the then much smaller BNP in 1967, and in that report it forms part of the Asteraceous (renosterbos) communities. More recently however, Vlok and De Villiers (2007) described this habitat in combination with the Breede River Thicket, and called it the Bontebok River and Floodplain, and refer to specific areas and landscape attributes in the habitat, from which the more specific species composition of the two habitat types could be derived. The tree and shrub component is similar to that of the Breede River Thicket (see section (g) below). These areas are not connected to perennial streams, as the Breede River Thicket is (Vlok and De Villiers, 2007). Here the grass and sedge component is well developed: The dominant grasses are *Andropogon appendiculatus, Cynodon dactylon, D. eriantha*, *Eragrostis capensis, E. curvula, Imperata cylindrica, Pennisetum macrourum, Pentaschistis colorata, Sporobolus africanus* and *Tristachya leucothrix*; and dominant sedges area *Cyperus fastigiatus, C. laevigatus, C. marginatus, C. textilis, Mariscus congestus* and *Schoenoplectus scirpoides* (Vlok and De Villiers, 2007). Portions of these seasonally wet drainage areas were historically heavily grazed by domestic stock (Robinson *et al.*, 1981). One area included in this type, formerly known as "Reisiesvlei" forms the convergence of a number of small valleys or drainage lines and was historically more inundated, which in the historical context was intensively grazed by livestock and also drained with a number of trenches that are still present in the landscape (Robinson *et al.*, 1981; Kraaij *et al.*, 2011). Some brackish areas also occur in this habitat type, where species like *Juncus acutus* and *J. punctorius* are abundant, and *Atriplex vestita,* three *Drosanthemum* spp., *Manochlamys albicans* and *Suaeda fruticosa,* are often present. The grass component is not well developed in the brackish areas where the drainage is poor (Vlok and De Villiers, 2007).

(e) **Inland Pans**, form 1% of the BNP, mapped at a scale of 1:10 000, using Georeferenced Orthophotos (Chief Director of Surveys and Land Information, 2010). Vlok and De Villiers (2007) mapped the presence of Inland Pans in the BNP landscape, calculated at a broader scale (1:50 000) as 5%. *Aponogeton junceus* and *Ornithogalum flexuosum*, *Elegia* spp., *Hypodiscus* spp. and *Erica quadrangularis* are noted as species present along the edges of pans in these areas. During summer, when the water surface of the pans are dried out, *C. dactylon* becomes a dominant species in this habitat type (Luyt, 2005), and forms an important species for bontebok during this season (Beukes *et al.*, 1989; Luyt, 2005; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010). A well-developed grass component along the pan fringe areas is visible in photographs in the report by Vlok and De Villiers (2007), which was confirmed by personal observation during this study.

(f) The **Grazing Lawns** habitat (Kraaij and Novellie, 2010) including the Kraal Lawn vegetation (Watson *et al.*, 2011), forms < 0.5% of the park area, and is dominated by *C. dactylon*. Watson *et al.* (2011) estimated the extent of the Kraal Lawn vegetation as 2% of the park area – the difference in proportional area could be attributed to the difference in mapping scale. These area estimates are also based on larger patches of Grazing Lawn vegetation that could be mapped at a ≥ 1:10 000 scale, and thus further investigation of the exact extent of the grazing lawns has been recommended by Luyt (2005), Kraaij *et al.* (2011) and Watson *et al.* (2011).

(g) **Breede River Thicket** forms 5% of the park area, and includes the riparian zone and the river. This type is a subset of the Breede River and Floodplain habitat mapped by Vlok and De Villiers (2007). This habitat has a prominent tree component, including the species *Acacia karroo*, *Buddleja saligna, Halleria lucida, Pittosporum viridiflorum, Sideroxylon inerme* and *Podocarpus elongatus* (Vlok and De Villiers, 2007). Spatially this habitat overlaps with the *Acacia karroo*, *Aloe*, *Olea* and *Podocarpus elongatus* communities of Grobler and Marais (1967). Shrubs are less dominant in this habitat, but species like *Grewia occidentalis* and *Leonotis leonurus* prevail, the latter being dominant after fire (Vlok and De Villiers, 2007).

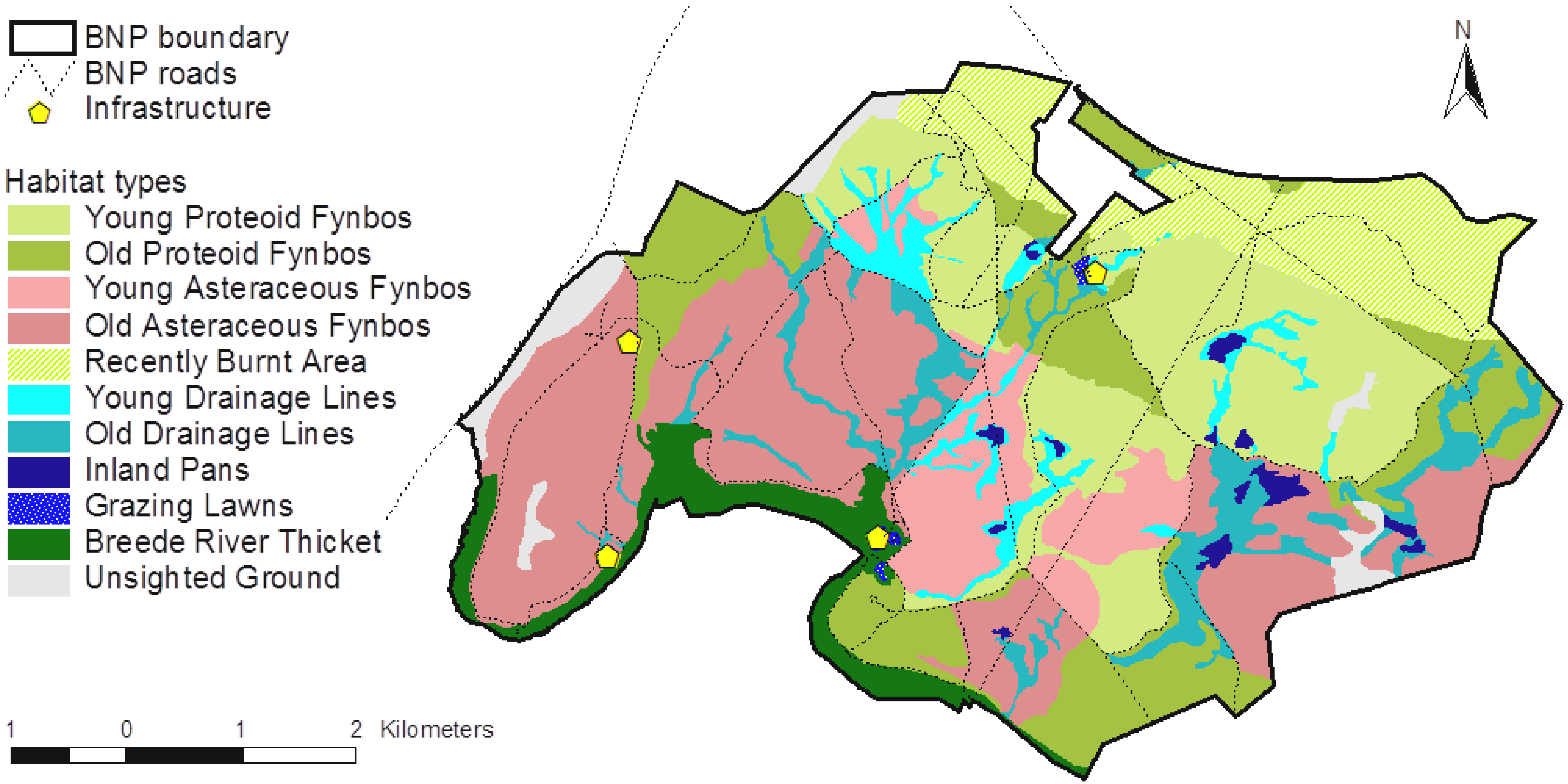


Figure 2.3: Habitat types available to mountain zebra in the BNP.

2.7. HERBIVORES

Ungulate species included in the historial range of the BNP would have included Cape grysbok (*Raphicerus melanotis*), grey duiker, grey rhebuck (*Pelea capreolus*), steenbok (*Raphicerus campestris*), bontebok, red hartebeest, Cape mountain zebra and bushpig (*Potamochoerus larvatus*), which are currently present in the BNP; as well as klipspringer (*Oreotragus oreotragus*), buffalo, eland (*Taurotragus oryx*), elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibious*) and black rhinoceros, which are currently not present in the park (Skead *et al.*, 2007; Kraaij *et al.*, 2011).

The Cape mountain zebra population was the main focus of this study, with observations of herds of bontebok and red hartebeest per habitat type noted. During 2012-2013 the study population of mountain zebra consisted of a total of 11 individuals in two herds, with a stallion in each herd, six adult mares, one sub-adult mare and three foals. In the early winter of 2012 there was one foal mortality in the smaller herd, reducing the study population to nine individuals. During the late winter / early spring there was one foal born in the larger herd, and another in autumn of 2013, bringing the study population to 11 animals for the remainder of the sampling term. Game counts by park staff during 2012 to 2014 estimated the number of Cape mountain zebra at 11, the number of bontebok at 240, and the number of red hartebeest at 49 (SANParks, 2014).

CHAPTER 3: HABITAT USE AND SUITABILITY

3.1. INTRODUCTION

Habitat selection is a hierarchical process during which a range of behavioural decisions are made by an animal about which habitat to use at the different scales in the available environment (Rosenzweig, 1981; Senft *et al.*, 1987; Bailey *et al.*, 1996). Since natural landscapes are heterogeneous, habitat types are used disproportionately (Jarman and Sinclair, 1979; Sinclair, 1979; Boyce and McDonald, 1999; Morris, 2003). The selection of habitat can be viewed at four levels: (a) The geographical range of a species at the regional scale; (b) The home range of the population in the landscape; (c) Habitat utilization based on plant communities, and (d) Selection of plant products at the feeding site (Johnson, 1980; Senft *et al.*, 1987; Orians and Wittenberger, 1991; Bailey *et al.*, 1996; Fortin *et al.*, 2002; Owen-Smith *et al.*, 2010). In the BNP, the presence of park boundaries replace the first order selection, since it is a fenced system from which grazers cannot migrate or extend their geographical range. The second order selection was not dealt with during the current study, while third order selections are analysed in this Chapter as the habitat preference of mountain zebra. The fourth order selection is dealt with in Chapter 4.

According to Bailey *et al.* (1996) factors such as thermoregulation and competition will influence habitat selection in terms of central areas chosen at the third order of selection, influencing the frequency of selection. Habitat selection based on plant communities will thus vary spatially, over time, and at various scales: in terms of large-scale movement patterns as well as specific site selection (Bailey *et al.*, 1996). If suitable habitat is in small patches, herbivores move between patches frequently, whereas if suitable habitat is in larger patches, herbivores may migrate over large areas over longer periods of time (Hopcraft *et al.*, 2010). According to Owen-Smith *et al.* (2010), herbivores will relocate to a suitable foraging area every one to four hours, constituting a new habitat patch. The factors that drive habitat selection include predation, water availability, thermoregulation, competition, forage abundance and food plant phenology (McNaughton and Georgiadis, 1986; Senft *et al.*, 1987; Bailey *et al.*, 1996; Hopcraft *et al.*, 2010).

As discussed in Chapter 1, the only potential large carnivore in the BNP region is leopard, and since predation by leopard on mountain zebra in the BNP is unlikely (Hayward *et al.*, 2006), predators appear not to be an important factor in determining mountain zebra distribution in the BNP. Human activity in the BNP may influence mountain zebra movements, and needs to be investigated in terms of habitat use (Barnes *et al.*, 1991; Knight, 1995; Reyna-Hurtado and Tanner, 2005; Averbeck *et al.*, 2012). Water is readily available and does also not appear to be a limiting factor in the BNP, due to a maximum of 2 km distance to water from any given point in the park (Kraaij and Novellie, 2010; Kraaij *et al.*, 2011).

Habitat selection could also be influenced by inter-specific competition among ruminant and non-ruminant species (who have been shown to have similar ecological niches when resources are limited), or communities depending on a common resource (Illius and Gordon, 1992; Bailey *et al.*, 1996; Young *et al.*, 2005). Mountain zebra is one of the three dominant grazing species in the BNP, along with bontebok and red hartebeest (Kraaij *et al.*, 2011; Watson *et al.*, 2011). Competition may influence habitat preference of mountain zebra in the BNP, as all three grazing species favoured young veld over older veld in the BNP (Kraaij and Novellie, 2010). Evaluating the role of competition between grazers in the BNP was not within the scope of this study specifically, though it may be an important factor, which warrants further investigation.

Habitat utilization is also strongly regulated by seasonal changes in forage abundance and quality: Strong seasonality would cause herbivores to move more frequently, whereas weak seasonality would cause animals to remain in local areas (Hopcraft *et al.*, 2010; Owen-Smith *et al.*, 2010). In order to sustainably manage herbivore populations within fenced ecosystems, there is a need to determine the preferred habitat and temporal movement dynamics within the habitat (Melton, 1987b; du Toit and Owen-Smith, 1989; Scoggings *et al.*, 1990; Seydack *et al.*, 2000; Cromsigt *et al.*, 2009).

Habitat quality and food resource availability are important factors driving habitat selection by large mammalian herbivores (Owen-Smith, 1982; McNaughton and Georgiadis, 1986; Owen-Smith, 2002; Watson *et al.*, 2005; Knoop and Owen-Smith, 2006). Herbivores will select areas which provide adequate forage within the landscape instead of being evenly spread throughout the system (Owen-Smith, 1982; Senft *et al.*, 1987; Bailey *et al.*, 1996; Owen-Smith *et al.*, 2010). Certain habitats will be used more frequently than others, both on an annual and a seasonal basis, the extent of which can be determined though resource selection functions (Neu *et al.*, 1974; Alldredge and Ratti, 1986; Boyce and McDonald, 1999; Manly *et al.*, 2002).

Habitat suitability estimation is another crucial component in the management of wild ungulates (Novellie and Winkler, 1993; Novellie, 1994; Bailey *et al.*, 1996; Henley, 2001; Owen-Smith, 2003; Rouget *et al.*, 2003; Traill, 2003; Watson *et al.*, 2005; Traill and Bigalke, 2007; Watson and Chadwick, 2007; Watson *et al.*, 2011). Habitat suitability is a measure of the quality of the resource available to large mammalian herbivores, and a useful method for estimating veld condition (Novellie and Winkler, 1993; Novellie, 1994; Riitters *et al.*, 1997; Owen-Smith, 2002; Owen-Smith, 2011). An assessment of the suitability of the habitat, serves as a more detailed analysis of the habitat quality of the preferred habitat than utilization alone (Franklin, 1995; Guisan and Zimmermann, 2000). One such measure is the Habitat Suitability Index (*HSI*), which assesses the abundance of dietary species in the available habitat (Novellie and Winkler, 1993). An assessment in the BNP suggested that all fynbos habitats included in the survey, besides the Grazing Lawns or Kraal Lawn vegetation are of low (*HSI* > 10.0) habitat suitability (Watson *et al.*, 2011).

Poor habitat quality appears to be an important limiting factor in dystrophic ecosystems, where the availability of preferred food species is limited (Scott, 1993; Watson *et al.*, 2005). The suitability of the habitat can be assessed using presence and/or absence data (Traill, 2003; Traill and Bigalke, 2007), or through a survey of the vegetation (Roux, 1963; Novellie and Strydom, 1987), combined with the acceptability index of known food species (Novellie and Winkler, 1993). The Habitat Suitability Index of Novellie and Winkler (1993) was considered the most suitable measure for this study, and employed to assess the grazing value of the habitats of the BNP to mountain zebra. This approach was also used for mountain zebra habitat suitability analyses in the MZNP (Novellie and Winkler, 1993), GMNR (Watson *et al.*, 2005), KNR (Watson and Chadwick, 2007) and BNP (Watson *et al.*, 2011). For the calculation of the *HSI*, a limitation in some of the studies in dystrophic ecosystems, was that acceptability indices from the more nutrient rich ecosystem of the MZNP were used, (Winkler, 1992; Novellie and Winkler, 1993), whereas this Chapter's analysis used the acceptability indices recorded for the BNP (Table 4.2).

The objectives of this Chapter were three-fold: Firstly, the size of the area used by all mountain zebra in the BNP was assessed, to determine the geographical extent of areas mountain zebra are utilizing in the BNP on an annual and seasonal basis; secondly, habitat preference of mountain zebra was analysed, both annually and seasonally; and thirdly, a Habitat Suitability Index was calculated for utilized and unutilized areas in the various habitats, to assess the suitability of these areas to mountain zebra in the BNP.

3.2. METHODS

3.2.1. STUDY SITE

For the study site description, refer to Chapter 2.

3.2.2. EXTENT OF PARK AREA USED

Sightings of breeding herds of mountain zebra were collected along drives done during three days per month, and monthly observations were grouped into seasons, three months per season (see section 2.4). Based on the estimated traversing time of large herbivores, counts were spaced at least 24 hours apart to ensure the independence of consecutive samples (Swihart *et al.*, 1988). Each sighting of a zebra herd was considered a single observation, based on individuals within the herd not being statistically independent (Alldredge and Ratti, 1986). Once a breeding herd was sighted, the geographical position of the herd was determined through triangulation, using a Global Positioning System (GPS), a rangefinder and a hand-held compass (Rathbun and Rathbun, 2006), and noted as a single observation per defined habitat (Alldredge and Ratti, 1986). The accuracy of the location calculation was within 5 m at a 150 m distance, determined from five fixes compared to their corresponding GPS positions.

For estimating the annual and seasonal extent of the park area used by mountain zebra in the BNP, a Kernel analysis was completed after Rodgers and Carr (1998). This technique is a standard and internationally accepted method for estimating the home range or extent of reserve area used of mammalian herbivores (Mohr, 1947; Hayne, 1949; Manly *et al.*, 2002; Burgman and Fox, 2003; Lent and Fike, 2003; Venter, 2006; Graham *et al.*, 2009), and zebra specifically (Penzhorn, 1982a; Thaker *et al.*, 2010; Bartlam-Brooks *et al.*, 2013).

Kernel analysis is a nonparametric statistical method for which probability densities can be estimated from point data (Worton, 1989; Rodgers and Carr, 1998; Lent and Fike, 2003). The Kernel method tests the probability of finding an animal in a particular place, using bivariate centering. A mean density estimate is then calculated from an superimposed grid (Rodgers and Carr, 1998). This results in an array of concentric contour lines which represent the volume of the distribution. The analysis is executed in the assumption that successive animal locations were independent (Rodgers and Carr, 1998). For the analysis of the extent of the area used by mountain zebra, the *href* smoothing parameter was used, using the adaptive method setting (Worton, 1989; Worton, 1995; Rodgers and Carr, 1998). Volume contouring at 50% and 90% probabilities was used, creating two contour lines for each of the four seasons. The 90% probability was used instead of a 95% probability, due to the 95% probability resulting in the inclusion of significant areas outside the reserve, which are not accessible to mountain zebra. The sizes of the 50% and 90% Kernel polygons were calculated using the XTools extension for Arcview 3.2 (ESRI, 2003).

3.2.3. HABITAT PREFERENCE

In order to determine the habitat preference of mountain zebra in the BNP, the frequency of use of the available habitat types was investigated geographically. Penzhorn (1982b) considers habitat preference to be one of the critical components of any ecological assessment of a species, and it is widely used as a measure of which habitat types are preferred in proportion to their availability (Penzhorn, 1982b; Byers *et al.*, 1984; Winkler, 1992; Winkler and Owen-Smith, 1995; Watson and Owen-Smith, 2000; Venter, 2006). Sightings of breeding herds of mountain zebra were collected (see section 3.2.2) to assess habitat utilization per season, using the utilization-availability technique of Byers *et al.* (1984). The reserve was stratified according to habitat types (see section 2.6.1), and the total area in km^2 of each habitat type was calculated using a GIS, employing the XTools extension for Arcview 3.2 (ESRI, 2003; O'Kane *et al.*, 2013; Unger *et al.*, 2013).

For annual and seasonal data, a chi-square goodness of fit test was used to compare the observed with the expected proportion of use (Zar, 1996). If significant, a Bonferroni analysis was used to determine whether habitat utilization between the four seasons was the same (Neu *et al.*, 1974; Byers *et al.*, 1984; Zar, 1996). First the proportion of each habitat type was converted to a proportion of the area of the whole park, this proportion representing the expected proportion of use (Byers *et al.*, 1984). Then the annual and seasonal number of observations of mountain zebra per habitat type was calculated as a proportion of the total number of observations, representing the observed proportion of use (Byers *et al.*, 1984). This approximation may be used as long as the average expected proportion across all categories is four or more at the 0.05 level (Roscoe and Byars, 1971). The average annual expected proportion for this analysis was 23, and the average seasonal expected was six for each of the four seasons.

Five of the seven habitat types defined in Chapter 2 formed the categories for the habitat preference analysis, namely Proteoid Fynbos, Asteraceous Fynbos, the Recently Burnt Area (with a veld age of less than one year), Drainage Lines, and the Inland Pans. The Proteoid and Asteraceous Fynbos, as well as the Drainage Lines were subdivided into Young (veld age of 1-5 years) and Old (veld age of > 5 years) habitat types. The Inland Pans were not subdivided into Young and Old pans for the analysis, due to the small size of these areas, and the minimum required relative area of habitat types for the analysis (Neu *et al.*, 1974).

The remaining two habitat types, the Breede River Thicket and the Grazing Lawns were not included in the analysis. Plains zebra prefer open habitat and avoid dense habitat to evade ambush predators (Sinclair, 1985; Boshoff and Kerley, 1999; Boshoff and Kerley, 2001; Landman and Kerley, 2001; Skinner and Chimimba, 2005; Chirima *et al.*, 2012; Barnier *et al.*, 2014). Thus the Breede River Thicket habitat, a dense thicket habitat, was not likely to be utilized by mountain zebra. Mountain zebra also appear to prefer more open habitat: In MZNP mountain zebra did not utilize riparian bush habitat, and used grassland habitat more readily than shrubland communities (Winkler and Owen-Smith, 1995). Also in the Baviaanskloof Nature Reserve, mountain zebra were not observed in woodlands, and the habitat suitability of the woodland areas was low, at 1.6 (Weel *et al.*, 2015). However, buffalo and red hartebeest, utilized slopes and valleys, which was linked to faecal nitrogen and phosphorus being greater in these species than in mountain zebra (Weel *et al.*, 2015). In KNR, mountain zebra were found to neutrally utilize thicket habitat (Watson and Chadwick, 2007).

To check if mountain zebra were going into the thicket habitat during this study, visible edges of the Breede River Thicket, and the accommodation camp of the park (which is surrounded by thicket) were sighted during sampling drives once a month. This was supported by monthly checks from vantage points of the western portion of the thicket habitat. Spot checks of the Grazing Lawns of the accommodation camp, as well as an area known as “Lang Elsie’s Kraal”, where mountain zebra dung piles had been observed in the past (Watson *et al.*, 2011) were also executed once a month. All other Grazing Lawns in the park were visible from sampling drives. Since no observations of zebra were made in the Breede River Thicket or on Grazing Lawns, these two habitat types were excluded from the analysis. Additionally, there were areas that could not be sighted from feasible access points and access roads (Unsighted Ground in Figure 2.3), which were also excluded from the analysis. Sightings of mountain zebra herds were grouped per habitat type. This constituted eight habitat types: Young Proteoid Fynbos, Old Proteoid Fynbos, Young Asteraceous Fynbos, Old Asteraceous Fynbos, Recently Burnt Area, Young Drainage Lines, Old Drainage Lines and Inland Pans.

3.2.4. HABITAT SUITABILITY

Initial observations of mountain zebra were used to determine areas used by mountain zebra in the study area. From these observations, as well as the Kernel analysis (section 3.3.1) it is clear that mountain zebra were only using specific sites within habitats, as opposed to preferring entire habitats. Areas used and unused by mountain zebra within habitat types were demarcated, for a comparative assessment of the habitat suitability of these areas. Within each of the habitat types, sites were randomly selected within used and unused areas. This consisted of a total of 14 sites, six used sites, and eight unused sites across habitat types.

A used site could be sampled in each of the following habitat types: Young Proteoid Fynbos, Old Asteraceous Fynbos, Young Drainage Lines, Old Drainage Lines, Young Inland Pans and Old Inland Pans. In both the Young and Old Asteraceous Fynbos, very few sites were used throughout the year, and mountain zebra mostly concentrated on small grassy patches such as termitaria in these areas. Thus used sites could not be delineated or surveyed for habitat suitability in Asteraceous fynbos. An unused site was sampled in each of the following habitat types: Young Proteoid Fynbos, Old Proteoid Fynbos, Young Asteraceous Fynbos, Old Asteraceous Fynbos, Young Drainage Lines, Old Drainage Lines, Young Inland Pans and Old Inland Pans.

For all these sites, a point survey of grass species cover was conducted (Novellie and Strydom, 1987; Novellie and Winkler, 1993). In order to assess the habitat suitability for these sites, the Habitat Suitability Index after Novellie and Winkler (1993) was used. This index is based on the proportional cover of the food plant species, as well as an acceptability index of each species. Strikes of all grass (Poaceae) species were recorded, as well as the two most preferred restio (Restionaceae) species (*Ischyrolepis capensis* and *I. triflora*), and the most preferred sedge (Cyperaceae) species (*Tetraria brachyphylla*). In each randomly selected plot, a 200 point survey for the selected graminoid species cover was performed (Novellie and Strydom, 1987), in ten rows of 20 points, spaced one meter apart. A strike was recorded if the point fell within an imaginary line drawn around the perimeter of the canopy of the plant (Roux, 1963). For the Recently Burnt Area habitat, a proportional cover was calculated from the number of plants per species in feeding quadrats (Chapter 4). This value may be an over-estimate, as feeding sites were targeted by mountain zebra, while in other habitats the sampling sites were randomly selected. However, the Recently Burnt Area was preferred annually and in three of the four seasons, and mountain zebra observations were scattered broadly across the habitat as opposed to other habitats.

For each site, a Habitat Suitability Index was calculated:

$$HSI = \sum a_i c_i,$$

where a_i is the acceptability index of species i, and c_i is the percentage cover of species i. The acceptability index for each species was obtained from diet preference surveys conducted during this study (see Table 4.2 and Appendix 1). Two of the 37 species encountered during habitat suitability surveys, were not present in feeding sites during the study (*Ehrharta villosa* and *Sporobolus fimbriatus*). For these two species, an acceptability index (ai) value was assigned based on the recognized grazing value (Van Oudtshoorn, 1999): An acceptability index of 0.1 was used for species of low grazing value, and 0.5 for species of intermediate grazing value. The mean HSI values for used and unused sites were compared using a Mann-Whitney U test (Zar, 1996).

3.3. RESULTS

3.3.1. EXTENT OF PARK AREA USED

A total of 185 observations of mountain zebra herds were recorded in the 12 month study period in the BNP. GPS localities of mountain zebra herds observed in the BNP showed particular seasonal patterns (Figure 3.1).

The 50% Kernel represents a density estimate for mountain zebra at a 50% probability in each season, while the 90% represents a density estimate at a 90% probability. The results for the 90% area use Kernel analysis was 16.95 km^2 annually, based on data for all seasons combined. The greatest seasonal park area use (Figure 3.2) was in the cool winter at 20.14 km^2, decreasing to 9.59 km^2 in the cool spring, 14.35 km^2 in the warm summer, and 8.07 km^2 in the warm autumn. The Kernel analysis of the 50% area size estimated these probabilities at 5.53 km^2 (16% of the park area) annually for all seasonal observations combined, and at its greatest seasonal extent, at 6.69 km^2 (19%) in the cool winter, declining to 2.79 km^2 (8%) in the cool spring, 3.68 km^2 (11%) in the warm summer and 2.04 km^2 (6%) in the warm autumn (Figure 3.2). The seasonal average 50% Kernel area size was 3.81 km^2, and the seasonal average 90% Kernel area size was 13.02 km^2.

3.3.2. HABITAT PREFERENCE

Chi-square goodness of fit analysis indicated that the observed frequency of use of the different habitat types by mountain zebra differed significantly from the expected frequency on an annual basis ($P < 0.0001$), and for each of the four seasons ($P < 0.0001$; Table 3.1).

The Young Proteoid Fynbos was preferred by mountain zebra on an annual basis, as well as in the cool winter season, and neutrally selected in the cool spring, warm summer and warm autumn seasons (Table 3.1). The Old Proteoid Fynbos was avoided on an annual basis, as well as in the cool spring or warm summer seasons; and neutrally selected in the cool winter and warm autumn.

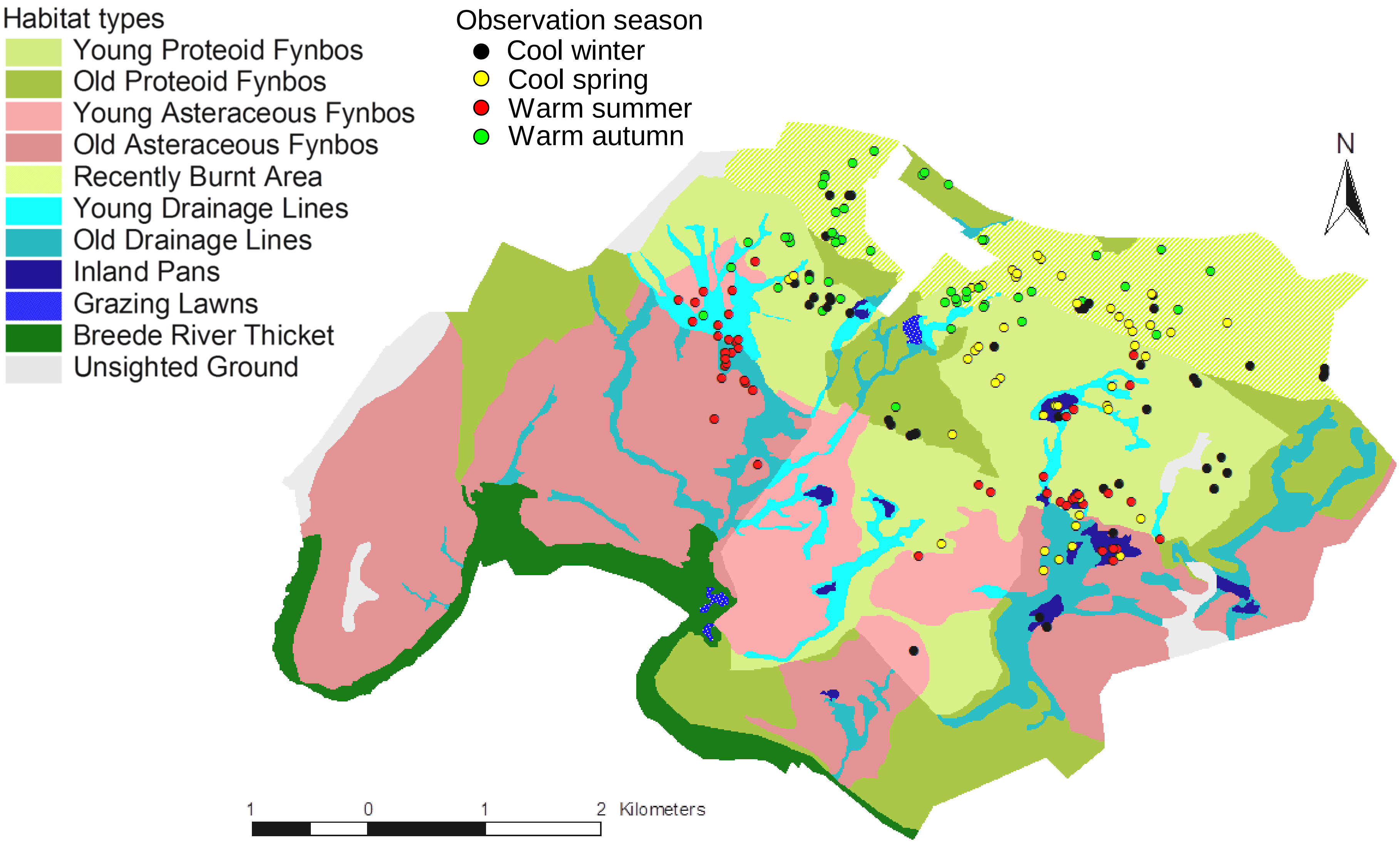
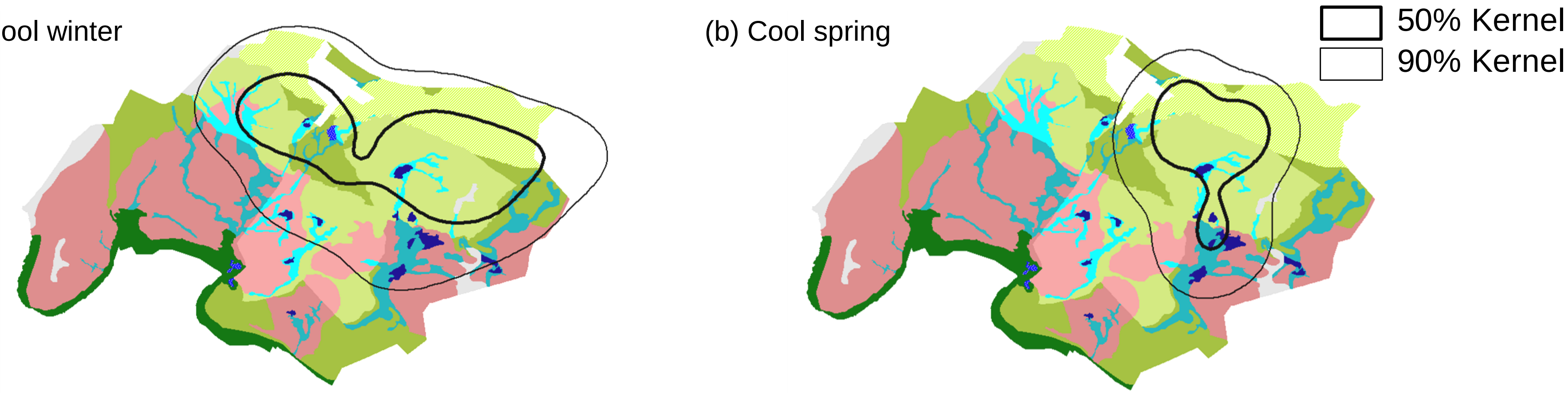


Figure 3.1: Seasonal point localities of observations of mountain zebra herds in the BNP.

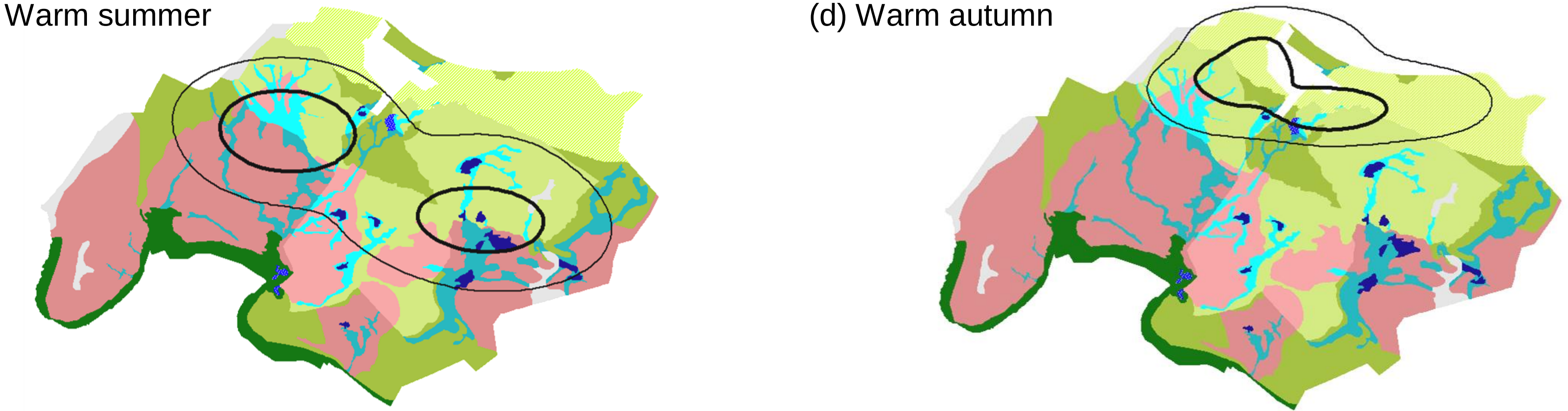


(a) Cool winter

50% Kernel: 6.69 km^2 (19% of the park)
90% Kernel: 20.14 km^2 (58% of the park)

(b) Cool spring

50% Kernel: 2.79 km^2 (8% of the park)
90% Kernel: 9.59 km^2 (28% of the park)



(c) Warm summer

50% Kernel: 3.68 km^2 (11% of the park)
90% Kernel: 14.35 km^2 (41% of the park)

(d) Warm autumn

50% Kernel: 2.04 km^2 (6% of the park)
90% Kernel: 8.07 km^2 (23% of the park)

Figure 3.2: The 50% and 90% seasonal Kernel analysis for the extent of park area used by mountain zebra in the BNP.

The Young Asteraceous Fynbos was avoided on an annual basis, and neutrally selected during the cool winter and warm summer seasons, with no observations in this habitat during the cool spring and warm autumn. The Old Asteraceous Fynbos was also avoided on an annual basis, as well as in the cool winter, cool spring and warm summer, with no observations in this habitat in the warm autumn.

The Recently Burnt Area was preferred on an annual basis, as well as in the cool winter, cool spring and warm autumn seasons, but no observations were recorded in this habitat during the warm summer season.

The Young Drainage Lines habitat was preferred on an annual basis, as well as in the warm summer season, and neutrally selected in the cool winter, cool spring and warm autumn. The Old Drainage Lines were neutrally selected on an annual basis and in the cool spring or warm summer seasons, and there were no observations in the cool winter or the warm autumn.

The Inland Pans were preferred on an annual basis, as well as in the warm summer season, but neutrally selected in the cool winter and cool spring, and there were no observations during the warm autumn in this habitat. Utilization of this habitat was mainly restricted to areas around the pans or “pan fringe”, where grass, restio and sedge species were utilized, as well as one observation on the lawn area of the inland pan itself, when it was dried out during summer.

3.3.3. HABITAT SUITABILITY

The Recently Burnt Area had the highest estimated *HSI* at 39.3 (Table 3.2). For all used sites, the *HSI* per site was > 19, while for the unused sites the *HSI* was < 10. For the used sites, the mean *HSI* and 95% confidence interval was 26.5 ± 6.2, while for the unused sites, the mean *HSI* and 95% confidence interval was 5.3 ± 2.2. The results of the Mann-Whitney U test showed a significant difference in the mean *HSI* value between used and unused sites (Z = 3.183; $P < 0.01$).

Table 3.1: Annual and seasonal habitat preference by Cape mountain zebra in the BNP, using Bonferroni z-statistic simultaneous confidence intervals.

		Annual **N = 185**			**Cool winter (May - July)** **N = 43**			**Cool spring (Aug - Oct)** **N = 47**			**Warm summer (Nov - Jan)** **N = 46**			**Warm autumn (Feb - Apr)** **N = 49**		
Habitat type[1]	Expected proportion of usage (P_i)	Observed proportion of usage (P_{io})	Bonferroni intervals for P_{io}	Pref[2]	Observed proportion of usage (P_{io})	Bonferroni intervals for P_{io}	Pref[2]	Observed proportion of usage (P_{io})	Bonferroni intervals for P_{io}	Pref[2]	Observed proportion of usage (P_{io})	Bonferroni intervals for P_{io}	Pref[2]	Observed proportion of usage	Bonferroni intervals for P_{io}	Pref[2]
PY	0.214	0.324	0.230 - 0.419	+	0.432	0.227 - 0.647	+	0.319	0.133 - 0.505	0	0.222	0.053 - 0.392	0	0.367	0.179 - 0.556	0
PO	0.171	0.059	0.012 - 0.107	–	0.114	-0.017 - 0.272	0	0.021	-0.036 - 0.079	–	0.000	-		0.102	-0.016 - 0.220	0
AY	0.081	0.016	-0.009 - 0.042	–	0.023	-0.039 - 0.084	0	0.000	-		0.022	-0.038 - 0.082	0	0.000	-	
AO	0.290	0.038	-0.001 - 0.076	–	0.023	-0.039 - 0.084	–	0.043	-0.038 - 0.123	–	0.089	-0.027 - 0.205	–	0.000	-	
RBA	0.122	0.308	0.215 - 0.401	+	0.318	0.126 - 0.510	+	0.404	0.208 - 0.600	+	0.000	-		0.490	0.294 - 0.685	+
DY	0.039	0.103	0.042 - 0.164	+	0.045	-0.040 - 0.131	0	0.021	-0.036 - 0.079	0	0.311	0.122 - 0.500	+	0.041	-0.037 - 0.118	0
DO	0.072	0.049	0.005 - 0.092	0	0.000	-		0.043	-0.038 - 0.123	0	0.156	0.008 - 0.303	0	0.000	-	
IP	0.011	0.103	0.042 - 0.164	+	0.045	-0.040 - 0.131	0	0.149	0.007 - 0.291	0	0.200	0.037 - 0.363	+	0.000	-	

P_i defined as the expected proportion of the total of number of mountain zebra breeding herds occurring in habitat *i*, calculated from the relative area of habitat *i*.
P_{io} defined as the observed proportion of the total of number of mountain zebra breeding herds occurring in habitat *i*.

[1] Habitat types:
PY = Young Proteoid Fynbos (1-5 years)
PO = Old Proteoid Fynbos (> 5 years)
AY = Young Asteraceous Fynbos (1-5 years)
AO = Old Asteraceous Fynbos (> 5 years)
RBA = Recently Burnt Area (Proteoid Fynbos / Drainage Lines < 1 year)
DY = Young Drainage Lines (1-5 years)
DO = Old Drainage Lines (> 5 years)
IP = Inland Pans

[2] Preference:
+ indicates utilization that is significantly greater than expected;
– indicates utilization that is significantly less than expected;
0 indicates that the observed utilization does not significantly differ from the expected.

Table 3.2: Habitat Suitability Index (*HSI*) for each used and unused site surveyed per habitat type.

Habitat	**Category**	***HSI***	**Category**	***HSI***
Young Proteoid Fynbos	Used	28.7	Unused	3.9
Old Proteoid Fynbos	Used	19.8	Unused	7.8
Young Asteraceous Fynbos	-	-	Unused	3.5
Old Asteraceous Fynbos	-	-	Unused	4.7
Recently Burnt Area	Used	39.3	-	-
Young Drainage Lines	Used	25.9	Unused	6.5
Old Drainage Lines	Used	19.2	Unused	9.9
Young Inland Pans	Used	28.1	Unused	1.7
Old Inland Pans	Used	24.1	Unused	4.6

3.4. DISCUSSION

3.4.1. EXTENT OF PARK AREA USED

Whether herbivores use a generalist or selective area selection strategy depends on the scale at which this is investigated (Boyce and McDonald, 1999; Oliver, 2007). Selectivity is also directly dependent on habitat quality (Jarman and Sinclair, 1979; Senft *et al.*, 1987). Thus although *Equus* species are considered to be able to utilize poor quality habitat better than ruminants (Owen-Smith, 1982; Duncan *et al.*, 1990; Menard *et al.*, 2002), poor habitat quality could necessitate a selective strategy in terms of space and time (Illius and Gordon, 1992). In terms of the extent of the area selected, *Equus* species have been found to demonstrate both low (Melton, 1987a; Ben-Shahar, 1991) and high area selectivity (Linklater *et al.*, 2000). Resource availability can also force large herbivore populations to move extensively between suitable habitats (Smuts, 1972; Wolanski *et al.*, 1999). As abundance of the food resource declines, there is an increase in habitat selectivity through the targeting of specific sites (Leuthold, 1978; Melton, 1987b; Bailey *et al.*, 1996). In large systems for example, when habitat quality declines, plains zebra migrate to areas with more suitable habitat (Bell, 1970; Bell, 1971; Maddock, 1979; Wolanski *et al.*, 1999).

In the BNP, the analysis of the park area used suggests that mountain zebra were using very specific sites within habitat types in the BNP on an annual basis, with only 16% of the park used based on the 50% Kernel analysis. On a seasonal basis the areas used was also selective, shifting in size and positioning to areas where adequate quality and quantity forage could be accessed. The maximum seasonal areas use was in winter, when the size of the area used according to the 50% Kernel analysis constituted 19% of the total area of the park, and the minimum was in autumn at 6%. Other work in the fynbos biome on mountain zebra did not use Kernel analysis to estimate area use, but the findings showed that mountain zebra use small proportions of the respective protected areas. In the GMNR, mountain zebra used habitats that constituted only 30% of the park area, attributed to low habitat suitability (Watson *et al.*, 2005). Similarly, in KNR, the only three preferred and suitable habitats, Arid Restioid Fynbos, Waboomveld, and the combined Renosterveld habitats formed 38%, 5% and <1% of the reserve, respectively (Watson and Chadwick, 2007). In DHNR, mountain zebra used an area of 30% of the reserve, concentrating in a habitat of 3.4% of the reserve, which was historically converted to agricultural grassland (Radloff, 2008; Smith *et al.*, 2011). Proportional area use by mountain zebra in the fynbos biome appears to be consistently low, and limited to suitable habitat with adequate grass cover.

3.4.2. HABITAT PREFERENCE

The habitat types of the BNP are primarily distinguished by the geology and associated soil, as well as the distribution of above-ground (pans, water courses) and below-ground (drainage lines) water sources (Cowling and Holmes, 1992; Low and Rebelo, 1996; Rebelo *et al.*, 2006; Vlok and De Villiers, 2007). Typical of fynbos, the unique nutritional and moisture regime of each habitat type leads to a specific vegetation structure and associated graminoid (grass, restio and sedge) component (Foth and Ellis, 1997; Germishuizen and Meyer, 2003; Germishuizen *et al.*, 2006), which provided the food resource for mountain zebra in the BNP during this study. The Proteoid and Asteraceous Fynbos are each associated with unique geological and associated soil formations in the park, the Proteoid Fynbos typically occurring on Enon Conglomerates with silcrete and ferricrete, and the Asteraceous Fynbos associated with alluvial and sandy loam (Theron, 1967; Vlok and De Villiers, 2007). The Drainage Line habitat or “Bontebok River and Floodplain” of Vlok and De Villiers (2007) has a diagnostic, well-developed grass and sedge component (see section 2.6.1) typically associated with this floodplain habitat (Grobler and Marais, 1967; Luyt, 2005; Vlok and De Villiers, 2007). Similarly, the vegetation of the Inland Pans is influenced by the unique character of the pans (Vlok and De Villiers, 2007). Only a few species are noted by Vlok and De Villiers (2007) for the Inland Pans, two restio genera (*Elegia* and *Hypodiscus*) of which were found in the diet of mountain zebra. The importance of fire affecting vegetation community structure in the park is well recognised (Grobler and Marais, 1967; Kraaij, 2004; Kraaij *et al.*, 2008; Novellie and Kraaij, 2010; Watson *et al.*, 2011), hence for this study the fire history was used to distinguish between the Recently Burnt Area, and Young and Old habitat types.

The preference for Young Proteoid Fynbos and avoidance of the Old Proteoid Fynbos is in line with other studies in the BNP which suggest that grazers prefer veld of less than five years post-fire to veld older than five years (Kraaij and Novellie, 2010). The seasonal preference of the Young Proteoid Fynbos in the cool winter and use in proportion to availability in each season suggests that this habitat provides a consistent habitat for mountain zebra in the BNP. The Old Proteoid Fynbos, however, was avoided annually, unused in two seasons and neutrally selected during the cool winter and warm autumn seasons. The Old Proteoid Fynbos is dominated by shrubs such as *Protea repens* and *Cliffortia ruscifolia* (Grobler and Marais, 1967; Vlok and De Villiers, 2007), and as the veld age increases over time, grass cover is reduced (Grobler and Marais, 1967). The suitability of Proteoid Fynbos to mountain zebra in the BNP is thus dependent on fire. In the KNR and GMNR, mountain zebra population growth was positively associated with the incidence of fire (Watson *et al.*, 2005; Watson and Chadwick, 2007), suggesting that mountain zebra benefit from utilization of young veld. The higher relative utilization of Young Proteoid Fynbos as opposed to both Young and Old Asteraceous Fynbos during this study could also be linked to the presence of silcrete in the soils of Proteoid Fynbos, which would make it more clay rich, resulting in a marginal increase in soil fertility (Specht and Moll, 1983; Allsopp *et al.*, 2014). Enon Conglomerate derived soils, which form the basis for the classification used for the Proteoid Fynbos in the BNP (Vlok and De Villiers, 2007; Kraaij, 2010; Kraaij and

Novellie, 2010; Watson *et al.*, 2011) are also slightly more alkaline than other fynbos soils, and have a better water holding capacity (Lambrechts, 1979; Hardy and Linder, 2007; Becker *et al.*, 2012). Grobler and Marais (1967) note the prevalence of the grasses *T. triandra* and *C. marginatus* in the Proteoid Fynbos, which also formed the greatest proportion of the diet of mountain zebra during this study (see Table 4.1). This habitat type also contains other grass species found to make an important contribution to the diet of mountain zebra during this study, namely *E. curvula* and *E. calycina* (Grobler and Marais, 1967).

The Asteraceous Fynbos occurs on a sandy loam with clay in parts and the drainage is poorer than in the gravelly soils of the rest of the park (Grobler and Marais, 1967). The general consensus in the literature is that sandstone, sand and limestone fynbos did not historically support large herbivore populations, that these animals would rather have focussed in renosterveld habitats with more nutrient-rich shale substrates (Morrow *et al.*, 1983; Johnson, 1992). Although *Dicerothamnus rhinocerotis* is a dominant shrub in the Asteraceous Fynbos of the BNP (Vlok and De Villiers, 2007; Kraaij, 2011), according to Rebelo *et al.* (2006) this type cannot be classified as true renosterveld, and thus it is not safe to assume that this area will be suitable to herbivores as other renosterveld habitats. Regional maps and other recent work however, suggest that the newly acquired section known as “Die Stroom” is supported by the moderately fertile Bokkeveld Shale soils (Cowling, 1983; Chief Director of Surveys and Land Information, 1984; Chief Director of Surveys and Land Information, 1993; Cowling and Heijnis, 2001; DWAF, 2004; DWAF, 2011). At the time of the study the veld age of this area was greater than five years, and mountain zebra were never observed to use this area. In the KNR, preference of favourable renosterveld habitat also declined in the absence of fire (Watson and Chadwick, 2007). The findings of this study support the hypothesis that (besides “Die Stroom” area, which may represent more typical of renosterveld habitat), the Asteraceous Fynbos as mapped for the current study is dissimilar to renosterveld (Rebelo *et al.*, 2006), which would be supported by more nutrient rich soils (Pierce and Cowling, 1984; Cowling *et al.*, 1986; Coetzee, 2002; Von Hase *et al.*, 2003; Midoko-Iponga, 2004; Curtis, 2013), as mountain zebra avoided both Old and Young Asteraceous Fynbos on an annual and a seasonal basis. For this analysis, “Die Stroom” area was included in the Old Asteraceous Fynbos habitat type, but since the soils in this area may be unique, it would be advisable to distinguish this habitat from the Asteraceous Fynbos for future research and management.

Grobler and Marais (1967) also note that *T. triandra*, a principal and preferred grass species in the diet of mountain zebra, is limited to small islands or patches such as termitaria in this habitat, which is frequently used by bontebok (Luyt, 2005). This phenomenon is confirmed by personal observation during this study. Another dominant grass in the southern portion of this habitat type is *Merxmuellera stricta* (Grobler and Marais, 1967), a C3 grass which becomes moribund in winter and in older veld (Cowling, 1983; Pierce and Cowling, 1984; Watson *et al.*, 2011). *Merxmuellera stricta* was only observed in feeding sites on less than 15 occasions, and was not utilized by mountain zebra.

The Recently Burnt Area habitat type was annually preferred by mountain zebra and for three seasons, which is to be expected of *Equus* species, who are one of the first grazers to appear on burnt veld (Grunow, 1980; Wilsey, 1996). In the grassland / Karoo veld of the MZNP, mountain zebra also prefer recently burnt areas. Mountain zebra have also been found to favour recently burnt areas, where grazing may reduce herbage yield by 50% in the first 18 months after fire (De Klerk *et al.*, 2001). Mountain zebra similarly favour recently burnt areas to older areas in fynbos (Watson *et al.*, 2005; Watson and Chadwick, 2007; Kraaij and Novellie, 2010; Watson *et al.*, 2011). This is supported by known grazer dynamics in recently burnt fynbos, where fire stimulates fire-climax species that provide good quality grazing for herbivores (Kruger and Bigalke, 1984; Mentis and Tainton, 1984). In semi-arid fynbos of GMNR, mountain zebra utilized burnt areas significantly within the first three years following fire, and there was also a strong relationship between population growth and fires in the reserve (Watson *et al.*, 2005). In the KNR, a positive relationship was evident between mountain zebra population size, rainfall and frequent fires, suggesting that habitat suitability for mountain zebra in the KNR is dependent on fire (Watson and Chadwick, 2007). In the BNP specifically, there is strong evidence that fire stimulates grasses, with an increase of over 50% recorded in important grass species cover in the first year after fire (Novellie, 1987). Mountain zebra significantly used areas with a veld age less than five years in the BNP, with the most intensive use when veld age was less than two years (Kraaij and Novellie, 2010).

An evaluation of defoliation of the principal species *T. triandra* in the BNP also showed the most intensive utilization in the first two years after fire (Novellie and Kraaij, 2010). Mountain zebra preferred recently burnt veld to young veld, though not as strongly as bontebok (Kraaij, 2010; Novellie and Kraaij, 2010). In the same way, the run-away fire which ran through the eastern portion of the BNP in February of 2012 played an important role in the movement strategies of the Cape mountain zebra of the BNP, and the preference of the Recently Burnt Area during this study confirms that grazers prefer recently burnt habitat in the BNP (Novellie, 1987; Beukes *et al.*, 1989; Kraaij and Novellie, 2010). The Recently Burnt Area was preferred in spring, during which the targeted grass species was the green and flushing *C. marginatus*, and in autumn, during which *E. curvula* was targeted (Table 4.3). The restio species *I. capensis* flowers in spring (Haaksma and Linder, 2000), and work by Stock *et al.* (1987) further suggests that during spring, restio species use nutrient resources for culm development.

In the warm summer, however, there were no observations of mountain zebra in the Recently Burnt Area. Lowland fynbos of the BNP region typically experiences a summer drought (Kruger, 1979; Raitt, 2005; Radloff, 2008). With fire having recently reduced vegetation load and shrub cover in the Recently Burnt Area, this habitat would have been more exposed to high temperatures and low rainfall of summer than habitat with older vegetation (see section 2.4). Bimodal climatic conditions with reduced summer precipitation and soil moisture is generally disadvantageous to warm-season grasses, which have shallow roots and exhibit seasonal dormancy (Weltzin and McPherson, 1997). The results of the plant attributes influencing forage selection in Chapter 5 provided evidence here, showing a significant decline in grass greenness of available plants during summer, specifically for *T. triandra* (Figure 5.4), and *E. curvula* (Figure 5.10). The leaf height of *T. triandra* was also low during this season, with a mean height of 44 mm above ground (Figure 5.5). This appears to be a further limitation, since zebra generally prefer taller grass (Grobler, 1983; Penzhorn and Novellie, 1991; Ben-Shahar and Coe, 1992; Groom and Harris, 2010). Low greenness and low leaf height in the Recently Burnt Area during the dry summer

(Kruger, 1979; Nahal, 1981; Raitt, 2005; Radloff, 2008) thus appears to negatively influence mountain zebra utilization. Summer drought conditions are presumably less pronounced in the Drainage Lines and Inland Pans, and possibly explain why mountain zebra moved here during the dry season.

The vegetation composition of the Drainage Line habitats is characterised by the availability of water in these areas (Vlok and De Villiers, 2007). Theoretically, grass benefits from intermediate soil moisture, with woody species invading as soil moisture increases (Tinley, 1982; Specht *et al.*, 1983; Knoop and Walker, 1985; Van Wilgen *et al.*, 1994; Weltzin and McPherson, 1997). Thus the preference of the Young Drainage Lines and neutral selection of the Old Drainage Lines on an annual basis can be linked to the increased availability of water in these areas, which would allow the utilization of grass species in this habitat despite summer drought conditions. The Young Drainage Lines habitat includes the old “Reisiesvlei” area, which has been drained with trenches to reduce water-logging, and historically subjected to nutrient input through domestic livestock practises (Robinson *et al.*, 1981; Novellie, 1987; Vlok and De Villiers, 2007). During a previous study in the BNP, Drainage Lines were found to contain greater dung group counts for mountain zebra than for other habitats (Watson *et al.*, 2011).

Seasonality appears to play a role in the preference of this type, in that Young Drainage Lines were significantly preferred during the warm summer, and neutrally selected during the rest of the year, while the observed and expected proportion of use of Old Drainage Lines was the same in the cool spring and warm summer, with no observations in the Old Drainage Lines in winter or autumn. The dry summer climate of the region (Kruger, 1979; Raitt, 2005; Radloff, 2008) and the preference of mountain zebra for the Drainage Lines and Inland Pans habitat during summer suggests that they target these areas during summer, due to the moisture retained in pans and drainage line habitats in summer. In the Kruger National Park (KNP), drainage line habitats also provided an important green and leafy grass component to the diet of herbivores during the dry season, due to the retention of moisture in these habitats, when other areas dried out (Grant *et al.*, 2000). Similarly, in the MZNP mountain zebra favoured ravines more readily in the dry season (Winkler and Owen-Smith, 1995), and in a previous study in the BNP, mountain zebra preferred the Drainage Lines habitat (Watson *et al.*, 2011). The current study now further supports the utilization for Young Drainage Lines habitat, and adds that preference of this habitat type is seasonal. During the warm summer, when C4 grasses typically experienced their growth season (Pierce and Cowling, 1984), *T. triandra* was targeted in the Drainage Line habitat (see Table 4.3).

The Inland Pan habitat (consisting of primarily pan fringe sites within the habitat type) was preferred annually, as well as in the warm summer, where species like *T. triandra* and *E. curvula* were targeted in this area (Table 4.3). The analysis by Watson *et al.* (2011) of habitat use in the BNP, based on dung groups per habitats showed mountain zebra not to prefer Inland Pans habitat specifically. Sampling of these areas occurred in the pan area itself, dominated by *C. dactylon*, and did not include the pan fringes, as in the current study. Notably mountain zebra were also not found to utilize the short lawn vegetation of the seasonally dry pans during this study. The dominant grass on the BNP pan surface, *C. dactylon*, was not preferred by mountain zebra, and both annual and seasonal diet composition of *C. dactylon* was < 2% (see sections 4.3.1 and 4.3.2). As mentioned in Chapter 2, Inland Pans are covered in water for most of the year, and dry out in summer and early autumn, and are dominated by *C. dactylon*. This is supported by the distribution of *C. dactylon* according to Beukes *et al.* (1989) and Luyt (2005), as well as the vegetation survey of Grobler and Marais (1967), who note that *C. dactylon* dominates in open patches throughout the park. During summer, as the water subsides from the Inland Pans, the *C. dactylon* in these areas is targeted by bontebok (Beukes *et al.*, 1989; Luyt, 2005; Watson *et al.*, 2011). In DHNR *C. dactylon* lawns were frequented by all grazers including mountain zebra, and *C. dactylon* also made a significant contribution to the mountain zebra diet (Radloff, 2008; Smith *et al.*, 2011). The results in Chapter 5 suggest that *C. dactylon* was not available to mountain zebra at the preferred height, possibly due to heavy utilization by bontebok (Appendix 4).

The differential feeding strategy used by grazers with hindgut fermentation as opposed to foregut fermentation is well-documented (Schoener, 1971; Owaga, 1975; Jarman and Sinclair, 1979; Grunow, 1980; Novellie, 1987; Duncan *et al.*, 1990; Novellie, 1990; Cromsigt and Olff, 2006; Venter *et al.*, 2014). Grazers with foregut fermentation like bontebok would thus be able to utilize short grass and lawns more effectively than mountain zebra. Springbok (*Antidorcas marsupialis*) in Victoria West, Central Karoo, also utilized pans at a greater frequency than adjacent plains and dunes (Milton *et al.*, 1992). Though investigated in an arid ecosystem, and the feeding strategies and digestive systems of springbok and zebra are quite different, the preference of pan areas by springbok suggests that the vegetation on and around seasonal pans can be more nutrient rich and favourable to herbivores than surrounding areas. This may be a very important driving factor in dystrophic ecosystems where soil nutrient concentrations are generally low. Milton *et al.* (1992) notes that the pans of that particular study area had higher levels of calcium, potassium, nitrogen and phosphorus, and plants remained green for longer and were of better quality in pans than surrounding areas. Grassy pans in savanna habitat also showed higher N and P values than surrounding veld (Mbatha and Ward, 2010), but no literature is available on the soils of pans compared to surrounding areas in dystrophic ecosystems. During the current study, bontebok herds were observed utilizing the *C. dactylon* lawn of the Inland Pans, and bontebok dung groups were also observed, which could be adding to the nutrient load of the pans. Further investigation into the nutrient concentration in BNP pans compared to other habitats is recommended.

3.4.3. HABITAT SUITABILITY

A veld condition assessment such as the *HSI* developed in the MZNP can serve to detect critical declines in grass availability, since areas may be subject to intensive grazing pressure over time (Novellie, 1994). Habitats with an *HSI* score < 10 are considered to represent poor quality habitat; an *HSI* between 10 and 20 represents a moderate quality habitat; and *HSI* scores > 20 represent good quality habitat (Novellie, 1994). The difference between habitat suitability of areas used by mountain zebra and unused areas in the current study suggests that areas preferred by mountain zebra in the BNP are targeted due to a greater availability of exploitable species compared to areas that were not utilized. The *HSI* range for the BNP of between 1.7 and 28.7 for all sites besides the Recently Burnt area, suggests that the habitat quality of the BNP is generally poor, and dependent on fire. This is in line with *HSI* analyses for mountain zebra in other dystrophic fynbos ecosystems (Watson *et al.*, 2005; Watson and Chadwick, 2007). In GMNR (Watson *et al.*, 2005) there was a clear separation between the habitats, with six of the ten habitats scoring ≥ 20, and the other habitats < 10. In KNR, only three of the eight habitat types comprised moderate to good quality habitat, only one site scoring an *HSI* > 20, and the remaining habitats being of poor quality (Watson and Chadwick, 2007). In BNR, the Baviaanskloof Sweet Grassland was of low habitat suitability, and only the Kouga Grassy Fynbos constituted suitable habitat (with an *HSI* of 20.2), (Weel *et al.*, 2015). By contrast, *HSI* values in the more nutrient-rich MZNP ranged between 13 and 44 (Novellie, 1994).

During previous work in the BNP, *HSI* scores were calculated at randomly selected sites in habitat types of varying veld age and fire history (Watson *et al.*, 2011). Fynbos sites were of low habitat suitability, while the Grazing Lawns appeared to represent suitable habitat to grazers, dominated by the stoloniferous *C. dactylon* (Watson *et al.*, 2011), which is similar to what has been observed in DHNR (Smith *et al.*, 2011). The results of this analysis in the BNP showed that there are other areas in the BNP that are used by grazers, where tussock grasses like *T. triandra* are targeted. Grazing Lawns and the lawn areas of the seasonal Inland Pans were not frequented by mountain zebra, nor was *C. dactylon* a targeted species at feeding sites (Table 4.3).

3.5. CONCLUSION

Mountain zebra were highly selective of both area and habitat type in the BNP on an annual and a seasonal basis. Seasonal extent of the park area used suggests that mountain zebra are targeting specific favoured feeding areas as opposed to moving between habitats indiscriminately. Young Proteoid Fynbos, the Recently Burnt Area, Young Drainage Lines and the Inland Pans were preferred by mountain zebra in the BNP. Preference of these types is in line with other work and with known grazer dynamics in relation to fire and seasonal water sources. Avoidance of fynbos older than five years is supported by recent work in the BNP and other dystrophic ecosystems. Asteraceous Fynbos being avoided irrespective of veld age confirms that this type is dissimilar to true renosterveld, which has richer soils. Park area and habitat selectivity by mountain zebra in the BNP is corroborated by the finding that used areas had a high Habitat Suitability Index (representing good quality habitat), and unused areas, a low Habitat Suitability Index.

CHAPTER 4: DIET COMPOSITION AND PREFERENCE

4.1. INTRODUCTION

Large herbivores face unique challenges in moist-dystrophic versus arid-eutrophic ecosystems (McNaughton and Georgiadis, 1986; Wrench *et al.*, 1996; Wrench *et al.*, 1997; Grant *et al.*, 2000; Grange and Duncan, 2006). In dystrophic ecosystems, forage is of low quality, resulting in large herbivores naturally occurring in low numbers in these habitats (Bell, 1982; McNaughton and Georgiadis, 1986; du Toit and Owen-Smith, 1989; Coetzee, 2002; Goldblatt and Manning, 2002; Grange and Duncan, 2006). Nutrient-poor soil is a dominant characteristic of fynbos (Morrow *et al.*, 1983). Forage for grazers is of low quantity in the fynbos biome, in that grass is not abundant, especially in the western part of the Cape Floristic Region (Cowling and Holmes, 1992). This warrants investigation of the strategies that grazers like mountain zebra use to overcome these challenges, particularly in the light of their historical distribution encompassing fynbos habitats (Boshoff and Kerley, 2001; Skead *et al.*, 2007).

During the last decade, a few studies have investigated aspects of diet and habitat selection by mountain zebra in the fynbos biome (Watson *et al.*, 2005; Watson and Chadwick, 2007; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Smith *et al.*, 2011; Watson *et al.*, 2011; Weel *et al.*, 2015), two of which investigated diet composition (Smith *et al.*, 2011; Weel *et al.*, 2015). The current study contributes to the knowledge base for mountain zebra in fynbos, using diet composition and diet preference to assess the forage base of mountain zebra in a fynbos system. This kind of information is needed to inform sustainable management of dystrophic ecosystems like the BNP, whereby impact on the vegetation can be monitored and animal numbers can be regulated accordingly (Holechek *et al.*, 1982b; Coetzee, 2002; Duncan and Poppi, 2008; Gaillard *et al.*, 2008; Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010).

Research in the field of dietary composition of ungulates primarily focuses on the plant growth forms (graminoids, succulents, forbs, dwarf shrubs and shrubs), plant parts (leaves, stems, culms and inflorescences) and taxonomically unique plant species that form the diet of the animal species in question (Petrides, 1975; Grunow, 1980; Everett *et al.*, 1992). Such analyses further distinguish between principal and preferred species in the diet of herbivores, principal species being species that occur in greatest quantity in the diet, and preferred species being species occurring in the diet more frequently than in the accessible environment (Petrides, 1975; Grunow, 1980; Johnson, 1980; Owen-Smith and Cooper, 1987; Everett *et al.*, 1992). Site availability indicates how often chosen food species were available in feeding sites, as an indicator of feeding opportunity (Owen-Smith and Cooper, 1987). The abundance and availability of preferred and principal species in ecologically suitable areas within the habitat are governed by seasonal changes in the ecosystem (Novellie *et al.*, 1988; Owen-Smith, 1994; Heitkönig and Owen-Smith, 1998). Seasonal fluctuations in diet composition, diet preference and site availability can be used to inform management of protected areas in terms of the adaptation of animal numbers, and the continued monitoring of the interactions between fire and herbivory for informing burning regimes (Novellie, 1987; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Weel *et al.*, 2015).

This Chapter deals with the species selection strategies of Cape mountain zebra in obtaining adequate quantity and quality food in the dystrophic ecosystem of the BNP. The objectives of this assessment of the diet of mountain zebra in the BNP were to gather information on: (a) Diet composition, the frequency with which the study animals were feeding on taxonomically unique food species at the feeding station, each bite taken by the animal representing a decision about which plant species to eat ; (b) Diet preference, the number of plants per species accepted, as a proportion of the number of sites in which the species occurred, estimating the acceptability of plant species utilized at the feeding site; and (c) Site availability, the seasonal proportion of sites in which utilized species occurred, as an indication of which species mountain zebra are targeting within the landscape.

4.2. METHODS

4.2.1. STUDY SITE

For the study site description, refer to Chapter 2.

4.2.2. FEEDING QUADRAT SURVEYS

The feeding quadrat method was used to collect data on the diet of mountain zebra in the BNP (Grobler, 1983; Winkler, 1992; Venter and Watson, 2008). Data were collected over a calendar year, in 12 monthly visits to the BNP, grouped into three months per season. Cape mountain zebra breeding herds were located by vehicle every morning for five to seven days each month. Once located, a focal animal was observed and the feeding path of the zebra noted at that site. Investigation of the feeding site commenced on foot once the animals had moved away from the feeding site. Within the site, quadrats of 1 m^2 were set out along an observed mountain zebra feeding path, spaced at least 2 m apart. On average five quadrats were sampled along the feeding path and data grouped as a feeding transect. A total of 644 quadrats were sampled along 124 transects, constituting 148 - 190 quadrats and 29 - 35 transects per season.

4.2.3. DIET COMPOSITION

At each quadrat, the number of bites taken per plant species was recorded. Mountain zebra bites from plants were taken to be ± 80 mm in diameter. Freshly taken plant matter was identified by the exudation of plant sap, the presence of saliva, or the absence of morning dew (Winkler, 1992). Upon close observation, old bite marks were identified by discolouration of the dried plant tissue (Winkler, 1992). In this way, interference from grazers previously foraging at the site was avoided (Winkler, 1992). For plant species from which mountain zebra utilized sparsely distributed seed heads or flowers (*Hypodiscus striatus* and *Watsonia laccata*), the estimated bite diameter was adjusted to include the same or similar volume as species for which mainly leaf blades were taken. The number of bites was summed per transect, and the relative percentage contribution (ps_i) of each species to the diet, the diet composition, was calculated, as a proportion of the total number of bites taken in that transect. An annual and seasonal mean ps_i was then calculated for each plant species. To test if the mean seasonal diet composition of each plant species was equal across all seasons, the Kruskall-Wallis and multiple comparison by mean ranks tests were used (Zar, 1996).

Species observed in feeding sites were mostly identified using the herbarium collection South African National Parks for the BNP (Kraaij, 2011). In selected cases, identification was done by taxonomic experts (see Acknowledgements). Plant nomenclature and growth form categorisation follow Germishuizen *et al.* (2006).

4.2.4. DIET PREFERENCE

Data on diet preference were recorded in the same quadrats used for diet composition. To assess diet preference the acceptability index of Owen-Smith and Cooper (1987) was used. During sampling, each quadrat was treated as an independent trial, in which the species present were recorded and scored as having being accepted or rejected by mountain zebra in the quadrat (Owen-Smith and Cooper, 1987). Plants were scored as available at the feeding station if the plant was alive if the roots were alive, irrespective of the level of desiccation or utilization of above-ground material (Owen-Smith, 1982). The diet preference of herbivore species was thus determined by recording the frequency at which a plant was either accepted or rejected by the animal at sampling sites. Only species that were found in more than ten sites annually were included in the analysis.

An acceptability index (ai_i) was calculated for grass species *i* annually, and for each season (Owen-Smith and Cooper, 1987), as:

$$ai_i = n_i / t_i,$$

where n_i is the number of quadrats in which grass species *i* was accepted, and t_i is the total number of quadrats in which grass species *i* was recorded as present. Annual and seasonal binomial 95% confidence limits were calculated for the *ai* values, followed by a chi-square contingency table analysis to test if acceptability index was independent across seasons (Zar, 1996). Species with an *ai* > 0.5 were regarded as preferred, species with an *ai* ranging from 0.3 to 0.5 were regarded as moderately acceptable, and species with an *ai* < 0.3 were regarded as being of low acceptability to mountain zebra in the BNP.

4.2.5. SITE AVAILABILITY

Data on site availability was recorded using the same feeding quadrats identified for diet composition and diet preference.

Annual and seasonal site availability was calculated for species *i,* measuring the relative availability of plant species *i* throughout the year and in each season respectively. Annual and seasonal site availability (s_i) was calculated for each species, as:

$$s_i = t_i / tn$$

where t_i is the total number of feeding sites where plant species *i* was recorded as available and *tn* is the total number of feeding sites surveyed for the relevant time interval (Owen-Smith and Cooper, 1987). As for diet preference, annual and seasonal binomial 95% confidence limits were calculated for the s_i values, followed by a chi-square contingency table analysis to test if acceptability indices were independent across seasons (Zar, 1996).

4.3. RESULTS

4.3.1. DIET COMPOSITION

In the 644 feeding quadrats sampled during the four seasons, 60 species were identified as being available to mountain zebra in feeding sites, 53 of which were utilized by mountain zebra. A total of 5646 bites from the 53 plant species were recorded over the 12 month period. Three grass species (*Themeda triandra, Cymbopogon marginatus* and *Eragrostis curvula*) and one restio species

(*Ischyrolepis capensis*) each formed > 5% of the annual diet, and were considered principal species (Table 4.1). Of the 53 species utilized, 26 species each formed ≥ 2% of the annual or seasonal diet. An additional two grass species, *Digitaria eriantha* and *Cynodon dactylon,* which composed < 2% of the diet, were included in Table 4.1 for comparative purposes. Appendix 1 lists all 60 species, including the remaining 32 species, of which 25 species showed an annual diet composition of < 2%, and seven species that were observed in feeding sites, but from which no bites were taken.

Grass species (Poaceae) formed 72.6% of the annual diet, restio species (Restionaceae) 11.8%, sedge (Cyperaceae) species 5.9%, geophytes 8.8%, dicotyledonous forbs 0.6% and dicotyledonous shrublets 0.2% (Appendix 1).

The four principal species (*T. triandra, C. marginatus, E. curvula* and *I. capensis*) dominated the annual diet, accounting for 56.2% of the total annual diet of mountain zebra in the BNP (Table 4.1). All other grasses contributed < 4% to the annual diet and of these, only four species contributed between 2% and 4% (*Merxmuellera disticha*, *Heteropogon contortus*, *Hyparrhenia hirta* and *Stipagrostis zeyheri*). In the cool winter, grass species contributed 81.2% to the diet. During the cool spring, the diet composition of grass species was at its lowest level, contributing 43.3% to the diet. In the warm summer, grass species diet composition increased to 67.9%, and during the warm autumn, grass species diet composition was at its highest, at 83.8%. One sedge species, *Tetraria brachyphylla* and two geophytes, *Moraea collina* (of which the bulbs were utilized) and the annual and seasonal diet composition of *Lanaria lanata* (from which the leaves were used) was between 2% and 4%.

On a seasonal basis, the four principal species each showed a significant ($P < 0.05$) peak in one of the four seasons. *T. triandra* contributed 20.9% to the annual diet, and reached its highest level in the diet during the warm summer (Table 4.1). The diet composition of *T. triandra* was also high in the cool winter and the warm autumn, but decreased in the cool spring. Annual diet composition of *C. marginatus* was 14.5%, and it was utilized at its highest level during the cool winter, declining in the cool spring and warm autumn, and to its lowest level in the warm summer. Annual diet composition of *E. curvula* was 13.3%, which was utilized at its highest level during the warm autumn season, with contribution to the diet being low in the cool winter, in the cool spring, and showing a marginal increase in the warm summer. The annual diet composition of *I. capensis* was 7.5%, reaching its highest level in the diet during the cool spring, lower levels in the warm summer, and at minimum levels in the cool winter and warm autumn.

Species that contributed > 5% to the seasonal diet were the C3 grasses *M. disticha* and *Ehrharta capensis* in the cool winter, the sedge species *Tetraria brachyphylla* and *Ficinia indica* in the cool spring, *Stipagrostis zeyheri,* and *T. brachyphylla* in the warm summer, and the geophyte *Moraea collina* in the warm autumn. Diet composition of *Moraea collina*, was 10.5% in autumn. The bulbs of this species were used at specific sites, where mountain zebra were observed to dig holes, dislodging the bulb, and shaking their heads to discard the husk around the bulb as well as the rest of the plant: leaf, stem and inflorescence. Up to four holes were dug in a single site, each recorded as a single bite.

4.3.2. DIET PREFERENCE

The annual and seasonal acceptability indices of the selected 28 species included in the diet composition analysis are shown in Table 4.2. All 28 species were found in more than ten feeding sites. Of the four species which formed the greatest proportion of the diet, *T. triandra*, *C. marginatus*, *Eragrostis curvula* and *I. capensis* (see Table 4.1), only the first three species were annually preferred, with an annual *ai* of 0.78, 0.60 and 0.81 respectively, while *I. capensis* was moderately acceptable.

A number of other grass species were also annually preferred, namely *M. disticha*, *H. contortus, H. hirta*, *S. zeyheri*, *Ehrharta calycina*, *P. dilatatum* and *D. eriantha* (Table 4.2). Furthermore, two restio species, *Calopsis muirii* and *H. striatus*, one sedge species, *T. brachyphylla* and three geophytes, *M. collina, L. lanata* and *W. laccata*, were preferred on an annual basis (Table 4.2).

Table 4.1: Variation in percentage diet composition of the 26 species with an annual or seasonal diet composition ≥ 2%, as well as two species with a composition < 2% (*C. dactylon* and *D. eriantha*), included for comparative purposes. Test-statistics indicate significance of differences between seasons.

Species	C3/C4	Annual mean ± 95% c.i. n = 124	Cool winter mean ± 95% c.i. n = 35	Cool spring mean ± 95% c.i. n = 29	Warm summer mean ± 95% c.i. n = 29	Warm autumn mean ± 95% c.i. n = 31	Statistic**
Grasses							
Themeda triandra$^{\#}$	C4	20.9 ± 4.9	23.9 ± 9.0^{ab}	8.6 ± 5.0^{a}	34.0 ± 13.4^{b}	16.9 ± 9.6^{a}	H = 12.853*
Cymbopogon marginatus$^{\#}$	C4	14.5 ± 3.6	26.8 ± 7.5^{b}	10.2 ± 4.6^{a}	4.1 ± 5.2^{a}	14.4 ± 8.5^{a}	H = 31.290*
Eragrostis curvula$^{\#}$	C4	13.3 ± 4.9	5.6 ± 6.3^{a}	4.6 ± 5.9^{a}	7.9 ± 5.7^{ab}	35.0 ± 14.7^{b}	H = 20.764*
Merxmuellera disticha	C3	3.7 ± 2.1	5.6 ± 5.1	3.9 ± 4.0	1.6 ± 3.3	3.5 ± 4.3	H = 5.759
Heteropogon contortus	C4	2.7 ± 1.7	3.3 ± 3.2	1.7 ± 3.4	3.9 ± 5.2	2.0 ± 2.2	H = 3.128
Hyparrhenia hirta	C4	2.5 ± 1.9	4.7 ± 5.5	0.4 ± 0.8	0.2 ± 0.3	4.1 ± 4.8	H = 6.845
Stipagrostis zeyheri ssp. *zeyheri*	C4	2.1 ± 1.9	–	–	8.2 ± 8.1	0.6 ± 1.1	Z = 0.769
Ehrharta capensis	C3	1.9 ± 1.2	6.4 ± 4.1	0.2 ± 0.5	0.1 ± 0.2	0.0	H = 26.446*
Brachiaria serrata	C4	1.9 ± 0.9	4.7 ± 2.5^{b}	0.3 ± 0.3^{ab}	0.4 ± 0.6^{a}	1.6 ± 2.3^{ab}	H = 23.314*
Ehrharta calycina	C3	1.7 ± 1.5	–	2.3 ± 3.5	–	4.5 ± 5.0	Z = 0.192
Paspalum dilatatum (exotic)	C4	1.3 ± 1.5	–	4.5 ± 6.5	–	0.9 ± 0.9	Z = 0.333
Pentaschistis curvifolia	C3	1.1 ± 0.9	–	3.7 ± 3.5	0.9 ± 1.0	–	Z = 0.949
Tribolium uniolae	C4	0.8 ± 0.5	–	2.1 ± 2.1	1.1 ± 0.9	0.0	H = 17.417*
Pentaschistis pallida	C3	0.7 ± 0.6	0.1 ± 0.2	–	2.6 ± 2.5	0.3 ± 0.6	H = 10.164*
Aristida diffusa ssp. *diffusa*	C4	0.5 ± 0.4	–	0.1 ± 0.2	2.0 ± 1.7	0.0	H = 16.696*
Digitaria eriantha	C4	0.3 ± 0.4	–	0.7 ± 1.3	0.5 ± 1.0	0.0	H = 4.665
Cynodon dactylon	C4	0.1 ± 0.2	0.1 ± 0.3	0.0 ± 0.1	0.4 ± 0.6	0.0	H = 2.319
Total		**70.0**	**81.2**^{b}	**43.3**^{a}	**67.9**^{b}	**83.8**^{b}	**H = 24.303***
Restios							
Ischyrolepis capensis$^{\#}$		7.5 ± 3.1	3.4 ± 3.5	18.5 ± 10.5	8.2 ± 5.9	1.2 ± 2.3	H = 13.080*
Calopsis muirii		1.2 ± 0.8	2.1 ± 2.3	2.0 ± 2.1	–	0.4 ± 0.8	H = 5.724
Hypodiscus striatus		1.0 ± 1.2	–	0.2 ± 0.4	4.1 ± 5.1	–	Z = 0.467
Ischyrolepis triflora		1.0 ± 0.9	–	–	4.0 ± 3.8	0.4 ± 0.8	Z = 1.183
Total		**10.7**	**5.5**^{ab}	**20.7**^{b}	**16.3**^{b}	**2.0**^{a}	**H = 20.932***
Sedges							
Tetraria brachyphylla		2.4 ± 2.0	–	5.3 ± 6.4	5.0 ± 5.9	–	Z = 0.124
Ficinia indica		1.8 ± 1.6	0.8 ± 1.0	5.9 ± 6.6	0.4 ± 0.6	0.3 ± 0.4	H = 2.894
Total		**4.2**	**0.8**	**11.2**	**5.4**	**0.3**	**H = 9.744***
Geophytes							
Moraea collina		3.4 ± 2.2	–	2.7 ± 2.8	0.5 ± 0.8	10.5 ± 8.2	H = 16.541*
Lanaria lanata		2.6 ± 1.7	4.1 ± 4.5	3.0 ± 4.2	–	2.9 ± 2.9	H = 5.361
Watsonia laccata		1.0 ± 0.9	–	4.3 ± 3.7	0.2 ± 0.3	–	Z = 1.602
Hypoxis villosa		0.9 ± 0.9	3.2 ± 3.3	0.0	–	0.0	H = 15.891*
Total		**7.9**	**7.3**	**10.0**	**0.7**	**13.4**	**H = 12.790***
Forbs							
Corymbium africanum ssp. scabridum		0.6 ± 0.7	–	1.9 ±	0.7 ± 0.7	0.0	H = 8.410*
Total		**0.6**	**0.0**	**1.9**	**0.7**	**0.0**	**H = 8.701***
Other species 1		6.6	5.2	12.9	9.0	0.5	
Total		**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	

[1] See Appendix 1

[a] different letters denote significant differences between seasons

[#] Principal species (annual *psi* > 5%)

* $P < 0.05$

** H = Kruskall-Wallis one-way ANOVA; Z = Mann-Whitney test

Preference of *T. triandra* was high throughout the year (Table 4.2). In contrast, *C. marginatus* was preferred in the cool winter season and cool spring season and of moderate preference in the warm summer and warm autumn. *E. curvula* followed a similar trend as *T. triandra*, in that *E. curvula* was preferred in all the seasons, but less so in the cool winter. *I. capensis* was only preferred in the cool spring season, preference declining to moderately acceptable in the cool winter and warm summer seasons, reaching its lowest point in the warm autumn. Other grass species that were preferred in a particular season include *Ehrharta capensis* and *B. serrata* which were preferred in the cool winter, and *A. diffusa* which was preferred in the warm summer (Table 4.2).

Species with a high annual acceptability other than grasses, included the restio *Hypodiscus striatus* of which the stems and seeds were used in spring and summer, as well the sedge *Tetraria brachyphylla*, of which leaves, stems and inflorescences were used, in spring and summer. Three geophytes with a high annual preference (*ai* > 0.5), as well as in particular seasons were *Moraea collina,* which was preferred in feeding sites during spring, summer and autumn; *Lanaria lanata*, which was preferred in winter, spring and autumn; and *Watsonia laccata*, which was significantly preferred in spring, as opposed to the low acceptability in summer (Table 4.2). From *M. collina*, the bulbs were used, while from *L. lanata* the leaves were used, and from *W. laccata*, the stems and inflorescences were used.

Plotting the diet composition of grass species that formed ≥ 2% of the annual or seasonal diet of mountain zebra and two additional species with a diet composition < 2% (*C. dactylon* and *D. eriantha*) against annual acceptability indices (Figure 4.1) enabled groupings of these species into three categories: (a) principal species that were also preferred (annual *psi* > 5%; *ai* ≥ 0.5; *T. triandra*, *C. marginatus* and *E. curvula*); (b) species with a low diet composition that were preferred (annual *psi* < 5%; ai ≥ 0.5; *Stipagrostis zeyheri*, *Paspalum dilatatum*, *Heteropogon contortus*, *Merxmuellera disticha*, *Hyparrhenia hirta*, *Ehrharta calycina* and *Digitaria eriantha*) and (c) species with a low diet composition and a moderate to low preference (psi < 5%; *ai* < 0.5; *Pentaschistis curvifolia*, *Tribolium uniolae*, *Pentaschistis pallida, Aristida diffusa, Ehrharta capensis*, *Brachiaria serrata* and *Cynodon dactylon*).

Table 4.2: Annual and seasonal acceptability indices of the 26 species with an annual or seasonal diet composition ≥ 2%, as well as two species with a composition < 2% (*C. dactylon* and *D. eriantha*), included for comparative purposes. Chi-square results indicate significance of differences among seasons.

Species	**Annual**	**Cool winter**	**Cool spring**	**Warm summer**	**Warm autumn**	**Chi-square**	**df**
Grasses							
Themeda triandra	0.78 (0.73, 0.82)	0.72 (0.63, 0.80)	0.71 (0.58, 0.82)	0.86 (0.77, 0.92)	0.83 (0.70, 0.92)	7.55	3
Cymbopogon marginatus	0.60 (0.55, 0.66)	0.77 (0.68, 0.85)	0.71 (0.59, 0.82)	0.42 (0.25, 0.61)	0.41 (0.31, 0.51)	36.82***	3
Eragrostis curvula	0.81 (0.73, 0.87)	0.56 (0.35, 0.76)	0.80 (0.52, 0.96)	0.78 (0.58, 0.91)	0.91 (0.82, 0.97)	14.76**	3
Merxmuellera disticha	0.72 (0.58, 0.83)	0.68 (0.46, 0.85)	0.71 (0.42, 0.92)	0.75 (0.19, 0.99)	0.80 (0.44, 0.97)	0.53	3
Heteropogon contortus	0.76 (0.61, 0.87)	0.62 (0.38, 0.82)	1.00 (0.48, 1.00)	0.85 (0.55, 0.98)	0.80 (0.44, 0.97)	4.42	3
Hyparrhenia hirta	0.71 (0.53, 0.85)	0.56 (0.31, 0.78)	1.00 (0.16, 1.00)	1.00 (0.03, 1.00)	0.85 (0.55, 0.98)	4.44	3
Stipagrostis zeyheri	0.95 (0.76, 1.00)	–	–	1.00 (0.81, 1.00)	0.67 (0.09, 0.99)	1.09*	1
Ehrharta capensis	0.25 (0.18, 0.33)	0.50 (0.37, 0.63)	0.05 (0.00, 0.26)	0.05 (0.00, 0.23)	0.00 (0.00, 0.12)	39.72***	3
Brachiaria serrata	0.22 (0.16, 0.29)	0.41 (0.29, 0.54)	0.06 (0.01, 0.17)	0.11 (0.01, 0.35)	0.16 (0.06, 0.31)	22.88***	3
Ehrharta calycina	0.63 (0.44, 0.79)	–	0.89 (0.52, 1.00)	–	0.52 (0.31, 0.73)	2.32	1
Paspalum dilatatum	0.95 (0.75, 1.00)	–	1.00 (0.75, 1.00)	–	0.86 (0.42, 1.00)	0.10	1
Pentaschistis curvifolia	0.43 (0.28, 0.59)	–	0.54 (0.33, 0.74)	0.28 (0.10, 0.53)	–	1.95	1
Tribolium uniolae	0.35 (0.24, 0.48)	–	0.48 (0.29, 0.68)	0.27 (0.14, 0.44)	0.00 (0.00, 0.84)	4.17	2
Pentaschistis pallida	0.31 (0.17, 0.48)	0.20 (0.01, 0.72)	–	0.39 (0.20, 0.61)	0.18 (0.02, 0.52)	1.85	2
Aristida diffusa	0.29 (0.16, 0.44)	–	0.06 (0.00, 0.30)	0.52 (0.31, 0.73)	0.00 (0.00, 0.46)	12.50**	2
Digitaria eriantha	0.57 (0.29, 0.82)	–	0.71 (0.29, 0.96)	0.60 (0.15, 0.95)	0.00 (0.00, 0.84)	3.27	2
Cynodon dactylon	0.06 (0.02, 0.14)	0.07 (0.00, 0.34)	0.06 (0.00, 0.29)	0.13 (0.02, 0.38)	0.00 (0.00, 0.15)	2.72	3
Restios							
Ischyrolepis capensis	0.39 (0.32, 0.46)	0.40 (0.24, 0.58)	0.59 (0.47, 0.71)	0.37 (0.24, 0.51)	0.05 (0.01, 0.17)	31.66***	3
Calopsis muirii	0.62 (0.42, 0.79)	0.83 (0.52, 0.98)	0.50 (0.23, 0.77)	–	0.33 (0.01, 0.91)	4.22	2
Hypodiscus striatus	0.92 (0.64, 1.00)	–	1.00 (0.03, 1.00)	0.92 (0.62, 1.00)	–	2.73	1
Ischyrolepis triflora	0.16 (0.09, 0.26)	–	–	0.19 (0.1, 0.31)	0.06 (0.00, 0.27)	1.07	1
Sedges							
Tetraria brachyphylla	0.94 (0.79, 0.99)	–	1.00 (0.78, 1.00)	0.88 (0.64, 0.99)	–	0.41	1
Ficinia indica	0.39 (0.26, 0.53)	0.15 (0.04, 0.35)	0.68 (0.43, 0.87)	0.5 (0.07, 0.93)	0.4 (0.05, 0.85)	13.23*	3
Geophytes							
Moraea collina	0.75 (0.63, 0.85)	–	0.75 (0.51, 0.91)	0.6 (0.26, 0.88)	0.79 (0.62, 0.91)	1.55	2
Lanaria lanata	0.92 (0.78, 0.98)	1.00 (0.79, 1.00)	1.00 (0.59, 1.00)	–	0.77 (0.46, 0.95)	5.79	2
Watsonia laccata	0.70 (0.50, 0.86)	–	0.85 (0.62, 0.97)	0.29 (0.04, 0.71)	–	5.44*	1
Hypoxis villosa	0.30 (0.17, 0.45)	0.38 (0.22, 0.56)	0.00 (0.00, 0.60)	–	0.00 (0.00, 0.46)	5.43	2
Forbs							
Corymbium africanum ssp. scabridum	0.43 (0.24, 0.63)	–	1.00 (0.59, 1.00)	0.26 (0.09, 0.51)	0.00 (0.00, 0.84)	12.96**	2

* $P < 0.05$; ** $P < 0.010$; *** $P < 0.001$

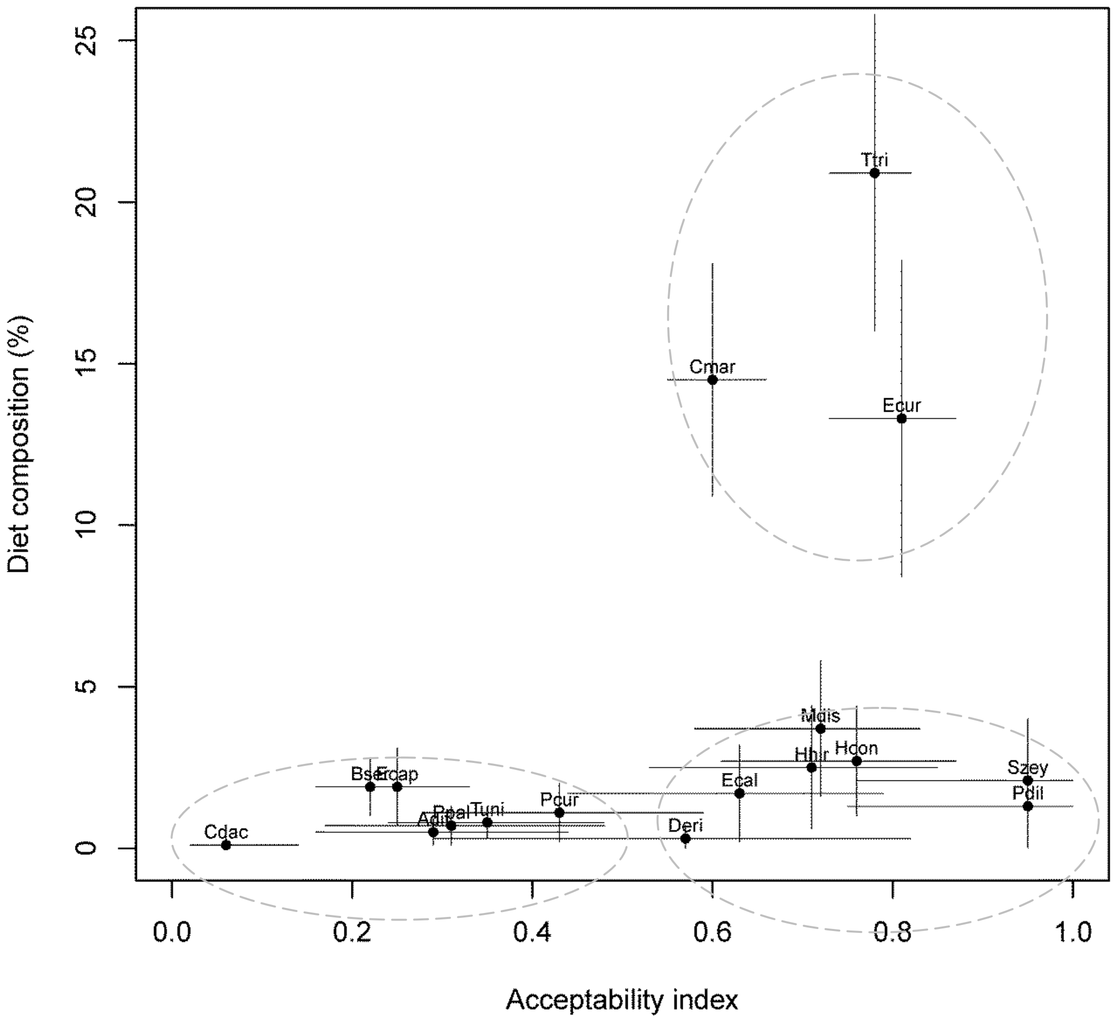


Figure 4.1: Annual diet composition (*psi*) in relation to acceptability indices (*ai*) of the grass species with an annual or seasonal diet composition ≥ 2%, as well as two species with a composition < 2% (*C. dactylon* and *D eriantha*), included for comparative purposes. Ttri = *Themeda triandra;* Cmar = *Cymbopogon marginatus;* Ecur = *Eragrostis curvula;* Mdis = *Merxmuellera disticha*; Hcon = *Heteropogon contortus;* Hhir = *Hyparrhenia hirta;* Szey = *Stipagrostis zeyheri* ssp*. zeyheri;* Ecap = *Ehrharta capensis;* Bser = *Brachiaria serrata;* Ecal = *Ehrharta calycina*; Pdil = *Paspalum dilatatum*; Pcur = *Pentaschistis curvifolia*; Tuni = *Tribolium uniolae*; Ppal = *Pentaschistis pallida*; Adif = *Aristida diffusa* ssp*. diffusa*; Deri = *Digitaria eriantha;* Cdac = *Cynodon dactylon.*

4.3.3. SITE AVAILABILITY

The results on annual and seasonal site availability of the 28 species included in the diet composition analysis showed that there were six species with an annual site availability > 0.2 (Table 4.3). These include five grass species *T. triandra*, *C. marginatus*, *E. curvula, Ehrharta capensis*, *B. serrata*, and one restio species *I. capensis*.

The seasonal site availability analysis showed that *T. triandra* was available in the greatest proportion in feeding sites during the warm summer season, followed by the cool winter season, with a significantly lower seasonal availability in the cool spring and warm autumn. *C. marginatus* showed greater site availability in the warm autumn and cool winter, than in the cool spring and warm summer respectively, and *E. curvula* was significantly more available in feeding sites during the warm autumn than in the other seasons. The restio species *I. capensis* was most available within feeding sites during the cool spring, with lower levels in the other three seasons.

Seasonal site availability of the remaining grass species was > 0.1. The site availability of *Ehrharta capensis* and *B. serrata* showed highest during the cool winter, and no grasses besides the three principal grass species (*T. triandra, C. marginatus* and *E. curvula*) showed a site availability > 0.1 in spring. In summer, *S. zeyheri* and *A. diffusa* showed the highest site availability, and *E. calycina* showed its greatest site availability in the warm autumn. Among other growth forms, the species with the highest seasonal site availability was *Moraea collina*, which was targeted in the warm autumn.

Table 4.3: Annual and seasonal variation in site availability of the 26 species with an annual or seasonal diet composition ≥ 2%, as well as two species with a composition < 2% (*C. dactylon and D. eriantha*), included for comparative purposes.

Species	**Annual**	**Cool winter**	**Cool spring**	**Warm summer**	**Warm autumn**	**Chi-square**	**df**
Grasses							
Themeda triandra	0.50 (0.46, 0.54)	0.59 (0.52, 0.66)	0.38 (0.3, 0.46)	0.65 (0.57, 0.73)	0.35 (0.27, 0.43)	14.412**	3
Cymbopogon marginatus	0.48 (0.44, 0.52)	0.57 (0.5, 0.64)	0.42 (0.34, 0.5)	0.21 (0.15, 0.28)	0.68 (0.6, 0.76)	29.601****	3
Eragrostis curvula	0.21 (0.18, 0.24)	0.13 (0.09, 0.19)	0.10 (0.05, 0.15)	0.18 (0.12, 0.25)	0.46 (0.38, 0.54)	44.457****	3
Merxmuellera disticha	0.08 (0.06, 0.11)	0.13 (0.09, 0.19)	0.09 (0.05, 0.15)	0.03 (0.01, 0.07)	0.07 (0.03, 0.12)	10.825*	3
Heteropogon contortus	0.08 (0.06, 0.1)	0.11 (0.07, 0.16)	0.03 (0.01, 0.07)	0.09 (0.05, 0.14)	0.07 (0.03, 0.12)	6.937	3
Hyparrhenia hirta	0.05 (0.04, 0.07)	0.09 (0.06, 0.15)	0.01 (0, 0.05)	0.01 (0, 0.04)	0.09 (0.05, 0.15)	19.612***	3
Stipagrostis zeyheri	0.03 (0.02, 0.05)	–	–	0.12 (0.07, 0.18)	0.02 (0, 0.06)	8.563**	1
Ehrharta capensis	0.21 (0.18, 0.24)	0.33 (0.26, 0.4)	0.12 (0.07, 0.18)	0.15 (0.09, 0.21)	0.20 (0.14, 0.28)	5.418*	1
Brachiaria serrata	0.27 (0.23, 0.3)	0.35 (0.28, 0.42)	0.31 (0.24, 0.39)	0.12 (0.07, 0.18)	0.26 (0.19, 0.33)	15.055**	3
Ehrharta calycina	0.05 (0.03, 0.07)	–	0.06 (0.03, 0.11)	–	0.16 (0.1, 0.22)	5.418*	1
Paspalum dilatatum	0.03 (0.02, 0.05)	–	0.08 (0.04, 0.14)	–	0.05 (0.02, 0.1)	0.887	1
Pentaschistis curvifolia	0.07 (0.05, 0.09)	–	0.15 (0.1, 0.22)	0.12 (0.07, 0.18)	–	0.297	1
Tribolium uniolae	0.15 (0.11, 0.18)	–	0.17 (0.12, 0.24)	0.25 (0.18, 0.33)	0.01 (0.00, 0.05)	26.82****	2
Pentaschistis pallida	0.08 (0.05, 0.10)	0.03 (0.01, 0.07)	–	0.15 (0.10, 0.22)	0.07 (0.04, 0.13)	15.63***	2
Aristida diffusa	0.07 (0.05, 0.09)	–	0.10 (0.06, 0.16)	0.15 (0.10, 0.22)	0.04 (0.02, 0.09)	10.319**	2
Digitaria eriantha	0.02 (0.01, 0.04)	–	0.04 (0.02, 0.09)	0.03 (0.01, 0.08)	0.01 (0.00, 0.05)	2.377	2
Cynodon dactylon	0.11 (0.08, 0.13)	0.07 (0.04, 0.12)	0.11 (0.06, 0.17)	0.11 (0.06, 0.17)	0.15 (0.10, 0.22)	3.922	3
Restios							
Ischyrolepis capensis	0.31 (0.27, 0.35)	0.18 (0.13, 0.25)	0.45 (0.37, 0.53)	0.36 (0.29, 0.45)	0.27 (0.2, 0.35)	16.79***	3
Calopsis muirii	0.05 (0.03, 0.06)	0.06 (0.03, 0.11)	0.09 (0.05, 0.15)	–	0.02 (0, 0.06)	6.001*	2
Hypodiscus striatus	0.02 (0.01, 0.03)	–	0.01 (0, 0.03)	0.08 (0.04, 0.14)	–	7.825**	1
Ischyrolepis triflora	0.12 (0.1, 0.15)	–	–	0.42 (0.34, 0.5)	0.12 (0.07, 0.19)	18.011****	1
Sedges							
Tetraria brachyphylla	0.05 (0.03, 0.07)	–	0.1 (0.05, 0.15)	0.11 (0.07, 0.18)	–	0.085	1
Ficinia indica	0.08 (0.06, 0.11)	0.14 (0.09, 0.19)	0.12 (0.07, 0.18)	0.03 (0.01, 0.07)	0.03 (0.01, 0.08)	17.808***	3
Geophytes							
Moraea collina	0.10 (0.08, 0.13)	–	0.13 (0.08, 0.19)	0.07 (0.03, 0.12)	0.23 (0.16, 0.31)	12.311**	2
Lanaria lanata	0.06 (0.04, 0.08)	0.08 (0.05, 0.13)	0.04 (0.02, 0.09)	–	0.09 (0.05, 0.15)	2.381	2
Watsonia laccata	0.04 (0.03, 0.06)	–	0.13 (0.08, 0.19)	0.05 (0.02, 0.09)	–	4.291*	1
Hypoxis villosa	0.07 (0.05, 0.09)	0.18 (0.13, 0.24)	0.03 (0.01, 0.06)	–	0.04 (0.02, 0.09)	25.371****	2
Forbs							
Corymbium africanum ssp. scabridum	0.04 (0.03, 0.06)	–	0.04 (0.02, 0.09)	0.13 (0.08, 0.19)	0.01 (0.00, 0.05)	15.493**	2

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ****; $P < 0.0001$

4.1. DISCUSSION

4.1.1. DIET COMPOSITION

Zebra are monogastric bulk grazers that require a large daily intake of fibrous material, feeding primarily on grass species (Bell, 1970; Owaga, 1975; Jarman and Sinclair, 1979; Murray and Illius, 1996; Stevens and Hume, 1996; Skarpe and Hester, 2008). In the semi-arid habitat of Kenya Plains, an ecosystem dominated by rich volcanic soils for example, plains zebra fed on 95-98% grass, with sedges and forbs comprising less than 5% of their diet (Owaga, 1975; Bell, 1982). The diet of mountain zebra in the MZNP likewise contained a high proportion of grass species (98% annually and 92-99% monthly) and sedges were avoided despite their relative abundance in the park (Winkler, 1992). In De Hoop Nature Reserve (DHNR), grass species formed 88% of the diet of mountain zebra, with inflorescence use of the family Restionaceae also recorded (Radloff, 2008; Smith *et al.*, 2011). In Baviaanskloof Nature Reserve (BNR) the mean annual diet composition of grasses to mountain zebra diet was 95.3% (Weel *et al.*, 2015). By comparison, the annual diet composition of grass species in BNP during the current study was 72.6%, which is substantially lower than the minimum annual grass component in mountain zebra diet in other studies. This warrants an evaluation of the seasonal patterns in diet composition, preference and site availability of grass species, with reference to the plant attributes that may influence forage selection of grass species (see Chapter 5).

The seasonal proportion of grass in the diet of mountain zebra in the BNP was significantly higher in the cool winter, warm summer and warm autumn (81.2%, 67.9% and 83.8% respectively) than in the cool spring at 43.3% (Table 4.1; H = 24.303; $P < 0.01$). By comparison, though the grass contribution to the mountain zebra diet was high in spring in DHNR, grasses that constituted the greatest proportion of the diet in spring were species such as *Aristida* spp., *C. dactylon*, *D. eriantha* and *Lolium* spp., which contributed between 10% and 20% to the diet (Smith *et al.*, 2011). These grass species were of low diet composition for mountain zebra in the BNP (Table 4.1). The use of *T. triandra* however, in DHNR was similar to the findings of the current study, showing its lowest contribution to the diet in spring (Smith *et al.*, 2011). This is noteworthy, since *T. triandra* formed the greatest proportion of the diet of mountain zebra in BNP. The increase in grass utilization in autumn during the current study also coincides with the findings of Smith *et al.* (2011), in that grass contribution to the diet was higher in autumn than summer in DHNR.

Principal grass species that were also preferred in the diet of mountain zebra, *T. triandra, C. marginatus, E. curvula* (grouped together in Figure 4.1), cumulatively accounted for 48.7% of the annual diet in BNP. Principal species *T. triandra*, *C. marginatus* and *E. curvula* are well documented as common species in the vegetation of the BNP (Grobler and Marais, 1967), as well as principal species in the diet of mountain zebra in other areas (Penzhorn, 1982b; Grobler, 1983; Novellie, 1987; Winkler, 1992; Smith *et al.*, 2011; Weel *et al.*, 2015).

Utilization of the C4 grass species *T. triandra* was significantly lower during spring than during the warm seasons in the current study. During spring, the diet was supplemented with restio and sedge species (Table 4.1). In DHNR *T. triandra* formed < 5% of the diet of mountain zebra (Smith *et al.*, 2011). In summer, grass utilization in BNP increased to 64.3%, primarily due to the high concentration of *T. triandra* in the diet in this season (34.0%). Summer grasses which use C4 photosynthetic pathways are typically targeted by grazers in fynbos in summer (Radloff, 2008), which is also the season during which most C4 grasses are actively growing (Pierce and Cowling, 1984). *T. triandra* typically experiences two growing seasons, namely summer and winter (Pierce, 1984; Pierce and Cowling, 1984), which coincides with the two seasons in which diet composition was greatest during this study. Other principal grasses were less favoured in the diet in summer, supported by a significant decline in the mean seasonal percentage greenness of *E. curvula* in the Recently Burnt Area, and of *C. marginatus* in feeding sites (see Chapter 5). Other grass species which also showed an increase in diet composition in summer included *E. curvula*, *S. zeyheri* and *A. diffusa* (Table 4.1), with *S. zeyheri* and *A. diffusa* contributing 8.2% and 2.0% to the summer diet respectively, of which stems with inflorescences made the greatest contribution to the diet (Figure 5.2; Appendix 2), and which were also in flower during this season (Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999; Clayton *et al.*, 2006).

C. marginatus was of moderate preference in summer and autumn, when the greenness for this species was lower, and the leaf height and diameter was higher (see Chapter 5). The diet composition of *C. marginatus* being greater during winter coincides with site availability of this species in winter, suggesting it was a targeted species in this season (Table 4.3). In the current study, winter was the first wet season after the February 2012 fire, which may explain the significantly greater proportion of accepted green plants during this season, particularly of *C. marginatus*, *Ehrharta capensis* and *E. curvula* (see Chapter 5). Fire typically increase forage production and quality (Mentis and Tainton, 1984). Frequent fires in the BNP since its proclamation, could also have increased the abundance of grasses like *C. marginatus* in the park (Mentis and Tainton, 1984; Novellie, 1987). In savanna communities with *Cymbopogon* spp. likewise offered favourable green leaf densities, and lower feeding deterrent properties during the wet season (Heitkönig and Owen-Smith, 1998). *C. marginatus* is predominantly a Mediterranean region species (Gibbs Russell *et al.*, 1990), and presumably adapted to growing during the cool wet conditions of winter. The mean utilization of *Ehrharta capensis* and *M. disticha* was also high in winter, though for *M. disticha*, the diet composition did not differ significantly from utilization in other seasons. *Ehrharta capensis* and *M. disticha* are C3 grasses, and thus utilization of these species in the cool wet winter would coincide with their growing season (Pierce and Cowling, 1984). C3 grasses are also more resistant to low temperatures during their growing season, which influences their distribution and availability to herbivores (Caldwell *et al.*, 1977).

The peak in the diet composition of *E. curvula* during the warm autumn season, is similar to findings in MZNP, where *E. curvula* was used most intensively in autumn, also showing highest level of greenness during autumn months (Winkler, 1992). Though not directly linked to seasonal use of *E. curvula*, the analysis in Chapter 5 suggests that both greenness and plant volume were important factors in the annual selection of *E. curvula*.

Grass species with a low diet composition that were preferred (see Figure 4.1; *S. zeyheri*, *P. dilatatum*, *H. contortus*, *M. disticha*, *H. hirta*, *E. calycina* and *D. eriantha*), cumulatively accounted for 14.3% of the annual diet. *M. disticha* and *D. eriantha* have also been utilized by mountain zebra in MZNP (Winkler, 1992), while *S. zeyheri* and *D. eriantha* were utilized by mountain zebra in DHNR (Smith *et al.*, 2011), and *H. contortus* was utilized by mountain zebra in BNR (Weel *et al.*, 2015).

The non-preferred grass species of low diet composition in Figure 4.1 (*P. curvifolia, T. uniolae, P. pallida, A. diffusa, Ehrharta capensis, B. serrata* and *C. dactylon*) constituted 7.0% of the annual diet. Of these species, *A. diffusa* was moderately utilized by mountain zebra in MZNP (Winkler, 1992), *Aristida* spp. and *C. dactylon* each contributed > 10% to the seasonal diet of mountain zebra in DHNR (Smith *et al.*, 2011), and *B. serrata* formed 0.7% of the diet of mountain zebra in BNR (Weel *et al.*, 2015). Rationales for the low utilization of *C. dactylon* in BNP, a species which constituted 15% of the mountain zebra diet in DHNR, is discussed in section 4.1.2 and in Chapter 5.

It is evident that although mountain zebra preferred grass in the BNP, the diet was supplemented with other graminoid and geophyte species. This is supported by other studies in which utilization of restios and sedges have been recorded for mountain zebra, particularly after fire, and declining subsequently (Novellie, 1987; De Villiers, 1999). During the spring and summer months, when grasses were of lower site availability, mountain zebra diet selection changed to include restios (20.7% and 13.0% respectively), sedges (13.0% and 5.4% respectively), and geophytes, with a diet composition of 10.0% in spring (3.0% attributed to the use of the inflorescences of the spring flowering species *W. laccata*). Mountain zebra targeted the inflorescences and photosynthetic stems of restios and sedges in spring and summer, when *I. capensis, H. striatus* and *Ischyrolepis triflora* were included in the diet, coinciding with the spring to summer flowering season for many Restionaceae species (Stock *et al.*, 1992; Haaksma and Linder, 2000). Restio and sedges also use C3 photosynthetic pathways, with an active growth period during the cool wet seasons (Pierce and Cowling, 1984; Stock *et al.*, 1992). Sedges were also utilized by bontebok in the BNP in the first year after fire, prior to the introduction of mountain zebra (Novellie, 1987). In DHNR, restios formed up to 1.5% of the seasonal diet of mountain zebra (Smith *et al.*, 2011), while restios were also utilized by mountain zebra in GMNR (De Villiers, 1999). Similarly, mountain zebra used non-grass species during the spring season in the MZNP, dwarf shrubs forming a significant monthly contribution of 4.7% to the diet in the spring month of August (Winkler, 1992).

Though not significantly different from utilization in other seasons, the sedge species *T. brachyphylla* and *F. indica* also formed > 5% of the diet in spring during the current study. Sedges use C3 photosynthetic pathways and are predominantly adapted to winter rainfall conditions and cooler climates (Stock *et al.*, 2004), which may explain why these species were utilized in spring. These plants may provide an important source of nitrogen during spring and summer, when maximum nitrogen is allocated to the culms and developing inflorescences (Stock *et al.*, 1987). The significant increase in nitrogen in mountain zebra dung in spring shown in Chapter 6 may be explained by the increase in the use of inflorescences of restios and sedges during spring.

Though grasses formed the bulk of the diet in the warm autumn, mountain zebra diet also included 13.4% geophytes during this season. This can be largely attributed to the opportunistic utilization of the bulbs of *Moraea collina* (Table 4.1), and of the fire-responsive species *Lanaria lanata* (Vlok and Schutte-Vlok, 2010). The leaves and flowers of *Moraea* species are deemed toxic to cattle (Joubert and Schultz, 1982; Snyman *et al.*, 2009; Snyman *et al.*, 2011), and thus the high use, preference and site availability of *Moraea collina* in the diet of mountain zebra in the BNP is surprising, and warrants further investigation. Utilization of *L. lanata* by mountain zebra was also recorded in the BNR (Weel *et al.*, 2015).

4.1.2. DIET PREFERENCE

Of the 26 species contributing ≥ 2% to the annual diet of mountain zebra, 15 (58%) were also annually preferred. The three principal grass species, *T. triandra, C. marginatus* and *E. curvula* were of high annual acceptability, as well as high annual site availability, and thus targeted by mountain zebra at feeding sites (Table 4.3). Of the species of high acceptability but low diet composition (Figure 4.1), species with the greatest diet composition, *M. disticha, H. contortus, H. hirta* and *D. eriantha are* included in this discussion. Of the species of both low acceptability and low diet composition (Figure 4.1), *C. dactylon* and *A. diffusa* are included in this discussion.

In the Northern Province Lowveld, *T. triandra* was preferred by plains zebra (Bodenstein *et al.*, 2000). Mountain zebra also prefer this species in the MZNP (Grobler, 1983; Winkler, 1992) and BNR (Weel *et al.*, 2015). Extensive work has been done on *T. triandra* in the BNP specifically, suggesting it is important grass species in the BNP for bontebok and other grazers in this ecosystem (Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Watson *et al.*, 2011). In both the MZNP (Winkler, 1992) and the BNP, preference for *T. triandra* was high throughout the year. As a Decreaser grass, *T. triandra* (Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999) is moderately sensitive to overgrazing, yet fire tolerant (Heady, 1966; Downing and Marshall, 1980; Belsky, 1992; Novellie and Kraaij, 2010; Ligavha-Mbelengwa and Bhat, 2013). Work in this regard showed *T. triandra* is not that sensitive to overgrazing in combination with fire (Novellie and Kraaij, 2010), and the historical short fire rotation aimed at stimulating grass production may have promoted the abundance of this grass in the BNP.

Cymbopogon species are preferred by mountain zebra in other studies, specifically in DHNR (Smith *et al.*, 2011), and the MZNP (Grobler, 1983; Winkler, 1992). The sward structure of grasses in the BNP, also suggests that it is utilized by grazers in the BNP (Novellie, 1990). *Cymbopogon pospischilli* (formerly *C. plurinoides)* showed higher protein levels in autumn in the MZNP (Grobler, 1983). During this study, *C. marginatus* was one of the three most preferred species on an annual basis, but preference was highest in the cool winter and lower in other seasons, increasing marginally in autumn. The preference in winter may have been influenced by the recent fire in the park, suggested by the high number of green flushing plants in the diet of mountain zebra during this season (see Chapter 5). *C. marginatus* is an aromatic grass of moderate palatability (Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999), which may be more important than its growing season as a C4 grass (Pierce and Cowling, 1984) in this context.

Eragrostis species were utilised or preferred by mountain zebra in both DHNR (Smith *et al.*, 2011) and MZNP (Winkler, 1992). *E. curvula* is an Increaser species, of important grazing value to mountain zebra (Novellie, 1990; Winkler, 1992; Van Oudtshoorn, 1999). Sites frequented by mountain zebra showed a moderate cover of

E. curvula in the MZNP (Novellie, 1990). Some overlap exists between the seasonal preference of *E. curvula* in the MZNP and the BNP: In the MZNP preference was significantly higher throughout autumn winter and spring that in summer (Winkler, 1992), while in BNP the peak was in autumn, but preference was also high in spring and summer (Table 4.2). *E. curvula* also showed higher protein levels in the MZNP during autumn (Grobler, 1983). In contrast, in BNR, *E. curvula* was a preferred species in the winter and early summer (Weel *et al.*, 2015).

Though considered an unpalatable grass (Van Oudtshoorn, 1999), *M. disticha* was preferred by mountain zebra in the current study, both annually and in all four seasons. Acceptability of *M. disticha* in MZNP was moderate to high (Winkler, 1992; Novellie and Winkler, 1993), while in another assessment *M. disticha* was not taken by mountain zebra in MZNP (Grobler, 1983). Notably, this species is a hard grazing grass that is grazed when young or when other available grazing is poor (Van Oudtshoorn, 1999). This is confirmed by observation during this study, as this species was utilized in young fynbos, when re-sprouting after fire, or when kept short by grazers on rocky outcrops in Proteoid Fynbos.

Mountain zebra preferred *H. contortus* throughout the year in the MZNP (Grobler, 1983; Winkler, 1992; Winkler and Owen-Smith, 1995). Preference of *H. contortus* in the BNP was also high throughout the year during the current study (Table 4.2). In BNR, *H. contortus* was moderately preferred on an annual and a seasonal basis (Weel *et al.*, 2015).

During this analysis preference of *H. hirta* remained high throughout the year. This species has not been recorded in other diet studies for mountain zebra to date. However *H. hirta* was found to be a preferred species in the diet of buffalo during the dry season, June to September, in DNR (Venter, 2006), a dominant species in the diet of roan antelope in the KNP (Knoop, 2004) and of moderate acceptability to sable antelope in Kgaswane Mountain Reserve, Magaliesberg, Limpopo Province (Parrini, 2006).

A species of moderate preference throughout the year to mountain zebra in the MZNP was *D. eriantha*, with an annual acceptability of 0.45 (Winkler, 1992), and a principal species (annual diet composition of 10%) in the diet of mountain zebra in DHNR (Smith *et al.*, 2011). In the BNP it proved to be a preferred species during the current study, with an annual *ai* of 0.57. In both MZNP (Winkler, 1992) and during this analysis in the BNP, there was no significant difference between seasonal acceptability indices of *D. eriantha*.

The couch grass *C. dactylon* has been identified as an important species in both BNP (Kraaij and Novellie, 2010; Novellie and Kraaij, 2010) and in the DHNR, forming 14% of the annual diet of mountain zebra in DHNR (Smith *et al.*, 2011). Other *Cynodon* species were of moderate acceptability to mountain zebra in the MZNP (Winkler, 1992), but not utilized by mountain zebra in a different study in the MZNP (Grobler, 1983). The current study found the preference and site availability of *C. dactylon* to be consistently low throughout the year, which can be attributed to low leaf height (see Chapter 5). This can be supported by the hypothesis that stoloniferous growth in grasses (like *Cynodon* species) evolved as an escape strategy from large herbivores (Wolfson and Tainton, 1999; Skarpe and Hester, 2008). Le Roux (2011) notes that *C. dactylon*, is of low acceptability to sable due to its short growth form, yet highly acceptable to short grass grazers such as wildebeest (Andere, 1981). This is in line with work in the BNP, where bontebok have been recorded to utilize *C. dactylon* grazing lawns in the BNP specifically (Luyt, 2005; Kraaij and Novellie, 2010; Watson *et al.*, 2011).

Aristida diffusa was seasonally preferred during this study, specifically in the warm summer, during which stems and inflorescences of this species were used (Figure 5.2; Appendix 2). This species was of low acceptability in MZNP (Winkler, 1992; Novellie and Winkler, 1993). In the assessment by Grobler (1983), *A. diffusa* and *A. congesta* were found to be available in the MZNP, but not used by mountain zebra. In DHNR *Aristida* spp. formed > 10% of the seasonal diet of mountain zebra (Smith *et al.*, 2011). A closely related species to *A. diffusa, A. junciformis*, was found to be of low preference to mountain zebra in BNR, forming 1.5% of the annual diet (Weel *et al.*, 2015). During in the current study, *A. junciformis* was not utilized, despite being present in feeding sites (Appendix 1).

4.1.3. SITE AVAILABILITY

The site availability indices of dietary species in the BNP ranged between 0 and 0.50, while site availability of utilized species in the MZNP ranged between 0 and 0.92 (Winkler, 1992). The low site availability of preferred species suggests that suitable habitat for mountain zebra in the BNP is limited. The low site availability (0.08) in BNP compared to the acceptability index (0.76) of a species such as *H. contortus* in particular, an important species for mountain zebra in the MZNP, is pertinent (Grobler, 1983; Winkler, 1992). In the BNP this may be attributed to the low grass availability in fynbos systems (Mentis and Tainton, 1984) and nutrient-poor conditions (Pierce and Cowling, 1984; Stock and Lewis, 1986; Witkowski and Mitchell, 1987; Cowling and Bond, 1991; Cowling, 1992; Coetzee, 2002), which have shown to influence nutrient availability to non-ruminants and ruminants alike (Illius and Gordon, 1992). This is underlined by findings in BNR, GMNR and KNR, where mountain zebra are resource limited (Watson *et al.*, 2005; Watson and Chadwick, 2007; Weel *et al.*, 2015), as well as in DHNR, where mountain zebra concentrate on transformed grassland instead of fynbos habitat (Smith *et al.*, 2011).

During this study, the site acceptability of each of the four principal species *T. triandra, C. marginatus, E. curvula* and *I. capensis* followed the same seasonal pattern as diet composition for these species, *C. marginatus* peaking in winter, *I. capensis* in spring, *T. triandra* in summer and *E. curvula* in autumn. This suggests that mountain zebra seasonally targeted these species at feeding sites, and that the seasonal changes in plant attributes determined whether and when these species were being targeted (Owen-Smith, 1982; Owen-Smith and Cooper, 1987; Owen-Smith, 2002).

The findings of this site availability analysis combined with the importance of grass volume in the selection of *T. triandra* (see Chapter 5) suggest that mountain zebra were frequenting sites where *T. triandra* was locally abundant at favourable quantities. Novellie (1987) identified *T. triandra* as an important species in the BNP, as this species was significantly utilized by grazers in the park at the time, which was before the introduction of mountain zebra to the BNP. The findings of this diet assessment suggest that *T. triandra* is also preferred by mountain zebra, and targeted in specific habitats and seasons. However, by comparison to site availability in the MZNP (Winkler, 1992), an annual site availability of 0.5 suggests that sites with *T. triandra* were restricted in the BNP, and thus monitoring of the impact of herbivory on this species is important.

4.2. CONCLUSION

Grass formed the greatest proportion of the diet of mountain zebra in the BNP, with a significant proportion of non-grass species as well. Three grass species (*T. triandra, C. marginatus* and *E. curvula*) and one restio (*I. capensis*) formed the bulk of the annual diet. *T. triandra* and *E. curvula* made the most significant contribution to the diet of mountain zebra during the warm seasons, which was in line with widely accepted trends for C4 grasses. Mountain zebra diet diversified during the cool spring, during which mountain zebra used less preferred grasses as well as restio and sedge species. Acceptability indices further informed the diet analysis, showing significant seasonal shifts between preferred species. *T. triandra* and *E. curvula* were preferred in all seasons, while *H. contortus* and *H. hirta*, two preferred and well-documented species that were of low annual diet composition in the BNP. Utilization of *C. marginatus* appeared to be linked to fire and greenness, and the low utilization of *C. dactylon* to its stoloniferous growth and low leaf height during the current study. These findings suggest that mountain zebra were applying season-specific and site-specific feeding strategies in obtaining adequate quantity and quality forage in the BNP throughout the year.

CHAPTER 5: FACTORS INFLUENCING GRASS SPECIES SELECTION

5.1. INTRODUCTION

Herbivore foraging behaviour is seen as an interaction between the characteristics of the herbivore and characteristics of the forage (Searle and Shipley, 2008). Besides the availability and chemistry of the food resource, forage selection by herbivores is also influenced by physical and phenological plant features (Heady, 1964; Owen-Smith, 1982; Owen-Smith and Novellie, 1982). Acceptance of food plants at the feeding site may be influenced by (a) palatability – plant chemistry and nutritive value; (b) physical plant characteristics – phenology, volume, thorns, hairs, prickles; and (c) prior feeding experience (Young, 1948; Erasmus *et al.*, 1978; Owen-Smith, 1982; Owen-Smith and Novellie, 1982; Grobler, 1983; Cooper and Owen-Smith, 1986; Senft *et al.*, 1987; Ben-Shahar and Coe, 1992; Winkler, 1992; Heitkönig and Owen-Smith, 1998). A number of grazer studies showed that grazing herbivores accept grass species on the basis of a combination of structural and seasonally fluctuating phenological characteristics (Heady, 1964; Owen-Smith, 1982; Owen-Smith, 1988; Winkler, 1992; Venter, 2006).

Plant part acceptability is recognised as a key component in herbivore dietary selection (Grunow, 1980; Owen-Smith, 1982; McNaughton and Georgiadis, 1986; Venter, 2006). Grazers prefer leaf material to stem material, because it is more digestible (Bell, 1970; Bell, 1971; Owen-Smith, 1982), and leaves have a higher nutrient to fibre ratio (Chapin and Stuart, 1980; Owen-Smith and Novellie, 1982). In the karoo, plant leafiness was an important grass selection criterion varying among species and seasons for buffalo, another bulk grazer (Venter, 2006). However, leafiness was only weakly correlated with acceptability for mountain zebra in the MZNP (Winkler, 1992). The selection of stems or culms by mountain zebra, is hypothesised to be strongly influenced by the targeting of graminoid inflorescences (Owaga, 1975; Winkler, 1992).

The phenological state of the plant influences the volume of photosynthetic green matter available to the herbivore (Winkler, 1992; Watson and Owen-Smith, 2002; Venter, 2006). Phenological state represents the temporal life phenomena in relation to varying climatic conditions, for example flushing, blooming, fruiting, foliation, defoliation and dormancy (Hanson, 1962; Harris, 1977; Cowling, 1992; Sinclair *et al.*, 2000; Baskin and Baskin, 2001; Arsenault and Owen-Smith, 2002). Plant attributes are strongly influenced by seasonal changes in the ecosystem, for example seasonal grass dormancy, which influences the movement patterns of grazers (Arsenault and Owen-Smith, 2002; Hopcraft *et al.*, 2010). This will cause grazers to choose areas where the growth state of grass is favourable, and move to more suitable patches if the state is not favourable. In fynbos ecosystems, grazer responses to seasonal changes in grass phenology require further investigation, as recommended by other work in the BNP (Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Watson *et al.*, 2011). Research informing this describes seasonal flushes or growth phases in graminoids by grouping species according to C3 or C4 photosynthetic pathways (Pierce and Cowling, 1984; Radloff, 2008). Restioids and C3 grasses growth occurs mostly in the cool wet season, while C4 grasses have either a summer growth season, or a summer and additional cooler growth season (Pierce and Cowling, 1984). This Chapter draws from the known phenological patterns in grass selection by herbivores, as well as the unique seasonal dynamics in dystrophic fynbos ecosystems, in order to better understand the role of phenology in grass selection by mountain zebra in the BNP.

Another plant attribute that influences herbivore grass selection is the availability of adequate quantity forage or plant volume (Bell, 1970; Bell, 1971; Owaga, 1975; Grunow, 1980; Arsenault and Owen-Smith, 2002). As a large non-ruminant grazer with hindgut fermentation, mountain zebra need a large daily intake of grass (Bell, 1971; Janis, 1976; Parra, 1978; Demment and Van Soest, 1985). However, recent research showed that the high quantity forage ingested by equids also needs to be of adequate nutritional value (Duncan *et al.*, 1990; Illius and Gordon, 1992). In older veld in fynbos for example, grass becomes moribund and low in nutrients (Mentis and Tainton, 1984; Bond *et al.*, 2003), which could be a limiting factor in the BNP.

It is widely accepted that *Equus* species also tend to select taller grass than other grazing ungulates, taking their food at between 50 and 150 mm from the ground (Bell, 1970; Grobler, 1983; Penzhorn and Novellie, 1991). Since zebra generally also move into areas with longer grass before other grazers do, they tend to open up the grass sward through grazing and trampling (Jarman and Sinclair, 1979; Novellie, 1987; Murray and Illius, 1996). Large body size may put mountain zebra in a position to be able to utilize taller grass, but the availability of the preferred grass at the preferred height may be limited in dystrophic systems. It is important to note that if other grazers such as bontebok keep the grass too short, mountain zebra may also not find sufficient grass quantity at the desired height (Bell, 1970; Grobler, 1983; Radloff, 2008; Smith *et al.*, 2011).

The focus of this analysis was only on grass species, which formed the bulk of the diet of mountain zebra in the BNP. The objectives of this Chapter are to investigate the role of three factors in the annual and seasonal forage selection by mountain zebra, namely: (a) plant part (the selection of leaves, stems and inflorescences); (b) plant phenological state (represented by grass greenness); and (c) plant volume (represented by grass leaf height and diameter).

5.2. METHODS

5.2.1. STUDY SITE

For the study site description, refer to Chapter 2.

5.2.2. SELECTION BETWEEN AND WITHIN SPECIES

Factors influencing selection were investigated (a) between species; and (b) within species selected. For the assessment between species, data were collected in the same feeding quadrat surveys as for diet composition and diet preference (Chapter 4). For the assessment within species two methods were used: (i) feeding quadrat surveys; and (ii) an independent grass surveys in and out of the Recently Burnt Area habitat.

5.2.3. FEEDING QUADRAT SURVEYS

Feeding quadrats were located and surveyed as in Chapter 4, using the feeding quadrat method (Grobler, 1981; Grobler, 1983). In each feeding quadrat, plant characteristics that may influence plant acceptance were recorded for a randomly selected accepted plant of each grass species, as well as for a randomly selected rejected plant, in accordance with the method used by Venter (2006).

In the cool winter, this consisted of 190 quadrats, in the cool spring 157 quadrats, in the warm summer, 149 quadrats, and in the warm autumn 148 quadrats (total n = 644). For each accepted grass species in the feeding quadrat, plant part utilization was measured in terms of the proportion of leaf and stem used. Rejected plants were excluded from this analysis, as utilization from these plants was nil. For this differentiation, “stems” included the stem of the leaf blade at the base of the plant, as well as the inflorescence-bearing culms (Gibbs Russell *et al.*, 1990; Yates, 2011).

Variables measured for both accepted and rejected plants included: (a) Percentage greenness – according to the eight-point Walker scale (Walker, 1976), with the score converted to a mid-point percentage of each category, for statistical analysis; (b) Leaf height – a measurement of the average predominant height (mm) of the grass tuft; and (c) Diameter – a measurement of the average diameter of the plant (mm).

5.2.4. GRASS SURVEYS IN THE RECENTLY BURNT AREA

In order to determine the seasonal change in greenness and leaf height of the available grass sward in and out of the Recently Burnt Area (RBA) habitat, an independent survey of these characteristics was conducted on a monthly basis. The three grass species surveyed were: *T. triandra*, *C. marginatus* and *E. curvula* (see Table 4.1). Once a month, a random area was selected in the Recently Burnt Area and as well as in Young Proteoid Fynbos, and a line transect was walked in each habitat. Every 2 m along the transect, greenness and leaf height measurements were taken from the closest plant of the three species, until 25 samples were obtained for all the three species per month.

5.2.5. STATISTICAL ANALYSES

5.2.5.1. FACTORS INFLUENCING SELECTION BETWEEN SPECIES

For factors influencing selection between species, a principal components analysis (PCA) was used to explore the importance of grass selection factors between grass species (Zar, 1996; Manly *et al.*, 2002; Hatcher and O'Rourke, 2014). Only data for accepted plants of grass species in feeding quadrats were included in the PCA. Continuous data formed the analytical variables for the analysis, namely percentage greenness, leaf height, diameter, percentage leaf use and percentage stem use, while inflorescence use per species per quadrat and season formed supplementary variables.

5.2.5.2. FACTORS INFLUENCING SELECTION WITHIN SPECIES

For the analysis of plant factors within species, grass species with a diet composition greater than 5% were selected (see Table 4.1), namely *T. triandra, C. marginatus* and *E. curvula*. The mean seasonal percentage greenness, leaf height, and diameter were calculated for each grass species per season respectively. The relationship between these factors in the various seasons needed to be established for both accepted and rejected plants. Since the data were non-parametric, and there is no generally accepted non-parametric equivalent for the two-way ANOVA, a combination of the Mann-Whitney and Kruskall-Wallis tests were used to analyse the data (Zar, 1996). The Mann-Whitney test was used to determine if mean values were the same between accepted and rejected plants for each species, within each season. The Kruskall-Wallis test was then used to determine if the means were the same between seasons, for both accepted and rejected plants per species independently, followed by a multiple comparison of mean ranks test to compare means between seasons.

The mean annual percentage greenness, leaf height and diameter of all grass species that occurred in more than ten feeding sites (23 grass species in total) were calculated, and the Mann-Whitney test used to determine if annual means for accepted and rejected plants per species were the same. Grass species that were never accepted in any quadrats (annually or seasonally), as well as grass species that occurred in less than ten sites during the year were excluded.

For the analysis of grass leaf height and greenness of the three principal grass species in the RBA, the Mann-Whitney test was used for each variable to determine if the mean values inside and outside of the RBA were the same (Zar, 1996). The Kruskall-Wallis test and the multiple comparison by mean ranks test was used to determine if the mean values were the same between seasons, for data collected in and out of the RBA respectively (Zar, 1996).

5.3. RESULTS

5.3.1. FACTORS INFLUENCING SELECTION BETWEEN SPECIES

Factor 1 (48.4%) and Factor 2 (26.0%) of the Principal Components Analysis (PCA) cumulatively accounted for 74.4% of the total variance in the data (Table 5.1), plotted on a two-dimensional plane in Figure 5.1. The data separated along the two axes, with the cool winter positioned on the negative side of the Factor 1 axis, the warm summer positioned on the positive side, the cool spring on the negative side of the Factor 2 axis, and the warm autumn on the positive side.

For Factor 1, percentage leaf use (32%) and stem use (32%) accounted for the greatest variance. Leaf use and percentage greenness (11%) were closely related to the cool winter on the negative side of the Factor 1 axis, while percentage stem use and inflorescence use were closely related to the warm summer.

For Factor 2, diameter and leaf height accounted for the greatest variance, at 38% and 26% respectively. Along this axis, both diameter and leaf height were positively related to the warm summer and autumn seasons, but negatively related to the cool winter and cool spring seasons.

5.3.2. FACTORS INFLUENCING SELECTION WITHIN SPECIES

5.3.2.1. PLANT PART USE

In terms of plant part use, from the mean annual percentage leaf and stem use (see Appendix 2), it is evident that leaf material was the preferred plant part for all grass species, with the exception of *Stipagrostis zeyheri*, *Aristida diffusa* and *Briza maxima*, for which stems with inflorescences were targeted, and *Brachiaria serrata*, from which equal proportions of leaf and stem were used.

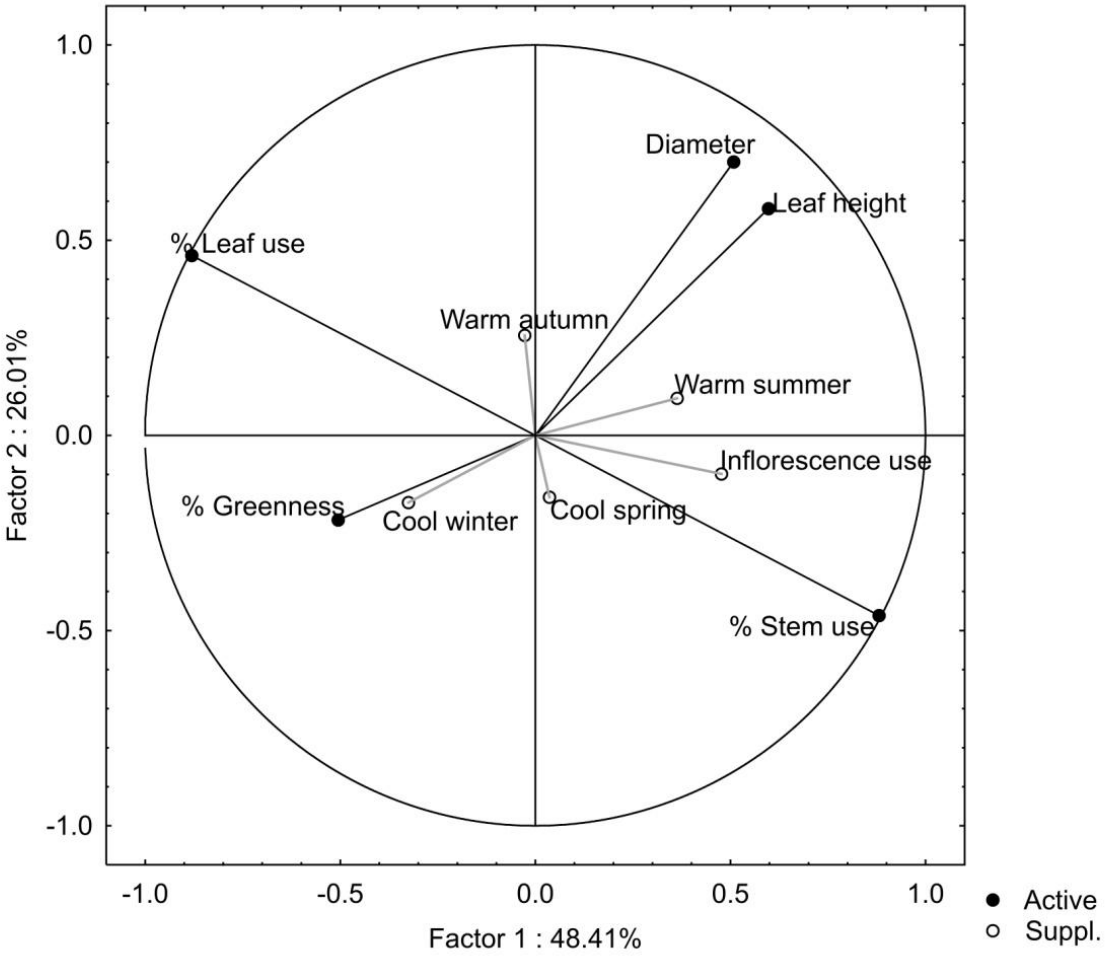


Figure 5.1: Plot of Factor 1 and Factor 2 of the principal components analysis of factors influencing grass selection in feeding quadrats, for accepted plants only.

Table 5.1: Variance and Eigen values for Factors 1 to Factor 5 of the principal components analysis.

Variable	**Factor 1**	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**
% Greenness	0.106	0.036	0.852	0.006	0.000
Leaf height	0.147	0.260	0.089	0.505	0.000
Diameter	0.107	0.377	0.034	0.482	0.000
% Leaf use	0.320	0.163	0.012	0.004	0.500
% Stem use	0.320	0.164	0.012	0.004	0.500
% Total Variance	**48.413**	**26.013**	**16.296**	**9.272**	**0.007**
Eigen value	**2.421**	**1.301**	**0.815**	**0.464**	**0.000**

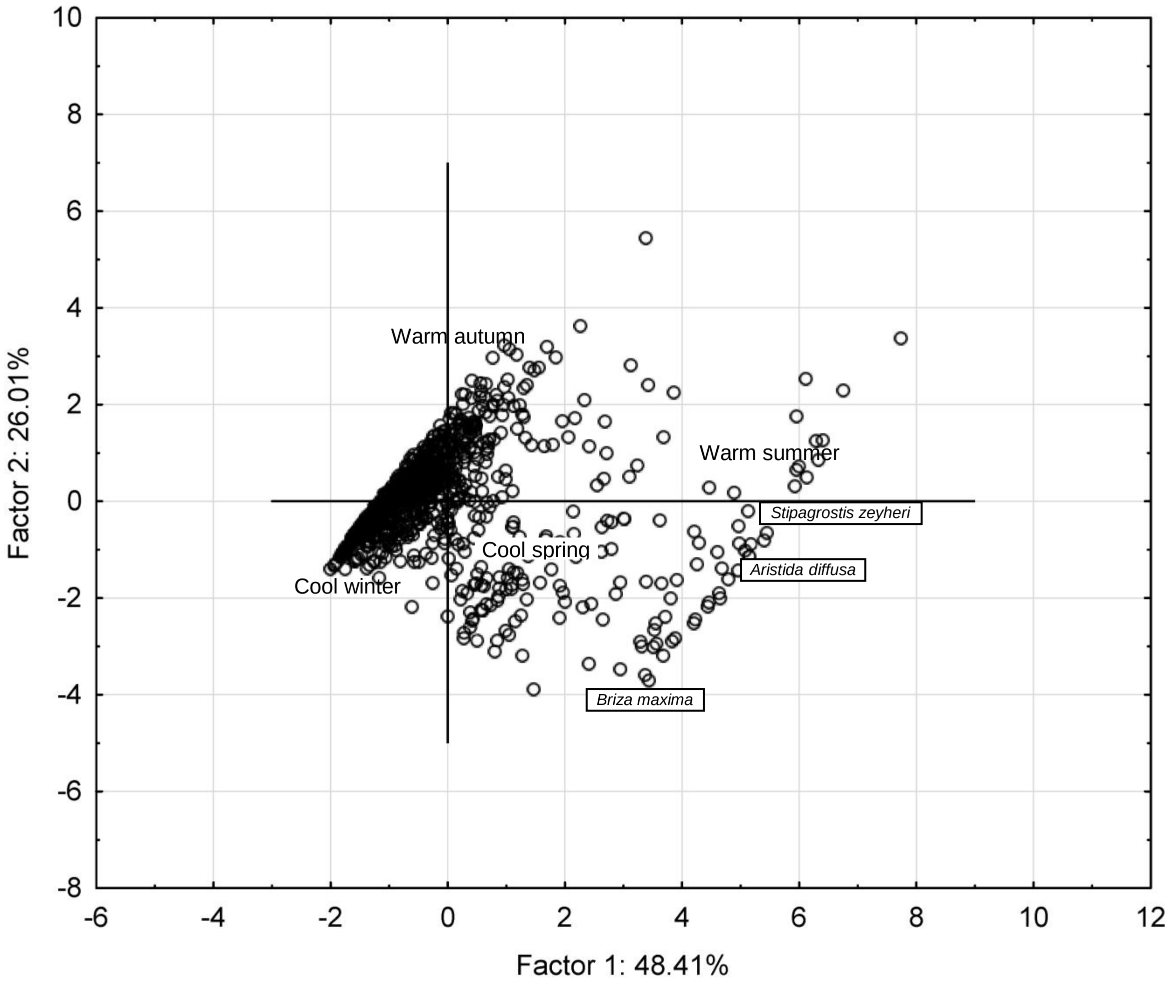


Figure 5.2: Data distribution plotted for Factor 1 and Factor 2, with reference to the positioning of the outliers, *Briza maxima*, *Stipagrostis zeyheri* and *Aristida diffusa*, in relation to the four seasons.

Figure 5.2 plots the data distribution of species measured on the PCA axes, indicating the positioning of the three outliers, S*. zeyheri, A. diffuse* and *B. maxima*. This data distribution indicated that *A. diffusa* and *S. zeyheri* were related to the warm summer season as thus also stem and inflorescence use, while *B. maxima* was related to the cool spring. All other grass species grouped together, according to leaf use and other variables. *B. serrata* plotted within this grouping and was not an outlier as the other three species for which stem use was important.

5.3.2.2. GREENNESS, LEAF HEIGHT AND DIAMETER

The mean seasonal percentage greenness of accepted plants of *T. triandra* in feeding sites varied between seasons (Figure 5.3; H = 9.135; $P < 0.05$), but the multiple comparison test did not indicate a difference between particular seasons. Rejected plants of *T. triandra* in feeding sites showed a significant drop in greenness during the warm autumn (H = 9.120; $P < 0.05$). There was no difference between the mean for accepted and rejected plants in each season (Figure 5.3; winter Z = 0.222; $P > 0.05$; spring Z = 0.307; $P > 0.05$; warm summer Z = 0.186; $P > 0.05$; warm autumn Z = 0.780; $P > 0.05$). The mean seasonal percentage greenness from surveys in the RBA differed between seasons in the RBA (Figure 5.4; H = 123.095; $P < 0.001$), and well as out of the RBA (H = 63.348; $P < 0.001$), in both analyses showing higher levels in the cool winter and spring, than the warm summer and autumn. There was also a difference between the mean percentage greenness in and out of the RBA, greenness being consistently greater in the RBA than out of the RBA for winter (Figure 5.4; Z = 8.395; $P < 0.001$), spring (Z = 3.328; $P < 0.001$), and autumn (Z = 4.913; $P < 0.001$), except for summer, when there was no difference in the mean percentage greenness between in and out of the RBA (Z = 0.731; $P > 0.05$).

The mean leaf height of *T. triandra* differed seasonally, for accepted (Figure 5.3; H = 59.026; $P < 0.001$), as well as rejected plants (H = 45.453; $P < 0.001$), increasing significantly in each consecutive season for the first three seasons, and then decreasing to a level between the two prior levels in autumn. Rejected leaf height followed the same trend as the diet composition of *T. triandra*, reaching its lowest level in spring and the highest level in the warm summer. The mean leaf height also differed between accepted and rejected plants per season, being greater for accepted than rejected plants in spring (Figure 5.3; $Z = 6.476$; $P < 0.001$), summer ($Z = 3.101$; $P < 0.01$) and autumn ($Z = 6.658$; $P < 0.001$). The only exception was in winter, for which mean leaf height levels for accepted and rejected plants were the same ($Z = 0.254$; $P > 0.05$). Mean leaf height in the RBA was higher in spring and autumn than winter and summer (Figure 5.5; $H = 49.305$; $P < 0.001$), but out of the RBA, mean levels decreased from higher levels in winter, spring and summer, to a lower mean level in autumn ($H = 23.392$; $P < 0.001$). The mean leaf height out of the RBA was higher than in the RBA in all seasons: winter ($Z = 9.292$; $P < 0.001$), spring ($Z = 7.110$; $P < 0.001$), summer ($Z = 8.666$; $P < 0.001$) and autumn ($Z = 2.586$; $P < 0.01$).

The mean seasonal diameter varied between seasons for accepted (Figure 5.3; $H = 28.695$; $P < 0.001$) and rejected plants, ($H = 29.617$; $p < 0.001$), from lower levels in winter and spring, to higher levels in the warm summer and autumn. *T. triandra* mean diameter was also consistently greater for accepted than rejected plants in winter ($Z = 4.634$; $P < 0.001$), spring ($Z = 4.164$; $P < 0.001$), summer ($Z = 4.328$; $P < 0.001$) and autumn (Figure 5.3; $Z = 3.390$; $P < 0.001$).

C. marginatus showed a decrease in mean percentage greenness in the warm summer, while means in the warm autumn, cool winter and cool spring seasons were similar, for both accepted (Figure 5.6; $H = 15.795$; $P < 0.01$) and rejected plants ($H = 48.363$, $P < 0.001$). Between accepted and rejected plants, mean percentage greenness was the same in winter ($Z = 0.032$; $P > 0.05$), spring ($Z = 1.067$; $P > 0.05$) and summer ($Z = 0.185$; $P > 0.05$), and different in autumn only, when mean percentage greenness of accepted plants was greater than for rejected plants ($Z = 3.592$; $P < 0.001$). Greenness of accepted and rejected plants followed a similar trend as diet composition of this species, decreasing from winter to spring, and again from spring to summer, when both greenness and diet composition were at a minimum. Both greenness and diet composition increased again in autumn. From the RBA surveys, there was a significant difference between the mean percentage greenness in (Figure 5.7; $H = 129.703$; $P < 0.001$) and out ($H = 115.581$; $P < 0.001$) of the RBA, with levels in the RBA being higher in the cool seasons than the warm seasons in both habitats. Mean percentage greenness was consistently higher in the

RBA than out of the RBA for all seasons: winter (Z = 7.544; $P < 0.001$), spring (Z = 6.956; $P < 0.001$), summer (Z = 5.245; $P < 0.001$) and autumn (Z = 7.123; $P < 0.001$).

The mean leaf height of accepted plants of *C. marginatus* varied seasonally, showing a lower level in winter than the other seasons (Figure 5.6; H = 44.590; $P < 0.001$). The mean leaf height of rejected plants followed a similar pattern, but showed lower levels in both cool seasons (winter and spring) than the warm summer and autumn seasons (H = 32.596; $P < 0.001$). Mean seasonal leaf height showed an inverse relationship to acceptability: leaf height was higher in seasons when acceptability was low, and higher in seasons when acceptability was high (Figure 5.6). The mean leaf height of accepted plants was the same as that for rejected plants in three seasons, winter (Figure 5.6; Z = 0.883; $P > 0.05$), summer (Z = 0.169; $P > 0.05$) and autumn (Z = 1.488; $P > 0.05$), and was greater that rejected plants in spring only (Z = 3.353; $P < 0.001$). From the RBA surveys, seasonal mean leaf height in the RBA was the same between seasons (Figure 5.8; H = 4.972; $P > 0.05$), but increased in autumn out of the RBA (H = 12.469; $P < 0.01$). The means were consistently lower in the RBA than out of the RBA: winter (Z = 8.619; $P < 0.001$), spring (Z = 8.985; $P < 0.001$), summer (Z = 7.273; $P < 0.001$), and autumn (Z = 7.828; $P < 0.001$).

The mean diameter of *C. marginatus* followed a similar trend as the mean leaf height, in that for accepted plants, seasonal means were lower in winter only (Figure 5.6; H = 23.777; $P < 0.001$), while for rejected plants, seasonal means were lower in winter and spring (H = 78.617; $P < 0.001$). As for leaf height, acceptability of *C. marginatus* was high in seasons when the mean diameter was low, and low when the mean diameter was high (Figure 5.6). The mean diameter of accepted plants was greater than that of rejected plants in winter (Figure 5.6; Z = 3.196; $P < 0.01$) and spring (Z = 2.222; $P < 0.05$), but was the same as that for rejected plants in summer (Z = 0.569; $P > 0.05$), and autumn (Z = 0.455; $P > 0.05$).

For *E. curvula* the mean percentage greenness for accepted plants was higher in autumn than winter, spring and summer (Figure 5.9; H = 11.007; $P < 0.05$), but remained consistent across seasons for rejected plants (H = 3.534; $P < 0.05$).

Accepted and rejected means were the same in winter ($Z = 0.623$; $P > 0.05$), spring ($Z = 1.385$; $P > 0.05$) and summer ($Z = 0.571$; $P > 0.05$), but the mean percentage greenness for accepted plants was higher than for rejected plants in autumn ($Z = 3.539$; $P < 0.001$). There was a significant decline in the available mean percentage greenness in the RBA during the warm summer (Figure 5.10; $H = 97.031$; $P < 0.001$), but out of the RBA, percentage greenness was at a minimum in winter instead ($H = 20.297$; $P < 0.001$). Means for in and out of the RBA were the same during spring ($Z = 1.131$; $P > 0.05$) and autumn ($Z = 0.118$; $P > 0.05$), but the mean percentage greenness was higher in the RBA than out of the RBA during winter ($Z = 7.227$; $P < 0.001$), and lower in the RBA than out of the RBA in summer ($Z = 5.409$; $P < 0.001$).

The mean seasonal leaf height for accepted plants of *E. curvula* was at a minimum in the warm autumn (Figure 5.9; $H = 13.094$; $P < 0.01$), while for rejected plants, means remained consistent (Figure 5.9; $H = 4.421$; $P > 0.05$). The mean leaf height for accepted plants was higher for rejected plants in winter, (Figure 5.9; $Z = 3.468$; $P < 0.001$), summer ($Z = 2.624$; $P < 0.01$) and autumn ($Z = 3.223$; $P < 0.01$), but were the same in spring ($Z = 1.714$; $P > 0.05$). From data collected during the RBA surveys, seasonal mean leaf height in the RBA remained consistent between seasons (Figure 5.11; $H = 5.232$; $P > 0.05$), while seasonal means for data collected out of the RBA were higher in summer than winter, spring and autumn ($H = 10.572$; $P < 0.05$). Levels were consistently lower in the RBA than out of the RBA, during winter ($Z = 4.170$; $P < 0.05$), spring ($Z = 4.199$; $P < 0.05$), summer ($Z = 5.154$; $P < 0.05$), and autumn ($Z = 5.700$; $P < 0.05$).

For accepted plants of *E. curvula*, the mean seasonal diameter differed between seasons (Figure 5.9; $H = 9.192$; $P > 0.05$), but the multiple comparison test did not show significant differences between any particular seasons. The mean diameter for rejected plants was the same across all seasons (Figure 5.9; $H = 5.523$; $P > 0.05$). The mean diameter for accepted plants remained higher than rejected plants in winter, (Figure 5.9; $Z = 2.812$; $P < 0.01$), spring ($Z = 2.077$; $P < 0.05$), summer ($Z = 2.320$; $P < 0.05$) and autumn ($Z = 2.767$; $P < 0.01$).

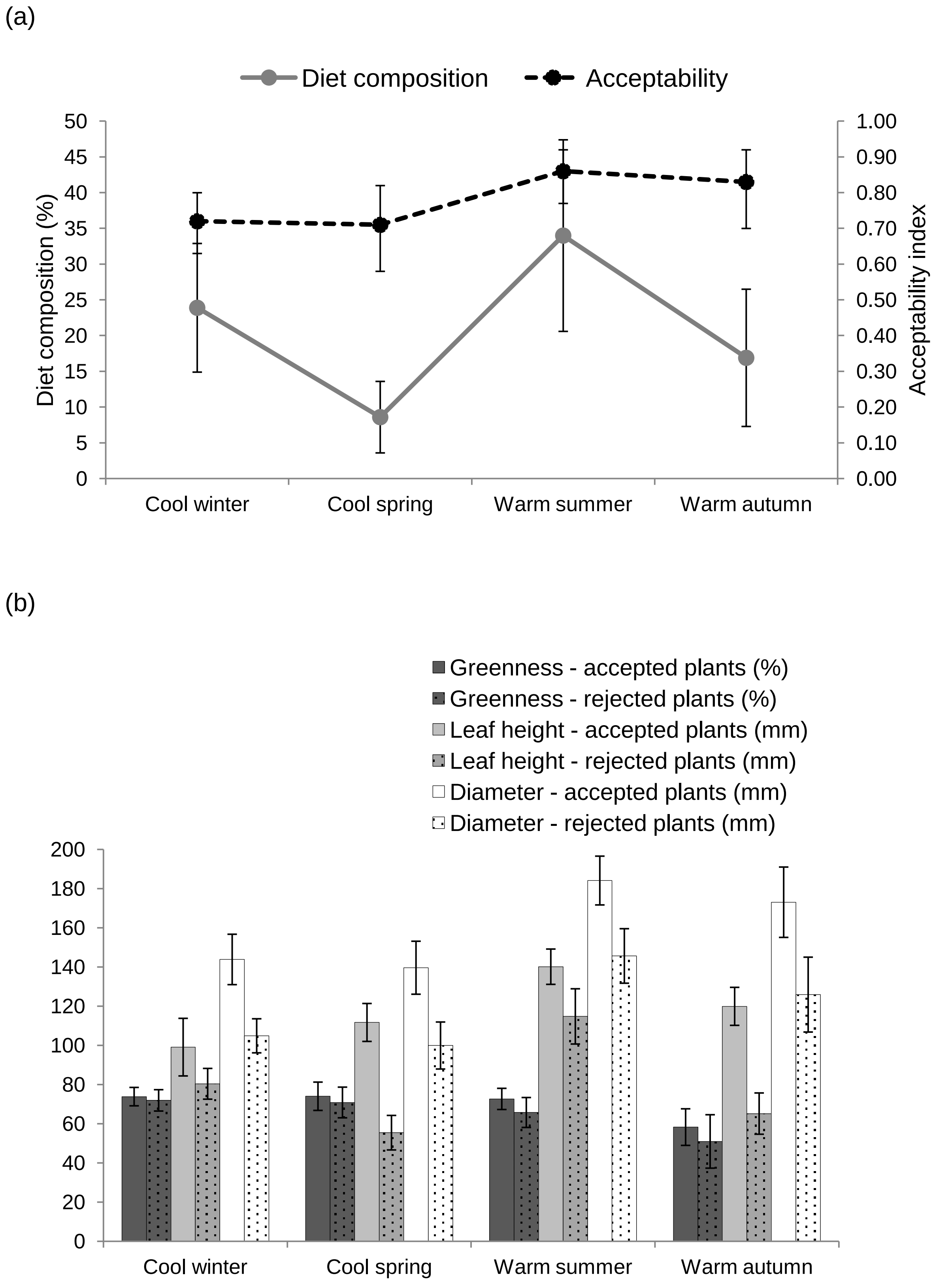


Figure 5.3: (a) Seasonal diet composition and acceptability of *T. triandra* (Chapter 4); (b) Accepted and rejected seasonal mean greenness, leaf height and diameter of *Themeda triandra*.

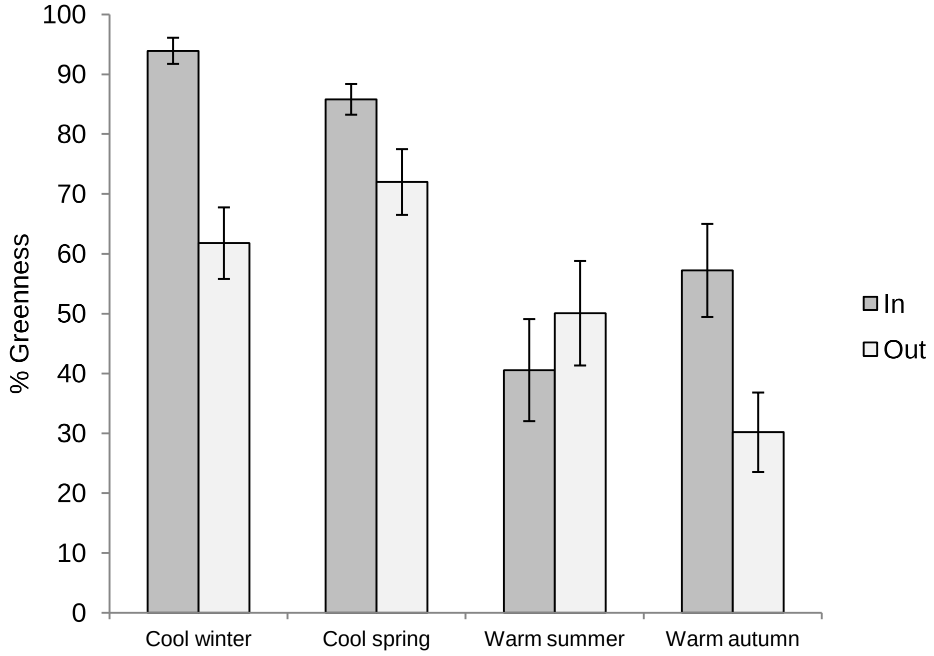


Figure 5.4: Seasonal mean percentage greenness of *T. triandra* in and out of the Recently Burnt Area.

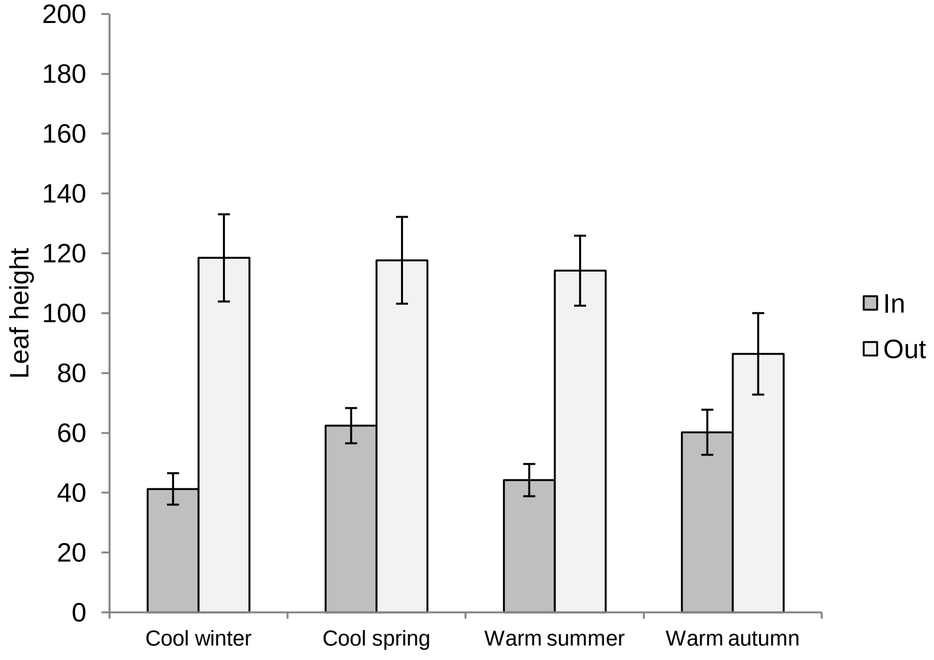


Figure 5.5: Seasonal mean leaf height of *T. triandra* in and out of the Recently Burnt Area.

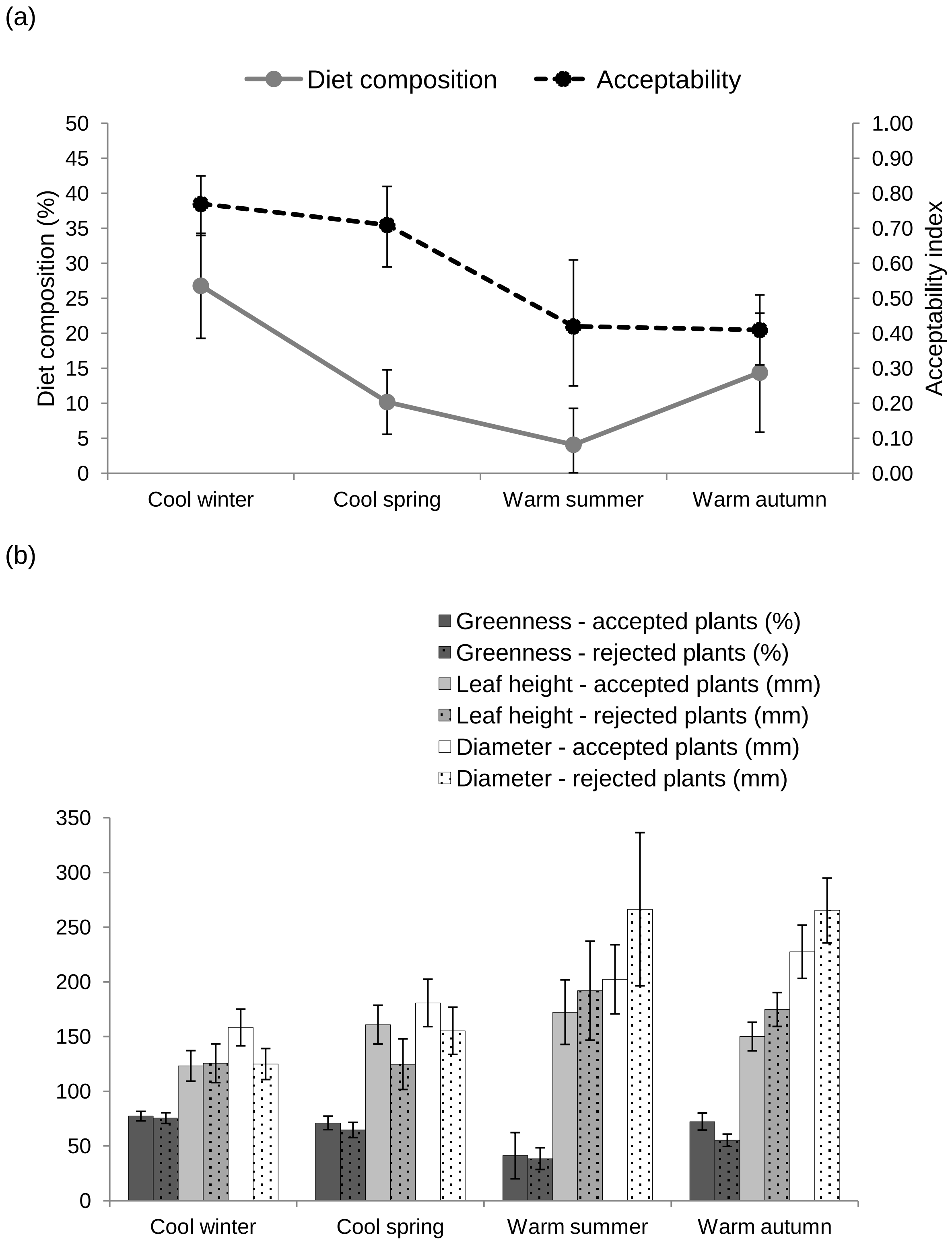


Figure 5.6: (a) Seasonal diet composition and acceptability of *C. marginatus* (Chapter 4); (b) Accepted and rejected seasonal mean greenness, leaf height and diameter of *C. marginatus.*

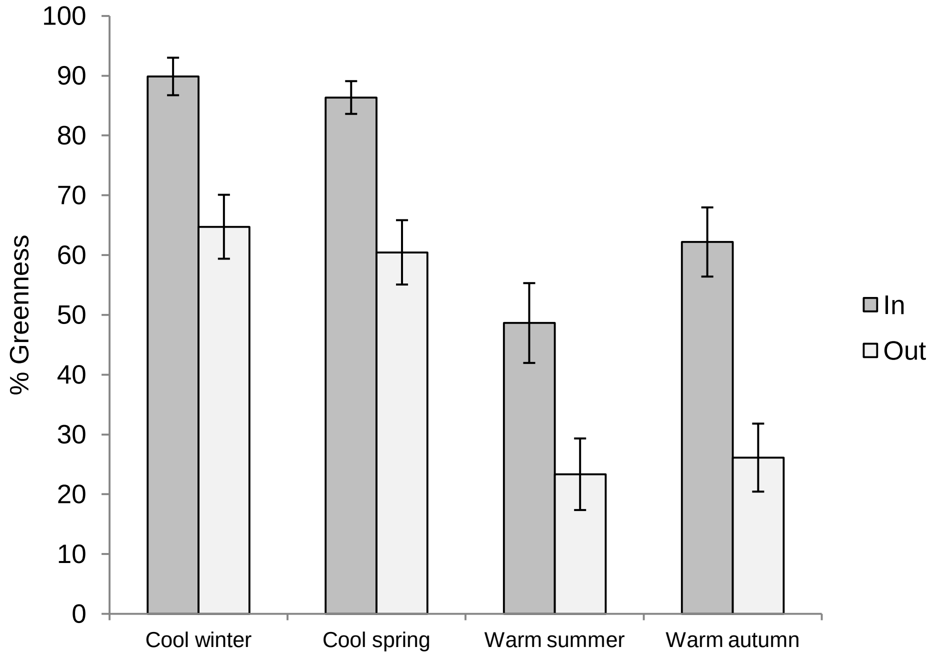


Figure 5.7: Seasonal mean percentage greenness of *C. marginatus* in and out of the Recently Burnt Area.

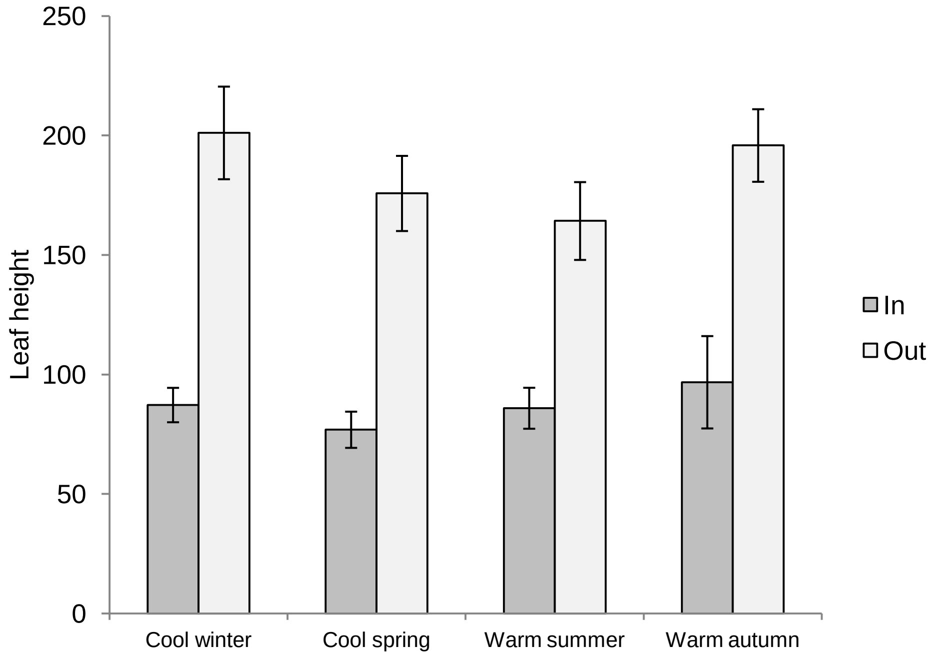
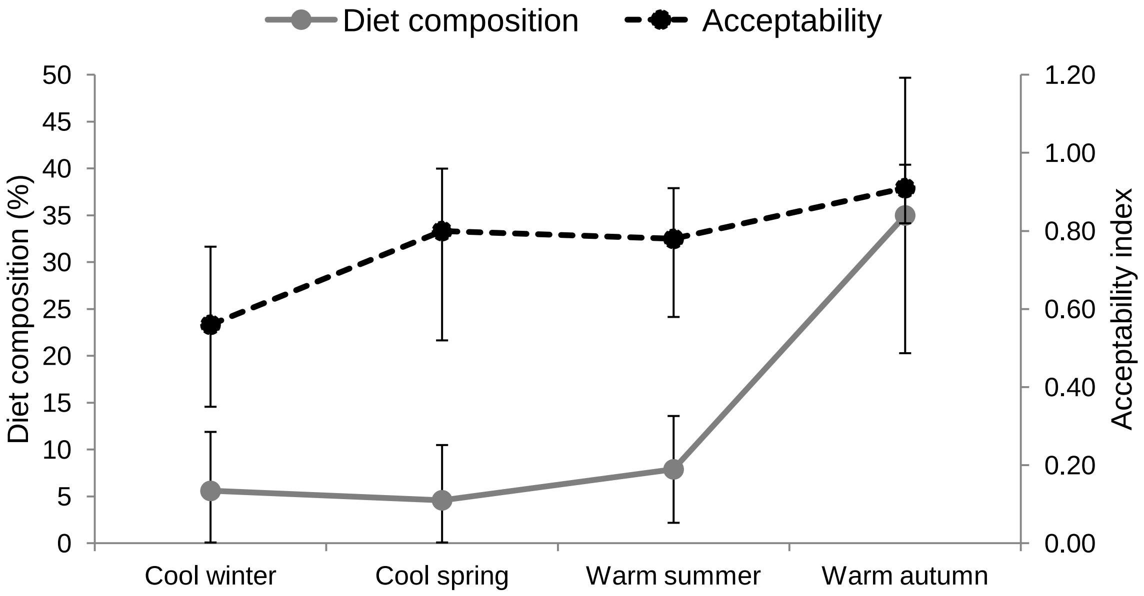


Figure 5.8: Seasonal mean leaf height of *C. marginatus* in and out of the Recently Burnt Area.

(a)



(b)

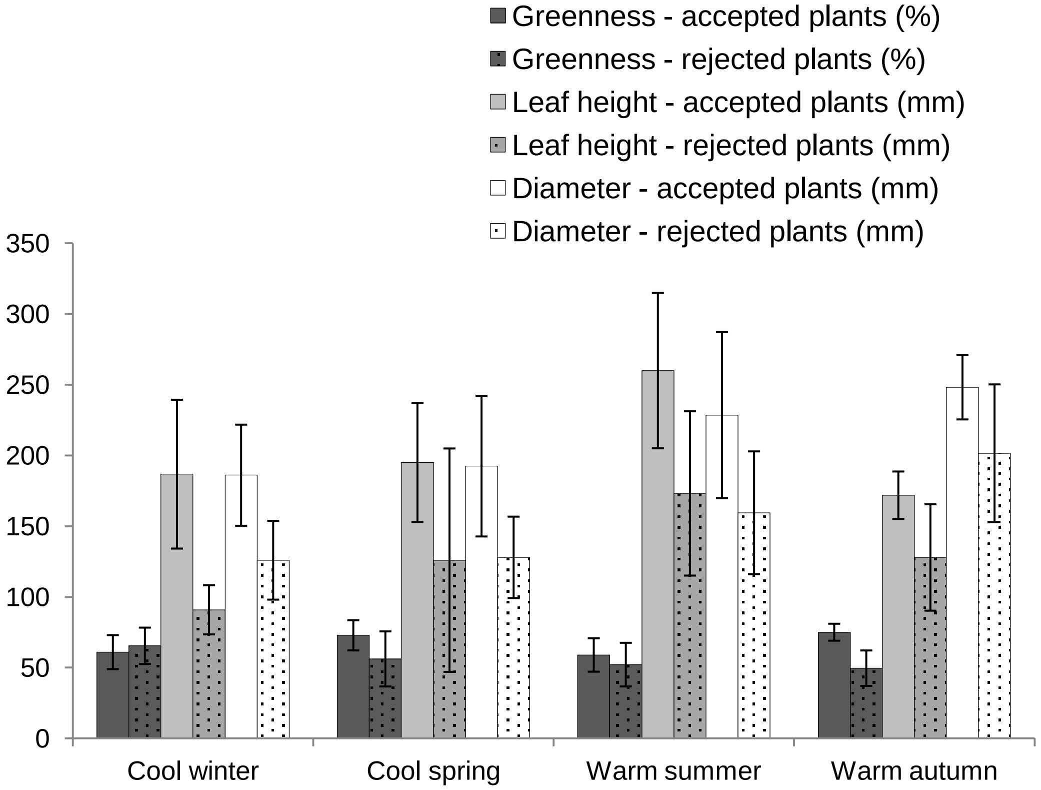


Figure 5.9: (a) Seasonal diet composition and acceptability of *E. curvula* (Chapter 4); (b) Accepted and rejected seasonal mean greenness, leaf height and diameter of *E. curvula.*

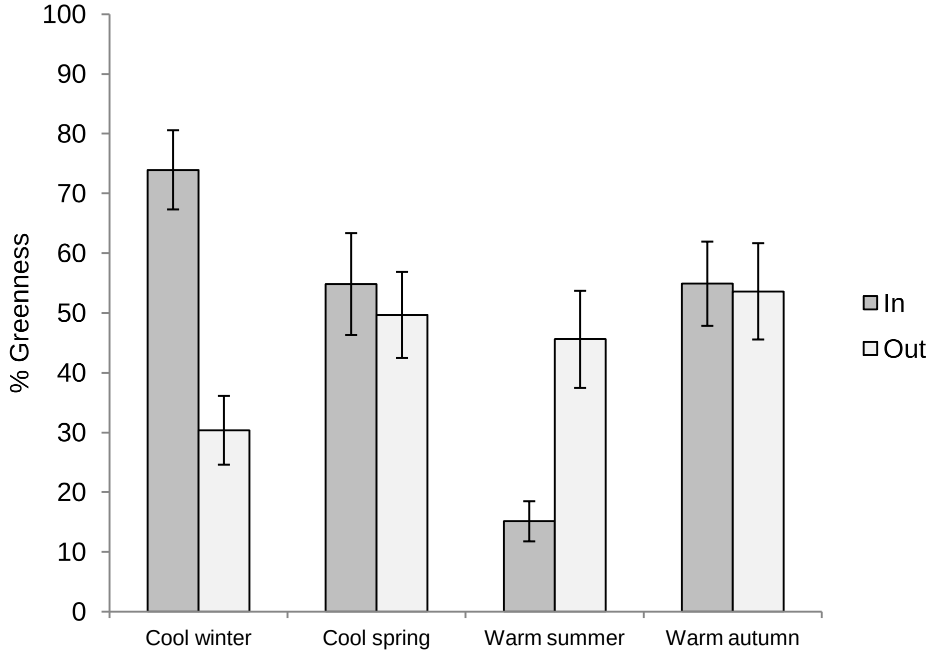


Figure 5.10: Seasonal mean percentage greenness of *E. curvula* in and out of the Recently Burnt Area.

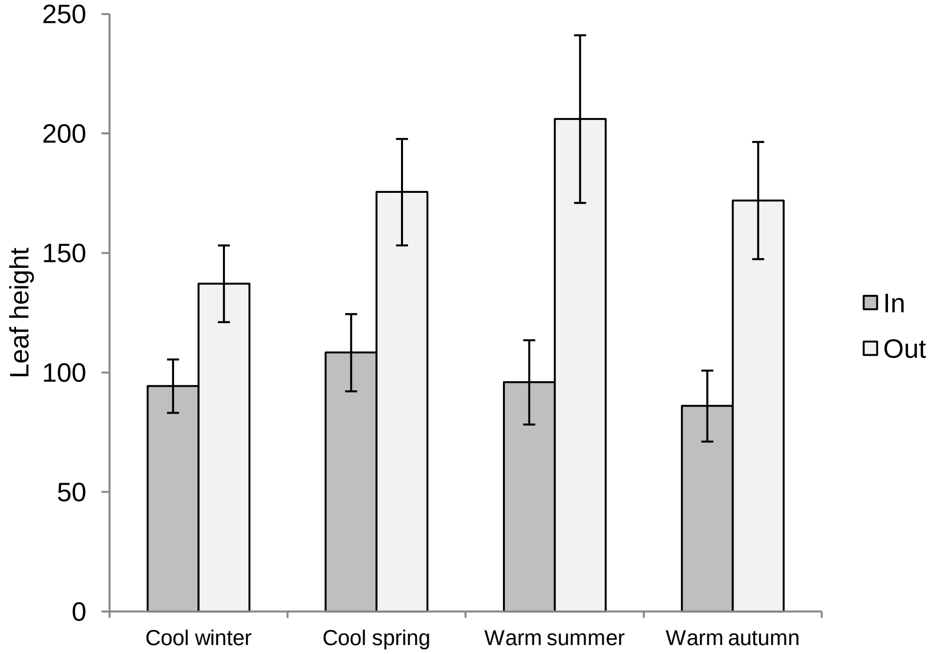


Figure 5.11: Seasonal mean leaf height of *E. curvula* in and out of the Recently Burnt Area.

5.4. DISCUSSION

5.4.1. FACTORS INFLUENCING SELECTION BETWEEN SPECIES

The results of the PCA suggest a strong seasonality in the factors determining mountain zebra grass selection in the BNP. Such seasonality in determining factors has also been detected for mountain zebra in the MZNP (Winkler, 1992), as well as in other dystrophic systems such as DHNR (Smith *et al.*, 2011). The results further emphasise the importance of phenological state (greenness), plant volume (leaf height and diameter) and plant part in grass selection by mountain zebra, suggesting species-specific responses. The findings of this analysis is in line with the findings of other studies, which suggest that forage selection by herbivores occurs as a unique combination of very specific factors for specific species, instead of a single factor applying to all species or to all seasons (Heady, 1964; Owen-Smith, 1982; Owen-Smith, 1988; Winkler, 1992; Venter, 2006).

The cool winter of 2012 was a season with a high number of flushing plants, influenced by the fire in late February 2012, which resulted in percentage greenness being closely related to this season in the PCA, as well as higher greenness levels in the RBA for all three principal grass species. In the same way, grass greenness being negatively related to the warm summer season in the PCA, and both acceptability and greenness of rejected plants of *T. triandra* and *C. marginatus* declining during the warm summer is to be expected, since high temperatures and low rainfall reduces grass greenness (Cowling, 1983; Novellie, 1986; Cowling and Holmes, 1992; Van Wilgen *et al.*, 1994; Cowling and Lombard, 2002; SANParks, Unpublished). This is in alignment with the Summer Nutritional Stress Hypothesis and the inadequate supply of green summer forage associated with the summer drought (Radloff, 2008), an important phenomenon in fynbos ecosystems. During the warm autumn, plant volume, in terms of leaf height and diameter was most influential, and moderately influential in the warm summer. This is supported by work in MZNP which showed plant size (tuft height) to be a factor of great importance in mountain zebra grass selection throughout the year, and especially in the dry seasons (Winkler, 1992). During the warm seasons, mountain zebra were selecting for sites and plants that offered the greatest bulk of grass, which is in line with the high intake needs of zebra (Bell, 1970; Bell, 1971; Janis, 1976; Owen-Smith, 1982; Owen-Smith, 1985; Owen-Smith, 1988; Duncan and Poppi, 2008).

5.4.2. FACTORS INFLUENCING SELECTION WITHIN SPECIES

5.4.2.1. PLANT PART USE

Plant part use played an important role in grass selection by mountain zebra in the BNP. The preference for leaf (annually and in specific seasons) is in accordance with work in other ecosystems, where zebra prefer leaf material to other grass parts (Bell, 1970; Owen-Smith, 1982; Owen-Smith and Novellie, 1982; McNaughton, 1985; Owen-Smith, 1988). Grass leaves also have a higher crude protein concentration than stems (Chapin and Stuart, 1980; Grobler, 1983; Prins and Beekman, 1989). *Equus* spp. do however also utilize grass sheath, stem and culm (Owaga, 1975; Ben-Shahar and Coe, 1992). For mountain zebra, Winkler (1992) found grass leafiness to be an important factor in grass species acceptance, while culms and inflorescences made a significant contribution to the diet during the cool winter months. In the current study, mountain zebra preferred grass leaves, but included culms and inflorescences from specific grasses during the warm summer.

The measurement of percentage leaf and stem use in the current study differs slightly from the assessment of leaf to stem ratio, where stem is sometimes portrayed as a feeding deterrent (Heitkönig and Owen-Smith, 1998). The approach of recording leaf and stem use rather expresses the use of plant parts such as leaf and stem as a particular feeding choice (Heady, 1964). Grass species for which stem and inflorescence was the principal plant part selected (*B. maxima*, *S. zeyheri* and *A. diffusa*), were targeted primarily during the warm summer (see Table 4.2 and Table 4.3). These species were mainly utilized in feeding sites in Drainage Lines and on the edges of the Inland Pans (Table 3.1).

During the current study, the use of inflorescences was recorded based on the structure of the rest of the plant. The height of use and the flowering and seeding parts of the remainder of the plant suggested that this was the part that was targeted, as opposed to the culm only. This same phenomenon is described by

Winkler (1992), who also suggests that the findings of other studies showing a high use of grass stem by zebra (Gwynne and Bell, 1968; Stewart and Stewart, 1970; Owaga, 1975), may also have been due to zebra targeting inflorescences rather than stem alone. Mountain zebra used the inflorescences of *E. curvula* specifically in the winter months in the MZNP (Grobler, 1983). This is supported by other studies, where mountain zebra and horses were found to supplement high volume but low-quality diet with grass flowers and seeds, which provide essential nutrients, especially in seasons where nutrition is inadequate (Ellis and Lawrence, 1980; Winkler, 1992). Mountain zebra in the BNP appear to be supplementing the diet with grass stems and inflorescences in summer, when nutrients are low, a phenomenon which is underlined by the Summer Nutritional Stress Hypothesis (Radloff, 2008).

5.4.2.2. GREENNESS

Research on the importance of greenness in grass selected by grazers suggests that most grass species will be accepted by grazers when in a young, green and growing condition, while the more favourable species are also utilized when mature (Vesey-FitzGerald, 1974; Venter, 2006). This can be explained by the increase in cell wall material over time, which decreases digestibility (Westoby, 1974; Owen-Smith and Novellie, 1982). Green leaves also have a higher crude protein content than green stalk (Prins and Beekman, 1989). In the MZNP, higher protein levels were found in grass that was green, declining by 50% during the dry season (Grobler, 1983).

During the current study, the difference between the seasonal mean percentage greenness of accepted and rejected plants of the three principal species (and for eight other grasses, see Appendix 2) showed that at the feeding site, mountain zebra accepted plants with a greater greenness than plants that were rejected, specifically for *T. triandra* in winter, spring and autumn; for *C. marginatus* in all seasons; and for *E curvula* in winter. From surveys in and out of the Recently Burnt Area, it is clear that there was a significant decline in grass greenness during both the warm seasons, the most pronounced decline being in the warm, dry summer. The effect of seasonality on leaf height was less pronounced than for the greenness of the three principal grasses surveyed, but differences do support the use and avoidance of species like *T. triandra* in the RBA habitat during specific seasons.

For both *T. triandra* and *C. marginatus*, the mean percentage greenness in both the cool seasons were different from the means in both the warm seasons, which is in line with the notion of a summer drought for the region (Nahal, 1981; Cowling, 1992; Raitt, 2005; Radloff, 2008). For all three species, greenness was generally greater in than out of the RBA, except during the drier and warm summer for *T. triandra* and *E. curvula*. The findings support the notion that fynbos plants are greatly influenced by harsh seasonal temperature fluctuations on burnt, un-shaded sites (Van Wilgen *et al.*, 1992). This phenomenon thus explains why there is a significant decline in greenness of *E. curvula* in the RBA during summer, but not out of the RBA, where grass would experience greater shading by taller fynbos shrubs. The decline in greenness for all three species during summer in the RBA also provides evidence for why this habitat was avoided during this season but preferred in all other seasons (Table 3.1). In the same way, the higher greenness in the RBA during winter, spring and autumn, substantiates why mountain zebra frequented the RBA during these seasons.

The annually high acceptability of *T. triandra* appears to be reflected by the consistent and relatively high level of greenness (between 61% and 74%) in feeding sites throughout the year, despite greenness levels in and out of the RBA declining to 40% in the warm seasons. This suggests that for this species, instead of selecting plants of adequate greenness at the feeding site, mountain zebra were selecting sites in which the greenness was favourable. This could be attributed to C4 grasses being better adapted to summer conditions, typically needing high temperatures for photosynthesis, and respiration being more water-use efficient than in C3 grasses (Mooney, 1997; Skarpe and Hester, 2008). Site availability for *T. triandra* was also high at 0.5 annually, the highest for all species (Table 4.3), which suggests that sites with this species were targeted by mountain zebra in the BNP, which peaked in summer (0.65). *T. triandra* was prevalent in certain areas in the park, such as the Drainage Line habitat associated with “Reisiesvlei”, which was targeted by mountain zebra in the warm summer (Table 3.1), but also occurred in association with termitaria in other habitats (Grobler and Marais, 1967; Novellie, 1987). The targeting of *T. triandra* at the feeding site scale is supported by known feeding dynamics for herbivores, where herbivores seasonally return to nutrient-rich patches with a high yield of preferred species (Bailey *et al.*, 1989; Bailey *et al.*, 1996).

Despite the lower greenness during summer for accepted species of *T. triandra, E. curvula*, these species were still preferred during this season (Figure 5.3; Table 4.2). This trend also applies to other preferred grass species *Hyparrhenia hirta* and *Heteropogon contortus* (Appendix 3). In fynbos, this may be explained by these C4, "summer rainfall" grasses typically experiencing their growing season during summer (Cowling, 1983; Pierce and Cowling, 1984; Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999), and consequently increasing their contribution to the diet of mountain zebra during this time. Seasonal use of *T. triandra* was also greater in summer in DHNR (Smith *et al.*, 2011), despite the summer drought conditions in the region (Radloff, 2008). Other herbivores have also been found to frequent lowland sites during the dry seasons, due to the soil moisture retention in these areas, which allows grasses to remain green at these sites (Sinclair, 1977).

Of the grass factors measured, greenness played the most important role in the selection of *C. marginatus* (Figure 5.6). *C. marginatus* is a dominant grass in the BNP (Grobler and Marais, 1967), also known as scented turpentine grass or lemon grass, an aromatic Increaser grass, with a low to medium forage factor, and reported medicinal uses (Watt and Breyer-Brandwijk, 1962; Hutchings, 1989; Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999). By implication, this species would only be acceptable to grazers while in a predominantly green and growing state (Westoby, 1974). In winter specifically, which is also the early rainy season (Cowling, 1983; Novellie, 1986; Van Wilgen *et al.*, 1994; SANParks, Unpublished), and the first season after the recent fire, plants with high greenness like *C. marginatus* were selected by mountain zebra. This consisted of flushing plants found in the RBA, as well as re-sprouting plants in Young Proteoid Fynbos (see Table 3.1).

On an annual basis, *E. curvula* greenness for accepted plants as well as plant volume was important in terms of plant selection within the feeding site. *E. curvula,* is an important grass in other mountain zebra diet studies (Grobler, 1983; Winkler, 1992; Weel *et al.*, 2015) and of high grazing value (Van Oudtshoorn, 1999), but site availability of *E. curvula* was seasonal. On an annual basis, at the feeding site scale, greenness levels of *E. curvula* was important, since the greenness of accepted plants was higher than rejected plants (Appendix 3; $Z = 3.600$; $P < 0.05$). Seasonally, the increase in percentage greenness of accepted plants from 59% in summer to 78% in autumn is in line with the pattern in diet composition for this species (Figure 5.9). In MZNP, *E. curvula* was also found to have higher leaf crude protein in March, which coincides with the autumn season of this study, during which it was most favoured by mountain zebra (Grobler, 1983).

5.4.2.3. LEAF HEIGHT AND DIAMETER

Based on the high intake requirement of zebra (Bell, 1970; Janis, 1976; Owen-Smith, 1982; Owen-Smith, 1988), the importance of leaf height and plant diameter in grass selection by mountain zebra during this study is to be expected. It is also widely accepted that *Equus* species tend to select taller grass than other grazing ungulates, taking their food at between 50 and 150 mm from the ground (Bell, 1970; Penzhorn and Novellie, 1991). Mountain zebra fed at a higher level than other grazers in MZNP, between 40 and 80 mm, and between 310 and 480 mm when selecting seed heads of *E. curvula* in the dry season (Grobler, 1983), or between 60 and 220 mm (Winkler, 1992). In MZNP, an analysis of the grass height of sites frequented by different grazers showed mountain zebra to prefer sites with taller Decreaser grasses, such as *T. triandra* (Novellie, 1990). For *T. triandra* and *E. curvula,* plant volume (leaf height and diameter) was a primary factor in grass selection (Figure 5.3; Figure 5.9). These species were also species with high annual and seasonal preference (see Table 4.2), and were also targeted at the feeding sites (see Table 4.3). These species also had a high acceptability in the MZNP (Winkler, 1992) and a moderate to high acceptability in the BNR (Weel *et al.*, 2015).

From the grass surveys in and out of the RBA, the mean accepted leaf height per species ranged between 56 mm and 311 mm. Leaf height being generally lower in the RBA than out of the RBA for all three the principal species is to be expected, based on the recent fire, and the high level of utilization by mountain zebra and bontebok in this habitat. In terms of habitat use, the preference of the RBA in spring and warm autumn by mountain zebra is supported by the leaf height of the targeted species *T. triandra* being higher in spring and autumn in the RBA.

The decline in the diet composition of *T. triandra* in spring, and the peak in use in the warm summer appear to be more closely related to plant volume (leaf height and diameter) than greenness. This is particularly evident during the warm summer, when the diet composition, acceptability, as well as leaf height and diameter of *T. triandra* were at maximum levels (Figure 5.3). During this season, mountain zebra did not utilize the RBA, and sites with *T. triandra* were frequented in the Young Drainage Lines (Table 3.1). The results suggest that in this habitat, mountain zebra targeted sites with plants of *T. triandra* of adequate volume. Mountain zebra preference for bulk grass is further underlined by both leaf height and diameter being consistently greater for accepted plants than rejected plants in all seasons (Figure 5.3). This shows that, at the feeding site, mountain zebra preferred plants of this species that offered more bulk feed, to plants of lower leaf height and diameter. In the MZNP the mean tuft height of accepted plants was consistent (between 180 mm and 190 mm) for all seasons, acceptability of this species was between 0.9 and 1.0 for all seasons (Winkler, 1992).

Utilization and preference of *C. marginatus* appears to be inversely related to leaf height and diameter (Figure 5.6). Acceptability and diet composition was at a maximum in winter, when leaf height and diameter was at their respective minimum levels (between 125 and 155 mm) for both accepted and rejected plants. Minimum acceptability and diet composition were in the warm seasons, when leaf height and diameter were at maximum levels (> 250 mm). This, and the greenness results suggest that *C. marginatus* is preferred by mountain zebra in a green, flushing state, when leaf height and diameter is low, with preference being low as plant volume increases. An investigation into possible changes in chemical composition that may influence utilization of *C. marginatus* is warranted.

Leaf height and diameter of *E. curvula* does not seem to indicate a clear pattern in terms of acceptability and diet composition of this species (Figure 5.9). There does however, appear to be a general trend of increased leaf height or diameter in the warm seasons, but there is a large degree of overlap in the data, which resulted in the findings not being statistically significant. In the MZNP there also appeared to be a weak correlation between the acceptability of *E. curvula* and greenness, tuft height and leafiness (Winkler, 1992). In the BNP habitat types of the current study, *E. curvula* was utilized along the edges of pans, roads and at specific sites in the RBA and Old Proteiod Fynbos, which suggest a possible opportunistic selection strategy by mountain zebra for this species. Site availability of *E. curvula* did show a sharp increase from low levels in the other seasons to 0.46 in the warm autumn (Table 4.3), which matched the pattern in diet composition of this species (Figure 5.9). This suggests that *E. curvula* is targeted at the site level during the warm autumn specifically. Botanical work on the pasturing performance of *E. curvula* (in sandy soils) suggests this species in particular could have a high yield outside of the most effective rainfall season, (Farrington, 1973). By implication it could be one of the grasses that would be more available when rainfall is lower, especially in the late warm season, which was the season in which it dominated in the diet of mountain zebra during the current study. The general growing season for this species is also indicated as summer to late autumn (FOA, 2014). Importantly, mountain zebra also utilized stems and inflorescences with leaves of *E. curvula* during this season. This overlaps with the flowering season for this species, which starts in summer and peaks in early autumn (Gibbs Russell *et al.*, 1990; Van Oudtshoorn, 1999). In the MZNP, mountain zebra specifically utilized inflorescence of *E. curvula* from May to June (Grobler, 1983), which coincides with the period during which it was preferred in the BNP.

5.5. CONCLUSION

The results of the principal component analysis of factors influencing grass selection by mountain zebra showed that greenness, and percentage leaf use were most important during winter. During spring a combination of factors influenced grass selection, when grass made a low contribution to the diet. During both the warm seasons, a bulk-feeding strategy was used by mountain zebra, targeting species that provide the greatest volume of forage, with an inclusion of grass stems or culms and inflorescences during the warm summer.

Greenness played the most important role in the selection of the aromatic species *C. marginatus*. For the principal and preferred species *T. triandra*, sites with a high greenness were chosen, and volume played the most important role in whether plants were accepted or rejected. For other important species like *E. curvula*, selection at the feeding site was based on a combination of factors, the results showing that both greenness levels and adequate volume were influential. Mountain zebra preferred the leaves of most grass species, using stems and inflorescences mainly from *A. diffusa* and *S. zeyheri*.

CHAPTER 6: NUTRITIONAL STATUS

6.1. INTRODUCTION

The nutritional requirements of ungulates play a vital role in their dietary choices (Penzhorn, 1982b; Grobler, 1983; Bailey *et al.*, 1996), as ungulates prefer habitats where the maximum rate of nutrient intake can be achieved (Owen-Smith, 1985; Melton, 1987b). The low grass cover (Mentis and Tainton, 1984) and low nutritive quality of fynbos habitats of the Cape Floristic Region (Joubert and Stindt, 1979; Goldblatt and Manning, 2002) suggest that feeding opportunities would be limited in this region (Weel *et al.*, 2015), and that adequate quantity and quality habitat is dependent on fire, or access to patches of disturbed, grass-dominated habitat (Watson *et al.*, 2005; Smith *et al.*, 2008).

The range quality of the habitat as a potential limiting factor to ungulate nutritional status can be assessed though soil analysis, grass analyses or faecal nutrient analysis (Holechek *et al.*, 1982a; East, 1984; Mitchell *et al.*, 1984; Novellie *et al.*, 1988; Ben-Shahar and Coe, 1992; Novellie and Bezuidenhout, 1994; Grant *et al.*, 1995; Wrench *et al.*, 1996; Wrench *et al.*, 1997; Grant *et al.*, 2000; De Klerk *et al.*, 2001; Augustine *et al.*, 2003; Novellie and Gaylard, 2013). Determining the current faecal nitrogen and phosphorus content for mountain zebra in the BNP after Grant *et al.* (2000) was considered suitable for this study. Thresholds for detecting nitrogen and phosphorus deficiencies in ungulates are particularly useful in assessing range quality (Moir, 1960; Leslie and Starkey, 1985; Irwin *et al.*, 1993; Wrench *et al.*, 1996; Wrench *et al.*, 1997; Grant *et al.*, 2000). Some criticism exists of the application of this method (Hobbs, 1987), which were refuted by Leslie *et al.* (2008). Nitrogen levels below 13 g/kg indicate dietary deficiency which could speed up nutritional stress in grazers (Grant *et al.*, 2000). In turn, faecal phosphorous levels of ≤ 2.0 g/kg over extended time periods have been linked to low reproductive success (Grant *et al.*, 2000). The data gathered during this study in the BNP could be evaluated based on known thresholds, but also compared to the nutrient status of mountain zebra in other fynbos ecosystems. For this purpose faecal samples were also collected from DHNR. Suitable habitat in DHNR has shown to be limited, as mountain zebra focussed on transformed areas (Radloff, 2008; Smith *et al.*, 2008). The mean annual rate of population increase of mountain zebra in DHNR has also shown a decline, from 6.6% between 1990 and 1995 to 4.5% between 1995 and 2008 (Radloff, 2008; Smith *et al.*, 2008).

The objective of this Chapter's analysis was to determine the seasonal nutritional status of mountain zebra in the dystrophic ecosystem of the BNP and DHNR, through analysing the concentration of nitrogen and phosphorus in the faeces of the study animals.

6.2. METHODS

6.2.1. STUDY SITE

For the study site description, refer to Chapter 2.

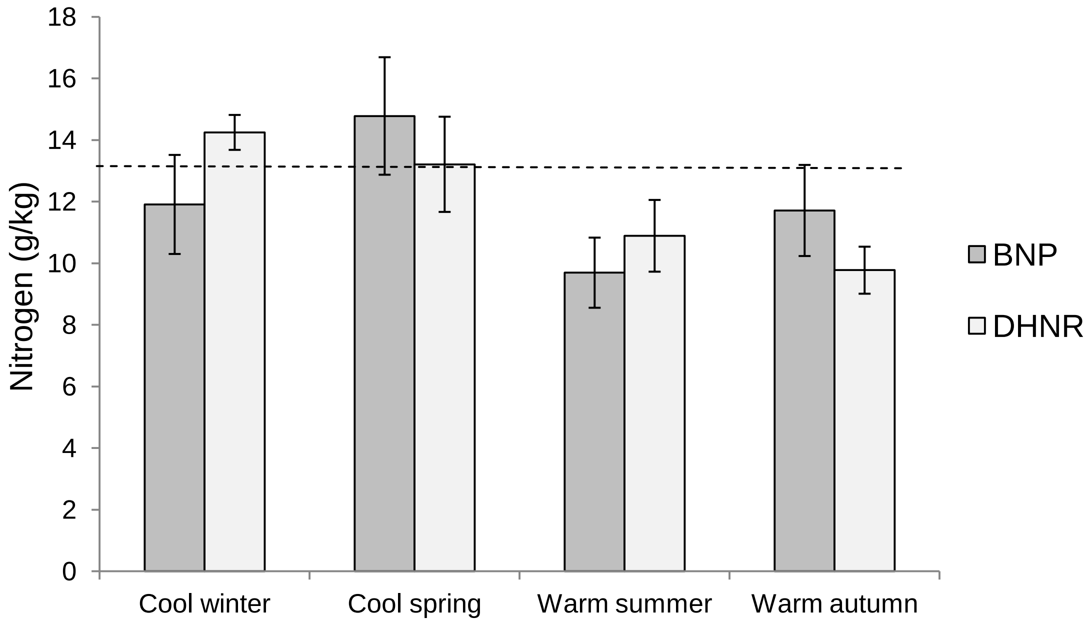
6.2.2. NUTRITIONAL STATUS

Faecal samples were collected from dung piles near feeding sites throughout the 12 month study period in the BNP, and during one day per season in DHNR. Two to five subsamples were collected from separate dung piles, which were combined to constitute a single sample, stored in brown paper bags and air-dried for nutrient analysis. A total of 51 samples were collected in the BNP, on average 13 per season, and 44 in DHNR, on average 11 per season. The dried faecal samples were milled and analysed for nitrogen and phosphorus content by Nutrilab, University of Pretoria. For nitrogen, the Kjeldahl method was used, which measures total organic nitrogen through digestion with hot concentrated sulphuric acid, after which a catalyst mixture is added to the acid to raise the boiling point (Kjeldahl, 1883). All nitrogen is converted to ammonia, which is measured by titration (AOAC, 2000a). The phosphorus content was determined using colourometric determination with ammonium molybdovanadate (AOAC, 2000b). Since the data were non-parametric, for each reserve, to assess whether the seasonal mean nitrogen levels were the same, the Kruskall-Wallis and multiple comparisons by mean ranks tests were used (Zar, 1996). For each season, the Mann-Whitney test was used to test if the mean nitrogen levels were the same between the BNP and DHNR (Zar, 1996). The same analyses were used to compare the seasonal mean phosphorus levels.

6.3. RESULTS

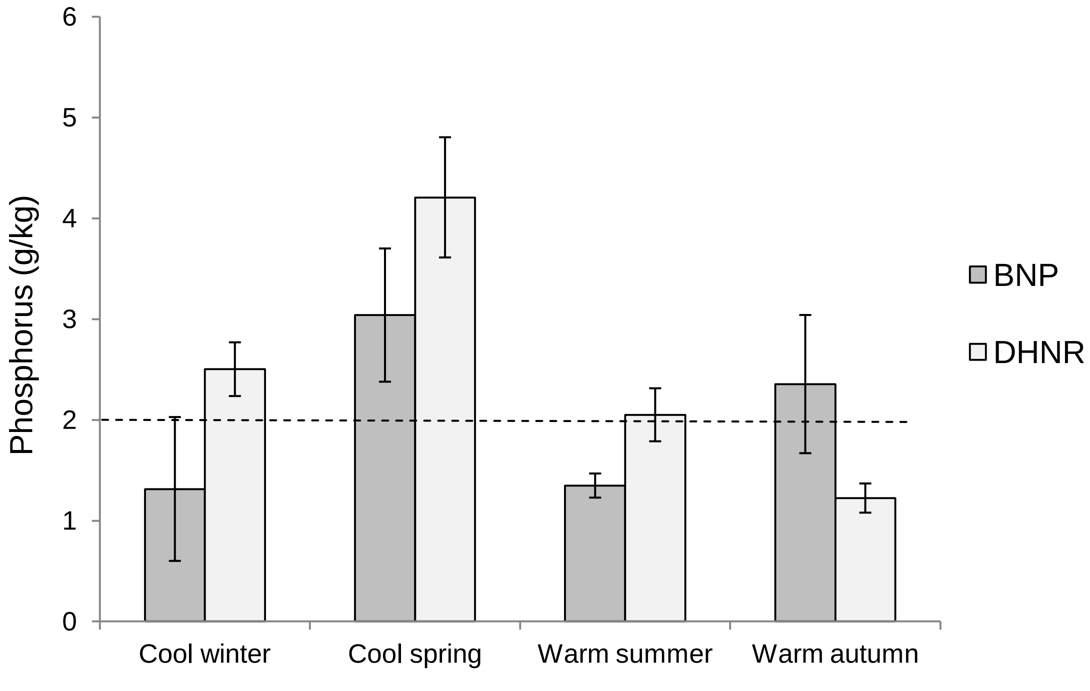
Faecal nitrogen from BNP was lower than that of the DHNR population during winter (Figure 6.1; $Z = 2.089$; $P < 0.05$), but greater than that of the DHNR during autumn ($Z = 2.298$; $P < 0.05$), with no difference during spring ($Z = 0.836$; $P > 0.05$) and warm summer ($Z = 1.671$; $P > 0.05$). The seasonal mean faecal nitrogen for BNP (Figure 6.1; $H = 11.720$; $P < 0.05$) and DHNR ($H = 14.291$; $P < 0.05$) varied significantly between seasons. The maximum seasonal mean faecal nitrogen levels for both reserves were in the cool seasons, for BNP in the cool spring, and for DHNR in the cool winter. The minimum seasonal mean faecal nitrogen for both reserves were in the warm seasons, for BNP in the warm summer, and for DHNR in the warm autumn. Seasonal mean nitrogen levels were below the threshold for nutritional deficiency (13 g/kg) in all seasons, except for the cool spring in BNP and the cool winter and spring in DHNR.

The mean faecal phosphorus levels did not differ between BNP and DHNR during winter, but was near significantly lower in BNP than DHNR (Figure 6.2; $Z = 1.671$; $P = 0.06$). The mean for BNP was lower than for DHNR during spring ($Z = 2.089$; $P < 0.05$) and summer ($Z = 2.507$; $P < 0.05$), but did not differ significantly in autumn ($Z = 1.671$; $P = 0.09$). The mean faecal phosphorus for BNP (Figure 6.2; $H = 11.160$; $P < 0.05$) and DHNR ($H = 17.103$; $P < 0.05$) also varied significantly between seasons. Maximum seasonal mean faecal phosphorus levels were in spring for both BNP and DHNR. Faecal phosphorus levels reached minimum levels for BNP in winter (1.31 g/kg) and summer (1.34 g/kg), and for DHNR during the warm autumn (1.22 g/kg). The seasonal mean phosphorus levels were below the threshold for nutritional deficiency (2.0 g/kg) in both winter and summer for BNP, and in autumn in DHNR, with levels above the threshold for both parks in the other seasons.



- - - - Dashed line indicates the threshold for nitrogen deficiency (13 g/kg)

Figure 6.1: Annual and seasonal mean faecal nitrogen levels with 95% confidence limits for mountain zebra in the BNP and the DHNR.



- - - - Dashed line indicates the threshold for phosphorus deficiency (2.0 g/kg)

Figure 6.2: Annual and seasonal mean faecal phosphorus levels with 95% confidence limits for mountain zebra in the BNP and the DHNR.

6.4. DISCUSSION

The soils associated with the fynbos of the CFR are dystrophic and particularly lacking in nutrients such as nitrogen and phosphorus (Kruger *et al.*, 1983; Specht and Moll, 1983; Mitchell *et al.*, 1984; Campbell, 1986). This poses nutritional challenges to herbivores in the ecosystem. Faecal nitrogen sustained below 13.0 g/kg in the diet of herbivores such as wildebeest, zebra, cattle and impala leads to poor body condition, while phosphorus levels sustained below the 1.9 to 2.0 g/kg level over time will result in reduced reproductive success (Moir, 1966; Grant *et al.*, 1995; Wrench *et al.*, 1997; Grant *et al.*, 2000).

Fynbos plants also show seasonal fluctuations in nitrogen and phosphorus content, caused by the specific climatic conditions, such as low winter temperatures and summer drought (Lamont, 1983; Mitchell *et al.*, 1986). The cool winter and cool spring seems to provide marginally improved nutrient levels, due to the good rainfall during these seasons (SANParks, Unpublished). The minimum nitrogen and phosphorus levels in the dung of mountain zebra in both the BNP and DHNR during the summer months of this study, are in line with the Summer Nutritional Stress Hypothesis of Radloff (2008). During summer, daily maximum temperatures, low rainfall and senescence in certain grass species are hypothesized to cause heat and feeding stress in ungulates (Radloff, 2008). This is in line with the findings in Chapter 5, where the decline in greenness levels suggests grass senescence in summer in the BNP. This was evident from greenness levels recorded in feeding sites for *C. marginatus* and in grass surveys in and out of the Recently Burnt Area (RBA) habitat for all three principal grass species (in and out of the RBA for *T. triandra* and *C. marginatus*, and in the RBA only for *E. curvula*). The results of the analysis of both faecal nitrogen and phosphorus in the BNP support this hypothesis, in that levels of both nutrients decreased significantly in the warm summer, and were also low in the warm autumn season.

Based on faecal nitrogen, the findings of this study suggest nitrogen deficiency in the mountain zebra of the BNP in all seasons except spring. This population has also suffered poor body condition and disease to date (Sasidharan, 2006; Marais *et al.*, 2007; Nel, 2007; Sasidharan *et al.*, 2011) and poor population growth (Lloyd and

Rasa, 1989; Novellie *et al.*, 2002; Kraaij and Novellie, 2010; Kraaij *et al.*, 2011; Watson *et al.*, 2011). The mean nitrogen levels for the mountain zebra of DHNR were also below the threshold in both the warm seasons. This supports recent work in the DHNR on mountain zebra, suggesting resource limitations (Smith *et al.*, 2011) and a decline in population growth in recent years (Smith *et al.*, 2008). Environmental conditions in fynbos have been shown to be optimal for nitrification during spring (Schaefer, 1973). Nutritional analysis of fynbos soils in the Malmesbury district (Stock and Lewis, 1986) showed maximum soil nitrate concentrations in both burnt and un-burnt fynbos sites from March to August (winter and spring for this study), and lowest levels in summer. A study near Cape Agulhas showed similar trends for results on sandstone soils dominated by Proteoid vegetation (Richards *et al.*, 1997). Though ammonium was high throughout the year, nitrates were at higher levels from April to August, which coincides with the winter and spring season of the current study, and lower from October to March, which corresponds with summer and autumn for the current study (Richards *et al.*, 1997). Another contributing factor to the high faecal nitrogen in spring could be the diversity of plant species of different life forms included the diet of mountain zebra in spring. In spring mountain zebra utilized 89% of the total number of identified plant species, as opposed to between 43% and 69% in other seasons (Table 4.1; Appendix 1). Restio species, which formed a large proportion of the diet in spring (see Table 4.1), also have maximum nitrogen levels in the photosynthetic culms during spring (Stock *et al.*, 1987).

The poor population growth of mountain zebra in the BNP (Lloyd and Rasa, 1989; Novellie *et al.*, 2002; Kraaij *et al.*, 2011) is likely to be related to the low level of phosphorus apparent in the results of the faecal analysis for BNP. Although levels were above the threshold in two of the four seasons, if seasonal deficiency persists in the long-term, due to a lack of phosphorus in the ecosystem, reproductive success would be impaired (Grant *et al.*, 2000). Population growth of mountain zebra has also been poor in GMNR and the KNR, which has been linked to poor habitat quality and the nutrient-poor status of these ecosystems (Watson *et al.*, 2005; Watson and Chadwick, 2007). Other studies in protected areas with nutrient-poor soils in the former range of mountain zebra (such as Baviaanskloof Wilderness Area, the Zuurberg section of the Addo Elephant National Park) also showed poor population growth (Novellie *et al.*, 2002). A recent study in another dystrophic fynbos ecosystem, the Baviaanskloof Nature Reserve, found both faecal nitrogen and phosphorus levels for mountain zebra to be below the respective thresholds for deficiency in all seasons (Weel *et al.*, 2015). Soil phosphorus in coastal fynbos of the Southern Cape showed seasonal peaks in spring and autumn, (Mitchell *et al.*, 1984; Richards *et al.*, 1997), which coincided with seasonal peaks in mountain zebra faecal phosphorus for BNP during the current study. The Cape Agulhas study showed an additional peak in soil phosphorus in December (Richards *et al.*, 1997). However, phosphorus absorption by plant roots is better in high moisture conditions (Stout and Hoagland, 1939; Barber *et al.*, 1963; Ho *et al.*, 2004), and thus plants and herbivores would not be able to utilize higher levels of phosphorus (such as a peak in phosphorus in December) as readily in the dry summer (Stock and Lewis, 1986; Radloff, 2008) as in other cool, wet seasons.

The influence of fire also needs to be taken into account, as mountain zebra concentrated in the Recently Burnt Areas in the BNP, especially in spring and autumn, when the observed frequency of use of this habitat were > 40% (Table 3.1). Fire increases the nutrient load in the topsoil and stimulates the growth of grass and legumes, which fix nitrogen in the soil (Cowling, 1992; Bond and Wilgen, 1996). However, this phenomenon may be short-lived, lasting up to a year (Boerner, 1982; Stock and Lewis, 1986; Shackleton and Mentis, 1992; Van de Vijver *et al.*, 1999; Wan *et al.*, 2001). There is an immediate increase in soil phosphorus availability following fire (Boerner, 1982; Van de Vijver *et al.*, 1999), though an increase in phosphorus through burning is less pronounced than in other nutrients (Van de Vijver *et al.*, 1999). Phosphorus has a higher temperature tolerance (> 500°) with less phosphorus being lost during a fire (Boerner, 1982). Thus the high use of the Recently Burnt Area in spring and autumn as opposed to its avoidance in summer, may have played a role in both faecal nitrogen and phosphorus being greatest in spring, and slightly greater in autumn than in summer (though the latter was not statistically significant according to the multiple comparison analysis).

6.5. CONCLUSION

The BNP and DHNR mountain zebra populations appear to be limited by the availability of both dietary nitrogen and phosphorus in the ecosystem, based on known thresholds for herbivore body condition and reproductive success. Seasonal fluctuations in faecal nitrogen and phosphorus follow similar trends in the two protected areas. Both populations seem to be experiencing the most intensive limitations in the warm summer and warm autumn seasons, supported by the Summer Nutritional Stress Hypothesis. Long-term monitoring of the condition and population growth of mountain zebra in the BNP through regular seasonal and annual faecal analysis is recommended. Sustainable management of the preferred habitats for mountain zebra is also recommended, with particular focus on burning regimes that promote both plant and animal conservation in the system.

CHAPTER 7: STUDY CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

7.1. INTRODUCTION

Resources available to herbivores vary in space and time, and are selected by herbivores at various scales (Johnson, 1980; Bailey *et al.*, 1996). Spatial scales of selection range from the landscape scale, to the habitat or plant community and feeding site, where plant growth form, plant species and plant part selection occurs (Senft *et al.*, 1987; Bailey *et al.*, 1996). The selection level is also a function of herbivore body size and foraging strategy (Johnson, 1980), and influenced by the suitability of the habitat and abundance of associated forage (Westoby, 1974; Johnson, 1980; Novellie, 1994; Grange and Duncan, 2006). Particularly in the dystrophic habitats of Cape fynbos, the relationship between large herbivores and their available food resource is complex and requires informed management decision making (Morrow *et al.*, 1983; Novellie, 1986; Novellie, 1987; Novellie, 1990; Johnson, 1992; Boshoff *et al.*, 2001; Watson *et al.*, 2005; Watson and Chadwick, 2007; Radloff, 2008; Kraaij and Novellie, 2010; Smith *et al.*, 2011; Watson *et al.*, 2011; Weel *et al.*, 2015). The findings of this study suggest that in the BNP, mountain zebra are selective at various levels in this hierarchical selection process: in terms of habitat preference, site selection, plant growth form and plant species, which is also shown to be dependent on plant part availability, phenology and bulk supply.

The 50% Kernel analysis showed that specific sections of the park area were used on a seasonal basis, 19% of the park area was used during winter, 8% during spring, 11% during summer and 6% during the warm autumn. The annual and seasonal habitat selection analysis of this study showed that mountain zebra were targeting specific habitats with suitable forage in the BNP. Mountain zebra preferred Young Proteoid Fynbos in the cool winter, and the Recently Burnt Area in all seasons except the warm summer, when they favoured Young Drainage Lines and Inland Pan areas. The Young Proteoid Fynbos is associated with Enon Conglomerate soils, which have marginally better soil moisture holding capacity and better nutrients than other fynbos soils (DWAF, 2004; Norman and Whitfield, 2006; Vlok and De Villiers, 2007), which may explain why this habitat type is preferred by mountain zebra in the BNP. Preference of the Recently Burnt Area is to be expected, given the increase in soil nutrient availability after fire (Van Wilgen and Le Maitre, 1981; Kruger *et al.*, 1983; Mentis and Tainton, 1984; Van Wilgen *et al.*, 1994), and findings from other studies (Grunow, 1980; Wilsey, 1996; Watson *et al.*, 2005; Watson and Chadwick, 2007; Kraaij and Novellie, 2010; Watson *et al.*, 2011). The preference of the Drainage Lines and pan fringes in summer are in line with the Summer Nutritional Stress Hypothesis of Radloff (2008), showing that drought conditions in the Southern Cape lowlands pose specific challenges for herbivores in these ecosystems (Stock *et al.*, 1992). Drainage Lines and Inland Pans, and also appear to be offering resources to mountain zebra in times of nutritional stress, caused by harsh environmental conditions, and may also have better soil moisture and nutrient regimes, which needs to be investigated specifically. The avoidance of habitat with a veld age greater than five years is in agreement with other work in the BNP (Kraaij and Novellie, 2010; Watson *et al.*, 2011). Habitat types older than five years also scored low in terms of habitat suitability (HSI < 10.0). Young and Old Asteraceous Fynbos were avoided and also do not constitute suitable habitat for mountain zebra in terms of habitat suitability (HSI < 5.0). This is in line with the classification of Swellendam Silcrete Fynbos, which states that although elements of both fynbos and renosterveld are present, this type cannot be characterised as “true renosterveld”, which is supported by more nutrient-rich soils (Low and Rebelo, 1996). The findings also showed that very specific sites were targeted by mountain zebra within habitat types, and used sites proved to have higher habitat suitability than unused sites.

Diet composition and preference analyses confirmed that the mountain zebra diet in BNP consisted mostly of grass species, although other graminoids (restios and sedges) and geophytes were also utilized, particularly in the cool spring. Three grass species, *T. triandra, C. marginatus* and *E. curvula* formed the bulk of the diet, and seasonal dietary shifts between these species occurred. *T. triandra* made the greatest contribution to the annual diet (20.9%), and was also the most consistently preferred of all species across seasons (seasonal ai ranging between 0.72 and 0.86), targeted at feeding sites across all seasons (seasonal s_i ranging between 0.35 and 0.65), and contributing its maximum proportion to the diet in the warm summer

(34.0%). The high utilization of *T. triandra* in summer corresponds with the greater leaf height and diameter in this season, as well as the summer growth season characteristic for this C4 grass (Pierce and Cowling, 1984). The preference and utilization of *C. marginatus* peaked in the cool winter (diet composition = 26.8%; *ai* = 0.77), when in flush after the fire, and when leaf greenness was high (see Chapter 5). Utilization of *C. marginatus* declined in summer and autumn when preference was intermediate (*ai* = 0.41 and 0.42 respectively). This trend coincided with a decline in greenness, but was inversely related to plant volume, preference increasing as leaf height and diameter increased. *E. curvula* became the dominant grass in the diet in the warm autumn (diet composition = 35.0%; *ai* = 0.91), and was of low diet composition in the other seasons (ps_i < 8%) though acceptability remained high (*ai* > 0.5). The marginal increase in summer and peak in utilization and preference in autumn, corresponds with the summer and autumn growth season of this C4 species, as well as the seasonal utilization of this species in other studies (Grobler, 1983; Pierce and Cowling, 1984; FOA, 2014). The seasonal shift in diet composition, preference and site availability of principal species suggests that mountain zebra feeding strategies are season-specific in the BNP.

In terms of the factors that influence the selection of grass species, mountain zebra preferred leaves to other plant parts, but stems and inflorescences were used from restios and sedges in the cool spring, and from specific grass species (*S. zeyheri, A. diffusa* and *B. maxima*) in the warm summer (see Chapter 5), and bulbs of *Moraea collina* were used in the warm autumn (see Chapter 4). Percentage greenness and percentage leaf use were the most important factors influencing grass selection during the cool winter, while a combination of greenness and percentage stem use influenced grass selection during the cool spring. During the warm summer and autumn seasons, mountain zebra appeared to focus on species that provided the greatest quantity of forage, measured as leaf height and diameter during this study. For the selection of the aromatic species *C. marginatus*, percentage greenness was the most important factor, and flushing plants of lesser volume were preferred. For *T. triandra*, mountain zebra selected sites where greenness levels in this species were high, and both leaf height and plant diameter played an important role in whether plants were accepted and rejected at the feeding site. Selection of *E. curvula* was related to both greenness and plant volume. These trends in seasonal acceptance according to the measured forage selection factors are in line with other work on the diet of mountain zebra (Grobler, 1983; Winkler, 1992; Smith *et al.*, 2011; Weel *et al.*, 2015).

In terms of ungulate nutritional status (Grant *et al.*, 2000), the mountain zebra populations of both the BNP and DHNR appear deficient in dietary nitrogen (< 12 g/kg) and phosphorus (< 2 g/kg). Deficiencies were greatest in the warm summer and autumn seasons. This is supported by the Summer Nutritional Stress Hypothesis, which suggests that ungulates in fynbos are limited by the low availability of sufficient quantity C4 grasses, caused by the harsh climatic conditions in summer (Radloff, 2008). Faecal nitrogen in the BNP only reached levels above the threshold for deficiency during the cool spring, and phosphorus during spring and autumn. During these two seasons the diet was supplemented with species from other growth forms (see Chapter 3), and the Recently Burnt Area habitat was used most frequently (> 40% of observations).

7.2. MANAGEMENT IMPLICATIONS

In the past, non-ruminant grazers like zebra were considered to be generalist feeders, linked to the high daily intake rate of fibrous material (Bell, 1970; Bell, 1971; Westoby, 1974; Janis, 1976; Ben-Shahar, 1991). However, recent work suggests that due to the lower gut retention rate of non-ruminants, the need for a high intake can be a limiting factor (Duncan *et al.*, 1990; Illius and Gordon, 1992), requiring non-ruminants to feed selectively to meet their nutritional and bulk forage requirements, especially in poor habitat (Duncan *et al.*, 1990; Illius and Gordon, 1992). For grazers, the concentration of nutrients and minerals is a principal determining factor in forage quality (Searle and Shipley, 2008). Nutrient concentrations also vary spatially, which drives the diet and movement strategies of ungulate grazers (Owen-Smith and Novellie, 1982; McNaughton, 1988; McNaughton, 1990). Grasses vary greatly in the nutritional gain provided to grazers, depending on habitat quality, which predisposes grazers to feed selectively (Fryxell, 1991; Searle and Shipley, 2008). Small herbivore populations aggregate in common feeding areas instead of exploiting the entire available habitat, especially in poor quality habitat (Fryxell, 1991). This is supported by more recent work in the BNR, where mountain zebra appear to have limited foraging opportunities (Weel *et al.*, 2015). The current study in the BNP corroborates the recent view, showing that mountain zebra are using a selective movement and feeding strategy, by using selected proportions of the park seasonally, selecting specific habitats in the park, and preferring certain sites with high *HSI* scores within each habitat type (Chapter 3). Furthermore, mountain zebra were selective in terms of seasonal utilization and preference of species in relation to availability in the environment, and targeted specific species seasonally (Chapter 4). Since mountain zebra are so selective in the BNP, a detailed management strategy of this population in such a small dystrophic ecosystem is required.

In terms of habitat management, the habitat types preferred by mountain zebra during this study can specifically inform management decision making in terms of veld condition monitoring and fire regimes, (Novellie, 1987; Kraaij and Novellie, 2010; Watson *et al.*, 2011). Personal observation during this study supports the notion that mountain zebra and bontebok are competing for young fynbos habitat in the BNP, as suggested by other work (Luyt, 2005; Kraaij and Novellie, 2010; Watson *et al.*, 2011), and thus sustainable management of grazer populations in the BNP is essential. The number of ruminants and non-ruminants, as well as veld condition thus needs to be monitored regularly (SANParks, 2008), to avoid overgrazing (Cowling and Bond, 1991; Coetzee, 2002; Kraaij and Novellie, 2010; Curtis, 2013). In the past, the BNP mountain zebra population increased when bontebok numbers were reduced (Watson *et al.*, 2011). In the period during which the data for this study was collected, the number of bontebok was in excess of 230 animals (SANParks, 2014). Subsequently the bontebok numbers have been significantly reduced, which would theoretically moderate the anticipated inter-specific competition between grazers, and ease grazing pressure on the vegetation. In the management of small parks, some of the literature suggests that animal numbers need to be managed more proactively (Novellie and Gaylard, 2013) than only through a monitoring approach (Bradshaw and Borchers, 2000; du Toit, 2003; Van Wilgen and Biggs, 2011). Due to the small size of the BNP, and the high number of rare and endangered plant and animal species in the BNP (Kraaij, 2011; Kraaij *et al.*, 2011), an integrated approach of a combination of an adaptive management strategy and a strategy based on thresholds for ungulate numbers, is recommended (Stalmans *et al.*, 2001). A continuous monitoring approach will provide data by which to inform management decision making (Bradshaw and Borchers, 2000; Yoccoz *et al.*, 2001), while management of animal numbers at a stocking rate below thresholds of potential concern in this small park (Lande, 1987; Novellie and Kraaij, 2010; Kraaij, 2012; Novellie and Gaylard, 2013), will prevent overgrazing or an increase in the extent of grazing lawns (Kraaij *et al.*, 2008; Kraaij, 2010; Watson *et al.*, 2011; Novellie and Gaylard, 2013) or a significant decline in game health as has been observed in BNP in the past (Sasidharan, 2006; Marais *et al.*, 2007; Nel, 2007; Kraaij *et al.*, 2011; Sasidharan *et al.*, 2011).

It is imperative that the fire management program promotes biodiversity (Kraaij, 2010; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Kraaij *et al.*, 2011). The intermediate disturbance hypothesis (Connell, 1978) suggests that intermediate disturbance levels promote species diversity and species co-existence. The fire regime of the BNP was revised in 2004, when the management objective of frequent burning was revised and brought in line with promoting biodiversity in the park (Kraaij, 2004; SANParks, 2008). However, a number of runaway fires from outside the park have recently burnt large portions of the BNP at shorter return intervals than what is optimal for this system (SANParks, 2013). Thus an integrated regional fire management plan is recommended, as well as a review of the extent and effectiveness of park boundaries and fire breaks (Fuggle *et al.*, 2009).

In the past, *T. triandra* was used as an indicator species in an assessment of veld condition in the BNP (Novellie and Kraaij, 2010). This would be an effective method in habitat types where *T. triandra* is abundant, such as Drainage Lines and recently burnt habitat. However, in other habitat types, such as Asteraceous Fynbos in the southern region of the park, *T. triandra* appears to be restricted to nutrient rich spots in association with termitaria (Grobler and Marais, 1967). Using *T. triandra* as the only indicator of veld condition might result in a misrepresentation of the suitability of the habitat type. It is thus recommended to also include other species such as *C. marginatus* and *E. curvula* in veld condition assessments. Implementing the habitat suitability assessment used during this study for example (Novellie and Winkler, 1993; Novellie, 1994), would incorporate multiple dietary species. The *HSI* can be used as a rapid measurement of herbivore impact and veld condition in relation to rainfall and fire, as well as a measurement of the suitability of the habitat, and its potential yield to grazers (Novellie and Winkler, 1993). For comparison to previous work in the BNP, veld condition assessments in terms of grass height and forage yield at the sites used by mountain zebra (as per the current study), would be informative to management (Novellie and Strydom, 1987; Novellie, 1990). Areas of high utilization by mountain zebra (as identified during this study) or other grazers (from other studies) should preferably be used for the placement of veld condition and habitat suitability monitoring sites. The GPS coordinates for recommended sites (based on mountain zebra focus areas as per the current study) are presented in Table 7.1.

The presence of rare and threatened lowland fynbos in this small National Park presents an opportunity for the conservation of Red-listed plant and animal species. Not only is the vegetation diverse (Kraaij, 2011), the soils are complex and the BNP is currently conserving a small remnant of a Critically Endangered fynbos type, Swellendam Silcrete Fynbos (Rebelo *et al.*, 2006; Kraaij, 2011). The small size of the park, and the high number of Red-listed and endemic plants in the park suggest that biodiversity in the BNP is particularly vulnerable to over-stocking and degradation (Kraaij, 2011). Coupled with the frequent fires which have historically occurred in the BNP, intensive herbivory potentially threaten plant biodiversity. Monitoring the impact of these disturbances on the rare and unique flora of the BNP has been recommended (Le Roux, 1988; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010). The increase of the extent of *C. dactylon* grazing lawns by intensive grazing has been of particular concern (McNaughton, 1984; Luyt, 2005; Archibald, 2008; Kraaij and Novellie, 2010; Novellie and Kraaij, 2010; Kraaij *et al.*, 2011; Watson *et al.*, 2011). During the current study bontebok were observed to habitually use these areas, while mountain zebra did not frequent grazing lawns, and rather fed along the edges of pans, where grass was taller. However, due to the high stocking rate of bontebok at the time, the grass on grazing lawns may have been too short for zebra to utilize. The continued monitoring of the influence of grazers on the extent of the grazing lawns is warranted.

Acquiring adjacent land to the BNP to increase the size of the park is another important factor to be considered (Cowling and Bond, 1991; Cowling and Heijnis, 2001; Boshoff *et al.*, 2002). This could eventually allow maintaining larger herbivore populations in the BNP, potentially promoting genetic diversity of the mountain zebra population, through mixing of all three the relict populations, which each represent a third of the genetic diversity of the meta-population (Lloyd and Rasa, 1989; Moodley, 2002; Sasidharan, 2004; Moodley and Harley, 2005; Sasidharan, 2006; Hrabar and Kerley, 2009; Sasidharan *et al.*, 2011; Watson *et al.*, 2011). Increase in reserve size is a big challenge for the BNP and in the Overberg district as a whole, as renosterveld habitat is now transformed and intensively used for agriculture (McDowell and Moll, 1992; Kemper *et al.*, 1999; Donaldson *et al.*, 2002). Thus until more land can be secured for conservation to increase the extent of the current BNP, a translocation-based management strategy to optimise the long-term genetic diversity and population viability of mountain zebra and other ungulates in the BNP is recommended (Dennis *et al.*, 1991; Novellie *et al.*, 1996; Watson *et al.*, 2005; Watson and Chadwick, 2007).

Ungulate nutritional status is a valuable measurement of ungulate health and performance (Grant *et al.*, 2000), and is highly recommended as a monitoring tool in the BNP. It is recommended that this monitoring technique be used by BNP management for the proactive detection of deficiencies and possible susceptibility to disease (Sasidharan, 2006; Marais *et al.*, 2007; Nel, 2007; Sasidharan *et al.*, 2011). This would involve the seasonal collection and processing of faecal samples from mountain zebra dung piles after Grant *et al.* (2000), and analysis at a laboratory for crude protein and phosphorus content (AOAC, 2000a; AOAC, 2000b)

Table 7.1: GPS coordinates of suggested monitoring sites in preferred habitat types.

Habitat type	**Decimal Degrees South**	**Decimal Degrees East**
Young Proteoid Fynbos	34.056734	20.479106
Recently Burnt Area	34.053255	20.488674
Recently Burnt Area	34.043364	20.473989
Young Drainage Lines	34.062184	20.486566
Young Drainage Lines	34.056242	20.456597
Inland Pans (fringe)	34.068464	20.487992

7.3. RECOMMENDATIONS FOR FUTURE RESEARCH

During this study, the preference of specific habitat types appears to be related to soil texture and nutrition, such as the diagnostic differentiation between the Proteoid and Asteraceous Fynbos types, which is based on associated geology and soils (Chief Director of Surveys and Land Information, 1993; DWAF, 2004; Vlok and De Villiers, 2007; Watson *et al.*, 2011). To better understand the variation in food plant quality and abundance, a fine-scale soil description, and soil nutrient content analysis of the habitat types is recommended (Coe *et al.*, 1976; Bell, 1982; Radloff, 2008). In this regard, the differences in soils, seasonal drainage and species composition between the Inland Pans (frequented by bontebok) as well as the pan "fringe" areas (utilized by mountain zebra during this study) are of particular research interest, especially in terms of how these dynamics influence game movement and utilization.

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APPENDICES

Appendix 1: Species recorded in the diet of Cape mountain zebra in the BNP with annual or seasonal percentage diet composition < 2%.

Species	**Annual psi ± 95% c.i.**	**Annual ai**
Grasses		
Themeda triandra	20.9 ± 4.9	0.78 (0.73, 0.82)
Cymbopogon marginatus	14.5 ± 3.6	0.60 (0.55, 0.66)
Eragrostis curvula	13.3 ± 4.9	0.81 (0.73, 0.87)
Merxmuellera disticha	3.7 ± 2.1	0.72 (0.58, 0.83)
Heteropogon contortus	2.7 ± 1.7	0.76 (0.61, 0.87)
Hyparrhenia hirta	2.5 ± 1.9	0.71 (0.53, 0.85)
Stipagrostis zeyheri ssp. *zeyheri*	2.1 ± 1.9	0.95 (0.76, 1.00)
Ehrharta capensis	1.9 ± 1.2	0.25 (0.18, 0.33)
Brachiaria serrata	1.9 ± 0.9	0.22 (0.16, 0.29)
Ehrharta calycina	1.7 ± 1.5	0.63 (0.44, 0.79)
Paspalum dilatatum (exotic)	1.3 ± 1.5	0.95 (0.75, 1.00)
Pentaschistis curvifolia	1.1 ± 0.9	0.43 (0.28, 0.59)
Tribolium uniolae	0.8 ± 0.5	0.35 (0.24, 0.48)
Pentaschistis pallida	0.7 ± 0.6	0.31 (0.17, 0.48)
Aristida diffusa ssp. *diffusa*	0.5 ± 0.4	0.29 (0.16, 0.44)
Eragrostis capensis	0.7 ± 0.7	0.32 (0.17, 0.51)
Melinis repens ssp. *repens*	0.6 ± 0.8	0.11 (0.05, 0.20)
Pentaschistis cirrhulosa	0.4 ± 0.7	0.13 (0.04, 0.27)
Vulpia myuros	0.3 ± 0.7	0.50 (0.16, 0.84)
Cymbopogon pospischilli	0.2 ± 0.4	0.17 (0.05, 0.37)
Digitaria eriantha	0.3 ± 0.4	0.57 (0.29, 0.82)
Koeleria capensis	0.2 ± 0.3	0.35 (0.14, 0.62)
Lolium perenne (exotic)	0.2 ± 0.3	0.80 (0.28, 0.99)
Cynodon dactylon	0.1 ± 0.2	0.06 (0.02, 0.14)
Aristida junciformis ssp. *junciformis*	0.0 ± 0.0	0.00 (0.00, 0.00)
Briza maxima	0.0 ± 0.1	0.07 (0.02, 0.18)
Briza minor	0.0 ± 0.0	0.00 (0.00, 0.00)
Festuca scabra	0.0 ± 0.0	0.00 (0.00, 0.00)
Hordeum murinum ssp*. glaucum*	0.0 ± 0.0	0.00 (0.00, 0.00)
Total	**72.6**	
Restios		
Thamnochortus cinereus	0.7 ± 1.5	0.29 (0.10, 0.56)
Elegia vaginulata	0.2 ± 0.3	0.30 (0.07, 0.65)
Staberoha distachyos	0.2 ± 0.4	0.17 (0.00, 0.64)
Cannomois parviflora	0.0 ± 0.1	0.50 (0.01, 0.99)
Ischyrolepis curviramis	0.0 ± 0.0	0.00 (0.00, 0.00)
Ischyrolepis capensis	7.5 ± 3.1	0.39 (0.32, 0.46)
Calopsis muirii	1.2 ± 0.8	0.62 (0.42, 0.79)
Hypodiscus striatus	1.0 ± 1.2	0.92 (0.64, 1.00)
Ischyrolepis triflora	1.0 ± 0.9	0.16 (0.09, 0.26)
Total	**11.8**	

Sedges

Species	**Annual psi ± 95% c.i.**	**Annual ai**
Cyperus thunbergii	0.0 ± 0.0	0.00 (0.00, 0.00)
Eleocharis limosa	0.4 ± 0.9	1.00 (0.54, 1.00)
Ficinia nigriscens	0.2 ± 0.2	0.46 (0.19, 0.75)
Ficinia nodosa	0.0 ± 0.1	0.09 (0.00, 0.41)
Ficinia oligantha	0.1 ± 0.1	0.13 (0.02, 0.40)
Scirpoides dioecus	0.8 ± 1.6	1.00 (0.40, 1.00)
Tetraria cf. pubescens	0.1 ± 0.1	0.07 (0.01, 0.22)
Tetraria cuspidata	0.1 ± 0.2	0.18 (0.02, 0.52)
Tetraria sp. nov.	0.0 ± 0.1	0.50 (0.01, 0.99)
Tetraria brachyphylla	2.4 ± 2.0	0.94 (0.79, 0.99)
Ficinia indica	1.8 ± 1.6	0.39 (0.26, 0.53)
Total	**5.9**	
Geophytes		
Annesorhiza nuda	0.5 ± 0.7	0.83 (0.36, 1.00)
Trachyandra revoluta	0.3 ± 0.3	0.50 (0.25, 0.75)
Babiana sp.	0.1 ± 0.2	0.20 (0.01, 0.72)
Drimia exuviata	0.0 ± 0.0	0.00 (0.00, 0.00)
Micranthus alopecuroides	0.0 ± 0.1	0.14 (0.00, 0.58)
Moraea collina	3.4 ± 2.2	0.75 (0.63, 0.85)
Lanaria lanata	2.6 ± 1.7	0.92 (0.78, 0.98)
Watsonia laccata	1.0 ± 0.9	0.70 (0.50, 0.86)
Hypoxis villosa	0.9 ± 0.9	0.30 (0.17, 0.45)
Total	**8.8**	
Forbs		
Corymbium africanum ssp. *scabridum*	0.6 ± 0.7	0.43 (0.24, 0.63)
Total	**0.6**	
Shrublets		
Aspalathus laricifolia ssp. *canescens*	0.2 ± 0.4	1.00 (0.40, 1.00)
Total	**0.2**	
Grand total	**100.0**	

Appendix 2: The mean percentage leaf and stem use of accepted plants in feeding quadrats.

Species	**% Leaf use mean ± 95% c.i.**	**n**	**% Stem use mean ± 95% c.i.**	**n**
Themeda triandra	95.4 ± 2.2	249	4.6 ± 2.2	249
Cymbopogon marginatus	90.4 ± 3.3	185	9.6 ± 3.3	185
Eragrostis curvula	84.4 ± 4.0	109	15.6 ± 4.0	109
Brachiaria serrata	58.6 ± 4.2	38	41.4 ± 4.2	38
Merxmuellera disticha	90.4 ± 7.6	38	9.6 ± 7.6	38
Heteropogon contortus	80.5 ± 10.8	37	19.5 ± 10.8	37
Ehrharta capensis	95.8 ± 6.2	33	4.2 ± 6.2	33
Hyparrhenia hirta	90.6 ± 6.8	24	9.4 ± 6.8	24
Tribolium uniolae	76.1 ± 10.1	23	23.9 ± 10.1	23
Ehrharta calycina	78.0 ± 14.4	20	22.0 ± 14.4	20
Stipagrostis zeyheri spp. *zeyheri*	17.5 ± 8.9	20	82.5 ± 8.9	20
Paspalum dilatatum (exotic)	72.4 ± 15.8	19	27.6 ± 15.8	19
Pentaschistis curvifolia	85.6 ± 12.2	18	14.4 ± 12.2	18
Aristida diffusa spp. *diffusa*	15.0 ± 20.9	13	85.0 ± 20.9	13
Pentaschistis pallida	96.7 ± 4.9	12	3.3 ± 4.9	12
Eragrostis capensis	88.6 ± 19.9	11	11.4 ± 19.9	11
Melinis repens spp. *repens*	70.0 ± 26.5	9	30.0 ± 26.5	9
Digitaria eriantha	98.8 ± 3.0	8	1.3 ± 3.0	8
Koeleria capensis	70.8 ± 35.5	6	29.2 ± 35.5	6
Pentaschistis cirrhulosa	99.0 ± 2.8	5	5.0 ± 10.8	5
Briza maxima	35.0 ± 20.5	4	65.0 ± 20.5	4
Cymbopogon pospischilli	83.8 ± 19.9	4	16.3 ± 19.9	4
Cynodon dactylon	76.3 ± 32.7	4	23.8 ± 32.7	4

Appendix 3: The mean percentage greenness of accepted and rejected plants in feeding quadrats.

Species	**Accepted mean % greenness ± 95% c.i.**	**n**	**Rejected mean % greenness ± 95% c.i.**	**n**	**Mann-Whitney**
Themeda triandra	75.0 ± 3.1	249	67.1 ± 3.9	263	Z = 1.959
Cymbopogon marginatus	72.1 ± 3.5	185	62.7 ± 3.4	265	Z = 3.392*
Eragrostis curvula	73.2 ± 4.4	109	55.0 ± 7.0	84	Z = 3.600*
Brachiaria serrata	74.9 ± 8.2	38	57.7 ± 4.9	165	Z = 2.836*
Merxmuellera disticha	71.9 ± 7.2	38	53.9 ± 12.8	29	Z = 1.860
Heteropogon contortus	69.6 ± 7.7	37	61.6 ± 13.2	32	Z = 0.319
Ehrharta capensis	97.0 ± 4.4	33	63.0 ± 7.8	130	Z = 4.159*
Hyparrhenia hirta	67.8 ± 7.6	24	55.5 ± 12.1	27	Z = 1.189
Tribolium uniolae	76.3 ± 10.3	23	56.6 ± 8.9	60	Z = 2.330*
Ehrharta calycina	83.4 ± 8.7	20	63.6 ± 15.3	24	Z = 1.367
Stipagrostis zeyheri spp. *zeyheri*	54.4 ± 11.2	20	44.9 ± 17.0	12	Z = 0.954
Paspalum dilatatum (exotic)	94.4 ± 3.8	19	93.0 ± 5.1	6	Z = 0.986
Pentaschistis curvifolia	65.4 ± 11.8	18	55.3 ± 11.5	36	Z = 0.688
Aristida diffusa spp. *diffusa*	37.0 ± 16.3	13	33.7 ± 7.9	36	Z = 0.215
Pentaschistis pallida	61.9 ± 14.5	12	35.8 ± 9.4	33	Z = 2.798*
Eragrostis capensis	68.6 ± 20.2	11	34.6 ± 12.8	29	Z = 2.544*
Melinis repens spp. *repens*	86.6 ± 10.7	9	71.5 ± 6.2	80	Z = 1.470
Digitaria eriantha	70.5 ± 8.7	8	48.4 ± 21.1	10	Z = 1.644
Koeleria capensis	85.7 ± 13.2	6	44.6 ± 17.7	15	Z = 2.569*
Pentaschistis cirrhulosa	71.0 ± 13.6	5	29.6 ± 10.7	37	Z = 2.272*
Briza maxima	92.0 ± 9.5	4	21.6 ± 10.1	54	Z = 2.746*
Cymbopogon pospischilli	81.0 ± 21.1	4	91.4 ± 7.8	23	Z = 2.013*
Cynodon dactylon	80.3 ± 31.9	4	57.2 ± 7.8	69	Z = 1.333

* $P < 0.05$

Appendix 4: The mean leaf height and diameter of accepted and rejected plants in feeding quadrats.

Species	**Leaf height (mm) Accepted (mean ± 95% c.i.)**	**n**	**Leaf height (mm) Rejected (mean ± 95% c.i.)**	**n**	**Mann-Whitney**	**Diameter (mm) Accepted (mean ± 95% c.i.)**	**n**	**Diameter (mm) Rejected (mean ± 95% c.i.)**	**n**	**Mann-Whitney**
Themeda triandra	118.5 ± 6.4	249	84.5 ± 6.2	263	Z = 8.421*	161.6 ± 7.3	249	119.4 ± 6.7	263	Z = 8.406*
Cymbopogon marginatus	142.2 ± 8.7	185	148.5 ± 10.7	265	Z = 0.530	182.5 ± 11.5	185	192.7 ± 15.7	265	Z = 1.125
Eragrostis curvula	193.3 ± 16.7	109	130.3 ± 22.4	84	Z = 5.730*	230.3 ± 18.3	109	162.9 ± 22.7	84	Z = 5.588*
Brachiaria serrata	76.7 ± 7.8	38	78.3 ± 4.8	165	Z = 0.092	107.7 ± 16.9	38	110.8 ± 8.0	165	Z = 0.282
Merxmuellera disticha	183.2 ± 18.6	38	198.1 ± 48.1	29	Z = 0.462	214.5 ± 37.8	38	176.6 ± 36.7	29	Z = 1.265
Heteropogon contortus	156.4 ± 24.3	37	106.3 ± 23.2	32	Z = 3.153*	176.9 ± 25.4	37	123.9 ± 18.3	32	Z = 3.032*
Ehrharta capensis	64.5 ± 10.8	33	61.1 ± 7.7	130	Z = 2.090*	107.6 ± 11.3	33	70.3 ± 6.5	130	Z = 5.592*
Hyparrhenia hirta	174.0 ± 32.7	24	113.5 ± 30.1	27	Z = 3.076*	173.1 ± 26.6	24	116.3 ± 14.8	27	Z = 3.312*
Tribolium uniolae	127.8 ± 22.6	23	75.8 ± 13.7	60	Z = 4.070*	143.9 ± 20.8	23	92.4 ± 11.1	60	Z = 4.304*
Ehrharta calycina	124.3 ± 18.4	20	70.2 ± 15.7	24	Z = 4.266*	148.8 ± 26.2	20	131.7 ± 26.9	24	Z = 1.155
Stipagrostis zeyheri spp. *zeyheri*	311.0 ± 46.4	20	245.0 ± 66.4	12	Z = 1.868	286.5 ± 49.9	20	232.5 ± 94.6	12	Z = 1.518
Paspalum dilatatum (exotic)	140.0 ± 19.9	19	93.3 ± 50.4	6	Z = 1.845	179.5 ± 27.8	19	166.7 ± 72.6	6	Z = 0.318
Pentaschistis curvifolia	146.7 ± 23.4	18	115.0 ± 25.1	36	Z = 1.881	149.4 ± 26.9	18	125.3 ± 18.8	36	Z = 1.697
Aristida diffusa spp. *diffusa*	295.4 ± 50.7	13	241.4 ± 44.5	36	Z = 1.574	319.2 ± 108.2	13	250.8 ± 57.2	36	Z = 1.393
Pentaschistis pallida	111.7 ± 25.2	12	78.3 ± 21.0	33	Z = 2.413*	165.0 ± 42.8	12	95.0 ± 19.1	33	Z = 2.887*
Eragrostis capensis	110.5 ± 19.0	11	98.4 ± 22.2	29	Z = 1.348	145.9 ± 32.3	11	119.0 ± 26.7	29	Z = 1.575
Melinis repens spp. repens	111.7 ± 24.5	9	79.5 ± 10.4	80	Z = 2.538*	153.9 ± 50.3	9	125.6 ± 13.3	80	Z = 1.354
Digitaria eriantha	101.3 ± 29.5	8	72.0 ± 21.0	10	Z = 1.688	158.8 ± 29.1	8	116.0 ± 25.5	10	Z = 2.266*
Koeleria capensis	153.3 ± 57.0	6	104.7 ± 24.1	15	Z = 1.868	106.7 ± 50.8	6	102.0 ± 23.3	15	Z = 0.039
Pentaschistis cirrhulosa	118.0 ± 25.4	5	78.6 ± 17.3	37	Z = 2.214*	102.0 ± 22.2	5	84.7 ± 17.1	37	Z = 1.495
Briza maxima	56.3 ± 17.6	4	47.5 ± 6.7	54	Z = 1.089	40.0 ± 23.4	4	37.8 ± 4.7	54	Z = 0.460
Cymbopogon pospischilli	105.0 ± 49.5	4	140.2 ± 27.8	23	Z = 1.160	108.8 ± 62.8	4	111.3 ± 24.4	23	Z = 0.239
Cynodon dactylon	57.5 ± 49.3	4	81.0 ± 12.6	69	Z = 0.788	148.8 ± 88.2	4	153.7 ± 16.7	69	Z = 0.012

* $P < 0.05$