

Cape mountain zebra in the Baviaanskloof Nature Reserve, South Africa: resource use reveals limitations to zebra performance in a dystrophic mountainous ecosystem

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Running title: Cape mountain zebra diet

Abstract

Resource use of Cape mountain zebra was studied in the Baviaanskloof Nature Reserve (BNR) over concerns of the poor performance in population growth. We assessed the seasonal diet, habitat suitability and forage quality of the Bergplaas area in BNR for mountain zebra. Grasses contributed 95.2 % to the annual diet of mountain zebra, *Tristachya leucothrix* contributing the most (39.4 %), followed by *Themeda triandra* (27.6 %). Seasonally, *T. triandra* contributed most to the diet in winter, while *T. leucothrix* became more important in the summer and also was the only species preferred in all seasons. Mountain zebra concentrated their feeding in Kouga Grassy Fynbos and from our assessment this was the only habitat suitable for mountain zebra. Our analysis of mountain zebra dung indicated that the seasonal nitrogen and phosphorus content was below the threshold values

prescribed for grazers, and our study suggests that mountain zebra at Bergplaas are severely resource limited. We emphasize the importance of fire and access to nutrient-rich lowlands in influencing the nutritional ecology of mountain zebra and provide conservation management recommendations.

Key words: nitrogen, phosphorous, habitat, nutrient analysis, fire, management, buffalo, red hartebeest

Introduction

Historically, Cape mountain zebra (*Equus zebra zebra*) occurred throughout most of the Western Cape and western parts of the Eastern Cape Provinces (Skead *et al.*, 2007). By the late 1980's, human impact confined the species to three protected areas; Mountain Zebra National Park (MZNP); Gamka Mountain Nature Reserve (GMNR) and Kammanassie Nature Reserve (KNR) (Novellie *et al.*, 2002) and is currently listed as Vulnerable (IUCN Red List; Novellie, 2008). The meta-population has experienced substantial growth since the re-introduction of mountain zebra onto private properties and other state protected areas, and presently the meta-population is estimated at > 2700 (Hrabar & Kerley, 2013). In comparison, the population in BNR has shown little growth (Reeves *et al.*, 2011) and this poor performance is typical of other protected populations in the predominantly dystrophic Cape Floristic Region (CFR) (Watson *et al.*, 2005; Watson & Chadwick, 2007; Watson, Kraaij & Novellie, 2011).

Palaeozoological evidence suggests that Cape mountain zebra were associated with open grassland habitats (Faith, 2012) and is supported by work in the predominantly eutrophic MZNP (Novellie *et al.*, 1988; Winkler & Owen-Smith, 1995). Although research on ungulate

resource use is essential for effective management (Gaillard *et al.*, 2008), little work has been done on mountain zebra resource use in the CFR, which typically has a low abundance of grasses (Goldblatt & Manning, 2002). This is concerning as the meta-population is well represented here and includes the relict GMNR and KNR populations. Of the CFR studies, most investigated habitat use and suitability (Watson *et al.*, 2005; Watson & Chadwick, 2007; Kraaij & Novellie, 2010; Watson *et al.*, 2011; Smith *et al.*, 2011), only one study assessed diet composition (Smith *et al.*, 2011) and none assessed diet preference. An important limitation of the habitat suitability studies is that they used grass acceptance values from MZNP.

An important aspect of ungulate nutritional ecology is the assessment of range quality and ungulate nutritional status (Holechek, Vavra & Pieper, 1982) and faecal nitrogen (N) and phosphorous (P) are commonly used for this purpose. Although Hobbs (1987) suggests this method is unreliable (but see Leslie, Bowyer & Jenks, 2008), several studies have used faecal N and P indices to investigate ungulate nutritional status, including plains zebra (*Equus quagga*) (Abaturov *et al.*, 1995; Grant, Peel & Van Ryssen, 2000; Codron *et al.*, 2007; Venter & Watson, 2008). This kind of study has not been done for mountain zebra in the CFR, where poor population growth performance appears to be influenced by poor range quality (Watson *et al.*, 2005). Our study had the objectives of determining: (a) the seasonal diet composition; (b) the seasonal species preference; (c) the habitat suitability of vegetation types; (d) the seasonal nutritional status of mountain zebra.

Study area

BNR (\pm 200 000 ha) is situated in the Eastern Cape Province, and includes the Kouga and Baviaanskloof mountains separated by a 75 km long valley (Fig. 1). The topography

includes; a central valley containing the perennial Baviaanskloof River; steep gorges and lower mountain slopes; mid-elevation plateaus; higher mountain slopes and peaks. The mountains (Cape Fold Belt), contain nutrient-poor soils from the Table Mountain Group, while the valleys have nutrient-rich soils from the Bokkeveld Shales and Enon Conglomerates (Rust & Illenberger, 1989).

The summers are generally hot, especially in the valleys where temperatures may exceed 45°C, while upper slopes are cooler (maximum of 25-30°C) and in winter may reach below 0°C (Boshoff, Cowling & Kerley, 2000). Typically most rainfall occurs in autumn and spring but varies with longitude and altitude, and generally the peaks are the wettest (1000 mm p.a.) and the valley bottoms the driest (200-250 mm p.a.) (Boshoff et al., 2000).

The vegetation of BNR is dominated by Fynbos on the plateaus and upper mountain slopes, Subtropical Thicket on the lower slopes and valleys and Nama Karoo on the western plains (Euston-Brown, 2006). Our study was done in the Bergplaas section (Fig. 1) of the BNR which includes the following vegetation types: Baviaans Thicket Savanna and Baviaans Renoster Sandolienveld in the valleys; Elands Woodland and Groot Woodland on the lower slopes; Baviaanskloof Sweet Grassland and Kouga Grassy Fynbos on the plateaus; Kouga Mesic Fynbos and Kouga Arid Fynbos on the upper slopes (Euston-Brown, 2006) (Fig. 1).



Fig. 1 A map indicating the location and topography of the study area in BNR. The distribution of the Cape mountain zebra and other key ungulate species, located during helicopter counts, which are relevant to the study, are also indicated. The vegetation types in the study are grouped into the following broad-scale habitat types adapted from (Euston-Brown, 2006): Grass - Baviaanskloof Sweet Grassland; Grassy Fynbos / Grassy Fynbos Mosaic / Renosterveld - Baviaanskloof Renoster Sandolienveld, Kouga Grassy Fynbos; Other Fynbos - (Elands Woodland, Groot Woodland, Kouga Arid Fynbos, Kouga Mesic Fynbos; Woody - Baviaanskloof Thicket Savanna Areas in white are non-reserve property.

Six reintroductions which accumulated to a total of 61 mountain zebra have occurred since 1990 (Fig. 2) And radio collar and count data indicate that they zebra use the mid-elevation plateaus in the eastern part of the reserve (Reeves *et al.*, 2011; ECPTA unpublished data). One of the sub-populations occurs at Bergplaas and formed the focus of our study. Other grazing ungulates in the area include; red hartebeest (*Alcelaphus buselaphus*), mountain reedbuck (*Redunca fulvorufula*) and Cape buffalo (*Syncerus caffer*). Domestic donkeys also

occur in BNR but outside the study area and are not considered further. The leopard (*Panthera pardus*) is the only large predator present in the reserve.

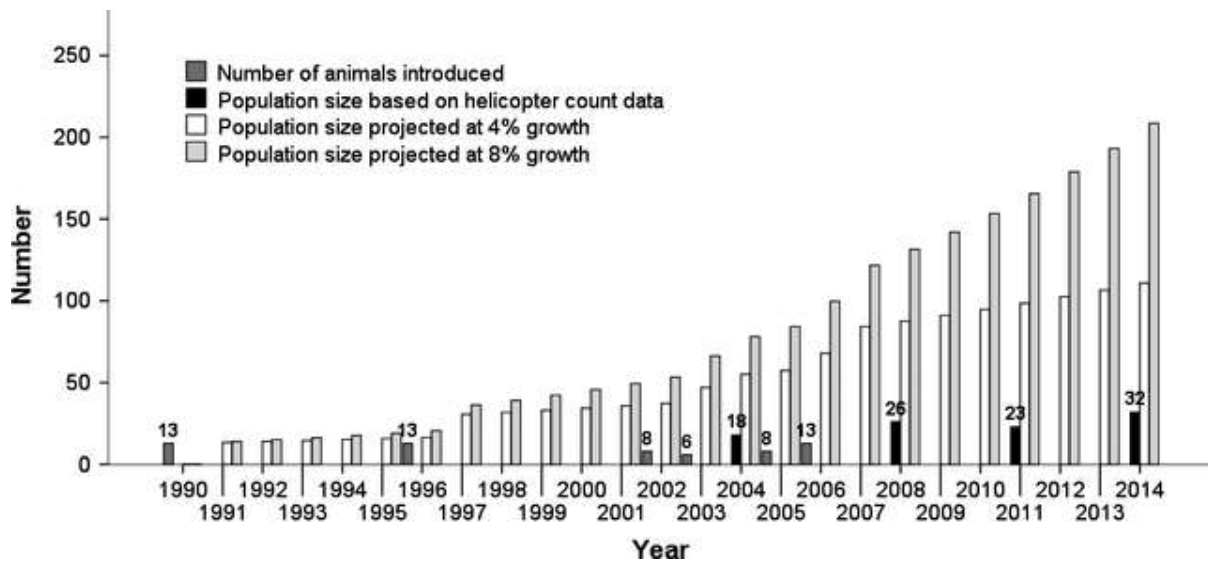


Fig 2 The population sizes of Cape mountain zebra, red hartebeest and buffalo as recorded during helicopter game counts. For each, the number of animals and the year they were introduced are indicated. For mountain zebra the projected 2014 number at 4% or 8% population growth are 115 and 225 respectively.

Our study (May 2011-March 2012) was divided into three seasons; winter with the lowest temperature but highest rainfall (May – July); early summer with intermediate temperatures and lowest rainfall (August – November); late summer with the highest temperature and intermediate rainfall (December – March).

Methods

Feeding surveys

Mountain zebra were located visually and observed while feeding and allowed accurate location of feeding sites. In feeding sites zebra bites were identified along feeding paths marked by spoor, dung and freshly eaten tufts. Along the feeding path, we surveyed between 4-5 quadrates (1 m²) and designated these to a single feeding transect. We sampled a total of

153 quadrates in 31 transects (Table 1). Buffalo and red hartebeest were never observed in zebra feeding sites and all bites were assumed to be that of zebra

Species contribution and acceptability

A 'zebra bite' was taken as the size of the researchers fist (± 80 mm diameter) and in each quadrate, the number of 'bites' taken per grazed plant, per species was recorded. For each transect, the percentage contribution (ps_i) of each species was calculated as the number of bites eaten, divided by the total number of bites recorded as eaten in that transect. For each species, a seasonal mean was calculated from the ps_i -values of all transects in that season. The Kruskal-Wallis and multiple comparisons by mean ranks tests were used to determine if the rank order of the contributions was the same between seasons.

To determine grass preference, we used an acceptability index (Owen-Smith & Cooper, 1987). In each quadrate, grasses considered available (*i.e.* visibly alive) were recorded as accepted or rejected. For each species, a seasonal acceptability index (ai_i) was calculated as the number of feeding quadrates in which it was accepted, divided by the total of feeding quadrates in which it was recorded. Grass species with an $ai_i \geq 0.50$ were regarded as preferred, those between 0.49-0.30 as moderately acceptable and those with an $ai_i < 0.30$ of low acceptability.

Habitat suitability

We selected a single representative site within in each of the four vegetation types used by mountain zebra. In each site, the vegetation was surveyed and a habitat suitability index calculated based on acceptability values from our study and percentage aerial cover of grass species (Novellie & Winkler, 1993).

Dung nutrient analysis

The dung analysis was used as an approximation for grass nutrient quality analysis. Fresh dung was collected from mountain zebra, buffalo and red hartebeest. Samples consisting of amalgamated dung piles, were stored in a brown paper bag and air-dried for analysis using standard procedures at Bemlab, Cape Town (Campbell & Plank, 1998; Miller, 1998). For mountain zebra, the Kruskal-Wallis and multiple comparisons by mean ranks tests were used to determine if N and P values were the same between season. We only collected buffalo and red hartebeest samples in early and late summer. These N and P values were compared to the summer mountain zebra values using the Kruskal-Wallis H and multiple comparisons by mean ranks tests.

Population numbers

Population numbers were determined using helicopter counts (Venter, Peinke & Peinke, 2008). The counts were done from a four-seat helicopter, flying at a height of 30 m along a predefined flight path consisting of parallel lines spaced 300 m apart. Counts were done using a data capturer and two observers and were triplicated to have a measure of precision (Reilly & Haskins, 1999). These counts were done every three years from 2008 to 2014, while the count in 2004 was done by flying and counting in only known zebra habitats (ECPTA unpublished data). In 2011 and 2014, population size estimates based on stripe pattern recognition from photographs were used and to supplement the helicopter counts (ECPTA unpublished data).

Results

Species contribution and acceptability

We recorded 1373 bites eaten from 25 plant species by mountain zebra (Table 1). Of these,

Table 1 The annual and seasonal percentage contribution of grass, other graminoid and dicotyledonous species recorded in the diet of Cape mountain zebra in Bergplaas (n = number of transects)

Species	Annual	Winter	Early summer	Late summer	Kruskal–Wallis ^b
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	
	n = 31	n = 9	n = 9	n = 13	
Grasses					
<i>Tristachya leucothrix</i>	39.4 ± 33.2	12.5 ± 11.9 ^A	43.9 ± 34.2 ^{AB}	54.8 ± 32.6 ^B	7.842 ^a
<i>Themeda triandra</i>	27.6 ± 26.7	51.8 ± 20.5 ^A	19.9 ± 25.4 ^{AB}	16.2 ± 21.1 ^B	10.136 ^a
<i>Trachypogon spicatus</i>	3.7 ± 9.0	0	7.1 ± 14.5	3.9 ± 6.6	
<i>Heteropogon contortus</i>	2.6 ± 5.4	2.7 ± 4.3	2.4 ± 4.5	2.7 ± 7.0	0.311
<i>Pentaschistis setifolia</i>	2.5 ± 7.9	8.5 ± 13.3	0	0	
<i>Eragrostis capensis</i>	2.3 ± 5.8	4.3 ± 10.1	1.1 ± 1.7	1.7 ± 2.9	0.194
<i>Eragrostis curvula</i>	2.2 ± 7.8	3.1 ± 9.2	4.5 ± 11.5	0	
<i>Eragrostis racemosa</i>	1.6 ± 9.0	0	0	3.8 ± 13.9	–
<i>Aristida junciformis</i>	1.5 ± 5.1	0.0 ± 0.0	4.8 ± 9.0	0.2 ± 0.7	
<i>Setaria sphacelata</i>	1.4 ± 4.64	0.7 ± 1.4	2.0 ± 5.9	1.4 ± 5.2	
<i>Poa bulbosa</i>	0.8 ± 4.2	0	0	1.8 ± 6.5	
<i>Brachiaria serrata</i>	0.7 ± 1.8	0.9 ± 1.4	1.4 ± 2.9	0.2 ± 0.5	2.418
<i>Diheteropogon filifolius</i>	0.7 ± 2.2	0	0.7 ± 2.0	1.2 ± 3.0	
<i>Triraphis andropogonoides</i>	0.2 ± 1.0	0.8 ± 1.7	0	0	
<i>Eragrostis chloromelas</i>	0.1 ± 0.3	0.2 ± 0.5	0	0	
<i>Unidentified</i>	8.0 ± 11.2	12.3 ± 11.3	7.6 ± 14.0	5.2 ± 8.6	
Total	95.2	97.7	95.2	93.3	
Other graminoids					

Species	Annual	Winter	Early summer	Late summer	Kruskal– Wallis ^b
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	
	n = 31	n = 9	n = 9	n = 13	
<i>Kyllinga sp.</i>	1.1 ± 4.1	0	1.4 ± 2.4	1.7 ± 6.0	
<i>Hypoxis villosa</i>	0.8 ± 3.3	0	2.3 ± 5.8	0.4 ± 1.3	
<i>Schoenoxiphium sparteum</i>	0.6 ± 1.5	1.5 ± 2.2	0.6 ± 1.5	0	
<i>Ficinia sp.</i>	0.6 ± 2.1	0.2 ± 0.5	0	1.3 ± 3.2	
<i>Bobartia orientalis</i>	0.1 ± 0.7	0	0.5 ± 1.4	0	
<i>Tetraria cuspidata</i>	0.1 ± 0.5	0	0	0.2 ± 0.7	
<i>Lanaria lanata</i>	0.1 ± 0.3	0.2 ± 0.5	0	0	
Total	3.4	1.9	4.8	3.5	
Dicotyledons					
<i>Hermania involucrata</i>	0.8 ± 3.3	0	0	1.8 ± 5.1	
<i>Aspalathus setacea</i>	0.3 ± 1.4	0	0	0.6 ± 2.2	
<i>Gazania linearis</i>	0.1 ± 0.7	0.4 ± 1.3	0	0	
<i>Unidentified</i>	0.3 ± 1.7	0	0	0.7 ± 2.7	
Total	1.5	0.4	0	3.2	
Total	100	100	100	100	

The same letter (Upper case) indicates no significant difference among the specified seasons.

^a $P < 0.05$.

^b Only calculated for species recorded in every season

16 grasses contributed 95.3 % to the annual diet, while other graminoids and browse formed low proportions of the diet. Grasses formed most of the diet in the cool, wet winter, but

decreased to the lowest level in the warm, dry late summer when other graminoids and browse contributed > 3 % to the diet. Only two grasses, *Tristachya leucothrix* and *Themeda triandra* formed > 5 % of the annual diet, of which the former was eaten the most (Table 1). Of the other grasses, only five formed between 2-5 % of the diet; *Trachypogon spicatus*, *Heteropogon contortus*, *Pentaschistis setifolia*, *Eragrostis capensis* and *Eragrostis curvula*.

Table 2 Annual and seasonal acceptability index (*ai*) of grasses contributing $\geq 2\%$ to the annual or seasonal diet of Cape mountain zebra in Bergplaas

Species	Annual <i>ai</i> (95% intervals)	Winter <i>ai</i> (95% intervals)	Early summer <i>ai</i> (95% intervals)	Late summer <i>ai</i> (95% intervals)
<i>Tristachya leucothrix</i>	0.86 (0.77, 0.93)	0.56 (0.30, 0.8)	0.93 (0.78, 0.99)	0.93 (0.80, 0.98)
<i>Themeda triandra</i>	0.54 (0.45, 0.63)	0.83 (0.68, 0.93)	0.39 (0.24, 0.55)	0.41 (0.26, 0.58)
<i>Eragrostis curvula</i>	0.43 (0.18, 0.71)	0.50 (0.12, 0.88)	0.43 (0.10, 0.81)	0
<i>Trachypogon spicatus</i>	0.30 (0.16, 0.47)	0	0.33 (0.13, 0.59)	0.26 (0.09, 0.51)
<i>Heteropogon contortus</i>	0.22 (0.11, 0.36)	0.38 (0.14, 0.68)	0.20 (0.04, 0.48)	0.14 (0.03, 0.35)
<i>Setaria sphacelata</i>	0.21 (0.08, 0.41)	0.29 (0.04, 0.71)	0.22 (0.03, 0.60)	0.17 (0.02, 0.48)
<i>Eragrostis capensis</i>	0.18 (0.10, 0.30)	0.33 (0.12, 0.48)	0.12 (0.02, 0.30)	0.17 (0.05, 0.37)
<i>Pentaschistis setifolia</i>	0.13 (0.05, 0.26)	0.43 (0.18, 0.71)	0	0
<i>Eragrostis racemosa</i>	0.13 (0.01, 0.38)	0	0	0.14 (0.02, 0.48)
<i>Aristida junciformis</i>	0.07 (0.02, 0.16)	0	0.14 (0.03, 0.35)	0.04 (0.0, 0.19)

Seasonally, *T. leucothrix* contributed 12.5 % to zebra diet in the cool, wet winter but most in the warm, drier summer seasons (Table 1). In contrast, *T. triandra* was eaten most in winter, but formed < 20.0 % of the diet in the summer. There was no clear seasonal pattern for the other principal grasses. Annually, *T. leucothrix* and *T. triandra* were the only grasses preferred while most other grasses were of low acceptability (Table 2). Seasonally, *T. leucothrix* was the only species preferred by mountain zebra in each season, and *T. triandra* was only preferred in the cool, wet winter. The only other species recorded as preferred was *E. curvula* in winter.

Habitat suitability

Of the eight vegetation types that were available to mountain zebra at Bergplaas, Kouga Grassy Fynbos was used the most, followed by Kouga Mesic Fynbos and Baviaanskloof Sweet Grassland (Table 3). Kouga Grassy Fynbos had the highest habitat suitability due to its relatively high abundance of *T. triandra* and *T. leucothrix*. Baviaanskloof Sweet Grassland had a high abundance of unacceptable grasses and thus a low habitat suitability. Bergplaas was a livestock farm prior to declaration of the reserve and overgrazing appears to have

Table 3 The habitat suitability scores (HSI) for habitats on the plateaus and upper slopes of Bergplaas

Vegetation type	% use	HSI	% grass	% <i>L. saligna</i>	% other dicots	Other	Total
Kouga Grassy Fynbos	81	20.2	36	32	6.5	24	98.5
Kouga Mesic Fynbos	16	17	28.5	34	13.5	23.5	99.5
Baviaanskloof Sweet Grassland	3	9.7	84	–	15	1	100
Groot Woodland	0	1.3	12.5	–	47.5	10	70

transformed this habitat. Mountain zebra were not observed in Groot Woodland and it had the lowest suitability score.

Dung nutrient analysis

The N content of mountain zebra dung varied significantly between seasons and was lower in winter than late summer, but there was no significant difference between winter and early summer nor early summer and late summer (Fig. 3A). The P content of mountain zebra dung did not vary significantly between seasons (Figure 3A). The N and P content of dung varied significantly between species and for both the values for mountain zebra were significantly lower than red hartebeest and buffalo but there was no difference between the red hartebeest and buffalo (Fig. 3B).

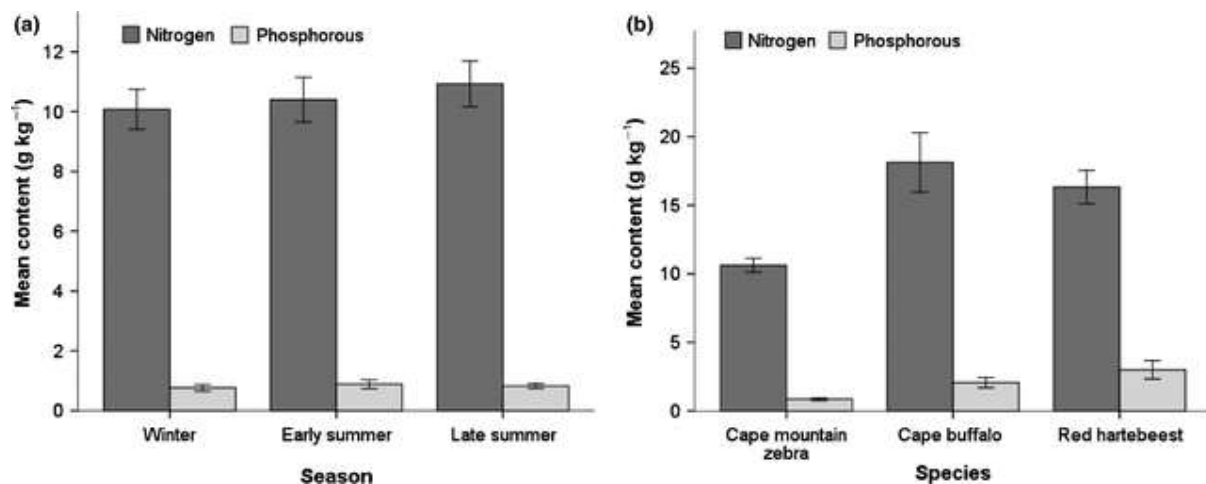


Fig 3 A comparison of the faecal nitrogen and phosphorous values of: (A) Cape mountain zebra in each season (for N, $H = 6.349$, $P < 0.05$; for P, $H = 3.447$, $P > 0.10$); (B) Cape mountain zebra, Cape buffalo and red hartebeest in the summer (for N, $H = 34.852$, $P < 0.001$; for P, $H = 35.813$, $P < 0.001$)

Population numbers

The helicopter counts indicate that mountain zebra numbers stayed relatively stable since 2008 (Fig. 2). Although counts based on striped pattern recognition suggest that zebra

numbers were underestimated by helicopter counts (23 versus 46 for 2011; 32 versus 51 for 2014), these still indicate poor population growth compared to the expected projected growth of between 4 and 8 % (Fig. 2). In contrast, buffalo numbers increased from an initial founder population of 37 to > 240 animals in 2014, while red hartebeest increased from 60 to > 170 in 2008 but have subsequently declined.

Discussion

The poor population performance of mountain zebra in BNR, dominated by CFR vegetation, is disappointing especially because it was seen as a high-potential site for range expansion of the species. A number of factors may contribute to poor population performance of mountain zebra in CFR systems: (a) Predation, but leopards are the only large predator in CFR protected areas and unlikely to be important (Hayward *et al.*, 2006); (b) Competition and facilitation could affect the ability of a species to persist in a system (Prins and Olf, 1998; Arsenault & Owen-Smith, 2002; Venter *et al.*, 2014.), but this has not been assessed in CFR systems; (c) Water availability may be important in KNR (Cleaver, 2004) but in other studies, water was readily available (Watson *et al.*, 2005; Watson *et al.*, 2011; Smith *et al.*, 2011) and it is yet to be determined how water availability influence mountain zebra in BNR; (d) Novellie *et al.*, (2002) suggest that small founder populations influence population viability, but this would apply to other systems where the species are successful; (e) Low genetic diversity influences population viability (Frankham, Ballou & Briscoe, 2002) and the low genetic diversity of mountain zebra is cause for concern (Sasidharan *et al.*, 2011). However, the genetically poor MZNP population (Moodley & Harley, 2005) has been the only source of both successful and unsuccessful re-introductions (Novellie *et al.*, 2002). (f) Recent archaeological evidence suggests that access to grassland was important in maintaining mountain zebra populations in the Pleistocene and that population numbers

declined in the Holocene as grassland was replaced by woody vegetation (Faith, 2012). Similarly, studies in the CFR indicate that limited suitable grassy habitat influences the poor performance of mountain zebra (Watson *et al.*, 2005, Watson *et al.*, 2011) and our study suggests that mountain zebra in BNR may be severely resource limited.

Mountain zebra in MZNP used a wide variety of landscapes and habitats, particularly those with habitat suitability scores > 20 (Novellie & Winkler, 1993; Winkler & Owen-Smith, 1995.) In BNR, mountain zebra only used the mid-elevation plateaus and have not been recorded in the nutrient-rich lower slopes or valleys. The latter are well used by buffalo and red hartebeest (Reeves *et al.*, 2011) and although competitive interactions between zebra and these grazers may be important, these landscapes are dominated by dense thicket habitats and may represent ‘landscapes of fear’ (Laundre, Hernandez & Ripple, 2010) due to human activity or potential predator attack (Winkler & Owen-Smith, 1995; Valeix *et al.*, 2009). Also, on the plateaus and mountain zebra mainly used Kouga grassy Fynbos, the only habitat with high habitat suitability score. This is similar to other CFR studies that indicate mountain zebra concentrate their foraging in a limited number of habitats (Watson *et al.*, 2005; Smith *et al.*, 2011).

Studies indicate that mountain zebra typically eat a wide variety of grasses (> 24) and that several grasses formed $> 5\%$ of the annual diet and were preferred throughout the year or seasonally (Winkler, 1992; Smith *et al.*, 2011). At Bergplaas, we only recorded 16 grass species in mountain zebra diet and only *T. leucothrix* and *T. triandra* formed $> 5\%$ of the annual diet. *T. leucothrix* also was the only species preferred throughout the year, while *T. triandra* and *E. curvula* were the only other grasses preferred in a season. This is reflected in our analyses of mountain zebra dung, which indicated that seasonal N and P concentrations

were constantly below the threshold prescribed for grazers, 13 g/kg and 2.0 g/kg respectively (Grant *et al.*, 2008). This is a surprising result and our values are the lowest recorded compared to other studies of *Equus* sp. (Abaturov *et al.*, 1995; Codron *et al.*, 2007, Barnier *et al.*, 2014). As protein is essential for mass gain and extended phosphorus deficiencies may lead to low reproductive rates of ungulates (Grant *et al.*, 2000), the poor performance of mountain zebra in BNR is perhaps not surprising. In contrast, the N and P values of buffalo and red hartebeest using the lower slopes and valleys were above these threshold values. This suggests that an unknown behavioural issue prevents mountain zebra from using the nutrient-rich landscapes and is highlighted as a future research priority.

It is apparent that mountain zebra at BNR were limited to a narrow range of foraging opportunities and were highly selective of grass species. The latter is unexpected as ungulates are expected to increase their dietary breadth as their nutritional status declines (Owen-Smith, 1994). Also, zebra as hind-gut fermenters are expected to be less selective to facilitate high intake rates of forage (Bell, 1971; Janis, 1976). We relate this to the moribund and unpalatable nature of the grass sward and suggest that although zebra are expected to be relatively tolerant of low quality graze (Janis, 1976; Bell, 1971), under these conditions zebra were unable to achieve the required intake rate of high quality forage (Duncan *et al.*, 1990; Illius & Gordon, 1992).

Management recommendations

Kerley *et al.*, (2003) indicate that conservation areas in the CFR are inadequate to conserve large mammal populations, including mountain zebra, and emphasize the need to improve understanding of factors determining mammal distribution and abundance in the CFR. Our study and others (Watson *et al.*, 2005; Watson & Chadwick, 2007) highlight the poor quality

of these systems to mountain zebra. Because conservation areas in the CFR are biased toward mountainous regions and suitable lowland habitat is limited (Rouget, Richardson & Cowling, 2003), potential management options could be to consider fire management and initiatives to promote access to nutrient-rich lowlands.

Presently, BNR is managed as a natural fire zone and the current fire regime appears appropriate for mountain fynbos (Reeves & Eloff, 2012). However, to meet the mountain zebra population growth objectives of BNR, an option could be to burn at appropriate intervals and season to favour reseeding of Proteaceae (Heelemann *et al.*, 2008; Kraaij *et al.*, 2013), and to allow sufficient new grass within the landscape for zebra (Kraaij & Novellie, 2010). This is an important consideration in dystrophic systems where palatable grasses become moribund with low nutritive value in the absence of fire (Mentis & Tainton, 1984; Bond *et al.*, 2003).

Although the contribution of the private sector toward the Cape mountain zebra meta-population cannot be over emphasised (Hrabar & Kerley, 2013), there is a need for greater stakeholder engagement of landowners around protected areas in the CFR (Knight, Cowling & Campbell, 2006), to allow mountain zebra access to suitable lowland habitat. Such engagement should aim to establish biodiversity stewardship agreements (Gallo *et al.*, 2009; Lindsey, Romanach & Davies-Mostert, 2009), that in the long-term will form part of the CFR conservation plan (Kerley *et al.*, 2003, Cowling *et al.*, 2003) and thus facilitate the long term security of the Cape mountain zebra meta-population. Expansion initiatives like these will also benefit general biodiversity conservation objectives.

An alternative option would be to reconsider whether BNR should be a key protected area for the conservation of mountain zebra and accept that the population has possibly reached its carrying capacity. Our study and others (Watson *et al.*, 2005; Watson & Chadwick, 2007) highlight the poor mountain zebra population growth in CFR systems. This is supported by archaeological evidence that mountain zebra mainly occurred in open grassland habitat and that climate change possibly forced them into mountainous areas (Faith, 2012). Later anthropogenic impacts probably just served to accelerate this effect. It could be that the main limiting factor in Cape mountain zebra's conservation efforts currently is the habitat association with the species name (see Kerley *et al.*, 2012). Continued efforts to establish or supplement populations in mountainous fynbos habitats without access to nutrient-rich lowlands could therefore be futile. The recommended low-risk option would thus be to focus on establishing growing populations in the eutrophic grassy Karoo habitats of the Eastern and Western Cape where reasonable population growth could be achieved.

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