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Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire

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Abstract

The small Cape mountain zebra population in Gamka Mountain Nature Reserve represents a third of the entire gene pool of this endangered species and is thus vital for it's conservation. Presently, management of this population is largely hands off, with the belief that it will grow to levels which will allow it to form a source for the mixing of mountain zebra stocks in the future. The growth of this population however, has been slow and we investigated the influence of habitat and fire on this growth. Firstly, we used a diffusion model to perform a population viability analysis. This analysis indicated that the population had a low probability of attaining quasi-extinction in the next 50 years ($G = 0.0032$). However, our findings indicated that less than 30% of the reserve was suitable for mountain zebra and that the preferred habitat would have to be burnt at unnaturally short intervals to sustain the present growth. We therefore argue that the risk of quasi-extinction to this population is greater than predicted and suggest that management options need to be implemented to reduce this risk. These options include; translocation to another protected area; acquisition of adjacent land; burning preferred habitat at unnaturally short intervals; forming a conservancy with adjacent landowners; leasing cultivated land for pasture. We suggest that only the latter two options are likely to stimulate mountain zebra population growth in the short term and that these should receive immediate attention.

Keywords: Mountain zebra; Population viability analysis; Habitat suitability; Fire; Conservation management

1. Introduction

Historically, Cape mountain zebra (*Equus zebra zebra* L.) occurred extensively in the mountainous regions of the southern parts of South Africa (Millar, 1970a; Millar, 1970b), but by the late 1980s this metapopulation had been reduced to only three natural populations; the Gamka Mountain Nature Reserve (GMNR), the Kammanassie Mountains and the Mountain Zebra National Park populations. Excluding the small GMNR and Kammanassie Mountains populations, currently there are more than 1200 Cape mountain zebra, occurring in some 30 protected areas and private game ranches through out their former range (Novellie et al., 2002). However, all these new populations have been founded from the Mountain Zebra National Park population. Recent genetic research on the three natural populations indicated that each population represented one third of the entire Cape mountain zebra gene pool (Moodley, 2002), making the GMNR population vital in the conservation of Cape mountain zebra.

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GMNR was established in 1974 to conserve the 13 remaining Cape mountain zebra in the area, but before the reserve was fenced, six were shot by a local farmer (Barry, 1997). By 2002, when our study was done, the population had grown to 30 individuals. While still constituting a population at risk (Caughley, 1994), management of this population has largely been hands off, with the belief that the population has the potential to grow to approximately 90 individuals, after which it can act as a source population for the mixing of stocks in other protected areas. The growth of the GMNR population however, has been slow relative to other mountain zebra populations also classified as performing well (Novellie et al., 2002). Although this growth may be influenced by stochastic factors such as genetic drift and natural catastrophes (e.g. a fire in 1997 killed five zebra), observations suggest that environmental factors such as habitat suitability and the influence of fire on the habitat, may also be important. For example, GMNR consists mainly of fynbos, which typically has a low abundance of grass, while mountain zebra require habitat with a high abundance of palatable grasses (Novellie and Winkler, 1993; Novellie, 1994). In addition, fynbos typically burns at 12–15 year intervals (Van Wilgen et al., 1992, 1994), while higher frequencies are required to stimulate grass production (Van Wilgen et al., 1992) essential for mountain zebra population growth. With these considerations in mind, our study had the following objectives: (a) To determine the probability that the mountain zebra population will attain quasi-extinction in the next 50 years. Quasi-extinction refers to a minimum number of individuals in the population which is considered critical to the management of the population (Ginzburg et al., 1982). (b) To determine the habitat use of mountain zebra. (c) To determine the suitability of the habitats in GMNR for mountain zebra. (d) To assess the influence of fire on mountain zebra population growth in GMNR.

2. Methods

2.1. Study site

Gamka Mountain Nature Reserve (9428 ha) is situated in the Western Cape, 33 km south west of the town of Oudtshoorn. The reserve is dominated by mountainous plateaus, incised with deep valleys and the underlying rock formations are of Table Mountain quartzite and shale, and Bokkeveld shale and sandstone (Allardice and Ince, undated). The veld types in GMNR after Acocks (1988) are Succulent Mountain Scrub, Succulent Karoo, False Fynbos and Mountain Renosterveld. Due to the topography of GMNR, the vegetation on GMNR is diverse and Lloyd and Allardice (1990) recognised 10 vegetation communities, which may represent distinct habitat types to mountain zebra: Riparian community dominated by the trees *Acacia karroo*, *Rhus lancea* and *Olea europaea africana*; *Portulacaria afra* community on the lower northern slopes; *Dodonaea angustifolia–Pteronia fasiculata* community on northern slopes; Dry Mountain Fynbos community on southern slopes dominated by *Phylica purpurea* and *Erica simulans*; *Rhodocoma fruticosa* community on higher northern slopes; *Themeda triandra–Merxmuellera stricta* community on eastern plateaus and slopes; *Protea repens–Protea neriifolia* community on southern slopes; *Mimetes chrysanthus* community on southern slopes; *Protea nitida–Themeda triandra* community on southern slopes; Dry Northern Slope community dominated by *Agathosma recurvifolia* and *Aloe ferox*.

GMNR receives rain throughout the year and the mean annual rainfall varies from 500 mm on the plateaus, to 300 mm on the lower slopes. Temperatures in summer may exceed 40 °C and fall below freezing in winter (Allardice and Ince, undated).

For the purposes of our study, GMNR was divided into three sections, the north (24%), the south east (38%) and the south west (38%). Fourteen fires were recorded in GMNR between 1940 and 2002, five pre-establishment and nine post-establishment. Of these fires, some burnt more than one section and nine fires were recorded in the north, nine in the south east and 11 in the south west. Although the mean interval between fires in each section was similar (7.0, 7.0, 5.7 years, respectively), 77% of the fires in the south east burnt more than 25% of this section, compared to only 11% and 27% of the fires in the north and south west, respectively. Of the nine fires recorded in GMNR since establishment of the Reserve (1974), six originated from outside the Reserve, two were due to lightning and one was controlled (Allardice and Ince, undated; GMNR records).

The south west section of GMNR is difficult to access and our studies were done in the north and south east sections of the reserve. These sections are also the sections in which the mountain zebra mostly occurred (GMNR records).

Prior to establishment, GMNR was divided into a number of farms and used for grazing by sheep, goats, cattle and donkeys. Since establishment, mountain zebra have been the dominant grazers, but five red hartebeest (*Alcelaphus buselaphus*) were introduced onto the reserve in 1998.

2.2. Population viability analysis

We used count data to perform a population viability analysis (PVA) on the mountain zebra population in GMNR. The count data were obtained from a zebra monitoring program in which field staff used ground counts to monitor the zebra population throughout the year between 1974 and 2002. To perform the PVA we used the model of Dennis et al. (1991). This model estimates the population growth parameters $\hat{\mu}$ (the arithmetic mean of the log population growth rate) and $\hat{\sigma}^2$ (the variance of the log population growth rate) and uses these estimates to determine the extinction probabilities of a population. For the zebra population, we used linear regression as described by Morris and Doak (2002) to estimate the parameters $\hat{\mu}$ and $\hat{\sigma}^2$. These estimates can then be used to derive a number of extinction parameters; the probability of attaining extinction; the mean, median and most likely times to extinction (Dennis et al., 1991). However, Morris and Doak (2002) suggest that a cumulative distribution of extinction times is more meaningful and we used the parameters $\hat{\mu}$ and $\hat{\sigma}^2$ to generate such a function for the mountain zebra population (Morris and Doak, 2002). The extinction time cumulative distribution function calculates the probability that the population will attain quasi-extinction (G) at some future time and can be used to derive the extinction parameters mentioned above. We set the quasi-extinction threshold at 10, a threshold approximating the size of the founder population. To allow the PVA to be relevant to management, we set the time horizon at 50 years.

The model of Dennis et al. (1991) relies on a number of assumptions (see Morris and Doak, 2002); population growth rate is density independent; the count data are not autocorrelated; population growth rate is not influenced by outliers in the data. To test for density independent versus density dependent growth in the zebra population, we used the parametric bootstrap likelihood ratio test of Dennis and Taper (1994). This test derives the maximum likelihood estimates for the parameters $\hat{a}$, $\hat{b}$ and $\hat{\sigma}^2$. These estimates are used to calculate a likelihood ratio test static (t) and an associated P value. The null hypothesis for the test is density independent growth and the alternative hypothesis is density dependent growth.

We used regression analysis as described by Morris and Doak (2002), to test for autocorrelation in the data and to test that the population growth rate was uninfluenced by outliers.

2.3. Habitat use and suitability

Observations of mountain zebra habitat use during the period 1994–2000 were used to determine mountain zebra habitat use in the study area. Individuals in a herd are not statistically independent and each sighting of a zebra herd was therefore considered a single observation (Alldredge and Ratti, 1986). To reduce auto-correlation of data, only records made 24 h apart were used (Swihart et al., 1988).

Habitat availability was measured as the proportional area of each habitat within the study area. For each habitat, the area was measured with a planimeter from the vegetation map of Lloyd and Allardice (1990). Chi-squared goodness-of-fit analysis was used to test for difference between the expected and the observed frequency of use of each habitat by mountain zebra (Byers and Steinhorst, 1984). The Bonferroni method was used to determine which habitats were positively selected or avoided by mountain zebra (Byers and Steinhorst, 1984).

In each habitat, the aerial cover of grass was estimated in three randomly selected quadrats (10×10 m), using the eight point scale of Walker (1976). The mean percentage grass cover for each habitat was calculated from the mid point of each rank (Walker, 1976).

In the two habitats most used by mountain zebra, 10 sites were rated from 1 to 10 according to observed use. For each site, the vegetation was surveyed as described by Novellie and Strydom (1987) and a habitat suitability index (HSI) calculated after Novellie and Winkler (1993):

$$\mathrm{HSI} = \Sigma a_i c_i,$$

where a_i is the acceptability index of grass species i and c_i is the percentage aerial cover of grass species i. The acceptability of the grass species encountered during the surveys was rated according to observations of mountain zebra feeding behaviour (M. Scott pers. comm., 2001). At each site, the number of mountain zebra dung piles were recorded in a 1 ha plot located around the site. The habitat surveys were done in 2001.

Spearman rank correlation coefficients were computed between the HSI of the site and the use of the site by mountain zebra as measured by observation and the number of dung piles.

2.4. The influence of fire

In the study area, mountain zebra use of burnt and unburnt areas was monitored between the fires of 1992 and 1996. The chi-square test of goodness-of-fit (Yates corrected) was used to test for difference in the frequency of use of burnt and unburnt areas by mountain zebra.

The number of foals produced by the mountain zebra population three years before and after the fires of 1982, 1992, 1996 and 1997 was compared using the chi-square test of goodness-of-fit (Yates corrected). For this analysis the 1996 and 1997 fires were treated as a single fire.

3. Results

3.1. Population viability analysis

The population growth of mountain zebra in GMNR between 1974 and 2002 is shown in Fig. 1. This growth is density independent (Table 1), and regression analysis

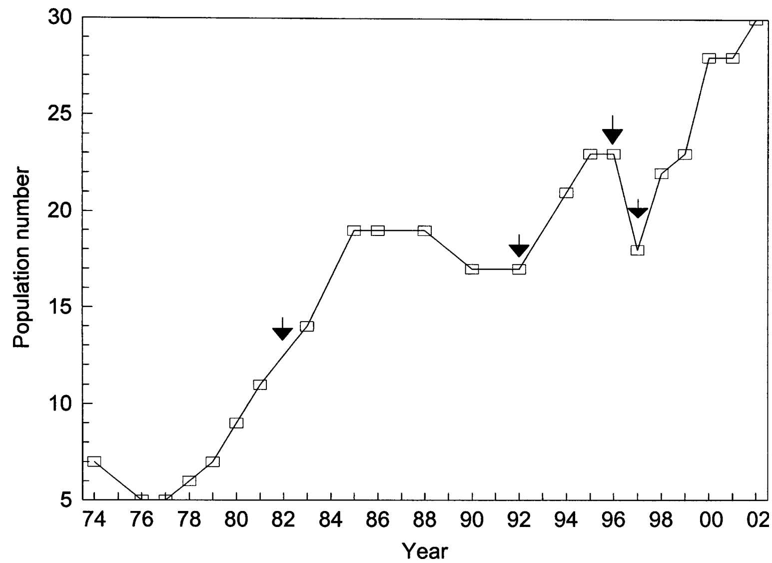

Fig. 1. The number of mountain zebra in GMNR between 1974 and 2002. Arrows indicate fires that occurred in the study area. The fire of 1997 burnt >90% of the reserve and killed five zebra.

Table 1
Maximum likelihood parameter estimates for density independent and density dependent growth models for the mountain zebra population

Model	â	$\hat{b}$	$2\hat{\sigma}$	Likelihood ratio statistics	
				t	*P*
Density independent	0.069		0.025		
Density dependent	0.14	−0.004	0.024	−0.887	0.547

The null hypothesis is density independent growth and the alternate hypothesis is density dependent growth. The estimates were calculated from 1000 bootstrap samples

indicated that the count data were not autocorrelated (first order autocorrelation $r = 0.190$, df = 20, $P > 0.20$) and that the population growth rate was uninfluenced by outliers (studentized residuals for all pairs in the regression were <2). The count data therefore conform to the assumptions of the PVA model of Dennis et al. (1991).

For the mountain zebra population, the estimates of the population growth parameters $\hat{\mu}$ and $\hat{\sigma}^2$ were 0.052 (95% confidence intervals; lower = −0.004, upper = 0.108) and 0.020 (95% confidence intervals; lower = 0.012, upper = 0.042), respectively. Importantly, although $\hat{\mu}$ was positive, the lower confidence interval of $\hat{\sigma}^2$ was negative and the probability that the slope of the regression was zero, was 0.0659. This analysis suggests that the probability of population growth over the long term is uncertain.

Using the estimates of $\hat{\mu}$ and $\hat{\sigma}^2$, the PVA model of Dennis et al. (1991) indicated that the mountain zebra population had a low probability of reaching the quasi-extinction threshold of 10 in the next 50 years ($G = 0.0032$; Fig. 2). However, the upper 95% confidence interval of G is less encouraging and indicated that the population had a 40% chance of attaining quasi-extinction in the next 50 years. Moreover, the distribution of the upper 95% confidence interval rises rapidly and indicates that the population has a high probability of reaching quasi-extinction in the next 15 years.

3.2. Habitat use and suitability

The observed habitat use of mountain zebra differed significantly from that expected from relative habitat area ($\chi^2 = 358.09$, df = 9, $P < 0.001$). Bonferroni analysis indicated that only two habitats, the *Themeda triandra–Merxmuellera stricta* and the *Protea nitida–Themeda triandra* habitats were favoured by mountain zebra, while the *Dodonaea angustifolia–Pteronia fasiculata* habitat was neutrally selected and all the other habitats were neglected by mountain zebra (Table 2).

Of these habitats, only the two favoured by mountain zebra had grass cover of >50% (Table 2). In contrast, habitats that were neutrally selected or neglected by mountain zebra typically had very little grass cover (0–16%; Table 2). Of the latter, the Dry Northern Slope habitat had relatively high grass cover (31%) but this mostly consisted of the unpalatable *Merxmuellera stricta*.

The *HSI* for the sites surveyed in the two habitats favoured by mountain zebra was positively correlated with both measures used to index mountain zebra site use (i.e.

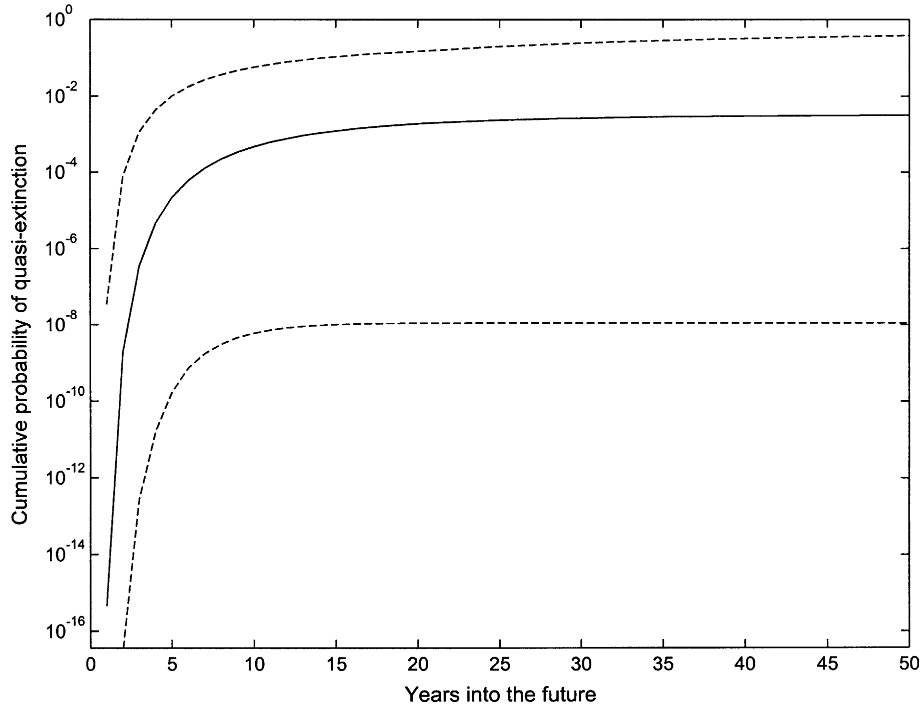

Fig. 2. The extinction time cumulative distribution function for the mountain zebra population in GMNR. The solid line indicates the best estimate of the probability of extinction, while the dashed lines indicate the 95% confidence intervals. The latter were determined by a bootstrap using a 1000 samples.

Table 2
Mountain zebra habitat preference in the study area for the period 1994–2000 (n = 489)

Habitat	Grass cover (%)	Expected use (p_{ei}) [a]	Observed use (p_{oi})[b]	95% limits	Preference[c]
Riparian	5.5	0.138	0.016	0.0–0.033	–
Portulacaria afra	0	0.035	0.004	0.0–0.012	–
Dodonaea angustifolia–Pteronia fasiculata	1.8	0.058	0.049	0.022–0.077	0
Dry Mountain Fynbos	13.5	0.155	0.09	0.054–0.126	–
Rhodocoma fruticosa	16.3	0.147	0.053	0.025–0.082	–
Themeda triandra–Merxmuellera stricta	53	0.241	0.421	0.359–0.484	+
Protea repens–Protea neriifolia	5.5	0.048	0.02	0.003–0.038	–
Mimetes chrysanthus	–	0.004	0	–	
Protea nitida–Themeda triandra	61.3	0.117	0.317	0.258–0.376	+
Dry Northern Slope	31.3	0.058	0.029	0.007–0.050	–

Codes: 95% limits = Bonferroni 95% confidence limits
[a] The relative area of the habitat.
[b] Calculated for habitat i as $p_{oi} = n_i/N$, where n_i is the number of times mountain zebra were located in that habitat and N is the total number of observations across all habitats.
[c] Preference: +, use significantly greater than expected; –, use significantly less than expected; 0, use no different to expected.

observation, number of dung piles; Table 3). Six of the sites had a *HSI* value ⩾ 20 while the remaining sites had values <10. According to Novellie (1994), the former represent good mountain zebra habitat while the latter indicate poor mountain zebra habitat.

3.3. The influence of fire

Between the fires of 1992 and 1996, observations indicated that mountain zebra favoured burnt areas over unburnt areas and mountain zebra with access to burnt areas were observed to use these areas 83% of the time (χ^2 = 26.266, df = 1, P = 0.001, n = 64). Access to burnt areas also influenced mountain zebra population growth. Since the establishment of GMNR, 30 foals were recorded for the mountain zebra population. A comparison between the number of foals produced three years before and after the fires in the study area, indicated that only two foals were produced pre-fire while 24 were produced post-fire (χ^2 = 16.962, df = 1, P = 0.001).

Table 3
The habitat suitability index of 10 sites in habitat favoured by mountain zebra in the study area

	Plots									
	1	2	3	4	5	6	7	8	9	10
Habitat suitability index	19.7	53.8	26.6	47.5	28.9	23	9.2	9.8	0.6	3.6
Rank of observed use	1	2	3	4	5	6	7	8	9	10
Number of dung piles	25	13	11	12	7	5	1	7	0	1

For observed use, rank 1 represents the most use.
Habitat suitability index vs rank of observed use: $r_s = 0.758$, df = 8, $P < 0.05$.
Habitat suitability index vs number of dung groups: $r_s = 0.756$, df = 8, $P < 0.05$.
Rank of observed use vs number of dung groups: $r_s = 0.909$, df = 8, $P < 0.001$.

4. Discussion

4.1. Population viability analysis

Population viability analysis is a modelling tool that predicts the likelihood of a population reaching some minimum size in the future (Coulson et al., 2001; Morris and Doak, 2002). The models that have been used most extensively are the simulation models (e.g. VORTEX, Lacy, 1993). These models use life-history data to predict extinction but require detailed demographic data and an estimate of carrying capacity. More over, accurate estimates of carrying capacity appear to be essential for realistic predictions (Brook et al., 1997). These data are unavailable for most wildlife populations, including the GMNR mountain zebra population. An alternative model, the diffusion model of Dennis et al. (1991) has recently been used for wildlife populations where demographic data and estimates of carrying capacity were unavailable (Dennis et al., 1991; Nicholls et al., 1996; Knight et al., 2001). This model predicts extinction from population growth rate and only requires regular census data, but population growth has to be density independent.

For the mountain zebra population in GMNR, the model of Dennis et al. (1991) predicted a low probability of quasi-extinction in the next 50 years. Although this prediction is favourable, the upper confidence limit is less encouraging and predicted a high probability of quasi-extinction in the next 15 years. The predictive accuracy of PVAs has recently been questioned, particularly when processes influencing population growth rate are likely to change and limit population growth in the future (Coulson et al., 2001). Our analysis of mountain zebra habitat use and the influence of fire on population growth suggests that the present population growth may not be sustained in the future (see below), and we argue that the PVA for the mountain zebra population in GMNR should be viewed in a cautionary rather than in an optimistic manner.

4.2. Habitat use and suitability

Ungulates favour habitats that maximise their rate of nutrient intake (Owen-smith, 1985). In GMNR, mountain zebra favoured habitats with high grass cover and within these habitats mountain zebra selected sites containing high abundances of highly acceptable grasses (e.g. *Themeda triandra*). These habitats however, only formed 30% of GMNR and using the classification of Novellie (1994), only approximately 60% of this qualified as good habitat for mountain zebra. Our analysis therefore indicated that suitable habitat for mountain zebra in GMNR is limited.

The carrying capacity for mountain zebra in the mountain complexes around GMNR is given as 66.78 ha/zebra (Boshoff and Kerley, 1999; carrying capacity – the potential of an area to support animals over an extended period without deterioration to the veld; Trollope et al., 1990). Considering that only 30% of GMNR is preferred by mountain zebra, the carrying capacity for the preferred habitat is 42 zebra. Although this estimate may be viewed as conservative (see Boshoff and Kerley, 1999), we suggest that the mountain zebra population is approaching the long term carrying capacity of GMNR. The management objective for mountain zebra in GMNR is given as follows; 'to conserve and actively manage the Cape mountain zebra population such that this population is encouraged to reach viable levels' (Barry, 2002). Although the number of zebra considered to be viable has not been stated, we take this to be 50 zebra (Caughley, 1994). However, the GMNR mountain zebra population will be a source population for introductions into other protected areas and the population will have to be larger than 50 before translocations can be considered (see Novellie et al., 2002). Given the limited suitable habitat for mountain zebra in GMNR and the finding that the lower confidence interval of $\hat{\mu}$ is negative, we argue that the probability of attaining these numbers in the near future is far from certain.

4.3. The influence of fire

Grazing ungulates are typically attracted to areas that have burnt (Bigalke and Willan, 1984). Similarly, mountain zebra in GMNR favoured burnt areas over unburnt areas. This behaviour had a marked influence on population growth and 80% of the recorded growth occurred within three years of fires burning the study area. Fire stimulates grass growth and increases the nutritive value of grass, while in sour veld such as GMNR, palatable grasses become moribund and of low nutritional value in the absence of fire (Mentis and Tainton, 1984). The observed pattern of mountain zebra growth in GMNR can therefore be related to the relatively long intervals between fire in the study area (mean = 7.0 years).

Most of GMNR is classified as fynbos and fynbos typically burns at intervals of 12–15 years (Van Wilgen et al., 1994). Burning at shorter intervals favours resprouting species and eliminates serotinous Proteaceae (Van Wilgen et al., 1994). The primary management objective of GMNR is to conserve biodiversity and the fire management policy therefore stipulates burning at 12 year intervals (Barry, 2002). Our findings however, indicate that burning at shorter intervals would be necessary if the growth of the mountain zebra population is to be sustained. From this it is clear that the primary management objective of GMNR and the management objective of mountain zebra are in conflict. If so, how then was the present population growth of mountain zebra in GMNR possible? Since the establishment of GMNR in 1974, all fires in the habitat favoured by mountain zebra have been uncontrolled and present population growth is thus incidental rather than managed.

4.4. Management options

Our findings indicate that the mountain zebra population in GMNR face a high risk of quasi-extinction in the near future and we suggest that viable management options need to be implemented to reduce this risk. We consider a number of management options but suggest that only two, the forming of a conservancy and the leasing of land, are likely to stimulate mountain zebra population growth in the short term and that these should receive immediate attention: (1) Translocation of mountain zebra in GMNR to another protected area within the region with more suitable habitat. As already mentioned, the likelihood for the mountain zebra attaining a population size from which zebra can be removed for translocation, under the present circumstances, is uncertain. This option can therefore only be considered once other options have been put in place to stimulate mountain zebra population growth (see Caughley, 1994). (2) The acquisition of adjacent land. This option is receiving high priority at present. Unfortunately, most of the land marked for acquisition lies to the west of GMNR and most of this land is similar to the unsuitable habitat in the south west section of GMNR. Although, some suitable habitat does occur within the land marked for acquisition, unsuitable habitat forms a barrier between it and the area presently used by the mountain zebra in GMNR. Dispersal into this suitable habitat is therefore only likely to occur in the long term and zebra in this habitat may also become genetically isolated from the source population in GMNR. Acquiring suitable land adjacent to the area presently used by the mountain zebra therefore needs to be considered. For reasons already mentioned, this may mean acquiring land that has low conservation value with respect to fynbos. (3) Burning the preferred habitat of mountain zebra at shorter intervals. As discussed, this option may compromise the primary management objective of GMNR (i.e. conserving biodiversity). However, this preferred habitat has historically burnt more extensively than other parts of GMNR and reseeding Proteaceae may already be lost from this habitat. Research indicating the status of reseeding Proteaceae in the habitat preferred by mountain zebra therefore needs to be done as a matter of urgency. Until such work has been completed, this option cannot be considered. (4) Forming a conservancy with the landowners adjacent to the area used by the mountain zebra. Financial constraints limit the purchasing of land and the forming of a conservancy with adjacent landowners that have suitable habitat needs to be pursued. An advantage of this option is that zebra already range up to the fence line of this land and dropping this fence will immediately extend the range of the mountain zebra. In addition, this land can be managed for a high fire frequency and thus ensure zebra population growth. (5) Leasing cultivated land adjacent to the area used by the mountain zebra. The land to the south of the habitat preferred by mountain zebra is extensively cultivated. This land could be leased and cultivated with pasture to stimulate mountain zebra population growth. As with the previous option, the zebra already range up to this fence line and this option will allow immediate access to high quality grazing.

Our findings indicate that limited suitable habitat for mountain zebra in GMNR and the strict application of the present fire policy will in the future reduce the population growth of mountain zebra relative to that experienced presently. We therefore suggest that the risk of quasi-extinction to the mountain zebra population in GMNR is greater than that predicted by our PVA (see Coulson et al., 2001) and suggest that this population can no longer be managed in a hands off manner, but that as a matter of urgency, viable management options need to be implemented to reduce the risk of quasi-extinction to this population.

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