



Recognition and management of ecological refugees: A case study of the Cape mountain zebra



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ABSTRACT

Anthropogenic activities have led to long-term range contraction in many species, creating isolated populations in ecologically marginal and suboptimal habitats. 'Refugee' species have a current distribution completely restricted to suboptimal habitat. However, it is likely that many species are partial refugees, where one or more populations are managed in ecologically unsuitable habitat. Here, we develop a framework to assess potential refugee populations in marginal habitats using a model species: the Cape mountain zebra. We assessed habitat quality by the abundance and palatability of grass and diet quality using proximate nutrient and element analysis. High grass abundance was associated with higher population growth rates and zebra density and less skewed adult sex ratios. Furthermore, faecal nutrient and dietary element quality was also positively associated with grass abundance. Our results show that poorly performing populations were characterised by suboptimal habitat, supporting the hypothesis that the Cape mountain zebra has refugee populations. In addition, we found more variance in sex ratio and population growth rates in smaller populations suggesting they may be more at risk for random stochastic effects, such as a biased sex ratio, compounding poor performance. We show how the 'refugee' concept can be applied more generally when managing species with fragmented populations occurring across marginal habitats. More broadly, the results presented herein highlight the importance of recognizing the range of habitats historically occupied by a species when assessing ecological suitability. Identifying and mitigating against refugee, relict and gap populations is especially critical in the face of on-going environmental change.

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1. Introduction

1.1. Current protected area coverage

Globally, protected areas are biased towards areas that have low value for human conversion for agriculture or development ("rock and ice" landscapes, Joppa and Pfaff, 2009). Given these biases, it is unsurprising that many species have distribution ranges that do not coincide with formally protected areas (Rodrigues et al., 2004a). In fact, over 92% of critically endangered fauna can be considered as 'gap species', as their ranges do not occur within any protected area (Rodrigues et al., 2004b). Many more species can be considered as 'partial gap species', where only a small proportion of their range is protected (Rodrigues et al., 2004b; Maiorano et al., 2006).

Whilst inadequate range overlap with protected areas is a clear impediment to successful conservation, confinement of a species in poor

quality or unsuitable habitat is an equal but often overlooked problem. Thus, a simple focus on protected area overlap with species' ranges may not be an appropriate measure of adequate protection. In addition to overlap, habitat suitability of protected populations needs to be considered. Species that are restricted or managed in marginal habitats may have poorer long-term prognosis than is apparent by evaluating protected area coverage. An extreme case is the 'refugee species' (Kerley et al., 2012), where anthropogenic pressures across a species' historical distribution leaves little available optimal habitat, and management interventions now restrict species to lower quality areas of their range where fitness is reduced. Whilst a gap species has a range that is absent from any protected area, a refugee species' range is confined to a protected area consisting of suboptimal or inappropriate habitat. The refugee concept builds on the ideal free distribution theory of habitat selection (Fretwell, 1972): population density will be highest in optimal habitats, but individuals will disperse into low quality habitat creating a gradient from high performing 'source' to low density 'sink' populations that are maintained by immigration from source populations (Pulliam, 1988) where reproduction and mortality rates vary across sites (Pulliam and Danielson, 1991). Habitat loss and

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fragmentation can lead to populations that are restricted to poor quality habitat. These populations will have a higher extinction risk than large, high-density populations in optimal habitats (Pulliam and Danielson, 1991), due to slow population growth rates and/or low population densities (Kerley et al., 2012). Convincing evidence for refugee status has been compiled for the European bison (*Bison bonasus*) and the Mediterranean monk seal (*Monachus monachus*) (Kerley et al., 2012; Bocherens et al., 2015; González, 2015).

Importantly, when range contraction occurs over several decades or longer, relict populations can be perceived as occurring in 'natural' or core habitat, due to the acceptance of an altered state as a baseline. 'Shifting baseline syndrome' has been discussed in detail with regard to fishing stocks (Pauly, 1995; Pinnegar and Engelhard, 2008), and has been identified as a real concern for conservation policy-making (Papworth et al., 2009). Counter-productive management strategies can be implemented under shifted baselines, for example translocations and introductions may be targeted towards areas of suboptimal habitat. As with partial gap species (those with a portion of their range outside a protected area) it is likely there are many cases of partial refugees, with at least some populations actively managed in protected, but marginal, habitat. In fact, many species may be both partial gap and partial refugees, where their current distribution is limited to poorly protected, suboptimal habitats. Thus, long-term conservation of species that have undergone extensive range contraction demands the recognition that relict populations may not occur in optimal habitats across their historical distribution. Successful management and conservation of such species relies on the implementation of novel interventions to overcome such constraints (Kerley et al., 2012).

A second consequence of long-term range contraction is habitat fragmentation leading to small, isolated populations. Such populations are more vulnerable to extinction as a result of multiple processes including environmental and demographic stochasticity and inbreeding (Lande, 1998). Thus, refugee populations are likely to be small, stochastic and isolated (Lesica and Allendorf, 1995), which can also result in Allee effects, where population performance is reduced in small or low-density populations. However, the causes of Allee effects are notoriously hard to document in vertebrate populations (Courchamp et al., 2008). Thus, historical fragmentation can impose both ecological and demographic challenges for populations.

1.2. Cape mountain zebra as a partial refugee

The Cape mountain zebra (*Equus zebra zebra*) is a candidate for partial refugee status (see Kerley et al., 2012 for assessment criteria). During the 20th and 21st centuries they underwent a large-scale population decline due to excessive hunting, persecution and habitat loss, leaving three relict populations with fewer than 80 total individuals. Active conservation has resulted in reintroduction across their historic range, with numbers now in excess of 4791 individuals (Hrabar and Kerley, 2015). Although this represents a great improvement and a rare conservation success story, many difficulties are still faced in their management. Cape mountain zebra occur as a complex of >75 small, fragmented and isolated populations, on both formally protected and privately-owned land. Individuals cannot freely disperse between these populations, rendering long-term natural metapopulation dynamics impossible without human intervention. Apart from one historical translocation, slow and stochastic growth in two of the relict populations has precluded the removal of individuals, such that 95% of the global population derives from the single relict population in the Mountain Zebra National Park. The prolonged bottleneck and isolation has resulted in the relict populations (and their daughter populations) becoming genetically distinct from one another (Moodley and Harley, 2006). Consequently, a large proportion of the remaining genetic diversity remains unrepresented by the majority of the subspecies, and is under threat of being lost altogether if the two relict populations

(Gamkaberg Nature Reserve and Kammanassie Nature Reserve) are not secured.

Cape mountain zebra are an ideal model species for understanding how confinement to marginal habitat impacts on population performance because the current populations, both relict and reintroduced, occur across a range of habitat types. Most of the Cape mountain zebra's current (and historic) range is found within the Cape Floristic Region in South Africa (Boshoff et al., 2015; Hrabar and Kerley, 2015). The north-eastern areas are characterised by summer rainfall and escarpment grasslands, whereas the southwest is dominated by winter-rainfall, with fynbos and succulent Karoo vegetation communities and low grass cover, much of which is not suitable for grazing animals (Boshoff et al., 2002; Kerley et al., 2003). The distribution of protected areas within the Cape Floristic Region is heavily biased towards marginal upland habitat (Rouget et al., 2003a), with few lowland areas large enough to support even small populations of large mammal herbivores (Kerley et al., 2003). Paleontological evidence suggests that Cape mountain zebra occupied open grassland, and persisted in low densities in fynbos habitat (Faith, 2012). There is evidence that, where possible, Cape mountain zebra seasonally move between habitat types and predominantly select areas with high grass cover (Penzhorn, 1982; Grobler, 1983; Winkler and Owen-Smith, 1995; Smith et al., 2008).

Two of the relict populations, Gamkaberg Nature Reserve and Kammanassie Nature Reserve, are dominated by fynbos vegetation and it has been suggested that <40% of each reserve is appropriate habitat for Cape mountain zebra (Watson et al., 2005; Watson and Chadwick, 2007). Most importantly, these populations have been actively managed in upland areas with restricted access to year-round grass-rich habitats and drinking water, which is likely a key factor leading to limited population growth. As relict populations were restricted to upland fynbos habitat in recent memory, these areas have been perceived by managers as core habitats for Cape mountain zebra, despite poor population performance. Thus, introductions and translocations of individuals into similar, and more arid, habitats have been supported as a key part of the species management plan (Novellie et al., 2002).

Here, we assess partial refugee status in the Cape mountain zebra by evaluating variation in habitat quality and population performance across reserves. We predict that: 1) populations in grass-poor habitats will have slower population growth rates and lower population densities, and 2) habitat quality (grass availability) and population performance will be associated with nutrient profiles derived from faecal diet analysis. We use three measures of population performance, which reflect different aspects of population health: population growth rate, zebra density and foal:mare ratio. We then provide a framework for identifying refugee populations both in Cape mountain zebra and other potential refugee species, and discuss the importance and application of this concept within conservation biology.

2. Methods

2.1. Vegetation index

Habitat assessments were made for a subset of 21 Cape mountain zebra populations (both public and private reserves, representing 28% of extant populations) where long-term population records were available, and which varied in terms of grassiness. We developed a *perceived grass vegetation index* (VI) that incorporates fine-scale differences in vegetation communities by qualitatively assessing the abundance of palatable grass species within each reserve. Although this technique does not quantify the biomass of palatable grass, it provides a systematic and repeatable assessment of grass dominance and richness that can be readily estimated across populations. The majority of the resources used (vegetation map and reserve boundaries) are freely available online (SANBI, 2006). Where geo-referenced maps were not available for private reserves, boundary information was obtained from reserve managers and shapefiles were created using Google Maps, with imagery

provided by 2015 AfriGIS (Pty) Ltd., Google Imagery 2015, CNES/Astrium, CNES/Spot Image, DigitalGlobe, Landsat and TerraMetrics TruEarth Satellite Imagery. The boundary of each reserve was overlain on the National Vegetation Map of South Africa, Lesotho and Swaziland (Mucina and Rutherford, 2006) using ArcGIS Desktop v.10, and the area of all vegetation types occurring in the reserve was estimated. Each defined vegetation type has an associated list of 'Important Taxa' that have a high abundance or frequent occurrence within the landscape, and also highlights dominant taxa (Mucina and Rutherford, 2006). The number of graminoid species in this list (excluding Cyperaceae, Juncaceae and Restionaceae) was used as a proxy for grass abundance; dominant species were weighted by a factor of two (see Table A1 for the list of vegetation types and the number of grass species present). Each grass species was ranked in terms of palatability (1 = low, 2 = medium, 3 = high) using information from published resources and online databases (see Table A2 for full list of species; Van Breda et al., 1990; Quattrocchi, 2006; Van Oudtshoorn, 2012; Andersson et al., 2015). Graminoid species listed in the 'Endemic Taxa' section (Mucina and Rutherford, 2006) were included. Graminoids, mainly endemic to a particular vegetation type, were excluded if there was no information available for palatability, which constituted 42 out of 154 described species or 65 out of 558 (~12%) of total occurrences. This resulted in a vegetation index for each vegetation type (VI_V) present within a reserve that was calculated by:

$$VI_V = \Sigma PT + \Sigma 2PD$$

where T is the total number of non-dominant grass species listed in the vegetation type description, D is the number of dominant grass species listed and P is the palatability of each grass species found within that vegetation type.

Finally, a standardised VI for each reserve was calculated as:

$$VI = \frac{\Sigma(CVI_V)}{VI_{MAX}}$$

where C indicates the percentage area of each vegetation type within a reserve and VI_{MAX} is the highest VI attained by any reserve in this study. The grass cover of three reserves was adjusted to reflect anthropogenic removal of fynbos habitat and replacement with disturbed, cultivated grasslands containing highly palatable grass species (De Hoop Nature Reserve: 1.70%, Swartberg Private Game Reserve: 21.52% and Welgevonden Game Farm: 41.72%). The boundaries of these disturbance grasslands were demarcated using Google Maps® and given the same VI_V as the high quality Karoo Escarpment Grassland as transformation of land in these reserves was managed for grazing stock and therefore constitutes a high abundance of palatable grass species.

2.2. Diet quality

Faecal analysis has been used to estimate diet quality across several wild herbivore taxa (Erasmus et al., 1978; Hodgman et al., 1996; Mésochina et al., 1998; Putman, 1984; Landman et al., 2013). We used this approach to evaluate Cape mountain zebra diet quality variation across reserves. During April and May 2014, a total of 106 faecal samples were collected from Mountain Zebra National Park, Gamkaberg Nature Reserve, De Hoop Nature Reserve, Camdeboo National Park, Mount Camdeboo Private Reserve and two sites in Karoo National Park (the Potlekertjie Loop and the Mountain View area in the east). Fresh samples (<1 h) were collected from as many individuals as possible, although if necessary older samples were also collected and age estimated (<24 h or >24 h). Samples were oven dried at 60 °C and milled using a 1 mm sieve, then subject to proximate diet analysis to estimate the content of crude protein, ash, fat, acid detergent fibre (ADF) and neutral detergent fibre (NDF) in the Cedara Feed Laboratory, South Africa (for full protocols see AOAC, 1980 and Goering and van Soest,

1970). The minerals Ca, Mg, K, Na, P, Zn, Cu, Mn, and Fe were determined by dry-ashing samples and atomic absorption spectroscopy. Faecal crude protein content from the proximate diet analysis was converted to faecal N by dividing by 6.25 (Rivera and Parish, 2010). Crude protein represents all sources of nitrogen in the faeces and is directly positively related to the palatability and digestibility of the diet (Erasmus et al., 1978), while ash represents the inorganic minerals. Conversely, the fibre content (shown here as NDF and ADF) coincides with low digestibility, where NDF represents the total amount of fibre in the diet and ADF the component of that fibre that is indigestible (Rivera and Parish, 2010). N and P are the most frequently measured elements as indicators of forage quality and both are limiting nutrients in South Africa (Wrench et al., 1997; Grant et al., 2000).

2.3. Study sites and population performance measures

Collection of demographic data took place at the following reserves (Fig. 1): Bakkrans Nature Reserve, Camdeboo National Park, De Hoop Nature Reserve, Gamkaberg Nature Reserve, Karoo National Park, Mount Camdeboo Private Reserve, Mountain Zebra National Park, Samara Private Game Reserve, Swartberg Private Game Reserve and Welgevonden Game Farm. Data were collected during seven sampling periods: Aug.–Sep. 2010, Feb.–June 2011, Dec.–Mar. 2012, Nov.–Dec. 2013, Apr.–May 2014, Jan.–May 2015 and Sep.–Dec. 2015; eight reserves were visited a minimum of four times across these sampling periods whilst the remaining two were visited twice. Each visit entailed a minimum of three reserve-wide surveys. Surveys were conducted both by vehicle and on foot, using public access and/or management roads. Whilst surveys are likely biased towards the areas covered by roads, the use of binoculars from key vantage points enabled most reserves to be surveyed extensively. The most notable exception to this is Karoo National Park, which is large, mountainous, and has a large section in the west not covered by a road network. Upon encounter, overall group size and each individual's sex and age class (foal \leq 12 months, sub-adult 13–36 months, adult >36 months) were recorded. Where possible, and for the majority of zebra sighted, each individual was photographed and repeated sampling of individuals was accounted for using HotSpotter identification software (Crall et al., 2013). The number of foals per mare observed at each reserve was averaged over all sampling periods to give the mean number of foals per mare (foal:mare). In addition, the following information for a further 16 populations was made available by the management team at each reserve from their records and 2015 ground and aerial counts: founding year, founding number, current population size, number of introductions and removals and the reserve area. Population growth rate was calculated using:

$$N_t = N_0 e^{rt}$$

solved for r:

$$r = \frac{\ln N_t - \ln N_0}{t}$$

where r is the rate of increase, N_t is the current population size, N_0 is the starting population size (or founding number), t is the time in years, e is the mathematical constant and ln the natural log. Current population size was adjusted for any recorded introduction or removal events since the population was founded: introductions were added to the founder population number and removals were added to the current population size. Populations range from 5500 to 146,000 ha, with the youngest founded nine years ago and the oldest relict population, Mountain Zebra National Park, established 79 years ago. Population density was calculated as current population size/reserve area (number of individuals/ha). Poorly performing populations were defined as scoring at least 50% worse than the best performing population on each measure. Mountain Zebra National Park was excluded from this

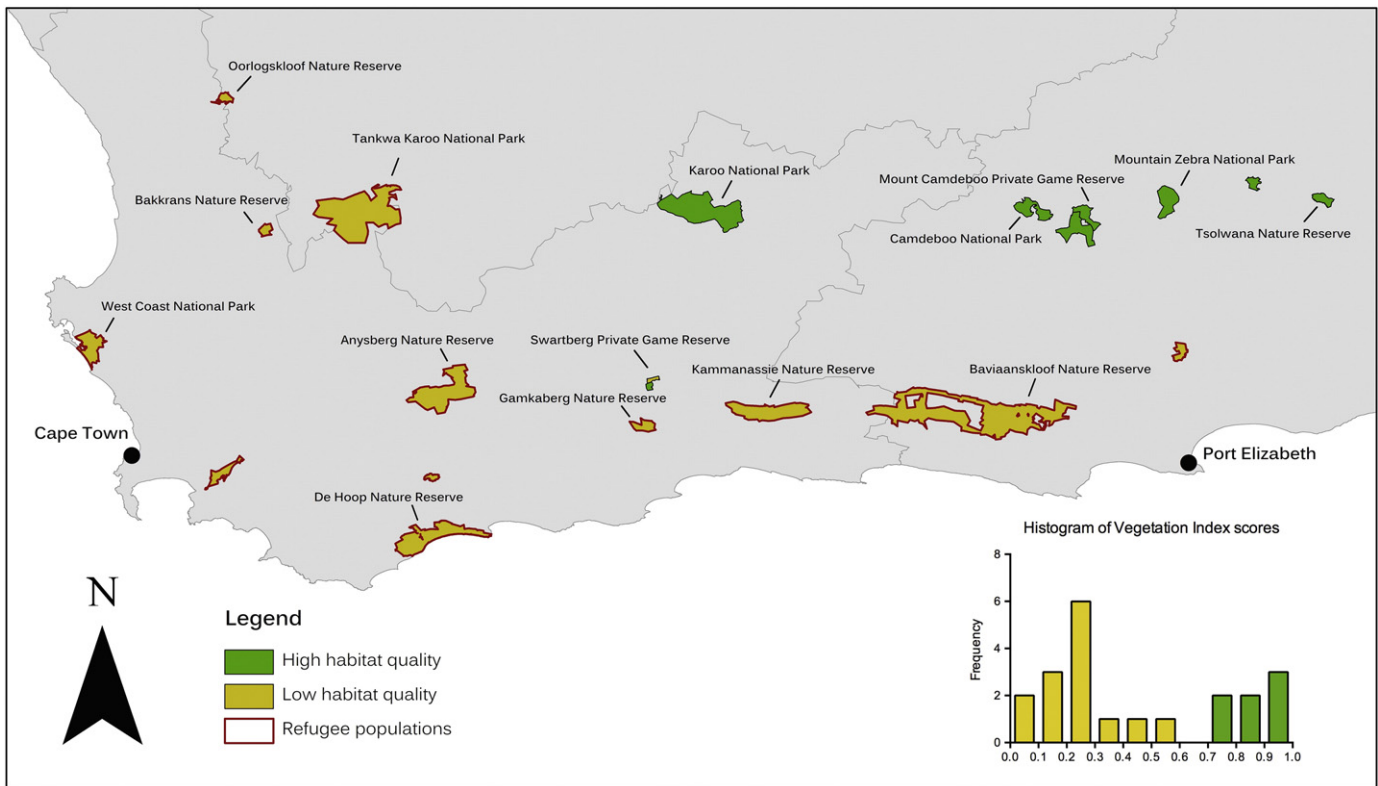


Fig. 1. Variation in Vegetation Index scores across populations where population performance and demographic data were available. Some focal populations are labeled.

calculation as it has an extremely high density of individuals that likely reflects its substantially longer time since establishment than any other reserve in similar habitat, and if included would unfairly make all other populations poorly performing on this measure. The three measures (growth rate, density and foal:mare) reflect different aspects of performance. Newly founded populations may still be growing quickly as they have not yet reached carrying capacity, whereas older established populations, such as in Mountain Zebra National Park, support a high density but have relatively moderate population growth rates. The observed number of foals per mare gives an indication of female fecundity at each site. In addition, the mean number of adult males and adult females observed from surveyed populations were used to calculate adult sex ratio (male:female).

2.4. Statistical analyses

Statistical analyses were performed using RStudio v.0.98.976 and IBM SPSS Statistics v.22. To reduce the proximal nutritional components (crude protein, ash, fat, NDF and ADF) to fewer explanatory variables, we performed a principal component analysis (PCA). Fat was removed as it formed its own principal component (PC), leaving the remaining four variables loading on to one PC (crude protein and ash loading positively and ADF and NDF loading negatively) that explained 46.6% of the variation with a Keiser-Meyer-Olkin (KMO) score of 0.610. A second PCA was performed on the mineral components of the diet analysis; Ca and K were removed as they did not load with the other minerals; the remaining eight minerals loaded onto two PCs (PC1: N, P, Na, Zn, Mg and PC2: Cu, Fe, Mn). The two components explained 65.6% of the variation in the analysis with a KMO score of 0.714. VI scores had a bimodal distribution (see histogram in Fig. 1), and are presented as both a categorical factor with 'high' and 'low' grass categories and a continuous variable in the performance measure analyses. Diet quality was compared across reserves and with categorical VI using Generalized Linear Models (GLM), with age of sample included as a factor and

subsequently removed if not significant ($p > 0.05$). GLMs were used to evaluate relationships between continuous and categorical VI and population growth rate, foal:mare ratio, zebra density and with continuous VI and adult sex ratio. Reserve size and years since establishment were included as fixed factors in the population performance analyses, and removed if not significant. Zebra density was cube root transformed before statistical analysis to normalise the data. F tests were used to compare variance in sex ratio and population growth rate between small (< 50 individuals) and large populations (stats library, R Core Team, 2016).

3. Results

3.1. Habitat and diet quality

The distribution of VI scores was bimodal; reserves with less than half the abundance of palatable grass than that of the highest of this study were characterised as having low habitat quality for Cape mountain zebra (Fig. 1). High VI scores are associated with summer rainfall areas on the Karoo escarpment where there is high abundance of palatable C4 grasses, whereas low VI scores are found in arid and/or winter rainfall regions, primarily, but not exclusively, in the fynbos biome. The levels of faecal nutrients ($F_{6,98} = 26.29$, $p < 0.001$) and macro ($F_{6,99} = 34.46$, $p < 0.001$) and microelements ($F_{6,99} = 18.52$, $p < 0.001$) varied significantly between reserves (Fig. 2). Faecal nutrient ($F_{1,104} = 9.74$, $p < 0.01$), macroelement ($F_{1,104} = 10.90$, $p < 0.01$) and microelement ($F_{1,104} = 14.87$, $p < 0.001$) content were all positively associated with VI. However, between-reserve differences in faecal diet profiles accounted for more variation than did grassiness. Overall, faecal samples from Camdeboo National Park and Karoo National Park Potlekkertjie Loop contained the highest levels of crude protein, macro and microelements, while samples from Gamkaberg Nature Reserve contained the lowest (Fig. 2; Table A3).

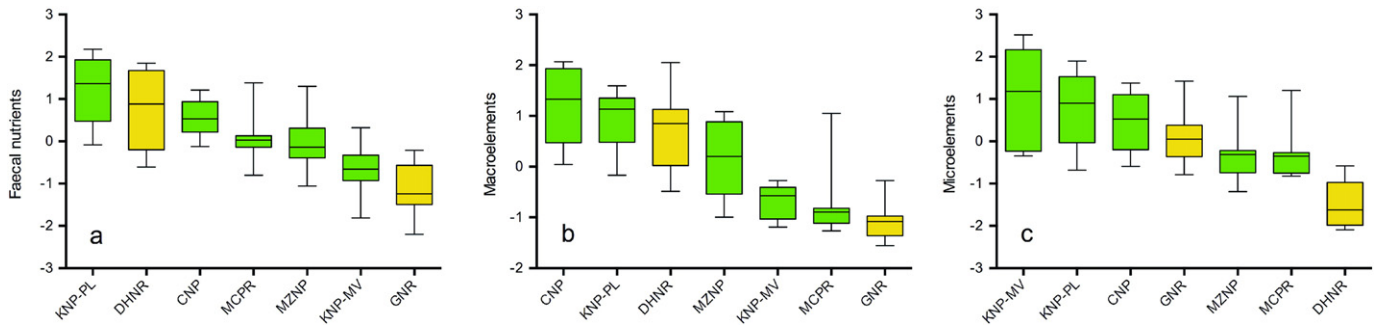


Fig. 2. Mean values of a) proximate diet component (crude protein, ash, acid detergent fibre (ADF) and neutral detergent fibre (NDF) content, where crude protein and ash load positively on the principal component and ADF and NDF load negatively), b) macroelement and c) microelement content of Cape mountain zebra faecal samples across reserves. Reserve abbreviations are: CNP: Camdeboo National Park, DHNR: De Hoop Nature Reserve, GNR: Gamkaberg Nature Reserve, KNP-MV: Karoo National Park, Mountain View, KNP-PL: Karoo National Park, Potlekertjie Loop, MCPR: Mount Camdeboo Private Reserve; MZNP: Mountain Zebra National Park. Colours represent the Vegetation Index score as in Fig. 1. Boxes show the median, upper and lower quartiles while the whiskers show the range of the data.

3.2. Population performance indicators

Performance measures and VI scores for each reserve can be viewed in Table 1. Population growth rate was significantly correlated with zebra density and foal:mare ratio ($R = 0.60$, 95% C.I. 0.24 to 0.82, $p < 0.01$ and $R = 0.72$, 95% C.I. 0.16 to 0.93, $p = 0.02$, respectively). There was a positive trend between zebra density and foal:mare ratio, though not significant ($R = 0.61$, 95% C.I. -0.03 to 0.90, $p = 0.06$). All three performance measures were significantly higher in reserves with a high VI (Fig. 3) when treated as a categorical variable (population growth rate: $\beta = -0.05 \pm 0.02$ s.e., $t_{1,19} = -3.01$, $r^2 = 0.29$, $p < 0.01$; zebra density: $\beta = -0.09 \pm 0.03$ s.e., $t_{2,18} = -3.33$, $r^2 = 0.44$, $p < 0.01$; foal:mare ratio: $\beta = -0.16 \pm 0.05$ s.e., $t_{1,8} = -3.45$, $r^2 = 0.55$, $p < 0.01$). Population growth rate and zebra density increased significantly with continuous VI (population growth rate: $\beta = 0.07 \pm 0.03$ s.e., $t_{1,19} = 2.22$, $r^2 = 0.16$, $p = 0.04$; zebra density: $\beta = 0.14 \pm 0.04$ s.e., $t_{2,18} = 3.62$, $r^2 = 0.48$, $p < 0.01$), and there was a positive trend between continuous VI and foal:mare ratio ($\beta = 0.20 \pm 0.09$ s.e., $t_{1,8} = 2.27$, $r^2 = 0.32$, $p = 0.05$). Zebra density decreased with increasing reserve size in both models ($\beta = -7.61e-07 \pm 3.52e-07$ s.e., $t_{2,18} = -2.16$, $r^2 = 0.48$, $p = 0.04$ and $\beta = -8.12e-07 \pm 3.63e-07$ s.e., $t_{2,18} = -2.24$, $r^2 = 0.44$, $p = 0.04$).

3.3. Demography and population performance

For the subset of populations with demographic data, sex ratio and population growth rate variance was higher across small populations (<50 individuals) than large populations ($F_{4,4} = 21.81$, $p = 0.01$ and $F_{8,11} = 4.26$, $p < 0.05$, respectively). The ratio of adult males to adult females was negatively associated with VI ($\beta = -0.96 \pm 0.41$ s.e., $t_{1,8} = -2.33$, $r^2 = 0.33$, $p = 0.05$), such that populations in grass poor habitats were more likely to have a male biased sex ratio. Adult sex ratio was marginally, but not significantly, associated with foal:mare ($\beta = -0.14 \pm 0.06$ s.e., $t_{1,8} = -2.04$, $p = 0.08$, $r^2 = 0.34$), but not with population growth rate ($\beta = -2.45 \pm 1.82$ s.e., $t_{1,8} = -1.35$, $p = 0.22$, $r^2 = 0.18$) or zebra density ($\beta = -0.004 \pm 0.004$ s.e., $t_{1,8} = -1.11$, $r^2 = 0.15$, $p = 0.30$), suggesting that VI had a stronger impact on population performance than demography.

3.4. Identification of refugee populations

The distribution of scores in the standardised Vegetation Index was bimodal (see histogram in Fig. 1); therefore populations in the lower half were highlighted as potential refugees. Populations were subsequently confirmed as refugees if they performed poorly in one or

Table 1
Population performance measures, relative assessment of palatable grass abundance (Standardised Vegetation Index), and refugee status for 21 Cape mountain zebra populations.

Reserve	Standardised Vegetation Index	Current population size	Population growth rate	Density (individuals/ha)	Mean foal:mare (\pm s.d.)	Refugee population?
Anysberg Nature Reserve	0.06	23	0.019	0.0003		Yes
Bakkrans Nature Reserve	0.02	43	0.066	0.0038	0.208 \pm 0.06	Yes
Baviaanskloof Wilderness Area	0.32	51	-0.009	0.0026		Yes
Bontebok National Park	0.25	9	0.025	0.0027		Yes
Camdeboo National Park	0.72	236	0.076	0.0122	0.347 \pm 0.13	No
Commandodrift Nature Reserve	0.95	136	0.075	0.0227		No
Coppermoon Private Reserve	0.49	46	0.068	0.0077		Yes
De Hoop Nature Reserve	0.13	100	0.038	0.0017	0.186 \pm 0.06	Yes
Gamkaberg Nature Reserve	0.24	42	0.047	0.0040	0.083 \pm 0.12	Yes
Hottentots-Holland Nature Reserve	0.27	6	-0.086	0.0003		Yes
Kammanassie Nature Reserve	0.13	80	0.067	0.0037		Yes
Karoo National Park	0.81	843	0.062	0.0091	0.369 \pm 0.06	No
Mount Camdeboo Private Reserve	0.89	71	0.076	0.0059	0.235 \pm 0.11	No
Mountain Zebra National Park	0.93	1191	0.078	0.0558	0.385 \pm 0.12	No
Oorlogskloof Nature Reserve	0.12	19	-0.022	0.0034		Yes
Samara Private Game Reserve	0.80	26	0.099	0.002	0.332 \pm 0.04	No
Swartberg Private Game Reserve	0.29	29	0.085	0.0145	0.278 \pm 0.16	No
Tankwa Karoo National Park	0.23	41	0.035	0.0003		Yes
Tsolwana Nature Reserve	1	144	0.074	0.0185		No
Welgevonden Game Farm	0.51	34	0.145	0.017	0.436 \pm 0.02	No
West Coast National Park	0.23	42	0.067	0.014		Yes

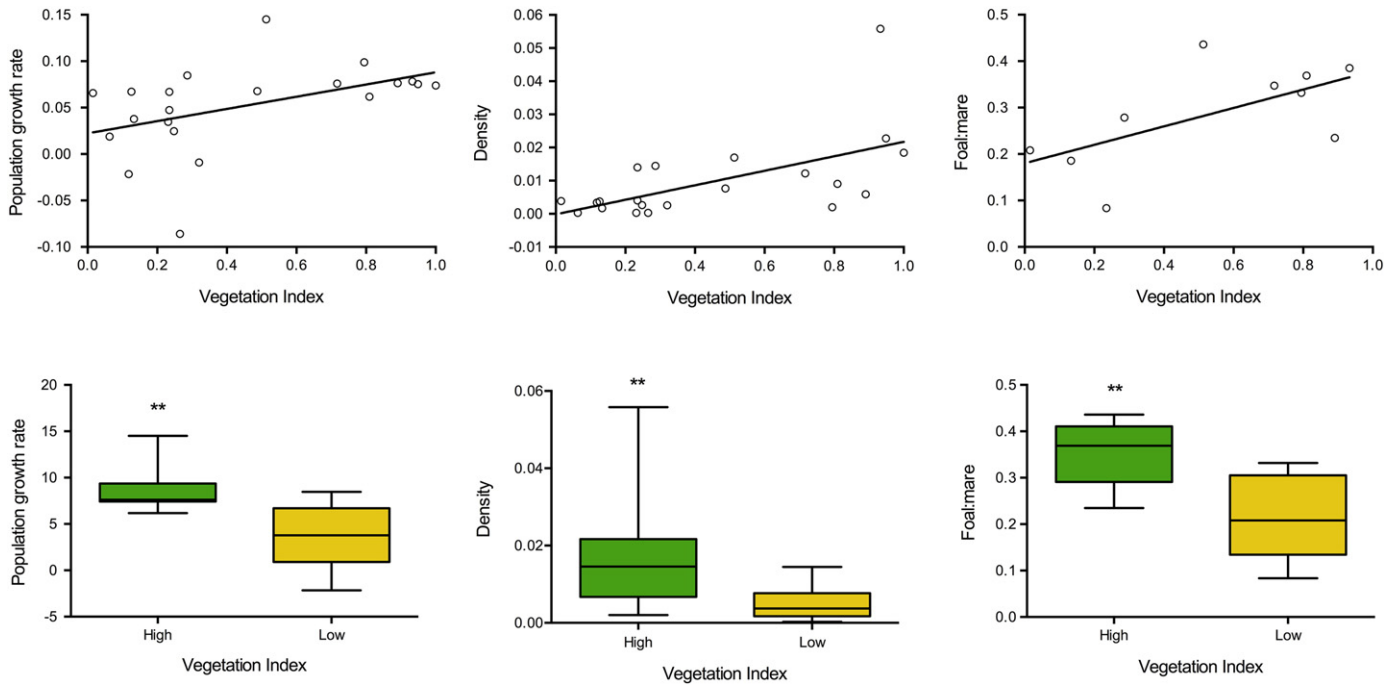


Fig. 3. Population growth rate, zebra density (individuals ha^{-1}), and female fecundity (foal:mare ratio) of Cape mountain zebra are all positively associated with habitat quality (Vegetation Index), shown as both a continuous and a categorical variable. Boxes show the median, upper and lower quartiles while the whiskers show the range of the data.

more of the population performance measures (scoring at least 50% worse than the highest performing population on each measure). Using this criterion, we identified 12 refugee populations out of a total of 21 (i.e. 57%) in this study (Fig. 4).

4. Discussion

4.1. A model partial refugee species: the Cape mountain zebra

Our results support the hypothesis that the Cape mountain zebra has refugee populations, which are confined to protected areas containing suboptimal habitat within its historic range and are characterised by poor population performance. The habitats currently occupied by Cape mountain zebra differ substantially in terms of their grass availability and nutrient and elemental dietary composition. We identified 12 refugee populations of Cape mountain zebra in this study, which have low habitat quality and score poorly in at least one performance measure. Populations in habitats with less palatable grasses performed worse across all performance indicators (population growth rate, foal:mare and density) and had more male-biased adult sex ratios. Low density populations were also associated with lower growth rates and male-biased sex ratios were weakly associated with female fecundity (foal:mare). This which raises two questions: 1) how does demography impact on population growth rates?, and 2) what is the cause of skewed sex ratios? That smaller populations had higher sex ratio and population

growth rate variance could either be the result of random demographic stochasticity or could suggest differential fecundity or survivorship in small populations. This also highlights potential feedback between habitat quality, population demography and long-term performance.

The three populations that contain the majority of the genetic diversity of the sub-species (Gamkaberg, Kammanassie and De Hoop Nature Reserves; Moodley and Harley, 2006) were all identified as refugee populations, suggesting that habitat, and specifically palatable grass availability, is limiting performance for these key populations. Moreover, other refugee populations recently re-introduced into reserves with a lower abundance of palatable grasses (e.g. Anysberg Nature Reserve and Bakkrans Nature Reserve) have performed worse than the two relic populations. These results corroborate studies that have argued that only small areas of some reserves have sufficient grazing for Cape mountain zebra (Watson et al., 2005; Watson and Chadwick, 2007; Smith et al., 2011; Weel et al., 2015). It is important to note that there are seasonal rainfall differences between reserves that could affect diet quality at different times throughout the year. It is likely this is a contributing factor leading to between-reserve differences in diet quality accounting for more variation than VI in this study. This said, faecal samples collected from individuals utilising different vegetation communities in the same reserve (Karoo National Park) reflect marked differences in nutrient and element quality (Fig. 2, Table A3). A large proportion of the Cape mountain zebra's historic range covers the Cape Floristic Region, where soil nutrients are often low (Goldblatt

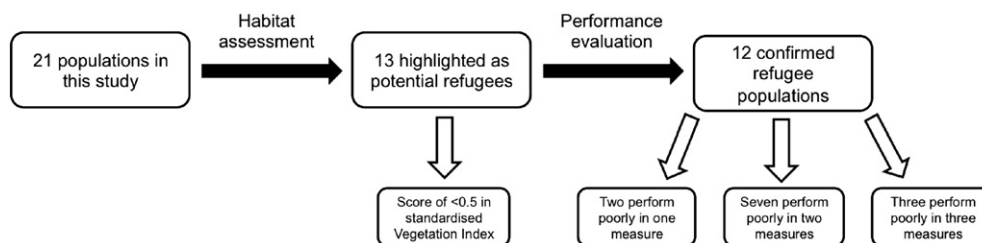


Fig. 4. Potential refugee populations were identified as those with relatively low habitat quality. Of these, 12 were confirmed as refugee populations as they performed at least 50% worse than the highest performing population in at least one of the following performance measures: population growth rate, zebra density (individuals ha^{-1}) and foal:mare ratio.

and Manning, 2002). The widespread transformation of lowland areas, where rainfall and fertility are sufficient for agriculture, has pushed wildlife out of these areas (Rouget et al., 2003b). Whilst the overall lower abundance of grasses in this region would have likely meant that Cape mountain zebra would have occurred at lower densities here than in the east, the inability of individuals to migrate to lowland habitat on a seasonal basis (Kerley et al., 2003), and on a larger scale between populations, is inhibiting the performance of individual populations and the metapopulation as a whole. This results in small populations that are vulnerable to the impacts of demographic stochasticity.

Whilst some Cape Floristic Region species have been completely extirpated, including the global extinction of the blue antelope *Hippotragus leucophaeus* (Kerley et al., 2009), others, such as Cape mountain zebra, now have disjunct populations often restricted to lower quality, ecologically unsuitable habitat within their historical distribution. To improve the performance of refugee populations, Cape mountain zebra require access to suitable habitat, either through land acquisition or by active management of the currently available habitat (e.g. burning regimes or ecological restoration in heavily grazed areas) (Watson et al., 2005; Watson and Chadwick, 2007; Smith et al., 2011). Ideally, this should be focused on securing the poor performing key relict populations, with the intention of increasing numbers to such an extent that individuals can be translocated to new areas of good quality habitat to form mixed stocks with individuals from other populations. Most importantly, our results highlight the on-going management of Cape mountain zebra populations in inappropriate habitat, often due to a misconception of what constitutes optimal, or core, habitat by conservation managers.

4.2. Implications and uses of the partial refugee species concept

Of the 21 Cape mountain zebra populations in this study, over half were identified as refugees. We propose a framework to assess species and populations for refugee status (outlined in Table 2). A potential partial refugee is likely to have undergone extensive range reduction, resulting in disjointed populations that occur across a range of environmental conditions. Refugee populations occur where there is low ecological suitability, which could be due to a number of factors including resource limitation, anthropogenic disturbance, or predation; such populations have little or no opportunity to disperse in order to find more suitable conditions. In confirming refugee status, it is important to develop objective measures of one or more ecological correlates and population performance, such as those used here, and a thorough analysis of the species' historical distribution and ecology. In some cases, where there is limited information available from historical records, population performance data from either closely related or ecologically similar species may provide a better baseline than do the potential refugee populations.

The prevalence of partial refugee species globally is potentially quite high, given the aforementioned bias of protected areas towards marginal upland habitat (Joppa and Pfaff, 2009). Partial gap species, or those species where protected areas cover fragments of their range, are particularly likely to also be partial refugee species. Using the framework provided here, such species could be readily identified. For example, the Mediterranean monk seal has already been identified as a refugee species, due to a reduction in its prehistoric range resulting in confinement to suboptimal breeding habitat (González, 2015). However, the Hawaiian monk seal (*Monachus schauinslandi*) is a likely candidate for partial refugee status as population growth rates vary widely, and physiological evidence suggests that poorly performing populations are resource limited (Gobush et al., 2014).

A key factor in the refugee species concept is the negative impact of active management, where the confinement process has been reinforced due to an inaccurate perception of what is ecologically suitable for the species (Kerley et al., 2012), the latter aspect being termed 'shifting

Table 2 Criteria for the assessment of candidate partial refugee species and potential mitigation strategies for refugee populations (following Kerley et al., 2012), with the Cape mountain zebra used as a model example.

	Initial indicators	Identification of refugee populations	Mitigation of partial refugee status
A candidate (partial) refugee species	<ul style="list-style-type: none"> Range reduction or population declines due to anthropogenic disturbance Disparity between current and historical distribution Exists as complex of fragmented populations with restricted movement and/or dispersal opportunities Occurs across heterogeneous landscape that can be expected to vary in habitat quality 	<ul style="list-style-type: none"> Evaluate variation in population performance (e.g. reproductive rates, mortality) Identify and measure important ecological factors across range (such as habitat/diet quality) Identify correlates of 'marginal' poorly performing populations 	<ul style="list-style-type: none"> Change in perception of optimal or core habitat by managers Expansion of poor quality reserves to include more optimal habitat Translocation of individuals from refugee populations to suitable habitat
A model partial refugee species: the Cape mountain zebra	<ul style="list-style-type: none"> Reduced to three populations totalling ~80 individuals in mid-20th century due to hunting and habitat loss Historical preference for grassy habitats (Faith, 2012; Boshoff et al., 2015) Currently > 75 populations found across diverse habitat types in southern mountainous South Africa with restricted dispersal (Hrabar and Kerley, 2015) 	<ul style="list-style-type: none"> Population growth rate, zebra density and foal:mare ratio vary between populations These measures are positively associated with habitat and diet quality Potential refugee populations have a low standardised Vegetation Index score Confirmed refugee populations score poorly in at least one performance measure (12 out of 21 in this study) 	<ul style="list-style-type: none"> Management and restoration of limiting ecological factor Immediate focus on poorest performing and key relict populations: De Hoop, Gamkaberg and Kammanassie Nature Reserves Where possible expand reserves into lowland areas with increased grass cover (priority for Gamkaberg and Kammanassie Nature Reserves) Form mixed stocks via translocation of individuals to areas of high grass abundance (priority for De Hoop Nature Reserve) Active management of existing land to promote an increase in grass abundance (e.g. burning, ecological restoration)

baseline syndrome' (Pauly, 1995). Identifying and understanding such misconceptions, and then managing accordingly, is vital for improvement in conservation planning. As is often the case, the conservation needs of one species may clash with another (such as that of Cape mountain zebra with the endemic fynbos flora); this said the needs of all species cannot be properly considered if they are not understood. Once refugee populations have been identified, the principal mitigation strategies are to expand and manage protected areas to promote more optimal ecological conditions and/or to translocate individuals to more suitable areas. This can only be successful if the historical distribution and ecology of the species is properly understood, and has broader implications for the areas targeted as conservation priorities. The indicators developed when evaluating refugee status could be used to assess new areas for species range expansion; indeed the framework presented here has the potential to be expanded and used to assess the suitability of protected areas for ecological communities rather than just single species. In any case, future conservation planning needs to avoid preconceived ideas about habitat suitability and incorporate a way to assess marginality and whether or not species (or communities) are adequately protected. More broadly, our results highlight the issue of inferring ecological preferences from current distribution patterns. Species distribution and climate envelope models are often based on current distribution patterns (Kerley et al., 2012). If ranges have undergone historical contraction, especially into marginal areas, then inferred suitability and adequacy of protected areas derived from such models would be strongly biased (Cromsigt et al., 2012). Using poorly informed assessments of habitat suitability or solely anecdotal evidence may grossly over-estimate the conservation value of existing protected areas. The importance of understanding ecological suitability within a historical context becomes even more critical in the face of on-going anthropogenic environmental change. As habitats shift with land use and climate change, the current distribution of protected areas may be inappropriate to meet our future conservation goals.

5. Conclusions

The conservation of species or populations in ecologically unsuitable conditions is extremely problematic and ineffective, and has far-reaching consequences for broad-scale conservation planning. A core issue lies in the active management of a species in suboptimal habitat due to the inaccurate or poorly informed perceptions of its historical distribution and ecology. Here, we provide a framework for identifying such species and apply it to a model species, the Cape mountain zebra. We identify 12 out of 21 populations as ecological refugees, due to low habitat and diet quality and poor performance. The framework provided here can be used to assess other species for refugee status, and will be most important in highlighting misconceptions by conservation managers in what habitats a species occupied historically, and where it should be conserved now.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.09.017>.

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