



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

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