Environmental change hastens the demise of the critically endangered riverine rabbit (Bunolagus monticularis)

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ABSTRACT

Declining population numbers coupled with the growing evidence of global change have focussed attention on the critically endangered riverine rabbit (Bunolagus monticularis) endemic to South Africa. The aim of this study is to develop a habitat model to aid in the identification of isolated populations, offer opportunities for re-introduction or introduction, and guide future conservation efforts by assessing the possible impacts of global change. We attempt a novel approach where plant species which afford the riverine rabbit cover from predation and its primary food sources are modelled utilising the same technique and are included as a predictor variable in the habitat model for both current and future projections of potential habitat. Inclusion of this proximal variable as well as riparian areas yields a more parsimonious habitat model than using climatic variables alone. Results suggest that unsurveyed suitable habitat east of Victoria West might harbour previously overlooked isolated populations or offer new opportunities for re-introductions. Future climatic conditions under the most severe general circulation model for the region (HADCM3) suggest that, on average, in excess of 96% of the current habitat could become unsuitable, mitigated only slightly by a possible 7% increase in range in adjacent upper catchment areas. Consideration of existing land transformation increases this range reduction by a further 1%. Given that ex situ captive breeding programmes have met with no success and that the bulk of future potential range lies well outside of the currently known and surveyed areas the current adaptation options of conservancy establishment and captive breeding need to be re-evaluated. Without positive human intervention the future of the critically endangered riverine rabbit under conditions of global change seems certain.

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1. Introduction

Rapidly declining numbers within known populations of the critically endangered (Collins et al., 2003) riverine rabbit (Bunolagus monticularis) along with unsuccessful captive breeding programmes (Dippenaar and Ferguson, 1994) have highlighted the urgent need for an evaluation of the in situ conservation of this South African endemic species. In situ conservation, implies, inter alia, a detailed knowledge of the species’ current, potential and future range. In the case of...
the riverine rabbit this knowledge is incomplete with exhaustive surveys of known and potential range yet incomplete. While conservationists have acknowledged climate and land-use change as a possible threat to Bunolagus monticularis (Ahlmann et al., 2000) these effects on remaining and future suitable habitat have not been explicitly analysed.

Habitat-based models have been increasingly used as a means to inform conservation (Engler et al., 2004; Lehmann et al., 2002; Li et al., 1999; Wu and Smeins, 2000) especially in the light of continued environmental change (Araújo et al., 2004; Aspinall and Matthews, 1994; Box et al., 1999; Midgley et al., 2002). Of interest to this study is their ability to aid in the identification of locations that might hold unknown populations (Guisan et al., 2006; Raxworthy et al., 2004), guide the introduction (Debeljak et al., 2001) or re-introduction of species (Glenn et al., 2001; Zimmermann and Breitenmoser, 2002) and restoration of habitats (Lehmann et al., 2002; Midgley et al., 2003) as well as assess the extent of future habitat (Hilbert et al., 2004; Teixeira and Arntzen, 2002).

This study aims to investigate some of the factors driving the distribution of the riverine rabbit, to delineate current suitable habitat in the hope of identifying unsurveyed areas which may harbour isolated populations or offer opportunities for re-introduction or introduction of the species, and guide future conservation efforts by assessing the possible impacts of global change and adaptation options through the development and validation of a habitat model.

Paleo-climatological research has highlighted that rapid changes in vegetation cover (over as little as ~100 years) may have led to a change in faunal composition (Post, 2003). The identification and inclusion of resource predictor variables, measured, modelled or inferred, in landscape scale habitat models is not uncommon, with examples including soil hardness for burrow excavation (Calvete et al., 2004), tree cavity availability (Lawler and Edwards, 2002), prey density (Glenn et al., 2001; Palomares et al., 2001) and potential fruit production (Pearce et al., 2001). While the dependence of species future ranges on vegetation under scenarios of climate change have been postulated (Huntley, 1995) models of faunal responses to climate change typically do not include the effects of proximal resource variables. In this study we attempt a novel approach where plant species which afford the riverine rabbit cover from predation and its primary food sources are modelled utilising the same technique and are included as a predictor variable in the habitat model for both current and future projections of potential habitat.

2. Materials and methods

2.1. Study species

The riverine rabbit is a lagomorph endemic to the semi-arid central Karoo region of the western and northern Cape provinces of South Africa. Bunolagus monticularis inhabits dense scrubby riparian areas along ephemeral rivers (Mills and Hes, 1997), produces relatively small litters of 1–2 young in a fur- and grass-lined subterranean chamber excavated in stable soils (Duthie, 1989) and is a nocturnal species spending daylight hours in a scrape beneath riparian vegetation (Skinner and Smithers, 1990). The decline in populations between 1903 (when the species was first described and was considered to be wide spread) and the present, where the species is considered to be critically endangered (Collins et al., 2003) are attributed to a number of factors. Habitat transformation to exploit the fertile alluvial floodplains adjacent to their riparian habitat for winter wheat production head this list, with in excess of 60% of this riparian habitat having been transformed (Ahlmann et al., 2000; Coetzee, 1994; Duthie, 1989; Duthie and Robinson, 1990; Duthie et al., 1989). Habitat degradation through fuel-wood collecting and overgrazing has lead to an increase in predation, while the reduction in streamflow owing to the construction of dams upstream, as well as hunting with dogs, have all played a role (Ahlmann et al., 2000).

2.2. Distribution data

Point distributions of known populations were compiled from a number of surveys undertaken by conservation agencies and researchers as well as field observation. The presence records of a recently discovered Touws River population in the Fynbos biome were excluded from this study for two reasons. Firstly, research to date has centred on the Karoo populations and observations for these may not be valid for this southerly population e.g. food species observed for the central Karoo population do not occur in the Fynbos biome, and secondly, genetic research suggests that this southerly population is indeed distinct from the Karoo population (Mathee, C., Pers. Comm., 2005).

Owing to the modelling technique requiring absence data and in order not to bias the modelling with the effects of prevalence (Manel et al., 2001), an equal number of pseudo-absence sites were inferred using the following technique. A grid of points was generated across the whole of South Africa in order to ensure that a complete response curve is generated as truncated response curves may lead to spurious results on projection (Thuiller et al., 2004). The presence observations were used to create a convex polygon, which by definition is the smallest convex set of points to include all of the points. Grid points within this convex polygon were excluded if they occurred within 1 km of ephemeral streams or occurred on terrain with a slope of less than 30%. A random sub sample of the remaining grid points was chosen such that an equal number of absence points were selected from within and without the convex polygon. The final distribution used in the modelling is illustrated in Fig. 1.

2.3. Ecological data

A thorough search of available literature along with field observations yielded the possible food sources on which the riverine rabbit relies as well as the plant species that it uses for cover from predation. Field observations identified Salsola glabrescens, Pteronia erythrochaeta and Osteospermum spinosum as food species as well as Ericopephalus spinosum and Lycium cinerium as the dominant cover plant species. Duthie et al. (1989) also identify Kochia pubescens (now Bassia salsoloides) and Mesembryanthemaceae (mesembs) as preferred foods. The commonly leaf-succulent Mesembryanthemaceae encompasses a very broad Family, with 182 species occurring within the range of Bunolagus monticularis, may well be impor-
tant sources of moisture (Duthie et al., 1989) and therefore should be included through identifying representative species. Comparative analysis of detailed plant survey information with the Bunolagus monticularis locality data yielded a small list of likely co-occurring mesembs. Of these Psilocaulon coriarium and Trichodiadema barbatum were selected as other studies had found browsing of these by Smith’s Red Rock rabbit, Pronolagus rupestris (Milton and Dean, 2001) and the Cape Hare, Lepus capensis (Kerley, 1990). Additional plant species noted in the literature (Duthie, 1989), as being favoured by Bunolagus monticularis are the flowers and leaves of Boegoe and Inkbush as well as grasses when they are available in the wet season. The use of common names posed a problem as their application does not appear to be consistent and may be applied to a range of species from more than one genus (Powrie, 2004). Powrie also notes that there are more than 95 grass species occurring in the Karoo, which makes this a vague categorisation of potential food sources. It was also felt that the exclusion of seasonal species was reasonable as the availability of food during the dry season would more likely be a limiting factor to the presence of Bunolagus monticularis. Distributions of the 8 key plant species were extracted from the Précis (Germishuizen and Meyer, 2003) and Ackdat (Rutherford et al., 2003) databases held by the South African National Biodiversity Institute.

2.4. Climate data

The Agroclimatic Atlas climate surface dataset (Schulze, 1997) covering southern Africa at a resolution of 1 min by 1 min (~1.6 km at this latitude) was used to represent current climate along with recently constructed rainfall surfaces (Lynch, 2003). Future (~2050) climate predictions were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HADCM3 General Circulation Model (Gordon et al., 2000) using the A1F1, A2, B1A and B2 IPCC SRES scenarios (Nakicenovic and Swart, 2000) in accordance with guidelines for climate impact assessment (IPCC-TGCIA, 1999) using a technique described by (Hewitson, 2003). The HADCM3 model was chosen as it represents the most pessimistic projection of future climate for the southern African region (Rousteenoja et al., 2003). Seven variables were selected based on their known effects on plant survival and growth (Midgley et al., 2002; Midgley et al., 2003): Annual and winter temperature, annual, winter and summer precipitation and annual and winter potential evapotranspiration. Potential evapotranspiration estimates were calculated using the FAO 56 Penman-Monteith combination equation (Allen et al., 1998). Winter temperature is likely to discriminate between species based on their ability to assimilate soil water and nutrients, and continue cell division, differentiation and tissue growth at low temperatures (lower limit), and chilling requirement for processes such as bud break and seed germination (upper limit). Potential evaporation discriminates through processes related to transpiration-driven water flow through the plant, and xylem vulnerability to cavitation and water transport efficiency. However, it is important to note that there is little experimental work on local indigenous species to guide in the choice of any bioclimatically limiting variables, and these were chosen...
as a hypothetical minimum basic set for defining bioclimatic niche-based models in indigenous flora. In the absence of clear information on climatic limiting factors for *Bunolagus monticularis*, these environmental parameters were considered to be an adequate representation of likely environmental factors affecting its distribution.

2.5. Additional habitat data

Data on land transformation covering southern Africa at a resolution of 1 min by 1 min were resampled from the 0.5 min resolution "Human Footprint" dataset (Sanderson et al., 2002). This represents a consistent source of land transformation expressed as the proportion transformed. The riverine rabbit is closely associated with riparian areas and this was reflected through the inclusion of a riparian variable expressed as the proportion of riparian area in each grid cell. Riparian areas were delineated by buffering a 1,250,000 scale rivers coverage by 400 m. This is believed to be reasonable as the average range size of the riverine rabbit is 15 hectares (Duthie and Robinson, 1990) and all locality data were accounted for by this delineation.

It was noted during the data exploration phase that the riverine rabbit appears to be closely associated with first and second order streams (Strahler, 1952) and does not appear to occupy areas of steep slope (>20%). These observations were not included into the model as their relationship with rabbit distribution is unclear and may be a function of limited land transformation associated with first and second order streams or soil stability affecting burrow excavation.

2.6. Habitat models

Generalised additive models (GAM) (Hastie and Tibshirani, 1990) relating the plant species distributions as well as the riverine rabbit distribution to the seven bioclimatic variables were calibrated using a random sample of the initial data (70%) and a stepwise (backwards and forwards) selection methodology with the most parsimonious models being selected using the Akaike information criterion (AIC). GAMs relating the riverine rabbit distribution to those bioclimatic variables selected in the initial process as well as combinations of the three environmental variables (resource, riparian areas and land transformation) were calibrated using a random sample of the initial data (70%) and a stepwise (backwards and forwards) selection methodology with the most parsimonious model being selected using the AIC. The explanatory power of the models was evaluated with the AIC, which assesses the fit of the model versus the complexity of the model, corrected for small sample size and associated metrics (Johnson and Omland, 2004; Rushton et al., 2004). The predictive power of each model was evaluated on the remaining 30% of the initial dataset using the values obtained for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (1-specificity) (Swets, 1988). Sensitivity is defined as the proportion of true positives correctly predicted, whereas specificity is the proportion of true negatives correctly predicted. The model that incorporated both strong explanatory and descriptive power was selected as the best model. The probabilities of occurrence from the *Bunolagus monticularis* models, with and without the additional variables, were converted to presence/absence using three thresholds, namely a threshold ensuring 90% sensitivity (Pearson et al., 2004), a threshold maximising the Cohen’s Kappa statistic (Fielding and Bell, 1997) and a threshold maximising jointly the sensitivity and specificity (Pearce and Ferrier, 2000). Selection of the appropriate threshold from these three was a function of summary statistics, visual analysis and model validation.

In the event that land transformation was not selected in the final habitat model it would still be of benefit to investigate its effect on the results. This was done by weighting the probabilities of occurrence with the degree of land transformation, for example if the probability of occurrence was 0.5 and the degree of transformation was 75% then the final probability of occurrence would be 0.125. Finally, the probabilities of occurrence from the filtered models were converted into presence/absence using the three thresholds described above. Future projections of the probabilities of occurrence were weighted in a similar manner and transformed into presence/absence using the same thresholds.

2.7. Habitat model scenarios

Climate, food and cover resources, land transformation and riparian areas were all considered as predictor variables. The models defined by the combination of these variables are outlined in Table 1.

Model Clim – The baseline model commonly utilised in studies of this type. The other models would be compared to this model to investigate whether the addition of these proximal variables would improve this model.

Model Clim.Res – The inclusion of a resource variable to account for both cover and food would allow investigation of the assumption that rabbit occurrence is more likely where more abundant food and cover is available. The transformed probability scores for the 8 modelled plant species for both the current and future time periods were grouped into two sub-classes, that of cover and that of food. The transformed probability scores were summed for each pixel and rescaled to a value between 0 and 1. The totals from the two sub-classes were then summed and rescaled to a value be-

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clim</td>
<td>Baseline climate model</td>
</tr>
<tr>
<td>Clim.Res</td>
<td>Inclusion of resource as defined by food and cover species</td>
</tr>
<tr>
<td>Clim.Trans</td>
<td>Inclusion of land transformation</td>
</tr>
<tr>
<td>Clim.Rip</td>
<td>Inclusion of delineated riparian areas</td>
</tr>
<tr>
<td>Clim.Res.Trans</td>
<td>Inclusion of resource and land transformation</td>
</tr>
<tr>
<td>Clim.Rip.Res</td>
<td>Inclusion of resource and riparian areas</td>
</tr>
<tr>
<td>Clim.Trans.Rip</td>
<td>Inclusion of land transformation and riparian areas</td>
</tr>
<tr>
<td>Clim.Res.Trans.Rip</td>
<td>Inclusion of resource, riparian areas and land transformation</td>
</tr>
<tr>
<td>Clim.Res.Rip.CC</td>
<td>Inclusion of climatic change</td>
</tr>
</tbody>
</table>
 tween 0 and 1 and used as a descriptor of available food and cover resources. In this manner both cover and food are given an equal weighting in the resource variable ensuring that distortion owing to high probability of one subclass did not occur.

Model Clim.Trans – Using climate variables plus the proportion of land transformation per pixel, the relationship of the riverine rabbit habitat with the degree of land transformation was explored.

Model Clim.Rip – Using climate variables plus a spatial definition of riparian habitat. The common name of riverine rabbit applied to *Bunolagus monticularis* accurately summarises the dependence of this species on riparian habitat. With limited ranges of approximately 15 hectares and riparian vegetation of approximately 200 m in width the inclusion of a riparian habitat indicator should narrow potential habitat to this specific habitat requirement and decrease the probability of occurrence of the species away from these areas.


Model Clim.Res.Rip.CC – Following the finalisation of the most parsimonious habitat model from the scenarios above

Fig. 2 – Comparison of the probability of occurrence of the food and cover resources under current (a) and the 4 future GCM climatic conditions, namely (b) A1F1, (c) A2 (d) B1A and (e) B2 simulations. Darker shades of grey indicate increasing probability of occurrence.
Table 2 – Predictive power of the different models assessed using AUC, Cohen’s Kappa Statistic, the Akaike Information Criterion corrected for sample size along with the AIC delta and weights

<table>
<thead>
<tr>
<th>Models</th>
<th>AUC</th>
<th>Kappa</th>
<th>AICc</th>
<th>AICc Delta</th>
<th>AICc Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clim</td>
<td>0.93</td>
<td>0.80</td>
<td>69.29</td>
<td>10.73</td>
<td>0.32</td>
</tr>
<tr>
<td>Clim.Res</td>
<td>0.88</td>
<td>0.74</td>
<td>61.39</td>
<td>2.70</td>
<td>17.85</td>
</tr>
<tr>
<td>Clim.Trans</td>
<td>0.94</td>
<td>0.80</td>
<td>73.44</td>
<td>14.75</td>
<td>0.04</td>
</tr>
<tr>
<td>Clim.Rip</td>
<td>0.96</td>
<td>0.75</td>
<td>66.32</td>
<td>7.62</td>
<td>1.52</td>
</tr>
<tr>
<td>Clim.Res.Trans</td>
<td>0.92</td>
<td>0.79</td>
<td>64.78</td>
<td>5.90</td>
<td>3.60</td>
</tr>
<tr>
<td>Clim.Res.Trans.Rip</td>
<td>0.95</td>
<td>0.80</td>
<td>65.58</td>
<td>4.45</td>
<td>7.43</td>
</tr>
<tr>
<td>Clim.Trans.Rip</td>
<td>0.97</td>
<td>0.90</td>
<td>69.05</td>
<td>10.16</td>
<td>0.42</td>
</tr>
<tr>
<td>Clim.Rip.Res</td>
<td>0.95</td>
<td>0.75</td>
<td>58.88</td>
<td>0.00</td>
<td>68.8</td>
</tr>
</tbody>
</table>

Table 3 – Summary of the threshold analysis results for each model where the 90% sensitivity (Pearson et al., 2004), presence/absence optimised (Pearce and Ferrier, 2000) and Cohen’s Kappa statistic (Fielding and Bell, 1997) thresholds are outlined

<table>
<thead>
<tr>
<th>Model</th>
<th>90% Sensitivity</th>
<th>Presence/absence optimised</th>
<th>Cohen’s Kappa statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clim</td>
<td>0.41</td>
<td>0.63</td>
<td>0.76</td>
</tr>
<tr>
<td>Clim.Res</td>
<td>0.35</td>
<td>0.47</td>
<td>0.45</td>
</tr>
<tr>
<td>Clim.Res.Trans</td>
<td>0.42</td>
<td>0.52</td>
<td>0.39</td>
</tr>
<tr>
<td>Clim.Res.Trans.Rip</td>
<td>0.34</td>
<td>0.34</td>
<td>0.37</td>
</tr>
<tr>
<td>Clim.Trans</td>
<td>0.50</td>
<td>0.56</td>
<td>0.76</td>
</tr>
<tr>
<td>Clim.Trans.Rip</td>
<td>0.55</td>
<td>0.55</td>
<td>0.62</td>
</tr>
<tr>
<td>Clim.Rip</td>
<td>0.55</td>
<td>0.56</td>
<td>0.51</td>
</tr>
<tr>
<td>Clim.Rip.Res</td>
<td>0.30</td>
<td>0.39</td>
<td>0.56</td>
</tr>
</tbody>
</table>
weaken the models. Application of the AIC corrected for sample size clearly highlighted that the Clim.Rip.Res model was the most parsimonious. In terms of both predictive and descriptive power the model incorporating climate, resources and riparian areas represented an improvement on the climate-only model.

Fig. 3 – Potential ranges for each of the model formulations (a) climate only, (b) clim.res, (c) clim.trans, (d) clim.rip, (e) clim.res.trans, (f) clim.trans.rip, (g) clim.rip.res and (h) clim.res.trans.rip. Note the spurious ranges predicted in the Springbok Area (square), Touws River (diamond) and south of Beaufort West (triangle) of models not selected. Note also the unexplored potential range east of Victoria West (ellipse).
3.3. Model validation

Validation of the selected model against independent data-sets indicated that, despite disparate levels of geo-reference accuracy, the model was robust with almost all historical survey locations and habitat suitability survey localities being accounted for (Fig. 4). Further corroboration stemmed from a comparison of the model with both a 1:250,000 vegetation map and the biomes constructed from this map. Almost all of the modelled range was restricted to the Nama Karoo biome with large portions of the range being confined to a few vegetation units, including the western and eastern upper karoo, karoo hardeveld and bushmanland vloere.

3.4. Model implications

A primary objective of the study was to identify any additional areas where isolated populations of the riverine rabbit might exist as the recent discovery of a genetically different yet related rabbit in the Touws River area (Mathee, C., Pers. fig. 1)
The conservation of critically endangered species is never easy, especially when adaptation options to global change need to be considered as well. Riverine rabbit conservation efforts to date have centred on the education of landowners and their employees, the establishment of private conservancies as opposed to the establishment of fixed reserves would offer a more flexible and cost-effective conservation option and should continue to be pursued. Whether this option will be able to afford the levels of protection that this critically endangered species will require for persistence in the wild will need to be assessed, especially as hunting by farm employees and their dogs has been high.

The robustness of the chosen model allowed for its projection into the future. Suitable future habitat for the rabbit was impacted negatively by climate change with range reductions greater than 93% being projected (see Table 4) for the most conservative prediction of future climate. The consideration of land transformation compounded this situation only slightly owing to the substantial effects of climate change. This additional effect could, however, prove deleterious especially as this was a conservative approach using current land transformation as a surrogate of future land transformation. The potential habitats under all four future climate predictions are illustrated in Fig. 5. Of note was that the bulk of future suitable habitats. Identification of these factors would greatly assist in the conservation of this species.

The current known range of the riverine rabbit lies entirely on privately owned land in both the western and northern Cape provinces of South Africa. Given that climate change is projected to promote a shift in suitable habitat to areas currently outside of the known range of the riverine rabbit and the fact that Karoo farms tend to be extensive, the establishment of private conservancies as opposed to the establishment of fixed reserves would offer a more flexible and cost-effective conservation option and should continue to be pursued. Whether this option will be able to afford the levels of protection that this critically endangered species will require for persistence in the wild will need to be assessed, especially as hunting by farm employees and their dogs has been highlighted as a significant threat (Ahlmann et al., 2000). With proposed legislation allowing for landowners to be compensated for limiting further development and employing conservation practices high priority areas of suitable habitat for both current and future climate should be identified as soon as possible. The model results from this study would be able to guide conservation authorities in this regard. However, it is important to note that semi-arid regions in southern Africa have an under-representation of hydro-meteorological stations and as such care should be taken when interpreting these modelled results as they are based in part on interpolated current climatic surfaces as well as modelled future climate with
its concomitant uncertainty. It is also recommended that other GCM’s be investigated as the HADCM3 model is acknowledged as providing a pessimistic view of future climate for the southern African region (Rousteenoja et al., 2003).

Owing to the fact that modelled current and future suitable habitat areas are disjunct, a translocation program is likely to be needed to ensure the long-term persistence of this species in the wild. Translocation of mammals between conservation areas has a long-standing history in conservation. However, recent concerns about the selection of populations to ensure success, the consequences of introducing novel genetic material (Heywood and Iriondo, 2003) and the unintended consequences of introduction, for example, invasion (Radosevich et al., 2003; Sakai et al., 2001) will need to be considered. Continued inter-provincial conservation agency cooperation will be a key factor in the short term survival of the riverine rabbit, especially as a third provincial agency will need to be included in deliberations of adaptation to climate change with the bulk of the future suitable habitat projected to lie in the eastern Cape. Given that the population numbers of this species have dipped alarmingly in the last decade, the amount of conservation planning that is still needed and the complications that climate change will introduce it is suggested that the cryo-preservation of genetic material be promoted as a safe-guard against the permanent disappearance if this species.

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