BIOLOGICAL CONSERVATION 141 (2008) 23–34

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

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

Gregory O. Hughes[a,d,*], *Wilfried Thuiller*[a,e], *Guy F. Midgley*[a,c], *Kai Collins*[b]

[a]*Kirstenbosch Research Centre, South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa*
[b]*Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa*
[c]*Center for Applied Biodiversity Science, Conservation International, 1919 M Street, NW Suite 600, Washington DC 20036, USA*
[d]*ADAS UK Limited, Woodthorne, Wergs Road, Wolverhampton, WV6 8TQ, UK*
[e]*Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Université J. Fourier, BP 53, 38041 Grenoble Cedex 9, France*

ARTICLE INFO

Article history:
Received 31 March 2005
Received in revised form
14 August 2007
Accepted 14 August 2007
Available online 7 November 2007

Keywords:
Riverine rabbit
Habitat model
Global change
Iand transformation
Conservation

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.

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

* *Corresponding author:* Address: Kirstenbosch Research Centre, South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa.
E-mail address: Hughesg@sanbi.org (G.O. Hughes).
0006-3207/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2007.08.004

the riverine rabbit this knowledge is incomplete with exhaustive surveys of known and potential range underway 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 (Glenz 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 (Glenz 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 heads 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 spinescens* as food species as well as *Eriocephalus spinescens* 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-

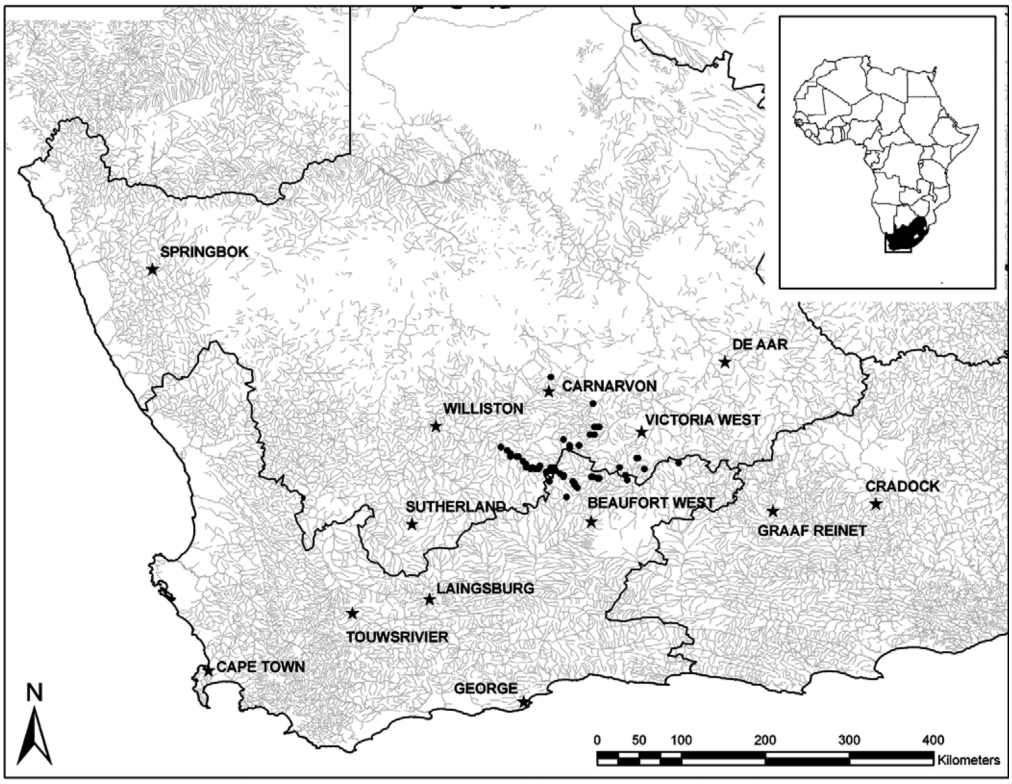

Fig. 1 – The study area indicating the presence records of surveyed populations used in the analysis in relation to nearby towns and the drainage network.

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, *Pronologus 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 assuring 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 untransformed probability scores for the 8 modelled plant species for both the current and future timeperiods were grouped into two sub-classes, that of cover and that of food. The untransformed 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 1 – Habitat models investigated during this study including the codes used to refer to each model and the variables included in the model formulation

Scenario	Description
Clim	Baseline climate model
Clim.Res	Inclusion of resource as defined by food and cover species
Clim.Trans	Inclusion of land transformation
Clim.Rip	Inclusion of delineated riparian areas
Clim.Res.Trans	Inclusion of resource and land transformation
Clim.Rip.Res	Inclusion of resource and riparian areas
Clim.Trans.Rip	Inclusion of land transformation and riparian areas
Clim.Res.Trans.Rip	Inclusion of resource, riparian areas and land transformation
Clim.Res.Rip.CC	Inclusion of climatic change

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.

Models Clim.Res.Trans, Clim.Trans.Rip, Clim.Rip.Res, Clim. Res.Trans.Rip – All combinations of the habitat factors described above. In this manner the relative impacts of each new variable and their combinations may be assessed.

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

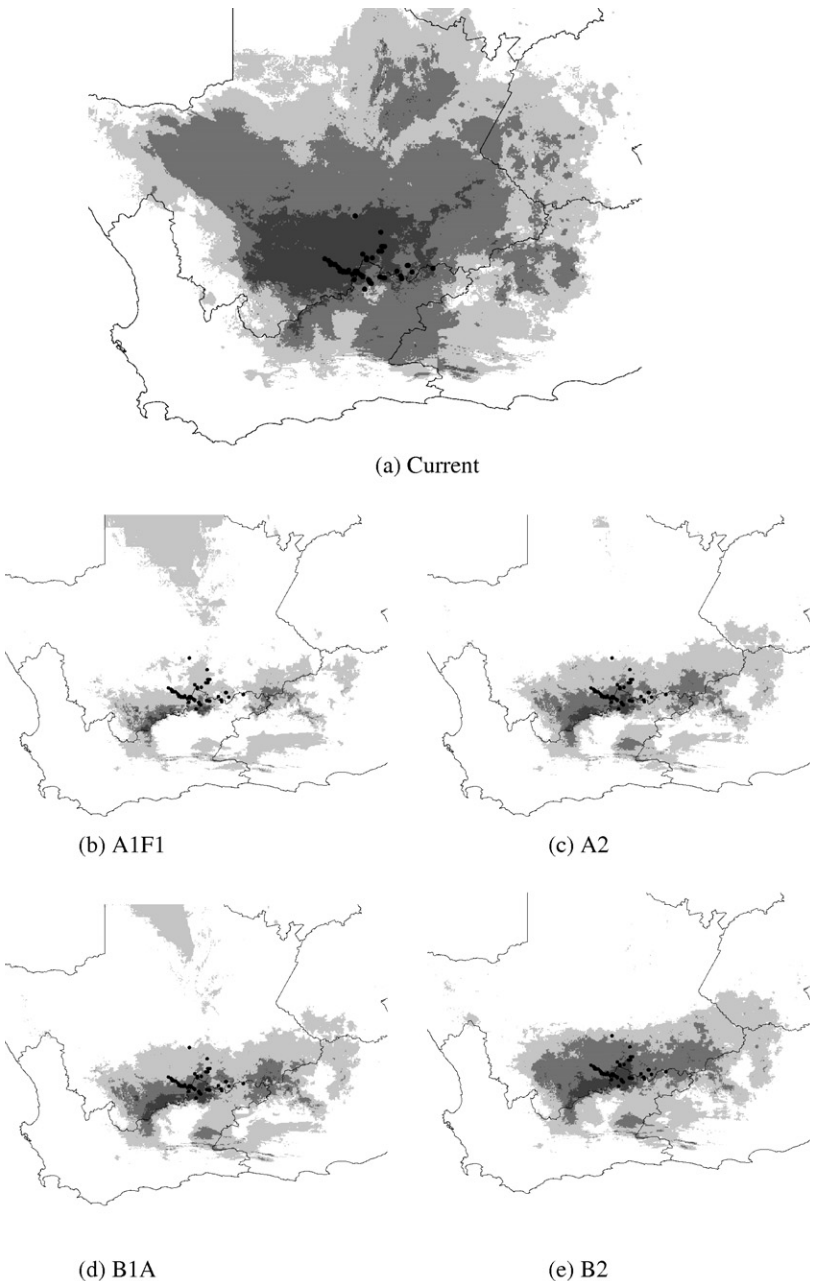

Fig. 2 – Comparison of the probability of occurrence of the food and cover resources under current (a) and the 4 future GCM climatic conditions, namely (b) A1F1, (c) A2 (d) B1A and (e) B2 simulations. Darker shades of grey indicate increasing probability of occurrence.

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

Models	AUC	Kappa	AICc	AICc Delta	AICc Weight
Clim	0.93	0.80	69.29	10.73	0.32
Clim.Res	0.88	0.74	61.39	2.70	17.85
Clim.Trans	0.94	0.80	73.44	14.75	0.04
Clim.Rip	0.96	0.75	66.32	7.62	1.52
Clim.Res.Trans	0.92	0.79	64.78	5.90	3.60
Clim.Res.Trans.Rip	0.95	0.80	63.58	4.45	7.43
Clim.Trans.Rip	0.97	0.90	69.05	10.16	0.42
Clim.Rip.Res	0.95	0.75	58.88	0.00	68.8

(namely model Clim.Rip.Res), this model including its climate dependant resource component was projected into the future using projections of future climate. We assumed that the most parsimonious model under current climate conditions would remain such into the future, and that despite changes in available moisture and runoff, the major drainage lines used to delineate the riparian areas would remain unchanged. It was also assumed that future land transformation is best described by the current land transformation dataset as this represents a conservative view of the future and limits additional uncertainty owing to future land transformation projections.

2.8. Model validation

In order to ensure that the final model selected was indeed appropriate it was compared with 2 independent sources of data, the survey data collected by Duthie (1989) and museum specimen locality information. Owing to the geo-referencing accuracy of both of these datasets being limited, approximately 5 km in the former and 15 km in the latter, this comparison was by visual inspection alone. These results were further compared with biomes constructed from a recent vegetation map of the area (Mucina and Rutherford, 2005).

3. Results

3.1. Resources

Modelling of the current food and cover resources suggest that riverine rabbit habitat is potentially extensive at present, especially to the east and north-east of its currently limited range. The current range of the riverine rabbit appears to be concentrated within the highest probability zones for food and cover resources (Fig. 2). The future food and cover resources under the 4 storylines of the HADCM3 GCM suggest that these will decrease radically by 2050 in both extent and probability of occurrence. It is important to note that the current range of the riverine rabbit is located within or adjacent to the higher probability areas identified under the future climate scenarios.

3.2. Habitat model

The conversion of the probability data to binary presence/absence data had a marked effect on the extent of the final modelled range. Selection of the threshold above which a species was considered to be present is primarily a function of model application. For example, the identification of habitat for the re-introduction of an endangered species would call for the use of a conservative (high) threshold (Pearson et al., 2004) while the definition of suitable range for impacts analysis would utilise a low threshold (Pearce and Ferrier, 2000). In order to meet the multiple objectives of this study, we analysed the results from the three thresholds explored (Table 3). Visual analysis suggested that for the purposes of this study that the threshold defined by the 90% sensitivity criterion was too liberal while that of Cohen's Kappa statistic was too conservative and hence the threshold optimising sensitivity and specificity was selected (Figs. 3 and 4).

The model that utilised climate alone was chosen as the baseline model against which the other models were compared to investigate whether the addition of further variables and combinations of variables yielded an improved model. What constitutes an improved model was a function of the study objectives and whether predictive or descriptive model accuracy was required. The area under the receiver operator characteristic curve and Cohen's Kappa statistic may be used as measures of a model's predictive power. The addition of variables and their combinations produced an increase in AUC/Kappa in some instances, (trans, res.trans.rip, trans.rip), while in others produced a decrease in the AUC/Kappa, (res, res.trans – Table 2). In two instances the AUC indicated an increase while Cohen's Kappa statistic indicates a decrease (rip, rip.res). In all cases these increases and decreases were not statistically significant (t-test) suggesting that inclusion of these additional variables did not significantly improve or

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

Model	90% Sensitivity	Presence/absence optimised	Cohen's Kappa statistic
Clim	0.41	0.63	0.76
Clim.Res	0.35	0.47	0.45
Clim.Res.Trans	0.42	0.52	0.39
Clim.Res.Trans.Rip	0.34	0.34	0.37
Clim.Trans	0.50	0.56	0.76
Clim.Trans.Rip	0.55	0.55	0.62
Clim.Rip	0.55	0.56	0.51
Clim.Rip.Res	0.30	0.39	0.56

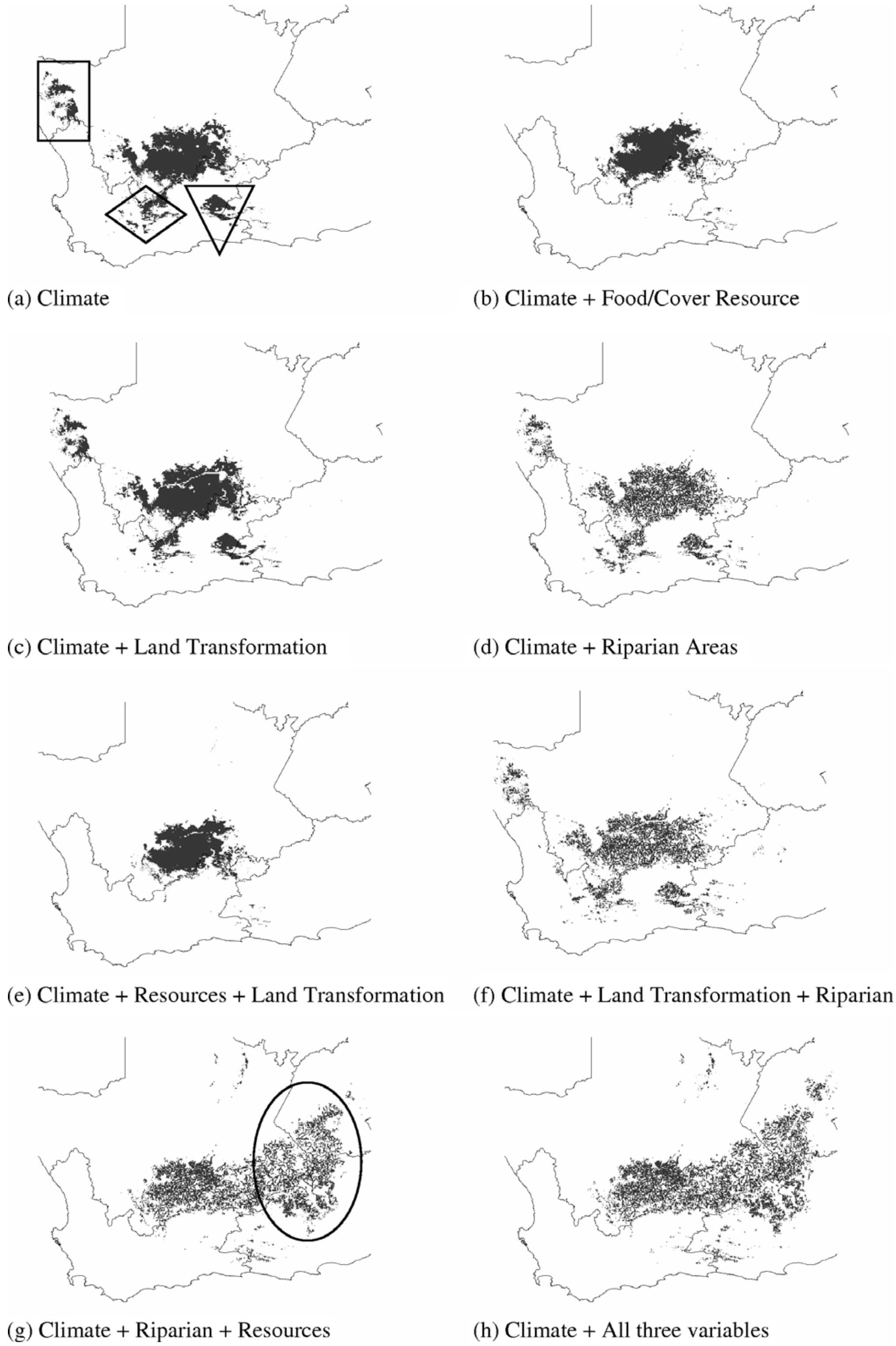

Fig. 3 – Potential ranges for each of the model formulations (a) climate only, (b) clim.res, (c) clim.trans, (d) clim.rip, (e) clim.res.trans, (f) clim.trans.rip, (g) clim.rip.res and (h) clim.res.trans.rip. Note the spurious ranges predicted in the Springbok Area (square), Touws River (diamond) and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

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.

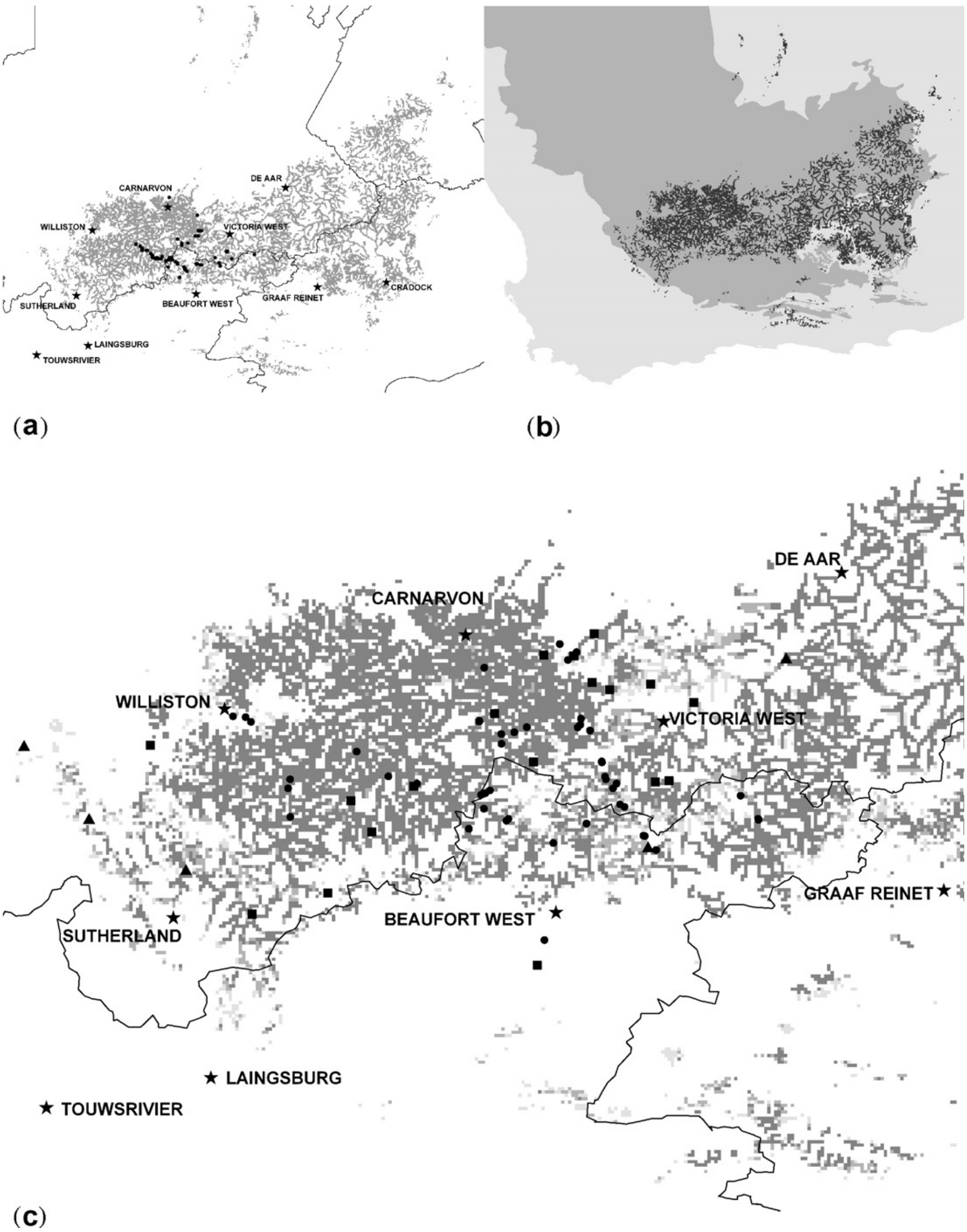

Fig. 4 – Modelled range according to the clim.rip.res model (model (g) in Fig. 3) in relation to the (a) current known localities, (b) biomes and (c) independent datasets, namely museum specimens (triangle), 1989 survey of Duthie et al. (square) and habitat suitability surveys (circle). Suitable habitat in (c) is defined such that presence/absence is optimised.

3.3. *Model validation*

Validation of the selected model against independent datasets 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.

Table 4 – Extent of current potential range could be lost, remain stable and possibly be gained for each GCM storyline excluding and including the effects of land transformation

Future climate	Lost	Persist	New	% Lost	% Persist	% New
2050 without land transformation						
A1F1	17154	51	902	99.70	0.30	5.24
A2	16677	528	1119	96.93	3.07	6.50
B1A	16258	920	1501	94.50	5.35	8.72
B2	16091	1114	1390	93.53	6.47	8.08
2050 with land transformation						
A1F1	16017	34	857	99.79	0.21	5.34
A2	15616	435	1116	97.29	2.71	6.95
B1A	15321	730	1498	95.45	4.55	9.33
B2	15115	936	1374	94.17	5.83	8.56

Comm., 2005) suggested that further isolated populations may as yet be undiscovered. The chosen model identified large tracts of possibly suitable habitat east of currently surveyed areas (see Fig. 3g and Fig. 4a). This objective also included the delineation of areas of suitable habitat away from the known populations that might offer alternative areas for introductions/re-introductions. The current model identified a host of high probability alternative options, including the following rivers and their tributaries: Ongers and Snyderskraal above the towns of Merriman and Murraysburg, respectively; Seekoie above Hanover; Riet and kromellenboog above the Kalkfontein dam; Sondags, Broederstroom and Swart above Graaf Reinett; Kleinbrak, Oompies, Grootbrak, Pauls, Rooispruit and Teebus surrounding Cradock; Oorlogspoort south of Colesburg; and Hondeblaf above Philipstown.

3.5. *Impacts of climate change*

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 habitat will comprise not only new range, but range which was currently well beyond the accepted current range. If the conservation of this species in the wild is a consideration then these areas need to be included as priorities in conservancy establishment.

4. Discussion

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 and ex situ captive breeding (RRCP, 2005). Given that the ex situ conservation option has been unsuccessful the continued existence of this species in the wild will require a comprehensive in situ conservation plan.

Detection of this rare nocturnal species has proved to be difficult. This coupled with the recent discovery of the Touws River population (RRCP, 2005), which has been shown to be genetically distinct (Mathee, C., Pers. Comm., 2005), suggests that further isolated populations may as yet be undiscovered. The modelled suitable habitat identifies large tracts of riparian areas that may yield further populations. Fieldwork targeting the high probability areas identified by our habitat model ensure optimal use of funding with iterative cycles of fieldwork and modelling progressively improving the habitat model (Guisan et al., 2006). Comparison of the modelled suitable habitat with the known range suggests that there may be additional factors that prevent this species from occupying all 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

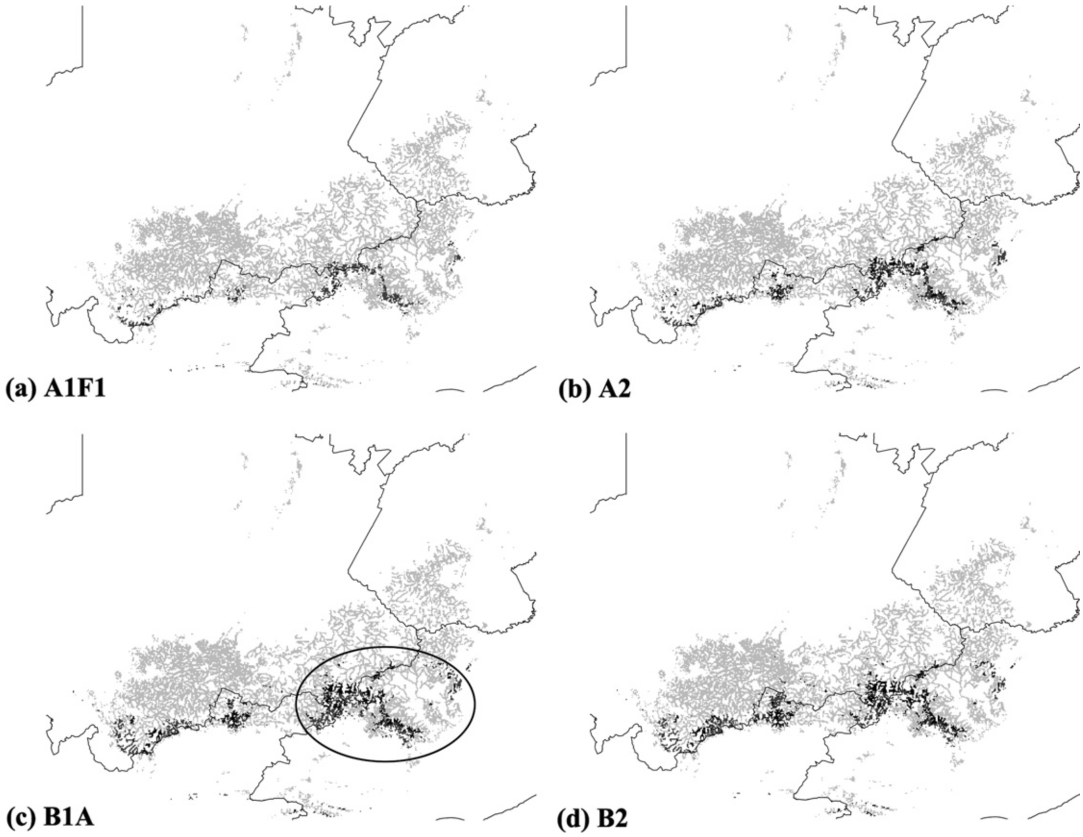

Fig. 5 – Potential range changes of *Bunolagus monticularis* between now and 2050 for the four GCM future climates as defined by the Clim.Rip.Res model. Light grey areas indicate areas that will no longer be suitable, black areas indicate areas of persistence and intermediate grey areas indicate expansion. Note that the majority of future range (ellipse) is located outside of what is currently accepted as known range.

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.

Acknowledgements

This work was supported by the AIACC AF04 project, a global collaborative initiative of the UNEP/WMO Intergovernmental Panel on Climate Change (IPCC) and funded by the Global Environment Facility. KC wishes to acknowledge funding and support from the START Doctoral Fellowship Program, the Wildlife Conservation Society, the Commonwealth Scholarship Commission and the Pittsburgh Zoo. WT and GFM received support from the International Research Network (GDRI) project 'France South Africa – Dynamics of biodiversity in Southern African ecosystems and sustainable use in the context of global change: processes and mechanisms involved'. This manuscript benefited from review by two anonymous reviewers.

REFERENCES

Ahlmann, V., Collins, K., Seal, U.S., 2000. Riverine Rabbit (*Bunolagus monticularis*): A population and habitat viability assessment workshop. Final Report., Conservation breeding specialist group (SSC/IUCN), Apple Valley, MN.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration Guidelines for computing crop water

requirements, FAO Irrig. and Drain. Paper 56. Food and Agriculture Organisation of the United Nations, Rome, pp. 300.
Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biol. 10, 1618–1626.
Aspinall, R., Matthews, K., 1994. Climate change impact on distribution and abundance of wildlife species: an analytical approach using GIS. Environ. Pollut. 86, 217–223.
Box, E.O., Crumpacker, D.W., Hardin, E.D., 1999. Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. Climatic Change 41, 213.
Calvete, C., Estrada, R., Angulo, E., S, C.-R., 2004. Habitat factors related to wild rabbit conservation in an agricultural landscape. Landscape Ecol. 19, 531–542.
Coetzee, K., 1994. The Riverine Rabbit (*Bunolagus monticularis*) and its habitat: Conservation implications of an unnaturally fragmented distribution. M.Tech. Diploma Thesis, Port Elizabeth Technikon, South Africa.
Collins, K., Ahlmann, V., Matthee, C., Taylor, P., Keith, M., Van Jaarsveld, A., 2003. *Bunolagus monticularis*. In 2004 IUCN Red List of Threatened Species. IUCN 2004 www.redlist.org Downloaded on 17 January 2005.
Debeljak, M., Dzerosky, S., Jerina, K., Kobler, A., Adamic, M., 2001. Habitat suitability modelling for red deer (*Cervus elaphus* L.) in South-central Slovenia with classification trees. Ecol. Model. 138, 321–330.
Dippenaar, S.M., Ferguson, J.W.H., 1994. Towards a captive breeding programme for the riverine rabbit *Bunolagus monticularis*. S. Afr. J. Sci. 90, 381.
Duthie, A.G., 1989. The ecology of the riverine rabbit *Bunolagus monticularis*. MSc Thesis, University of Pretoria, South Africa.
Duthie, A.G., Robinson, T.J., 1990. The African rabbits. In Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. In: Chapman, J.A., Flux, J.E.C. (Eds.). IUCN/SSC Lagomorph Specialist Group, pp. 121–127.
Duthie, A.G., Skinner, J.D., Robinson, T.J., 1989. The distribution and status of the riverine rabbit, *Bunolagus monticularis*, South Africa. Biol. Conserv. 47, 195–202.
Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. J. Appl. Ecol. 41, 263.
Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.
Germishuizen, G., Meyer, N.L., 2003. Plants of southern Africa: an annotated checklist, Strelitzia. National Botanical Institute, Cape Town, South Africa.
Glenz, C., Massolo, A., Kuonen, D., Schlaepfer, R., 2001. A wolf habitat suitability prediction study in Valais (Switzerland). Landscape Urban Plan. 55, 55–65.
Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B., Wood, R.A., 2000. The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. Clim. Dynam. 16, 147–168.
Guisan, A., Broennimann, O., Engler, R., Yoccoz, N.G., Vust, M., Zimmermann, N.E., Lehmann, A., 2006. Using niche-based models to improve the sampling of rare species. Conserv. Biol. 20, 501–511.
Hastie, T.J., Tibshirani, R., 1990. Generalized additive models. Chapman and Hall, London.
Hewitson, B., 2003. Developing perturbations for climate change impact assessments. EOS 84, 337–339.
Heywood, V.H., Iriondo, J.M., 2003. Plant conservation: old problems, new perspectives. Biol. Conserv. 113, 321–335.
Hilbert, D.W., Bradford, M., Parker, T., Westcott, D.A., 2004. Golden bowerbird (Prionodura newtonia) habitat in past, present and future climates: predicted extinction of a vertebrate in tropical highlands due to global warming. Biol. Conserv. 116, 367–377.
Huntley, B., 1995. Plant species' response to climate change: implications for the conservation of European birds. IBIS 137 (Suppl.1), S127–S138.
IPCC-TGCIA (Ed.), 1999. Guidelines on the use of scenario data for climate impact and adaptation assessment. Intergovernmental panel on climate change, task group on scenarios for climate impact assessment, pp. 69.
Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evolut. 19, 101–108.
Lawler, J.J., Edwards, T.C.J., 2002. Landscape patterns as predictors of nesting habitat: building and testing models for four species of cavity-nesting birds. Landscape Ecol. 17, 233–245.
Lehmann, A., Overton, J.M., Austin, M.P., 2002. Regression models for spatial prediction: their role for biodiversity and conservation. Biodivers. Conserv. 11, 2085–2092.
Li, W., Wang, Z., Ma, Z., Tang, H., 1999. Designing the core zone in a biosphere reserve based on suitable habitats: Yancheng Biosphere Reserve and the red crowned crane (Grus japonensis). Biol. Conserv. 90, 167–173.
Lynch, S.D., 2003. Development of a raster database of annual, monthly and daily rainfall for southern Africa. WRC Report No. 1156/1/03, School of Bioresources Engineering and Environmental Hydrology, Pietermaritzburg, South Africa.
Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921–931.
Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Global Ecol. Biogeogr. 11, 445–451.
Midgley, G.F., Hannah, L., Millar, D., Thuiller, W., Booth, A., 2003. Developing regional and species-level assessments of climate change impacts on biodiversity: A preliminary study in the Cape Floristic Region. Biol. Conserv. 112, 87–97.
Mills, G., Hes, L., 1997. The Complete Book of South African Mammals. Struik, Cape Town, South Africa. pp. 356.
Milton, S.J., Dean, W.R.J., 2001. Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. J. Arid Environ. 47, 465–483.
Mucina, L., Rutherford, M.C., 2005. Vegetation Map of South Africa, Lesotho and Swaziland, Strelitzia. National Botanical Institute, Pretoria, South Africa.
Nakicenovic, N., Swart, R. (Eds.), 2000. Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 570.
Palomares, F., Delibes, M., Revilla, E., Calzada, J., Fedriani, J.M., 2001. Spatial ecology of the Iberian lynx and abundance of its primary prey, the European rabbit, in a heterogeneous environment. Wildlife Monogr. 148, 1–36.
Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225–245.
Pearce, J.L., Cherry, K., Drielsma, M., Ferrier, S., Whish, G., 2001. Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. J. Appl. Ecol. 38, 412–424.
Pearson, R.G., Dawson, T.P., Liu, C., 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27, 285–298.
Post, E., 2003. Climate-vegetation dynamics in the fast lane. Trends Ecol. Evol. 18, 551–553.
Powrie, L.W., 2004. Common names of Karoo plants, Strelitzia. National Botanical Institute, Pretoria, South Africa. pp. 119.

Radosevich, S.R., Stubbs, M.M., Ghersa, C.M., 2003. Plant invasions – process and patterns. Weed Sci. 51, 254–259.
Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2004. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426, 837–841.
Rousteenoja, K., Carter, T.R., Jylha, K., Tuomenvirta, H., 2003. Future climate in world regions: an intercomparison of model-based projections for the new IPCC emissions scenarios. Finnish Environment Institute, Helsinki, Finland.
RRCP, 2005. Riverine Rabbit Conservation Project.www.riverinerabbit.co.za Downloaded on 17 January 2005.
Rushton, S.P., Ormerod, S.J., Kerby, G., 2004. New paradigms for modelling species distributions? J. Appl. Ecol. 41, 193–200.
Rutherford, M.C., Powrie, L.W., Midgley, G.F., 2003. ACKDAT: a digital spatial database of distributions of South African plant species and species assemblages. S. Afr. J. Bot. 69, 99–104.
Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G., 2001. The population biology of invasive species. Ann. Rev. Ecol. Syst. 32, 305–332.
Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. BioScience 52, 891–904.
Schulze, R.E., 1997. South African Atlas of Agrohydrology and Climatology. Report TT82/96, Water Research Commission, Pretoria, South Africa.
Skinner, J.D., Smithers, R.H.N., 1990. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria, South Africa.
Strahler, A.N., 1952. Dynamic basis of geomorphology. Geol. Soc. Am. Bull. 63, 923–938.
Swets, K.A., 1988. Measuring the accuracy of diagnostic systems. Science 240, 1285–1293.
Teixeira, J., Arntzen, J.W., 2002. Potential impact of climate warming on the distribution of the Golden-striped salamander, *Chioglossa lusitanica*, on the Iberian Peninsula. Biodivers. Conserv. 11, 2167–2176.
Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. Ecography 27, 165–172.
Wu, X.B., Smeins, F.E., 2000. Multiple-scale habitat modelling approach for rare plant conservation. Landscape Urban Plan. 51, 11–28.
Zimmermann, F., Breitenmoser, U., 2002. A distribution model for the Eurasian lynx (Lynx lynx) in the Jura Mountains, Switzerland. In: Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.B., Samson, F.B. (Eds.), Predicting species occurrences – Issues of accuracy and scale. Island Press, Washington, pp. 653–659.