

A modelling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns

## CHAPTER 2

B.F.N. Erasmus<sup>1</sup>, M. Kahariya<sup>1</sup>, M.W. Mansell<sup>2</sup>, S.L. Cloven<sup>3</sup> & A.S. van Jaarsveld<sup>1,4\*</sup>

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<sup>1</sup>Conservation Planning Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002

<sup>2</sup>Phytosystematics Division, ARC – Plant Production Research Institute, Private Bag 11201, Pretoria, 0001 South Africa

<sup>3</sup>Department of Zoology & Entomology, University of Pretoria, Pretoria, 0002 South Africa

<sup>4</sup>Centre for Environmental Studies, University of Pretoria, Pretoria, 0002 South Africa

**Key words:** species distribution, predicted climate change, antlion

\*To whom correspondence should be addressed. [AgvJaarsveld@zoology.up.ac.za](mailto:AgvJaarsveld@zoology.up.ac.za)

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B.F.N. Erasmus<sup>1</sup>, M. Kshatriya<sup>1</sup>, M.W. Mansell<sup>2</sup>, S.L. Chown<sup>3</sup> & A.S. van Jaarsveld<sup>1,4\*</sup>

<sup>1</sup>Conservation Planning Unit, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002 South Africa.

<sup>2</sup>Biosystematics Division, ARC – Plant Protection Research Institute, Private Bag X134, Pretoria, 0001 South Africa.

<sup>3</sup>Department of Zoology & Entomology, University of Pretoria, Pretoria, 0002 South Africa.

<sup>4</sup>Centre for Environmental Studies, University of Pretoria, Pretoria, 0002 South Africa

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**ABSTRACT**

The application of a model modified from Jeffree & Jeffree (1994) for investigating the distribution responses of selected antlion species to a climate change scenario was explored in this study. Modifications include a multivariate capability that facilitates the incorporation of precipitation seasonality, and provides useful outputs in the form of probability of occurrence values for each species. The model can be used to interpolate the distributions of poorly sampled taxa as well as predict responses to a changing climate. It is predicted that species from the more arid western parts of South Africa will be subject to severe range contraction and range shifts whereas the species from the more mesic eastern parts will experience range contraction with limited range shift. The likelihood of successful range shifts will be affected by the nature of novel communities, habitat suitability and the degree of land transformation encountered. Given the extent of the predicted spatial responses, conservation planners can no longer afford to ignore future climate impacts on species distribution patterns.

conservation plans, however, predictive modelling remains one of the few practical alternatives likely to provide information on species distribution patterns and their range dynamics at a time-scale relevant to conservation.

A recent model developed by Jeffree & Jeffree (1994) investigated the distribution patterns and their response to climate change. This model (Jeffree & Jeffree 1994; Climate Change 1992) was investigated during this study. The model is a multivariate model which could potentially be applied to large numbers of taxa in a taxon-by-taxon manner. The original model was modified by adding a multivariate capability for species-pair matching (Tilbe & Richardson 1994; Ealey et al. 1992). The output from this modified model is a spatially explicit set of probabilities of occurrence values for each species.

To demonstrate the potential value of this modified modelling approach, it was attempted to derive interpolated distributions of selected and poorly surveyed antlion species and generate climate-affected distribution patterns for these species under future climate conditions. Because antlions generally prefer arid areas (Mansell 1963) and current climate models predict general aridification in southern Africa (Howarth 1994), these antlion species were considered appropriate for exploring the value of such a predictive distribution modelling procedure for poorly sampled taxa.

## INTRODUCTION

The conservation of poorly sampled taxa presents special challenges to conservation biology. Information on the geographic distributions of such taxa should ideally be extended through intensive biodiversity surveys before conservation decision-making (Balmford & Gaston 1999), although this strategy is usually confounded by time and resource constraints (Freitag *et al.* 1998). Acknowledging that the use of poor distribution data may significantly affect land use and related economic efficiency of conservation practice (Balmford & Gaston 1999), an alternative strategy is to model the predicted distributions of species based on suitable broad-scale environmental parameters, *e.g.* soil, climate and vegetation types (Margules & Redhead 1995). In many instances this approach may require a number of assumptions, including: linear relationships between species' physiological tolerances and their distribution limits, minimal effects of interspecific interactions on species distributions, and that fewer rather than many abiotic variables determine distributions (Chown & Gaston 1999). In the context of the conservation crisis, however, predictive modelling remains one of the few practical alternatives likely to provide information on species distribution patterns and their range dynamics, at a time scale relevant to conservation practitioners.

A recent model developed by Jeffree & Jeffree (1994, 1996) to predict species' distribution patterns and their response to climate change (Intergovernmental Panel on Climate Change 1992) was investigated during this study. The model is straightforward and could potentially be applied to large numbers of taxa in a cost effective manner. The original model was modified by adding a multivariate capability that transcends pure climate matching (Tribe & Richardson 1994; Eeley *et al.* 1999). The output from this modified model is a spatially explicit set of probabilities of occurrence values for each species.

To demonstrate the potential value of this modified modelling approach, it was used to derive interpolated distributions of selected and poorly surveyed antlion species, and to generate climate-affected distribution patterns for these species under climate change conditions. Because antlions generally prefer arid areas (Mansell 1985a) and climate change models predict general aridification in southern Africa (Hewitson 1998), these neuropteran species were considered appropriate for exploring the value of such a climate-based distribution modelling procedure for poorly sampled taxa.

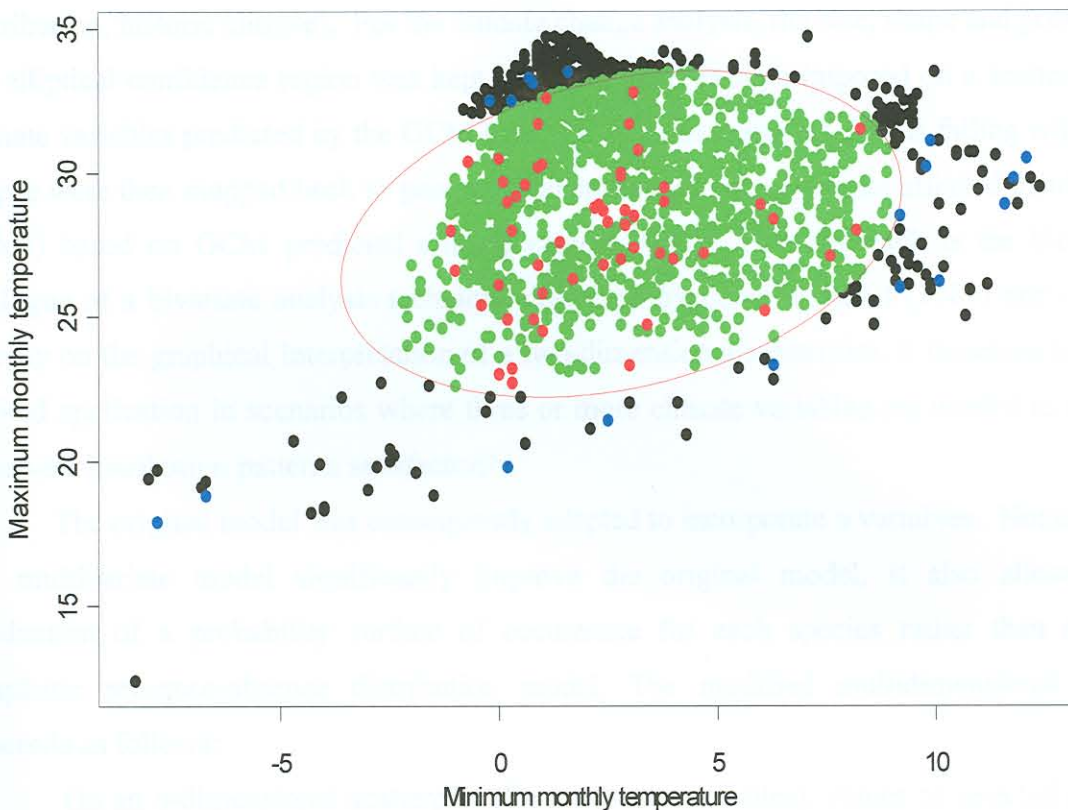
## METHODS

The study was conducted at a subcontinental scale using climate data and antlion (Neuroptera: Myrmeleontidae) distribution data for South Africa. Data resolution was resolved to quarter degree grid cells (approximately 25 km × 25 km). The Computing Centre for Water Research (CCWR, University of Natal) provided climate data for 1858 grid cells encompassing South Africa. Neuroptera distribution data were extracted from the Plant Protection Research Institute (PPRI) database (see Freitag & Mansell 1997) which, for the antlions, comprises 606 records for 49 species. Expert opinion showed that model output based on less than nine sampling records produced spurious predictions and therefore sampling density together with biome representation and expert assessment of sampling bias were used to select appropriate species for inclusion in the model. Five species were selected to test the modelling approach, to illustrate the principles on which the model is based, and to demonstrate the ways in which the model can highlight potential conservation concerns. The selected species were Palpares caffer (Burmeister), a species endemic to southern Africa with the largest proportion of its distribution in the moister eastern parts of South Africa (Mansell, unpubl.); Palpares speciosus (Linnaeus), a species endemic to the Eastern and Western Cape provinces; Palparellus dubiosus (Péringuey), a species endemic to the arid western parts of South Africa; Pamexis luteus (Thunberg), a range-restricted species endemic to the Western Cape Fynbos biome (Low & Rebelo 1996) and Pamexis namaqua (Mansell), a range-restricted species from the Succulent Karoo biome of Namaqualand (Mansell 1985b). Although only five species were selected, they account for 26 % of the 606 records in the PPRI database and were regarded as representative for the purposes of this study.

The climate data initially selected were the mean minimum temperature of the coldest month and the mean maximum temperature of the hottest month for each grid square. Jeffree & Jeffree (1994, 1996) considered these two variables to be sufficient for their models of the distribution changes of European insect and plant species expected under scenarios of climate change. However, exploratory modeling in the present study revealed that these variables were insufficient for realistically describing antlion spatial distributions, partly as a result of the seasonal rainfall patterns in the southern African region. As there are strong east to west rainfall gradients across the subcontinent that have a marked influence on the biota (Schulze 1997; Harrison *et al.* 1997; Le Lagadec *et al.* 1998; Davis *et al.* 2000), and because antlions are generally xerophilous (Mansell 1985a), measures of precipitation were included as

additional explanatory variables to increase the predictive power of the proposed model. Mean annual precipitation and precipitation seasonality were included. The latter can be seen as a joint measure reflecting when precipitation occurs as well as the amount recorded. Precipitation seasonality was calculated as the difference between the mean rainfall for February and the mean rainfall for August. These months were selected based on a factor analysis of the 12 monthly rainfall means which showed that February rainfall contributed most to Factor 1, explaining 56 % of the variance in monthly rainfall, and August rainfall contributed most to Factor 2 that explained an additional 37 % of the variance in monthly rainfall. A negative precipitation seasonality value indicates winter rainfall and a positive value summer rainfall. All mean values were calculated from climate data from the last 30 years. Two sets of climate data were used for the four variables employed; one set based on historic climate data and the other on a General Circulation Model (GCM) predicting climate change. The Hadley Centre Unified Model (HadCM2 with no sulphates) ([http://www.metogovt.uk/sec5/NWP/NWP\\_sys.html](http://www.metogovt.uk/sec5/NWP/NWP_sys.html)) GCM was used because it represents a worst-case scenario for South Africa, predicting the most extreme changes in climate (G. Kiker, pers. comm.). It predicts a temperature rise of 2.5 – 3 °C for South Africa by the time that atmospheric carbon dioxide levels have doubled from their pre-industrial levels. Erring on the side of caution, this means that significant changes in the regional climate can be expected by the year 2050 (Hewitson 1998) but possibly sooner. These changes can be expected to be significant given that climate fluctuations of similar magnitude led to biotic range shifts during the last glacial period (Allen *et al.* 1999).

The original bivariate Jeffree & Jeffree (1994) modelling approach proceeded as follows. A scatterplot of the values of all grid cells for any two chosen climate variables was defined as the climate space. The grid cells where a particular species was recorded was referred to as the known records (KR). The values of these two climate variables for all KR cells were used to construct an elliptical confidence region that was superimposed on the scatterplot (Fig. 1). The choice of an ellipse to define the confidence region implies the assumption that the shape of the realised niche in climate space is elliptical. The ellipse was chosen partly based on the work of Jeffree & Jeffree (1994, 1996) but also based on the need for a simple basic model that can be used for broad scale modelling for a large number of species. Although it would be possible to build a species-specific model that uses a more complex shape to define the realised niche in climate space, such a model would not be generalisable across species.



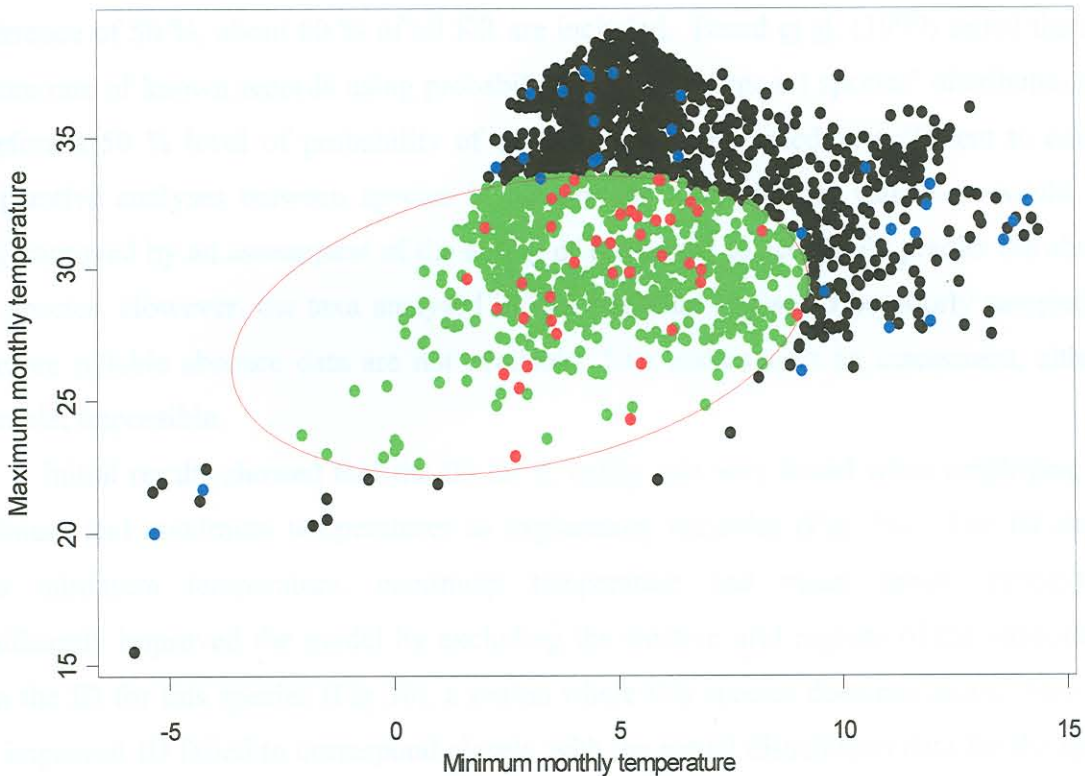
**Fig. 1.** Scatterplot of the minimum and maximum temperature values for 1858 quarter degree grid squares covering South Africa. Superimposed on this scatterplot is an elliptical confidence region whose size and shape was derived from historic temperature values in grid squares where *Palpares caffer* was recorded. Red dots represent known records for *P. caffer* falling inside the confidence region, blue dots represent known records that fall outside the confidence region, green dots represent the distribution predicted for this species by the climate data (interpolated distribution (ID) in the text), and black dots represent the grid squares where this species does not occur and where it was not predicted to occur.

All points falling within this elliptical confidence region were then mapped back on to geographical space to form an interpolated distribution where this species could occur. This interpolated distribution based on historic climate data was referred to as ID (interpolated distribution, historic climate). For the climate change analysis, the size, shape and position of the elliptical confidence region was kept constant, but it is superimposed on a scatterplot of climate variables predicted by the GCM (see Fig. 2 for an example). Points falling within the ellipse were then mapped back to geographical space to depict a climate affected distribution (CAD) based on GCM predicted climate change values. This approach is the biological analogue of a bivariate analysis technique described by Sokal & Rohlf (1981) and it relies heavily on the graphical interpretation of a two-dimensional scatterplot. It therefore has very limited application in scenarios where three or more climate variables are needed to explain observed distribution patterns satisfactorily.

The original model was consequently adapted to incorporate  $n$  variables. Not only did the multivariate model significantly improve the original model, it also allowed the production of a probability surface of occurrence for each species rather than a more simplistic presence-absence distribution model. The modified multidimensional model proceeds as follows:

On an  $n$ -dimensional scatterplot (for  $n$  climate variables), values of selected climate variables were plotted for each KR grid cell and subtracted mean climate values to generate transformed values for each grid cell. This procedure centres values around the origin of the multidimensional scatterplot. An  $n \times n$  covariance matrix was calculated and then this matrix was used as an input to calculate eigen values and eigen vectors for the covariance matrix. The climate variable values of all grid cells were then transformed into this eigen vector space. The transformed climate variables were then divided by the eigen values and the distances of these points from the above origin follows a  $\chi^2$  distribution. This allows one to read the probability of occurrence of a species in any grid cell off a  $\chi^2$  probability table at the appropriate degree of freedom (KR-1). The technique is relatively straightforward and does not require considerable computing power. The outcome of this analysis is a probability of occurrence surface for each species across the country.



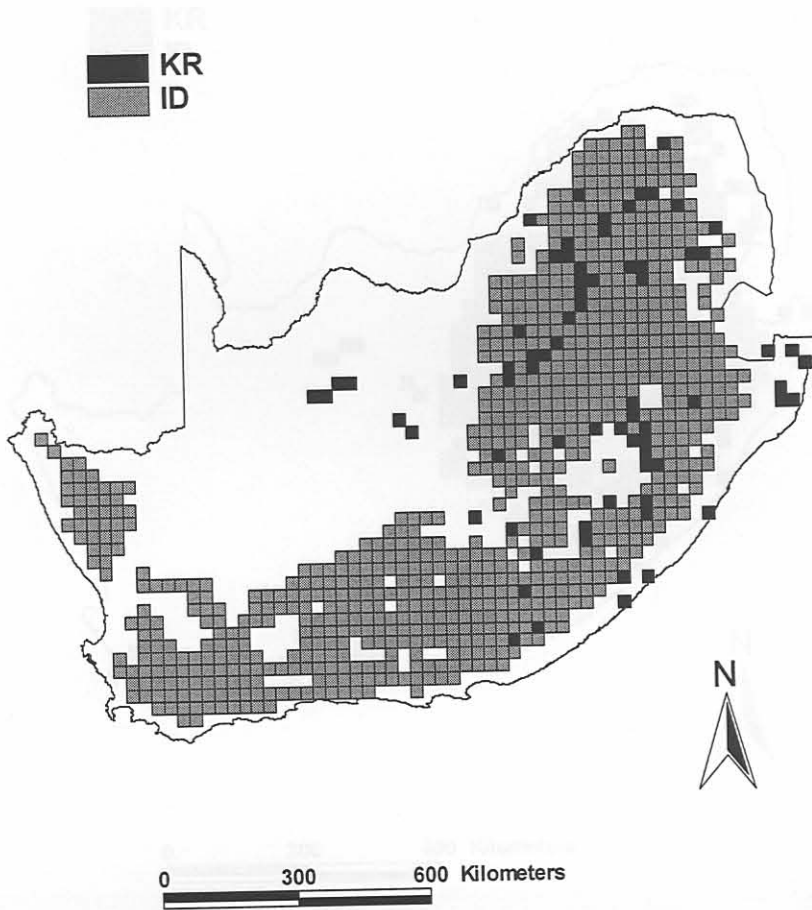


**Fig. 2.** Scatterplot of the GCM predicted minimum and maximum temperature values for 1858 quarter degree grid squares covering South Africa. Superimposed on this scatterplot is an elliptical confidence region whose size and shape were derived from historic temperature values in grid squares where *Palpares caffer* was recorded. Red dots represent known records for *P. caffer* falling inside the confidence region, blue dots represent known records that fall outside the confidence region, green dots represent the distribution predicted for this species by the climate data (climate affected distribution (CAD) in the text), and black dots represent the grid squares where this species does not occur and where it was not predicted to occur.

## RESULTS

Because this modified multivariate model (Jeffree & Jeffree 1994) provides a probability of occurrence value for each grid cell, it was necessary to select an appropriate probability level to employ across the study for comparing results from different species. At a probability of occurrence of 50 %, about 60 % of all KR are included. Beard *et al.* (1999) found the same capture rate of known records using probabilistic models to model species' distributions and therefore a 50 % level of probability of occurrence was regarded as sufficient to conduct comparative analyses between species in the present study. Model validation would have been improved by an assessment of the ability of the model to accurately predict the absence of a species. However, the taxa analysed in this study are known to be poorly sampled and therefore reliable absence data are not available. This makes such an assessment, although desirable, impossible.

Initial results showed that the ID for *P. caffer* was very broad when employing only minimum and maximum temperatures as explanatory variables (Fig. 3a). The ID derived from minimum temperature, maximum temperature and mean annual precipitation significantly improved the model by excluding the western arid regions of the subcontinent from the ID for this species (Fig 3b), a region where this species does not occur. However, this improved ID failed to correspond closely with the actual distribution data for the species (Fig. 3b) because it predicted that the species would occur in the eastern summer rainfall region of South Africa and along the southern coastal region that has a predominantly winter rainfall pattern. Similar results for the other species confirmed that employing temperature and mean annual rainfall in the model does not adequately represent distributions that are strongly affected by seasonal rainfall patterns. For this reason the mean annual precipitation variable was replaced with a precipitation seasonality value. This resulted in a further improved predicted ID pattern for *P. caffer* (Fig. 4), using minimum and maximum temperature and precipitation seasonality as explanatory variables. Here the ID is limited to the eastern portions of South Africa, which is more consistent with the distribution data derived from the PPRI database. The improved predictions using precipitation seasonality together with minimum and maximum temperatures were consistent for all species except *P. dubiosus*, which yielded similar ID's when using either of the precipitation variables in conjunction with minimum and maximum temperatures.



**Fig. 3(a).** These figures (3a and 3b) illustrate the modelling process. Black squares represent known records (KR) and grey squares represent the interpolated distribution. This figure shows the Interpolated distribution (ID) from historic climate data for *Palpares caffer* using minimum monthly temperature and maximum monthly temperature.

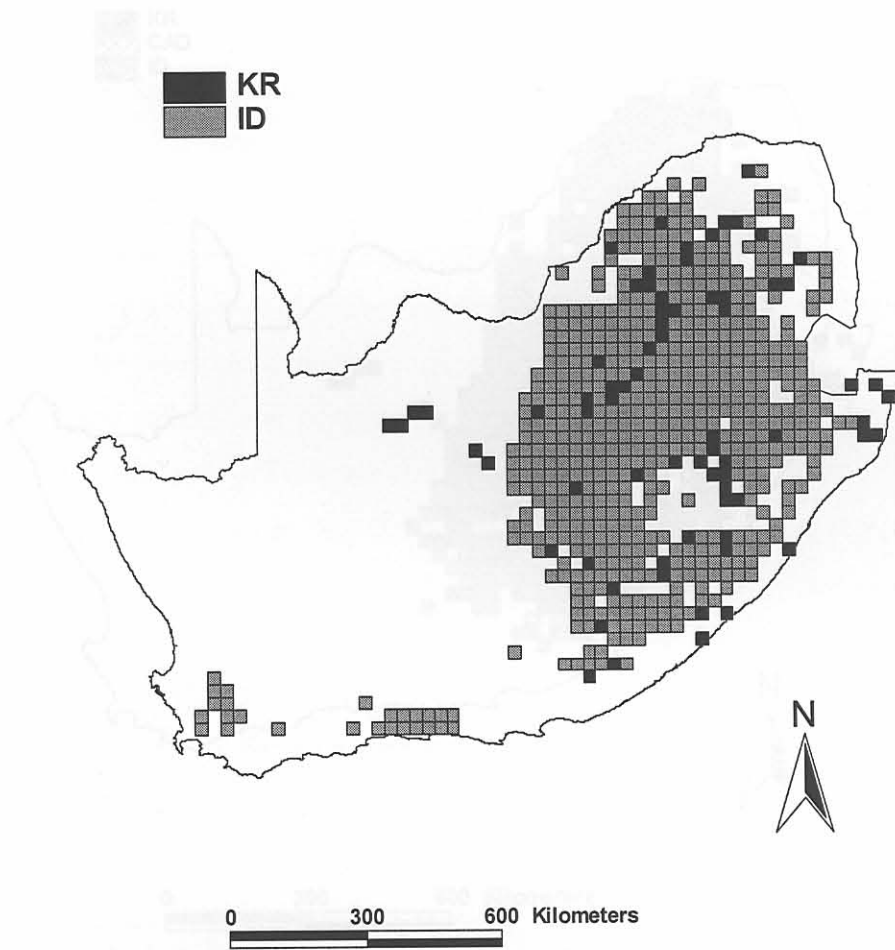
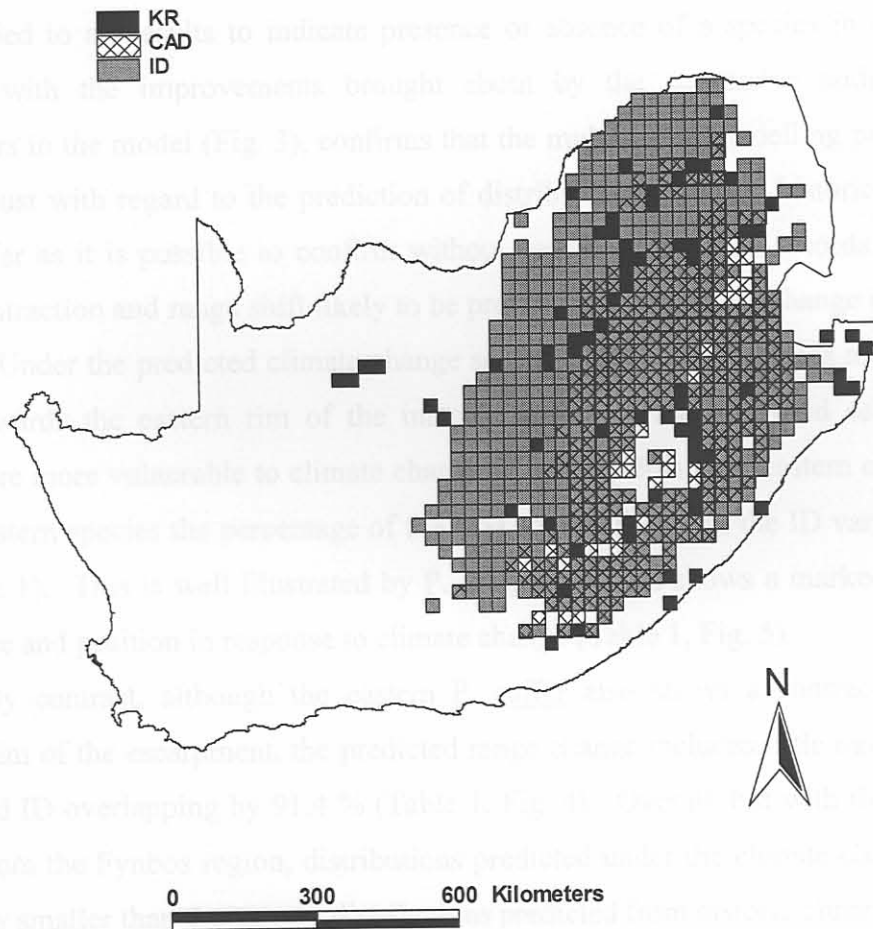


Fig. 4. Predicted distributions for *Palpares caffer* derived from minimum monthly temperature, maximum monthly temperature and precipitation seasonality. Black squares represent known records (KR) for the species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution (ID).

**Fig. 3(b)** Interpolated distribution (ID) from historic climate data for *Palpares caffer* using minimum monthly temperature, maximum monthly temperature and mean annual precipitation.



**Fig. 4.** Predicted distributions for *Palpares caffer* derived from minimum monthly temperature, maximum monthly temperature and precipitation seasonality. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data

Nonetheless, following the seasonality-based procedure, on average 51.7 % ( $\pm$  SD 4.9) of the PPRI database-derived records fell within their respective ID's generated by the modified multivariate model. This is consistent with the 50 % probability of occurrence cut-off that was applied to all results to indicate presence or absence of a species in this study. This, together with the improvements brought about by the successive addition of rainfall parameters in the model (Fig. 3), confirms that the multivariate modelling procedure appears to be robust with regard to the prediction of distributions based on historic climate data, at least as far as it is possible to confirm without confirmed absence records. The degree of range contraction and range shift likely to be precipitated by climate change is summarized in Table 1. Under the predicted climate change scenario, the antlion species mostly show range shifts towards the eastern rim of the inland escarpment and it would seem that western species are more vulnerable to climate change (Figs 5-8) than their eastern counterparts.. For these western species the percentage of the CAD coinciding with the ID varies from 0 - 33.8 % (Table 1). This is well illustrated by *P. dubiosus* which shows a marked change in both range size and position in response to climate change (Table 1, Fig. 5).

By contrast, although the eastern *P. caffer* also shows a contraction towards the eastern rim of the escarpment, the predicted range change includes little range shift, with the CAD and ID overlapping by 91.4 % (Table 1, Fig. 4). Overall, but with the exception of *P. luteus* from the Fynbos region, distributions predicted under the climate change scenario are markedly smaller than the current distributions predicted from historic climate data (Table 1)

## DISCUSSION

### Model characteristics

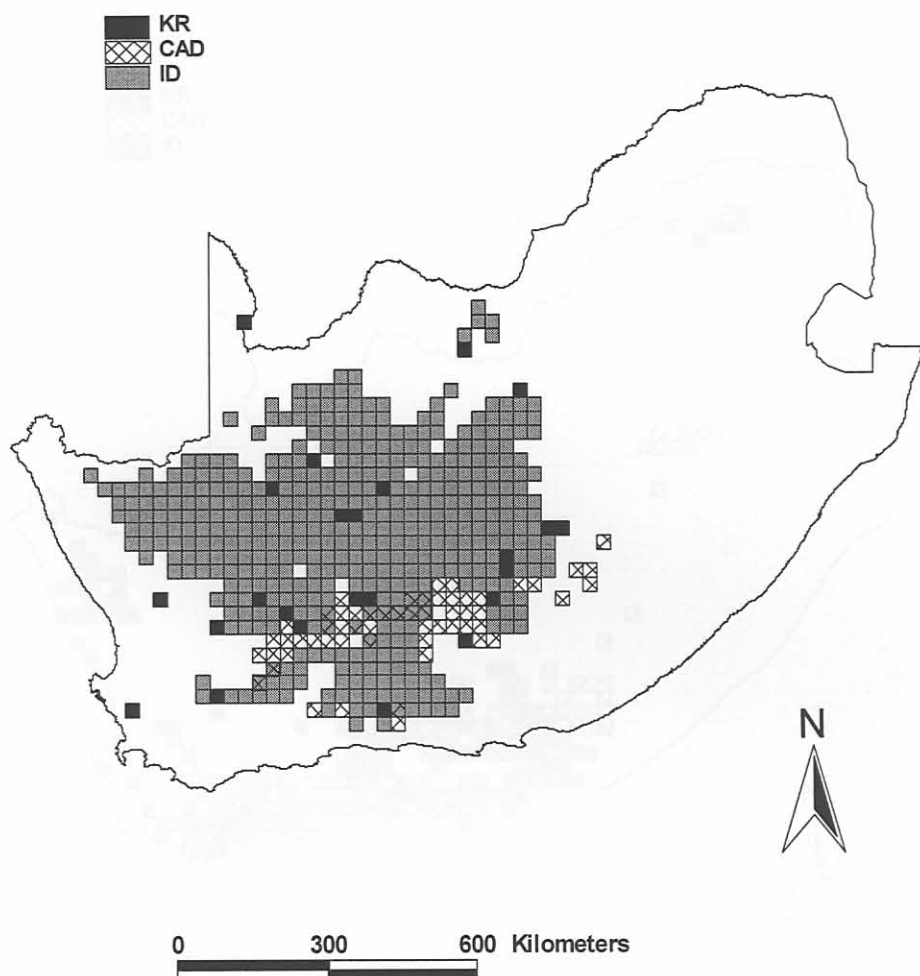
It is clear from this analysis that the modified model's ability to accurately predict distributions decreases if the distribution of the species being modelled straddles seasonal rainfall regions. For example, *P. speciosus* occurs in regions with markedly different seasonal rainfall patterns (Figs 6 & 9) resulting in the disjunct ID in Fig. 6. This distribution is unlikely to be biologically realistic, and clearly some additional improvements to the model are required to adequately deal with species that show this type of distribution pattern. These improvements may include more detailed information on the biology of this particular species to identify appropriate variables that drive its distribution pattern and a subsequent adjustment in the model to include such variables. Such adjustments might include modelling

**Table 1.** The number of grid cells occupied by each species. The values in brackets indicate percentages. Abbreviations: KR – Known records, ID – interpolated distribution from historical climate data, CAD – Predicted distribution from predicted climate data<sup>1</sup>. The results are from the multivariate improvement on Jeffree & Jeffree (1994) model at a 50% probability of occurrence

Species	KR	ID	CAD (CAD as % of ID)	KR falling inside ID (% of KR)	Overlap between ID and CAD (%CAD inside ID)
<u>Palparellus dubiosus</u>	24	461	59 (12,7)	12 (50)	16 (27,1)
<u>Palpares caffer</u>	74	684	361 (52,8)	43 (58,1)	330 (91,4)
<u>Palpares speciosus</u>	27	187	65 (34,8)	13 (48,1)	22 (33,8)
<u>Pamexis luteus</u>	15	16	18 (112,5)	7 (46,7)	1 (5,3)
<u>Pamexis namaqua</u>	9	12	6 (50,0)	5 (55,6)	0 (0)

Fig. 5. Predicted distributions for Palparellus dubiosus derived from multivariate monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, white squares represent the climate affected distribution (CAD), and grey squares represent the interpolated distribution from historic climate data (ID).

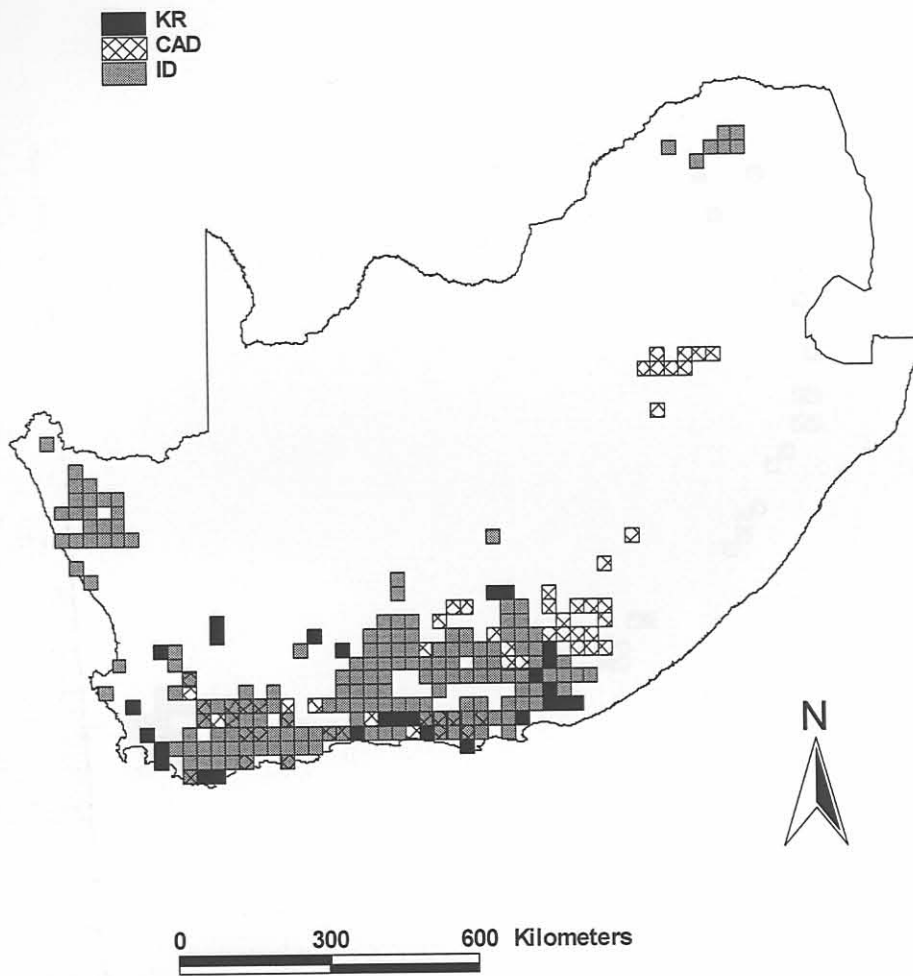
<sup>1</sup>The percentage overlap between ID and CAD was calculated using proportional overlap (Prendergast et al. 1993) where the number of coinciding grids cells is divided by the maximum number of possible overlapping grid cells, i.e. the number of grid cells containing records of the smallest distribution.



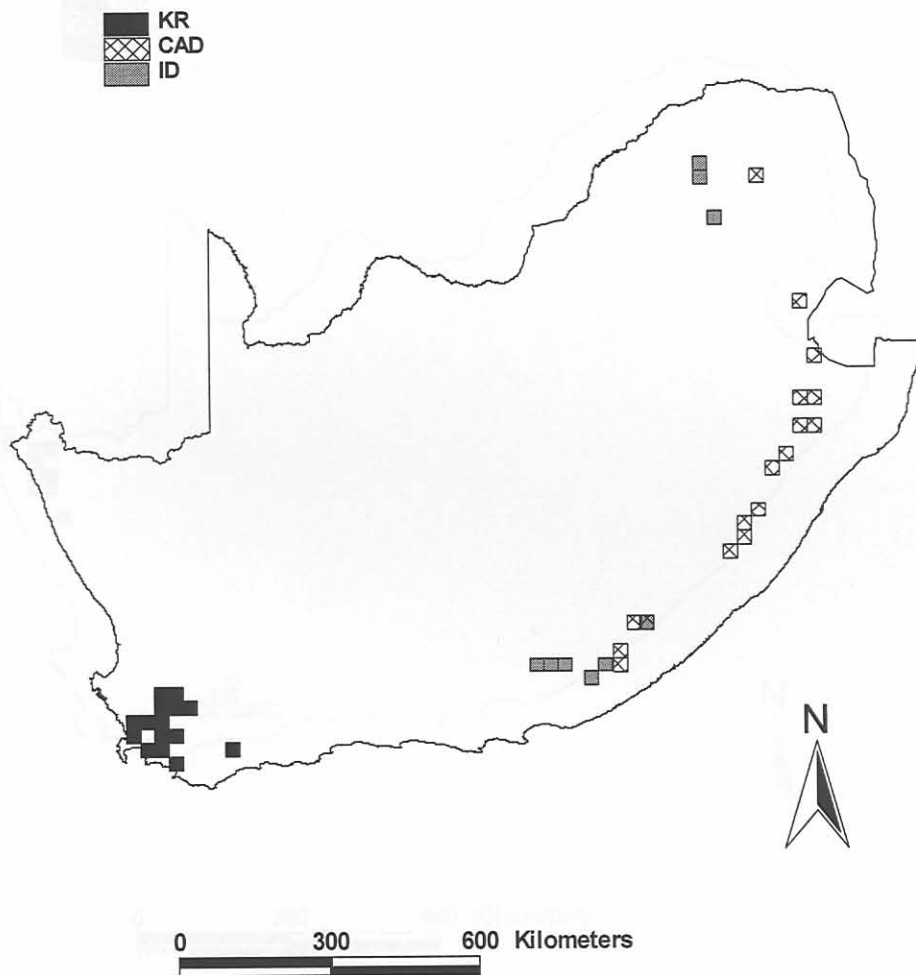
**Fig. 5.** Predicted distributions for *Palparellus dubiosus* derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.

distribution from historic climate data.

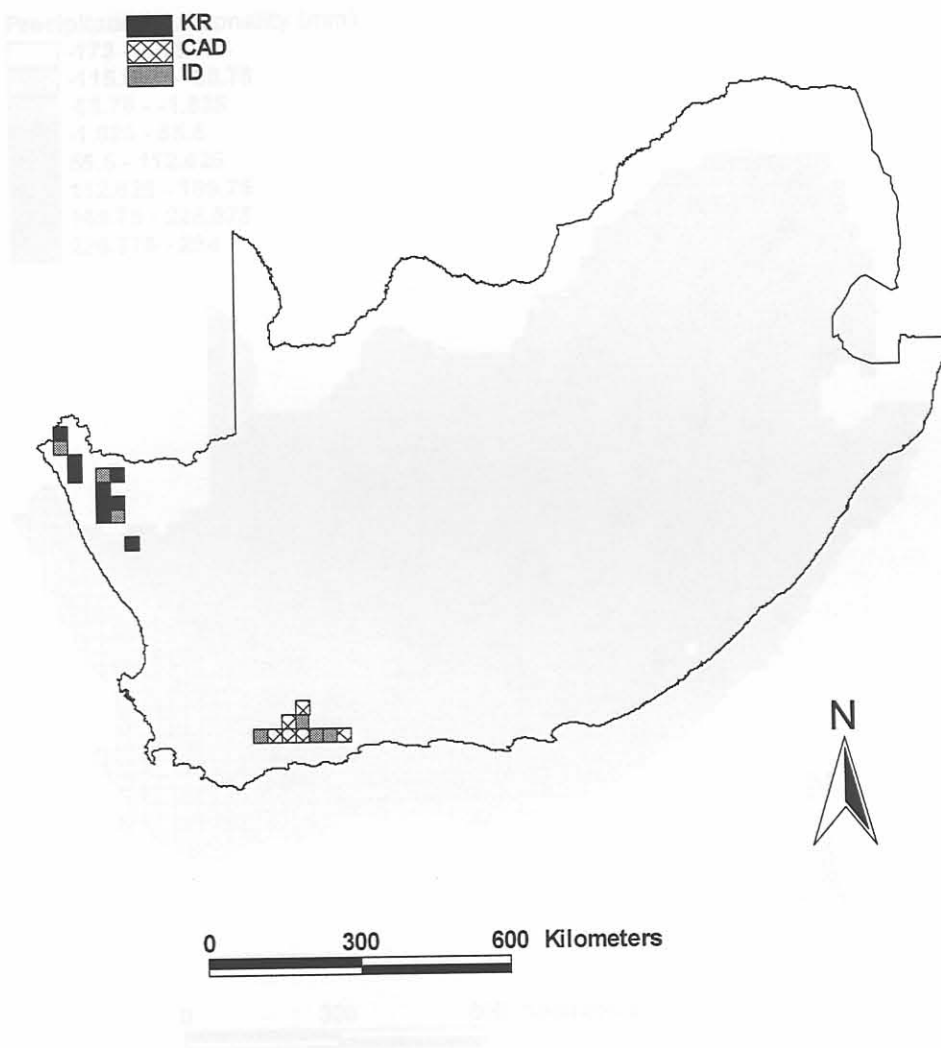




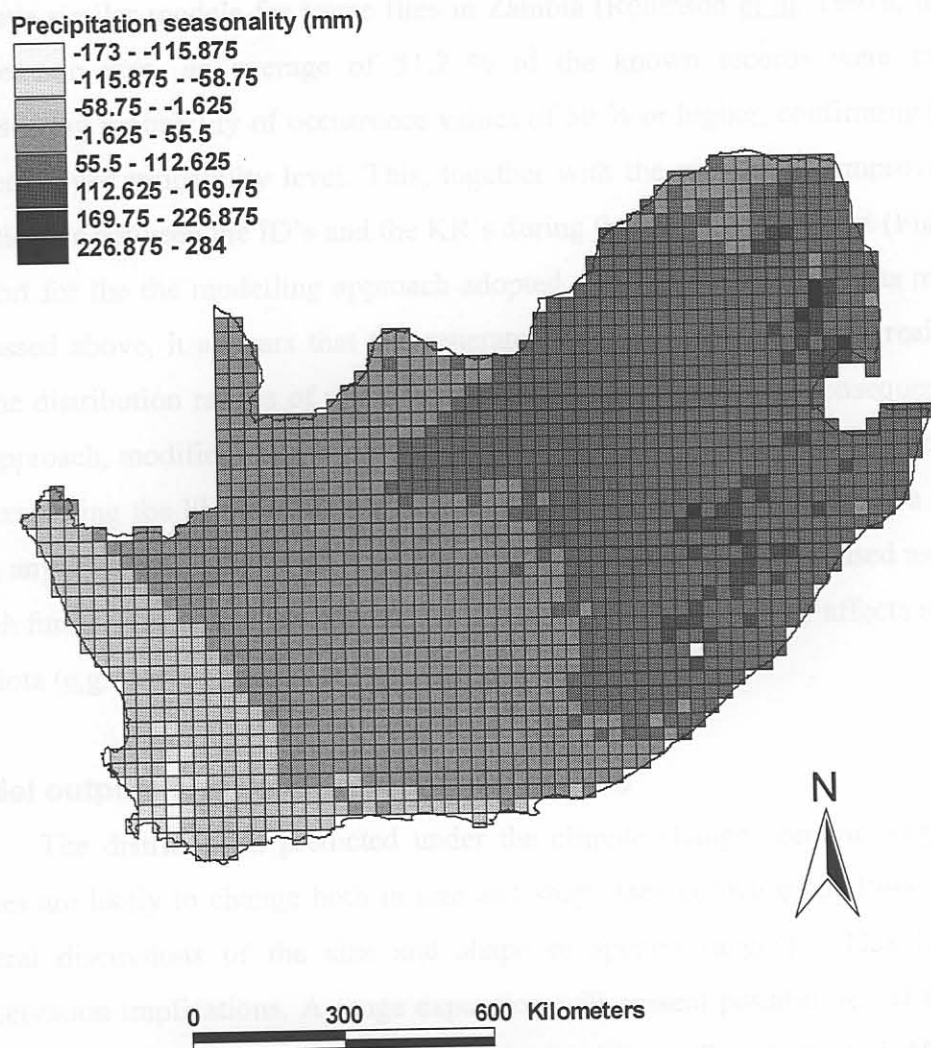
**Fig. 6.** Predicted distributions for *Palpares speciosus* derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.



**Fig. 7.** Predicted distributions for *Pamexis luteus* derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.



**Fig. 8.** Predicted distributions for *Pamexis namaqua* derived from minimum monthly temperature, maximum monthly temperature and mean annual precipitation. Black squares represent known records (KR) for this species, hatched squares represent the climate affected distribution (CAD) and grey squares represent the interpolated distribution from historic climate data.



**Fig. 9.** Precipitation seasonality for South Africa, measured in mm, expressed as the difference in mean rainfall for February and August. A positive value indicates summer rainfall and a negative value winter rainfall.

distributions in the two major climate regions separately, a technique that has been used to improve similar models for tsetse flies in Zambia (Robinson *et al.* 1997a, b). Despite these problematic taxa, an average of 51.7 % of the known records were captured by IDs representing probability of occurrence values of 50 % or higher, confirming the relevance of this employed probability level. This, together with the progressive improvement in spatial coincidence between the ID's and the KR's during the modelling process (Figs 3a-b), provide support for the the modelling approach adopted. Apart from the obvious model limitations discussed above, it appears that the generated ID's provide reasonably realistic predictions for the distribution ranges of poorly sampled species (Figs 4-8). It consequently appears that the approach, modified from Jeffree & Jeffree (1994, 1996), and presented here will be useful for examining the likely effects of climate change on the distributions of a range of species from any specific region (Van Jaarsveld *et al.* 2000), and can also be used as a platform from which further, more detailed approaches to understanding the likely affects of climate change on biota (*e.g.* Davis *et al.* (1998a,b)), can be undertaken.

### Model outputs and conservation implications

The distributions predicted under the climate change scenario suggest that species ranges are likely to change both in size and shape (see Brown *et al.* 1996; Gaston 1994 for general discussions of the size and shape of species ranges). This has a number of conservation implications. A range expansion will present possibilities of novel interactions with previously unencountered species, and assemblages (Parmesan *et al.* 1999; Pounds *et al.* 1999). The likely outcome of such novel interactions is difficult to predict, as the biological invasion and biological control literature illustrates, (Williamson 1996; Lonsdale 1999; McEvoy & Coombs 1999), although many species have survived exposure to such changes in the past (Coope 1979). Nonetheless, some progress could be made toward understanding the outcome of novel interactions by basing microcosm-type experiments (see *e.g.* Davis *et al.* 1998a,b), on the new species combinations predicted by climate modelling procedures such as the current one.

Over and above any novel species interactions, of immediate conservation concern is the contraction in range sizes predicted for four of the five species modelled in this study. A reduction in range size may also result in a decline in the local abundance of a species (see Gaston *et al.* 1996 for a general overview of the range size abundance relationship). Species subjected to both range size contraction and population decline are clearly at substantial conservation risk, the double jeopardy of Gaston (1998). Although *P. caffer* is vulnerable in

terms of range contraction for the reasons outlined above, it may be less susceptible than the other species because it is widespread and shows little range shift under the climate change scenario.

The remaining four species all display range shifts as well as range contractions with ID's and CAD's revealing an average coincidence of 16 % ( $\pm$  SD 16,  $n = 4$ , Table 1). Arid-adapted antlion species from the western parts of South Africa will thus experience more severe shifts in distribution than their eastern counterparts (Figs 4-8). This predicted pattern is not unexpected given the general aridification predicted by the HadCM2 general circulation model. However, the likelihood of a species successfully colonising a new habitat during a range shift depends primarily on habitat suitability. In the case of antlions, many of the predicted range shifts are into areas that have been highly transformed for intensive agriculture (Fairbanks *et al.* 2000). They will consequently be largely unsuitable for antlion colonisation. Predicted range shifts may thus actually represent range contractions, thereby exacerbating the likelihood of species extinction. In effect, our results suggests that arid areas in South Africa may become too arid to support previously xerophilous species, while previously marginal temperate areas may be unsuitable because of land transformation.

Finally, the expected response of *P. luteus*, the fynbos endemic, raises an important point regarding modelling exercises of this kind (Chown & Gaston 1999). The ID encompasses not only the known records for this species (Fig. 7), but also various habitat patches in what is known as the Afromontane phytogeographical region (Cowling & Hilton-Taylor 1997). Fynbos-related elements do occur in these Afromontane patches in the form of ericaceous shrublands (Killick 1978; White 1978), but *P. luteus* apparently does not. This example therefore illustrates that although the model is useful for many species, there are clearly cases where other biological variables such as specific habitat requirements will ultimately determine potential habitat occupancy (Chown & Gaston 1999).

A model previously developed for predicting the effects of climate change on insects and plants in Europe is shown here to be applicable to southern Africa, after modification to account for seasonal rainfall patterns. An added advantage of this modified multivariate approach is that the model provides probability of occurrence values for each grid cell in contrast with the presence absence outputs generated by the original bivariate approach (Jeffree & Jeffree 1994). Most importantly, it is shown that range contractions and shifts in the positions of species ranges are likely to be significant consequences of climate change for antlions in South Africa. If this applies to other animal taxa, and it seems that it does (Van Jaarsveld *et al.* 2000) then the message to the conservation community is clear. The likely

impacts of climate change on our ability to conserve our fauna can no longer be ignored, but must now form an integral part of conservation planning.

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