Climate change and tick-host relationships in Africa

by

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Abstract

The concerns that vectors and vector-borne diseases will expand, contract or shift their ranges in response to climate change revived investigations into the magnitude of these range alterations in worldwide species. By use of predictive species models and modelled or interpolated climate data, the current and future distribution of many insects, pests and pathogens in many parts of the world have been predicted using their major climate drivers. In sub-Saharan Africa studies on the impacts of climate change on the current distribution of vectors that transmit diseases to humans has also increased over the past few years but similar studies in vectors that transmit diseases in livestock or wild animals remains inadequate. Yet ticks and tick-borne diseases alone remain a burden to the livestock industry particularly the rural households whose livelihood may depend on a few heads of cattle. Under climate change conditions, the devastation is unknown and it needs to be investigated and incorporated in future control strategies. Furthermore, the current knowledge of the distribution and proximity of other domestic and wild animals to tick infested areas is inadequate and yet forms a vital role in proper management of ticks and tick-borne diseases since ticks use these hosts to complete their life cycles and tick borne disease pathogens reside in them.

This thesis addresses these concerns using a modelling approach in which current, future climate and tick/host distribution data were combined in a GIS environment. Different statistical methods were employed in the analysis of the predicted current and future distribution of various species of the tick genus *Rhipicephalus* and selected vertebrate species that act as hosts. A comparison of how different climate data sets predict the current distribution of four *Rhipicephalus* species revealed different distribution per climate datasets. It is therefore important to assess the suitability of a climate data before use. The current and future prediction of 30 *Rhipicephalus* species showed that East Africa and South Africa are considered the most vulnerable regions on the continent to climate-induced changes in tick distributions and tick-borne diseases. More than 50% of the species examined show potential range expansion and more than 70% of this range expansion is found in economically important tick species. There is also an increase in tick species richness in the south-western regions of the sub-continent. More than 20 % of the species experienced range shifts of between 50 and 100 %. The predicted impacts of climate change on the tick-borne disease, East Coast Fever (ECF) showed a potential increase in Northern Cape and Eastern Cape provinces of South Africa, Botswana, Malawi, Zambia and eastern DRC. Contraction was the main range alteration predicted for the vertebrate species that act as hosts of *R. appendiculatus* under climate change conditions. However, more generalist species expanded their ranges. It was also clear from the whole study that different tick species reacted differently to predicted changes in climate and different areas in Africa experienced varying degrees of impacts. The ability of tick and host species to shift their ranges depends on the degree of land degradation and transformation and not to mention the existing ecological interactions. The existing social, economic and environmental policies in individual counties will determine the actual vulnerability.

Key words: Climate change, sub-Sahara Africa, ticks, *Rhipicephalus* spp., tick-borne diseases, predictive species modelling, DARLAM, host assemblages

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Disclaimer

This thesis consists of chapters that have been prepared for submission to, or published in, a range of scientific journals. As a result styles may vary between chapters in the thesis and overlap may occur to secure publication entities. Figures have been added at the end of the respective chapters.

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CHAPTER 1

Introduction

SAVING the world used to be the job of superheroes.
But now, with millions of plant and animal species facing extinction
It's down to us mere mortals.
Where do we begin?
We don't even know how many species are out there
and even if we did, the numbers are overwhelming
until we know how the organisms that we can see
What we need is a way to make predictions
based on the information we already have
But the fledgling science of ecology
has struggled to offer us general models of where creatures live
Like early astronomers, ecologists are too focused
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Arran Frood, New Scientist 18 August 2001

The current concerns about global warming has stimulated considerable interest in species distributions, especially the knowledge of how their current distributions may change. The urgency to acquire this knowledge is augmented by the evidence of numerous IPCC reports to the fact that the global climate is changing at an unprecedented rate, most likely due to anthropogenic activities, and that these changes in climate are causing severe, and possibly irreversible, changes in physical and biological systems (http:// www.ipcc.ch). Since in the past, large-scale extinctions and species movements were precipitated by major climatic changes (Gates 1993; Roy et al. 1996), it is crucial for us to use our understanding of distribution pattern drivers to predict how future climatic change will affect species distributions and biological processes. Acquisition of this knowledge should not be delayed until a complete understanding of the mechanisms determining species distributions patterns has been achieved. Some form of environmental change (human induced habitat destruction, global climate change) will

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But the fledgling science of ecology
has struggled to describe the natural world, let alone understand it.
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to scientific methods such as experimentation, replication or manipulation.
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The current concerns about global warming has stimulated considerable interest in species distributions, especially the knowledge of how their current distribution, may change. The urgency to acquire this knowledge is augmented by the existence of numerous IPCC reports to the fact that the global climate is changing at an unprecedented rate, most likely due to anthropogenic activities, and that these changes in climate are causing severe, and possibly irreversible, changes in physical and biological systems (http:// www.ipcc.ch). Since in the past, large-scale extinction, and species movements were precipitated by major climatic changes (Gates 1993; Roy *et al.* 1996), it is crucial for us to use our understanding of distribution pattern drivers to predict how future climatic change will affect species distributions and biological processes. Acquisition of this knowledge should not be delayed until a complete understanding of the mechanisms determining species distributions patterns has been achieved. Some form of environmental change (human induced habitat destruction, global climate change) will likely have precipitated considerable species losses in the interim (Chown and Gaston 1999).

The importance of climate to explain animal and plant distribution was recognised as early as the 18th century (Guisan & Zimmermann 2000) and a vast body of literature from past and current field experiments exists in support of this. The relationships between sensitivity of species to climate change and their ecological properties has also been reported in current literature (Thuiller *et al*. 2005) while the primary importance of climatic factors in explaining the link between latitude and the spatial pattern of human pathogens has also been reported (Guernier *et al*. 2004). With the looming global climate change, the issue is not how climate defines the current distribution of species but how the current distribution will react to climate change. There is no alternative to long – term field studies to provide proof for such a hypothesis. But what does one do when the issues are very complex or the scale is unmanageably large, and the time is forthcoming? How then can we be anticipatory, if no meaningful physical experiment can be performed? (Schneider 1992) and in this case no fieldwork can be done? We can turn to a surrogate lab, not a room with bunsen burners, but a small box with transistors and microchips. We can build mathematical models and perform our "experiments" in computers. Although models are not usually faithful simulations of the full complexity of reality, they can tell us the logical consequences of explicit sets of assumptions (Schneider 1992).

The use of geographical predictive models to predict the distribution of both plants and animals species has recently gained importance not only as a research tool in autecology but also as a tool to assess the impacts of accelerated land use and other environmental change on the distribution of organisms (for review see Guisan & Zimmermann 2000). These models, though static and comparative often remain the only approach for studying the possible consequences of a changing environment on species distribution since only very few species have been studied in detail in terms of their dynamic responses to environmental change (Woodward & Cramer 1996). In response to the inevitable climate change and a call for assessment of impacts, adaptations and vulnerability by IPCC

(IPCC 2001), various studies have attempted to predict the current and future distribution of species based on major environmental factors that influence their distribution. In this issue in which the projected climate change impacts on Africa were elucidated, the health and agricultural sectors were among those that were reported to show high vulnerabilities. This is not only as a result of limited or deteriorating infrastructure in the public health system but also because insect-vector diseases and water-borne diseases are prevalent in Africa and their distribution is influenced by climate. Climate change may alter the distribution of vector species—increasing or decreasing the ranges, depending on whether conditions are favourable or unfavourable for their breeding places (e.g., vegetation, host, or water availability).

The World health organisation report on the effect of climate change on health sector in Africa reported that climate plays an important role in vector-borne diseases -- a major cause of illness and death in tropical countries. Insects such as mosquitoes, ticks, sandflies and tsetse flies transmit these diseases. These cold-blooded vectors are sensitive to direct effects of climate such as temperature, rainfall patterns and wind. Temperature alone directly influences the reproduction and maturation rate of the infective agent within the vector organism, as well as the survival rate of the vector organism, thereby further influencing disease transmission (IPCC (TAR) 2001). Climate also affects their distribution and abundance through its effects on host plants and animals". WHO (2001) (http://www.who.int/mediacentre/factsheets).

Accurate and verified models that translate these physiological climate-related processes into more detailed maps of disease distribution are scarce. Such maps and models are necessary to set the baseline of current levels and limits of transmission against which projected impacts of climate change can be measured (IPCC 2001). Also it is clear in this report that the assessment of the response of vectors and vector-borne diseases to climate change has been attempted but mainly in human related vectors as opposed to vectors that transmit pathogen to livestock and other wild animals. And yet ticks alone are exposed to more than 80% of the world's cattle population resulting in global annual losses of up to US $7 billion (McCoster 1979). This is because ticks exceed any arthropod groups in being pests, parasites and vectors both in the tropics and temperate regions. They are very successful vectors because they transmit a greater variety of microorganisms to humans and livestock than any other arthropods, (Soneshine 1991).

In Africa, East Coast fever (ECF), devastating disease of livestock transmitted mainly but not exclusively by a tick *Rhipicephalus appendiculatus,* threatens over 25 million cattle, costing farmers more than US$170 million a year in direct losses. This loss may be underestimation since most devastation from ticks is in remote areas in Africa where pastoralists continue to move their herds in search of green pastures. For instance in 2001, 120 cattle died daily per sub-county from various tick-borne diseases in Kotido District in the Northern part of Karamoja, North Eastern Uganda. (http://www.cahnet.com). Under climate change accentuated by insufficient mitigation options and inadequate health facilities, Africa may suffer under the heavy burden of these livestock diseases. Currently, the main form of control by use of chemicals to target either the parasite or the habitat may not be sufficient if the future world is a world more suitable for ticks. Predicting the suitability of areas for ticks may solve the pressure and urgency that goes with chemical control and may also save the control agents time and resources because the actions will be targeted to already identify specific areas. Also this traditional chemical control of ticks may benefit from new ecological approaches to tick control by including the knowledge of the preferred and reservoir hosts of the vector and the pathogen respectively. It was under this background that this study was initiated to explore the impacts of climate change on the distribution of ticks and their hosts in Africa, deduce how the predicted change in distribution may impact tick-borne diseases.

Tick data was obtained mainly from three sources (Cumming 1999b; Walker *et al.* 2000, I. G. Horak private collection). The hosts' data was obtained from Boitan *et al.* 1999). The multivariate predictive distribution modelling procedure developed by Erasmus *et al.* (2000) was employed throughout the current study and current and future climate data was provided by DARLAM (Division of Atmospheric Research limited-area model climate data). DARLAM is a high resolution limited area model that was developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in

Melbourne, Australia for use in both short-term mesoscale atmospheric studies and longer-term climate simulation experiments (Walsh & McGregor, 1995). The model is a two-time-level, semi-implicit, hydrostatic primitive equations model. It uses an Arakawa staggered C-grid (Mesinger & Arakawa, 1976) and semi-Lagrangian horizontal advection (McGregor, 1993) with bi-cubic spatial interpolation, and has 18 horizontal sigma (σ) levels in the vertical (Phillips, 1957). DARLAM employs a wide range of physical parameterization schemes to represent atmospheric processes such as cumulus convection that exist at sub-grid scale. A one-way nesting technique (Davies, 1976) is used with lateral boundary conditions supplied by the CSIRO-9 Mk 2 GCM with R21 spectral resolution.

In the present study nine separate 30-day simulations were performed for both January (representing mid-summer conditions) and July (representing mid-winter conditions). The monthly average of the nine simulations constitutes the model climatology for the month. Engelbrecht *et al.* (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables like near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does; however, tend to overestimate rainfall totals over regions with a steep topography. The DARLAM simulations used in this study were performed by my colleagues at the Laboratory for Research in Atmospheric Modelling (LRAM) in the Meteorology Department at the University of Pretoria on a Pentium III workstation with two 550 MHz processors. It took approximately 11-minutes (CPU time) to simulate a model day at the specified model resolutions. The climate variables employed in this study were mean maximum temperature of January and July, mean minimum of January and July, and mean rainfall of January and July.

The predictive species model used was originally developed by Jeffree & Jeffree (1994, 1996). It was used as a standard base for predicting species (ticks and vertebrate hosts) current and future distribution patterns and for evaluating the relative performance of the different climate data sets. This model was recently modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus *et al.*, 2000). The original model was adapted to incorporate a variety of climatic predictor variables. Not only does this improve the original model, but it also allows the production of a probability surface of suitability for each species (Erasmus *et al*., 2000), rather than merely a presence-absence distribution model. This multivariate modelling approach uses the values of selected climate variables for each cell where a species had been recorded. These are plotted on an n-dimensional scatter plot (for the n-climate variables), and mean climate values subtracted to center values around the origin of the multidimensional scatter plot. An $n \times n$ covariance matrix is calculated and this matrix is used as an input to calculate eigen values and eigen vectors for the covariance matrix. These eigen vectors form the orthogonal principle axes of an n-dimensional hyperspace with the origin representing the theoretical core of the species' fundamental niche, as defined by the predictor climate variables (also see Robertson *et al*., 2001).

The climate variables (temperature and rainfall) values of all grid cells are then transformed into this eigen vector space. These transformed climate variables are subsequently divided by the eigen values and in the resulting n-dimensional hyperspace, the distance of any particular unsampled grid cell from the origin represents a measure of the suitability of that locality for the specific species (Robertson *et al*., 2001). According to Austin & Meyers (1996), the fundamental niche of an organism follows a broad Gaussian distribution. Such a Gaussian distribution is best approximated by a normal distribution but given that the distance from the origin of the hyperspace is calculated by the sum of the squared eigen vector axis scores, and that a squared normal distribution is equal to a chi-square distribution, the probability of any grid cell to be suitable for the selected species, can be read off a chi square probability table at the appropriate degrees of freedom (m, the number of climatic variables) (Robertson *et al*., 2001).

The input data comprises 3000 grid cells covering sub-Saharan Africa populated with climate variables. Grid cells, in which particular tick /host species were recorded, are referred to as *known records* following Erasmus *et al*. (2002). Thus, on a scatter plot of climate variables (multivariate climate space), the values of climate variables from localities where species have been recorded are used to construct a confidence region where there is a high probability that the records reflect the core range of the species.

Points falling within this confidence region are then mapped back to geographic space to represent an *interpolated distribution* (ID), represented as a probability of climate suitability (see Erasmus *et al*., 2000 for a detailed model description. Each grid cell was assigned a tick presence, climate value and hosts as the analysis permitted. Geographic information system (GIS) analysis was conducted in ArcView ESRI (2000) and modelling was performed in S-Plus (2000). Throughout the various chapters, different methods of comparing the predicted distributions have been employed and discussed fully in the respective chapters. Also the implications of the results and the shortcomings of the methods used have been highlighted.

Recent developments in geographic information systems and easy accessibility of climate data from different climate models have fostered the development and use of many climate models in the exploration of the response of a changing climate on species distribution. Occasionally, the researcher is faced with a problem of selecting the best climate data for a particular study. To evaluate the impact different climate dataset have on the resultant predicted distribution, in chapter two three climate datasets (2 interpolated and 1 modeled) have been used to evaluate the relative performance of the climate datasets in simulating the present distributions of ticks in sub-Saharan Africa. In this chapter, distribution data of four tick species from the genus *Rhipicephalus* were used. The results showed that the use of data derived from high-resolution nested climate models (e.g. DARLAM) provided equal or even better species distribution-modelling performance (Olwoch *et al*. 2003). As the model is dynamic and process based, the output data are available at the modelled resolution, and are not hamstrung by the sampling intensity of observed climate datasets.

Genus Rhipicephalus is one of the largest genera and includes some of Africa's most economic important species. Chapter three focuses on the likely climate induced changes in the distributions of this genus. Analysis of predicted range contractions, shift and changes in species richness pattern were performed for the whole study area, per region and lastly an analysis of different aspects of range alterations were compared between the economic important ticks and non -economic ones. The latter was done to establish the indirect effects of these range alterations to tick-borne diseases. The results showed that East Africa followed by South Africa are considered the most vulnerable regions on the continent to climate-induced changes in tick distributions and tick-borne diseases. More than 50% of the species examined show potential range expansion and more than 70% of this range expansion is found in economically important tick species. There is also a predicted increase in tick species richness in the southwestern regions of the sub-continent and more than 20 % of the species experienced range shifts of between 50 and 100 % under predicted climatic conditions.

One of the most devastating tick-borne diseases in sub-Saharan Africa is East Coast fever (ECF). It is transmitted by a protozoan parasite, *Theileria parva* that is transmitted by the brown ear-tick, *Rhipicephalus appendiculatus*. Since the results of chapter three revealed that economic important ticks were severely affected by climate change, in chapter four the potential present and future distribution of ECF based on the present and potential future distribution of the tick and cattle assemblage was assessed. The criticisms of this method were two fold: there are several different tick species that are vectors of ECF, and there are a number of different hosts, why use only *R. appendiculatus* and cattle? The available data and literature provides compelling evidence in support of the approach in this thesis. There are other species that have been mentioned as capable of transmitting the pathogen that causes ECF, but there is no evidence in the literature that these species are actually possible transmitters in the field. Whereas transmission clearly can occur via other tick species and probably does (Cummings pers.comm.), there is no evidence to date to support this. This thesis is therefore inclined to stay with the dominant view point that *R. appendiculatus* is the main, if not the only tick vector that is capable of transmitting the protozoan parasite *Theileria parva* that causes ECF in the field. The results obtained in this chapter are therefore based on the *R. appendiculatus* and cattle ranges only. The results show that the predicted general increase in minimum temperature has favoured the establishment of ticks and ECF. The Northern Cape and Eastern Cape provinces of South Africa, Botswana, Malawi, Zambia and eastern DRC are predicted to show increases in ECF prevalence.

Many of the emerging infections in wild life are usually caused by generalist pathogens transmitted by arthropods that "spill over" (Daszak *et al.* 2000) from other species, often from domestic animals and to a certain extent from human especially in cases where the population of other preferred hosts decline. The first three chapters relate the current and predicted future ticks distribution to climate. However, ticks exhibit a dual lifestyle in which they must constantly alternate between hiding in protected spaces and climbing up vegetation to quest for hosts (Londt & Whitehead 1972). Prediction of hosts, though very complicated (Estrada-Peña 2001b) forms an important part in establishing the prevalence of ticks and tick-borne diseases in a changing climate. Chapter five uses the same modelling approach on *R. appendiculatus* and its community of hosts to assess how the current host assemblage will be influenced by climate change. Furthermore it is now established that diversity in host communities can influence tick and tick-borne diseases through two pathways i) by increasing infection rates and ii) by increasing the density of vectors. Using predicted host ranges of R. *appendiculatus* for the current and future, the probable effect of that change on the current and future tick-host assemblages were analysed and conclusions were made regarding this change on tick abundance and infection rates of the pathogen that causes East Coast fever. Different host species reacted differently to climate change conditions. Although contraction was the main range alteration predicted, the future predicted distribution of the more generalist species expanded. The results also showed reduction in the range of the total host assemblage in the future climate. The predicted future range of the host assemblage intimately involved in ECF transmission was also altered at different degrees in different areas in sub-Saharan Africa. Increased probability of this assemblage was predicted in Tanzania, Angola and Mozambique.

Tick distributions are known to vary through space and time due to interactions of many factors, including climate, host diversity, levels of resistance of hosts, absence of tick control measures and management practices that affect host behaviour. The use of a simple climate model (as the one used in this study) often termed "climate envelope" or "correlative" as opposed to a more complex physiologically based model has therefore been reportedly not valid (Davis *et al.* 1998a, b). However, limitations regarding the use of physiologically based models exist especially where specific information regarding the species is sketchy (Pearson and Dawson 2003). On the other hand, relatively simple bioclimatic envelope models can provide a useful starting point when applied to suitable species and at appropriate spatial scales. In many cases, bioclimatic envelope models provide perhaps the best available guide for policy making at the current time (Hannah *et al.* 2002). The use of this simple model in this study is therefore appropriate since most areas in Africa are poorly sampled and the distribution of Africa ticks is relatively incomplete. Furthermore correlative /simple techniques do not require detailed physiological data about individual species; they can be applied to a large number of species as has been done in this study. This enables conclusions regarding the impacts of climate change on a wide range of species, thus habitat assemblages, to be made (Berry *et al.* 2002). Though not to be underestimated, model predictions should be interpreted with caution and should be viewed as first approximations indicating the potential magnitude and broad pattern of future impacts, rather than as accurate simulations of future species distributions (Pearson & Dawson 2003). The resultant predictive maps are also important because they fill in gaps in the primary observations and update the distributions as they shift with changing environmental conditions.

A tick - host - disease system is by no means a simple one. Unresolved viewpoint vis-à-vis host – tick relationships and limited knowledge concerning the relative importance of different hosts on tick and tick borne disease prevalence compounds this challenge. By use of a predictive species model and climate provided by DARLAM, this study has highlighted the importance of a suitable climate dataset in climate envelop studies. In addition, the study has identified the vulnerability of different areas in sub-Sahara Africa for ticks and tick-borne diseases under climate change conditions. The predicted ranges of vertebrate species that act as hosts of *Rhipicephalus appendiculatus* have complemented the climatic determinant of tick ranges. This approach neither disregards the need for more detailed and comprehensive eco-physiological approaches nor does it pretend to predict the future. What it does is define the role of climate as a factor in determining the potential for future vector establishment when all other factors are not included (Sutherst 2003). Therefore, what I present in this thesis is an initial but essential step towards the production of tick risk maps for the current and future. Because vulnerabilities of specific areas are identified, these results also serve as a warning of the probable changes in tick distribution under a changed climate. They also serve to attract attention of tick-control agencies to those areas of tick expansions. Furthermore, these results serve as way of increasing awareness to the close relation between climate and vector distribution and the importance of all the parts of a tick-host-diseases system in selecting a tick control method. The results presented in this thesis must therefore be viewed as an initial step towards developing current and future tick risk maps for Africa and as base for more field oriented studies on the effect of climate change on African ticks.

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CHAPTER 2

Simulating tick distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces

Simulating ticks distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces.

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ABSTRACT

Aim

A broad suit of climate datasets is becoming available for use in predictive species modelling. We compare the efficacy of using interpolated climate surfaces (CRES and CRU) or high-resolution model derived climate data (DARLAM) for predictive species modelling, using tick distributions from sub-Saharan Africa.

Location

The analysis is restricted to sub-Saharan Africa. The study area was sub-divided into 3000 grids cells with a resolution of 60 x 60 km.

Methods

Species distributions were predicted using an established multivariate climate envelope modelling approach and three very different climate datasets. The recorded variance in predicted species distributions across the climate datasets was quantified by employing omni directional variograms. To further compare the interpolated tick distributions that flowed from using three climate data sets, we calculated true positive (TP) predictions, false negative (FN) predictions as well as the proportional overlaps between observed and modelled tick distributions. In addition, the effect of tick dataset size on the performance of the climate datasets was evaluated by performing random draws of known tick distribution records without replacement.

Results

The predicted distributions were consistently wider ranging than the known records when using any of the three climate datasets. However, the proportional overlap between predicted and known distributions varied as follows: for *Rhipicephalus appendiculatus* Neumann (Acari: Ixodidae), these were 60%, 60% and 70%; for *Rhipicephalus longus* Neumann (Acari: Ixodidae) 60%, 57% and 75%; for *Rhipicephalus zambeziensis* Walker, Norval & Corwin (Acari: Ixodidae) 57%, 51%, and 62%, and for *Rhipicephalus* capensis Koch (Acari: Ixodidae) 70%, 60%, and 60% using the CRES, CRU and DARLAM

climate datasets respectively. All datasets were sensitive to data size but DARLAM performed better when using smaller species datasets. At a 20% data sub-sample level, DARLAM was able to capture more than 50% of the known records and captured more than 60% of known records at higher sub-sample levels.

Main conclusions

The use of data derived from high-resolution nested climate models (e.g. DARLAM) provided equal or even better species distribution-modelling performance. As the model is dynamic and process based, the output data are available at the modelled resolution, and are not hamstrung by the sampling intensity of observed climate datasets (~ 1 sample / 30 000 km^2 for Africa). In addition, when exploring the biodiversity consequences of climate change, these modelled outputs form a more useful basis for comparison with modelled future climate scenarios.

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INTRODUCTION

Predictive species modelling is rapidly becoming a routine analytical procedure (for review see Guisan & Zimmermann 2000), and with rapid advances in climate data interpolation and modelling techniques, it is now possible to predict the distributions of an array of insects, pests and pathogens using their major climate drivers (Messenger, 1959; Sutherst & Maywald, 1985; Meats, 1989; Perry *et al*., 1990; Randolph & Rogers, 1997; Sutherst *et al.,* 1995; Coakley *et al.,* 1999; Cumming, 2000a; Rogers & Randolph, 2000; Randolph, 2001, 2002; Erasmus *et al.,* 2000, 2002; Harvell *et al.*, 2002). Many of these approaches are static and probabilistic in nature but remain the primary approach available for studying the possible consequences of changing environments on species distributions.

The principal sources of climate data used for predictive distribution modelling are climate surfaces, generated by interpolating observed climate data that was sampled at varying intensities from across a region. Consequently, any differences between these climate surfaces can usually be attributed to the spatial and temporal evenness of the observed data used for interpolation. Most modern interpolation techniques are pattern based and statistically incorporate horizontal as well as vertical (altitudinal) adjustments (see Hutchinson, 1989, 1991; Hutchinson & Gessler, 1994).

General circulation models (GCMs) have now become the primary method of simulating climates. These are coupled ocean-atmosphere models that provide 3-dimensional simulations of the atmosphere. To date, general circulation models (GCMs) have produced climate data at a horizontal resolution that is too coarse for use in predictive species modelling (> 100 km x 100 km grid point resolution), especially for species that are habitat specialists or that are influenced by fine scale environmental gradients. Computational requirements usually prevent GCMs from being run at mesoscale grid resolutions (10 - 100 km). A potential alternative source of high-resolution climate data for use in predictive species modelling is nested limited-area models. Nested climate modelling involves the nesting of a high-resolution limited area model within a GCM over the area of interest (for review see McGregor, 1997). The GCM supplies the limited area model with initial and boundary conditions. With a grid resolution of 10-100 km, the limited area model is able to simulate some of the meso-scale properties of the circulation. This technique provides a viable alternative to the use of observed/interpolated climate surfaces for fine scale climatic data. The resolution attained by this dynamic modelling process is essentially limited by the computing power available to the modellers.

The present study used one species distribution modelling procedure (Erasmus *et al.*, 2000) and three climate datasets (2 interpolated and 1 modeled) to evaluate the relative performance of the climate datasets in simulating the present distributions of ticks in sub-Saharan Africa. We employed distribution data from 4 tick species from the genus *Rhipicephalus.* These tick species are taxonomically well known, are poorly sampled and their environmental dependencies not adequately documented (Tukahirwa, 1976; Rechav, 1981; Short & Norval, 1981; Norval *et al.*, 1982; Horak *et al.*, 1983, 1995; Perry *et al.*, 1990; Rogers & Randolph, 1993; Cumming, 1998, 1999a, Walker *et al.*, 2000). As principal vectors of numerous cattle diseases these tick species are also of significant economic importance to the continent.

MATERIALS AND METHODS

CRES climate data

The first climate dataset used forms part of a topographic and climate database for Africa developed by the Center for Resource and Environmental Studies (CRES)(Hutchinson *et al.,* 1996) at the Australian National University. These data contain grid box values of elevation (Hutchinson, 1989), monthly mean climate of rainfall as well as daily values for maximum and minimum temperatures at a spatial resolution of 0.05 x 0.05 degrees. Climate grid box values were calculated by fitting topographically dependent climate surfaces to point climate data using procedures described in Hutchinson (1991) and Hutchinson & Gessler (1994), thereafter the surfaces were interrogated using elevations from the topographic data (McMahon *et al.*, 1995). Climate data at a sufficient spatial density to support reliable spatial interpolation were compiled. In addition to data already obtained by CRES, monthly climate data were acquired from many other research agencies. Data were collected over all available years to maximize spatial coverage, subject to the condition that rainfall averages were calculated from records of at least five years. The data set comprises data collected between 1920 and 1980 from approximately 1 500 temperature and 6 000 rainfall stations. The error of grid values depends mainly on the accuracy of the underlying climate surfaces. The standard errors of the temperatures are about 0.5 °C, while standard errors for rainfall range between 5% and 15 % (depending on data density and the spatial variability of observed mean monthly rainfall values). The mean monthly rainfall values as well as maximum temperatures for January and July are depicted in Figure 1. The climate surfaces are relatively smooth due to their dependency on low-resolution point observations. These data were re-sampled to the finest common resolution between climate data sets, which is the 60km x 60km DARLAM grid cells. This resulted in data for 3000 grid cells which was within the limitations imposed by the available hardware and software. The mean values of CRES data cells contained within each 60km x 60km grid cells was used as the new re-sampled CRES data value for that particular grid cell. Although some variation was lost in this procedure, between-cell variation before re-sampling was small due to interpolation between remote data points, and therefore the predictive ability of this data was not affected. After re-sampling, 92% of the grid cells had standard deviations smaller than 5% of the mean value for that particular grid cell. The variograms of re-sampled data in Fig 2 confirms this fact, with neighbouring cells remaining highly autocorrelated at small distances (~60km). We regard this small change in variation as reasonable for our purposes.

CRU climate data

The 1961 - 1990 climate dataset from the Climate Research Unit (CRU) was used as a second dataset (New *et al.*, 1999). The database consists of mean monthly climate fields with a 0.5° x 0.5° grid resolution across the global terrestrial areas, excluding Antarctica.

The mean climate surfaces were constructed from a 30-year (1961-1990) station observation field. The station data were interpolated as a function of latitude, longitude and elevation using thin-plate splines. The accuracy of the interpolations are assessed using cross-validation and by comparison with other climate surfaces (New *et al.,* 1999). Considerable spatial and temporal variance of climate surface variables over southern Africa can be observed in the CRU data (Engelbrecht *et al.,* 2002). Despite this, the climate surfaces remain smooth due to their dependence on low-resolution point data. The mean monthly rainfall values as well as maximum and minimum temperatures are depicted in Figure 1. These data were also re-sampled to 60km x 60km grid cells in the same manner as the CRES data.

DARLAM climate data

The Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Melbourne, Australia, developed the high-resolution limited-area model DARLAM (Division of Atmospheric Research limited-area model) for use in both short-term mesoscale atmospheric studies and longer-term climate simulation experiments (Walsh & McGregor, 1995). The model is a two-time-level, semi-implicit, hydrostatic primitive equations model. It uses an Arakawa staggered C-grid (Mesinger & Arakawa, 1976) and semi-Lagrangian horizontal advection (McGregor, 1993) with bi-cubic spatial interpolation, and has 18 horizontal sigma (σ) levels in the vertical (Phillips, 1957). DARLAM employs a wide range of physical parameterization schemes to represent atmospheric processes such as cumulus convection that exist at sub-grid scale. A one-way nesting technique (Davies, 1976) is used with lateral boundary conditions supplied by the CSIRO-9 Mk 2 GCM with R21 spectral resolution.

In the present study nine separate 30-day simulations were performed for both January (representing mid-summer conditions) and July (representing mid-winter conditions). The simulations were performed at a horizontal grid resolution of 60 km x 60 km using a domain of 100 x 100 grid points that covers sub-Saharan Africa. The monthly average of the nine simulations constitutes the model climatology for the month. The climatologies of rainfall and minimum and maximum temperature obtained in this manner are shown in Figure 1. Engelbrecht *et al.* (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables like near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does, however, tend to overestimate rainfall totals over regions with a steep topography.

The DARLAM simulations were performed at the Laboratory for Research in Atmospheric Modelling (LRAM) at the University of Pretoria on a Pentium III workstation with two 550 MHz processors. It took approximately 11-minutes (CPU time) to simulate a model day at the specified model resolutions.

Predictive species modelling

We used a single predictive species modelling approach, originally developed by Jeffree & Jeffree (1994, 1996), for predicting species distribution patterns in the present study as a standardised base for evaluating the relative performance of the different climate data sets. This model was recently modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus *et al.*, 2000). The original model was adapted to incorporate a variety of climatic predictor variables. Not only does this improve the original model, but it also allows the production of a probability surface of suitability for each species (Erasmus *et al.*, 2000), rather than merely a presence-absence distribution model. The multivariate predictive distribution modelling procedure developed by Erasmus *et al.* (2000) was employed throughout the current study. In short, this multivariate modelling approach uses the values of selected climate variables for each cell where a species had been recorded. These are plotted on an n-dimensional scatter plot (for the n-climate variables), and mean climate values subtracted to center values around the origin of the multidimensional scatter plot. An $n \times n$ covariance matrix is calculated and this matrix is used as an input to calculate eigen values and eigen vectors for the covariance matrix. These eigen vectors form the orthogonal principle axes of an n-dimensional hyperspace with the origin representing the theoretical core of the species' fundamental niche, as defined by the predictor climate variables (also see Robertson *et al.*, 2001).

The climate variable values of all grid cells are then transformed into this eigen vector space. These transformed climate variables are subsequently divided by the eigen values and in the resulting *n*-dimensional hyperspace, the distance of any particular unsampled grid cell from the origin represents a measure of the suitability of that locality for the specific species (Robertson *et al.*, 2001). According to Austin & Meyers (1996), the fundamental niche of an organism follows a broad Gaussian distribution. Such a Gaussian distribution is best approximated by a normal distribution but given that the distance from the origin of the hyperspace is calculated by the sum of the squared eigen vector axis scores, and that a squared normal distribution is equal to a chi-square distribution, the probability of any grid cell to be suitable for the selected species, can be read off a chi square probability table at the appropriate degrees of freedom (*m*, the number of climatic variables) (Robertson *et al.*, 2001). The input data comprises 3000 grid cells covering sub-Saharan Africa populated with climate variables. Grid cells, in which particular tick species were recorded, are referred to as *known records* following Erasmus *et al.* (2002). Thus, on a scatter plot of climate variables (multivariate climate space), the values of climate variables from localities where species have been recorded are used to construct a confidence region where there is a high probability that the records reflect the core range of the species. Points falling within this confidence region are then mapped back to geographic space to represent an *interpolated distribution* (ID), represented as a probability of climate suitability (see Erasmus *et al.*, 2000 for a detailed model description). Differences in model performance when employing a suit of different climate datasets were evaluated by comparing the interpolated species distributions.

Tick data

Point localities of recorded tick observations were obtained from Cumming (1999b). These data were compiled from various tick collections (see Cumming (1999b) for a detailed list of sources). Combining data sets from different sources invariably compounds identification and distribution errors and for this reason data congruence with Walker *et al.* (2000) were used to assess data quality. This later reference provides well-illustrated distributions of *Rhipicephalus* species. Synonyms provided in this reference also solve the common problem of referring to one species using two different names. The tick species selected for this study belong to the phylum Arthropoda, Class Arachnida and Family Ixodidae. Four species (*R. appendiculatus, R. capensis, R. longus* and *R. zambeziensis*) were selected from the 74 *Rhipicephalus* species found in Africa because their life history parameters and host preferences are relatively well known (Walker *et al.,* 2000). Tick point localities were assigned to particular 60km x 60km grid cells by means of a spatial intersect. A conservative estimate of the accuracy of these point localities is 0.2 degrees (Cumming, pers.comm.) and therefore this approximation is considered reasonable.

Climate variables

In the present study the climate variables employed were mean maximum temperature of January and July, mean minimum of January and July, and mean rainfall of January and July.

Comparison of interpolated species distributions across climate datasets.

Interpolated tick distributions emanating from the three climate data sets were compared by first calculating the true positive predictions (TP), that is the number of grid cells where the probability of climate suitability was equal or greater than 50% and where a tick had previously been recorded. The number of false negative (FN) predictions were also recorded, that is when the probability of climate suitability was less than 50% but where a tick had previously been recorded. The comparison among climate data sets was conducted using the proportional overlap method (Prendergast *et al.,* 1993; Lombard, 1995; Reyers *et al.,* 2000). Proportional overlap was calculated as TP / TP + FN where TP is the number of true positive predictions and FN + TP represents the number of negative plus the number of positive predictions, or, the maximum number of overlapping grid cells between observed and modeled tick distributions. This method was the most appropriate vehicle of comparison as absence data for tick distributions were not available. Although ROC analyses has been shown to be robust to the assumption of absence data in unsampled cells (Cumming, 2000a), the low prevalence of presence data (varying between 0.027 and 0.179) in this study means that ~2500 absence records would be added if this assumption was made. We are not confident that such a large change in the number of records can still yield robust model outputs. Therefore, in this case, the absence of absence data precludes the use of ROC analyses (Erasmus *et al.,* 2002).

Modelling random sub samples of known records

To evaluate the role played by tick dataset size on the performance of the climate datasets, we performed single random draws of varying percentages of the known tick distribution records without replacement (20%, 40%, 60%, 80%, 100% of known records). By varying the input dataset size and summing the proportional overlaps between predicted occurrences and known records across tick species, we were able to evaluate climate data performance for different levels of species data availability. A Kruskal-Wallis rank test between the proportional overlap values of the three climate data sets at every level of dataset reduction was performed (20%, 40%, 60%, 80& and 100%).

RESULTS

Comparing climate data sets

The observed variance in the CRES temperature data only becomes distance invariant after approximately 22 degrees, which is almost 3 times greater than that found for the DARLAM and CRU datasets (Fig. 2a). When the variogram is interpreted at the distance of reliability (Kaluzny *et al.,* 1998), which is half the maximum distance over the field of data for an experimental variogram, CRES data are still influenced by more remote data points, whereas the autocorrelation of CRU and DARLAM data have become distance invariant. This means that any particular value in the CRES data is more strongly influenced by data up to15 degrees away than either the CRU or DARLAM datasets where the sphere of influence is much more localized (~ 7 degrees). The relatively small number of observations used as inputs to create the CRES climate surface, forced interpolations over larger distances than for CRU, where more observational data were available for creating the climate surface. The slope of the curve for DARLAM temperature data appears to be steeper than the other curves over short distances (Fig. 2a). This illustrates how DARLAM, a process model, is very sensitive to topography and topographical features which are usually expressed over short distances, i.e. ~2 degrees. DARLAM's precipitation variogram (Fig. 2b) also displays a non-monotonic behaviour.

Interpolated tick distributions

The multivariate climate envelope model used in the present study provides probability of climate suitability values ranging from 0 - 1 across all grid cells. It was therefore necessary to select an appropriate probability level to use for comparison between the different species. In this study a 50% probability level of occurrence was used. This means that a tick was assumed present where the model predicted a probability of occurrence of ≥ 50% and the reverse. This follows a frequently employed convention in the field of predictive species modelling (Beard *et al.*, 1999; Brito *et al.,* 1999; Erasmus *et al.*, 2002; van Staden *et al.*, in press; also see Walker *et al.*, 1990 for even lower thresholds). When the proportion of the correctly predicted cases (true positives) were evaluated, it was found that in *R. appendiculatus*, a well-studied tick species, a true positive coverage of 70% (using DARLAM data) was obtained at a probability of occurrence level of ≥ 50%. This percentage of known records captured in the interpolated distribution is considered good, bearing in mind that the observed known records are not only determined by climate but also by the presence of suitable host species and other species specific micro-ecological or habitat selection factors which are not incorporated in this model.

The interpolated distribution for *R. appendiculatus* (Fig 3), when using any of the three datasets, was both visually and statistically broader than the extent of the known records, but the true positive predictions corresponded satisfactory with the known records (60%, 60% and 70% overlap using the CRES, CRU and DARLAM datasets respectively) (Table 1a, Fig. 4). There was a noteworthy positive congruence between the interpolated distributions and the known records in most areas of East, Central and Southern Africa: Uganda, Tanzania, Zambia, Zimbabwe and South Africa.

Unlike *R. appendiculatus* that is well studied and therefore presents a more comprehensive recorded distribution, the other tick species are poorly sampled and the actual distributions are still contested in the literature. While Walker *et al.* (2000) maintain that *R. capensis* is strictly South African; Cumming (1999b) reported it mainly in South Africa with some scattered records in Rwanda, DRC, Angola and Zambia (Fig. 3). The proportional overlap correlation between interpolated distribution and known records for *R. capensis* were 70%, 60%, and 60% for the CRES, CRU and DARLAM climate datasets respectively (Table 1b Fig.4). The highest overlap occurs in South Africa and Namibia with more than 90% of all true positive records found in RSA for the three climate data sets. This resultant interpolated distribution compares favorably with the Walker *et al.* (2000) distribution pattern and improves the suggested Cumming (1999b) distribution by eliminating a few scattered records in the north of South Africa and Namibia. The interpolated distributions of the other 2 tick species (Fig. 3) were also broader than the known records, with a 60%, 57% and 75% proportional overlap using CRES, CRU and DARLAM data for *R. longus* (Table 1c, Fig. 4) and 57%, 51%, and 62% for *R. zambeziensis* (Table 1d, Fig 4) respectively. One of the interesting and consistent results that emerged from these analyses is the ability of DARLAM to produce a higher proportion of true predictions across all species examined (Figs. 4 & 5).

Modelling random sub samples of known records

All three examined climate datasets seemed to be sensitive to the tick dataset size in terms of their ability to correctly predict tick distributions. However, DARLAM consistently performed better with higher degree of overlap between the interpolated distributions and known records (Figs. 5 & 6). Even with a 20% sub-sample of known records across the tick species, DARLAM was able to capture more than 50% of the known records and was consistently above 60% at higher levels of sub-sampling. However, none of these differences in proportional overlap reached statistical significance ($P < 0.05$) suggesting that DARLAM performs at least as well as any of the observed datasets.

DISCUSSION

Comparing spatial datasets

When interpreting the output of climate envelope based predictive species distribution models, it is necessary to take cognizance of differences in climate data that can be used as inputs. The datasets used in the present study represent 3 different types of climate data, namely: (i) observed data with variable coverage in space and time together with elevation influenced smoothing (CRES), (ii) better coverage and 30-year averaged observed data with elevation influenced smoothing (CRU), and (iii) purely process derived modeled climate data (DARLAM). Although some differences among the climate datasets are obvious, even to visual inspection (see Figures 1), a more quantitative measure of the difference in underlying climate parameters was obtained by comparing omnidirectional variograms (Kaluzny *et al.,* 1998; Rossi *et al.,* 1992; Nielsen & Wendroth, 2001) for these data sets. In a variogram the variance of the property being measured, i.e. rainfall or temperature, is statistically expressed as a function of the distance between observations within a given spatial domain, i.e. sub-Saharan Africa (Nielsen & Wendroth, 2001). The difference between pairs of observations separated by a specific distance is plotted and the slope, position and shape of this graph gives an indication of the scale at which the underlying processes might operate. These variograms can therefore be interpreted as a measure of the degree of difference between the various datasets. For example, the emergence of non-monotonic behaviour in the DARLAM dataset (Fig. 2b) is indicative of spatial variation at scales other than the sampling units (Nielsen & Wendroth, 2001). Given the fact that precipitation is the result of complex atmospheric interactions at different scales, such a non-monotonic variogram can be expected from a process-based model such as DARLAM. In the analyses conducted here, the CRES dataset varied over larger spatial scales than either the CRU or DARLAM datasets. Thus, the three data sets used in this study do not only appear different to a casual visual inspection (Fig. 1), but are also different with respect to the spatial dependencies of database characteristics which influence adjacent climate values (Fig. 2).

Model evaluation

Usually the validity of a predictive species distribution model is assessed by its ability to predict both negative and positive cases (Fielding & Bell, 1997). However, the opportunistic manner in which the tick distribution data were collected precludes rigorous model evaluation. This is as true absence data are not available for these species, mainly because some areas were simply poorly sampled (Fig. 3). This same climate envelope model was however previously subjected to rigorous evaluation using presence-absence data resulting from a coordinated and systematic survey effort. Erasmus *et al.* (2002) used the distribution records of 34 bird species and tested model performance using receiver operator characteristic analyses (Fielding & Bell, 1997). The model performed significantly better than a random model with no discriminatory ability. The model also accurately predicted the complete known distributions for 24 of the 34 bird species, using a 20% sub-sample of the known records (Erasmus *et al.,* 2002). In sum, the model performed satisfactorily and is therefore considered adequate for the purposes of the present study.

Predicting tick distributions

At the outset it is important to acknowledge that, although we use a climate envelope approach in this study, we are not suggesting that this is an adequate basis for predicting the fine scale distributions of tick species across the African continent. Tick distributions and abundances are likely to be impacted by factors other than climate, such as host abundance, host resistance to ticks, acaricide use and grazing management (see

Cumming, 1998, 1999a, 2002). Most of these changes interact with temperature and rainfall regimes and in the absence of experimental data. It is impossible to separate the effects of these interrelated factors. This, compounded by the fact that the broad scale ecology of only a few tick species have been studied in detail (Cumming, 2002), means that employing climate variables as the main limiting factors for tick distributions remains the best option available. Minimum temperature, maximum temperature and rainfall have similar predictive abilities to one another; when considered together; their predictive ability increases substantially (Cumming, 2002). This is probably a consequence of their being correlated with one another. The intimate relationship between climate and tick distributions has also been reported elsewhere (Rechav, 1981; Minshull & Norval, 1982; Walker, 1974; Walker *et al.*, 2000). Taken in the context of current knowledge, we agree with Cumming (1999a) that the direct effects of climate typically determine the distributions of African ticks, but that biotic variables such as vegetation type and host distributions, may be important in creating heterogeneity in tick distributions at finer scales (Minshull & Norval, 1982) and play a subordinate role in limiting the species ranges of ticks at broad spatial scales (Cumming, 2002).

Against this background we proceeded to employ distribution data from a number of tick species that are considered sound taxa and that are widely collected. This was to evaluate the use of three different climate datasets for carrying out predictive species distribution modelling. These datasets varied in terms of the manner in which they were generated. Two datasets (CRES and CRU) represented the traditionally used datasets (see Guisan & Zimmermann, 2000; Robertson *et al.,* 2001; Erasmus *et al.,* 2002) for this type of predictive modelling activity. These are based on observed climate data and were subsequently interpolated to generate climate surfaces for the continent (Hutchinson, 1991; Hutchinson & Gessler, 1994; McMahon *et al.*, 1995; Hutchinson *et al.*, 1996; New *et al.,* 1999). The third dataset was derived from a nested limited-area model, is entirely based on a simulation of climate processes and does not use any observed meteorological data to generate climate surfaces (DARLAM - Engelbrecht *et al.,* 2002). In all instances explored here, cross species and degrees of data sub-sampling, the DARLAM dataset was equal to or marginally outperformed the interpolated climate surfaces in predicting the distributions of species. This suggests that process-based modeled datasets, such as DARLAM, should in the future be considered viable or even preferred datasets for modelling the predicted distributions of species, especially when considering their ability to capture climate at fine scales relative to range sizes of species.

A further advantage of employing process-based modeled climate surfaces for predicting species distributions is that this provides improved compatibility when using these predictions as a basis for exploring the consequences of climate change for future species distributions. This improved compatibility flows from the fact that future climate surfaces can easily be generated from nested limited-area models such as DARLAM. Thus, we can easily model the future using similar process-based models as used here in DARLAM but, in contrast, we cannot observe the future in order to generate climate datasets for direct comparison with the observed data derived climate datasets (CRES and CRU).

In conclusion, the recent availability of high-resolution nested limited-area models (DARLAM – Engelbrecht *et al*., 2002) now means that there are alternative climate surfaces available for modelling species distributions at broad scales. The results obtained here suggest that the use of data derived from a nested limited-area or process model for predicting species distributions, offer a viable and even a preferred alternative to using interpolated climate surfaces derived from observed climate data. This is especially true when the spatial and temporal coverage of observed datasets are poor, resulting in climate data surfaces that are strongly spatially autocorrelated over large distances.

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Table 1: The number of true and false predictions generated for four different tick species by a predictive species distribution model (Erasmus *et al.* 2002) using different climate datasets (CRES, CRU, DARLAM) and complete species datasets. KR = known records, TP = true positive predictions, FN = False negative predictions.

(a) Rhipicephalus appendiculatus			
	CRES	**CRU**	**DARLAM**
KR	538	538	538
TP	315	320	372
FN	223	217	166
Proportional overlap (TP/TP + FN)	**60%**	**60%**	**70%**
(b) R. capensis			
KR	189	189	189
TP	128	119	108
FN	60	70	81
Proportional overlap	**60%**	**60%**	**57%**
(c) R. longus			
KR	129	129	129
TP	78	74	97
FN	51	55	32
Proportional Overlap	**60%**	**56%**	**75%**
(d) R. zambeziensis			
KR	82	82	82
TP	47	42	51
FN	35	40	31
Proportional Overlap	**60%**	**50%**	**65%**

FIGURE LEGENDS

FIGURE 1. Maximum temperature (deg C) and rainfall (0.1mm/day) for January and July as represented by three climate datasets (CRES, CRU and DARLAM) (a) Mean maximum temperature for January, (b) mean maximum temperature for July, (c) mean rainfall for January and (d) mean rainfall for July

FIGURE 2a. Variogram of January maximum temperature across sub Saharan Africa for the CRES, CRU and DARLAM data sets. Distance is measured in geographical degrees. Spatial dependence (gamma) is calculated following Nielsen & Wendroth (2001).

FIGURE 2b. Variogram of January rainfall across sub Saharan Africa for the CRES, CRU and DARLAM data sets. Distance is measured in geographical degrees. Spatial dependence (gamma) is calculated following Nielsen & Wendroth (2001).

FIGURE 3. Recorded known records (KR) and interpolated distributions (ID) of ticks obtained using species predictive modelling based on each of the three climate datasets (CRES, CRU and DARLAM) (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*.

FIGURE 4. Known records (KR) and true predictions (TP) for all tick species generated for each climate dataset (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*.

FIGURE 5. Degree of proportional overlap between known records and predicted presence of all tick species for each climate dataset. These proportional overlap values were calculated at different levels of random sub-sampling of

known records (a) *R. appendiculatus*, (b) *R. capensis*, (c) *R. longus*, (d) *R. zambeziensis*

FIGURE 6. Mean value of proportional overlap (mean ± s.d) across all tick species at different levels of random sub-sampling of known records . This analysis is repeated for each climate dataset.

Figure 1

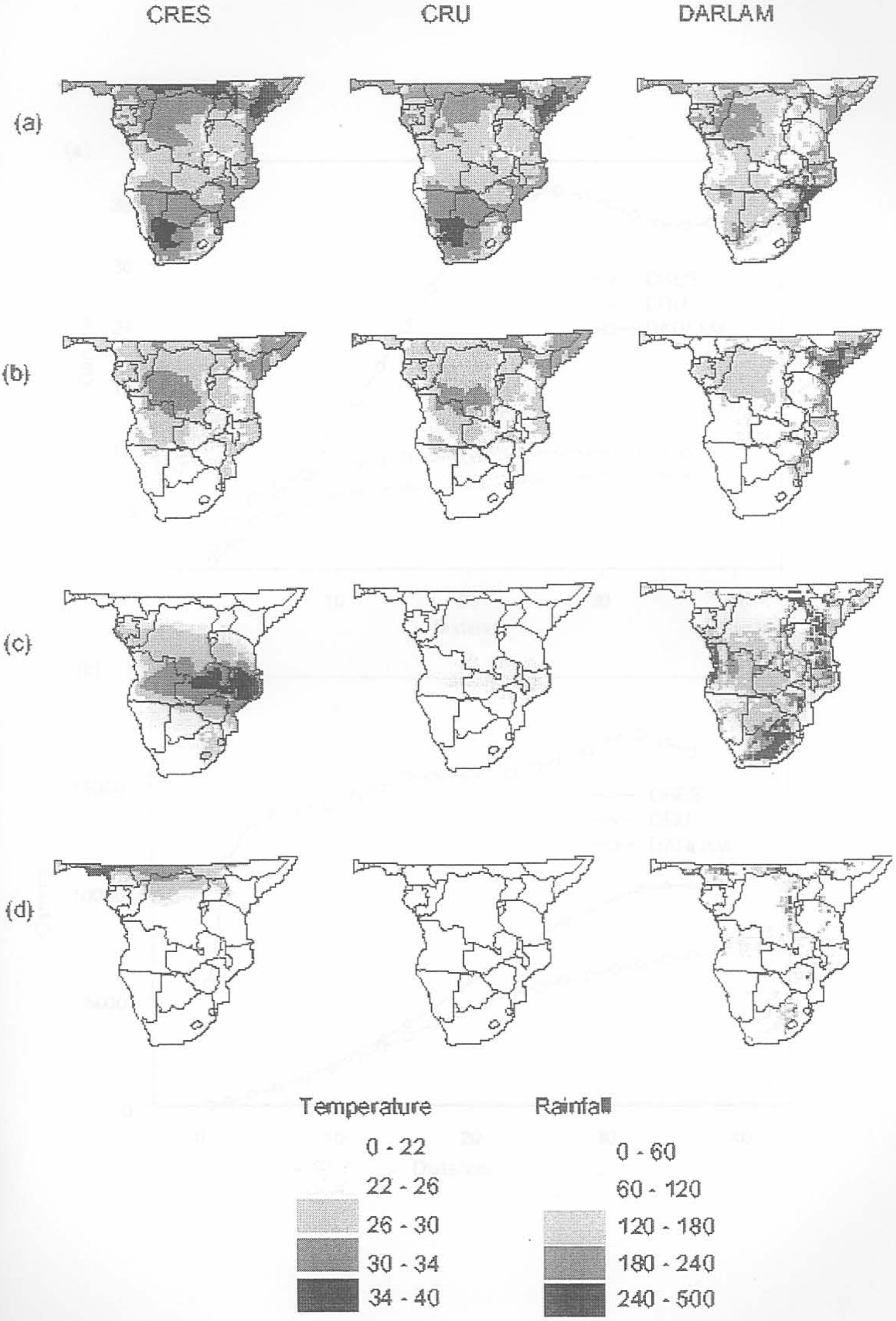

CRES
CRU
DARLAM
(a)
(b)
(c)
(d)
Temperature
0 - 22
22 - 26
26 - 30
30 - 34
34 - 40
Rainfall
0 - 60
60 - 120
120 - 180
180 - 240
240 - 500

Figure 2

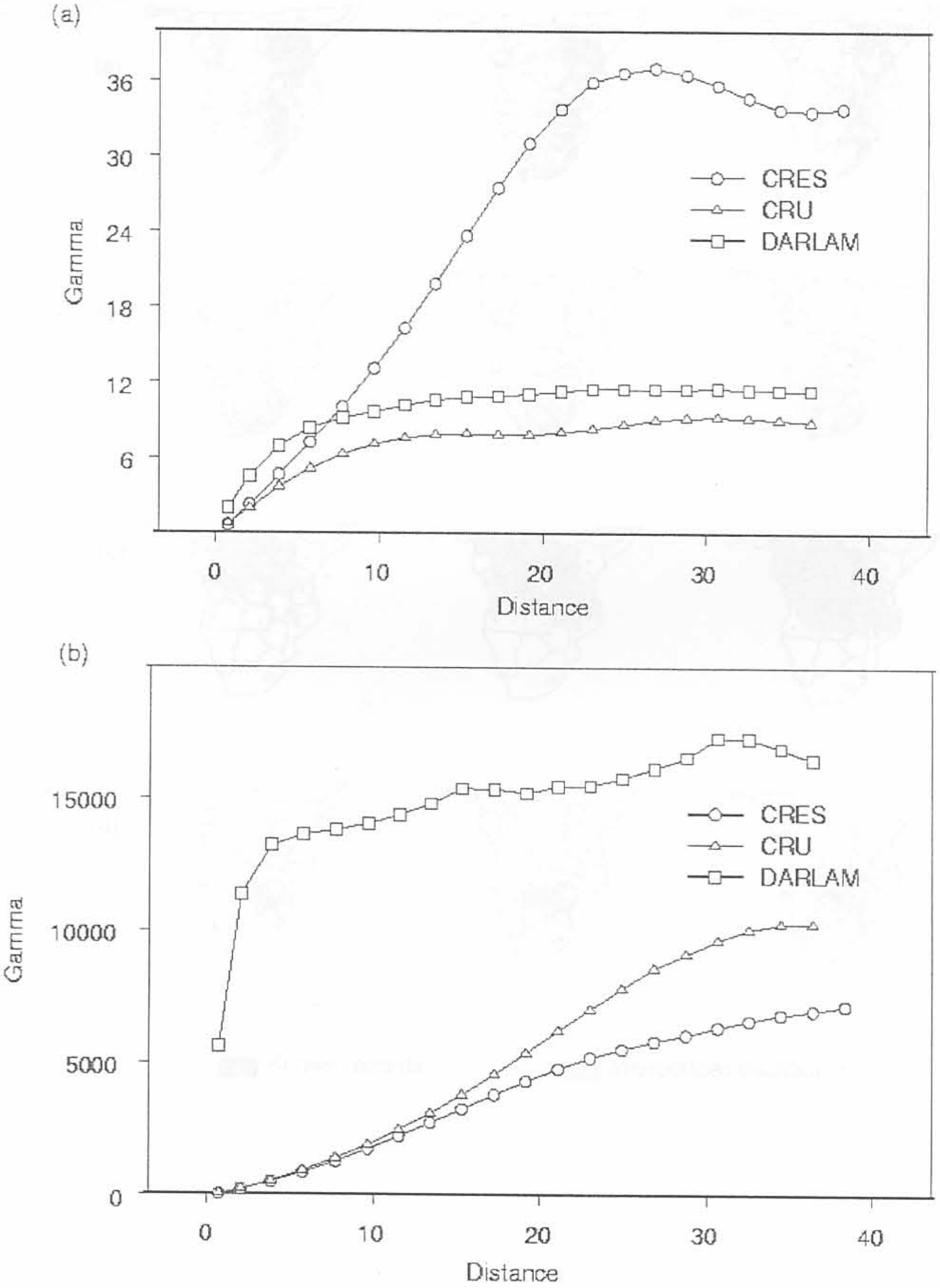

(a)
Gamma
36
30
24
18
12
6
0
10
20
30
40
Distance
CRES
CRU
DARLAM
(b)
Gamma
15000
10000
5000
0
0
10
20
30
40
Distance
CRES
CRU
DARLAM

Figure 3

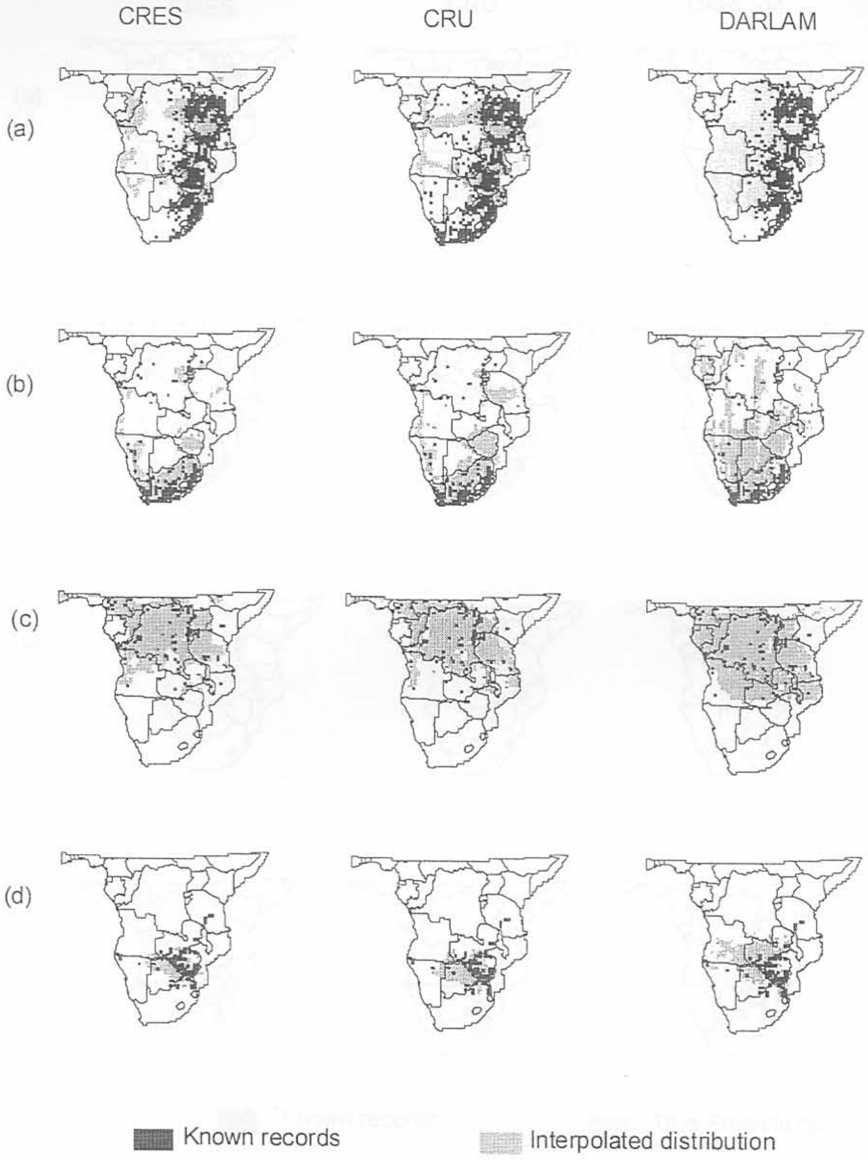

CRES
CRU
DARLAM
(a)
(b)
(c)
(d)
Known records
Interpolated distribution

Figure 4

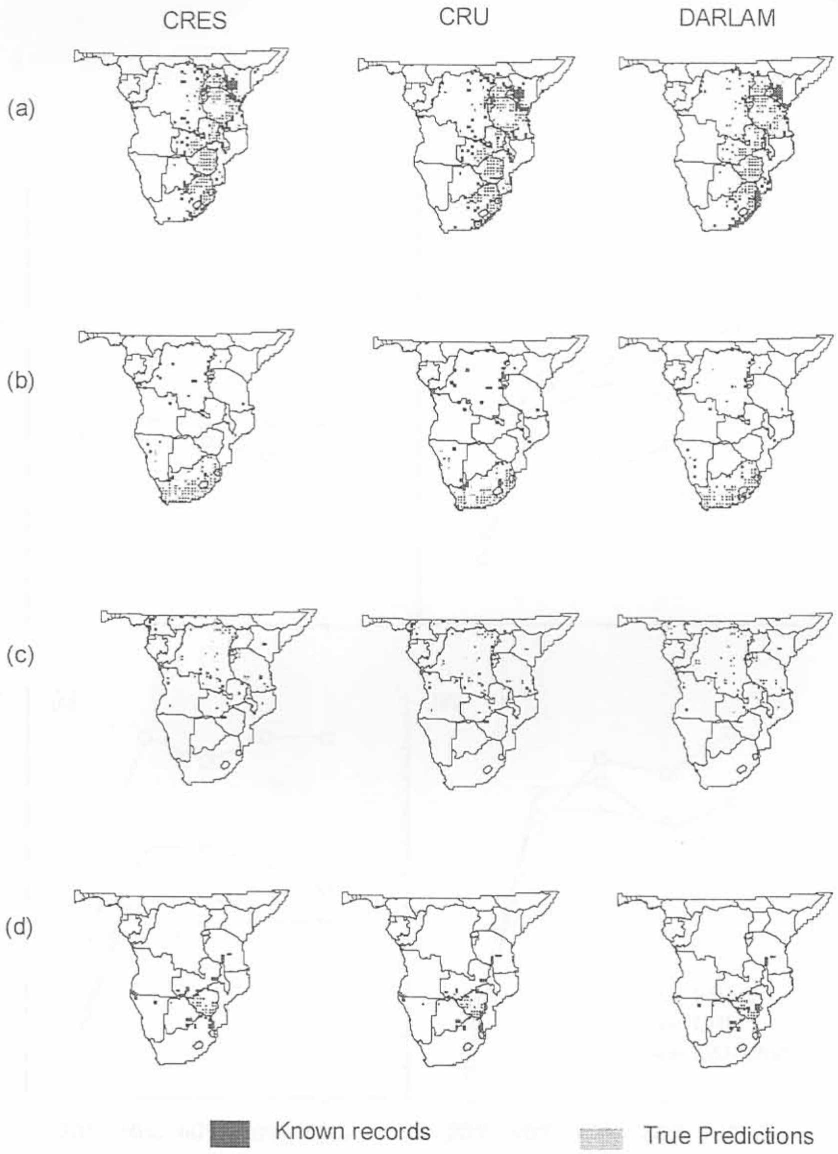


Figure 5

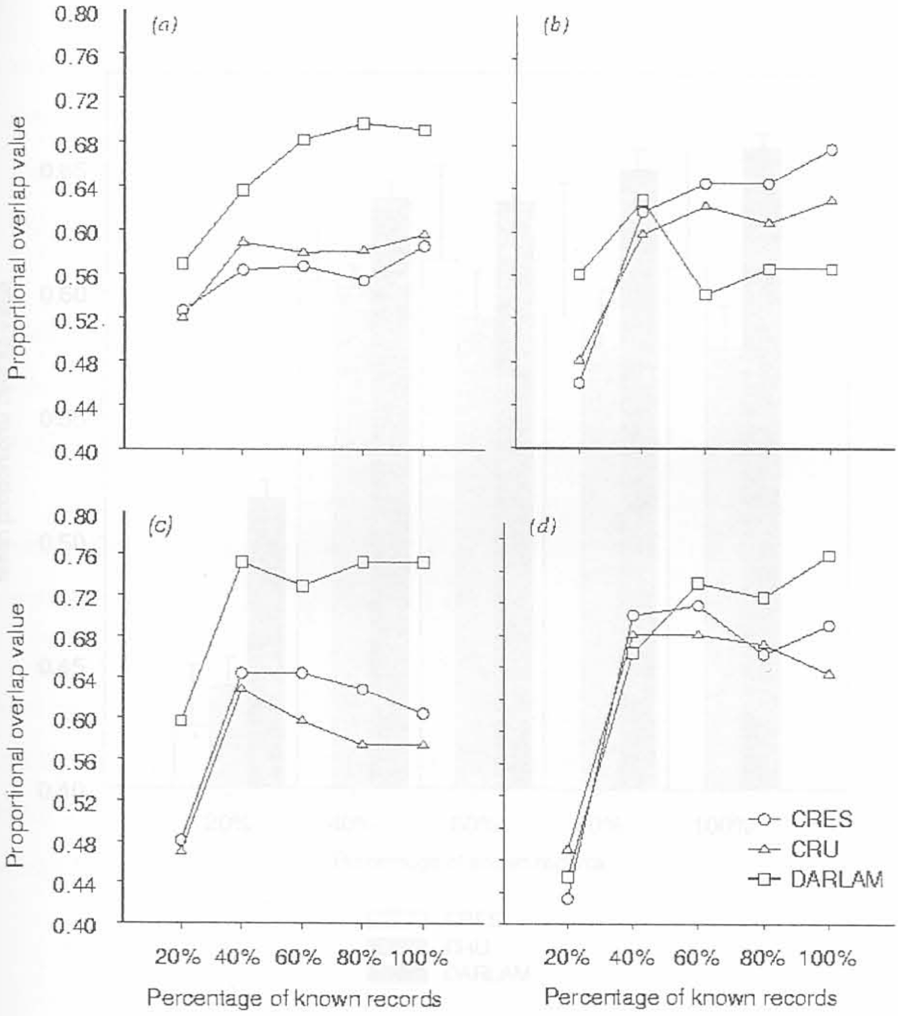
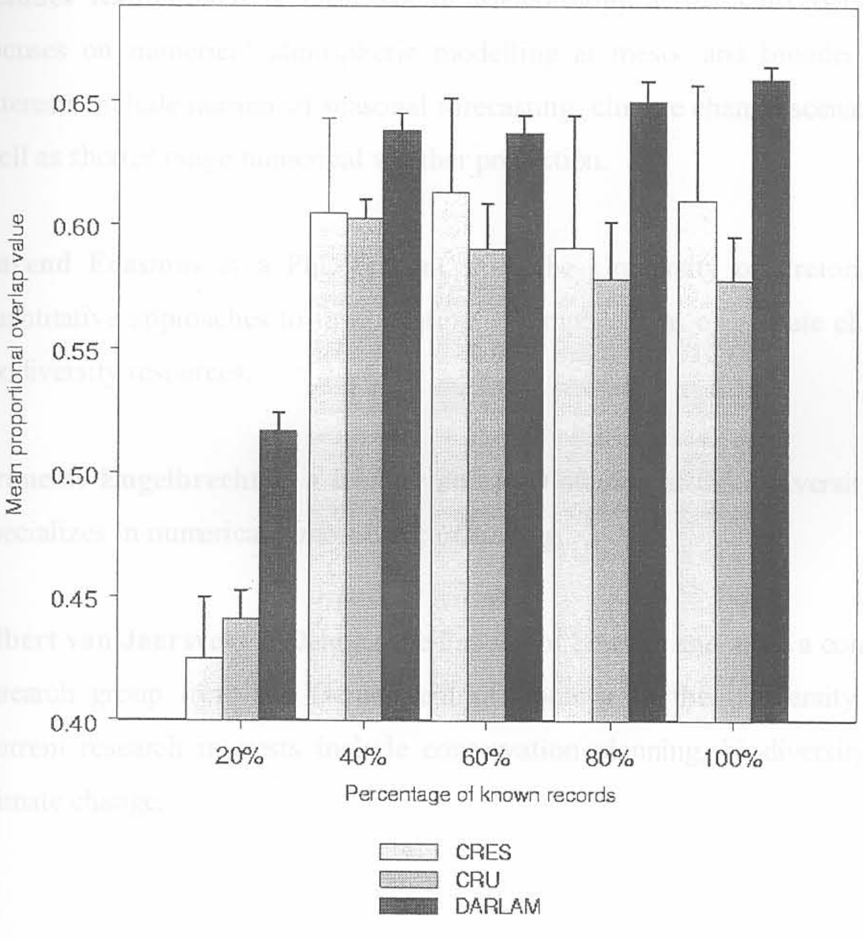

(a)
(b)
(c)
(d)
Proportional overlap value
0.80
0.76
0.72
0.68
0.64
0.60
0.56
0.52
0.48
0.44
0.40
20%
40%
60%
80%
100%
Percentage of known records
CRES
CRU
DARLAM

Figure 6


Mean proportional overlap value
0.65
0.60
0.55
0.50
0.45
0.40
20%
40%
60%
80%
100%
Percentage of known records
CRES
CRU
DARLAM

BIOSKETCHES

Jane Olwoch is a PhD student at the University of Pretoria on a START studentship. Her main interests are in the area of climate change and its consequences for vectors and vector-borne diseases in Africa.

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CHAPTER THREE

Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

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3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

ABSTRACT

The suitability of current and future climates for 30 *Rhipicephalus* species in Africa are predicted using a simple climate envelope model as well as a regional nested climate model, Division of Atmospheric Research limited-area model - DARLAM. DARLAM's predictions are also compared with the mean outcome from two Global Circulation Models (GCMs). East Africa and South Africa are considered the most vulnerable regions on the continent to climate-induced changes in tick distributions and tick-borne diseases. More than 50% of the species examined show potential range expansion and more than 70% of this range expansion is found in economically important tick species. There is also an increase in tick species richness in the south-western regions of the sub-continent. More than 20 % of the species experienced range shifts of between 50 and 100 %. Actual range alterations under climate change may be even greater since factors like land degradation and population increase have not been included in this modelling process. However, these predictions are also subject to the effect that climate change may have on the hosts of the ticks, particularly those that favour a restricted range of hosts. Where possible, the anticipated biological implications of the predicted changes are explored.

Keywords: Climate change, *Rhipicephalus* species, sub-Saharan Africa, tick-borne disease

3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

INTRODUCTION

The recognition that species distributions are significantly influenced by climate has placed considerable emphasis on acquiring information about how the present distributions of organisms will be affected by climate change. In response to this challenge the topic of vector distributions has recently gained much deserved attention. Numerous studies (Sutherst & Maywald 1985; Nix 1986; Perry, Lessard, Norval, Kundert & Kruska 1990; Norval, Perry, & Young 1992; Rogers & Randolph 1993; Sutherst, Maywald & Skarratt 1995; Randolph & Rogers 1997; Estrada-Peña 1999; Rogers & Randolph 2000; Randolph 2001; 2002; Erasmus, Kshatriya, Mansell, Chown & van Jaarsveld 2000; Erasmus, Van Jaarsveld, Chown, Kshatriya & Wessels 2002; Olwoch, Rautenbach, Erasmus, Engelbrecht & Van Jaarsveld 2003; van Staden, Erasmus, Roux, Wingfield & van Jaarsveld 2004; Thomas, Cameron, Green, Bakkenes, Beaumont, Collingham, Erasmus, Ferrierra, Grainger, Hannah, Hughes, Huntley, Van Jaarsveld, Midgley, Miles, Ortega-Huerta, Peterson, Philips & Williams 2004) have attempted to predict the distribution of species based on the major environmental factors that influence their distributions.

This approach neither disregards the need for more detailed and comprehensive eco-physiological approaches nor does it pretend to predict the future. What it does is define the role of climate as a factor in determining the potential for future vector establishment when all other factors are not included (Sutherst 2003). This paper also accents the urgent need to acquire more detailed information about the biology and environmental sensitivities of each and every species against the background of likely climate change. In the absence of more detailed and comprehensive eco-physiological information, relatively straightforward statistical methods that seek correlations between environmental factors and animal or plant presences are likely to remain our best pragmatic approach for exploring the expected future distributions of large numbers of species. This study focuses on the climate induced changes likely to occur in the distribution of some species of an economically important African arthropod, the tick genus *Rhipicephalus*.

The intimate relationship between climate and the requirements of ticks for growth and reproduction is well documented (Tukahirwa 1976; Rechav 1981; 1982; Short & Norval 1981; Minshull & Norval 1982; Norval, Walker & Colborne 1982; Dipeolu 1989; Perry *et al.* 1990; Norval *et al.* 1992; Okello-Onen, Tukahirwa, Perry, Rowlands, Nagda, Musisi, Heinonen, Mwayi & Opuda-Asibo 1999). Subsequently, predicting the distributions of African ticks using climate has also received considerable attention (Rogers & Randolph 1993; Randolph 1993; 2001; Randolph & Rogers 1997; Norval, Sutherst, Kurki, Kerr & Gibson 1997; Cumming 2000a; c; Estrada-Peña 2001b; Olwoch *et al.* 2003). Collectively these results suggest that accurate predictions of tick distributions at different temporal and spatial scales would be feasible. This approach would naturally be especially valuable and useful for investigating poorly sampled regions and species in Africa. The climate data used in earlier studies were garnered mainly from interpolated climate databases at 25 km resolution (Perry *et al.* 1990) or 6 km x 6 km resolutions (Cumming 2000c).

The genus *Rhipicephalus* is the fourth largest in the Family Ixodidae (Walker, Keirans & Horak 2000). There are 74 species currently recognized. It is essentially an African genus with about 60 species recorded only in the Afro-tropical region and ten species that are recognized outside this region. One species, *Rhipicephalus evertsi evertsi* Dönitz, 1910, whose distribution was originally confined to the Afro-tropical region has now gained a foothold on the Arabian Peninsula and its distribution is expected to spread even further (for a recent detailed review of this genus see Walker *et al.* 2000). Only 30 species are included in this paper. They are those whose ecological, life history strategies and climatic requirements are relatively well known. Also, as two main distribution data sets have been used, these ticks are the ones whose current distributions are relatively well plotted. The manner in which these distributions will be influenced by climate change is poorly documented and forms the essence of this paper.

The use of climate-matching models to predict tick distributions

One of the earliest climate matching approaches was CLIMEX (Sutherst & Maywald 1985). In Northern Australia the use of CLIMEX, which calculates the climatic suitability of geographic regions for species using a temperature-dependent growth index moderated by four growth indices: hot, cold, dry and wet, was considered a great success for predicting the distribution of an arthropod, *Rhipicephalus* (*Boophilus*) *microplus* Canestrini, 1887. It was anticipated that this initial success could be translated into predicting distributions of African tick species. However, early studies tended to over-predict the distribution of *R.* (*Boophilus*) *microplus* across Africa, and the predicted high incidences for *Rhipicephalus appendiculatus* Neumann, 1901 in West Africa also failed to correspond to its actual presence. After the Sutherst & Maywald (1985) study it was believed that CLIMEX could successfully predict the possible spread of *R. appendiculatus* into western and central Ethiopia (Perry *et al.* 1990; Norval, Perry, Gebreab & Lessard 1991). Moreover, when the distributions of *Amblyomma* spp. in Africa were modelled using CLIMEX, these were found to be dissimilar to their known distributions. These conflicting results led Norval, Perry, Meltzer, Kruska & Boothroyd (1994) to conclude that the predicted climatic suitability of *Amblyomma hebraeum* Koch and *Amblyomma variegatum* Fabricius, 1794, is almost the opposite of the actual distribution of these ticks, both in Zimbabwe and also in the rest of Africa (Norval *et al.* 1991; 1992).

BIOCLIM was the second climate-based approach employed to model tick distributions (Nix 1986; Norval *et al.* 1992). For each of a selection of geographic points throughout the distribution range of a tick species, BIOCLIM generates 24 climatic attributes from which annual and seasonal mean conditions, extreme values and intra-year seasonality are derived. Computer-selected thresholds and limits of each of the indices are matched across a geographical grid to predict the potential species distribution. This model generally provided a better fit between the predicted and known distributions of *R. appendiculatus*, although at a finer scale the match in some areas of the East African highlands was less useful (Norval *et al.* 1992). The climate database used was also interpolated, in this instance, but at an increased resolution (8 km). This factor alone may explain the increased accuracy when compared to the earlier CLIMEX-based attempts. A subsequent logistic regression approach (Cumming 2000c), based on interpolated climate and elevation data for Africa (Hutchinson *et al.* 1996), and with a resolution of 25 km, achieved even better accuracy. Such an approach, however, normally requires the existence of a training data set that includes presence and absence data (Estrada-Peña 2003). While it is relatively easy to ascertain where ticks have been collected, it is more difficult to confirm the reliability of surveys in which a tick species is cited as not present. Consequently the assumption that non-presence always implies absence may limit the application of this modelling approach (Estrada-Peña 2003).

The use of an advanced very high-resolution radiometer (AVHRR) on the National Oceanic and Atmospheric Administration's (NOAA's) meteorological satellites was used in the 1990s. This feature allowed the direct detection of environmental factors at an 8 km resolution (Lessard *et al.* 1990). The main predictor for this method is the satellite derived maximum mean monthly Normalized Difference Vegetation Index (NDVI). However, this procedure was reportedly very complicated when used to predict the distribution of *R. appendiculatus* (Kruska & Perry 1991). There are current initiatives to revive confidence in the NDVI approach as a predictive tool in research (Randolph 2002).

The present study used a single species distribution modelling procedure (Erasmus *et al.* 2000), originally developed by Jeffree & Jeffree (1994; 1996), for predicting species distribution patterns and for evaluating the relative performance of predicted future climate data sets. This model was subsequently modified to accept multivariate inputs to yield probability of occurrence maps for species (Erasmus *et al.* 2000). When used to predict the current potential distribution of African ticks (Olwoch *et al.* 2003) the model achieved more than 70 % positive predictions for the four species tested.

Climate data used for predicting African tick distributions

The principal sources of climate data used for predictive distribution modelling are climate surfaces, generated by interpolating observed climate data sampled at varying intensities across a region. Consequently any differences between these climate surfaces can usually be attributed to the spatial and temporal evenness of the observed data used for interpolation. Most modern interpolation techniques are pattern based and statistically incorporate horizontal as well as vertical (altitudinal) adjustments (Hutchinson 1989; 1991; Hutchinson & Gessler 1994). These climate surfaces are, however, relatively smooth because of extensive interpolation between low-resolution point observations.

Another source of climate data is general circulation models (GCMs). These are coupled ocean-atmosphere models that provide 3-dimensional simulations of the atmosphere. To date GCMs have produced climate data at a horizontal resolution that is generally too coarse for use in predictive species modelling (> 100 km x 100 km grid point resolution), especially for species that are habitat specialists or that are influenced by fine scale environmental gradients. Computational requirements usually prevent GCMs from being run at meso-scale grid resolutions (10 - 100 km).

The present study used data generated from a regional climate model (DARLAM) as the main climate data set. DARLAM is a potential alternative source of high-resolution climate data that involves the nesting of a high-resolution limited area model within a GCM over the area of interest (for review see McGregor 1997). The GCM supplies the limited area model with initial and boundary conditions. With a grid resolution of 10-100 km, the limited area model is able to simulate some of the meso-scale properties of the circulation. This technique provides a viable fine scale alternative to the use of observed or interpolated climate surfaces or very coarse scale GCMs climate surfaces. The resolution attained by this dynamic modelling process is essentially limited by the computing power available to the modellers. The implication of using these different datasets for predicting current tick distributions has been assessed by Olwoch *et al.* (2003). In this study DARLAM's future predictions are compared with the predictions obtained by using mean climates from two GCMs (CGCM and CCSR/NIES).

MATERIALS AND METHODS

Study area

The study area covers sub-Saharan Africa (Fig. 1) and was divided into 3000 grids cells of 60 x 60 km resolution. This resolution was determined by the DARLAM climate data.

Tick data

Recorded point localities of tick recoveries were obtained from Cumming (1999 b), who compiled the data that he used from various collections of ticks, and from recent collections made by one of us. Combining data sets from different sources invariably compounds identification and distribution errors and for this reason data congruence with Walker *et al.* (2000), who provide well-illustrated distributions of *Rhipicephalus* species, was used to assess data quality in the final compiled dataset. Synonyms provided by the latter authors also solve the common dataset problem of referring to one species but using different names or referring to a group of species as a single species. The species selected for this study belong to the phylum Arthropoda, Class Arachnida, Family Ixodidae, and Genus *Rhipicephalus*. Tick point localities were assigned to particular 60 km x 60 km grid cells by means of a spatial intersect in ArcView GIS. A conservative estimate of the accuracy of these point localities is 0.2° (G. S. Cumming, personal communication 2003) and consequently this approximation is considered reasonable. About 63 *Rhipicephalus* species occur only in Africa but only 30 of them have been included in this study. The species selected are those whose distribution and life history strategies are relatively well known and it is our hope that these results will provide a baseline model for future modelling of other tick species.

Predictive species modelling

A simple climate envelope model was used to predict the future distribution of the focal species (Erasmus *et al.* 2000; 2002). The input data comprised 3000 grid cells of 60 x 60 km size populated with climate variables covering sub-Saharan Africa. Reliable presence records of the ticks selected and the present climate values at these locations were used to construct a climate envelope, using a principal components-type approach. This climate envelope represents the range of climates within which a particular tick is known to occur, and can be interpreted as the realized niche, as defined purely by climate. To arrive at a predicted distribution under a climate change scenario, the existing climate envelope is applied to a climate surface representing future climates, and a new geographical interpretation of distribution is derived [see Erasmus *et al.* (2000; 2002) and Olwoch *et al.* (2003) for a more detailed explanation]. This was used as a standardized base for evaluating the relative performances of the DARLAM and the mean GCM climate data sets, and allows the production of a probability surface of climate suitability for each species modelled.

DARLAM present and future climate data

The Australian Commonwealth Scientific and Industrial Research Organisation (CSIRO) developed the high-resolution limited-area model DARLAM for use in both short-term meso-scale atmospheric studies and longer-term climate simulation experiments (Walsh & McGregor 1995). In the present study ten separate 30-day simulations were performed for both January and July for different 10-year periods. The periods selected are the 1990's and 2020. The simulations were performed at a horizontal grid resolution of 60 km x 60 km using a domain of 100 x 100 grid points that cover sub-Saharan Africa. The monthly average of the ten simulations constitutes the model climatology for the month. The CSIRO Mark 2 GCM was used to force DARLAM at its lateral boundaries. The GCM was integrated for the period 1960-2100, with greenhouse gas forcing corresponding to the A_2 SRES (Special Report on Emission Scenario, issued by the Intergovernmental Panel on Climate Change) scenario.

Engelbrecht, Rautenbach, MacGregor & Katzfey (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables such as near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does, however, tend to overestimate rainfall totals over regions with a steep topography. The DARLAM simulations were performed at the Laboratory for Research in Atmospheric Modelling (LRAM) at the University of Pretoria on a Pentium III workstation with two 550 MHz processors. In the present study the six climate variables used were mean maximum temperature for January and July, mean minimum temperature for January and July, and mean rainfall for January and July (Fig.2)

GCM future climate data

All the GCM climate data used in this study were downloaded from the IPCC/DDC website. Through various stages in ArcView GIS, the original GCM data were processed to fit the 60 x 60 km resolution of DARLAM. The Canadian Global Coupled Model (CGCM2) was the first GCM climate used in this study. It is based on the earlier CGCM1, but with some improvements aimed at addressing shortcomings identified in the first version. In particular, the ocean mixing parameterization has been changed (Gent & McWilliams 1990), and following Flato & Hibler (1992) sea-ice dynamics has been included. The version of GCM2 used for control and doubled CO_2 experiments has ten levels in the vertical with the lowest prognostic level located at approximately 200 m above the surface. A description of CGCM2 and a comparison, relative to CGCM1, of its response to increasing greenhouse-gas forcing can be found in Flato & Boer (2001). The climate change projections used in this study are those from the newer IPCC SRES A2 scenario.

The second GCM model used was developed by the Center for Climate System Research/ National Institute for Environmental Studies, (Japan) (CCSR/NIES) CGCM (Nozawa, Emori, Numaguti, Tsushima, Takemura, Nakajima, Abe-Ouchi & Kimoto 2001). This model is also based on Emission Scenarios (SRES) of the Intergovernmental Panel on Climate Change (IPCC). It is a Transient Coupled Ocean-Atmosphere Model, which was developed to investigate the direct and indirect climate impacts of the anthropogenic sulphate and carbonaceous aerosols in future projections of climate change. The data used here are from the A2 scenarios. Direct radiative forcing of the carbonaceous aerosols nearly nullifies that of the sulphate aerosols for all scenarios. Estimated total indirect radiative forcing is about –1.3 Wm–2 for the A1, B1, and B2 scenarios, and is about –2.0 Wm–2 for the A2 scenario in the latter half of the 21st century. Global and annual averages of the surface air temperature increase for all scenarios because of the dominance of the radiative forcing of the increased CO_2. Global warming is decelerated with an increase in the anthropogenic sulphate and carbonaceous aerosols, because indirect forcing due to the aerosols has a significant cooling effect. Geographical distribution of the surface warming does not depend much on the scenarios. Cloud feedback becomes dominant in the latter half of the 21st century, and this introduces further warming at the surface.

Predicting current and future distribution of *Rhipicephalus* species

The predicted current distributions were initially obtained using the DARLAM predicted current climate. This represents a valuable comparison between predicted distributions and known records (see Olwoch *et al.* 2003). To obtain future predicted distributions the grid cells are populated with future climate variables. The predicted current distributions were obtained using the predictive species model (Erasmus *et al.* 2000) and six climate variables of current and future mean maximum temperature, mean minimum temperature and mean rainfall of January and July provided by DARLAM. The predicted future distributions were obtained by using both DARLAM and the mean GCM climates. The predictive modelling was executed in S-Plus (S-Plus 2000), while maps of the results were drawn in ArcView GIS. The resultant potential distribution maps represent the probability values of their suitability for ticks based on climate.

Analysis of predicted tick range changes

A number of analyses were performed to compare the predicted current and future distributions of ticks. These included: 1) analysis of species range expansion; 2) an analysis of range contraction; 3) change in species richness pattern; 4) species range shifts; and 5) an assessment of overlap between DARLAM and GCM predicted future distributions. These range changes were initially analysed for the whole study area and subsequently, in some cases, on a regional basis in some cases. In the second analysis, ticks were grouped into the following regions depending on their principal regional distribution, namely East Africa, Central Africa and southern Africa, and a fourth group of ticks that were termed "general ticks". The East African tick species include *Rhipicephalus aquatilis* Walker, Keirans & Pegram, 1993; *Rhipicephalus armatus* Pocock, 1900; *Rhipicephalus bequaerti* Zumpt, 1949; *Rhipicephalus carnivoralis* Walker, 1966; *Rhipicephalus humeralis* Rondelli, 1926; *Rhipicephalus kochi* Dönitz, 1905; *Rhipicephalus maculatus* Neumann, 1901; *Rhipicephalus muehlensi* Zumpt, 1943; *Rhipicephalus planus* Neumann, 1907 and *Rhipicephalus pulchellus* Gerstäcker, 1873.

The Central African species include *Rhipicephalus complanatus* Neumann, 1911; *Rhipicephalus compositus* Neumann, 1897; *Rhipicephalus dux* Dönitz, 1910; *Rhipicephalus longus* Neumann, 1907; *Rhipicephalus lunulatus* Neumann, 1907; *Rhipicephalus masseyi* Nuttall & Warburton, 1908; *Rhipicephalus punctatus* Warburton, 1912; *Rhipicephalus senegalensis* Koch, 1844; *Rhipicephalus supertritus* Neumann, 1907;and *Rhipicephalus ziemanni* Neumann, 1904.

The southern African species include *Rhipicephalus capensis* Koch, 1844; *Rhipicephalus distinctus* Bedford, 1932; *Rhipicephalus exopthalmos* Keirans & Walker, 1993;

Rhipicephalus oculatus Neumann, 1901; *Rhipicephalus zambeziensis* Walker, Norval & Corwin, 1981 and the subspecies *Rhipicephalus evertsi mimeticus* Dönitz, 1905.

There were also species that have wide ranging distributions that overlap in different areas in Africa. These species, termed "general ticks" include *R. appendiculatus; R. evertsi evertsi* Neumann, 1897*; Rhipicephalus pravus* Dönitz, 1910; and *Rhipicephalus simus* Koch, 1844. The above groupings are presented to facilitate interpretation of the present findings and do not imply that the ticks placed in particular geographical regions are restricted to these areas, but rather localise their distribution with extensions into neighbouring regions.

Range expansion and contraction

In order to obtain range changes in terms of contractions or expansions, predicted current or future distributions were first obtained. The predicted current or future distributions were taken as the number of grid cells in which the probability of occurrence is equal to or greater than 50 %. The difference in the number of grid cells between the predicted *present distribution* (DP) and predicted *future distribution* (DF) constitutes *distribution range change* (DC). These range changes may either represent contractions or expansions. We initially performed this analysis on a sub-Saharan scale and later on a regional scale in order to establish which regions in Africa would experience greater changes in predicted tick distribution ranges (current and future) and therefore appear more vulnerable to climate change. We analysed the differences between the predicted distributions using the Kolmogorov-Smirnoff two-sample test. Furthermore, we divided the ticks into economically important and unimportant species. A comparison of range changes between the current and future predictions was performed on this latter grouping to assess which of the two groups is more vulnerable to climate change. In all of the above analyses we assessed the proportion of species that experienced expanded or contracted range changes and the degree of the predicted expansion/contraction.

Analysis of change in species richness pattern and degree of range shifts

Species richness patterns were calculated as the number of species in the predicted current or future distribution per grid cell following Erasmus *et al.* 2002. This analysis was performed for the whole of sub-Saharan Africa. Range shifts were calculated as the number of additional grid cells in the predicted future distribution as a proportion of the current predicted distribution. We used the current predicted distribution instead of current known records because most regions in Africa are poorly sampled.

Comparing predicted future distributions of ticks based on climates simulated by DARLAM and GCM

The accuracy of any climate model is as good as the initial conditions that are used to configure it. Since there is no climate model that provides an accurate projection of the future, it seemed prudent to use the results from more than one climate model in this study. A comparison was therefore made to assess the differences between the predicted future climate suitability for tick species using a regional climate provided by DARLAM and a mean of two GCMs described above. The analysis was performed on a sub-Saharan scale and also on a regional scale. We assessed the degree of proportional overlap between the predicted current distribution and the predicted future distribution (DARLAM and GCM) by means of the proportional overlap method (Prendergast, Quinn, Lawton, Eversham & Gibbons 1993; Reyers, van Jaarsveld & Krüger 2000). In this case the proportional overlap was calculated as Nc / Ns where Nc is the number of common grid cells between a pair of areas under comparison and Ns is the number of grid cells in the smallest set of areas containing data for both groups or the maximum number of overlapping grid cells possible.

RESULTS

Model Validation

Model validation was not performed in this study because the same climate envelope model had previously been subjected to rigorous evaluation using presence-absence data resulting from a coordinated and systematic survey effort. Erasmus *et al.* (2002) used the distribution records of 34 bird species and tested performance of the model using receiver operator characteristic analyses (Fielding & Bell 1997). The model performed significantly better than a random model with no discriminatory ability. It also accurately predicted the complete known distributions for 24 of the 34 bird species, using a 20 % sub-sample of the known records (Erasmus *et al.* 2002). This satisfactory documented performance of the model and the relatively good predictions that were obtained when used to predict the current distributions of four African ticks (Olwoch *et al.* 2003) are sufficient reasons to consider the model adequate for the present study.

Future climate – DARLAM

The climatological anomalies for the 2020's vs. the 1990's as predicted by DARLAM are depicted in Fig. 2. January minimum and maximum temperatures are simulated to increase by more than 2 °C over certain regions of sub-Saharan Africa. Many of the eastern regions are expected to become drier with an associated pattern of higher sea-level pressure, whilst the western subcontinent is expected to become wetter. An interesting feature of the July anomaly fields is that parts of the central subcontinent are simulated to become cooler and wetter.

Species distribution changes

Broad scale range changes (Fig.3a, b)

The predicted current and future distributions of the selected *Rhipicephalus* spp. using DARLAM are provided in figures 10-39. On a sub-Saharan scale, the ranges of 46 % of the tick species namely *R. appendiculatus, R. capensis, R. distinctus, R. humeralis, R. kochi, R. longus, R. masseyi, R. oculatus, R. planus, R. punctatus, R. senegalensis, R. simus, R. zambeziensis and R. ziemanni* are predicted to contract. The ranges of 54 % of the species namely *R. aquatilis, R. armatus, R. bequaerti, R. carnivoralis, R. complanatus, R. compositus, R. dux, R. evertsi evertsi, R. evertsi mimeticus, R. exopthalmos, R. lunulatus, R. maculatus, R. muehlensi, R. pravus, R. pulchellus* and *R. supertritus* are predicted to expand over the same period (Fig. 3a & b). These results translate into an area expansion of 3 502 800 km^2 (12%) in total tick range with a total reduction of 64 0800 km^2 (2%).

Central African species (Fig. 4a, b)

Fifty-five percent of species in central Africa are predicted to show range reductions (*R. longus, R. masseyi, R. punctatus, R. senegalensis* and *R. ziemanni*) while 45 % (*R. lunulatus R. compositus, R. complanatus,* and *R. dux*) are predicted to show range expansions. Although the ranges of most ticks are predicted to contract, the total area of expansion is 81% while the total area of reduction is only 19%. The tick species that is predicted to expand its range most in this region is R. *lunulatus* with a total expansion of 252 000 km^2 (Figs. 4a & b, 15, 16, 22, 24, 30, 31, 35, 37and 39).

East African species (Fig. 5a, b)

In East Africa 70 % (*R. aquatilis, R. armatus, R. bequaerti, R. carnivoralis R. maculatus, R. muehlensi* and *R. pulchellus*) of the species are predicted to show range expansions, while 30 % (*R. humeralis, R. kochi* and *R. planus*) are predicted to show range contractions. This translates into a total area expansion of 1760400 km^2 (91 %) with a mere 169200 km^2 (9 %) reduction in total area. The predicted greater expansions are mainly attributed to *R. bequaerti* which more than doubles its present range and *R. pulchellus,* which is predicted to expand its range by some 921600 km^2 (more than 50%) (Figs. 5a & b, 11, 12, 13, 14, 20, 21, 23, 25, 27and 29).

Southern African species (Fig. 6a, b)

In southern Africa some 66 % (*R. capensis, R. distinctus, R. oculatus* and *R. zambeziensis)* of the tick species are predicted to contract their ranges under the future climate conditions generated by DARLAM. Although only 33 % (*R. evertsi mimeticus* and *R. exopthalmos*) of the ticks are predicted to expand their current ranges, the total range expansion is 439200km^2 (23%) while the total range reduction is only 64800km^2 (1%). Most of the expansion in this area is attributed to *R. evertsi mimeticus* (Figs. 6a & b, 17, 18, 19, 26, 34 and38).

"General" tick species (Fig. 7a, b)

The "general" ticks are those *Rhipicephalus* species that are widely distributed with current distributions overlapping within various geographical regions of the subcontinent. This does not necessarily mean that these species are not specialists with regard to their ecological requirements. For example, *R. appendiculatus* is confined to parts of eastern, central and south-eastern Africa (Walker *et al.* 2000). It is a species of significant economic importance in Africa because it transmits *Theileria parva,* the cause of East Coast Fever (ECF), which is major cause of cattle mortality and also causes significant production losses in cattle in most African countries (Okello-Onen *et al.* 1999). In this category 75 % of the ticks, namely *R. evertsi evertsi, R. pravus* and *R. simus* are predicted to expand their ranges. The total range expansion in this region is equivalent to 864 000 km^2 (7%). This expansion is mainly as a result of *R. simus*, which is predicted to expand its range by 601 200 km^2 grid cells (70%). The only tick species predicted to contract its range in this group is *R. appendiculatus*, which is predicted to contract its range by 212 400 km^2 (5%) (Fig. 7a & b,10, 28, 32 and 36).

Changes in species richness patterns and range shifts

The future climate predicted by DARLAM will alter the species richness distribution pattern of African *Rhipicephalus*. Compared to the current species richness pattern (Fig. 8a) the predicted richness pattern is spatially different and broader (Fig. 8b) with encroachment of ticks into new areas. These regions, which include Angola, Namibia and the Northwest Province of South Africa, are forecast to experience more than 50 % increase in tick species richness (Fig. 8c). This may be related to increased rainfall in these regions, rendering the western regions of sub-Saharan Africa more suitable for ticks. However, the general west-east shift in species ranges reported by Erasmus *et al.* (2002) is not supported in this tick study, but rather varying degrees of shift into different directions appears to be the emergent pattern for this taxon. Analysis of range shifts further indicate that 80 % of the species show less than a 50% range shift while 20 % of the species show a range displacement of more than a 100 %. The latter species are mainly those that occupy the western arid regions of Africa (Fig. 8).

Species range changes and tick-borne diseases implications

Thirty percent of the ticks included in this study are classified as economically important because they are vectors of diseases of livestock or other animals (Table 1). These species are responsible for 52 % of the predicted range expansion under future climate conditions. The remaining 70 % are responsible for only 48 % of future tick range expansions.

Predicted future distributions using DARLAM and GCM climate data

The predictions of future climate suitability for ticks when using DARLAM are generally broader than those generated when using the combined GCM climates. With the exception of five species (*R. capensis, R. compositus, R. evertsi mimeticus, R. exopthalmos* and *R. oculatus*), DARLAM predicts wider ranges of climatic suitability than the combined GCM climate surfaces. DARLAM's total predictions are 31 %

broader than the GCMs. The average difference in the range sizes predicted for DARLAM and GCM is 511, 200 km ^{2}. Statistically there is no significant difference between the predictions by DARLAM and GCM using a Kolmogorov-Smirnov test ($p > 0,1$; $n = 30$). However, when the climate data simulated by DARLAM and GCM are analysed for statistical significance, there is a highly significant differences between the two data sets (Kolmogorov-Smirnov test $p < 0.001$ was obtained for all variables; also see Fig. 9). This difference was especially noticeable in the predictions for mean maximum temperature for July, and mean rainfall for January and July where the GCM data predicted hotter and drier climates than DARLAM.

The regional analysis of DARLAM and GCM predicted tick distributions has revealed consistently broader ranges for DARLAM, except for South Africa where the GCM predictions are broader than DARLAM in 66 % of the species studied. These species, *R. capensis, R. evertsi mimeticus, R. exopthalmos* and *R. oculatus* are species that occupy arid and semi-arid areas in South Africa with an annual mean rainfall of 100-600 mm. The other two species from southern Africa (*R. compositus* and R. *muehlensi*) for which GCM predictions were found to be broader than DARLAM occupy a wide variety of habitats.

Proportional overlap tests between the GCM and DARLAM fields on a sub-Saharan scale yield overlap values ranging from 24 % to 72 %. Regional comparisons show moderate overlap between DARLAM and GCM predictions. The lowest average overlap in tick ranges is found in East Africa with a mean proportional overlap of 43 %, while for the "general ticks" category the overlap is the highest at 52 %. This result is expected to change as the area of analysis increases.

DISCUSSION

Using models to predict tick distributions

This study employed a climate envelope model (Erasmus *et al.* 2000) and a regional climate model DARLAM (Engelbrecht *et al.* 2002) to predict the present and future distribution of some African species of the genus *Rhipicephalus*. A climate compiled from values from two GCMs was also used on a comparative basis with DARLAM for modelling future tick distributions. Earlier work (Olwoch *et al.* 2003) indicated high accuracy levels between the predicted and recorded distributions of *R. appendiculatus, R. capensis, R. longus and R. zambeziensis* in Africa using DARLAM. With this as background we have proceeded to predict the future distributions of certain African tick species. The perceived advantages of this approach over the previous studies include:

(i) The climate surfaces produced by DARLAM are capable of capturing climate at sufficiently fine scales relative to the range sizes of species, are entirely based on a simulation of climate processes and do not use any recorded meteorological data to generate climate surfaces (Engelbrecht *et al.* 2002). Furthermore the 25 km or 8 km or 6 km resolution of most long term interpolated climate data sets provides a false picture because it depends on the original low-resolution point observations (for a comparison of different climate datasets see Olwoch *et al.* 2003).

(ii) The multivariate capabilities of a predictive species modelling procedure (Erasmus *et al.* 2000) and its ability to provide probabilities of occurrence as opposed to mere absent-present predictions gives a comparatively better picture especially when tackling species that have been poorly sampled. This model can also operate effectively using only presence records and any number of available climate variables. The model has been validated for bird species (Erasmus *et al.* 2000) and tested on four species of African ticks (Olwoch *et al.* 2003).

(iii) The use of satellite imagery (e.g. the use of NDVI) is gaining ground as a basis for predicting tick distributions, but only works for predicting current distributions and cannot capture NDVI for the future.

This paper relates the possible effect that the predicted climate changes, without taking other factors into account, may have on tick distribution in sub-Saharan Africa. It would, however be naïve not to address the importance of some of these other factors. One of these is host species, particularly as climate change may drastically affect their distribution even more than it would that of the ticks. Ixodid ticks are obligate, albeit temporary parasites of mammals, birds or reptiles during their larval, nymph and adult stages. Several species attach to a very wide range of hosts, while others have a restricted range of hosts that they will attach to during their adult or immature stages. This part of the discussion is be limited to those species of *Rhipicephalus* of which one of us (I.G.H) has considerable field experience, namely *R. appendiculatus, R. capensis, R. distinctus*, R. *evertsi evertsi. R. evertsi mimeticus, R. exophthalmos, R. kochi, R. maculatus, R. muehlensi, R. oculatus*, *Rhipicephalus* spp. of the pravus group, *R. simus* and *R. zambeziensis*.

Ticks that have a wide host range can be considered as generalists, namely *R. appendiculatus, R. evertsi evertsi, R. evertsi mimeticus* and *R. zambeziensis*. In addition, their larvae and nymphs feed on the same domestic or wild ruminant or equine hosts as the adults (Walker *et al.* 2000), with the further proviso that the larger the host animal or species the greater the number of adult ticks it is likely to harbour (Horak, Boomker, Spickett & De Vos 1992; Horak, Boomker & Flamand 1995). Although these host species are likely to be affected by climate change, it is probable that there will still be domesticated animals around to act as hosts for the ticks.

Rhipicephalus maculatus and *R. muehlensi*, which both prefer coastal bush as habitat, can be considered restricted generalists in that all stages of development of the former tick prefer thick-skinned animals such as African buffaloes, bushpigs and rhinoceroses as hosts, and those of the latter tick tragelaphine antelope species such as kudus, nyalas and bushbuck (Horak *et al.* 1995; Walker *et al.* 2000).. Climate change will thus not only affect the preferred coastal woodland habitat of the ticks, but also the distribution of their hosts and these could prove to be major constraints to the predicted future distributions of these ticks.

The preferred hosts of all stages of development of *R. kochi* are medium-sized and larger antelopes and scrub hares, and the preferred hosts of adult *R. exophthalmos* are medium-sized and larger domestic and wild ruminants and scrub hares (Walker *et al.* 2000). The preferred hosts of all stages of development of ticks of the *R. pravus* group are scrub hares, but their adults will also be found on medium-sized and larger domestic and wild ruminants (Walker *et al.* 2000). It would, however, appear as if elephant shrews are excellent hosts of the immature stages of each of the latter three ticks (Fourie, Horak & Woodall in press). Depending on the extent of reliance that the immature stages have on elephant shrews compared to the larger animals as hosts, the effect of climate change on the distribution of these small mammals may be greater than its predicted effect on the distribution of the tick species they harbour.

The host preferences of two of the more "specialist" group of ticks, namely *R. capensis sensu strictu* and *R. simus sensu strictu* are nearly identical, with their adults on equids, large carnivores and large bovids and their immature stages on murid rodents, but whereas *R. capensis* is a tick of the western, winter rainfall, coastal regions, *R. simus* is found mainly in the moister inland summer rainfall regions of South Africa (Walker *et al.* 2000). The predicted future distributions may thus be determined not only by the presence of large mammal and murine hosts for their adult and immature stages respectively, but also by the differences in their seasonal climate preferences. The remaining two ticks, namely *R. distinctus* and *R. oculatus* are both very specific in their host requirements with all stages of the former virtually exclusively infesting hyraxes and of the latter hares (Walker *et al.* 2000). Any predicted changes in these ticks' distributions will depend heavily upon changes in the distribution of their specific hosts.

The above analysis and the fact that different tick species prefer different ecological and climatic requirements imply that the effect of climate change on the distribution of one tick species will not necessarily reflect the manner in which other species would react, emphasizing the importance of assessing its effect on as many species as possible. It should also be noted that predicted data, figures and risk maps presented here in no way represent the current / future presence or absence of species, but rather an inclination to habitat suitability. Moreover, this study supports the view put forward by Randolph (2002) that if the objective of a risk map is to warn of potential threat, to alert control services and to direct attention to hitherto uncharted localities where the tick may be lurking, it may be better to err, within limits, on the side of false alarms than of false complacency. In the light of the foregoing this paper represents an attempt to produce maps, using a regional climate model, for the predicted future distribution of tick species belonging to a genus of considerable veterinary and medical importance on the African continent.

Predictive species modelling is particularly useful in Africa where field surveys on most ticks are not conducted on a regular basis and consequently species inventories are not updated as required. By using the recorded distributions of well-sampled tick species and models the gaps in the existing records of poorly sampled species can be filled in. Even if up- to- date field data on the distribution of tick species are available, studies on the future distribution of species will still depend on the use of models. Thus good data and predictive species modelling are complementary in the study of the distribution of species in a changing environment. Since some of the African tick species have been adequately sampled this data can be used as an input in a model and the response to climate change of lesser-sampled species can be obtained.

Implications of the findings

The predicted effect of climate change on the distribution of ticks varies by region and species, and several species are forecast to experience range alterations in the form of contractions, expansions or shifts. It is also envisaged that climate change will alter the overall pattern of tick species richness. Though range alterations are in some cases minimal, they nevertheless may prove catastrophic on small African farms if prior warnings are not issued. The extent to which these predicted changes coupled with possible landscape changes will translate into realized alterations in distributions will depend on numerous other factors. These may include the effect of climate change on the hosts as discussed above, acaricide usage, land degradation and human population increase. In the following paragraphs each of these predicted changes are analysed separately before broad conclusions are made, and where possible the biological implications of the predicted range alteration are discussed.

Range expansions

As could be expected, not all tick species reacted to the predicted climate changes in a similar manner. However, specific information concerning how physiological tolerances and behavioural patterns influence species ranges is limited to a few African taxa and has not been researched sufficiently to allow for entirely accurate predictions (Van Jaarsveld, Chown, Erasmus, Kshatriya & Wessels 2002). More than half of the tick species studied expanded their ranges under future climate conditions. This has implications for the future, as some of them are vectors of pathogens. The close correlation between climate variables and many vectors of disease has been pointed out by Rogers & Randolph (1993). Climate change may increase the reproductive rate of some pathogens or alter the selection pressures on others and possibly accelerate the rate at which new pathogen types evolve. Because of the number of new types of pathogens that may evolve, mutations will probably also increase and there are likely to be more disease cycles per year in a warmer world (Sutherst 1996).

The expected range expansions simulated for East African ticks could be in response to the predicted general decrease in maximum temperatures. Since temperature determines rates of invertebrate development, reproduction and mortality, a decrease in temperature could accelerate rates of population increase, especially in areas where these are currently limited by high temperatures (Sutherst 1996) through reduction in death of eggs by desiccation. DARLAM's predicted decrease in January maximum temperatures could increase the likelihood of egg survival and thus result in greater hatching percentages. These moderate temperatures are responsible for the expected general expansion of tick ranges in sub-Saharan Africa. Climate changes predicted for the east African horn region and northern Kenya favour range expansion by *R. pulchellus*, which prefers harsh environmental conditions (Walker *et al.* 2000). Range expansion by this tick corresponds with field observations that indicate that it is already expanding its range in the northern parts of east Africa (J. Mukani, *personal communication 2002*). On the other hand the specific reasons behind the predicted range expansion of *R. bequaerti* are not clear since very little information exists in the literature on the ecological preferences of this species. Its range expansion may, however, be in response to the predicted increase in minimum temperatures accelerating development and shortening generation times, possibly leading to higher tick populations in some areas (Sutherst 1996). The predicted decrease in maximum temperatures at the same time may reduce the limiting effect on such development that excessively high temperatures may have had.

In Southern Africa range expansions are predicted for those species that currently occupy the drier regions of the subcontinent, namely *R. evertsi mimeticus* and *R. exophthalmus*. Furthermore the predicted decrease in maximum temperatures and increase in rainfall in Namibia may result in shorter generation times and therefore more tick generations per year and higher tick populations. The fact that extensive range expansions are predicted for some of the economically important tick species implies that a future climate may also be favourable for an increase in tick-borne diseases. Range expansions of ticks in South Africa in particular may be in response to the observed effect of temperature on the pre-hatch period of the eggs. Various authors (Londt 1977, Robertson 1981, Spickett & Heyne 1990) reported that the length of this period is inversely dependent on increased temperatures. They observed that eggs laid in late summer; autumn or winter for instance took longer to hatch than those laid in summer and that there was a synchronous hatching of these eggs that occurred as the temperatures increased in spring. This observation was also recently supported by the field data of Horak, Spickett & Braack (2000) for *R.*

(*Boophilus*) *decoloratus* in the Kruger National Park (KNP) in South Africa. Any predicted range expansion for this tick will also be in agreement with the marked increase in the number of free-living ticks of this species collected from vegetation in the KNP in 1998, corresponding to the exceptionally warm temperatures recorded during that year. In fact, their results show that there was a double seasonal peak in tick numbers in 1998 implying that an additional generation of ticks had been completed (Horak *et al.* 2000). This result is also in agreement with experimental data on the spread of the tick *Ixodes ricinus* in northern Europe (Lindgren, Talleklint & Polfeld 1998). A worrying aspect of these predicted range expansions is that, by implication, larger numbers of cattle will be exposed to certain economically important tick species thus increasing the encumbrance of effective tick control measures.

In the "restricted generalist" and "specialist" tick categories the distributions of *R. pravus* and *R. simus* respectively, that currently already occupy wide ranges, are predicted to expand further. However, a reason for the apparently wide current distribution of these two ticks could be due to the fact that it is only recently that their specific identities have been unresolved; in the past and still today authors refer to them as ticks of the *R. pravus* and *R. simus* groups (Walker *et al.* 2000). It is probable that the distribution data used in this study also contain data on ticks of the latter broader groups, and consequently it is not possible to state whether the predicted distributions represent those of true *R. pravus* and *R. simus* or those of ticks belonging to these groups.

Range contractions

The ranges of nearly half the tick species studied displayed varying degrees of contraction. The degree of range contraction is usually of concern because of the known negative relationship between range size and the probability of extinction (Gaston 1994). However in this case this aspect is not of much concern considering he relatively small scale of contraction found. Compared to other species some may view the extinction of parasites as an advantage, but it may have unexpected consequences. In Cote d'Ivoire for instance Gouteux & Jarry (1998) examined five species of tsetse fly and found that each species occupied different habitats and that populations were displaced in time. Partial removal of *Glossina palpalis* resulted in the invasion of its territory by two less dominate species, namely *Glossina pallicera* and *Glossina nigrofusca* resulting in the continued transmission of trypanosomiasis (Sutherst 2001). Additionally, the suppression of *R.* (*Boophilus*) *decoloratus* in south-eastern African countries by chemical control, coupled with the warm, moist climate of these countries, has partially been responsible for the invasion of its habitat by its more vigorous relative R. (*Boophilus*) *microplus* (Sutherst 2001). Although the later is also subject to the same chemical control, this shows that in reality suppression of one parasite may result in unexpected consequences. Thus a contraction in the distribution range of one parasite species may increase competition and initiate the invasion of its erstwhile range by another species, which may, as is the case with *R.* (*Boophilus*) *microplus*, transmit economically more important diseases than the indigenous *R.* (*Boophilus*) *decoloratus* (Sutherst 2001).

The general range contraction for most of the Central African tick species included in this study is in response to the predicted decrease in the July minimum temperatures over this region. Similarly, increase in January temperatures and intense desiccation predicted for Zimbabwe and some parts of South Africa may be detrimental to tick growth and development leading to contraction of tick ranges in this region. The 'generalist' tick, *R. appendiculatus* that flourishes in areas of high rain-fall and moderate temperature is forecast to lose ground under the predicted dehydration of most of the East African coast. These results are in agreement with field observations on the decrease of free-living *R. appendiculatus* in the KNP following the drought 1991/1992 (Horak *et al.* 2000). An explanation for these results appeared to be that the greater proportion of bare ground compared to ground cover in the years following the drought led to heat stress and dry stress, which adversely affected the free-living stages of *R. appendiculatus* and consequently resulted in a reduction in the population on the vegetation. An increase in maximum temperatures in Zimbabwe is likely to drive *R. appendiculatus towards* the cooler areas of East Africa. This forecast is in agreement with earlier predictions by

Rogers & Randolph (1993) that under global warming South African ticks are likely to retreat to the mountainous eastern region near the border of South Africa with Mozambique and that this effect will be more noticeable near the peripheries of their present ranges. This would imply that areas currently showing corridor as an emerging disease may become vector free in the future. The contraction of *R. appendiculatus* may be looked at as a relief since it is the most important vector of tick-borne diseases on the African continent; transmitting the pathogen that causes ECF (Corridor diseases in South Africa). However, the contraction is too small to affect livestock ranching

Range shifts and species richness

The overall results indicate that climate change will result in an increase in species richness in the current western arid areas of the sub-continent. This is attributed to more favourable climatic conditions in the future. However, because of specific ecological requirements, this pattern is not common to all ticks. For instance *R. appendiculatus* demonstrates a clear west to east shift in its distribution range and therefore supports the west to east shift hypothesis (Erasmus *et al.* 2002).

Future climate predictions using DARLAM and GCMs

The notable differences between the predicted climate outputs of the two modelling approaches is reflected in the variations in tick distribution range predictions. The hotter and drier climates predicted by GCMs are expected to result in greater decreases in tick distribution ranges than those forecast by DARLAM, an indication of model output differences. One would have expected proportionally significant differences in the resultant distribution ranges predicted by the two models corresponding to the highly significant differences in the two climates that they predict. However, moderate to high proportional overlapping between the DARLAM and GCM predictions implies that there are other factors operating at local levels other than climate. Because DARLAM is a process driven model it is able to capture today's conditions and comparatively more local interactions at a higher spatial resolution. GCMs on the other hand operate at a very low spatial resolution and have been criticized for being unable to capture the present day features of the global climate (Goodess & Palutikof 1993). Ticks are habitat specialists and spend more that 90 % of their lives on the ground and are thus likely to be affected by local variations in climate. In this regard climate simulations provided by a regional model such as DARLAM are intuitively more appropriate to use in such studies than the GCM outputs.

Tick-borne diseases and climate change

A warmer climate will favour the range expansion of some of the economically important ticks, and domestic stock in sub-Saharan Africa would thus experience increased prevalence of ticks that act as vectors of disease. With weak mitigation capacity the livestock industry in sub-Saharan Africa would be severely affected and effective chemical control may be applied too late. Tick-borne disease control measures used during and after outbreaks and epidemics have not always been successful as they are usually crisis management tactics that do not allow for the incorporation of untreated controls in their evaluation (Carpenter, Appel, Erickson & Novilla 1976; Burrows, Hofer & East 1994). Most of these approaches target the disease in the infected animal and ignore the importance of all other interacting organisms in maintaining the disease in the population in a stable state. In this regard a more holistic ecological approach to disease management may be called for. Nevertheless tick-borne disease control will still rely heavily on chemical control due to its accessibility and "quick-fix" results. However, for a more permanent and sounder management of these diseases the incorporation of our knowledge about vectors and hosts, climate and other requirements, both now and in the future is of paramount importance. The impact of climate change on these tick-host-disease systems can no longer be ignored.

Future direction

The results presented here are essentially based on a climate matching method that relies firstly on the model used and secondly on the available current distribution data for the species. When these variables are projected into the future, caution is advised. Moreover, the overall effect of climate change on tick distribution will also depend on how these changes affect the interactions between ticks, hosts and parasites collectively. Equally complex models will be required to include all of these specific interactions. In the absence of suitable modelling approaches to accommodate all of these biotic and abiotic interactions, simple climate matching models offer the best means available for exploring likely future biological consequences. On the whole, the effects of climate change on ticks and tick-borne diseases in Africa are likely to be expressed in several ways, from short-term epidemics to long-term gradual changes in disease trends. Field studies in Kenya already support this in that climate variability accounts for up to 26 % of the anomalies in hospital-based highland malaria cases (Githeko, Lindsay & Confalonieri & Patz 2000). In most cases there are few published data that provide this essential information partly because the science of climate and health is as yet not well developed. The actual proportion of changes in vector-borne diseases attributable to climate change is therefore still unknown. Furthermore, there are also bureaucratic obstacles to evidence-based health policy change (Githeko *et al.* 2000).

These results would have benefited from data generated by regular interval long-term surveys of tick distribution in Africa so that local trends could be identified. Although some ticks in some areas have been properly sampled, this sampling needs to be intensified to include all regions and all species. Where it has been, as in the case of *R. pulchellus*, the results are in agreement with field surveys in the horn of Africa where this species is already expanding its range. In the absence of such surveys and more robust models, the present predictions serve as a starting point for understanding the broad scale climatic requirements of African ticks and how these may be influenced by climate change. The prediction that some economically important tick species will be favoured by climate warming, puts pressure on African governments and on vector control agencies to introduce measures that will integrate the tick's ecological requirements in the appropriate tick control measure. Predicted range expansions in East and South Africa should not be taken lightly because of the dependency of these regions on livestock production. Holistic ecological control measures should be developed and resources for field studies should be provided to validate these results. In addition resources to promote the continued study of the science of climate change must be made available for future research.

In conclusion, this study has identified those areas on the African continent south of the Sahara that will be most vulnerable to disruption by certain ticks of the genus *Rhipicephalus* under climate change. This is an important first step in disease management because it provides a key to the direction future efforts should take and also to avoid much unproductive effort on systems that may be sensitive to change, but for which there are sustainable and robust adaptation options already available. However, with the resources at hand, it is still possible to give guidance as to the current and future distribution of a number of tick species.

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TABLE 1 *Rhipicephalus* spp. and the diseases associated with them or the toxins they produce

Disease and causal agents	**Animal affected**	**Vectors**
EAST COAST FEVER *(Theileria parva)*	Cattle	*R. appendiculatus* *R. zambeziensis*
TICK TOXICOSIS	Cattle	*R. appendiculatus*
CORRIDOR DISEASE OR BUFFALO DISEASE *(Theileria lawrencei)*	Cattle Buffalo	*R. appendiculatus* *R. zambeziensis*
Gall sickness *(Anaplasma marginale)*	Cattle	*R. evertsi evertsi* *R. simus*
EQUINE BILLIARY FEVER OR EQUINE PILOPLASMOSIS	Horses, Mules Donkeys	*R. evertsi evertsi*
SPRING LAMB PARALYSIS	Lambs, Calves	*R. evertsi evertsi*
CANINE BILIARY FEVER OR CANINE TICKFEVER (*Babesia canis*), RICKETTSIOSIS (*Ehlichia canis)*	Dogs	*R. sanguineus*
PARALYSIS	Sheep, Lambs Calves	*R. lunulatus*
NAIROBI SHEEP DISEASE	Sheep, Humans	*R. pulchellus*

TABLE 2. Proportional overlaps between pairs of grid cells between the predicted ranges from DARLAM and the ranges predicted using mean values for two GCMs

SPECIES	DARLAM 2030	GCM 2030	COMMON GRIDS	POP
"General" ticks				
R. appendiculatus	969	858	476	55 %
R. evertsi evertsi	1220	945	611	65 %
R. pravus	1300	868	621	29 %
R. simus	1209	858	597	60 %
East Africa				
R. aquatilis	33	17	5	29 %
R. armatus	153	116	29	25 %
R. bequaerti	215	40	11	28 %
R. carnivoralis	205	111	67	60 %
R. humeralis	79	33	12	55 %
R. kochi	797	491	326	29 %
R. maculatus	425	173	98	56 %
R. muehlensi	**699**	**678***	315	67 %
R. planus	719	413	278	55 %
R. pulchellus	841	217	179	25 %
Central Africa				
R. complanatus	626	595	400	67 %
R. compositus	**699**	**737***	443	60 %
R. dux	201	192	77	40 %
R. longus	1020	990	642	25 %
R. lunulatus	897	518	308	28 %
R. masseyi	450	338	202	60 %
R. puntatus	458	440	262	28 %
R. senegalensis	803	622	415	56 %
R. ziemanni	611	558	352	72 %
South Africa				
R. capensis	**485**	**547***	309	56 %
R. distinctus	707	352	254	72 %
R. evertsi mimeticus	**423**	**577***	49	49 %
R. exopthalmos	**212**	**236***	116	15 %
R. oculatus	**386**	**434***	293	49 %
R. zambeziensis	299	226	169	60 %

Bold* = GCM predictions wider than those of DARLAM

POP: Proportional overlap value

LEGENDS TO FIGURES

FIG. 1: Study area

FIG. 2: DARLAM's climatological anomalies for the 2020s vs 1990s

FIG. 3a: *Rhipicephalus* species in sub-Saharan Africa that are predicted to show range size contraction

FIG. 3b: *Rhipicephalus* species in sub-Saharan Africa that are predicted to show range size expansion

FIG. 4a: *Rhipicephalus* species in Central Africa that are predicted to show range size contraction

FIG. 4b: *Rhipicephalus* species in Central Africa that are predicted to show range size expansion

FIG. 5a: *Rhipicephalus* species in East Africa that are predicted to show range size contraction

FIG. 5b: *Rhipicephalus* species in East Africa that are predicted to show range size expansion

FIG. 6a: *Rhipicephalus* species in the southern Africa that are predicted to show range size contraction

FIG. 6b: *Rhipicephalus* species in southern Africa that are predicted to show range size expansion

FIG. 7a: *Rhipicephalus* species in the "General ticks" that are predicted to show range size expansion

FIG. 7b: *Rhipicephalus* species in the "General ticks"group that are predicted to show range size contraction

FIG. 8: Species richness pattern of Rhipicephalus species in sub-Saharan Africa (a) Current (b) Future (c) areas with more than 50% increase

FIG. 9: Box Plots based on Kolmogorov-Smirnov test that compared climate predicted by DARLAM and a combined GCM

Figs 10-39 Predicted probability distribution of *Rhipicephalus* species using DARLAM and GCM future climates: (a) DARLAM (b) GCM

FIG. 10: *R. appendiculatus*

FIG. 11: *R. aquatilis*

FIG. 12: *R. armatus*

FIG. 13: *R. bequaerti*

FIG. 14: *R. carnivoralis*

FIG. 15: *R. complanatus*

FIG. 16: *R. compositus*

FIG. 17: *R. distinctus*

FIG. 18: *R evertsi mimeticus*

FIG. 19: *R. exophthalmus*

FIG. 20: *R. humeralis*

FIG. 21: *R. koch*

FIG. 22: *R. longus*

FIG. 23: *R. maculatus*

FIG. 24: *R. masseyi*

FIG. 25: *R. muehlensi*

FIG. 26: *R. oculatus*

FIG. 27: *R. planus*

FIG. 28: *R. pravus*

FIG. 29: *R. pulchellus*

FIG. 30: *R. punctatus*

FIG. 31: *R. senegalensis*

FIG. 32: *R. simus*

FIG. 33: *R. supertritus*

FIG. 34: *R. zambeziensis*

FIG. 35: *R. ziemanni*

FIG. 36: *R. evertsi evertsi*

FIG. 37: *R. lunulatus*

FIG. 38: *R. capensis*

FIG. 39: *R. dux*

Fig. 1

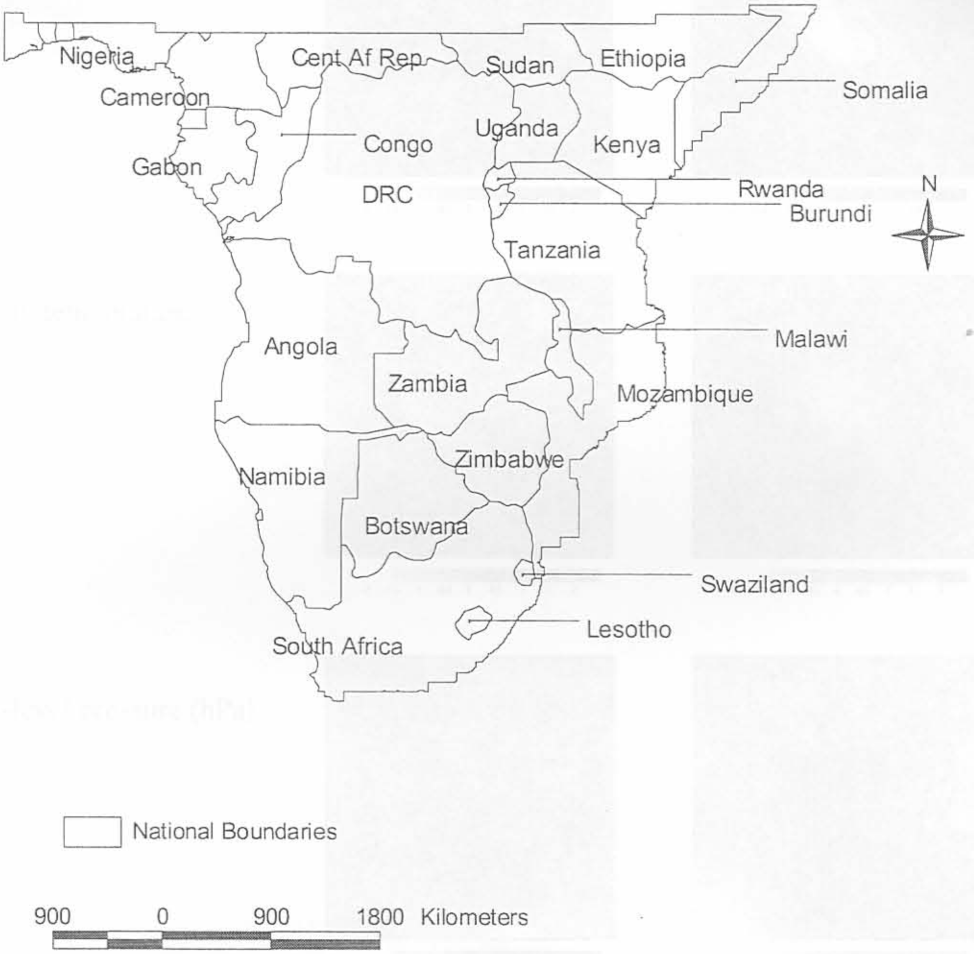
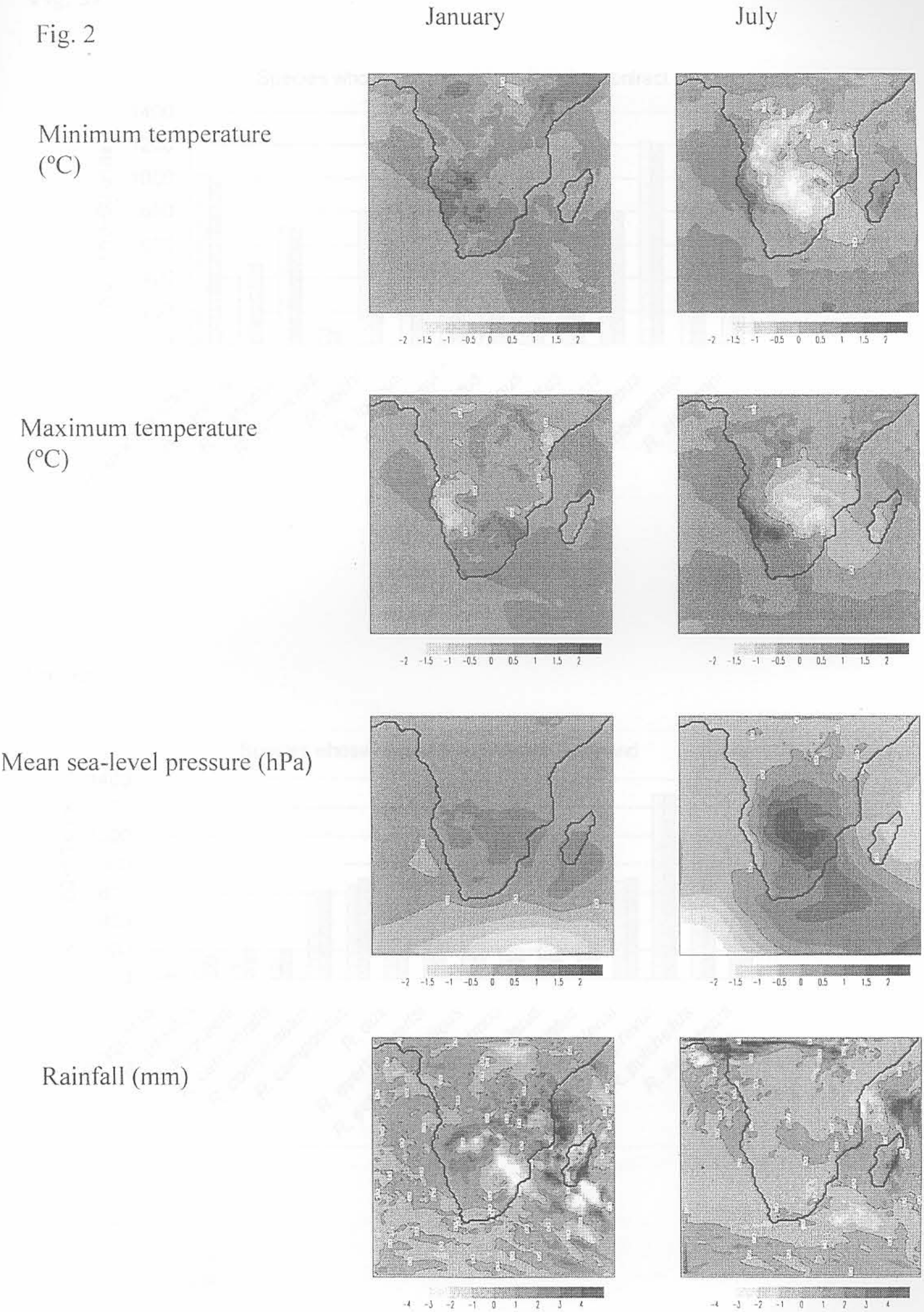

Nigeria
Cent Af Rep
Sudan
Ethiopia
Somalia
Cameroon
Congo
Uganda
Kenya
Gabon
DRC
Rwanda
Burundi
N
Tanzania
Malawi
Angola
Zambia
Mozambique
Zimbabwe
Namibia
Botswana
Swaziland
Lesotho
South Africa
National Boundaries
900
0
900
1800
Kilometers

Fig. 2


January
July
Minimum temperature (°C)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Maximum temperature (°C)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Mean sea-level pressure (hPa)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Rainfall (mm)
-4 -3 -2 -1 0 1 2 3 4

3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

Fig. 3a

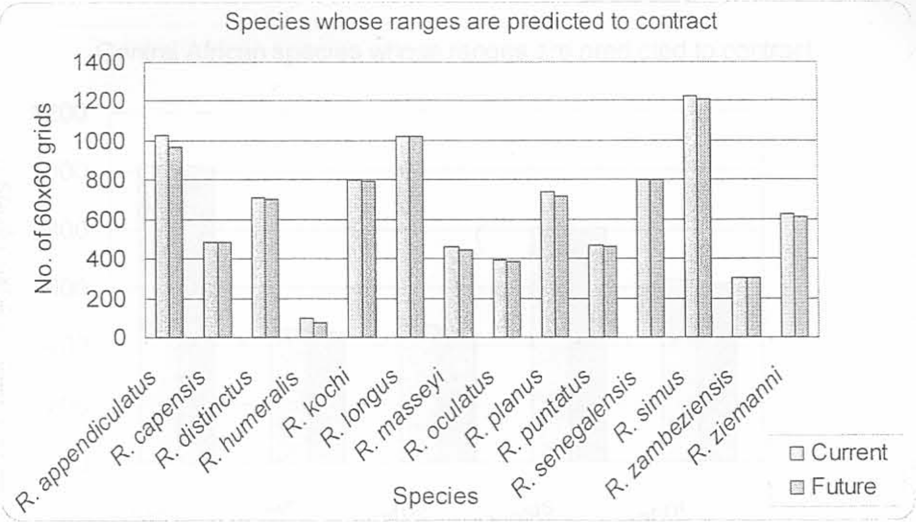


Fig.3b

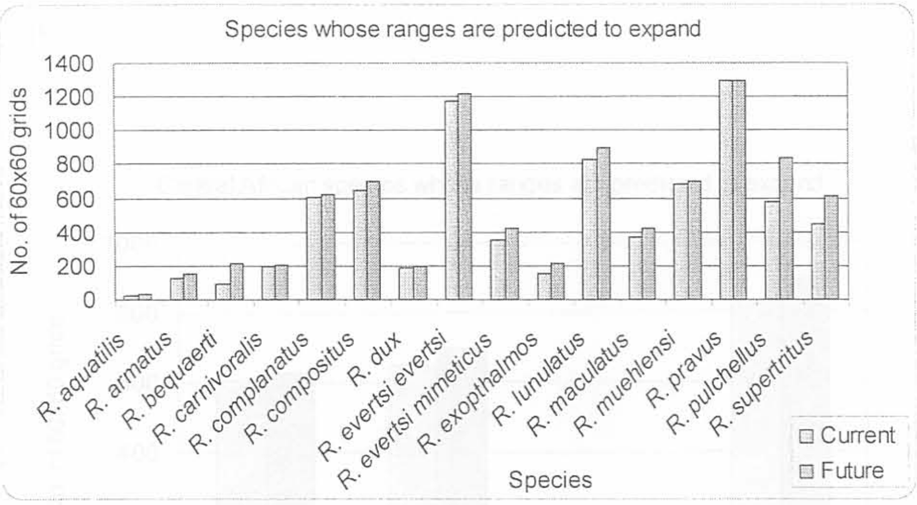


Fig. 4a

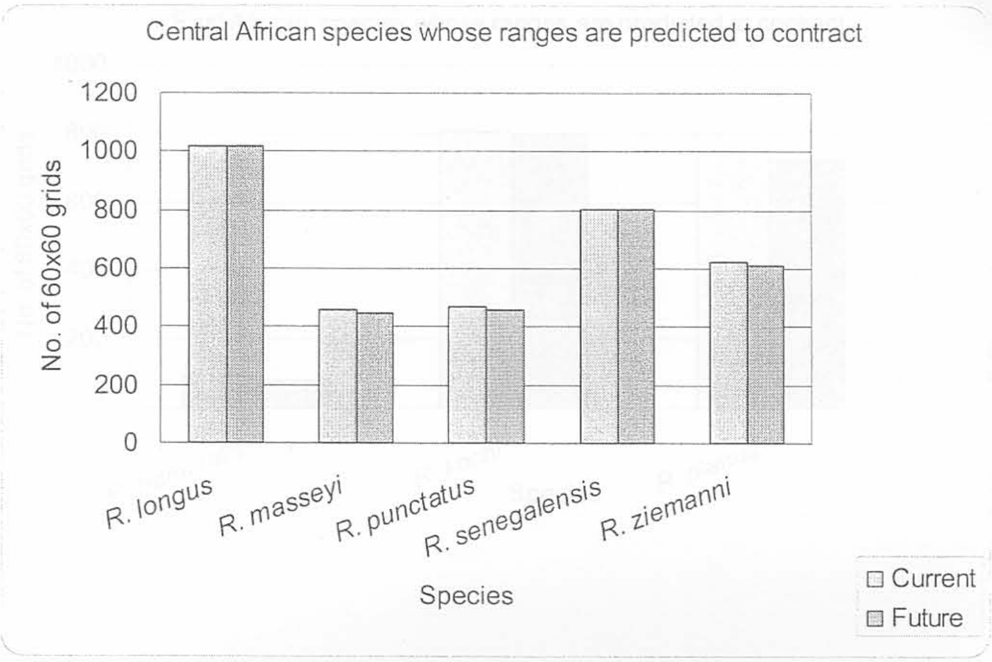

Central African species whose ranges are predicted to contract
1200
1000
800
600
400
200
0
No. of 60x60 grids
R. longus
R. masseyi
R. punctatus
R. senegalensis
R. ziemanni
Species
Current
Future

Fig. 4b

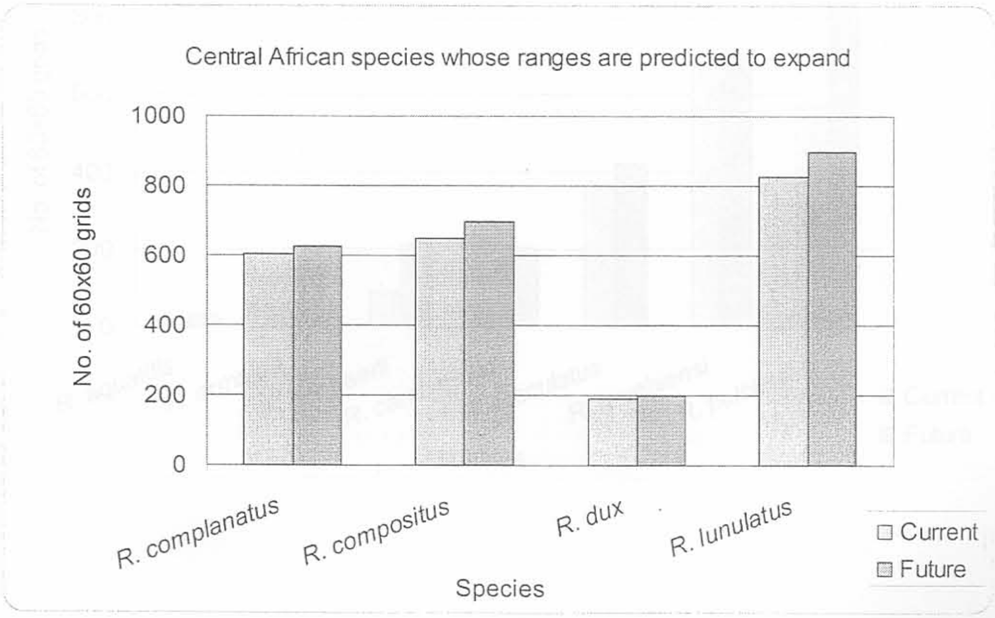

Central African species whose ranges are predicted to expand
1000
800
600
400
200
0
No. of 60x60 grids
R. complanatus
R. compositus
R. dux
R. lunulatus
Species
Current
Future

Fig. 5a

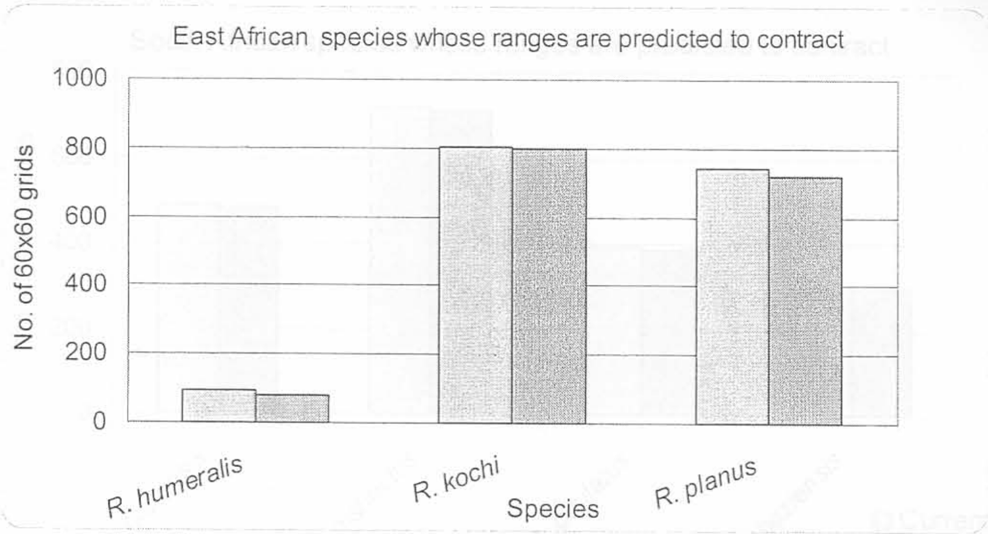

East African species whose ranges are predicted to contract
No. of 60x60 grids
1000
800
600
400
200
0
R. humeralis
R. kochi
R. planus
Species

Fig. 5b

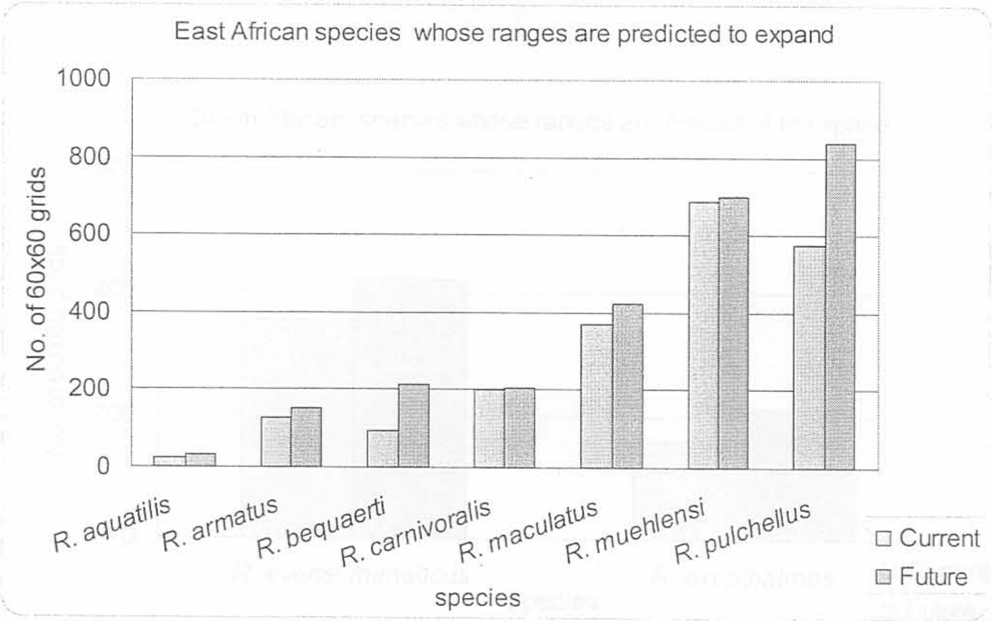

East African species whose ranges are predicted to expand
No. of 60x60 grids
1000
800
600
400
200
0
R. aquatilis
R. armatus
R. bequaerti
R. carnivoralis
R. maculatus
R. muehlensi
R. pulchellus
species
☐ Current
▨ Future

Fig. 6a

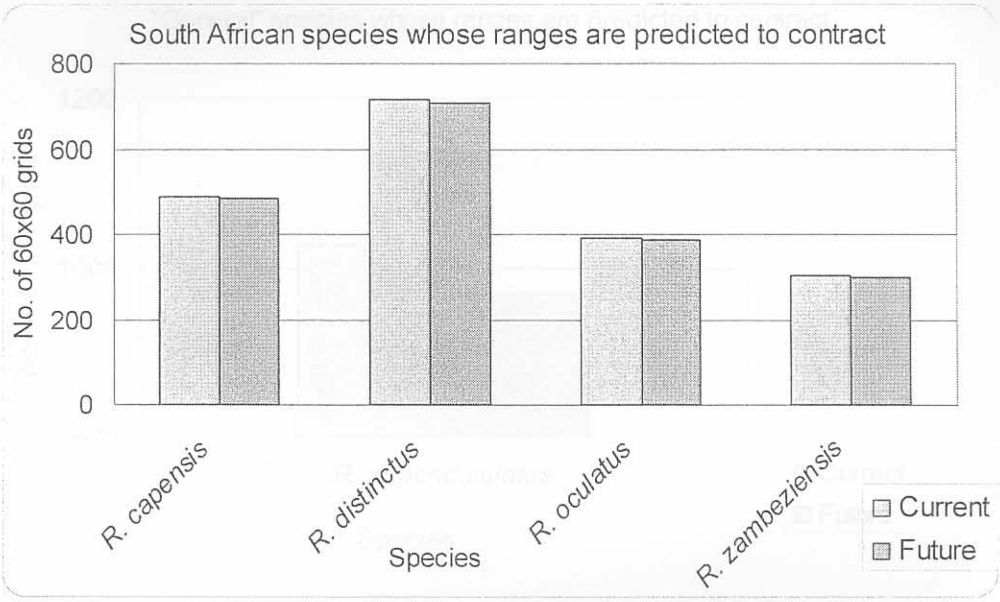
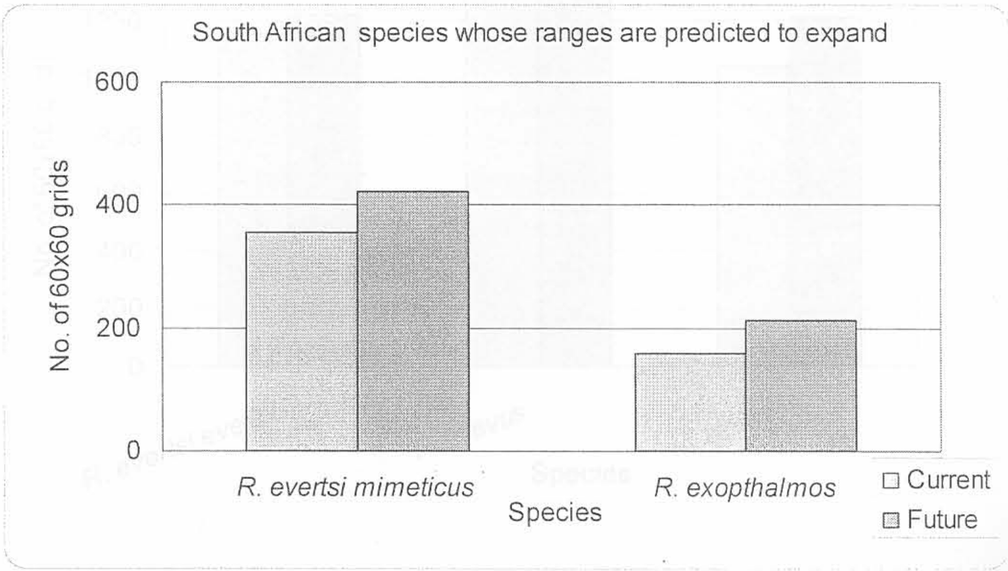

South African species whose ranges are predicted to contract
800
600
400
200
0
No. of 60x60 grids
R. capensis
R. distinctus
R. oculatus
R. zambeziensis
Species
Current
Future

Fig. 6b


South African species whose ranges are predicted to expand
600
400
200
0
No. of 60x60 grids
R. evertsi mimeticus
R. exopthalmos
Species
Current
Future

3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

Fig. 7a

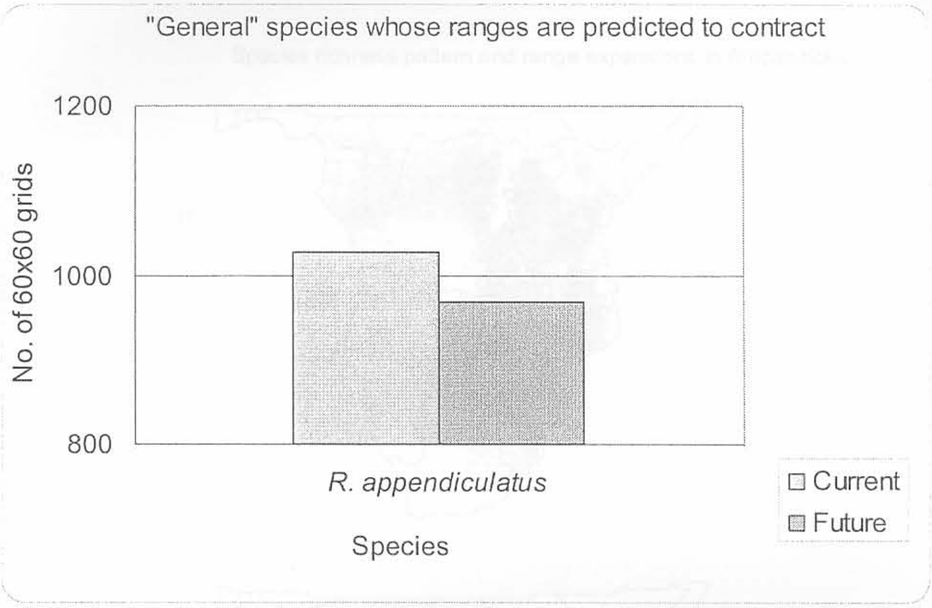


Fig. 7b

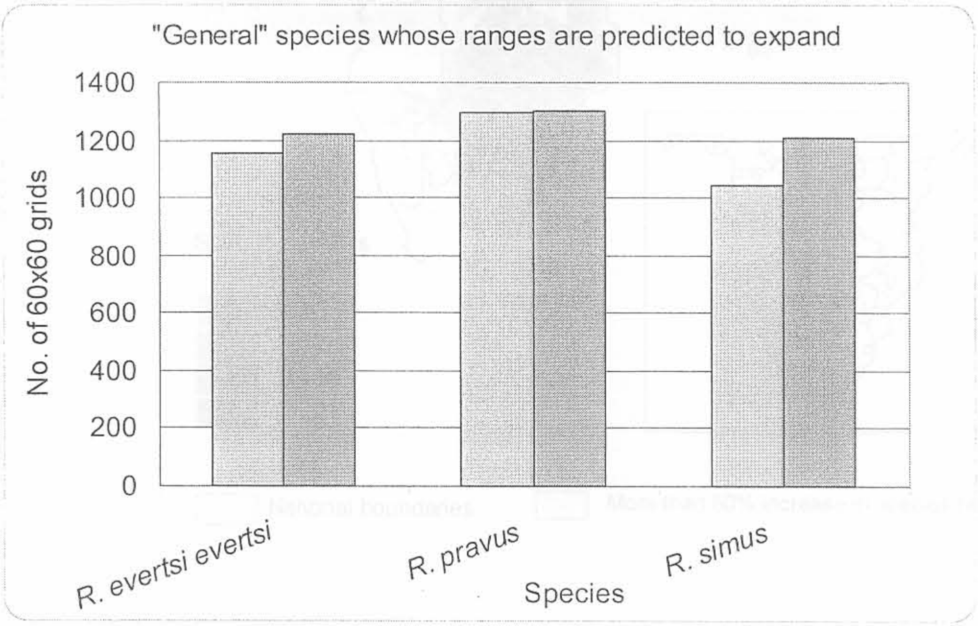


Fig. 8

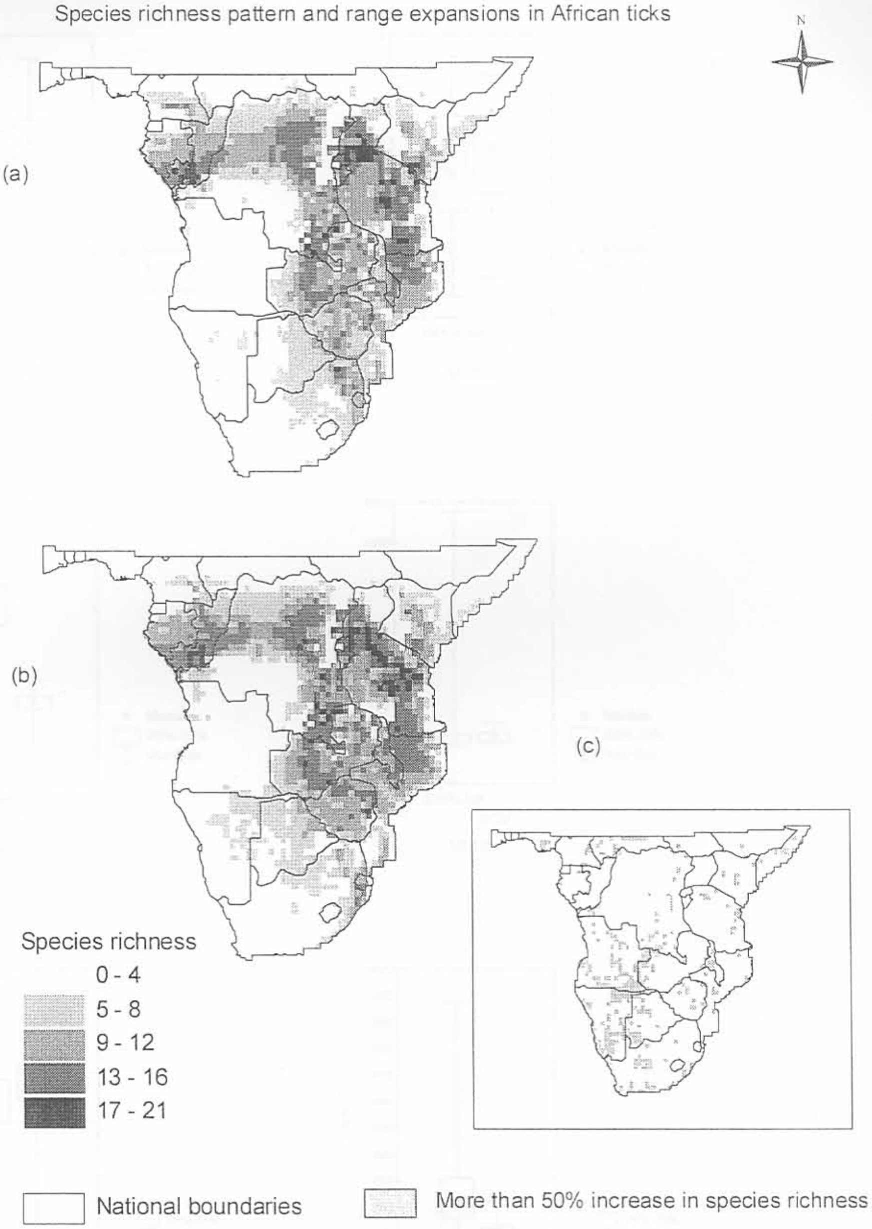

Species richness pattern and range expansions in African ticks
N
(a)
(b)
(c)
Species richness
0 - 4
5 - 8
9 - 12
13 - 16
17 - 21
National boundaries
More than 50% increase in species richness

Fig. 9

BoxPlots representing climate predicted by DARLAM and GCM

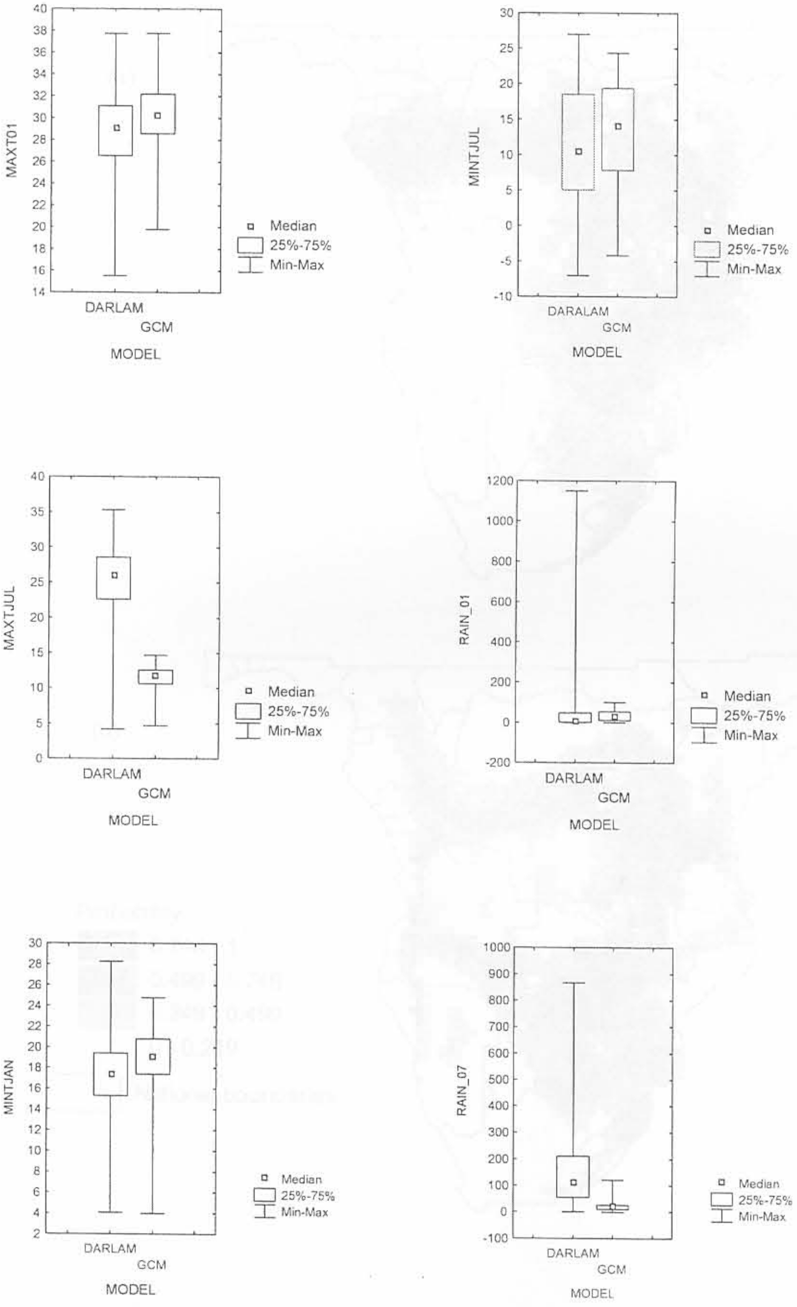


Fig. 10

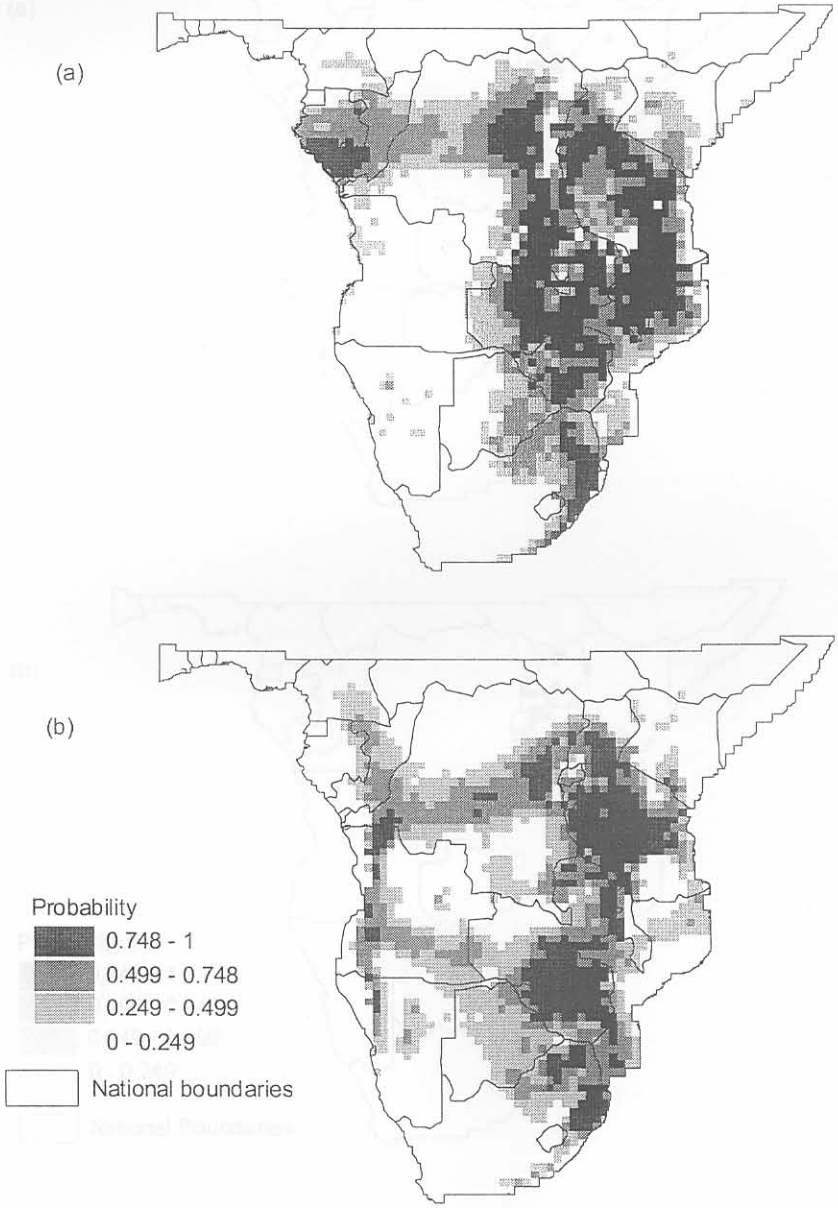

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 11

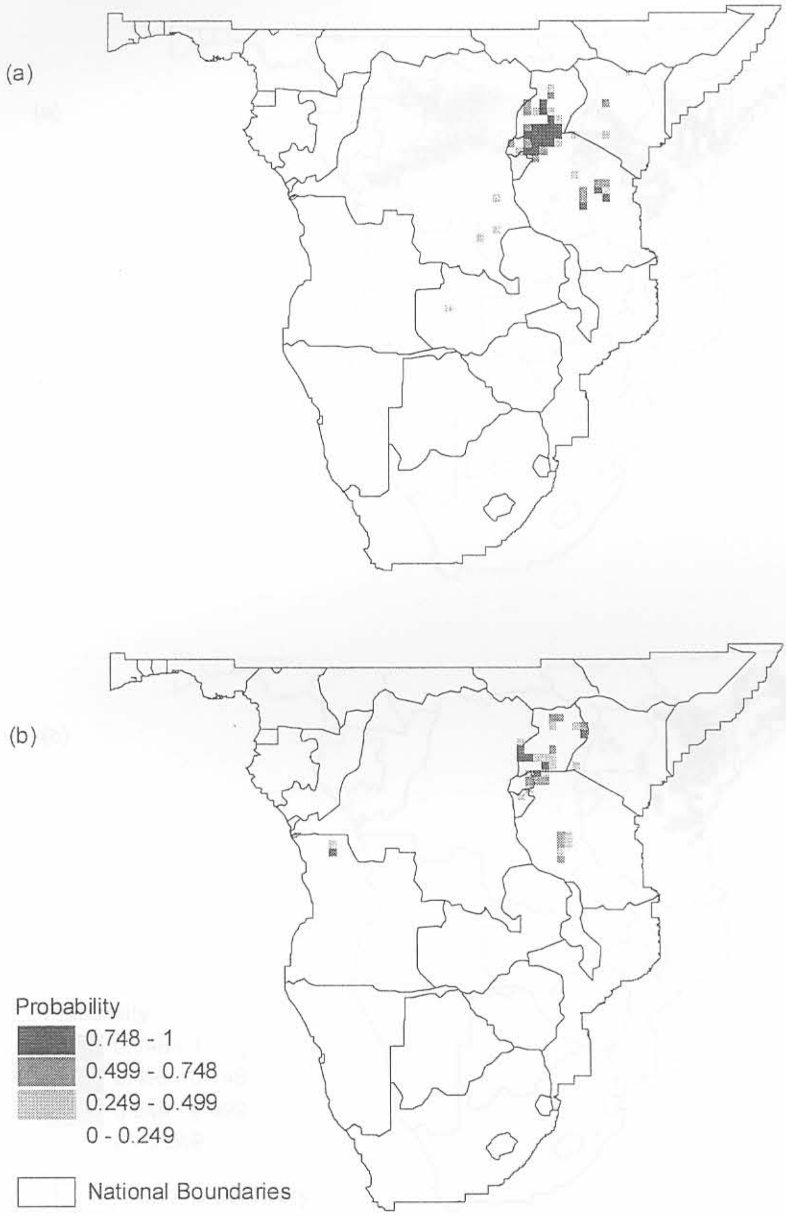

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National Boundaries

Fig. 12

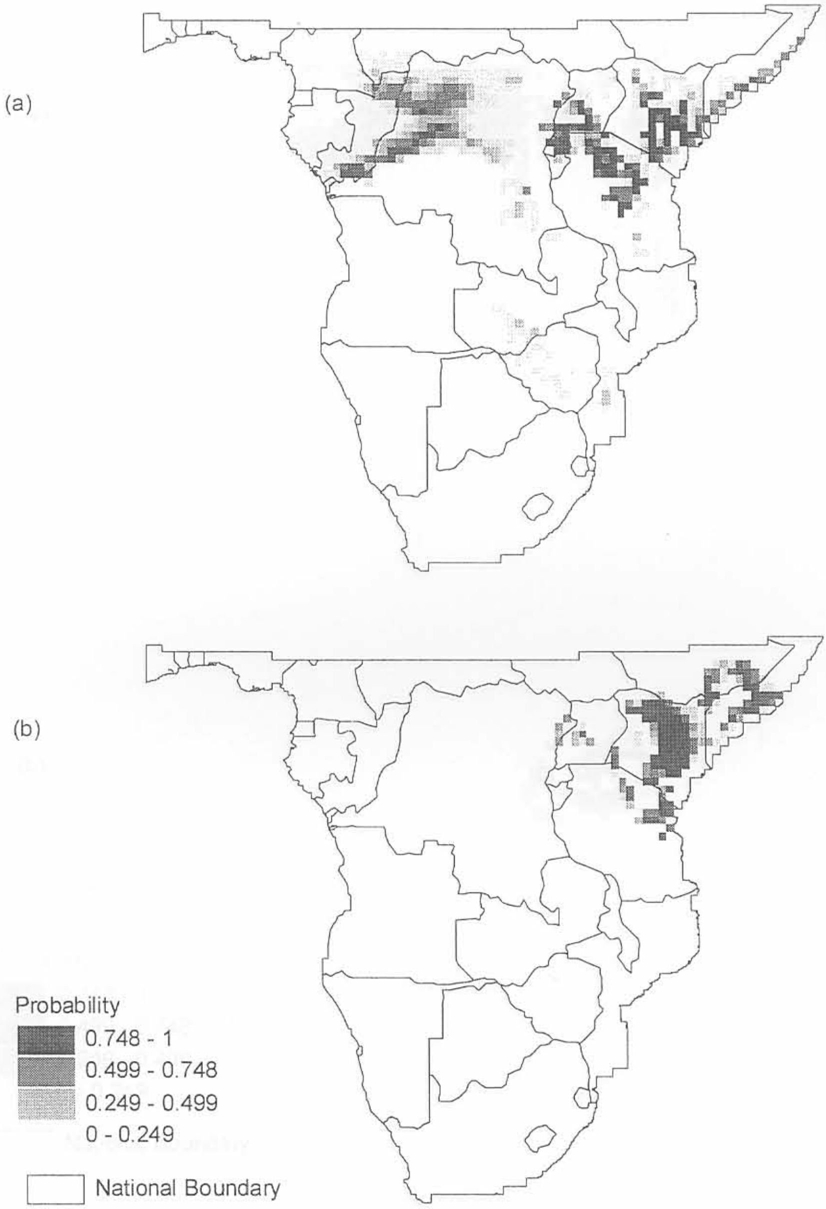

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National Boundary

Fig. 13

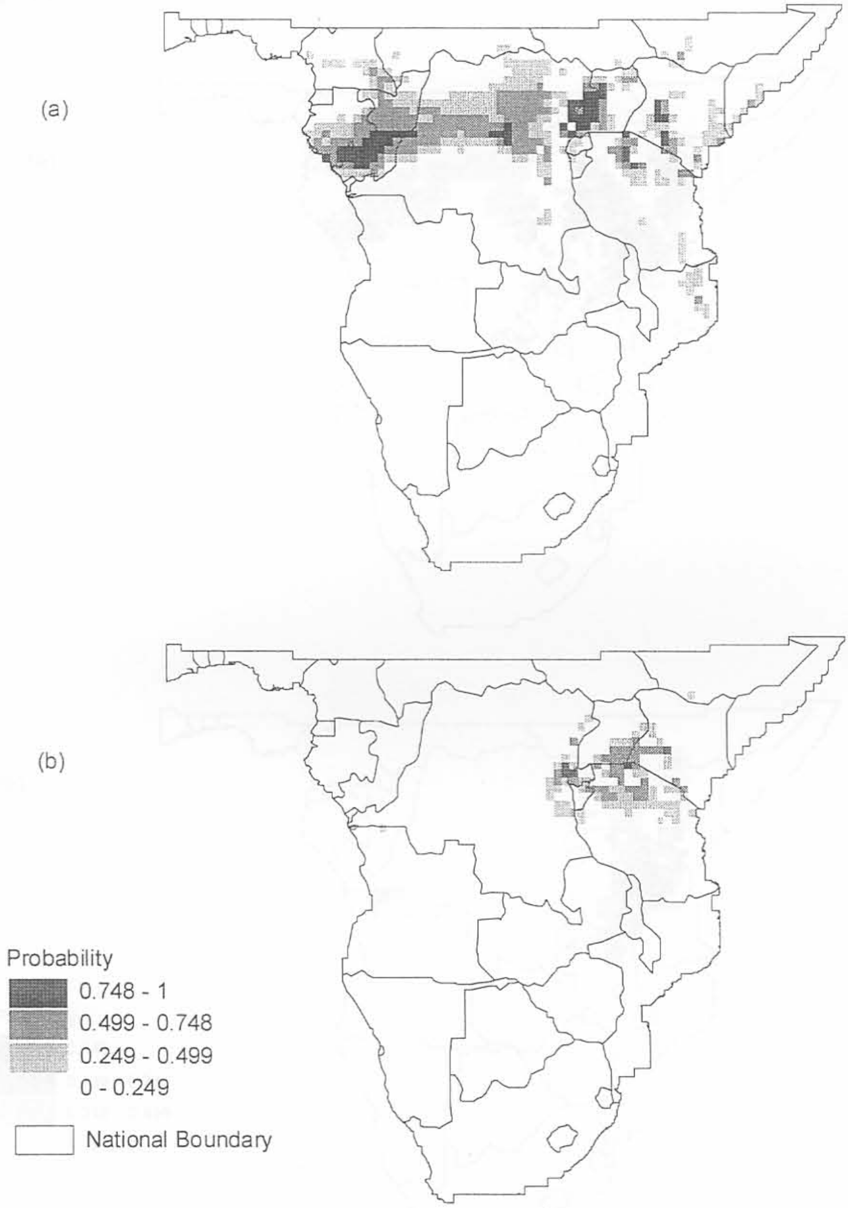

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National Boundary

Fig. 14

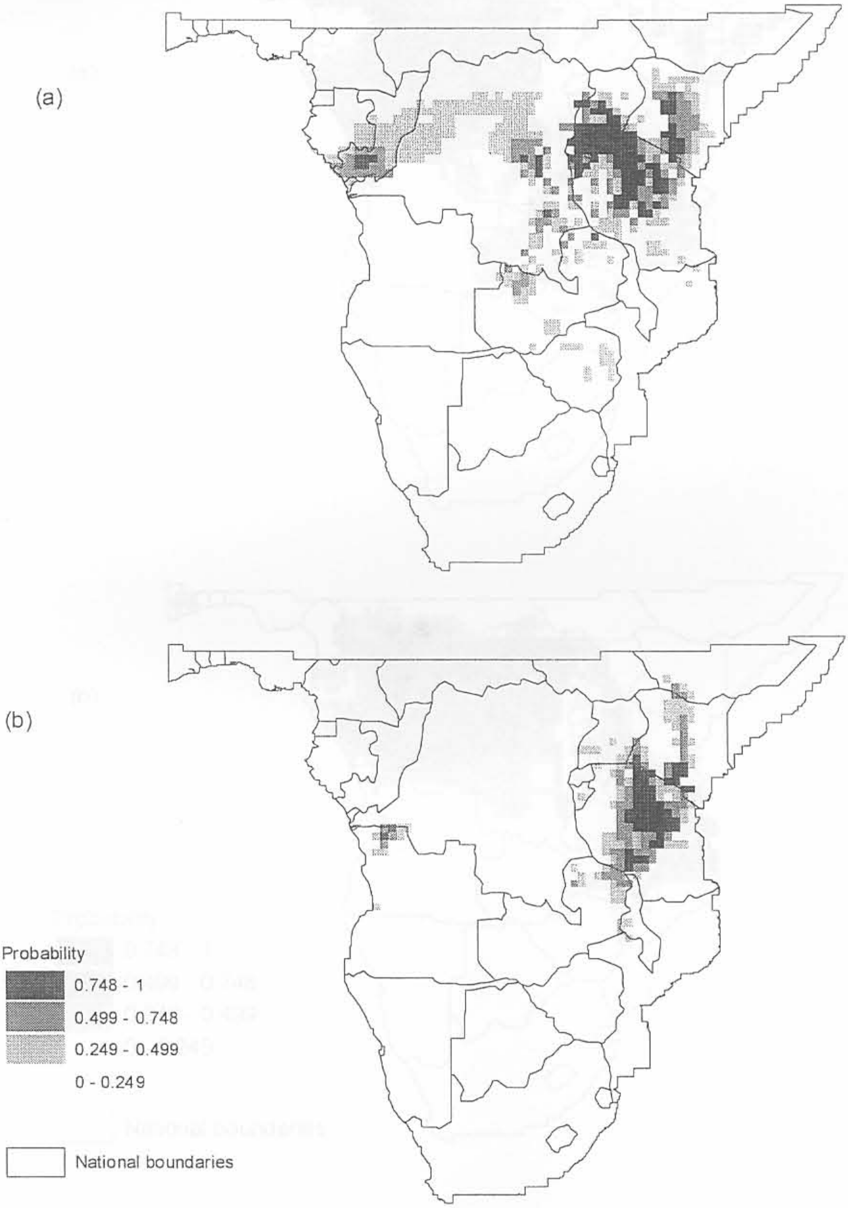

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 15

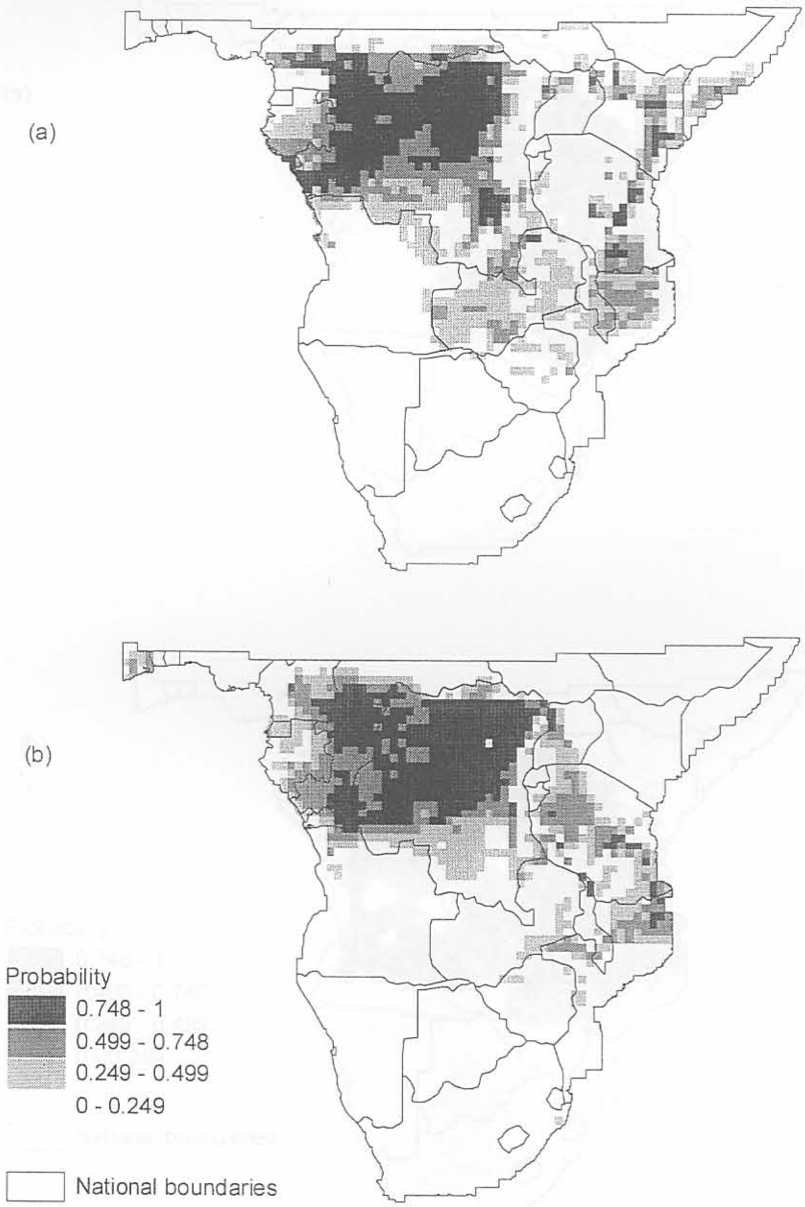

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 16

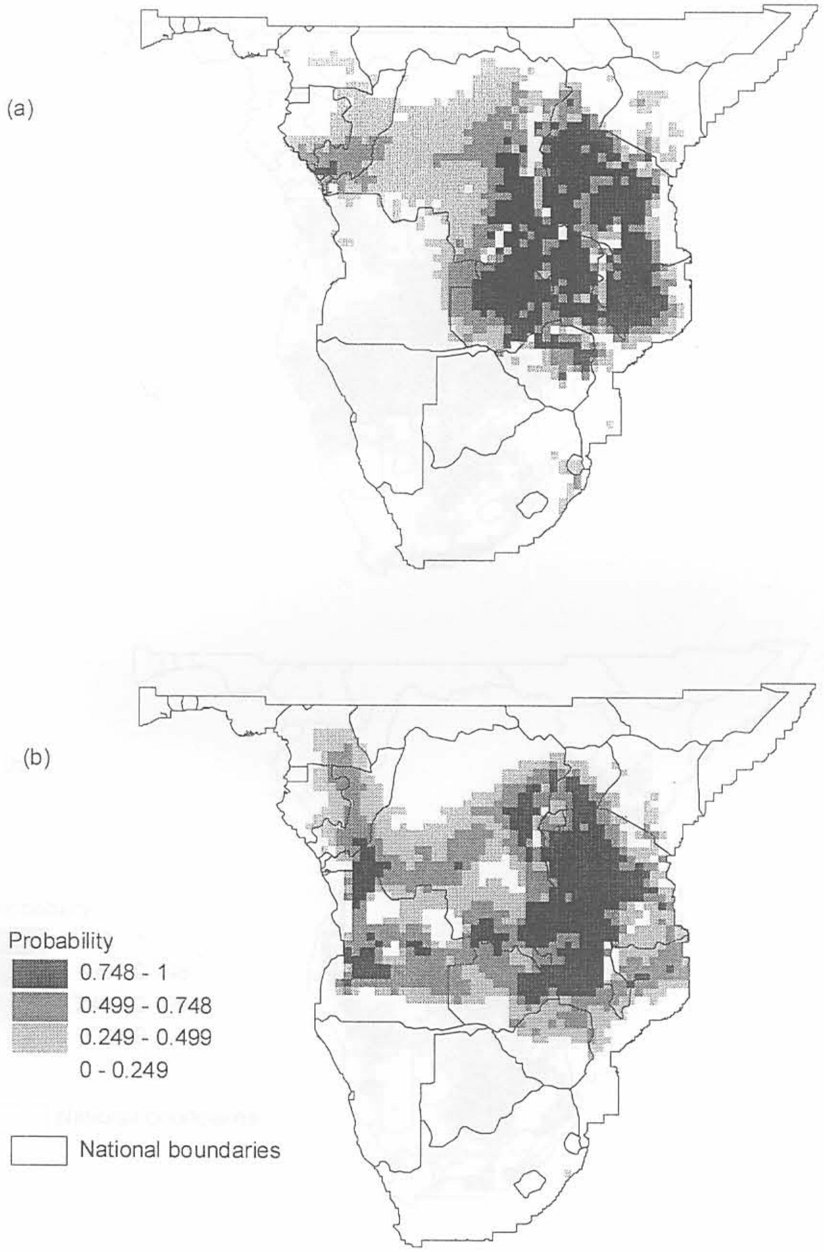

(a)
(b)
Probability
▩ 0.748 - 1
▨ 0.499 - 0.748
░ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 17

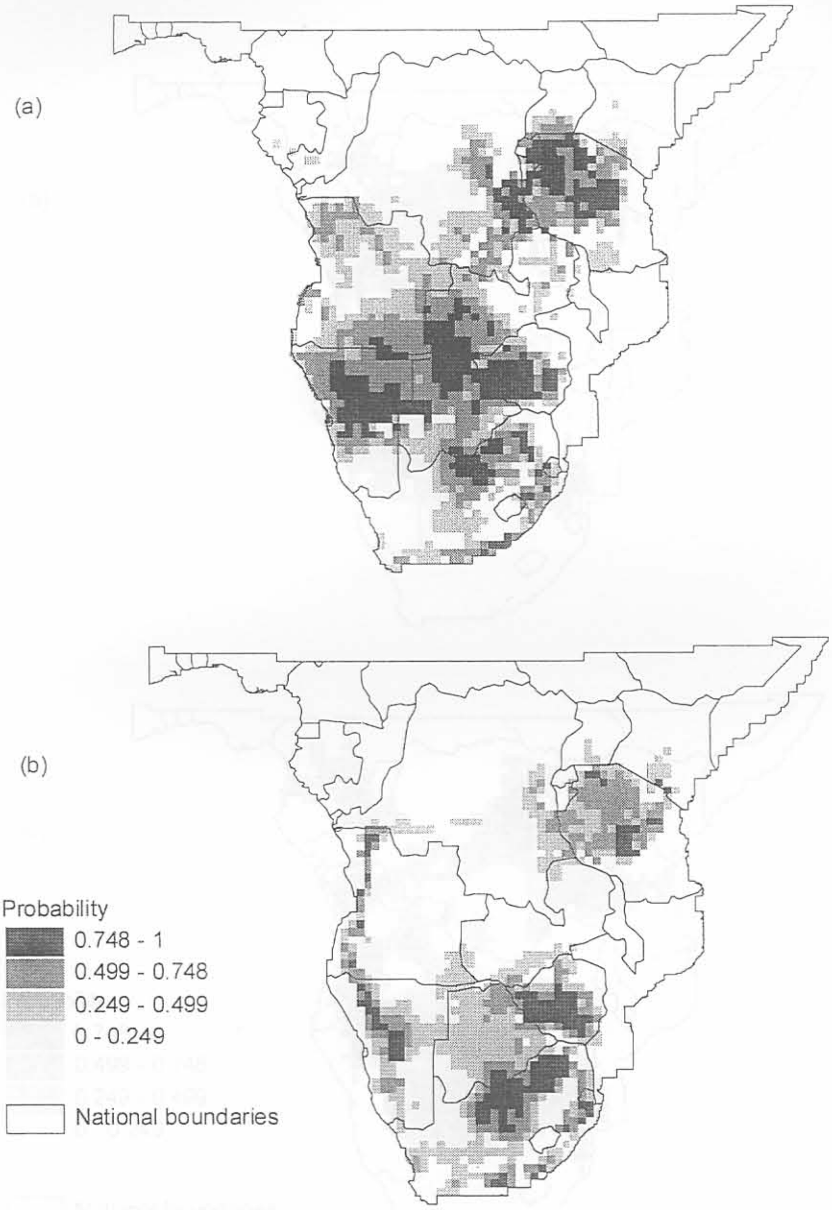

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 18

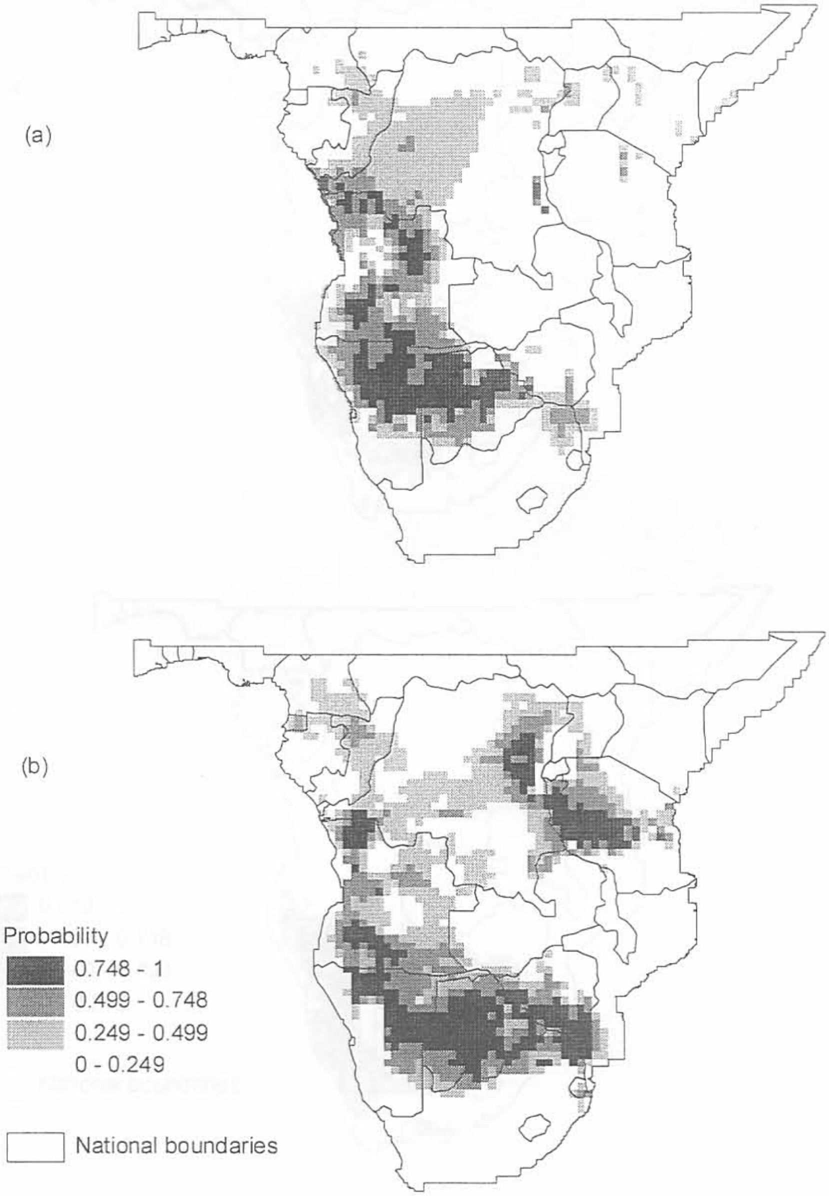

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 19

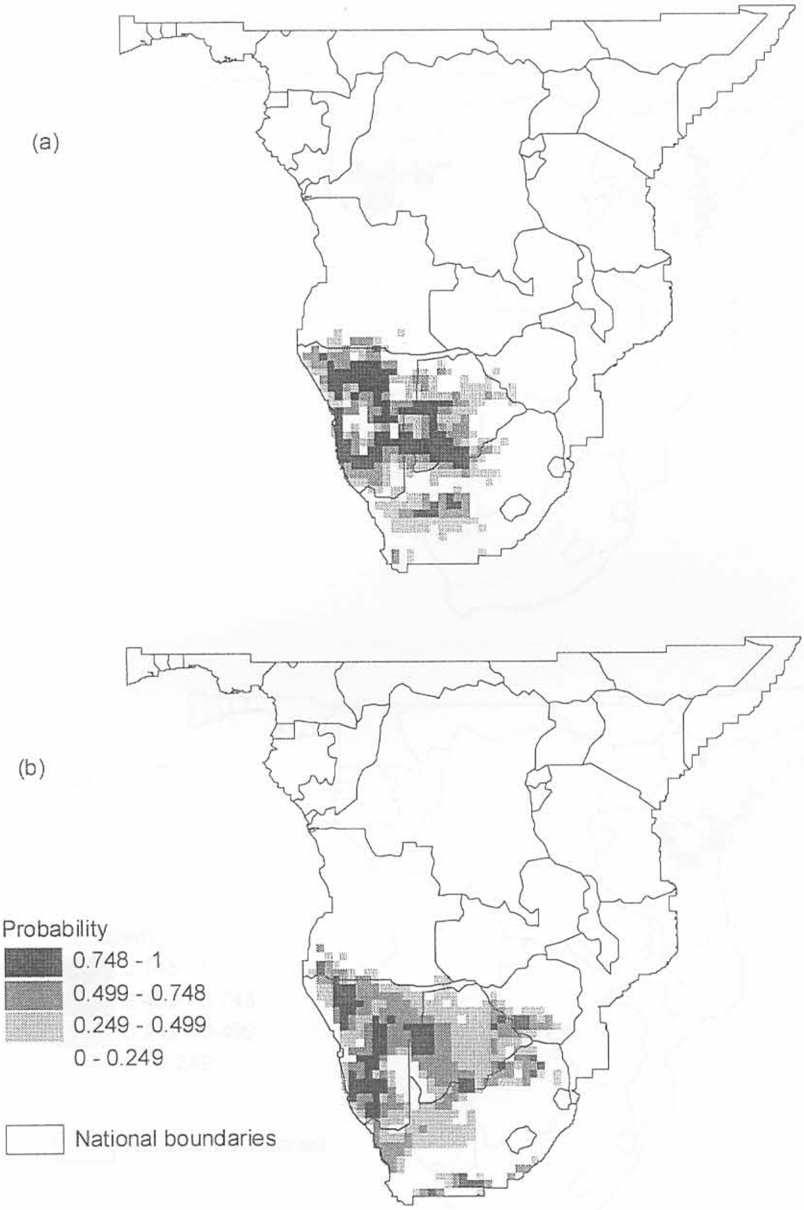

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 20

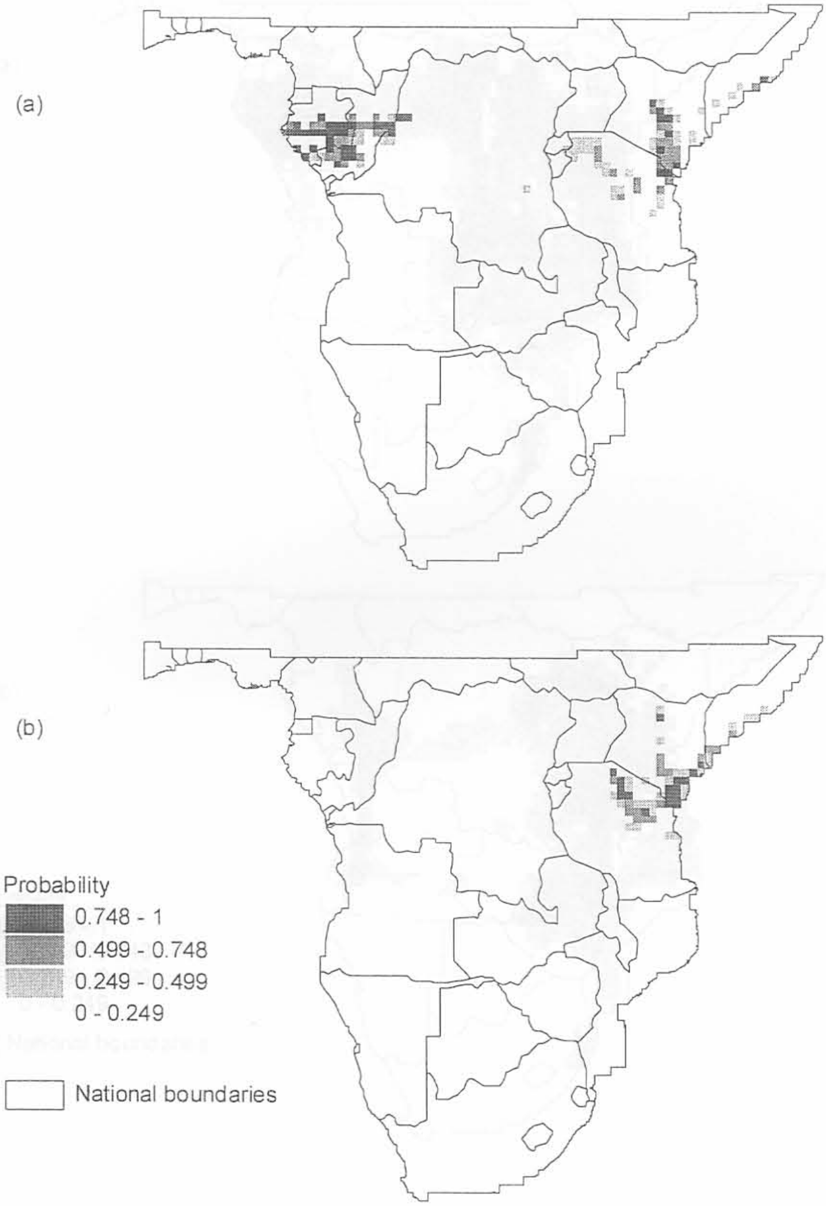

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 21

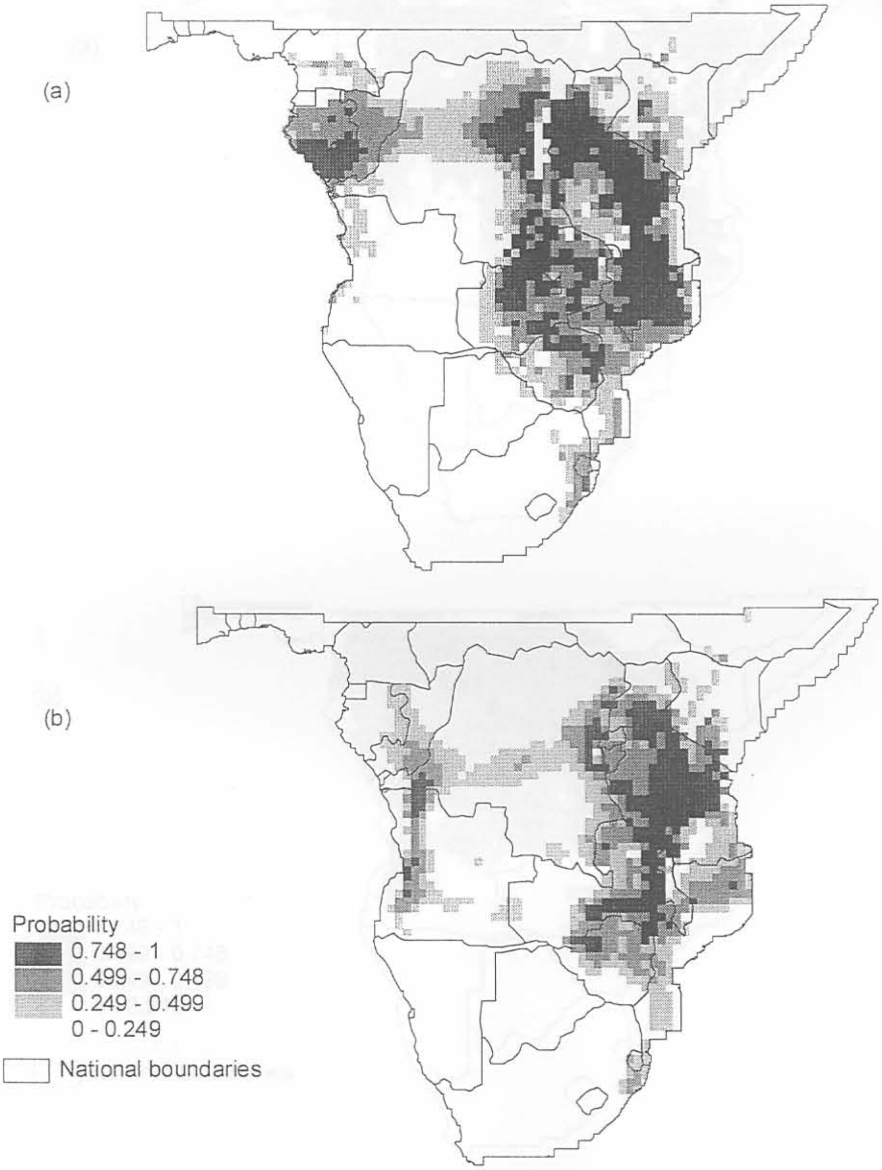

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 22

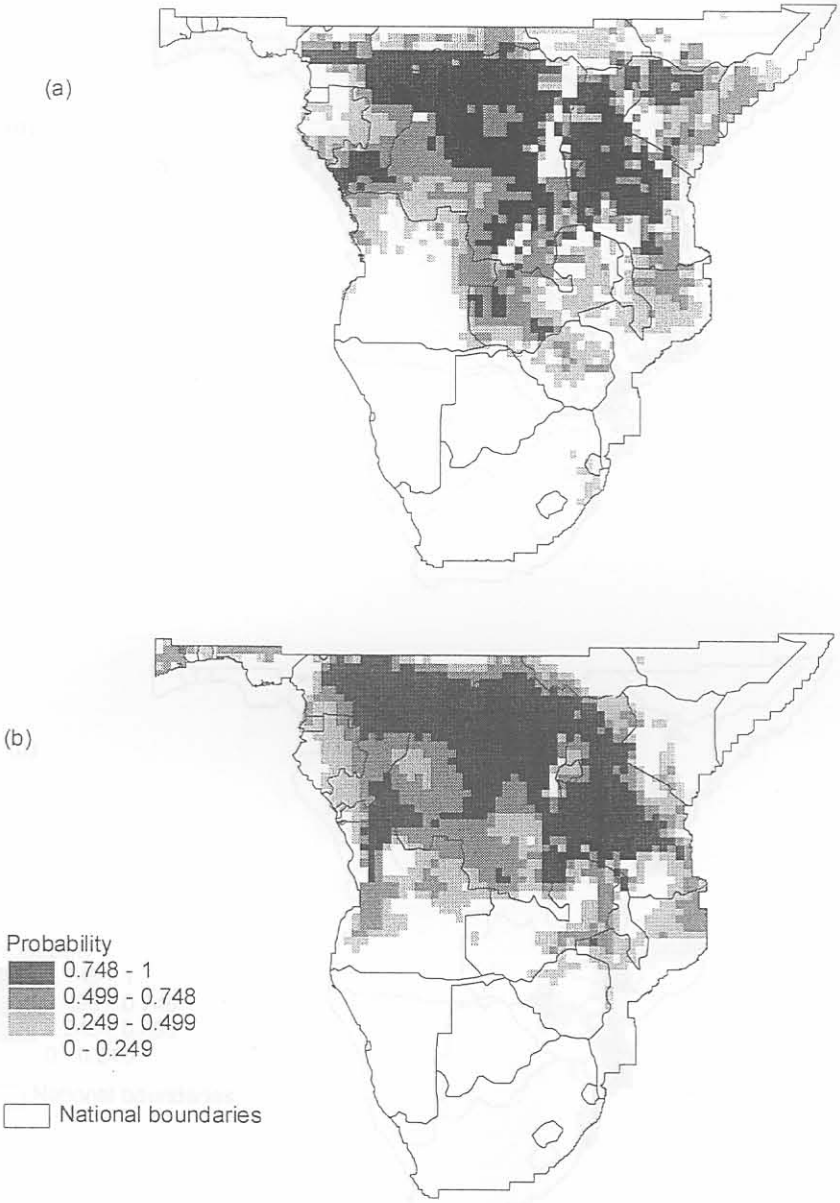

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 23

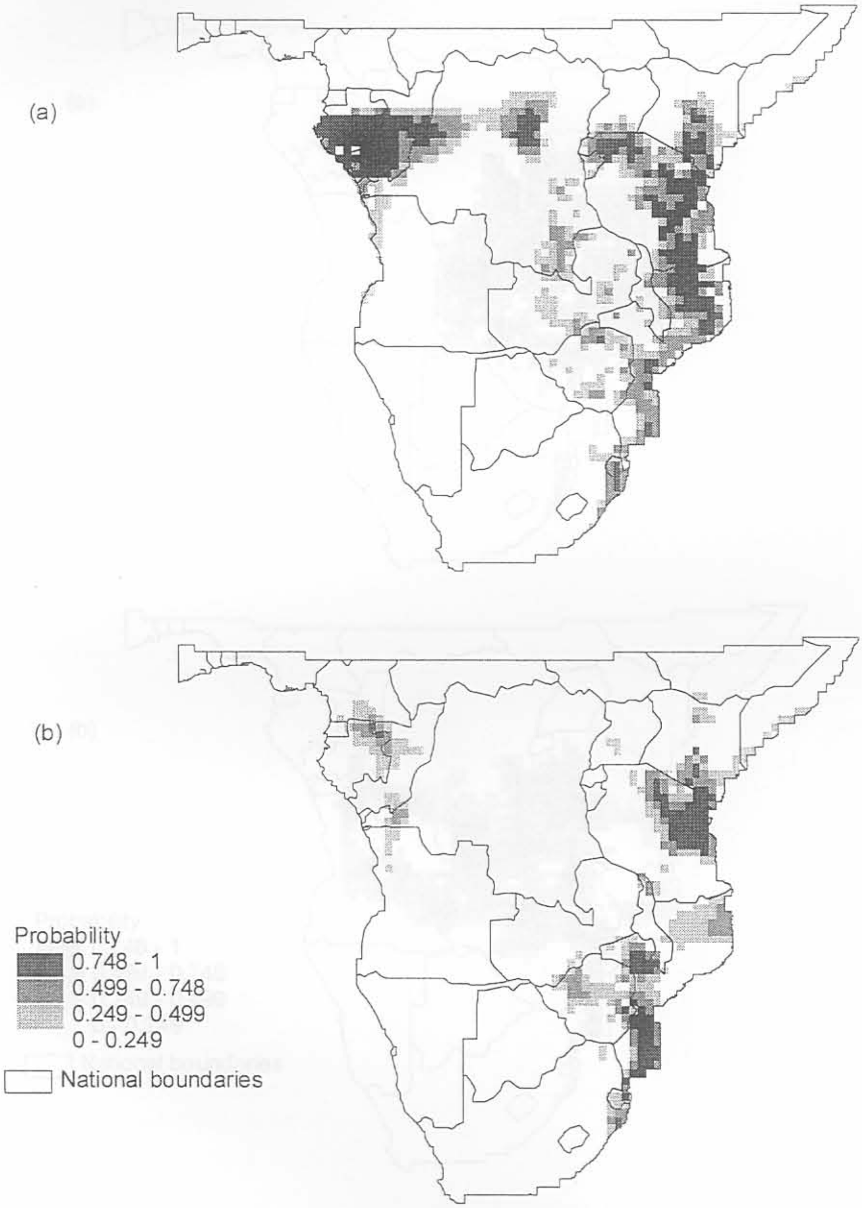

(a)
(b)
Probability
▩ 0.748 - 1
▨ 0.499 - 0.748
░ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 24

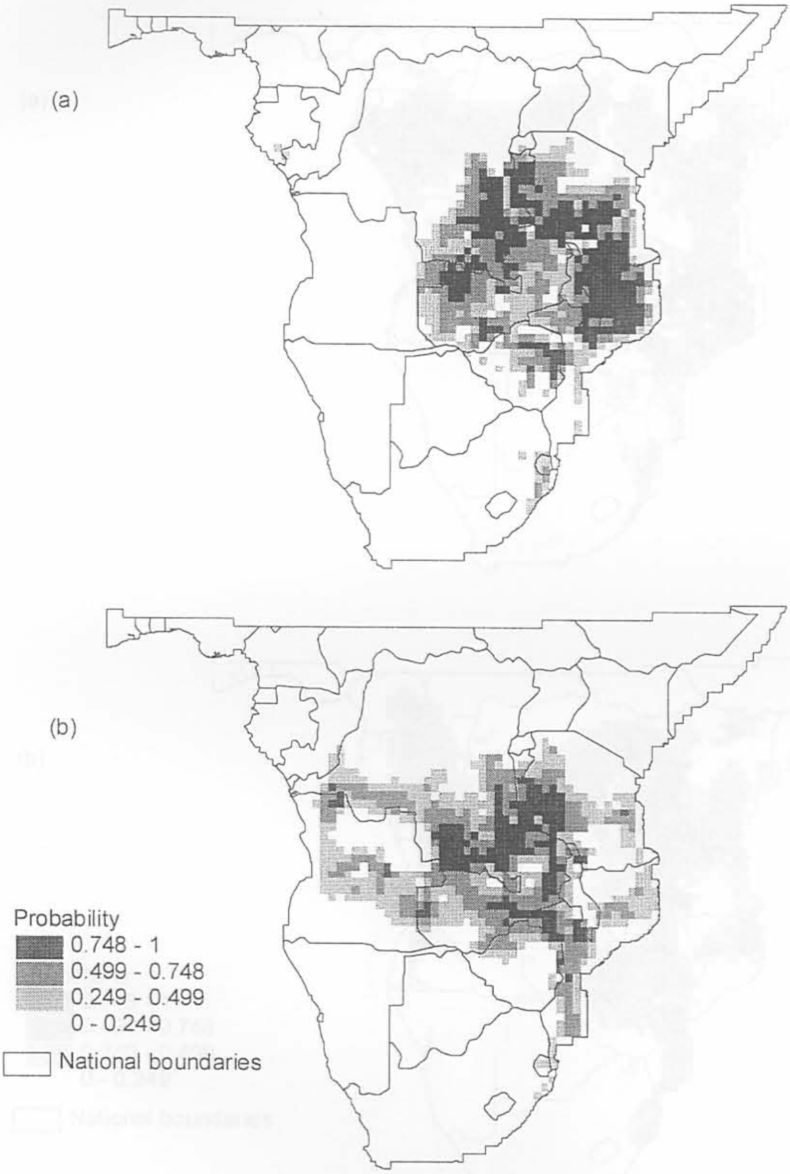

(a)
(b)
Probability
▩ 0.748 - 1
▩ 0.499 - 0.748
▩ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 25

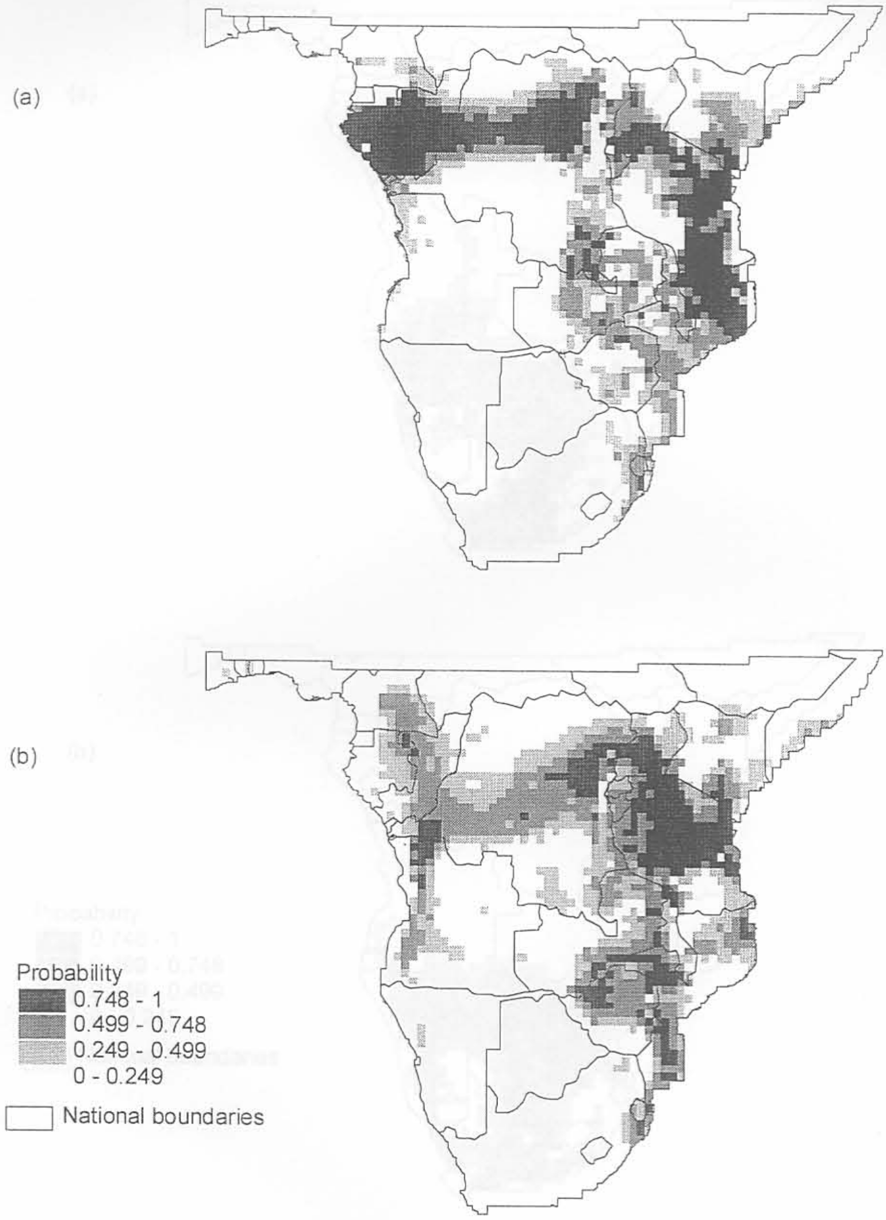

(a)
(b)
Probability
▨ 0.748 - 1
▨ 0.499 - 0.748
▨ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 26

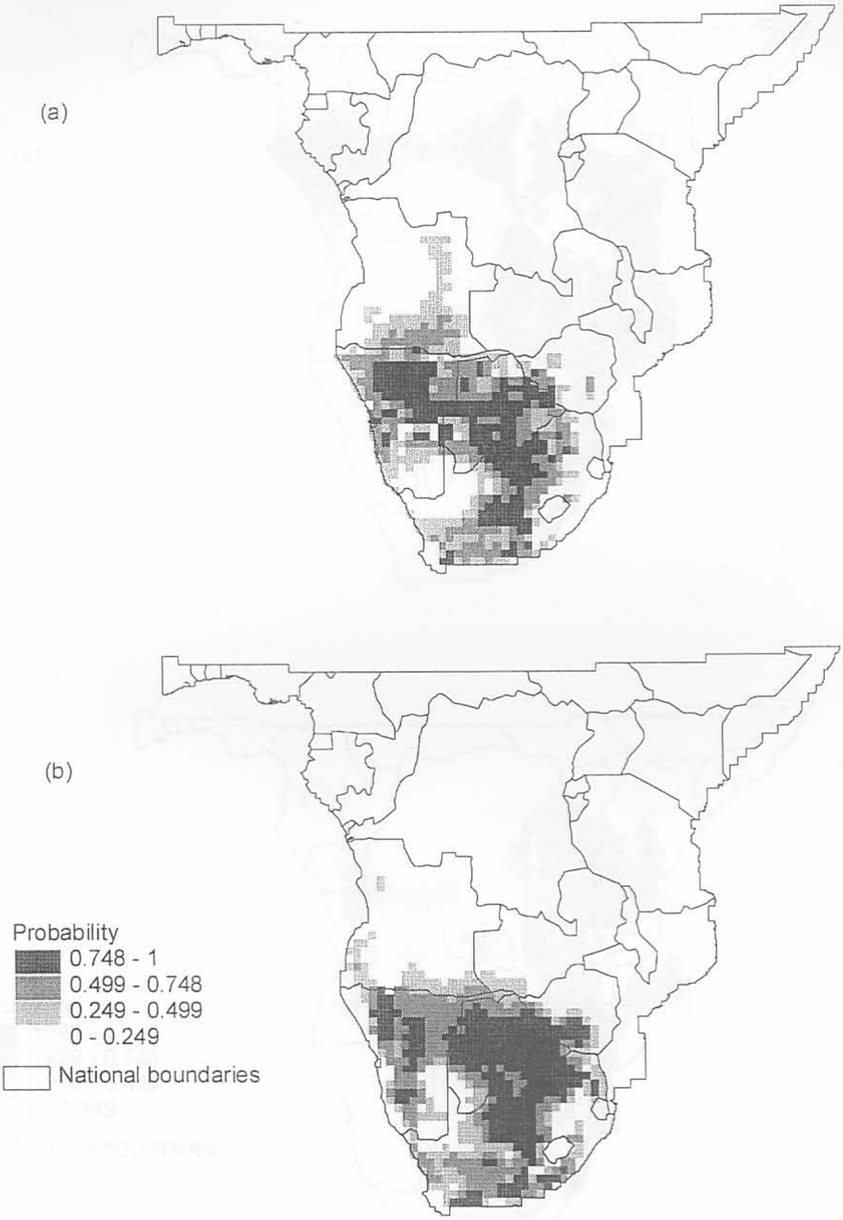

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 27

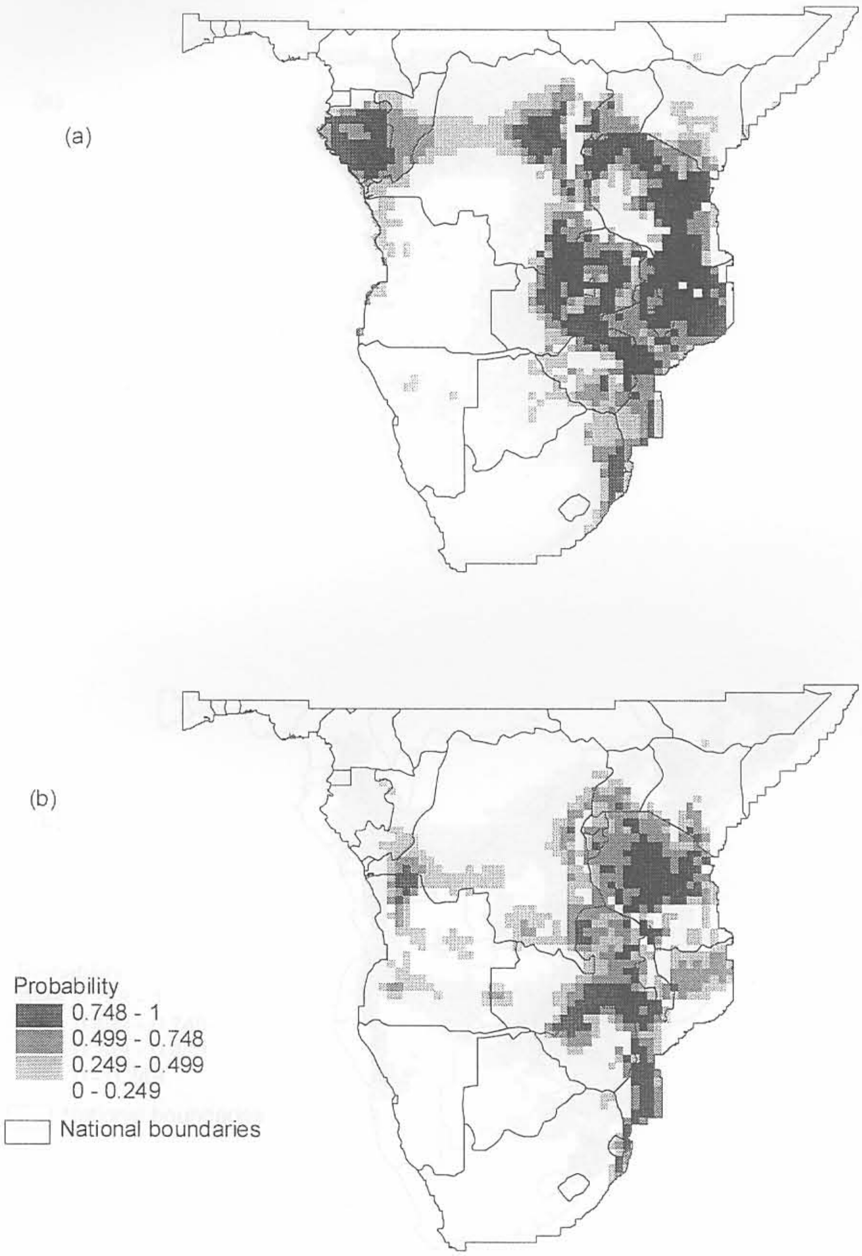

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 28

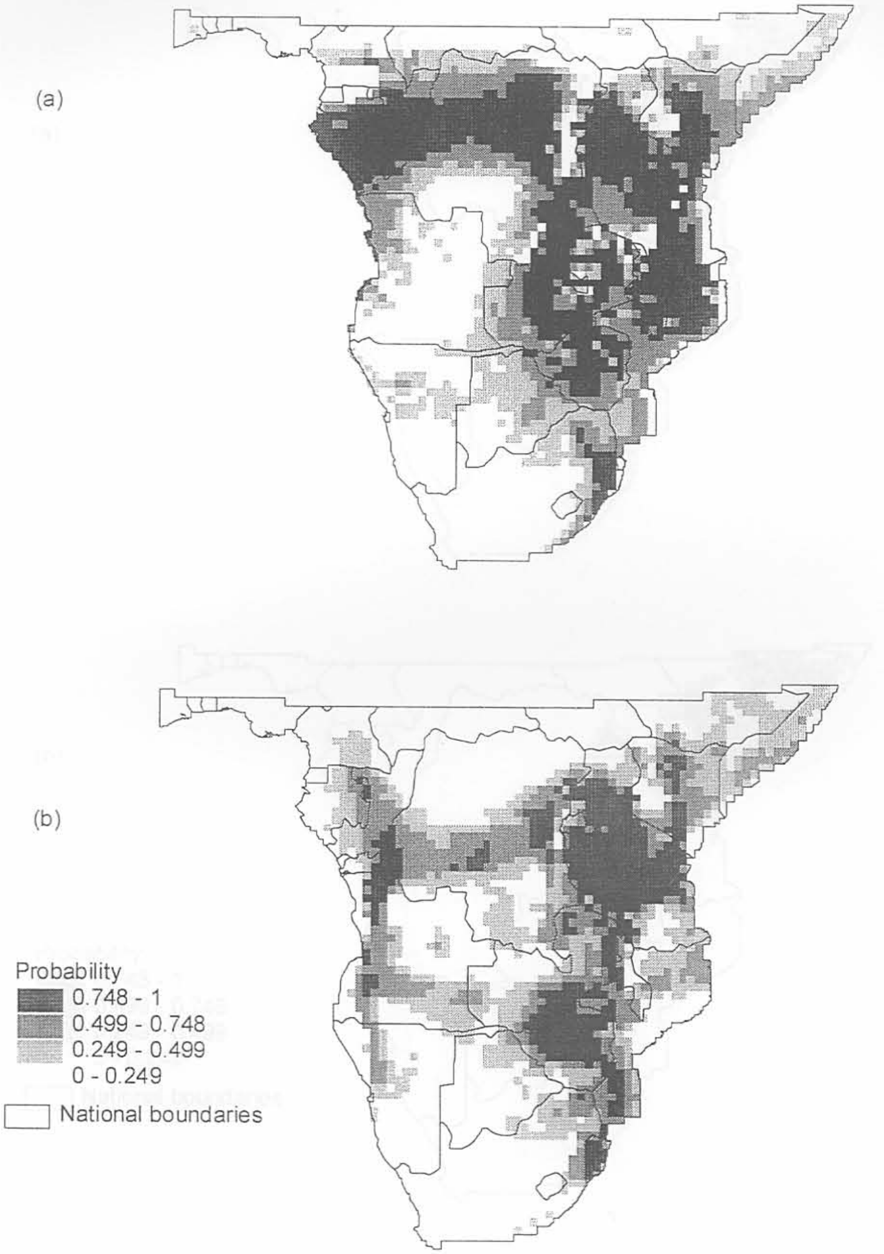
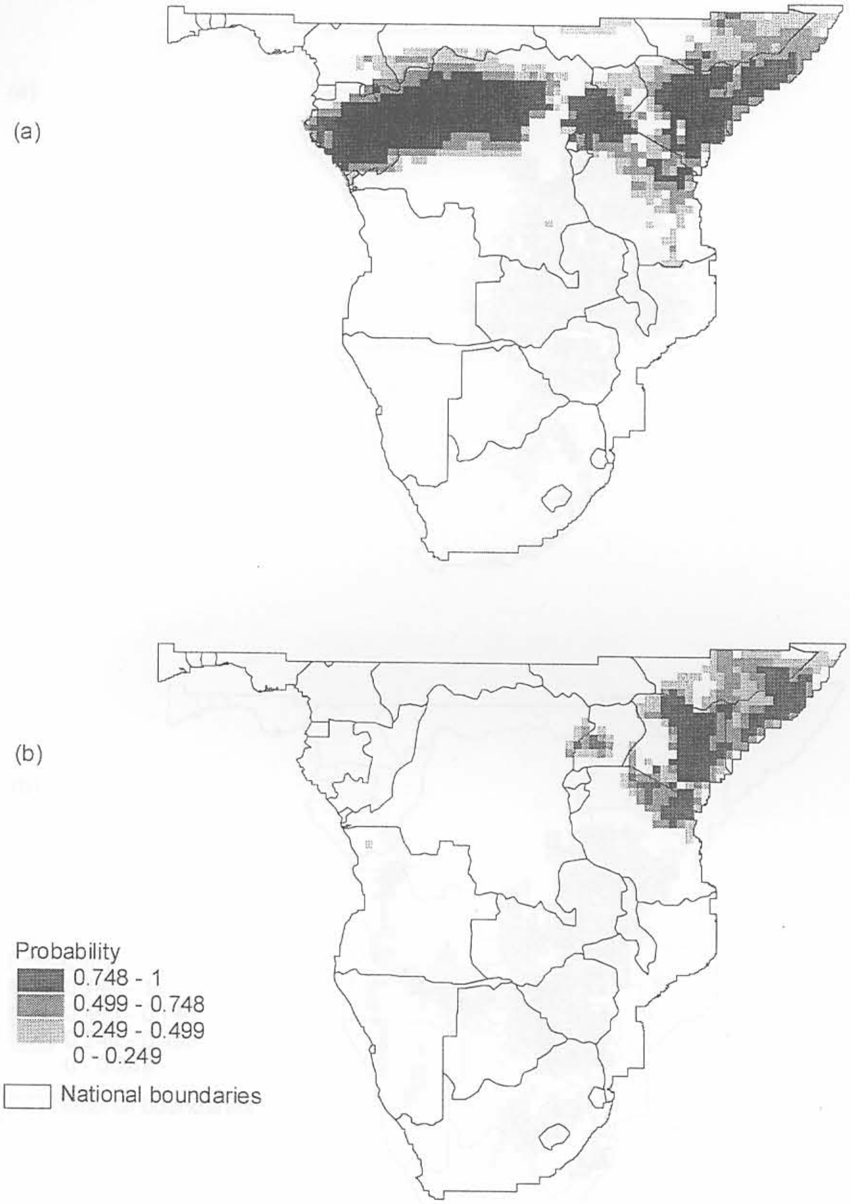

(a)
(b)
Probability
▩ 0.748 - 1
▨ 0.499 - 0.748
░ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 29



(a)
(b)
Probability
▩ 0.748 - 1
▨ 0.499 - 0.748
░ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 30

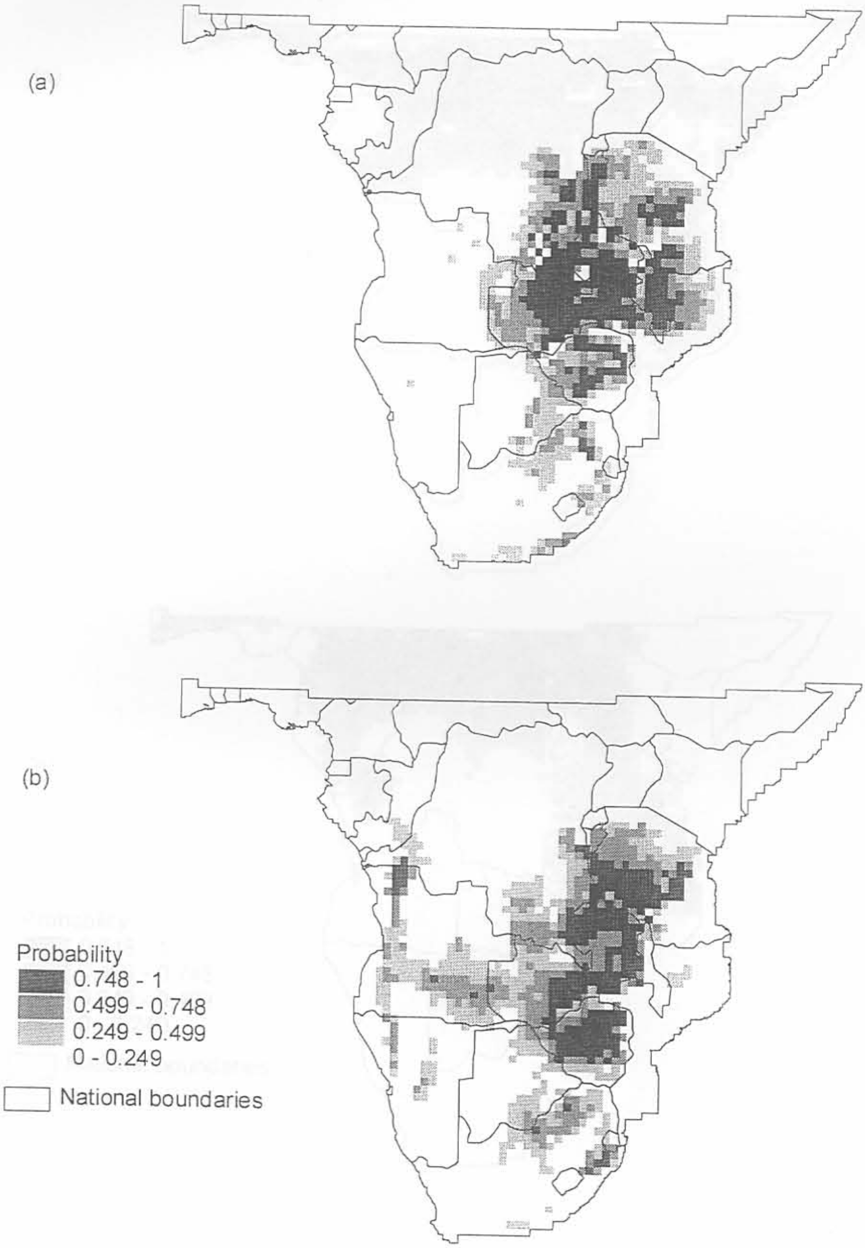

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 31

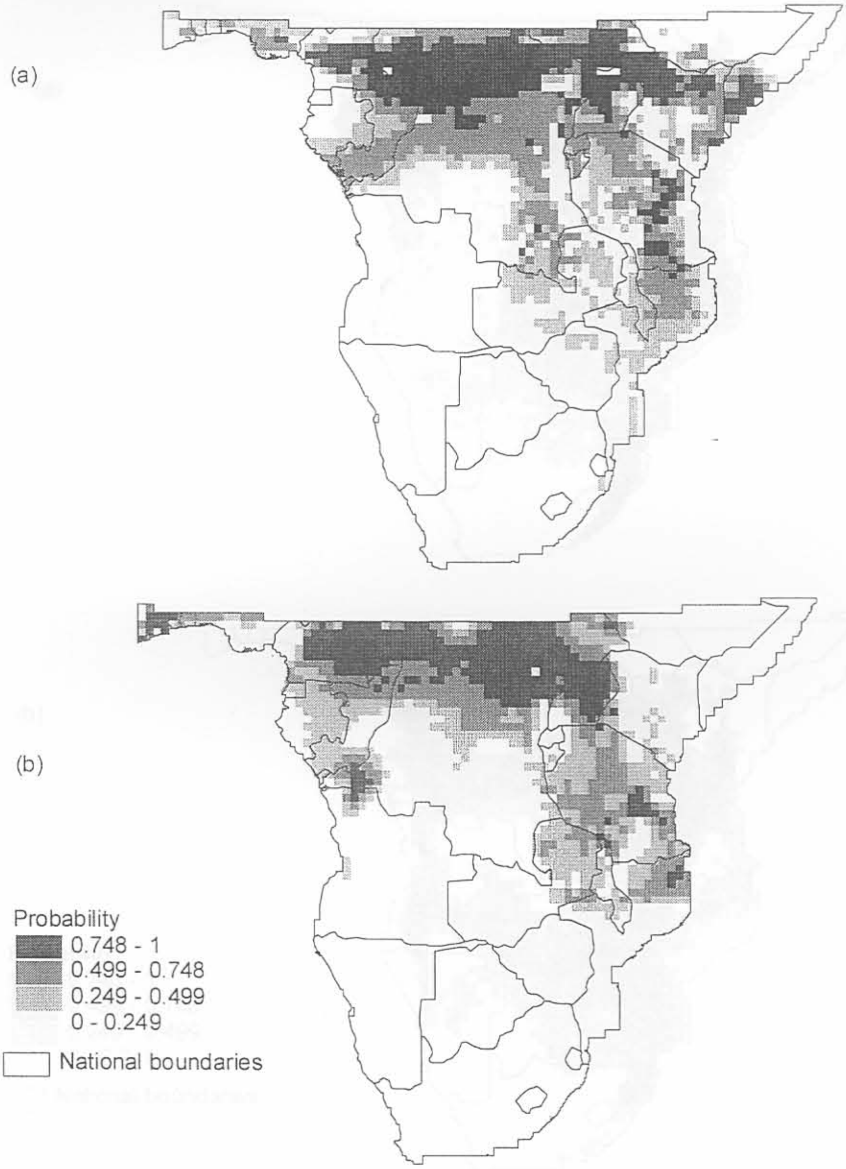

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 32

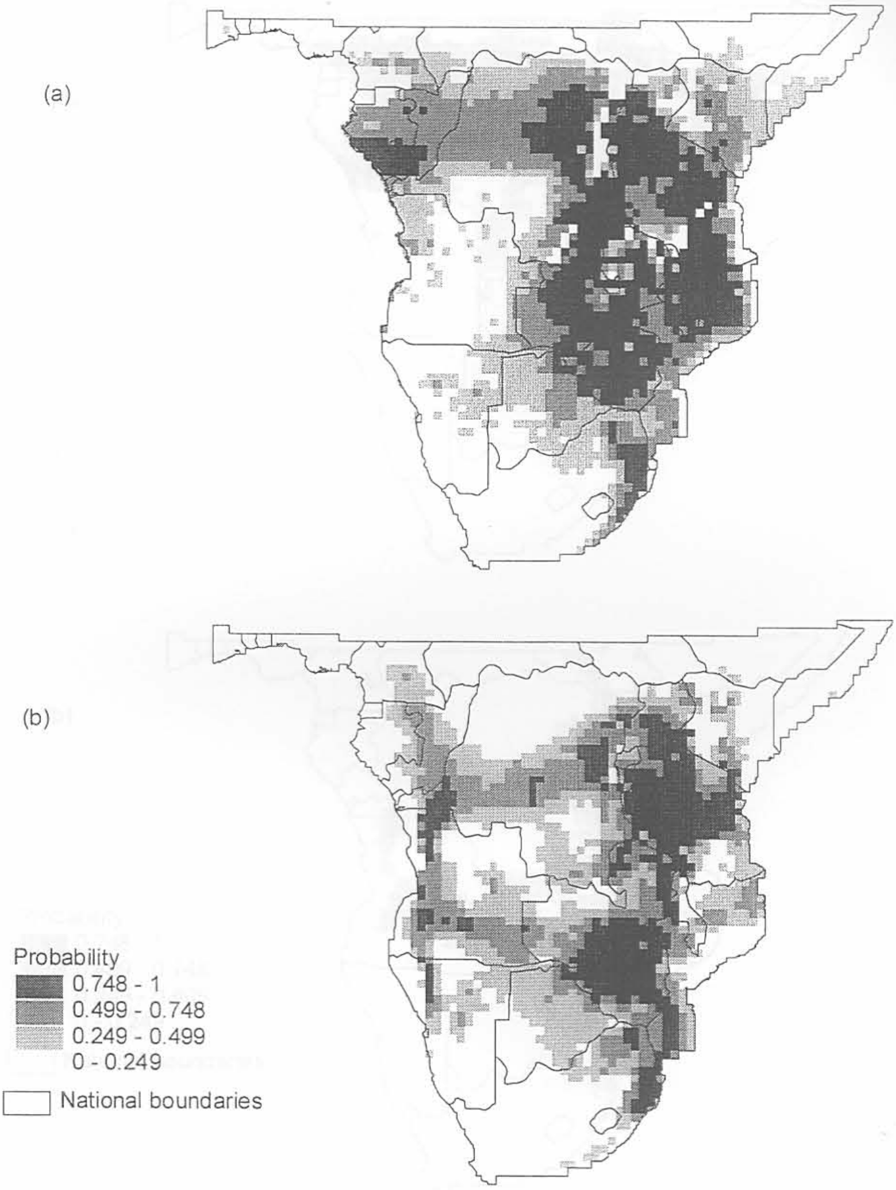

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 33

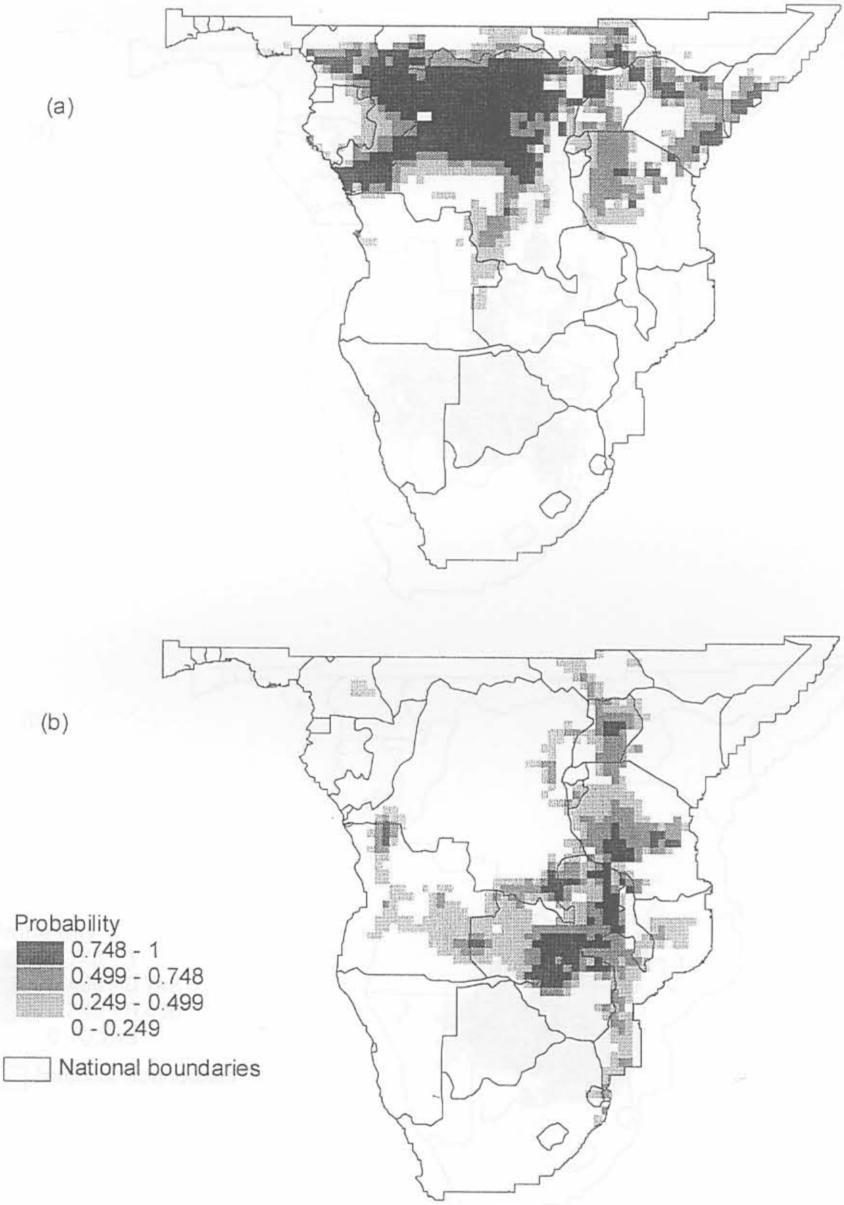

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 34

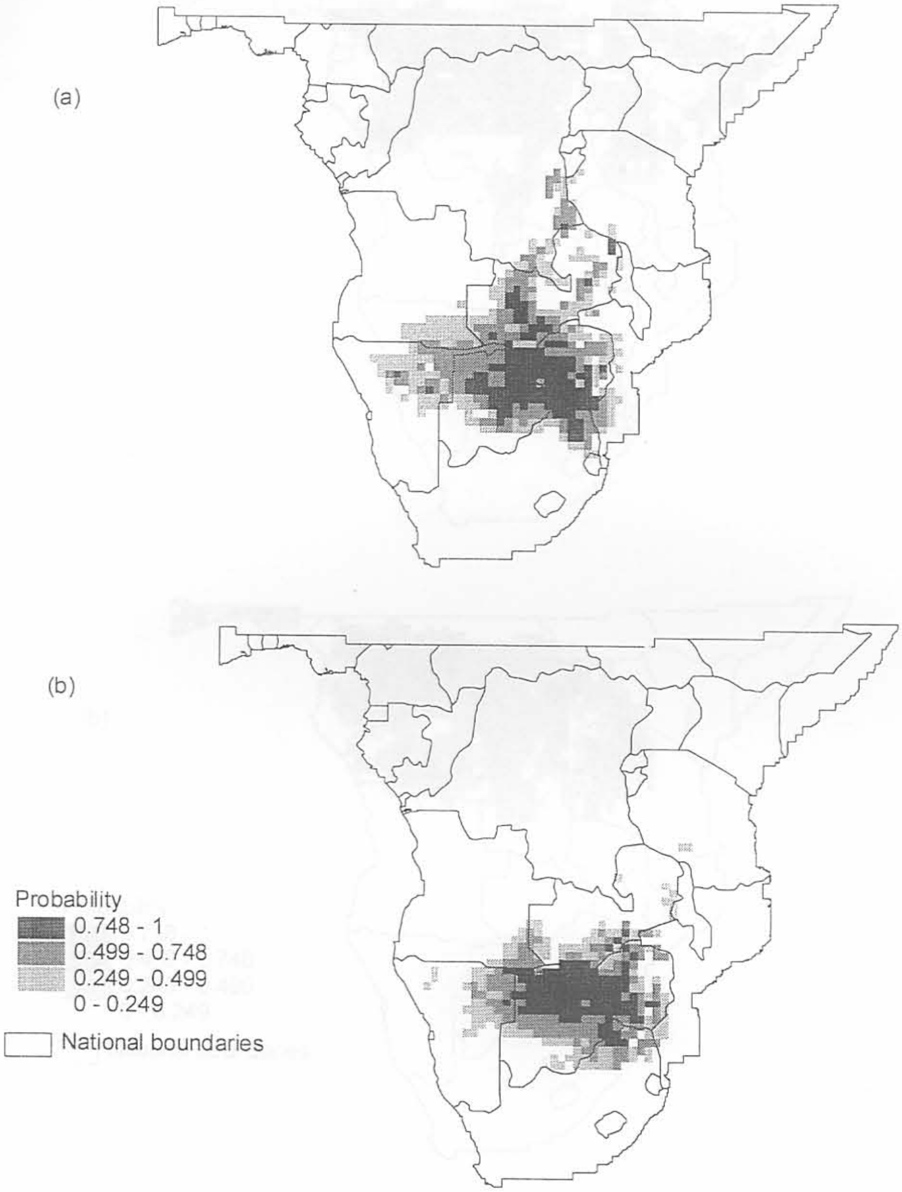

(a)
(b)
Probability
▨ 0.748 - 1
▨ 0.499 - 0.748
▨ 0.249 - 0.499
0 - 0.249
☐ National boundaries

Fig. 35

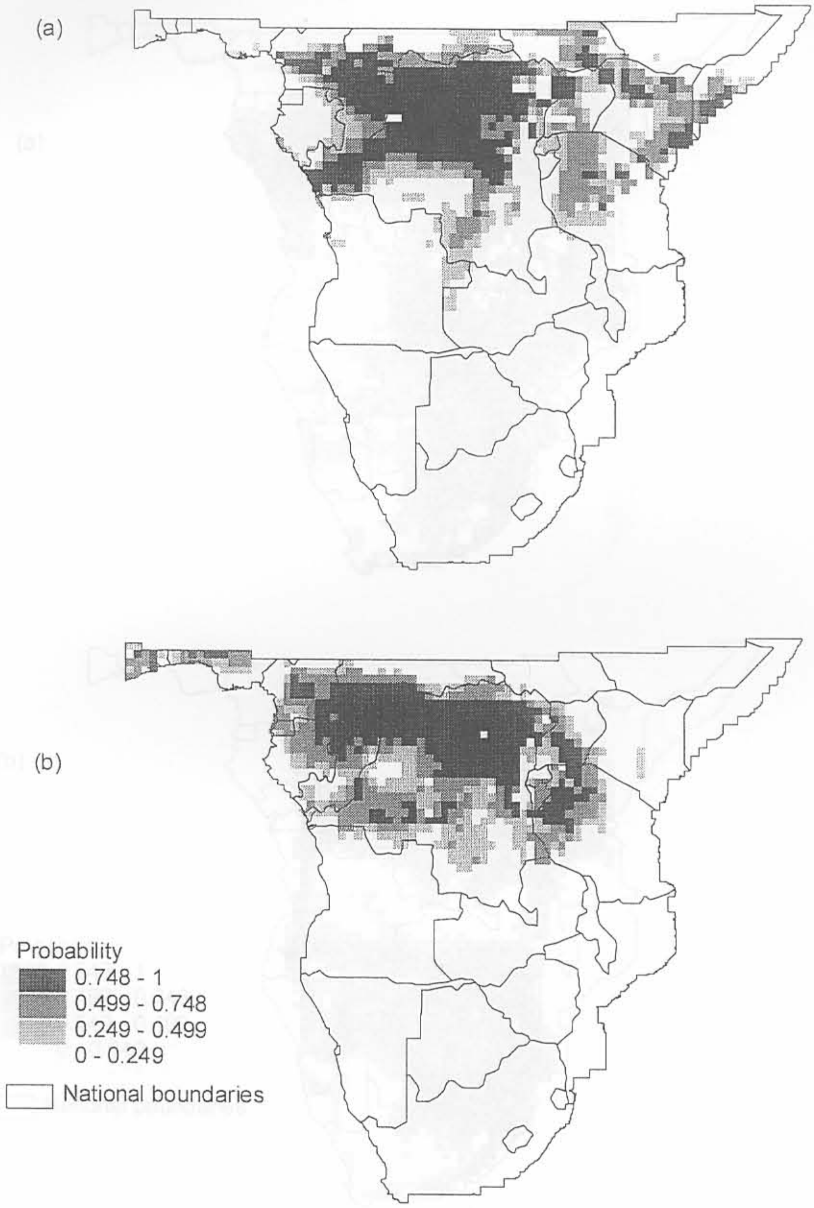

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 36

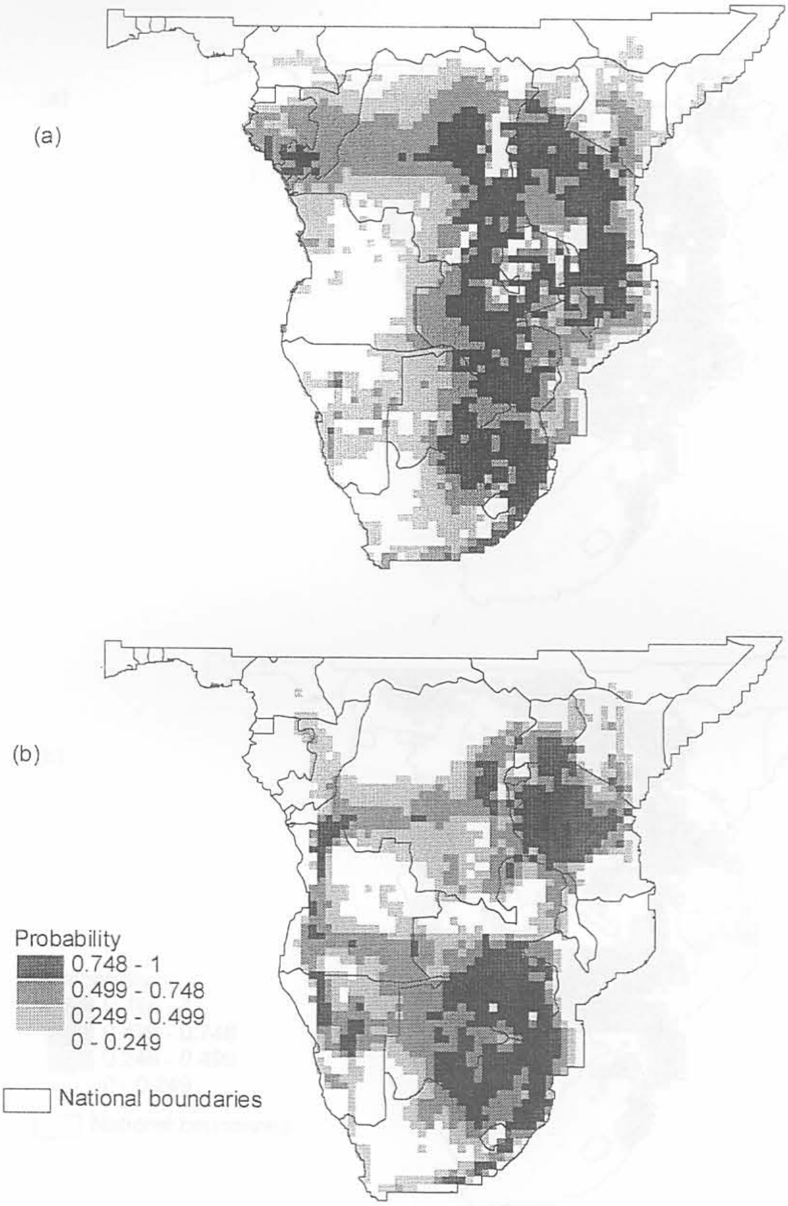

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 37

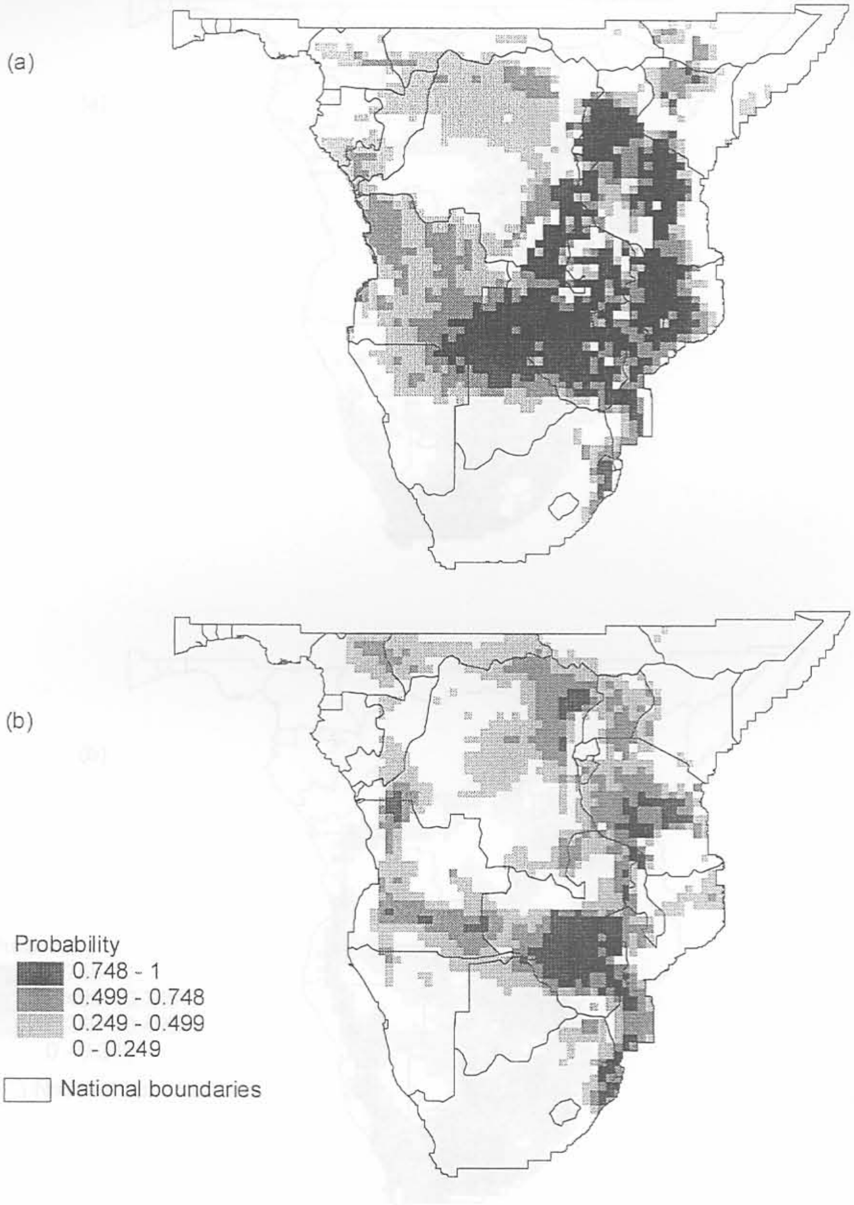
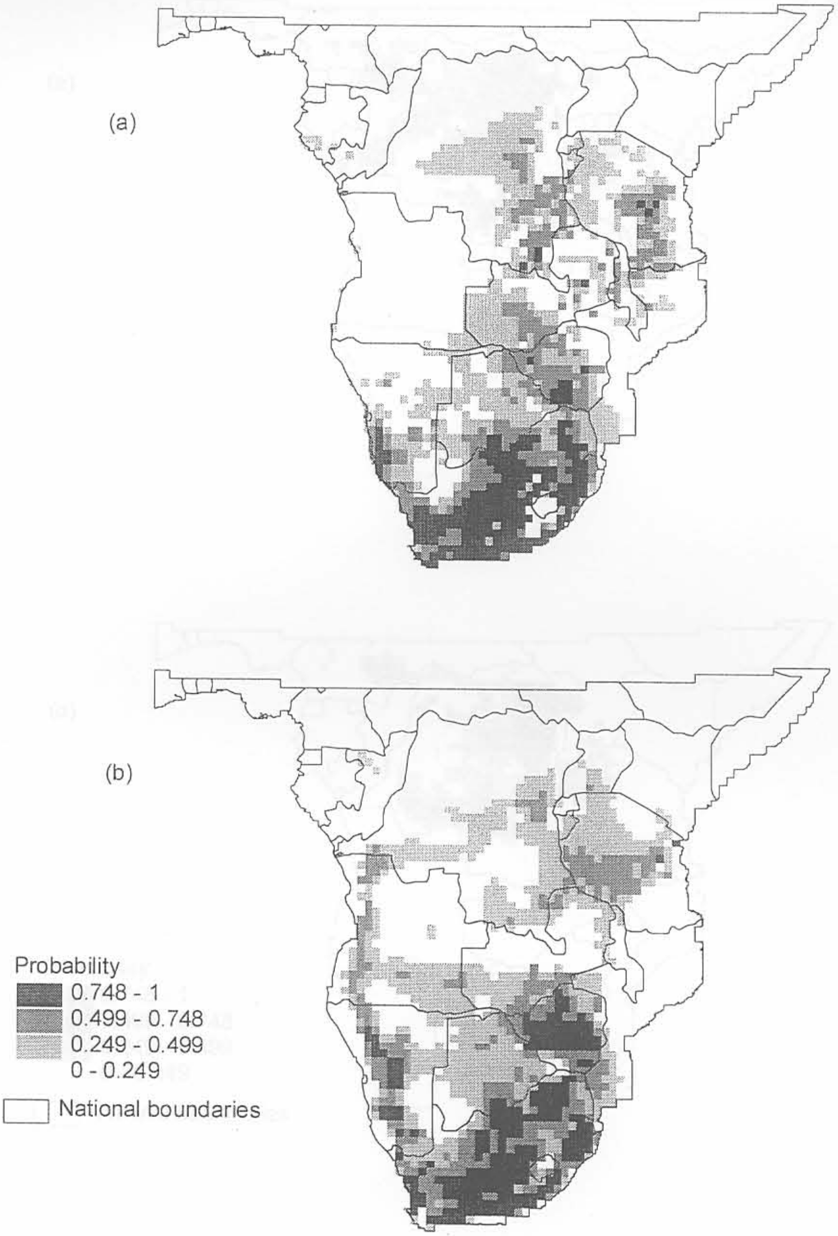
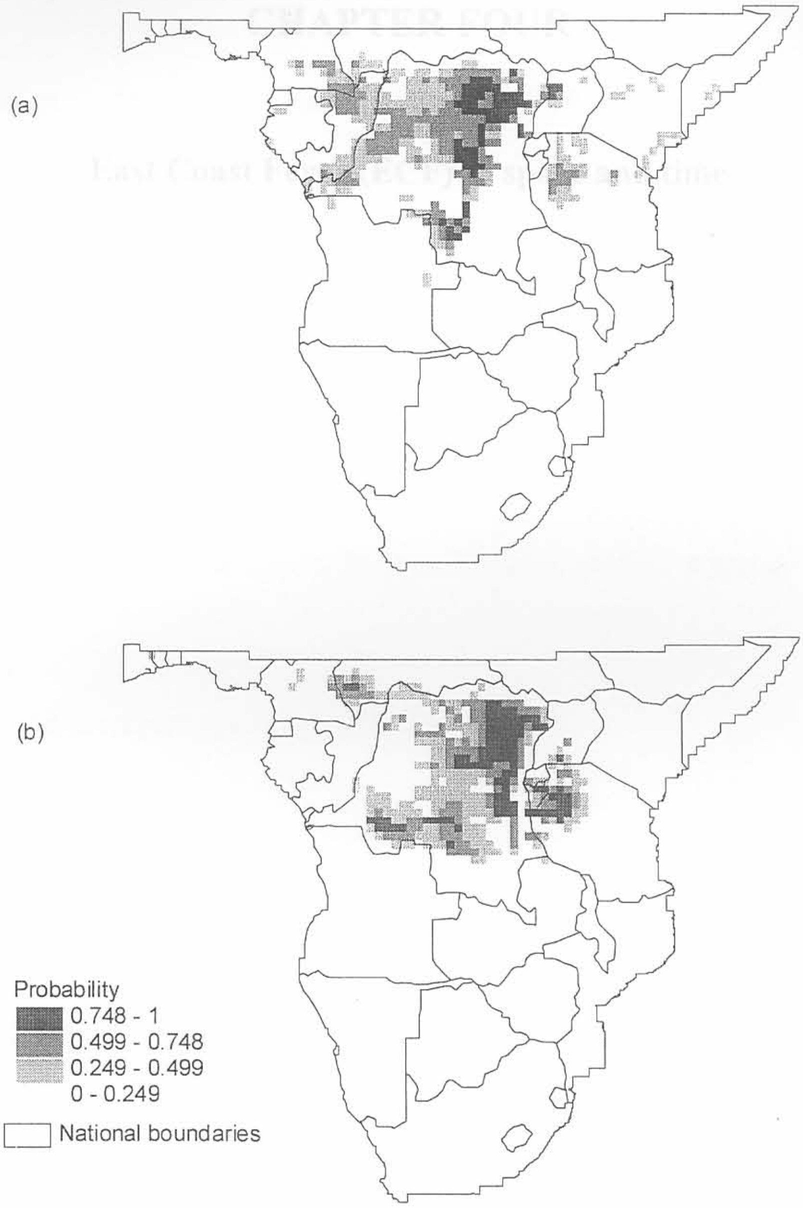

(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

Fig. 38


(a)
(b)
Probability
0.748 - 1
0.499 - 0.748
0.249 - 0.499
0 - 0.249
National boundaries

3. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa

Fig. 39



CHAPTER FOUR

East Coast Fever (ECF) in space and time

East Coast Fever (ECF) in space and time

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Key words: ECF, sub-Saharan Africa, *R. appendiculatus,* predictive species modelling

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ABSTRACT

East Coast Fever (ECF), caused by a protozoan parasite *Theileria parva,* is one of the most important livestock diseases in Africa. For its transmission it depends on the tick *Rhipicephalus appendiculatus* Neuman 1901, which parasitises mainly cattle. The distribution of ECF is therefore restricted to those areas where cattle and *R. appendiculatus* coexist. The failure of tick chemical control programs in Africa, the lack of sufficient knowledge on the ecology of ECF and the lack of proper diseases surveillance has put a heavy burden on the livestock industry. These concerns and the implications of climate change for the diseases, necessitates exploration of other means of disease management. An ability to predict the current and future potential locations of ECF and its vectors would be a valuable development. In this sub-Saharan study, a predictive species distribution model and a nested regional climate model DARLAM was used to predict the present and future potential distribution of ECF. Kolmogorov-Smirnov test and a proportional overlap test were used to compare the current and future predictions of both ECF and *R. appendiculatus*. The results show that the predicted general increase in minimum temperature has favoured the establishment of ticks and ECF. The Northern Cape and Eastern Cape provinces of South Africa, Botswana, Malawi, Zambia and eastern DRC are predicted to show increases in ECF prevalence. These results serve as a caution to other areas in Africa where the tick is known to occur. Constant country-specific surveillance of ticks and the resultant disease is necessary so that changes are known at local scales. This paper also calls for a more active role for control agencies in Africa to provide more resources for proper monitoring.

INTRODUCTION

Ticks (Acarina, Metastigmata) are obligate blood feeders. Although only 10% of ticks parasitise humans and their livestock, they are of particular concern because they transmit pathogenic microorganisms. In fact ticks are vectors of more kinds of microorganisms than any other single arthropod taxon, including mosquitoes (Diptera: Culicidae) (Oliver, 1989). Some of these microorganisms are known to cause diseases in humans and their livestock. East Coast Fever (ECF), caused by a protozoan parasite *Theileria parva* is one of the most important livestock diseases in Africa (Lessard *et al., 1988*; Muraguri *et al.*, 1999). It depends on the tick *Rhipicephalus appendiculatus* Neuman 1901, a three-host tick, which has been collected mainly from cattle for its transmission. The distribution of ECF is therefore restricted to those areas of East and southern Africa where cattle and ticks coexist (Norval *et al.*, 1992). This area extends south from southern Sudan to eastern South Africa and as far west as the Democratic Republic of Congo (DRC). The disease kills 1.1 million cattle and causes an economic loss of $168 million annually (Norval *et al.*, 1992). Mortality is higher (up to 100%) in the more expensive exotic cattle than in the indigenous Zebus, where the average mortality is estimated at 10% (Lawrence *et al.*, 1988). If uncontrolled, ECF can cause over 90% mortality of susceptible cattle following its introduction into a region (Lawrence *et al.*, 1988).

Apart from direct losses due to cattle mortality in endemic areas where chronic ECF occurs, other less quantifiable effects of the disease are apparent including poor weight gain, low fertility rates, reduced growth and milk production, paralysis, and secondary attacks from other parasites (Pegram *et al.*, 1989). ECF is therefore a major reason for tick control in most African countries. A main form of control, the use of acaricide, is however complicated by its high cost, development of tick resistance (Cox, 1991), stock movement during drought, inefficient supervision of ECF quarantines, abundant tick-carrying wildlife and lack of adequate dipping facilities; not to mention concerns about the potential environmental consequences of this control program (Cox, 1991). Other socio-economic factors such as inadequacy of the main tick control facilities make individual farmers undertake fewer control efforts than are optimal for the society at large. The failure of tick chemical control programs in Africa is accentuated by the fact that annual fluctuations in tick abundance, ecology of the ticks, as well as their habitat preferences are largely unknown and thus do not currently inform decisions about appropriate chemical or other tick control measures (Sutherst, 1987a). With these concerns of lack of knowledge on ECF biology and the implications of climate change for the diseases, an ability to predict the current and future potential locations of ECF vectors would be a valuable development (Cox, 1991).

Despite these concerns, this disease does not rank among the most important emerging vector-borne diseases for a variety of reasons including the almost total eradication of the main tick vector *R. appendiculatus* in South Africa and other parts of Africa. It is also known that after prolonged infestations, cattle can acquire enough resistance to ticks resulting in controlled field populations and can limit *T. parva* infection rates in ticks and therefore reduce field challenge. These reasons form part of the general feeling among epidemiologists that ECF is well contained in the areas where it occurs. However, when considering parasite survival, ticks transmit the disease more rapidly when feeding on tick-resistant cattle (Lawrence *et al.*, 1988). In addition, the impacts of global climate change on cattle, ticks and ECF would disrupt the current contained nature of the diseases through invasion of pastures by pastoralists or translocations of game to new areas. Newly introduced cattle, whether exotic, Taurine (*Bos taurus*) or the indigenous Zebu (*Bos indicus*) and Sanga (*Bos indicus*) breeds, during displacement driven by climate change, are much more susceptible to ECF than cattle from endemic areas.

Furthermore, under conditions of global warming, there is a possibility that the current range of the main tick vector, *R. appendiculatus,* may expand or shift and together with the current reduction in available grazing land and the consequent cattle movements to greener areas, the introduction of ECF to new areas is inevitable. In addition to this, there is an increasing demand for livestock products in Africa (Thornton *et al.*, 2000) and consequently, there is a move by most African rural farmers from indigenous cattle breeds to exotic ones that are believed to produce more milk, but are more susceptible to ECF.

Tick abundances are known to vary through space and time due to interactions of many factors, such as climate, host diversity (Norval & Lightfoot, 1982), levels of resistance of hosts, absence of tick control measures and management practices that affect host behaviour. More importantly, the seasonal activity and occurrence of ticks are known to fluctuate from species to species and country to country due to variations in photoperiod (Rechav, 1981; 1982; Minshull & Norval, 1982; Short & Norval, 1981; Norval *et al.*, 1992, Okello –Onen *et al.,* 1999). As far as *R. appendiculatus* is concerned, in southern Africa for instance, there are marked annual cycles of abundance of each life-stage, punctuated by near total absence for several months of each year (see Rechav, 1981). This is due to a behavioral diapause in the adult tick, which is controlled by photoperiod and allows it to survive during the long hot dry seasons (Rechav, 1981; Norval *et al.,* 1992).

Nearer to the equator these ticks usually feed throughout the year and numbers vary far less, but still show discernible seasonality especially in the immature stages (Randolph & Rogers, 1997). This is because developmental rates of *R. appendiculatus* are reported to be temperature dependant, while survival is humidity influenced (Tukahirwa, 1976; Okello–Onen *et al.,* 1999). These reported tick seasonal dynamics, which are a function of climate, exert a major influence on the dynamics of transmission of tick-borne pathogens (Randolph & Rogers, 1997). They determine not only seasonally variable vector-host ratios but also the time delay between acquisition and transmission of pathogens.

The effect that climatic factors exert on tick distribution and abundance is therefore well documented, but the way in which these parameters will change under possible climate change is still uncertain. Studies on European ticks have shown that ticks and tick-borne disease systems will shift or be disrupted following predicted climate change (Randolph & Rogers, 2000; Randolph, 2001). This may lead to the introduction of disease and disease vectors in new areas and may prove catastrophic if prior warnings are not issued. In South Africa, research on the effect of climate change on other animal species

(Erasmus *et al.,* 2002) has illustrated that 25% of the species investigated showed more than 90% shifts in their range. This general pattern of species showing limited overlap between their existing distributions and predicted distributions is most marked in reptiles and invertebrates (van Jaarsveld *et al.,* 2000). Studies in the prediction of African tick distributions remain inadequate, but there is a general prediction that under global warming South African ticks are likely to retreat to the mountainous eastern region near the border of South Africa with Mozambique (Rogers and Randolph, 1993). This effect will be more drastic near the edge of their present ranges.

Most ticks of the genus *Rhipicephalus* are generalists and therefore climate, and not host availability, is assumed to be the most important limiting factor. The host may be limiting factor where all climatic factors become suitable. Cattle are the preferred domestic hosts of all stages of development of *R. appendiculatus* (Norval *et al.,* 1982; Okello-Onen *et al.,* 1999). The preferred wild hosts of all stages of development are African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), sable (*Hippotragus niger)* impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus ellipsiprymnus)* (Horak *et al., 1*983, 1995; Norval *et al*., 1992). African buffalo are also the main wild reservoirs of *T. parva* infection, and may suffer clinical disease. The less specific the tick-host relationship, the less likely it is that hosts will be a limiting factor (Randolph, 2002), because such a tick can use any available host to complete its life cycle. For this reason, spatial distribution of ticks may be analysed by simple statistical methods that seek correlations between known tick presence/absence and climatic factors (Rogers & Randolph, 1993; Cumming, 2000c; Estrada-Pena, 1999; Estrada-Pena, 2003, 2005 & Olwoch *et al*., 2003).

However, analysis of the spatial and temporal distribution of tick-borne diseases is more complex and multifaceted. It requires the analysis of tick and host distribution, pathogen reproduction, growth, development and mutation. It also requires the analysis of the nutritional conditions of the pastures, because they affect the ability of the host to withstand infection. A more robust and comprehensive biological model is needed to predict the effect of climate change on this complex system accurately. However such a biological system does not exist (Randolph, 2002). With the birth of predictive habitat distribution modelling (for review see Guisan & Zimmermann, 2000), and reliable climate data, the distributions of many insects, pests and pathogens have been predicted using their major climate drivers (Messenger, 1959; Meats, 1989; Sutherst & Maywald, 1985; Sutherst *et al.,* 1995; Perry *et al.*, 1990; Coakley *et al.,* 1999; Rogers & Randolph, 2000; Randolph& Rogers, 2000; Randolph, 2001; 2002; Harvell *et al.,* 2002; Erasmus *et al.,* 2000, 2002). Recently, a multivariate model has been used to predict the location of future climate envelopes of South African fauna (Erasmus *et al.*, 2002). These predictions have shown acceptable success rates in the way they predict known records.

In a previous study (Olwoch *et al*., 2003), this multivariate habitat model and high resolution climate data simulated by a limited-area atmospheric model, DARLAM (Division of Atmospheric Research limited-area model) (Engelbrecht *et al.,* 2002) in combination with existing known tick distribution records provided potential distribution predictions for selected tick species. The same habitat model and DARLAM are used in this study to identify potential areas of *R. appendiculatus* distribution after possible climate change. Like all other vector-borne diseases, risk of infection of ECF depends on the degree of contact between cattle, the main host animal, and infected *R. appendiculatus* vectors determined by both biological and non-biological factors.

The aim of this paper is therefore to establish the present and potential future distribution of ECF based on the present and potential future distribution of the tick and cattle assemblage and to assess the impacts of these range shifts on tick-born disease control by use of a predictive species model. The use of predictive distribution models in tick research is still in its infancy, especially in Africa where biological requirements of ticks are not sufficiently known. Consequently, robust mechanistic models that are reported to yield superior results (Pearson and Dawson, 2003) are not suitable for this study. Correlative models that make use of species-environment relations are more suitable and more specifically, profile models that rely only on presence data are preferred because of the uncertainty around true or false absence of *R. appendiculatus.* These models as represented by the modified multivariate technique (Erasmus *et al*., 2000) have successfully predicted South African fauna (Erasmus *et al.*, 2002) and African ticks (Olwoch *et al.*, 2003).

MATERIALS AND METHODS

Study area

This study covers Sub-Saharan Africa (Fig. 1). The study area was divided into 3000 grids cells of 60 x 60 km resolution. This resolution was determined by DARLAM climate data.

Tick Data

Point localities of recorded tick observations restricted to sub-Saharan Africa were obtained from Cumming (1999b). These data were compiled from various tick collections (see Cumming, 1999b for a detailed list of sources). Combining data sets from different sources invariably compounds identification and distribution errors. For this reason data comparison with Walker *et al.*, (2000) was used to assess data quality. This latter reference provides well-illustrated distributions of *Rhipicephalus* species. Synonyms provided in this reference also solved the common problem of species synonyms. The distribution of *R. appendiculatus* was used in this study as the main determinant of ECF transmission. There are other tick species that are capable of transmitting ECF but only under laboratory conditions and their distribution has therefore not been included in this study. The present distribution of *R. appendiculatus* (Fig. 2) was used as an input to the habitat model (Olwoch *et al.*, 2003). These point localities were used to assign each 60x60 km grid a tick presence or absence.

Cattle data

Cattle density data were obtained from Kruska *et al.*, (1995) (Fig. 2). This database is a result of International Livestock Research Institute's (ILRI) work in which country level cattle census data was collated to create a cattle density layer for Africa. The census figures are not usually conclusive because they are reported on the basis of administrative boundaries, which can vary widely in resolution (province, district, division). These figures were therefore improved by attaching an administrative boundary layer that was obtained from Food and Agricultural Organisation (FAO) (Kruska *et al.*, 1995. The best available cattle data from the census was attached to this administrative boundary layer. During this process, areas of zero cattle population such as protected areas and water bodies were not included in order to improve density calculations. Because of the variation in the quality of census data from country to country, additional attribute fields were added to the density database that included administration level information and date of the census (see Kruska *et al.,* 1995). The cattle density layer used includes both the indigenous and exotic breeds.

The purpose of the cattle data used was to refine the predicted current and future range of *R. appendiculatus* in order to predict ECF habitat suitability. It might be argued that the current density data for cattle would not suffice as a refinement of the future predicted distribution of the ticks, and instead a map of future cattle densities would have to be used. But predicting cattle distribution changes would need a comprehensive review of at least the following factors: human population distribution changes resulting from population growth and urbanization; economic changes affecting trade and market development; agro-ecological changes affecting livestock systems, including the impacts of climate change on feed supplies from pastures and crops; and estimation of the effects on livestock production of changes in grazing and land use caused by human use, and finally an ability to model people's behaviour. Such elaborate data does not exist at the moment and given the capabilities of the modelling approach used in this study, it is not possible at the moment to include all these factors. Furthermore, an analysis of the existing cattle records (FAO) showed that there was no marked increase in cattle numbers from 1990 to 2003. However this does not suggest that no change will take place over the long term, but at the moment there are no better available resources that indicate how cattle numbers will change in the future. The cattle distributions used for refining the predictions of ticks in the present and future were therefore kept constant.

DARLAM present and future climate data

The Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Melbourne, Australia has developed the high-resolution limited-area model DARLAM for use in both short-term mesoscale atmospheric studies and longer-term climate simulation experiments (Walsh & McGregor, 1995). In the present study ten separate 30-day simulations were performed for both January and July for different 10-year periods. The periods selected are the 1990's and 2020. The simulations were performed at a horizontal grid resolution of 60 km x 60 km using a domain of 100 x 100 grid points that cover sub-Saharan Africa. The monthly average of the ten simulations constitutes the model climatology for the month. The CSIRO Mark 2 GCM was used to force DARLAM at its lateral boundaries. The GCM was integrated for the period 1960-2100, with greenhouse gas forcing corresponding to the A_2 SRES (Special Report on Emission Scenario, issued by the Intergovernmental Panel on Climate Change) scenario. Engelbrecht *et al.*, (2002) illustrated that DARLAM is capable of simulating the regional characteristics of atmospheric variables like near-surface temperature, low-level wind patterns and rainfall over sub-Saharan Africa with considerable detail. The model does however tend to overestimate rainfall totals over regions with a steep topography.

The climatological anomalies for the 2020s vs. the 1990s as predicted by DARLAM are shown in figure 3. January minimum and maximum temperatures are simulated to increase by more than 2ºC over certain regions of the subcontinent. Much of the eastern regions are expected to become drier with an associated pattern of higher sea-level pressure, whilst the western subcontinent is expected to become wetter. An interesting feature of the July anomaly fields is that parts of the central subcontinent are simulated to become cooler and wetter.

Predictive species modelling

A simple climate envelope model was used to predict the future distribution of the focal species. (Erasmus *et al.*, 2000; 2002). The input data comprised 3000 grid cells of 60 x

60 km size covering sub-Saharan Africa populated with climate variables. There were 548 known presence records of *R. appendiculatus* and the present climate values at these locations were used to construct a climate envelope, using a principal components-type analysis. This climate envelope represents the range of climates within which the tick is known to occur, and as such, can be interpreted as the realised niche, as defined purely by climate. To arrive at a predicted distribution under a climate change scenario, the existing climate envelope is applied to a climate surface representing future climates, and a new geographical interpretation of distribution is derived (see Erasmus *et al*., (2000, 2002) and Olwoch *et al.,* (2003) for a more detailed explanation). Both the predicted current and future distributions were obtained using this predictive species model and 6 climate variables of current and future mean maximum temperature, mean minimum screen temperature and mean rainfall of January and July.

The perceived main draw back of this method is that it is based on the current species-environment relationships and may not be a reliable guide of the future interactions. Also most of the tick data used (*with exception of few new records, Horak private collection*) were collected at a different time scale form the cattle data. Furthermore, most of the climate data available for predictive species modelling is at a much coarser scale than the site-specific conditions in which the ticks and other vectors operate. However with the evolution of climate data used in predictive studies from long-term climate datasets (Hutchinson *et al*., 1996) to GCMs (General circulation models) and to RCMs (Regional Climate models) such as DARLAM, we are confident that these results are useful. When this method was evaluated on how it predicts the current distribution of South African birds (Erasmus *et al*., 2003) and African ticks (Olwoch *et al*., 2003) relatively accurate results were obtained. It is the same confidence that we attach to the predicted future distribution. However caution should be exercised when interpreting these results because of the model and data gaps. Thus a record of ECF for at least two centuries is needed to evaluate these results. Proper monitoring and experimental research on vector borne diseases is necessary to comprehend future predictions.

Predicting the current and future distribution of *R. appendiculatus* and ECF

From the 548 known distribution records of *R. appendiculatus*, the predicted current distribution was initially obtained using six variables of the current climate as an input into the model. This is useful because it represents a valuable comparison of how the model predicted distribution compares with the known records (see Olwoch *et al*., 2003 for details). To obtain the future predictions, the grid cells are populated with future climate. In order to predict the potential current and future distribution of ECF, the predictive species model was used to get an idea of where the ticks could survive currently and in the future based on current and future climatic variables, and then refined these by adding the ranges of cattle. The predictive modelling was executed in S-Plus (S-Plus 2000) while maps of the results were drawn in ArcView GIS. The resultant potential distributions are maps of probability of occurrences per 60 km by 60 km grid cell based on climate. A simplified diagram representing this methodology is shown in figure 4.

Comparison of the predicted present and future distribution of *R. appendiculatus* and ECF

Several analyses were performed to compare the predicted current and future distributions of *R. appendiculatus*. These included: 1) a comparison of the probability of occurrence values per grid cell between current and future predictions; 2) an analysis of range contraction, expansion and shift; 3) an assessment of overlap between current and future distributions. These analyses were done for the entire study area, per region and per country. By using only the areas where *R. appendiculatus* is currently distributed three regions were defined and assessed: Southern Africa which includes; South Africa, Botswana, Zimbabwe, Zambia, Malawi, Angola and Mozambique; Central Africa which includes Democratic Republic of Congo (DRC), Rwanda and Burundi; and East Africa which includes Uganda, Kenya and Tanzania.

The comparison in the probability values of tick occurrence between the present and the future were analysed by using Kolmogorov-Smirnov two-sample test (StatSoft, Inc. (2001). This was done for all probability values and then a comparison was made between the number of grid cells in various probability classes in the current and future predictions. These probability classes were: 0-<20%, 20- <40%, 40 - <60%... 80-100%. Range changes between the current and the potential future distribution of *R. appendiculatus* were assessed. The predicted current or future potential distribution was taken as the number of grid cells where the probability of occurrence is equal or greater than 50%. This threshold has been used before (Beard *et al*., 1999; Erasmus *et al*., 2002; van Staden *et al*., 2003; and Walker, 1990 for even lower thresholds). The difference in grid cells between the predicted current distribution (CD) and predicted future distribution (FD) constitutes distribution range change (DC). These range changes may either be range contraction or range expansion. There is range expansion if FD > CD and there is range contraction if FD< CD. Maps of range shifts were obtained by overlaying the number of grid cells with probability values > 50% before climate change with the number of grid cells with probability values > 50% after climate change. The number of grid cells outside the intersection constitutes range shifts in a specified direction.

Finally, the degree of proportional overlap between the predicted current and the predicted future distributions of *R. appendiculatus* was assessed by means of proportional overlap method (Prendergast *et al*., 1993 and Reyers *et al*., 2000). In this case the proportional overlap was calculated as Nc / Ns, where Nc is the number of common grid cells between a pair of areas under comparison and Ns is the number of grid cells in the smallest set of areas containing data for both groups or the number of grid cells in the smallest set minus the number of grids that are not common in these two sets.

These assessments of future range changes done for the tick distribution were then repeated for ECF distribution. The present and potential future ranges of ECF were obtained by superimposing the distribution of cattle with the predicted current and predicted potential future distribution of *R. appendiculatus*. Again cells with a probability greater or equal to 50% that fell within the current cattle distribution were assigned a presence value for ECF. The degree of range change was been calculated as outlined above.

RESULTS

R. appendiculatus predicted distribution

Under the current and future climates, the predicted probability values of *R. appendiculatus* distribution based on the current and future climate are shown in Fig. 5. These values range from 0-1 (0% - 100%). The probability that the area will be climatically suitable for ticks decreases as one moves from 1-0. Visually, the current and future predicted distributions are not clearly differentiated, but when the number of grid cells in various probability classes was compared statistically, a significant difference between the current and future probability values was found (Kolmogorov-Smirnov two sample test, $p <. 005$). When the number of grid cells falling into different probability classes were analysed for the whole of sub-Saharan Africa (Table 1), there were no major changes in the number of grid cells in the lower probabilities (0-20%). The biggest change in the number of grids occurred in the 20 – 40% and 40 - 60% probability classes. This tick suitability class showed increases of 31 and 33 grid cells respectively in the future (Table 1). Also of interest was the reduction in the number of grid cells grid cells with a probability greater than 80% for the predicted future distribution.

Regional analysis of probability classes for predicted *R. appendiculatus* distribution revealed that the East Africa is predicted to be most affected region. There is greater than 100% increase in the number of grid cells in the 60-80% probability class. In the other regions (Central and South) there were no major changes for the current and future distributions (Fig. 6a). A further analysis of probability classes for individual countries revealed that in most of the countries tick suitability would stay the same. However, the following exceptions were noted: Burundi, Kenya, Rwanda, Zambia, Zimbabwe and Uganda showed significant increases in the number of grid cells with higher probabilities (60-80%) (Fig. 6b) while DRC showed increases in the number of grids in the 20-40 % probability classes in the future (Fig. 6b).

When assessing range changes, a tick was assumed present where the model predicted a probability value of ≥ 50%. On a sub-Saharan scale, the analysis revealed that there was a general reduction of 23.3% in *R. appendiculatus* range between predicted present (CD=1263 grid cells) and predicted future (FD = 969 grid cells) (Table 2) (Fig. 7). Range shift was mainly from west to east with most of the range reduction-taking place in the west. Regional analysis revealed less than 1% decrease of *R. appendiculatus* range in all regions. The country analysis showed that Botswana, Malawi, South Africa and Zimbabwe are predicted to show increases while Mozambique, Tanzania, Uganda, DRC and Zambia show slight decreases. The countries that are predicted to show no change are Burundi, Rwanda and Kenya (Table 3). Analysis of the spatial congruence between predicted current and future *R. appendiculatus* ranges by means of the proportional overlap method showed high congruency between current and future predicted distributions. On a sub-Saharan scale there was 89% congruence between current and future predicted distribution of *R. appendiculatus* (Table 2). On a regional scale, there is 90% congruence in Central and East with 87% congruence in the South (Table 2). Country proportional overlaps vary from 77% for Botswana, 78% for south Africa, 85% Zimbabwe and 87% DRC. The rest show 90% apart from Rwanda, Burundi, and Malawi that show 100% congruency (Table 3).

Once the cattle distributions were superimposed on the present and future potential tick distribution, an analysis of the change in potential ECF distribution was possible. On a sub-Saharan scale, there was a slight increase in ECF range between present and future (Table 4). The difference between the maps (Fig. 8) of ECF predicted range under the current climatic conditions and future climate scenarios showed that 100 grid cells which were suitable for ECF under the current climatic conditions become unsuitable in the future while 102 grid cells which were unsuitable in the current climate become suitable in the future. Visually, most of the south western African countries of Angola, Namibia, western and southern Botswana, western Zambia and central DRC are predicted to become unsuitable for East Coast Fever in the future. Regionally, there is a predicted increase of ECF in Southern and Central Africa while East Africa stays the same (Table 4). An analysis of individual country ECF changes revealed that the range is predicted to increase in Botswana, DRC, Malawi, and South Africa. Predicted decrease in ECF is expected in Tanzania and Uganda (Table 5). ECF in the rest of the countries (Burundi, Kenya, Mozambique, Zambia and Zimbabwe) stays the same. Analysis of the predicted ECF ranges for the present and future using proportional overlap method showed the lowest congruency in Kenya, followed by Botswana and South Africa (Table 5).

DISCUSSION

Implications of the findings

Changes in *R. appendiculatus* distribution

The climate predicted by DARLAM in the future renders the western arid regions of Africa unsuitable for *R. appendiculatus*. I propose here that increase in temperature in an already hot and dry area limits population increase, and any further rise in temperature may result in slowing down developmental rates and later limit or halt survival due to water loss under dry conditions. Angola, Namibia, southern DRC become climatically unsuitable for *R. appendiculatus* infestation. However the northern and eastern Cape provinces of South Africa as well as Botswana, Zambia and eastern DRC that are currently unsuitable are rendered climatically suitable for *R. appendiculatus* under future climate scenarios. This may be because of enhanced rainfall in these areas. Rises in temperature (especially the minima) as predicted over most of tropical Africa and southern Africa may contribute to the increases in suitability of *R. appendiculatus* in these regions. These effects would shorten generation time and may allow populations to pass through additional generations, possibly leading to higher pest populations in some cases. Increase in tick numbers, as well as shifts in the timing and duration of each generation time may overwhelm areas that may become more suitable for tick infestations. This would increase the absolute amount of production loss of cattle. Thus strategic dipping may not be a sufficient strategy in such an environment.

Changes in the range of East Coast Fever (ECF)

The predicted ECF range was mainly deduced from *R. appendiculatus* predicted distributions and cattle ranges. It will therefore follow the predicted range of these two factors. The slight increase in *R. appendiculatus* distribution in cattle inhabited areas leads to a slight increase in ECF on a sub-saharan scale. Minimum temperature is the main factor that influences tick abundance and length of generation time. The predicted general increase in minimum temperature in most areas therefore means an increase in tick density and a shorter generation time. This scenario is particular applicable to southern Africa which currently experiences only one generation of *R. appendiculatus* per year compared to the tropical African countries. Thus it is possible to say that southern Africa and central Africa are the regions predicted to show increases in ECF suitability in the future. Elsewhere, the climatic suitability of ECF in most of its core areas is predicted to stay the same. However at the edges of its range, there are observable changes in the suitability because the dynamics of any organism at the edge of its range are likely to be determined by a single limiting factor, while at the core of its range, an organism is more often subject to multivariate constraints (Randolph, 2001).

Country analysis of ECF changes show increases in ECF suitability in eastern DRC, Botswana, Malawi, and South Africa. The key factor linked to this response is the predicted decrease in temperatures during wetter winters (making conditions less harsh) (Botswana and Malawi), and increasing rainfall in the austral summer (South Africa and the eastern DRC). On the other hand, central Tanzania with its predicted future increase in rainfall and slight warming does not show the expected increase in ECF future suitability; a clear indication that although climate alone may be used to give acceptable biological explanations of the responses, more explicit models need to be developed to tackle such complex relationships. In this case other factors operating at local scales that are also crucial to tick seasonal dynamic such as the absence of the main hosts in this arid part of Tanzania may be responsible for the observable anomaly. Moreover it is important to note here that the reduction in ECF range does not necessarily mean reduction in the severity of the disease, because unfavorable climatic conditions may also render pastures unpalatable or not available and thus result in hosts with very poor nutrition conditions.

These underfed hosts are more prone to tick infections because cattle under stress appear to suffer more from each unit of tick attack (Sutherst, 1983). Studies in Australia have reported that the nutritional condition of cattle will decline in northern Australia due to reduced protein levels in pastures at high temperatures and carbon dioxide concentrations, leading to both heavier tick infestations and greater losses for each tick attaching under stressful conditions (Sutherst, 1983). An additional effect may be on the hosts' availability and well being. In this case, cattle may change their distribution and thereby disrupt the lifecycles of ticks. Other indirect effects may also come into play such as increases in the rate of evolution of the parasites thus the frequency of mutation. In such a case the hosts will be subjected to a multitude of new parasites at all times and the issue of resistant hosts does not arise (Harvell, 2002).

The assessment of biodiversity as a fundamental important factor in reducing the risk of exposure to tick-borne diseases (Ostefeld & Keesing, 2000) does not form part of this chapter but needs to be explored for East Coast Fever in future. The dependence of *R. appendiculatus* on different hosts to complete its life cycle means that changes in the population of those hosts within communities is a very important factor to consider when dealing with this tick-borne disease. Therefore, changes and proximity to wild host populations plays a great role in East Coast Fever transmission even more so for those hosts that act as reservoirs for this disease infection. Movement and displacement of some of these hosts as may happen after climate change may result in changes in host population and/or diversity which may lead to disruption in life cycles of the tick. This will influence the timing of tick borne infections and therefore place a huge burden on control programs. We suggest here that predicting the hosts' distribution would give an indication of the diseases prevalence. The use of changes in host numbers to predict disease outbreaks is being explored in the case of desert gerbils (*Rhombomys opimus)* and the plague in the Soviet Union. The findings of the gerbil study confirmed long held theory that plague and other infectious diseases erupt when host populations reach a critical threshold. For the plague, bigger populations of hosts make it easy for the vector to jump from one animal to another and the pathogen survives (Davies *et al.*, 2004).

The tick-host and disease relationships are very complex and are not fully understood at this moment. At the same time there are no equally complex models to deal with these relationships. However, there are good species distribution and climate data. With these, the distribution of vectors and diseases has been attempted using simpler climate envelope approaches. By using these models, it is now possible to understand the relationships between current climate, tick, host distribution and population in order to predict their future ranges. By doing this we provide a relatively acceptable picture of the disease's implications for the present and future. In Africa, economic crises and wars hinder proper surveillance of tick and host populations, but by observing changes in climatic conditions that are linked to vector and host reproduction and development, outbreak of diseases can be anticipated long before they occur. The tick *R. appendiculatus* being a three- host tick, the immature stages mainly depend on small hares to develop. These hosts respond quickly to heavy rains. Monitoring and predicting these hosts may be the practical key factor in the control and prevention of ECF in Africa. Understanding the dynamics of vector borne diseases rather than chemical control is the key. Moreover chemical control has proved unsuccessful partly because partial removal of one parasite results in invasion of others. For instance removal of *Glossina palpalis* in Cote d'Ivoire resulted in invasion of lesser dominant species, *Glossina pallicera* and *Glossina nigrofusca*. Also the eradication of *Boophilus decoloratus* in southeastern countries resulted in the invasion of its competitor, *B. microplus* (Sutherst, 2001).

This study does not suggest that climate is the only factor influencing the distribution of *R. appendiculatus* and ECF. Neither does it mean to imply that the distribution of *R.*

appendiculatus and the presence of cattle are the only determinant factors for ECF transmission and prevalence. Other factors such as host population size and density, habitat modification, vector control programs and the social environments play a significant role. In Africa for instance, lack of enforcement of animal movement restrictions and invasion of game parks for grazing land play a very crucial role in ECF infection and spread. These results present the broad scale climatic limits within which finer scales operate and are therefore a valuable tool for understanding the relationship between ticks, tick-borne diseases and climate. In the absence of a more comprehensive and versatile model, these results are also the best alternative we have.

In an African context, predicted increase in ECF in areas such as Botswana, DRC and South Africa would be disastrous especially if other control measures arrive too late. A more active role for the control agencies is suggested especially in Africa to provide more resources for proper monitoring. Changes in human behaviour as well as tick-host distribution following a changed climate should also be included in future planning.

Future direction

These results can benefit from the inclusion of ECF distribution records over the last century. More importantly, research into the development of more comprehensive tick models that include both the biological and non-biological factors should be motivated so as to predict not only the distribution ranges but also their reproduction and developmental rates. Country surveillances of tick- borne diseases should be revived so that changes are known at local scales. Also increases in hosts that are linked to these vector borne diseases should also be reported for a better understanding of the interaction between vectors, vector-borne disease and their hosts.

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TABLES

Table 1: Number of 60km x 60km grid cells falling into various probability classes for the presence of *R. appendiculatus* under the predicted current and future distribution.

Probability class	**Current no. of predicted grid cells**	**Future no. of predicted grid cells**	**Common grids**	**Overlap**
0-20%	1428	1486	1341	94%
20-40%	376	357	166	46%
40-60%	369	383	165	45%
60-80%	372	369	178	48%
80-100%	455	405	321	79%

Table 2: Number of 60km x 60km grids cells for which *R. appendiculatus* is present in the predicted current and future distribution at a sub-Saharan and regional scale. Proportional overlap values between current and future ranges are also shown. Presence assumed at a threshold of 50%.

Region	**Current no. of predicted grid cells**	**Future no. of predicted grid cells**	**Common grid cells**	**Overlap**
SUB-SAHARA	1233	969	867	89%
CENTRAL	437	403	373	93%
EAST	254	234	213	91%
SOUTH	572	563	490	87%

Table 3: Number of 60km x 60km grids cells for which *R. appendiculatus* is present in the predicted current and future distribution at a country scale. Proportional overlap

values between current and future ranges are also shown. Presence assumed at a threshold of 50%.

Country	Current no. of predicted grid cells	Future no. of predicted grid cells	Common grid cells	Overlap
BOTSWANA	39	44	34	74%
BURUNDI	13	13	13	100%
KENYA	21	20	14	93%
MALAWI	35	38	35	100%
MOZAMBIQUE	156	119	114	93%
SOUTH AFRICA	86	78	61	78%
RWANDA	12	12	12	100%
TANZANIA	191	182	168	93%
UGANDA	42	32	31	91%
ZAIRE	283	250	231	87%
ZAMBIA	157	155	148	95%
ZIMBABWE	91	100	83	85%

Table 4: Number of 60km x 60km grids cells for which ECF is present in the predicted current and future distribution at a sub-Saharan and regional scales. Proportional overlap values between current and future ranges are also shown. Presence assumed at a threshold of 50%.

Region	Current no. of predicted grid cells	Future no. of predicted grid cells	Common grids	Overlap
SUB-SAHARA	739	741	639	86%
CENTRAL	90	102	88	98%
EAST	228	212	191	90%
SOUTH	401	410	347	87%

Table 5: Number of 60km x 60km grids cells for which ECF is present in the predicted current and future distribution at a country scale. Proportional overlap values between current and future ranges are also shown. Presence assumed at a threshold of 50%

Country	**Current no. of predicted grid cells**	**Future no. of predicted grid cells**	**Common grids**	**Overlap**
BOTSWANA	39	44	34	77%
BURUNDI	12	12	12	100%
DRC	66	78	64	97%
KENYA	20	20	14	70%
MALAWI	28	31	28	100%
MOZAMBIQUE	45	45	43	96%
RWANDA	12	12	12	100%
SOUTH AFRICA	78	86	61	78%
TANZANIA	171	164	150	91%
UGANDA	37	28	27	96%
ZAMBIA	99	99	95	96%
ZIMBABWE	97	97	80	82%

FIGURE LEGENDS

Figure 1: Map showing the countries of sub-Saharan Africa that were included in this study

Figure 2: The relationship between recorded cattle density for sub-Saharan Africa and the recorded *R. appendiculatus* distribution.

Figure 3: DARLAMs climatological anomalies for the 2020s vs 1990s

Figure 4: Simplified diagram of how the current and future distribution of *R. appendiculatus* and East Coast Fever (ECF) were predicted

Figure 5: The current and future predicted probability values of *R. appendiculatus* obtained by using the predictive species model (Erasmus *et al*., 2002) and DARLAM climate surfaces (a) Current (b) Future 2030

Figure 6a: Changes in number of 60kmx60km grid cells in various probability classes between the current and the future for different regions

Figure 6b: Changes in the number of 60kmx60km grid cells in various probability classes between the current and the future for different countries

Figure 7: Predicted current and future *R. appendiculatus* distribution obtained by using the predictive species model (Erasmus *et al*., 2002) and DARLAM climate surfaces (a) Current (b) Future. Presence assumed at a threshold of 50%.

Figure 8: East Coast Fever future risk map obtained by using by the predictive species model (Erasmus *et al*., 2002) and DARLAM climate surfaces. Presence assumed at a threshold of 50% of *R. appendiculatus* and cattle presence.

Figure 1

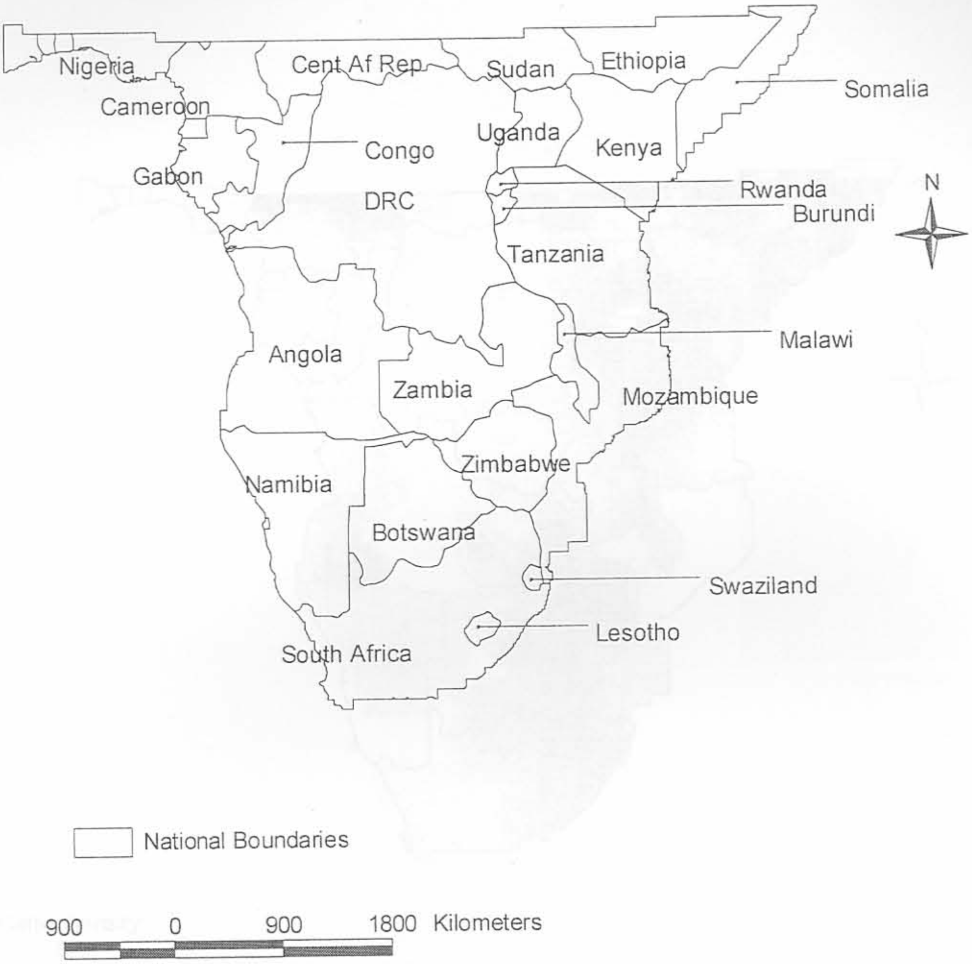

Nigeria
Cent Af Rep
Sudan
Ethiopia
Somalia
Cameroon
Uganda
Congo
Kenya
Gabon
DRC
Rwanda
Burundi
N
Tanzania
Malawi
Angola
Zambia
Mozambique
Zimbabwe
Namibia
Botswana
Swaziland
Lesotho
South Africa
National Boundaries
900
0
900
1800
Kilometers

Figure 2

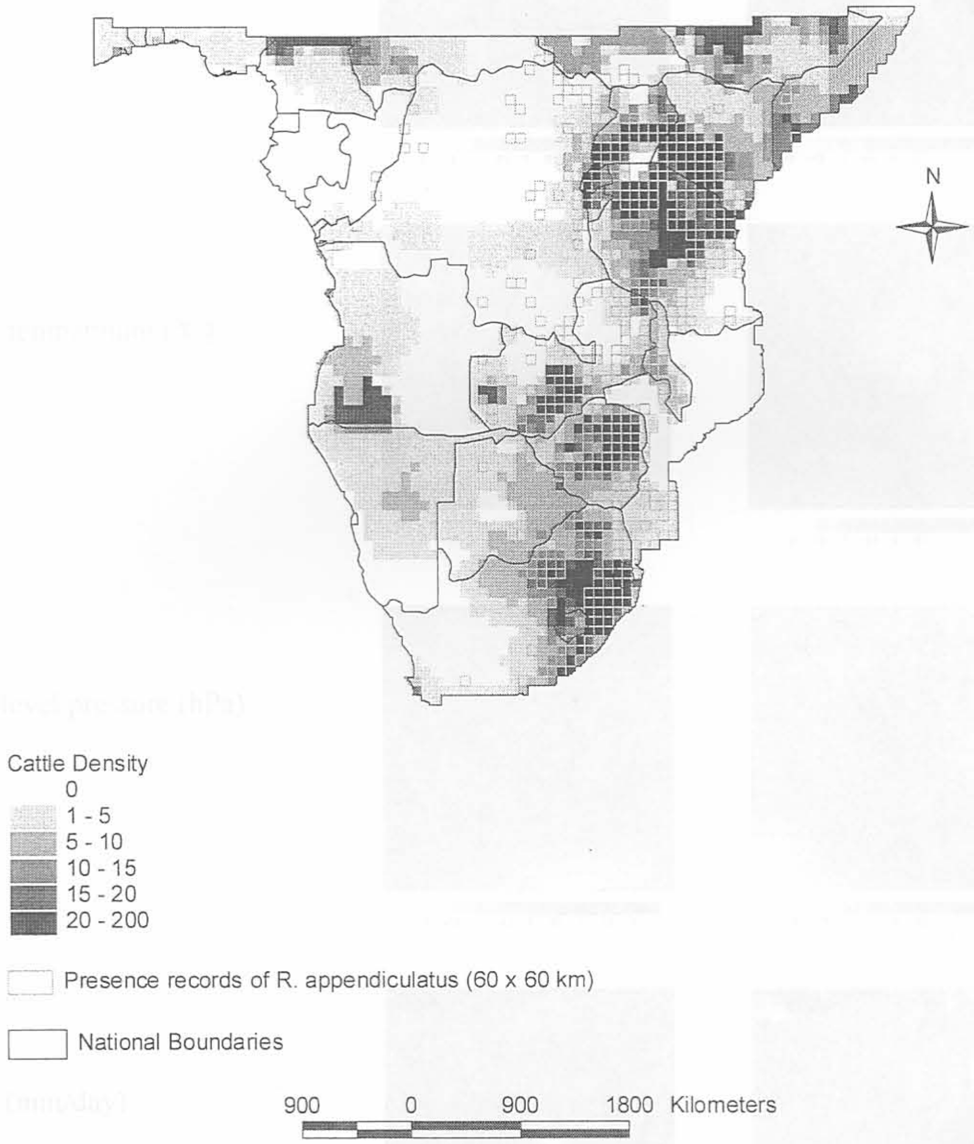

N
Cattle Density
0
1 - 5
5 - 10
10 - 15
15 - 20
20 - 200
Presence records of R. appendiculatus (60 x 60 km)
National Boundaries
900
0
900
1800
Kilometers

Figure 3

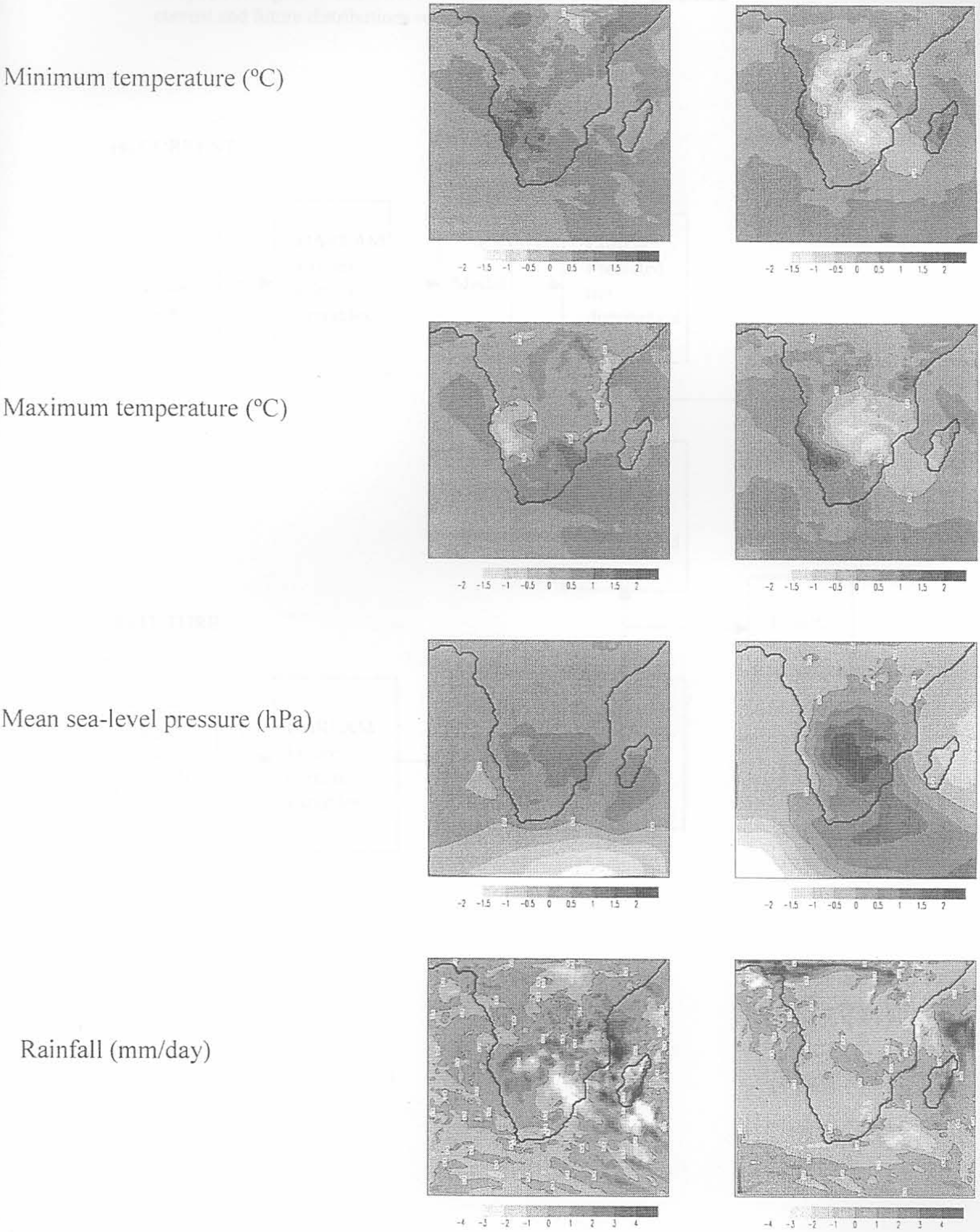

Minimum temperature (°C)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Maximum temperature (°C)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Mean sea-level pressure (hPa)
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
-2 -1.5 -1 -0.5 0 0.5 1 1.5 2
Rainfall (mm/day)
-4 -3 -2 -1 0 1 2 3 4
-4 -3 -2 -1 0 1 2 3 4

Figure 4

Simplified diagram of how the *R. appendiculatus* and ECF predicted current and future distributions were obtained

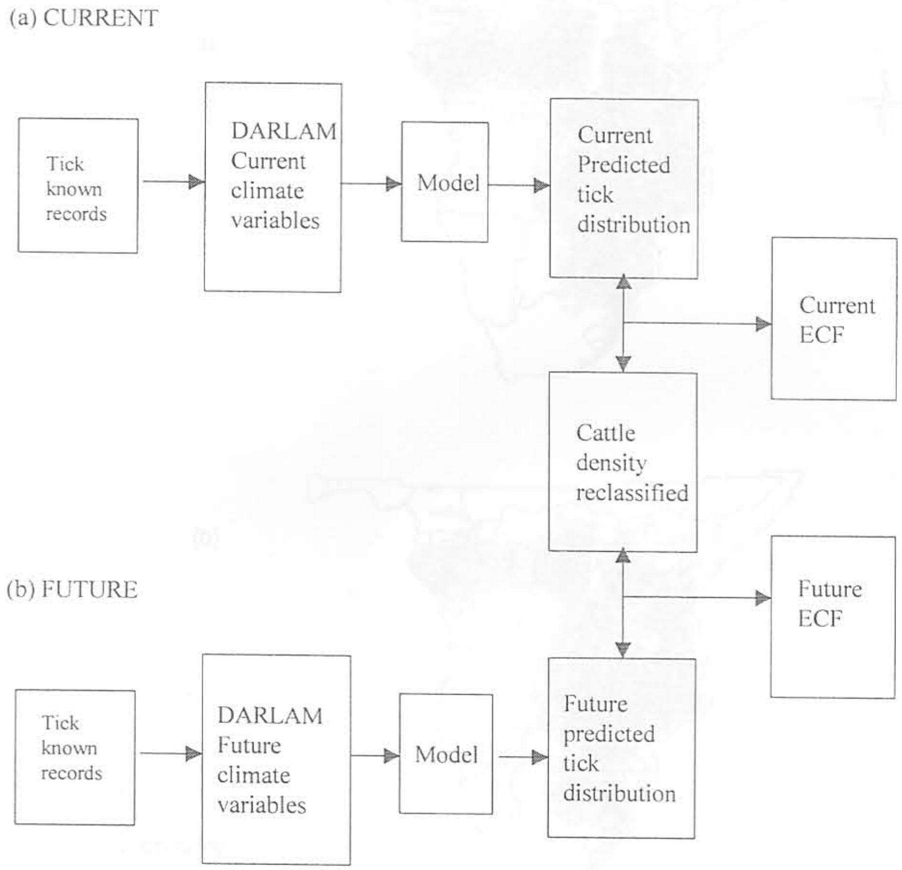


Figure 5

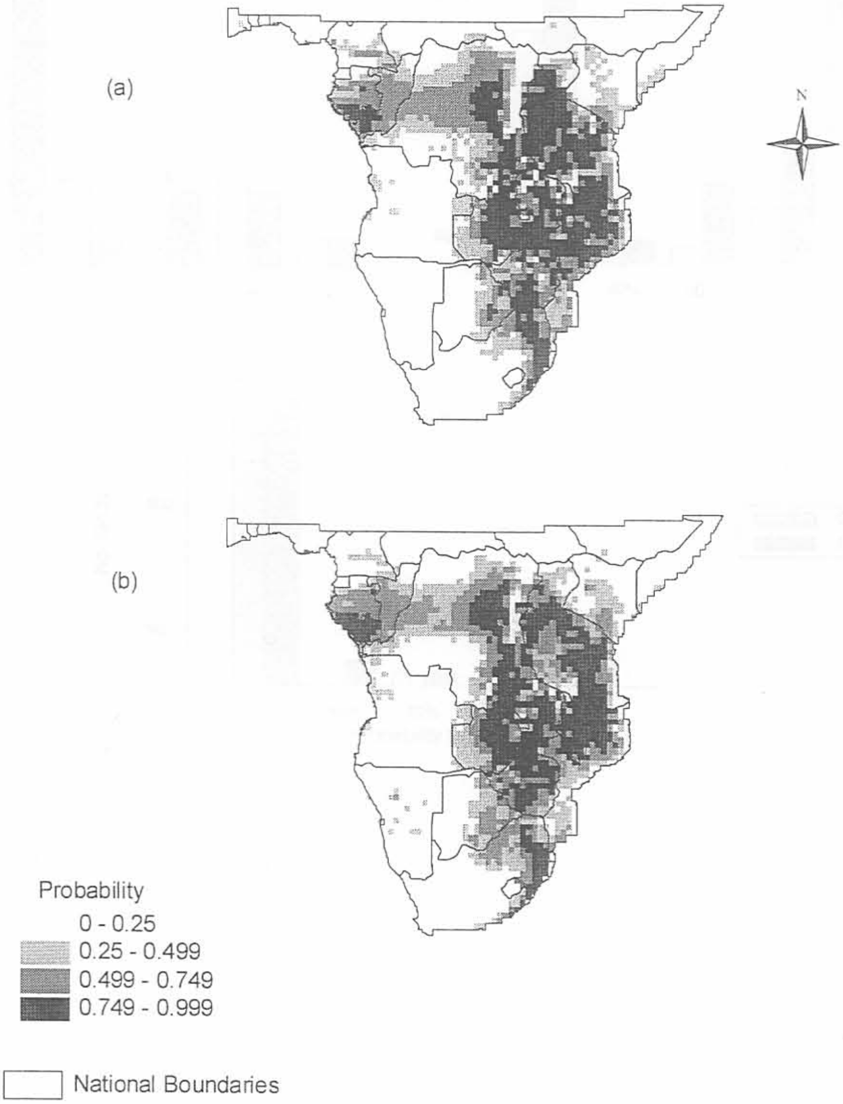

(a)
N
(b)
Probability
0 - 0.25
0.25 - 0.499
0.499 - 0.749
0.749 - 0.999
National Boundaries

Figure 6a

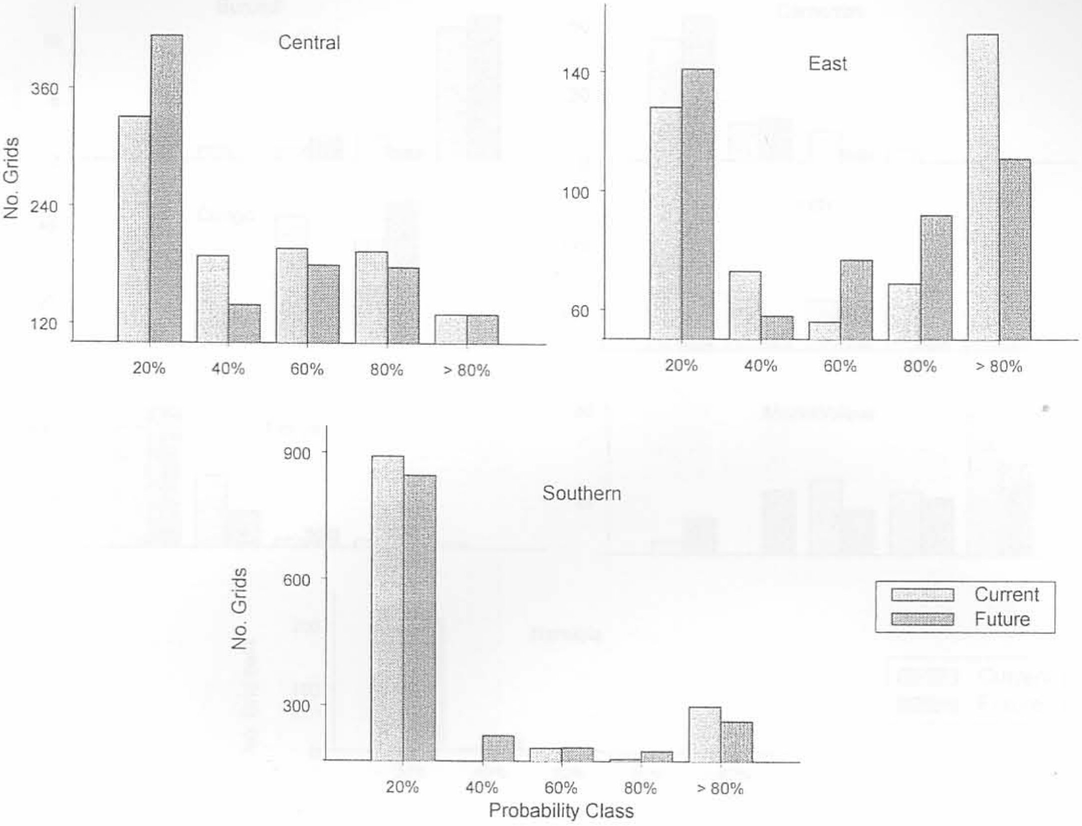

Central
No. Grids
360
240
120
20%
40%
60%
80%
> 80%
East
140
100
60
20%
40%
60%
80%
> 80%
Southern
No. Grids
900
600
300
20%
40%
60%
80%
> 80%
Probability Class
Current
Future

Figure 6b

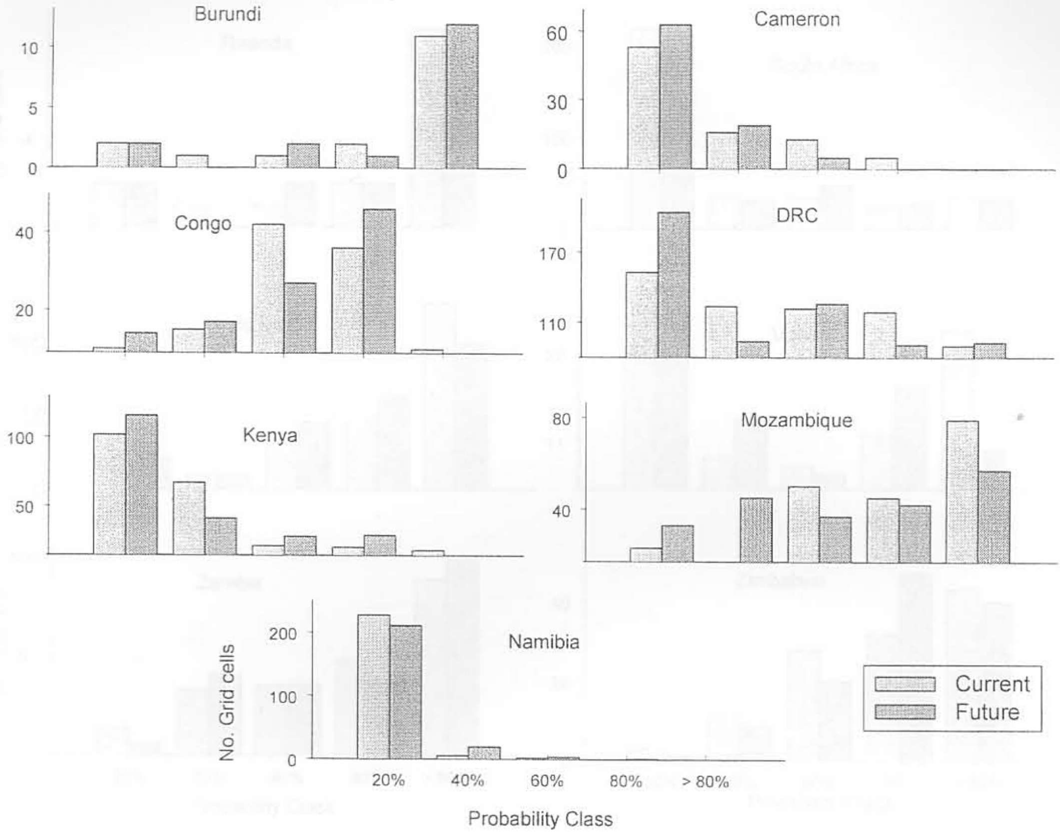

Burundi
10
5
0
Camerron
60
30
0
Congo
40
20
DRC
170
110
Kenya
100
50
Mozambique
80
40
Namibia
200
100
0
No. Grid cells
20%
40%
60%
80%
> 80%
Probability Class
Current
Future

Figure 6b continued

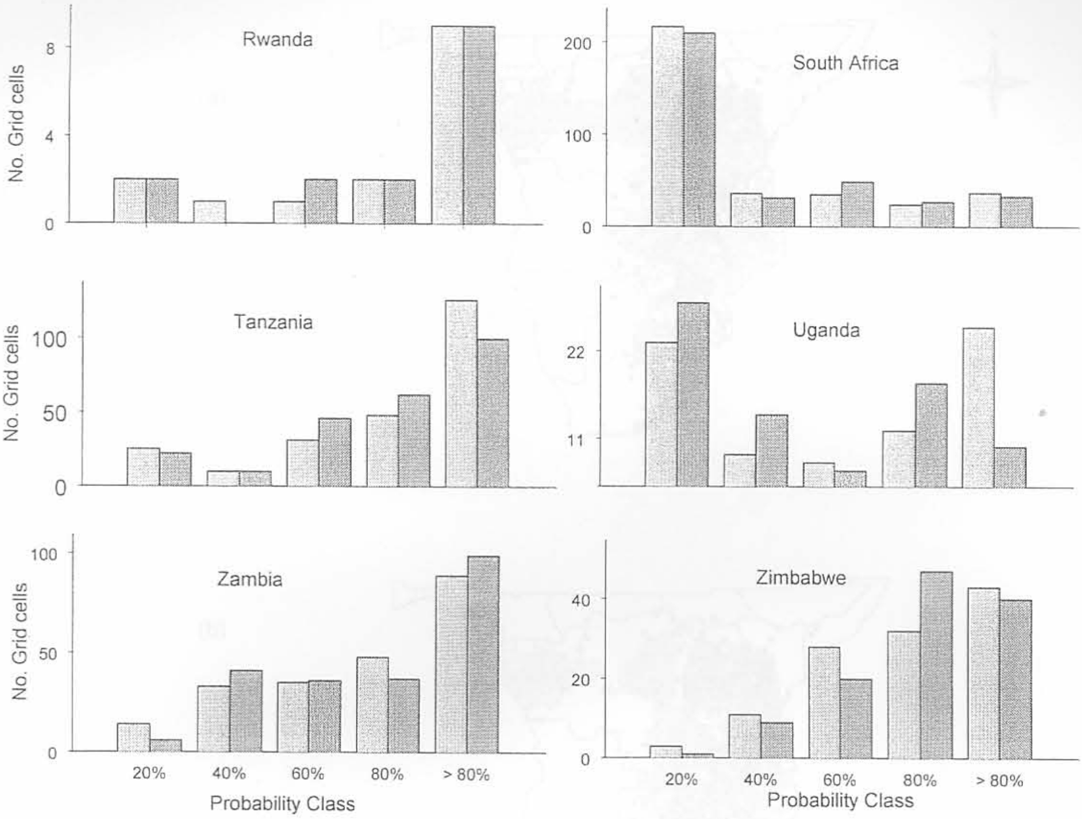


Figure 7

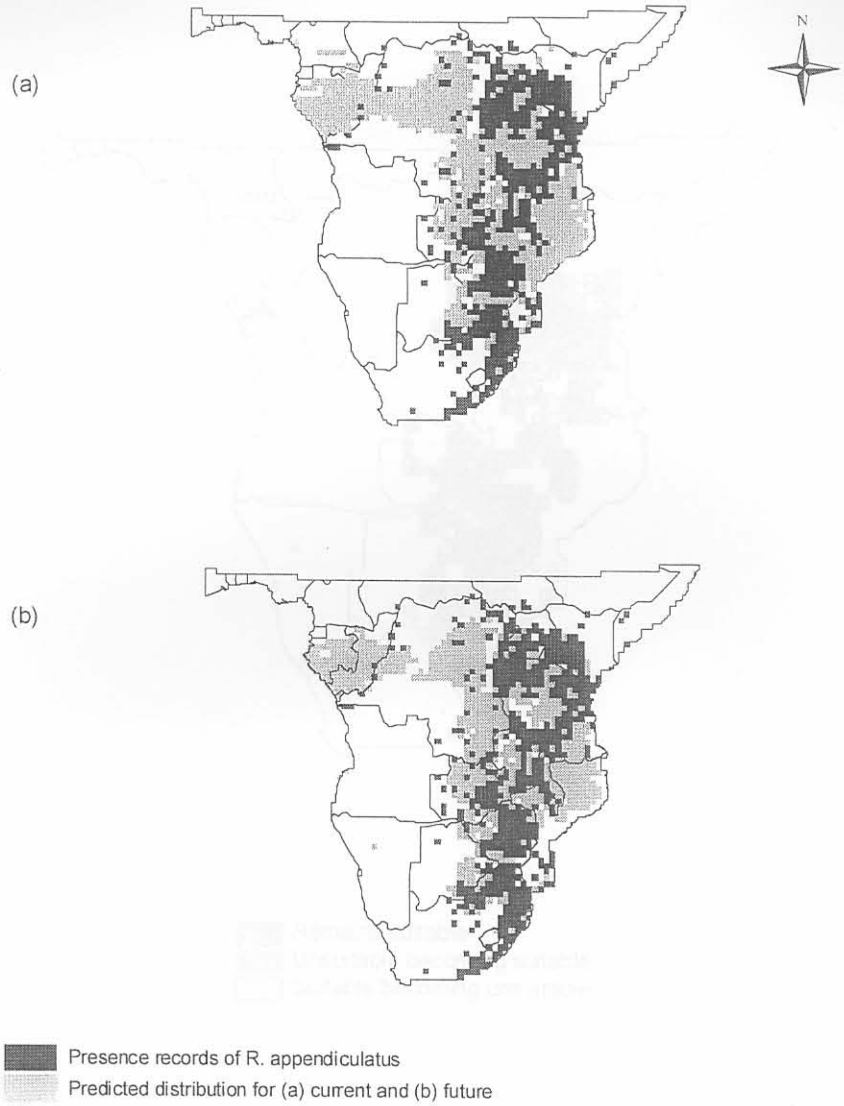
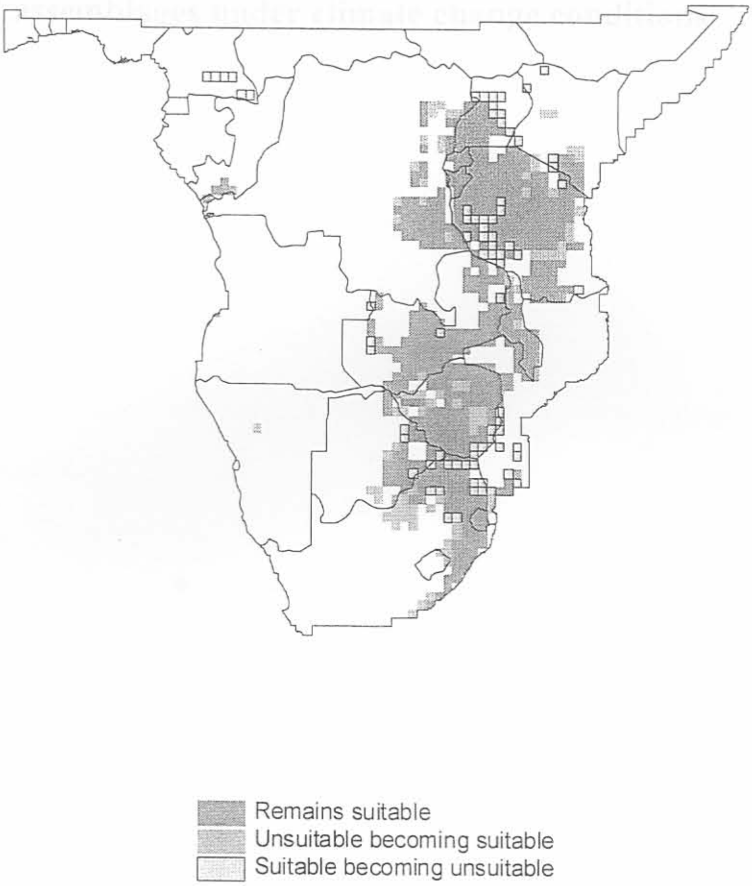

N
(a)
(b)
Presence records of R. appendiculatus
Predicted distribution for (a) current and (b) future

Figure 8


▨ Remains suitable
▨ Unsuitable becoming suitable
☐ Suitable becoming unsuitable

CHAPTER FIVE

Host assemblages under climate change conditions

Host assemblages under climate change conditions

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Key words: Host assemblages, sub-Saharan Africa, *R. appendiculatus,* predictive species modelling, "dilution effect".

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ABSTRACT

The predicted current and future ranges of ten preferred vertebrate host species of *Rhipicephalus appendiculatus* were obtained using a predictive species model and 6 climate variables provided by a regional climate model DARLAM (Division of Atmospheric Area Model). Visually and statistically significant differences between the current and future predicted ranges (probability of occurrence) for individual host species were evident from these results. Different host species reacted differently to climate change conditions. Although contraction was the main range alteration predicted, the future predicted distribution of the more generalist species expanded. The results also showed reduction in the range of the total host assemblage in the future climate. The predicted future range of the host assemblage intimately involved in ECF transmission was also altered at different degrees in different areas in sub-Saharan Africa. Increased probability of this assemblage was predicted in Tanzania, Angola and Mozambique. The implication of these results on future tick abundance and ECF transmission were discussed using the Lyme disease "d*ilution effect"* model. In order to minimise the anticipated climate change impacts, country specific concerted conservation efforts should be put in place. The knowledge of the existence and proximity of wild animal species to livestock production areas is vital in future tick-borne disease and particularly ECF control in sub-Saharan Africa.

INTRODUCTION

The specific climate requirements of tick species are well recognised both in field studies and modelling exercises (see chapters 2-4). These and other previous studies have undoubtedly emphasised that a suitable climate is key in influencing the distribution of ticks. Under a range of climate change scenarios, significant range alterations for ticks have been postulated. However, ticks exhibit a dual lifestyle in which they must constantly alternate between hiding in protected spaces and climbing up vegetation in a quest to obtain suitable hosts (Londt & Whitehead 1972). It is this latter part of the ticks' existence that forms the core of this chapter. While a large number of studies report that suitable hosts play a significant role in ticks and tick-borne disease systems, (Norval & lightfoot, 1982, Norval *et al.* 1982; Perry *et al.* 1990; Oliver 1989; Gallivan & Surgeon 1995; Randolph & Rogers 1997; Uilenberg 1999; 2000; Randolph 2002; Estrada-Pena 2003), there are limited field studies in Africa to adequately support this claim.

The two principal requirements for a successful tick population are known to be a suitable environment for the survival of the free-living stages and the presence of suitable hosts in sufficient numbers (Norval & Lightfoot 1982). In a given environment, it can therefore be assumed that the density of suitable hosts must exceed a certain threshold level before a tick population can become established (Estrada-Pena 2003). Moreover, it follows that this host density threshold must increase as environmental suitability declines to compensate for increased mortality in the free living stages of the ticks i.e. lower tick survival rates must be counteracted by increased probability of finding a suitable host. This leads to the expectation that when host densities in suitable climates exceed a certain threshold level, then the size of the tick population is expected to increase (Estrada-Pena 2003). However, different host species also differ in their ability to support tick numbers and in their ability to contain a specific pathogen.

Host species are not only important for ticks because they act as suitable hosts but because biodiversity per se plays an important role in the maintenance of ticks and tick-borne diseases (Ostfeld & Keesing 2000a; Schmidt & Ostfeld 2001). The phenomenon known as the '*dilution effect*' assumes that communities of hosts characterised by high species richness or evenness are likely to contain a higher proportion of hosts that are inefficient in transmitting the disease agents to a suitable feeding vector. The greater the abundance of weakly competent reservoir species, the stronger the '*dilution effect*' and the lower the probability of disease transmission for any given bite. However, these communities of incompetent reservoirs could increase the density of vectors by providing the vector population with more feeding opportunities than they would have in species poor communities. Thus more diverse communities of incompetent hosts could simultaneously decrease infection prevalence and increase the population density of vectors, with unpredictable net effects on disease risk in humans and livestock (Schmidt & Ostfeld 2001). An understanding of this relationship underpins a more sustainable management basis for these diseases and a better approach towards their epidemics.

Epidemics of vector-borne diseases are usually followed by attempts to eradicate the vector, the reservoir host or both. Eradication programs appear to be rooted in classical disease ecology that disease transmission is determined by a single intermediate and definitive host (Schmidt & Ostfeld 2001). This classical framework promotes the logic that knocking out the system's dominant players is both necessary and sufficient to reduce diseases transmission. Such efforts often use a non-specific chemical treatment that results in the destruction of vector or host habitat, both of which may foster unintended and undesirable ecological consequences. These eradication programs rarely succeed in eliminating the diseases (Schmidt & Ostfeld 2001). The reason for this is that in reality, pathogens often reside in many species of vectors and hosts, which vary in their ability to support survival and reproduction of the pathogen population. Thus an exclusive focus on the perceived dominant players may fail to take advantage of natural ecological processes that influence disease transmission (Schmidt & Ostfeld 2001).

In Africa, detailed field data regarding the relative importance of hosts and biodiversity in determining the distribution and abundance of ticks and the prevalence of tick-borne diseases remain limited and vague. In this chapter initial modelling attempts are made to explore how climate change may affect species diversity and evenness in the community of hosts for *R. appendiculatus*. From these results, conclusions were made regarding relationship between tick abundances, host ranges and the transmission potential of ECF. East Coast Fever was used as a model system because it is the most common tick-borne disease in sub-Saharan Africa (Okello-Onen *et al.* 1999) and because the natural history of the pathogen (*Theileria parva*), the primary tick vector (*Rhipicephalus appendiculatus*) and its vertebrate hosts are all relatively well understood (Walker *et al.* 2000). Consequently, this chapter will i) review the available information regarding the relative importance of hosts in determining the distribution and abundance of ticks and tick-borne diseases ii) review the available information regarding the importance of biodiversity for the maintenance of ticks and tick-borne diseases iii) summarise ECF natural history iv) obtain the predicted current and future climatic suitability of African environments for the hosts using a simple climate envelope model and a regional climate model DARLAM, v) from this modelling exercise assess anticipated host assemblage changes vii) use the Lyme disease "dilution effect" model to assess the implications of these changes for tick abundance and ECF prevalence in sub-Saharan Africa.

It may be argued that the Lyme disease model is not suitable for ECF since Lyme disease is biodiversity driven and ECF is mainly driven by a single host (cattle). However, the effect of other wild animals in ECF transmission is well acknowledged and the exclusion of wild animals from cattle-grazing environments is advocated as a measure to reduce the risk of the disease in cattle (Grootenhuis *et al.* 1987a). Therefore, wild hosts play a vital role in ECF transmission and any change in climate suitability that may result in reduction/ expansion/ shift in the ranges of these wild animals would impact heavily on ECF prevalence. It is hoped that these results will complement the work done in previous chapters and also initiate field studies that look at the importance of hosts' assemblages for tick distributions and abundances as well as tick-borne disease prevalence.

REVIEW: HOSTS AND BIODIVERSITY IN TICK-BORNE DISEASE TRANSMISSION

Importance of hosts in limiting tick ranges

In order to study the importance of hosts in limiting ticks and tick borne disease ranges under current and future climates, long-term field studies are essential because they provide the only means of detecting those climatic and biotic variables that affect the population processes and that lead to fluctuations in the numbers of parasites (Estrada-Pena 2001b). These long-term studies are complicated, first by the mobility of hosts and the existence of numerous 'unknowns' in the tick-host-disease system. They are also very laborious and time consuming and usually lack sufficient funds to effectively execute them. These studies are also complicated because they would ideally involve translocations of some of the hosts so that the relative importance of each host species can be evaluated. Where hosts have been used, like in the *Boophilus decoloratus* model (Estrada-Pena 2002), only cattle density was used because the distributions of other hosts are reportedly difficult to map. Yet, they form an important feature of any tick life cycle model, especially as they play a major role in regulating the host-finding period and the subsequent mortality of the host-finding larvae (Estrada-Pena 2001b).

Furthermore, tick life cycles vary from those that require a single host species, in which the ticks develop from larva to adult, to two or three-host species, in which the ticks feed on two or three different host species before they complete their development. This would therefore necessitate studying more than one host species. Throughout the life of a tick suitable hosts are therefore crucial because of the dependence of each tick developmental stage on a blood meal. Hard ticks such as the family Ixodidae, to which *R. appendiculatus* belongs, take very large meals (10-100) times their body weight only once per life cycle stage. This intimate relationship between ticks and hosts characterised by feeding, development, elimination of excess ions and water and the exchange of microorganisms form fundamental and crucial parts of a tick's life cycle (Randolph 2002). Furthermore, the seasonal dynamics of ticks is to a greater degree influenced by the availability of hosts. Detailed quantitative analysis of published tick datasets summarised by Randolph & Rogers (1997) reported that three of five factors that determine the seasonal dynamics of ticks, were host related. These factors are i) facultative diapause, manifested as a delay in the onset of host-questing behaviour ii) very strong density dependence in the interstadial mortalities caused by hosts' response and iii) tick questing activity characterised by a certain level of daily mortality plus a certain probability of successfully contacting a host.

The importance of a host for the successful growth and reproduction of a tick cannot be understated but it is not clear whether ticks are primarily habitat specialists that feed on any available hosts within their chosen environment, or whether they select certain hosts and are constrained to habitats where these hosts are found (Klompen *et al.* 1996). In an attempt to clarify this association, Cumming (1998); (1999a), analysed numerous recorded data of African tick species and their hosts and concluded that the overwhelming majority of African tick spp are not host-specific and show no evidence of being host-limited. Of the 55 species frequently collected from cattle, 48 were far less widely distributed than cattle; a further 22 species are absent from a large part of the range of their particular non-cattle hosts. Thus it appears that ticks occupy only a sub-set of their hosts' ranges, with the broad-scale boundaries to their ranges being set by abiotic factors (Cumming 1999a). This general analysis of a large data set was recently questioned (see ICCTD News letter December 1999) (http://www.uu.nl/tropical.ticks).

In addition to this, field studies on the importance of hosts elsewhere have reported that at local scales the absence or scarcity of hosts in any part of a region within a tick-permissive environment will cause patchy distributions, so that, for example, ticks may be absent in fields or residential areas but present in adjoining woodlands inhabited by appropriate vertebrate species (Randolph 2001). There is also some compelling evidence (reviewed by Spielman *et al.* 1985; Barbour & Fish 1993), that in the US deforestation and the elimination of deer during the 18th and 19th centuries destroyed the pre-existing conditions suitable for *Ixodes scapularis* populations. These conditions were subsequently re-established from 1926 onwards, first through the reintroduction and proliferation of deer, and finally by the spread of ticks from their refuges on certain undisturbed islands. The effects of fallow deer (*Dama dama*) on *Ixodes ricinus* abundance has also been documented in Ireland, where tick densities were significantly higher inside than outside a fenced deer park (Gray *et al.* 1992).

The conclusion that the overwhelming majority of African tick spp are not host-specific (Cumming 1999a) was supposedly contrary to field observations that found that ticks do not feed on any available hosts since some ticks are known to feed only on a particular group of hosts and not others (see ICCTD News letter December 1999 and chapter three). Moreover, from numerous field observations (Short & Norval 1981; Norval & Lightfoot 1982; Perry *et al.* 1990; Oliver 1989; Norval *et al.* 1982; Gallivan & Surgeon 1995; Uilenberg 1999; 2000), it appears that *R. appendiculatus* for instance is far more abundant on cattle or buffalo than any other hosts. In addition, cattle are not often regarded as the natural hosts of these species (Uilenberg 1999; 2000). Other known tick-host specific relationships are *Rhipicephalus sanguineus* that is reported to feed exclusively on dogs and other wild canines (Uilenberg 2000) while *Rhipicephalus distinctus* feeds on Hyraxes, *Rhipicephalus occulatus* on scrub hares and other hares (Horak pers. comm). The fact is that many species appear to have clearly defined 'preferred' hosts or host groups (Uilenberg 2000).

Additionally, ticks do not fly and the nest-dwelling Argasid (soft) ticks live in semi permanent close association with their hosts and their mortality rates are more closely related to biotic than abiotic factors (Randolph 1998), Ixodid ticks (hard) though not nidiculous, climb on to vegetation where they contact a passing host. In instances where there is no shortage of hosts, the next location of this waiting tick depends on the distance that the host travels. Dispersal of the tick is therefore largely dependent on host mobility. In Africa, Minshull & Norval (1982) reported that the spatial distribution of *R. appendiculatus* larvae, nymphs and adults is determined by the spatial distribution of the hosts over different seasons. Seasonal changes in habitat use of the hosts may also affect the timing of the activity periods of ticks and therefore the likely infestation rates. Gallivan and Surgeon (1995) also reported delayed infestation due to a lack of hosts in

Swaziland. In this latter study, it was reported that seasonal shifts in habitat use by kudu and impala determined the activity periods of the tick.

Furthermore, hosts play an important role in determining the numbers of ticks and tick-borne diseases. Randolph and Rogers (2000) attributed the increases in *Ixodes ricinus* and Tick-borne Encephalitis Virus (TBEV) to the increased availability of livestock hosts for adult ticks, leading to higher tick densities in sites accessible to humans. Also in the US the high incidences of Lyme borreliosis (Randolph & Rogers 2000) corresponded with areas of high deer populations to support the tick population (Dister *et al*., 1997) and mice and birds as competent reservoirs (Wilson *et al.* 1985). There is also evidence to the effect that infection rate of ticks in the field range between 30-80 % (Fleetwood *et al.* 1984) and can rise even higher during unusual events such as mouse plagues. From these reports, it appears that hosts do play an important role in setting the geographical limits of tick distributions and tick-borne diseases. However, more field studies are necessary to clarify the parts played by different hosts for different tick species and the contributions made by biodiversity in reducing tick-borne diseases.

Biodiversity and the risk of exposure to tick-borne diseases

Ticks and tick-borne diseases have plagued many parts of the world, and Africa in particular, for a very long time. As pointed out by Randolph (2004), "Vector-borne diseases are bad enough in the northern hemisphere, but in Africa they have scarred the entire continent. Diseases carried by ticks and the tsetse fly have made it impossible for Africans to keep livestock successfully, and this has had a devastating impact on the history of the continent" (http://www.anapsid.org/lyme/riseinticks.html). So far no proper control practice has managed to reduce this impact to manageable levels. One of the main reasons for this is that control usually follows an outbreak and in order to alleviate this epidemic the quickest acting methods of control are preferred and these are mainly directed at treating the disease or the eradication of the vector. In most cases farmers are advised to increase dipping to reduce tick numbers. Such a method of control is not successful partly because most ticks that are of economical importance in Africa are generalists that not only feed on cattle and other domestic animals but also use a number of wild reservoirs. Therefore controlling the disease in cattle only is not sustainable because the infections can be maintained in the reservoir hosts until such a time as they are transferred back to the domestic animals. Taking into account current human population expansions, overexploitation of our natural resources and concurrent climate change, African livestock farmers are likely to move in search of greener pastures. This inevitable movement, which is exacerbated by low levels of law enforcement, means that encroachments into nature reserves or other areas in close proximity to wild animals can be anticipated. In this case the issue of the knowledge and inclusion of reservoir hosts in tick control efforts becomes increasingly important.

It is imperative to understand and identify how the disease flows through the host population and more specifically which host individuals are responsible for the majority of the transmissions (Perkins *et al.* 2003). In the case of tick-borne disease transmission, the key hosts are those that support large numbers of vectors. A particularly important variable in macro parasites-host systems is the observation that the majority of hosts harbour a minority of the parasites and that a minority of hosts support the majority of the macro parasite population (Shawn & Dobson 1995). Woolhouse *et al.* (1997) examined contact rates between vectors and their hosts and showed that not only were these highly variable between individual hosts but also displayed a negative binomial distribution. This has a major impact on the basic reproductive number, R_o (the ability of a pathogen to invade or persist within a population). An infection can establish if $R_o > 1$ but if $R_o < 1$ then an infection cannot invade or persist. The study also identified that 20% of hosts contributed some 80% of the transmission potential, conforming to the '20/80' rule. This pattern has important consequences for the control of parasites and pathogens, since if the 20% of hosts that account for 80% of diseases transmission can be identified and targeted to the extent that R_o falls below one, the impacts of control efforts would be maximised. Also, it is fundamentally important in vector-borne disease control to identify the reservoir of infection, that is the epidemiologically connected populations or environments in which the pathogen can be permanently maintained and from which infection is transmitted to the target population (Woolhouse *et al.* 1997).

In other parts of the world, the theory termed the "dilution effect" (Van Buskirk & Ostfeld 1995; 1998: Ostfeld & Keesing 2000 a; b) described in earlier paragraphs is gradually being explored for other vector-borne diseases. A model was used to explore the effects of changes in the community of hosts for juvenile ticks on the abundance and infection prevalence of nymphs. This model was used on *Ixodes scapularis* and its host communities in the eastern and central United States, with one competent reservoir and one to several alternative hosts with low or non-existent transmission efficiencies. As *I. scapularis* ticks feed successfully from a variety of vertebrate hosts, the simulation model found that tick density was relatively insensitive to changes in the relative abundance of competent versus incompetent reservoirs. The infection prevalence of nymphal ticks however was dramatically reduced when the relative abundance of non-mouse hosts was increased. The model varied the species diversity (species richness + evenness) within the host community and showed that increasing the diversity of hosts reduced disease risk as measured by the infection prevalence of nymphal ticks. Therefore from this modelling study it seems that any factor that decreases the representation of the White-footed mice relative to other hosts in the vertebrate community would reduce the proportion of ticks infected with the Lyme disease spirochete. This reduction can be achieved in two ways i) to reduce the abundance of White-footed mice while maintaining the presence of alternative hosts species, ii) to increase the number of alternative hosts, which typically are incompetent reservoirs. In this chapter a predictive species model was used to test this outcome on the tick vector, *R. appendiculatus,* its community of hosts and ECF transmission in sub-Saharan Africa.

Transmission Cycle of ECF

East Coast Fever (ECF) is caused by a protozoan parasite *Theileria parva*. It is an acute, tick-borne disease causing high rates of morbidity and mortality in cattle in 12 countries in sub-Saharan Africa (Norval *et al.* 1992). One million cattle die each year from ECF with an annual economic cost estimated to be $168 million (Dolan 1999). As the livelihood of smallholder farms, often managed by women, depend on one or two cattle, the financial burden due to loss of income and livestock products impacts on the quality of all aspects of family life. The brown-ear tick, *Rhipicephalus appendiculatus*, transmits the parasite (*T. parva*) through sporozites released in feeding activity (Norval *et al.* 1992). Normally, for transmission to occur, the infected tick must be attached for several days to enable sporozites to mature and be emitted through the tick's saliva (Chen *et al.* 1991). However, under high ambient temperatures, ticks on the ground may develop infective sporozites, which can be transmitted to cattle within a few hours of attachment (Norval *et al.* 1992).

Before the life cycle of ECF is reported, a short summary of the *R. appendiculatus* life cycle is provided in order to ensure that the transmission route of *T. parva* is clear. The life cycle of *R. appendiculatus* begins as an egg on the ground that hatches into a larva. The larva climbs onto a suitable host and feeds for about a week before detaching. This larva then changes into a nymph after about 1 week to 8 months depending on the climate. The nymph climbs, feeds on a suitable host, engorges for 3 to 11 days, detaches, and changes after about a month into an adult male or female. This adult tick climbs up grass/ plants and waits for a suitable host. When a warm-blooded animal walks past, the tick can crawl onto them and begin feeding. Ticks insert their mouthparts, attach to their prey and engorge themselves with a blood meal. During feeding tick saliva can get into the host's body and blood stream. Any tick infected with *T. parva* can then inadvertently spread it to the host. Male and female ticks usually mate while attached to the host. A few weeks later, the engorged female detaches from the host and lays her eggs (1000 - 8000 eggs) on a leaf.

The full life cycle of *T. parva* is complex and some stages are poorly understood. It begins when a *R. appendiculatus* tick bites a host and introduces sporozites, which invade lymphocytes where they develop into intracytoplasmic, multinucleated schizonts. The infected animal then develops a lymphoma-like disorder that is rapidly degenerative and usually fatal; many animals die within 3-4 weeks of infection (Norval *et al.* 1992). This disease is not transmitted to ticks transovarily (Harwood & James 1979) and all eggs are therefore free of the diseases. The newly hatched larvae are therefore free of the pathogen but can acquire the pathogen during its first feed. Cattle are the preferred domestic hosts of all stages of development of *R. appendiculatus* (Norval *et al.* 1982; Okello-Onen *et al.* 1999). The preferred wild hosts of all stages of development are African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), sable antelope (*Hippotragus niger)* impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus ellipsiprymnus)* (Horak *et al. 1*983; 1995; Norval *et al.* 1992). The African buffalo (*Syncerus caffer*) is a reservoir of *T. parva* infection, and it has recently been demonstrated that waterbuck (*Kobus* spp.) also act as reservoirs (Norval *et al.* 1992). Buffaloes may suffer clinical symptoms from *T. parva* infection, but its effects on waterbuck are unknown.

MATERIALS AND METHODS

Study area

This study covers sub-Saharan Africa as defined in the previous chapters. The area was divided into 3000 grids cells of 60 x 60 km resolution, a resolution that was determined by DARLAM (Engelbrecht *et al.* 2002) climate fields.

Modelling species distribution

The distribution of *R. appendiculatus,* cattle density layer and climate data used in this chapter were described in the previous chapters. The distribution data of indigenous host species were obtained from a Databank for the Conservation and Management of the African Mammals (AMD) (Boitani *et al.* 1999). The 'original data' about host distributions were obtained from numerous published maps and converted into GIS (Arc/Info, ESRI, USA) polygon coverages. Known extent of occurrence of the "preferred host group" was used in this study (Boitani *et al.* 1999). For comparative purposes, the extent of occurrence of those host species that support the immature tick stages is represented. This was done as it is established that changes in the numbers of hosts will influence tick abundances (Horak *et al.* 2000). This Horak *et al.* (2000) study showed that an increase in the abundance of larvae and nymphs of *R. simus* and *R. turanicus* in 1994 was in response to the rodent population explosion towards the end of 1993. There was however, no concomitant increase in the population of *R. appendiculatus* that does not feed on rodents. However, smaller antelope species and hares are considered good hosts of immature stages of *R. appendiculatus* (Walker *et al*. 2000). Thus, for this study the following additional host species were considered: *Lepus capensis* (Cape or brown hare), *Lepus saxatilis* (Scrub hare) and *Lepus victoriae* (African Savanna hare). Using the same six-climate variables (chapters 2-4), the known extent of occurrence of the relevant host species were used as input variables into the habitat model (Erasmus *et al*. 2002). These point localities were imported into ArcView GIS and by means of a spatial intersect; each 60 x 60 km grid was assigned a host presence or absence and allocated its relevant climate variables. The modelling was executed in SPLUS. From the known distribution records of the accepted host species, the predicted current distribution was initially obtained using the current climate as described in the previous chapters. To obtain the future distributions of the host species, the grid cells were populated with future climate data (see chapter 3).

Current and future distributions of host species

The current and future predicted distributions of 10 host species that are known to support the life cycle of *R. appendiculatus* were generated using the modelling process described previously. The suitability of this model for predicting species geographic ranges was assessed in previous studies for South African fauna (Erasmus *et al*. 2002) as well as African tick species (Olwoch *et al*. 2003). This evaluation resulted in acceptable comparisons at a probability of occurrence level of 50% and above. In the present study, when the predicted current distribution for buffalo was compared with the known extent of occurrence (≥ 50% probability of occurrence), more than 90% of the predicted range corresponded with the known extent of occurrence (Figure 1). From this high degree of overlap and on the strength of previous model validations (Erasmus *et al*. 2002; Olwoch *et al*. 2003) the same model was applied to all host species in the present study.

Analysing host distribution range changes

The following analyses were performed to compare the current and future predicted distributions of hosts in response to climate change i) analysis of changes in the overall geographical distributions of individual host species (probability of occurrence) between the current and the future climates. Whether or not these differences were significant was analysed by Kolmogorov-Smirnov two-sample test (StatSoft, Inc. (2001) ii) a comparison between the number of grid cells occupied in various probability of occurrence classes (0-<20%, 20- <40%, 40 - <60%... 80-100%) between the current and future distributions per host species iii) analysis of host assemblage changes (all hosts) between the current and future predicted distributions iv) analysis of shifts in the distribution of the cattle-buffalo assemblage. The degree of range change was recorded and analysed and the expected implications of these changes for tick abundance and the prevalence of ECF were documented.

Host assemblage distribution changes

Analysis of host assemblage changes due to anticipated shifts in distributions were quantified as the combined probability of occurrence value for all host species per grid cell. This was used as a measure of the climatic suitability of the grid cell for the complete assemblage of hosts. The probability product rule (Wadsworth 1990) was used to combine the individual probabilities for the host species. This analysis was conducted on the "effective range" of the species. The "effective range" was taken as the areas where minimum conditions for the existence of a host were present and means that all areas of zero probability of occurrence for host species were excluded from this analysis. In addition, a separate assemblage range for two important host species (cattle - *Bos indicus* and buffalo – *Syncerus caffer*) that play important roles in ECF transmission was constructed for the present and future climate conditions.

RESULTS

Broad scale range alterations

The predicted current and future host species ranges are visibly different (Figures 1-10). Statistically, a comparison between range sizes (number of 60 x 60 grid cells occupied) between the predicted current and future distributions for host species revealed highly significant differences (Kolmogorov-Smirnov; $p < 0.001$, $N = 3000$) for the following species: cattle, Burchell's zebra, Waterbuck, Cape shrub hare, African savanna hare and Buffalo There were no significant differences between the predicted current and future range sizes of the other host species: Eland, Sable antelope, Impala and Scrub hare. Differences in the number of grid cells in different probability classes were also evident in these results revealing increases or decreases in suitability of grid cells for a host species under climate change conditions. These changes, which vary per species and probability class, are presented in table 1 and figure 11.

Analysis of distribution range changes between the current and the predicted future climates further revealed that range contractions are the main range alteration predicted for most of the host species. Ninety percent of the hosts are predicted to show range contractions ranging from 8% to 33% (Figure 12 a & b). This predicted range contraction is evident in both the hosts that support the development of all stages of *R. appendiculatus* and those that support only the larvae and nymphs. The only species predicted to show range expansion was the Cape hare, which gained some 12% in suitable area compared with its current range. The range expansion in this species may be related to its wide ecological tolerance/requirements. The Cape hare is known to occur primarily in open environments, including cultivated lands, from rich savannas to desert grasslands. It is also found in lightly wooded or bushed areas or mountain ranges.

Host assemblage distribution changes

From the range analyses it appears that under future climatic conditions (DARLAM) the range of the total host assemblage of *R. appendiculatus* is likely to decrease. Also the range size of the host assemblage considered especially important for ECF transmission decreases. The predicted current and future range for the complete host assemblage is depicted in figure 13a & b respectively. The areas that are currently most suitable for all host species (probabilities of occurrence values 0.4-0.9) are in the eastern DRC, western Tanzania, and southern Zambia, western and central Zimbabwe. The rest of sub-Saharan Africa has relatively low suitability (less than 0.4) for the entire host assemblage. There are visual reductions in the anticipated extent of occurrence of these respective host assemblages under future climate conditions (Figure 13b). The total area occupied by the probability range (0.4-0.9) visibly decreases.

The predicted current range of the host assemblage that is intimately involved in ECF transmission (cattle & buffalo) is shown in figure 14a. High to moderate probabilities of occurrence is predicted in the Gabon, Congo, southern and eastern DRC, northern Angola, Tanzania, Mozambique, Zimbabwe, northern Botswana, and eastern Namibia. Under the predicted future climates, a reduction in the anticipated ranges is noted. Very high probabilities of occurrence for the assemblage however persist in the Eastern DRC, North and central Tanzania and southwest Zambia (Figure 14b).

A comparison of the current and future predicted total host assemblage range revealed notable reductions in Congo, Gabon, the DRC, northern Tanzania, Angola, Botswana, Mozambique and in the northeastern parts of South Africa. Range expansions are evident in central Namibia, eastern DRC, southeastern Angola, eastern Tanzania, and some parts of central Zimbabwe, eastern Malawi and in the eastern parts of South Africa (Figure 15a). Comparison of the current and future host assemblages involved in ECF transmission also revealed that the general trend is towards range reduction. Eastern and southern DRC, north-western Angola, northern Namibia, North eastern parts of South Africa, western and northern Zambia, western Tanzania, southern Zimbabwe and Mozambique all show various degrees of range contraction. Increased probability of occurrence values are predicted in eastern parts of Tanzania, Angola and Mozambique (Figure 15b).

DISCUSSION

Modelling host distributions

The precise current and future part played by hosts in determining the abundance, distribution of ticks and the prevalence of tick-borne diseases in Africa is poorly documented. This is as a result of numerous difficulties in studying host distributions over time. In this chapter, the current and predicted future ranges of host species have been provided through a modelling exercise. The data and figures provided are therefore an aid to understanding how climate change may impact ticks and tick-borne diseases through their impacts on the domestic and wild animals that act as hosts for the ticks and as reservoirs to the pathogens. It can be argued that assessment of these results using existing tick-host distribution inventories is necessary. However, not all species check lists are accurate and in some instances, vast areas may not have been sampled adequately. This will mean that we have access to incomplete distribution records. This is especially true in Africa where accessibility into area and resource availability can dictate the availability of research data. Nevertheless, the climate requirements of numerous tick species and some vertebrates are well documented. Therefore using the climate requirements obvious from well sampled areas to predict species occurrences in lesser-known areas remains one of the most achievable method of assessing the likely impact of climate change on the distributions of these species. However, the precise impact of these anticipated changes on *R. appendiculatus* abundance and ECF prevalence cannot be determined since other major human-mediated factors have not been incorporated in this modelling exercise. Thus, these results are based on climate parameters alone and should be interpreted as such.

Implication of the findings

ECF and the "dilution effect"

For the "dilution effect" to work the following conditions must be applicable (i) the vector must be a generalist that parasitises at least several host species, including humans; (ii) hosts parasitized by the vector must vary strongly in their reservoir competence, such that some are highly infective and others are dilution hosts; (iii) vectors must acquire the pathogen via blood meals rather than relying predominantly on transovarial transmission; and (iv) the most competent reservoir host(s) must be dominant members of the host community, feeding a high proportion of the tick population (Ostfeld & Keesing 2000b). Since the ECF-tick-host system satisfies all of these conditions, it is assumed that the "dilution effect" model would give a satisfactory explanation of this system under conditions of a changing climate. Consequently, the impacts of the reported predicted changes in host ranges on tick abundance and ECF prevalence will be explored using the "dilution effect" model.

A decline in the suitability of most areas in sub-Saharan Africa for the host species in response to climate change would likely translate into loss of suitable habitat and possibly, at worst species losses. This conclusion is based on the existence of two major mechanisms of species loss - a decline of area and a decline in suitable habitat (Triantis *et al.* 2003). Additionally, if this change is not concurrent with a decline in the suitability of these areas for cattle rearing (suitable conditions for cattle could be supplied by humans), this would mean an increase in the probability of ticks feeding on cattle, which is considered a competent reservoirs for the parasite that causes ECF. Consequently, there will be disproportionately higher representation of cattle resulting in a high percentage of the ticks taking meals from this competent reservoir and therefore higher infection prevalence in tick populations. This higher infection prevalence in cattle may also secondarily increase disease prevalence in wildlife because many of these emerging infections in wildlife are usually caused by a generalist pathogens that "spills over" (Daszak *et al.* 2000) from other species, often from domestic animals and to a certain extent from humans, especially in cases where the population of other preferred hosts decline. These generalist pathogens maintained in one species can spill over and potentially cause devastating and repeated epidemics (Laurenson *et al.* 2003).

Furthermore, climate change may also result in land fragmentation and transformation, which may result in both demographic and living preferences for humans and wildlife a like (Daszak *et al.* 2000). In the long run this could also increase disease risk because habitat destruction and habitat fragmentation is known to cause reductions or even the elimination of some vertebrate species, particularly those larger species that occupy high trophic levels (Rosenblatt *et al.* 1999) thus reducing biodiversity even further. This reduction in vertebrate populations in some parts of sub-Saharan Africa (Woodroffe 2000) may increase disease risk both via reduction in feeding opportunities from these incompetent hosts and via the loss of regulatory effect of higher trophic level predators on typically more reservoir-competent hosts (Ostfeld & Keesing 2000a).

Moreover, if the predicted reduction in the ranges of hosts species occurs, this will almost inevitably mean an increase in their risk of at least local extinction. This is due to the negative relationship between range size and extinction probability (Gaston 1994). Such small populations are more prone to local extinction, especially through disease, since several well documented extinctions and near extinctions of threatened mammal populations have been directly caused by diseases (Woodroffe 1999) and in all cases the populations were considered small (Lawrence *et al*. 1994). For example, long term monitoring of bighorn sheep (*Canis canadensis*) populations, in California in which disease is the major cause of local extinction, has shown that small populations (=< 50 animals) are more prone to extinction than larger populations numbering 100 animals or more (Berger 1990). From the results presented, it is possible that T. *parva* infection in cattle populations might be instrumental in reducing the populations of wild hosts because most extinctions or near extinctions are caused by generalist pathogens with a wide host range which are usually contracted from domestic species. The role played by domestic hosts in wildlife disease is shown by the disappearance of rinderpest from wild ungulates following its eradication (Plowright 1982).

The predicted reduction in range sizes for host species in the more westerly parts of sub-Sahara Africa confirms earlier reports (Erasmus *et al*. 2002) for South African species. It is also in agreement with the fact that desert in Africa and the grasslands of eastern and southern Africa appear particularly vulnerable to climate change (IPCC 1997). Furthermore, the results also confirm earlier reports that different species will reacted differently to climate change (van Jaarsveld *et al.* 2000). It is evident from these results that generalists' species such as the Cape shrub hare will flourish under conditions of climate change.

This predicted general decrease in suitable habitat for the suite of host species together with the predicted increase in areas suitable for tick establishment (see chapters 3 & 4) means that a greater tick burden is likely for the available hosts. It can be argued that under these conditions increased tick mortalities will increase due to the unsuccessful host questing behaviour. But, the realised impacts of these collective changes on the tick-borne disease system will also depend on the unexplored shifts in pathogen geographic ranges, possibly putting them into contact with new host populations or species (Bergot *et al.* 2004) resulting in potential disease outbreaks as severe as those observed following pathogen imports (Harvell *et al.* 2002).

The vulnerability of the tick-host-disease system to climate change could be further influenced by other climate change consequences such as land transformation, increased human populations and subsequent activities in rural areas. These changes could place humans, their livestock and their pets into more direct contact with wild animals and the ticks that feed on them. Consequently, parasite life cycles that have been established between wild animals and ticks may now be able to include livestock, pet animals and humans as well. For instance the effect of forest fragmentation alone on the rodent hosts of Lyme disease has resulted in an increase in human exposure to the parasite (Allan *et al.* 2003).

Conclusion and recommendations

The importance of biodiversity as a source of medicine or food supply has been well documented (MA 2003). The central role played by species diversity in the performance of ecosystem functions such as primary production and for resource extraction purposes is also rapidly emerging (MA 2005). However, the importance of biodiversity in the ecology of infectious diseases is still poorly understood. The inevitable links between climate change and the emergence of new diseases including HIV/AIDS, Lyme disease, Ebola, SARS and the likely redistribution of old diseases such as Malaria and TB and associated species losses is also poorly documented. Scant information exists regarding the effects of climate change on livestock diseases in Africa and even less information regarding the importance of host species in tick abundance and tick-borne disease prevalence exist. For proper management of ticks and tick-borne disease, field studies looking at the relative importance of these hosts' assemblage are vital and will improve the existing tick-borne disease control methods in Africa. Also the regular monitoring of the reservoir hosts of infection is useful not only in devising appropriate tick-borne disease control programmes but also for the protection of the threatened wildlife species. This may incorporate managing the disease in reservoir hosts, limiting the size of the reservoir host which in turn would reduce contact rates and therefore lower the probability that the infection could persist. Also managing the diseases reservoir host would contribute significantly towards the effective control of tick borne diseases. Similar programmes were established in the past; vaccinating domestic dogs against rabies to protect lions and wild dogs and vaccinating domestic dogs to protect the Ethiopian Wolf (*Canis simensis*) (Woodroffe 1999). More important to the tick-host-disease system would be to limit the size of the reservoir host population so as to reduce the contact rate between the domestic and wild reservoir hosts.

This chapter presents a first attempt at modelling the current and future distributions of vertebrate hosts that act as suitable hosts for the tick *R. appendiculatus*. Range alteration of these hosts as a result of climate change is of concern both in terms of tick-borne disease control and in terms of conservation objectives. Since different areas in sub-Saharan Africa are predicted to show varying range alterations, country specific concerted efforts such as facilitated range shifts", protection of their remaining habitats (Hannah *et al.* 2005) and creation of corridors that will allow species to track climate change (Hannah *et al.* 2002) are necessary to counteract these climate change impacts. As far as tick-borne diseases are concerned, regulation of cattle movement is an important step towards minimising the distance between cattle and wild animals.

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TABLE 1

Percentage change in the number of grid cells between the predicted current and future distributions in different probability classes for the different hosts analysed

EBURCHEL	% CHANGE
0-20%	-3.53
20-40%	**16.14**
40-60%	**25.26**
60-80%	-17.34
80-100%	-3.37

LCAPENSIS	% CHANGE
0-20%	**23.82**
20-40%	**29.36**
40-60%	**18.86**
60-80%	-10.71
80-100%	-21.81

TORYX	% CHANGE
0-20%	-0.58
20-40%	**23.78**
40-60%	7.81
60-80%	-60.76
80-100%	**100.00**

EMELAMPUS	% CHANGE
0-20%	**4.26**
20-40%	-10.56
40-60%	**9.94**
60-80%	**2.13**
80-100%	-10.60

LSAXATILIS	% CHANGE
0-20%	**0.55**
20-40%	-28.81
40-60%	**10.00**
60-80%	-5.19
80-100%	0.00

CATTLE	% CHANGE
0-20%	-0.81
20-40%	**29.08**
40-60%	**18.23**
60-80%	**12.12**
80-100%	-20.71

HNIGER	% CHANGE
0-20%	-0.37
20-40%	**5.92**
40-60%	-10.37
60-80%	-3.92
80-100%	**7.59**

LVICTORIAE	%CHANGE
0-20%	-7.43
20-40%	**16.90**
40-60%	**72.00**
60-80%	**14.69**
80-100%	-36.80

KOBUS	% CHANGE
0-20%	**3.04**
20-40%	**44.95**
40-60%	**28.38**
60-80%	-7.10
80-100%	-20.11

SCAFFER	% CHANGE
0-20%	**11.59**
20-40%	**28.45**
40-60%	**10.24**
60-80%	-8.78
80-100%	-18.67

FIGURE LEGENDS

FIGURE 1: Predicted probability distribution of Buffalo- *Syncerus caffer* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future.

FIGURE 2: Predicted probability distribution of cattle- *Bos indicus* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future.

FIGURE 3: Predicted probability distribution of Impala- *Aepyceros melampus* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 4: Predicted probability distribution of Burchell's Zebra- *Equus burchelli* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 5: Predicted probability distribution of Sable antelope – *Hippotragus niger* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 6: Predicted probability distribution of Waterbuck- *Kobus ellipsiprymnus* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 7: Predicted probability distribution of Eland- *Taurotragus oryx* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 8: Predicted probability distribution of the Cape hare – *Lepus capensis* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 9: Predicted probability distribution of Scrub hare – *Lepus saxatilis* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 10: Predicted probability distribution of African Savanna hare – *Lepus victoriae* obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 11: Changes in the number of grid cells (60x 60 km) in different probability classes predicted in the current and future host distributions

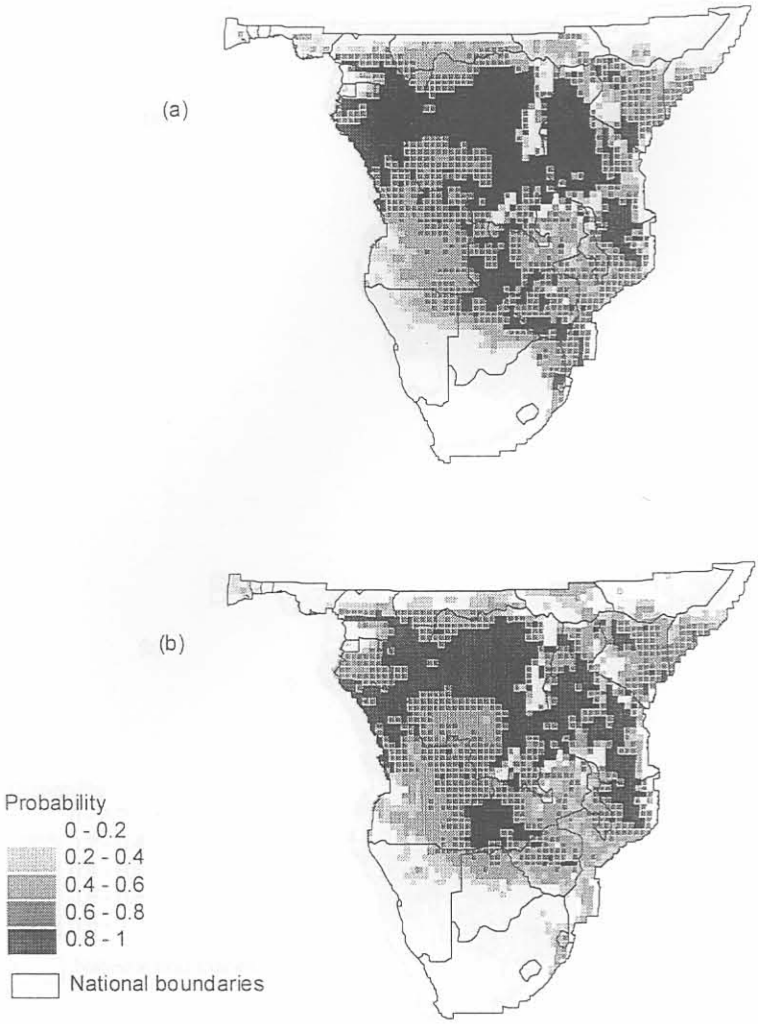
FIGURE 12: Predicted total range size changes for all host species between the (a) current and the (b) future predicted distribution under climate change

FIGURE 13: Predicted probability distribution of the complete host assemblage obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 14: Predicted probability distribution of the host assemblage that is intimately involved in ECF transmission obtained using species predictive modelling and DARLAM climate fields (a) current (b) future

FIGURE 15: Differences in the predicted probability of occurrence between the current and future predictions (a) complete host assemblage (b) cattle & buffalo assemblage

Figure 1



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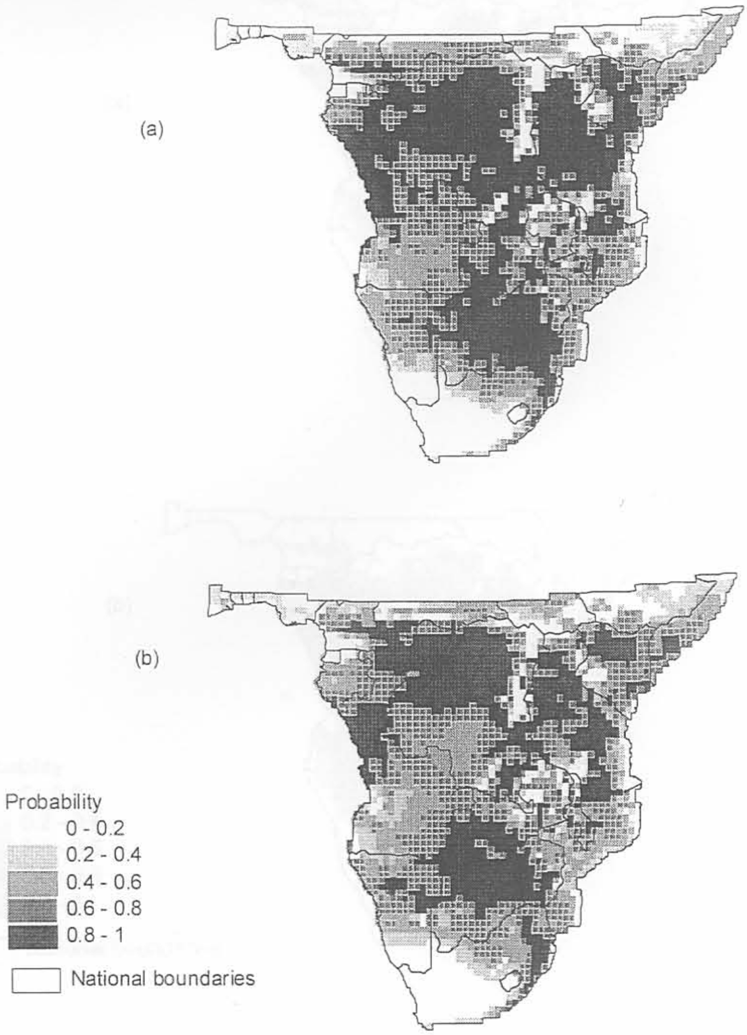

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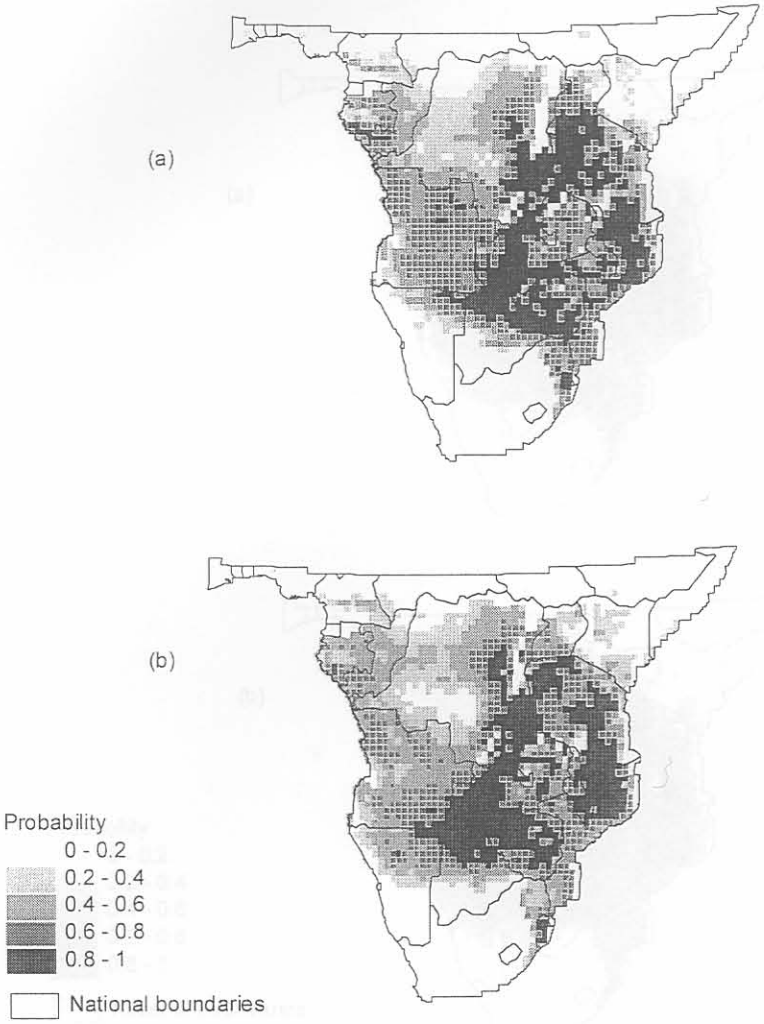

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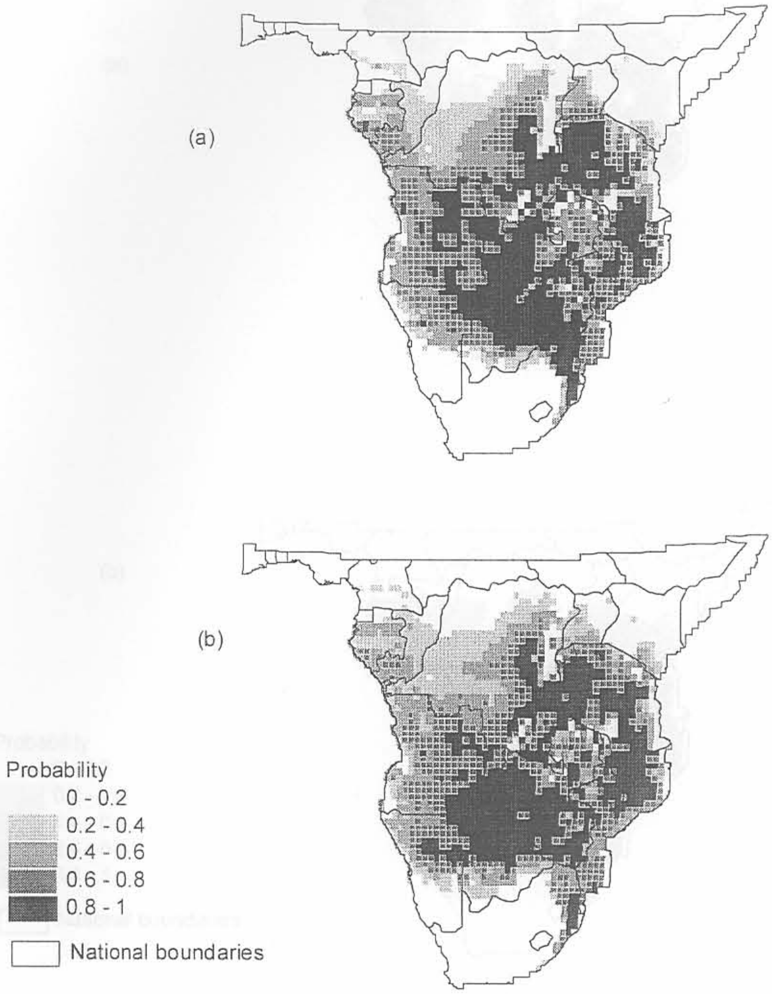

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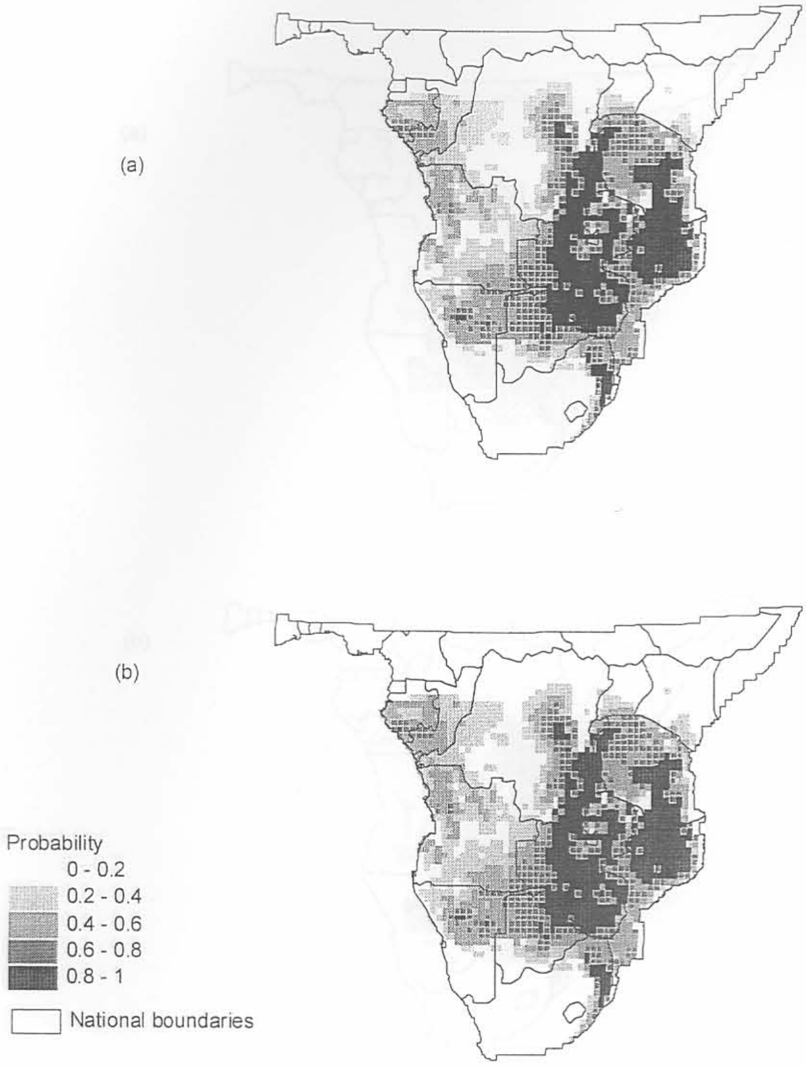

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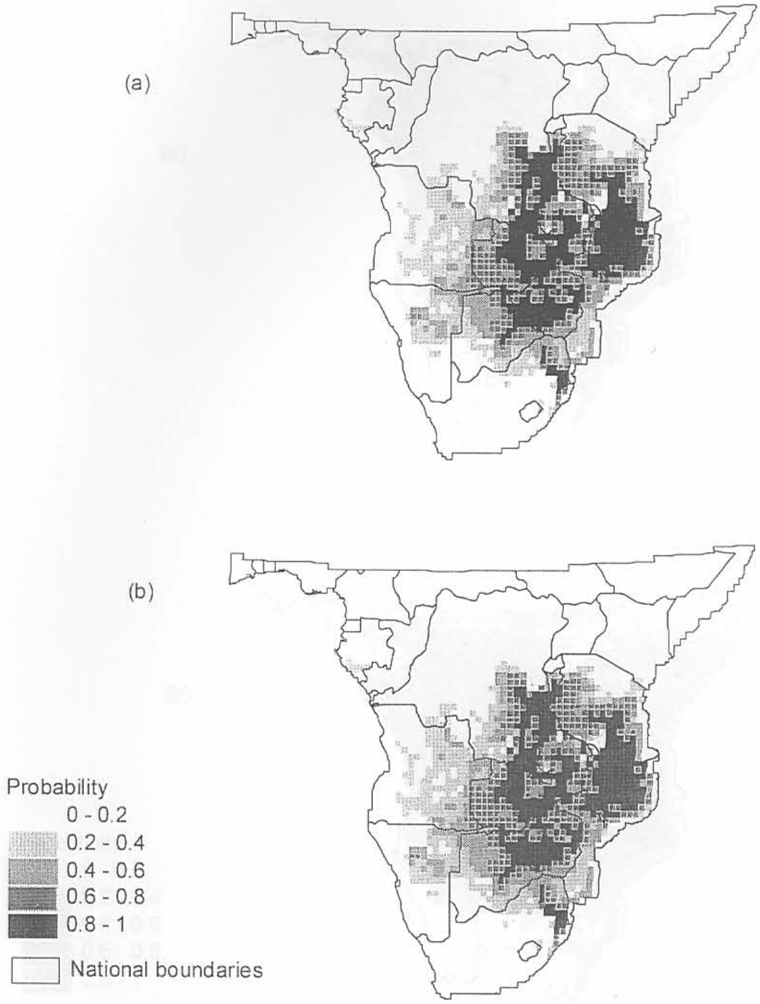

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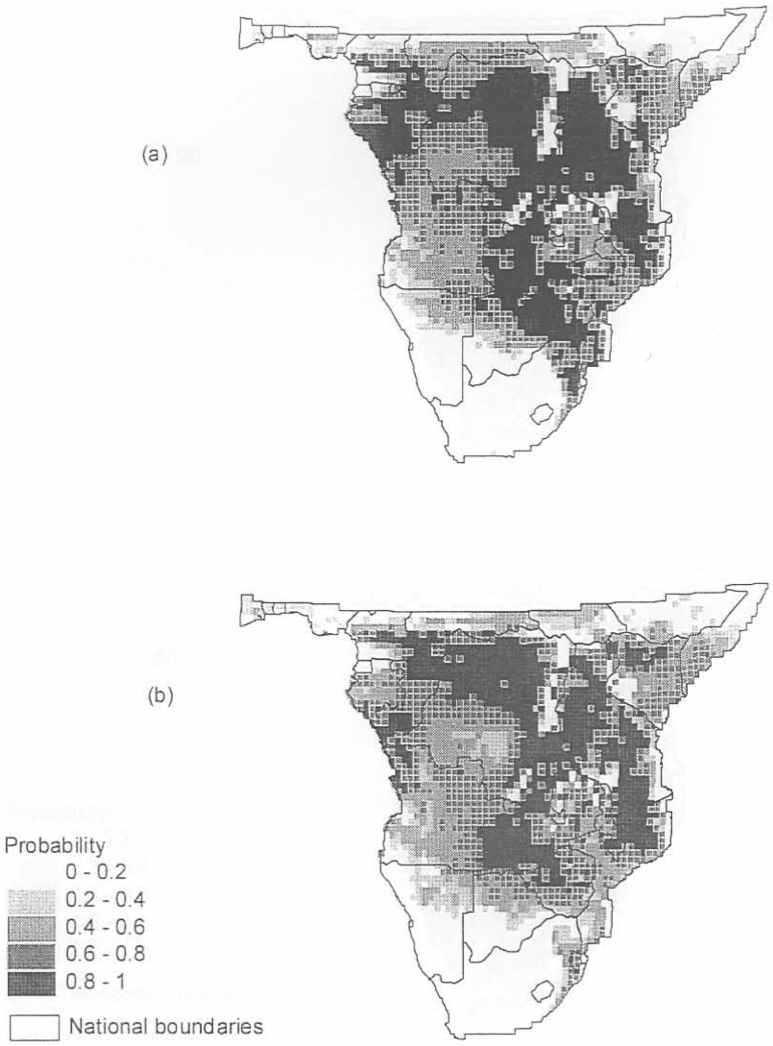

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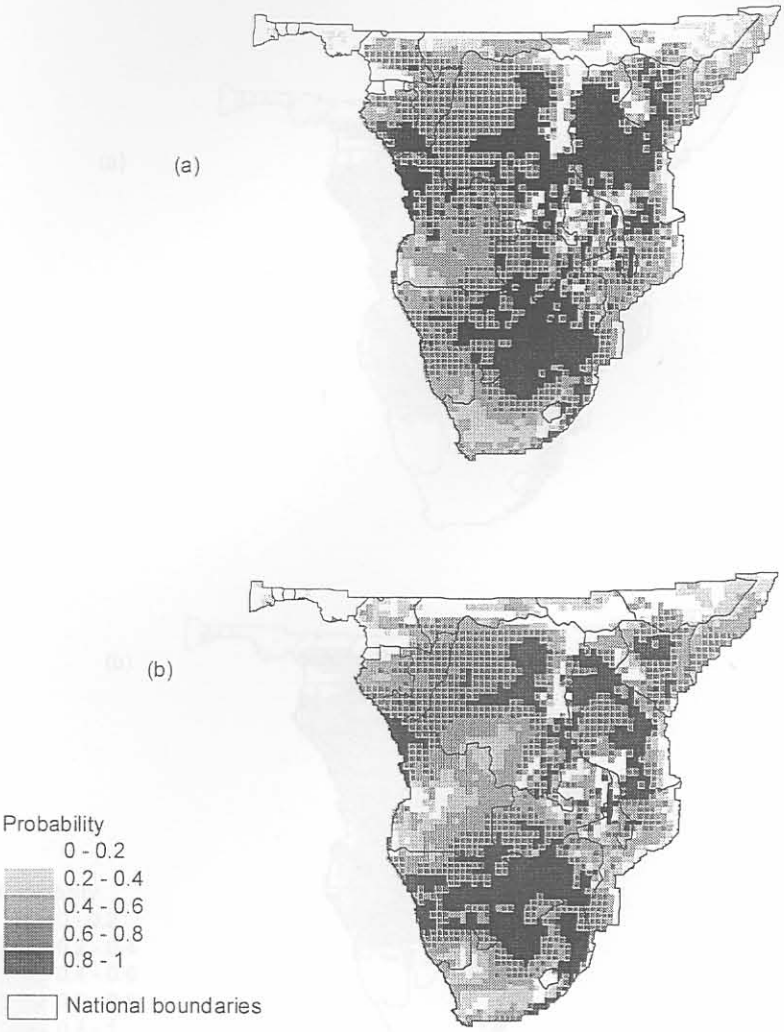

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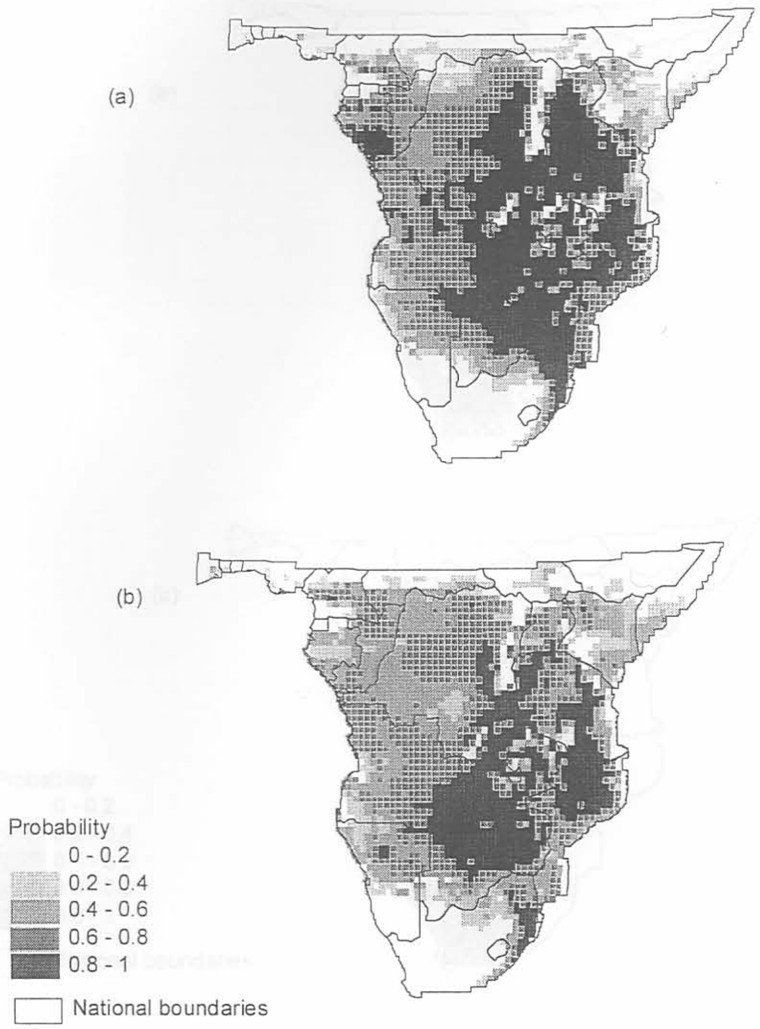


Figure 10

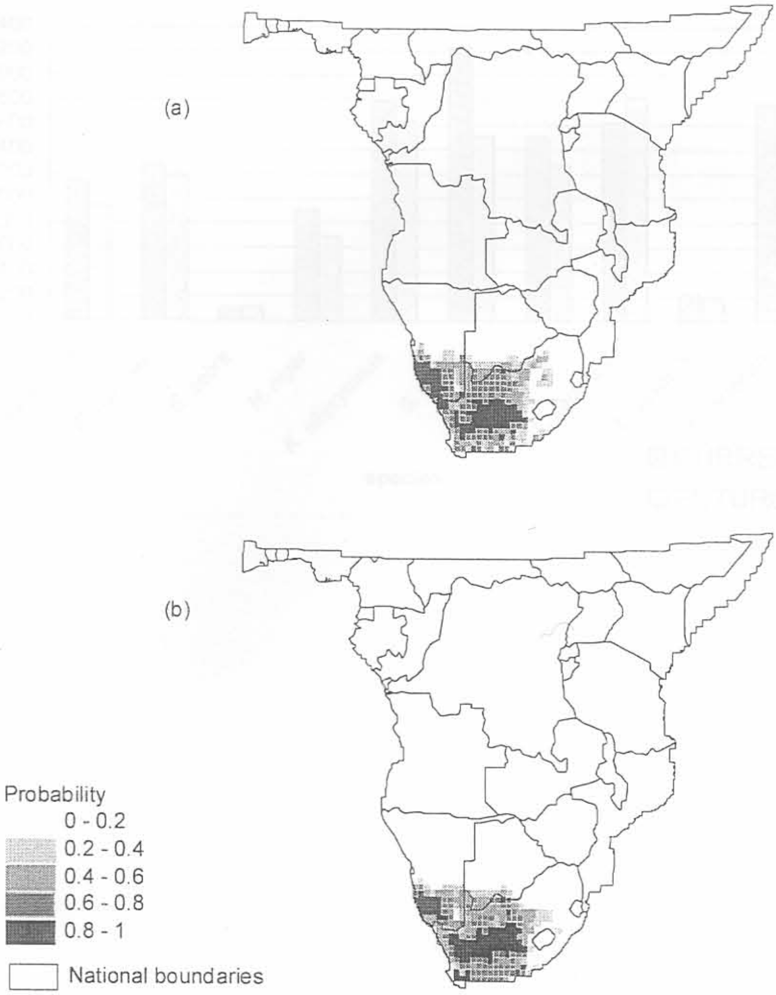


Figure 11

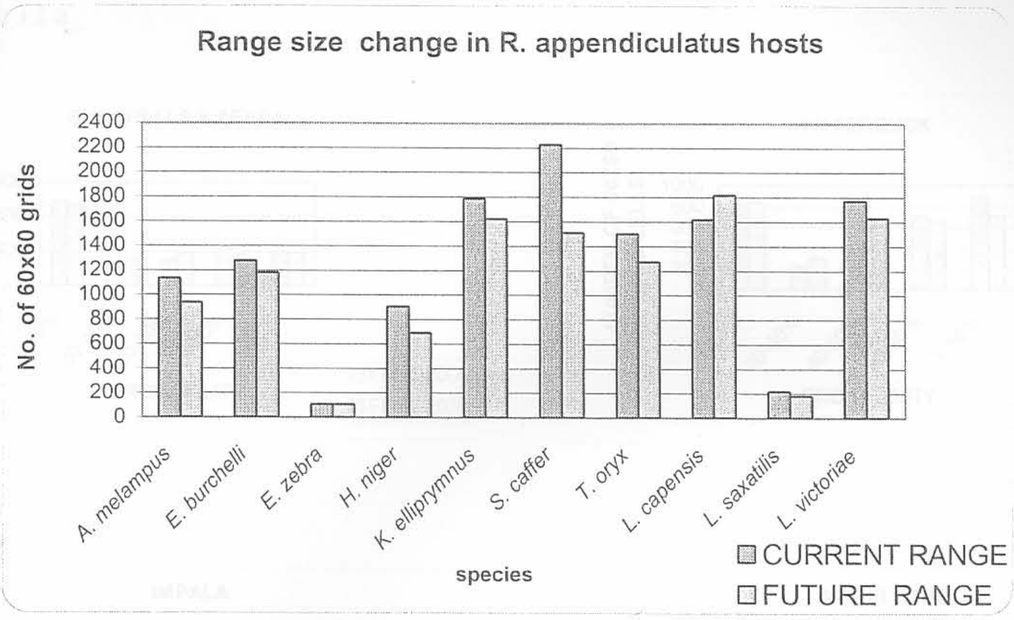

Range size change in R. appendiculatus hosts
No. of 60x60 grids
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
A. melampus
E. burchelli
E. zebra
H. niger
K. elliprymnus
S. caffer
T. oryx
L. capensis
L. saxatilis
L. victoriae
species
▨ CURRENT RANGE
▨ FUTURE RANGE

Figure 12 a

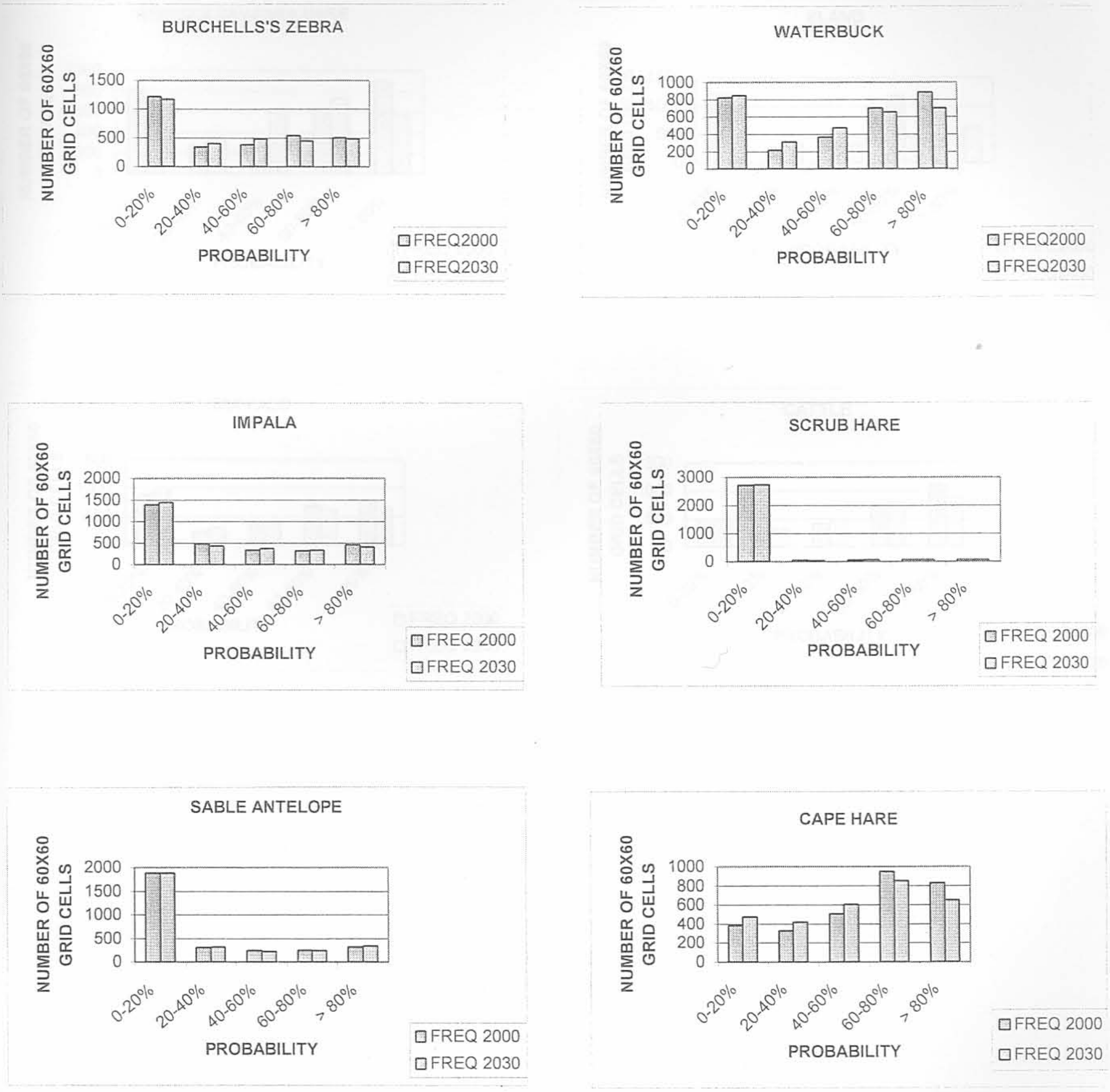

BURCHELLS'S ZEBRA
NUMBER OF 60X60 GRID CELLS
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ2000
☐ FREQ2030
WATERBUCK
NUMBER OF 60X60 GRID CELLS
1000
800
600
400
200
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ2000
☐ FREQ2030
IMPALA
NUMBER OF 60X60 GRID CELLS
2000
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ 2000
☐ FREQ 2030
SCRUB HARE
NUMBER OF 60X60 GRID CELLS
3000
2000
1000
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ 2000
☐ FREQ 2030
SABLE ANTELOPE
NUMBER OF 60X60 GRID CELLS
2000
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ 2000
☐ FREQ 2030
CAPE HARE
NUMBER OF 60X60 GRID CELLS
1000
800
600
400
200
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
▨ FREQ 2000
☐ FREQ 2030

Figure 12 b

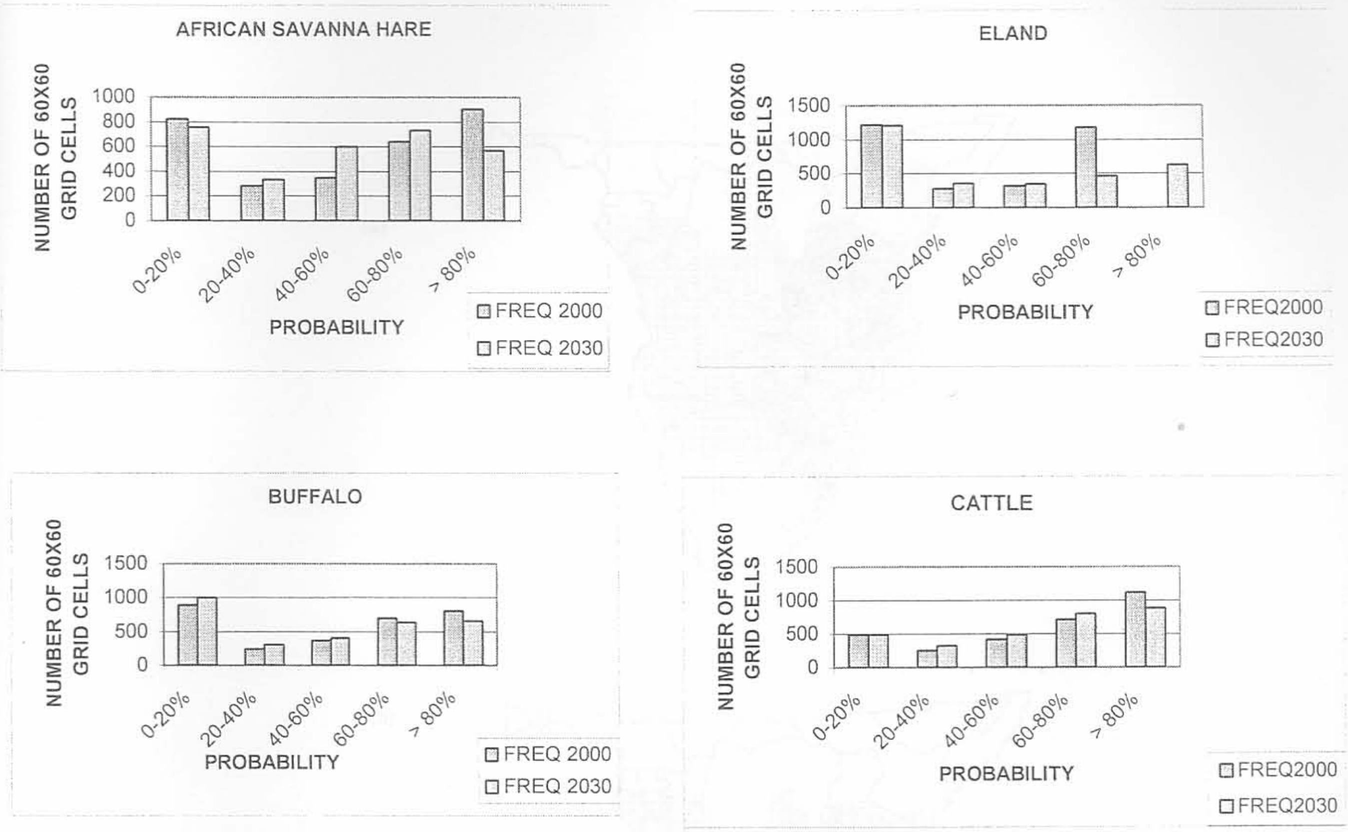

AFRICAN SAVANNA HARE
NUMBER OF 60X60 GRID CELLS
1000
800
600
400
200
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
FREQ 2000
FREQ 2030
ELAND
NUMBER OF 60X60 GRID CELLS
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
FREQ2000
FREQ2030
BUFFALO
NUMBER OF 60X60 GRID CELLS
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
FREQ 2000
FREQ 2030
CATTLE
NUMBER OF 60X60 GRID CELLS
1500
1000
500
0
0-20%
20-40%
40-60%
60-80%
> 80%
PROBABILITY
FREQ2000
FREQ2030

Figure 13

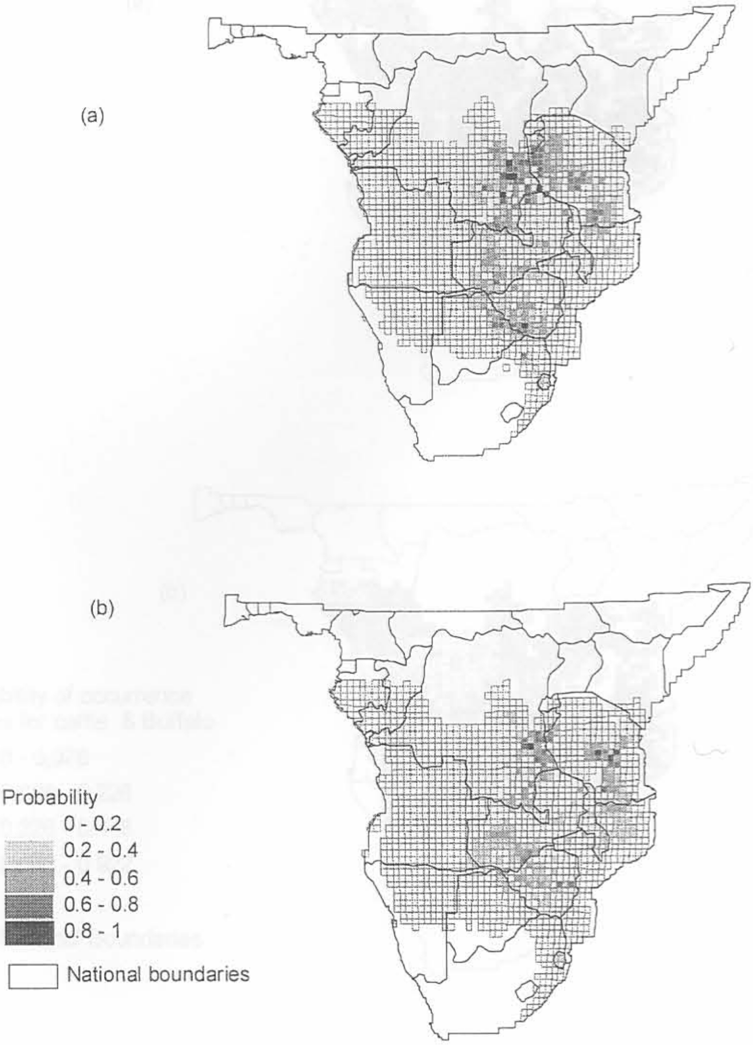


Figure 14

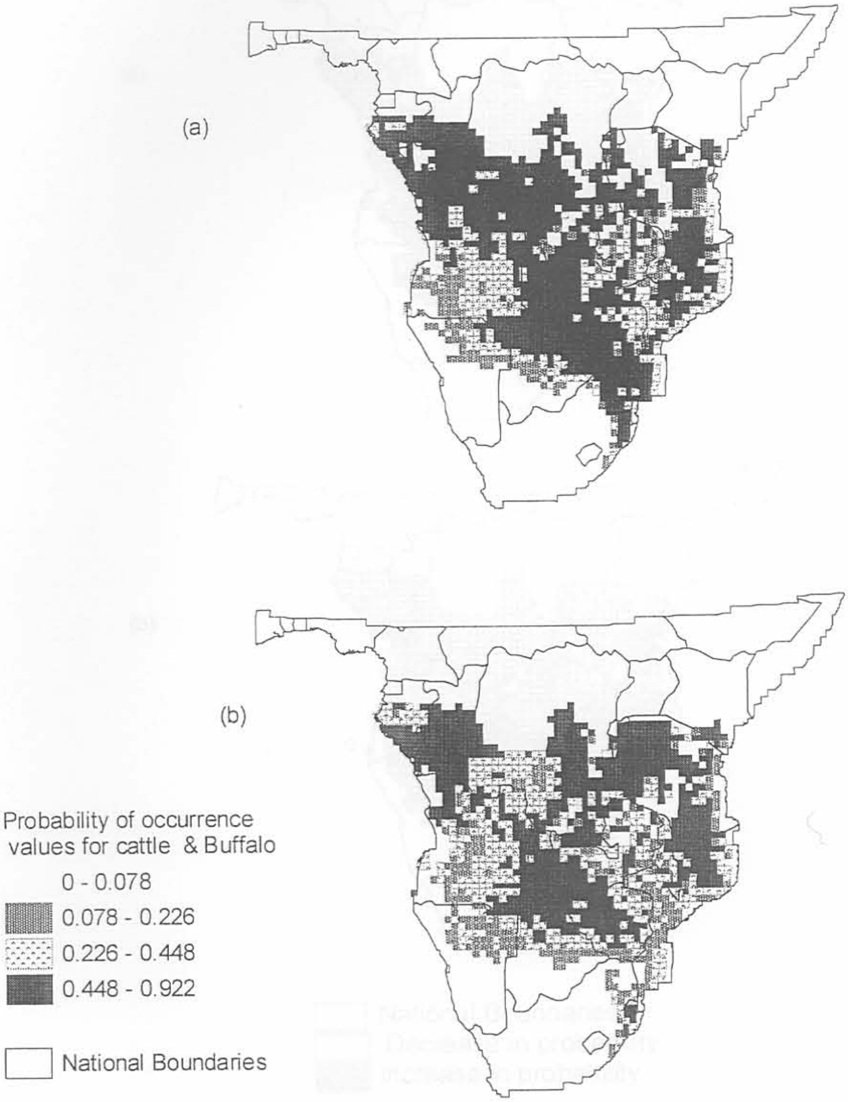
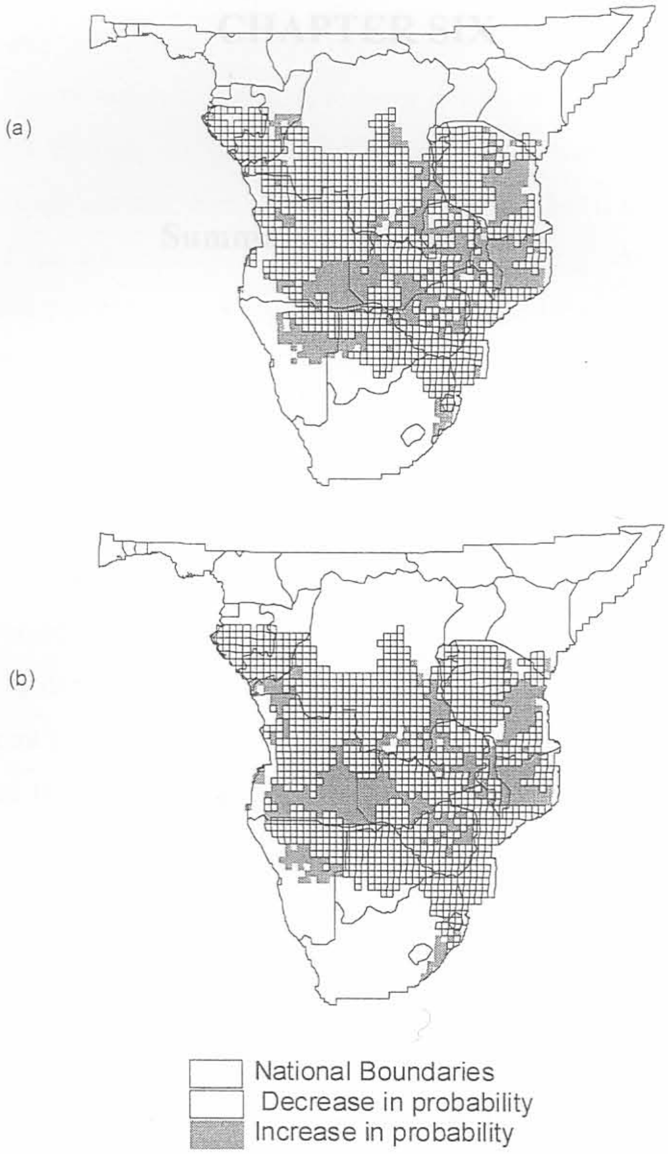

(a)
(b)
Probability of occurrence values for cattle & Buffalo
0 - 0.078
0.078 - 0.226
0.226 - 0.448
0.448 - 0.922
National Boundaries

Figure 15


(a)
(b)
National Boundaries
Decrease in probability
Increase in probability

CHAPTER SIX

Summary and conclusion

Summary and conclusion

As the controversy on climate change rages, some fossil fuel companies and other interest groups mount active campaigns to raise doubts and create confusion about the spectre of climate change; including some scientists, the world and all its inhabitants stand defenceless against this imminent disaster, a disaster that is partly brought about by various kinds of human overexploitation of natural resources. Available observational evidence indicates that regional changes in climate, particularly increases in temperature, have already affected a diverse set of physical and biological systems in many parts of the world. Examples of observed changes include the shrinkage of glaciers, thawing of permafrost, later freezing and earlier break-up of ice on rivers and lakes, lengthening of mid- to high-latitude growing seasons, poleward and altitudinal shifts of plant and animal ranges, declines in some plant and animal populations, and earlier flowering of trees, emergence of insects, and egg-laying in birds (IPCC 2001). This means that climate change is not something likely to affect us "The *Day After Tomorrow*"! It is a present reality that global temperatures have increased by approximately 0. 6^0 C over the 20^{th} century and that additional warming of 0. 6 ° C to 3.5 ^{0} C is expected over the present century (IPCC 2001).

In Africa, evidence of climate change includes a general decrease in diurnal temperature ranges, while deviations in precipitation are increasing. Increases in temperatures precipitating the melting of glaciers on Africa's major mountains are also evident. Observations have also shown that the frequency and intensity of El Niño and la Nina events has increased. Major coral bleaching events have occurred in recent times. More importantly, there are recorded direct and indirect impacts of climate change on diseases that are endemic to Africa. Following the 1997-1998 El Niño event for instance, malaria, Rift Valley fever, and cholera outbreaks were recorded in many countries in East Africa (UNEP Vital Climate Graphics Africa 2002). Furthermore, the meningitis belt in the drier parts of West and Central Africa is expanding into the eastern regions of the continent.

These climate change impacts, superimposed upon existing weak infrastructure, land-use change, and drug resistance against pathogens such as *Plasmodium falciparum, Vibrio cholerae*, *Theileria parva*, and others could impact heavily on the social, cultural and economic fabric of Africa if timely steps are not taken to reduce their consequences. Climate change is real, and it has great significance for sustainable development plans, life and livelihoods in Africa, even more so than on other continents. The diversity in climatic regimes across this vast continent from arid and seasonally arid tropical regimes to humid equatorial regimes, with differing degrees of temporal variability make discussions of climate change for Africa challenging (Desanker 2001). However, the uncertainties about climate change, the magnitude of the change to physical and biological systems should not shift attention from focusing on ways to reduce, combat and understand how ecosystems will react.

Natural systems are more vulnerable to climate change than societal systems because species and ecosystems have a more limited ability to adapt. Besides, ecosystems do not shift as a whole; instead individual species will migrate at different rates (IPCC 2001). New ecosystems will be formed and composed of different assemblage of species. Under climate change some species are unable to move in pace with shifting climatic zones because their paths of migration have been blocked by barriers resulting in extinctions (Thomas *et al*. 2004). "*Climate change is asking species to move when there is no place to move to*," Hannah 2004. This risk to natural habitats from climate change is far more serious because development has already put ecosystems under stress through habitat destruction, fragmentation and pollution. Preliminary studies in South Africa have shown that 25% of the species investigated are expected to require more than a 90% shift in their range (Erasmus *et al*. 2002). This general pattern of species showing limited overlap between their existing distributions and predicted future distributions is most marked for reptiles and invertebrates (van Jaarsveld *et al*. 2000). The implications of climate change on disease- vectors systems is an additional concern. Studies in Europe have so far shown that ticks and tick-borne disease systems will shift or be disrupted during climate change (Randolph & Rogers 2000 & Randolph 2001). This will lead to the introduction of disease and disease vectors in new areas and may prove catastrophic if prior warnings are not issued. Africa with its warm climate and diverse habitats renders it a haven for various species of vectors and an understanding of how their distributions will change under conditions of climate change is one of the most important and basic requirements for developing responses to future challenges.

Research looking at the impacts of climate change on vectors in Africa have mainly concentrated on vectors that affect human beings and there have hardly been any studies that have looked at the effect of climate change on vectors of livestock and wild animals. And yet these diseases place a considerable burden on the livelihoods of many African farmers. Also, altering landscapes can change the transmission dynamics and location of many serious diseases, not to mention the fact that parasitic life cycles existing in humans may include livestock and wild animals in cases of displacement and encroachment of areas not currently used by man. Therefore the goal of this study was not only to investigate the impacts of climate change on ticks and tick-borne diseases in sub-Saharan Africa but also to highlight the need for an ecosystem approach to the management of vectors and vector–borne diseases. The control of vector-borne zoonoses should not be considered in isolation from the control of vector-borne diseases in other animals. The relationships and interdepencies between all these systems must govern any vector borne diseases control approach. Here the tick-host- disease system in Africa is used as a model for exploring vector-borne diseases in Africa. This sub-Saharan tick study is concluded by focusing on the following issues: 1) the advantages of the climate data used here over other climate data used in previous studies 2) implications of the predicted range alterations 3) the advantages and shortcomings of the predictive modelling approach and 4) and finally some recommendations for future research and action.

As the urgency to assess the effects of climate change and other habitat changes on the distributions of species mounts, with the subsequent rise in new statistical approaches and the use of geographic information systems (GIS), more and more scientists are employing different models to predict the distributions of species. Consequently, the availability of suitable climate data becomes increasingly important. In general an evaluation of climate data sets is encouraged before use so that the best data are picked for a particular study. In this thesis, the predictions of the current distributions of ticks using climate data derived from DARLAM, a nested regional model, proved superior to the predictions derived from two other climate data sets (Olwoch *et al.* 2003 – Chapter two). The reasons for this are that DARLAM is able to capture climate at a sufficiently fine scales relative to the range sizes of species, is entirely based on a simulations of climate processes and does not use any observed meteorological data to generate climate surfaces (Engelbrecht *et al.* 2002). This is particularly useful in Africa where meteorological observation stations are inadequate.

The alternative climate datasets, e.g. CRES and CRU, although they have been resampled to increase the data resolutions, are still relatively smooth because they depend on the original low-resolution point observations. Differences observed in the predicted future distributions of ticks using future GCM and DARLAM further confirm the need to assess climate data before commencement of a study. Broader range sizes predicted by DARLAM are again a reflection of the existence of differences in climate model results and in this case the predicted GCM climate was much drier than that generated by DARLAM. Since DARLAM is a process driven model, it is able to capture today's conditions, it is sensitive to more local variations particularly in topography and more local interactions at a higher spatial resolution. GCMs on the other hand operate at a very low spatial resolution and have been criticized for their inability to capture the present day features of the global climate (Goodess & Palutikof 1993). Ticks are known to be habitat specialists, spend more that 90% of their lives on the ground and are more affected by local variations. In this regard, the use of climate simulations provided by a regional model such as DARLAM are more appropriate that broad scale GCM data in studies of this nature.

Range alterations, in the form of expansions, contractions and possible shifts in response to climate change are evident from this thesis. These results give support to the IPCC predictions that climate change may alter the distribution of vector species — increasing or decreasing the ranges, depending on whether conditions are favourable or unfavourable for the breeding places of vectors (e.g., vegetation, host, or water availability). Range expansions of ticks across sub-Saharan Africa, with its fragile economy and non-existent support systems in the livestock and health sectors may prove catastrophic if prior warnings are not provided and acted upon. Whether or not these tick ranges are correlated with increases in tick-borne diseases depends intimately on the availability of hosts that are involved in the transmission of vectors. Nevertheless, in an environment where the expansion of tick ranges is accompanied by predicted range contractions of the hosts, considerable uncertainty prevails. The tick mortality rates as a result of host finding behaviour might increase and may result in reduction in the number of ticks completing a life cycle. Though studies to date have emphasised that climate and not host influences the range of African ticks, in conditions of climate change as predicted in this thesis, the host are more probable to become limiting.

The main concern attributed to species range contraction is usually because of the negative relationship between range size and extinction probability (Gaston 1994). A reduction in the absolute range of a species will almost inevitably mean an increase in its risk of extinction. Extinction of parasite may in all cases be a welcome sign. However, since different tick species occupy different habitats and are influenced by different degrees of climate factors, contraction of one major tick species may give way to introduction of a lesser-known species. This displacement of populations in time has already reported in *Glossina* species in Cote d'Ivoire Gouteux & Jarry (1998) and also in *Boophilus* species in South Eastern Africa countries (Sutherst 2001).

The range shifts following climate change reported in this thesis are consistent with range shifts reported in other species in other parts of the world, in Europe (Randolph & Rogers 2000), in diseases (Harvell *et al.* 2002), in South African species (Erasmus *et al.* 2002), in plant and animals (Root *et al.* 2003 and globally (Parmesan & Yohe 2003). Range shifts reported here are likely to increase the vulnerability from tick-borne diseases in livestock populations in these new areas. In vector ecology, range shifts have an additional problem in that shifting in vectors is likely to introduce pathogen in a new area and these introduced pathogens are likely to be more virulent in the host populations. Increase in species richness in the drier western parts of the continent is consistent with the earlier assessment of how South African ticks will respond to climate change (Hulme1996) and this is obviously in response to the enhanced rainfall predicted for these areas.

Increased vulnerability of sub-Sahara Africa to tick-borne diseases revealed by this thesis through the predicted increase in ECF and increase in ranges of economically important ticks are again consistent with the IPCC predictions that climate change may favour the increase of vector-borne diseases. These predictions based solely on the current and future climatic suitability of *R. appendiculatus* and cattle should not be underestimated because the relative importance of other factors has not been thoroughly investigated. These factors including other competent hosts of *R. appendiculatus*, other reservoir hosts of the pathogen, tick-control policy, will increase or reduce ECF infection from the existing state of affairs determined by the two main factors; cattle and *R. appendiculatus* distribution. These results are an important measure of the expected vulnerability on which other broader studies could be done taking into account more factors. Since the occurrence of ticks is a potentially important variable in predicting the incidence of the pathogens that they transmit (Cumming 1999), these results are based on the available information and understanding and gives the most logical presentation of this complex system under climate change. Furthermore, cattle are neither the only hosts that support R. *appendiculatus* nor the only hosts that can carry the pathogen, *T. parva*, but despite the economic importance of ticks only a few countries have been thoroughly studied and the sampling regime under which tick collections have been made has been highly biased towards cattle ticks (Cumming 1999). Therefore, cattle provided the most reliable and consistent data than any other host.

The degree of range expansion, contraction and shifts and overall decrease in host diversity reported here might not be the same magnitude as the realized alterations because even without climate change, ticks and their hosts are already under stress from habitat-fragmentation, destruction and land use transformation. The combined effects of these factors and climate change on tick and tick-borne diseases distribution in sub-Saharan Africa may be different from the one presented in this thesis. Climate change and habitat fragmentation for instance are likely to be opposing shifting factors, with climate change forcing a distribution shift and habitat fragmentation preventing that shift through absence of suitable land (Warren *et al*. 2001). In this instance the net result is likely to be local extirpation of the population, rather than a shifted population (Erasmus 2003). In a tick-host diseases system this would disrupt the established relationships and likely result in a greater degree of change in species diversity than predicted in this thesis. This has a direct link with disease transmission rates. What I present in this thesis is therefore a foundation on which more elaborate studies could be done and wider conclusions made.

The predictive species model used in this thesis has been criticised as being unable to incorporate detail information regarding the factors that influence distribution of these species. In the first instance, such elaborate information regarding species does not exist. Furthermore even in field ecological study, it is impossible for a researcher to imply that all the factors affecting a species have been included because some factors are created by the mere presence of others. It has also been criticised as being simple and static. In most cases a mechanistic model would be the preferred choice. However, Robertson *et al.* (2003) have shown that an equilibrium type model can perform at least as well, if not better, than a mechanistic model that is based on explicit and known ecophysiological constraints. Such a mechanistic model effectively uses the fundamental niche to determine the bioclimatic envelop of the species; however, if the fundamental niche is not realised at the present, then it is unlikely to be realised in the future. Bioclimatic envelops based on observed distributions effectively capture the realised niches, and are likely to be more adept at predicting future distributions since some measure of factors determining the realised niche is implicitly included (Pearson & Dawson 2003).

Furthermore this model with its multivariate capabilities as opposed to provision of mere absent-present predictions gives a better estimate especially when dealing with poorly sampled species. Since this can operate effectively using only presence records and any number of climate variables available, it is one of the most practical models since most of the species in sub-Saharan Africa are poorly sampled. This approach neither disregards the need for a more detailed and comprehensive eco-physiological approach nor does it pretend to predict the future but it defines the role of climate as a factor in determining the potential for establishment when all other factors are not included (Sutherst 2003). Nevertheless, in spite of modelling efforts focused on single species or entire ecosystems, a few preliminary surveys of impact of climate change on different ecosystems and evidence of climate change-mediated shifts in several species, the likely effects of climate change on species' distributions remain little known, and fauna-wide or community-level effects are almost completely unexplored (Townsend *et al.* 2002). It is also one of the realisations of this thesis that more detailed and specific field studies are needed to allow the development of more comprehensive predictive models. Unfortunately, such detailed information is rarely available and managers have to make decisions based largely published information and local experience (Booth *et al.* 2002).

The rate at which African societies will be vulnerable, and whether or not they will effectively adapt to this change depends on numerous factors. Large-scale environmental changes such as, population movement, forest clearance and land-use patterns, human population density, and the population density of insectivorous predators all affect the vulnerability of a society to vector-borne infectious diseases. However an understanding of the vulnerability, which has been achieved by this thesis, is the first step towards adaptation. Adaptation measures can however benefit from easy access to information, including early warnings of extreme climate events and also constant dispensations of information on the relationship between local disease vector distribution and climate by the local control programs. Furthermore, improving the current level of public health infrastructure is the initial and most effective way of adapting to climate change induced effects. In very many countries in Africa, this infrastructure has declined in recent years. Many diseases and public health problems that otherwise may be exacerbated by climate change could be prevented substantially or completely with adequate financial and public health resources. These resources would encompass public health training programs, research to develop and implement more effective surveillance and emergency response systems, and sustainable prevention and control programs. As provided by this thesis, different countries will have different rates of vulnerability and adaptation will depend on several societal systems, including access to financial resources (for individuals and populations), technical knowledge, public health infrastructure, and the capacity of the health care system. Thus, individual, country community and geographical factors will also determine vulnerability.

The realised ecological consequences of climate change to ticks, hosts and tick-borne disease will however depend on many interacting variables and the results presented here may be different if all those other factors are included in the model. Despite this and other shortcomings of the model, this thesis has succeeded in identifying which tick species and vertebrate hosts are likely to show greater responses. Furthermore, this study has succeeded in identifying the importance of using a suitable climate data in predictive species modeling, has also provided an understanding of the magnitude of how regions and countries in sub-Saharan Africa are vulnerable to climate changes by using tick-host and tick-borne diseases system. Since an understanding of how a society is vulnerable to climate change is the first step towards identifying adaptation capacity, this thesis has been useful in that regard. This thesis, realizing the intricate relationships between different components in the ecosystem, has called for an ecological approach to vector-borne diseases management in sub-Saharan Africa. What this thesis has not made clear is the actual magnitude of the vulnerability and how the African people will adapt to this climate change impacts. The actual magnitude of future responses is not known but current vulnerability must be assessed through field studies. Further research is needed to identify actual vulnerabilities through field studies, adaptation needs, evaluate adaptation measures, assess their environmental and health implications, and set priorities for adaptation strategies ensuring active surveillance for important ticks and the diseases they transmit; and continuing research to further our understanding of associations between weather, extreme events, and tick-borne diseases. In addition, continuing research into ecological approaches to tick-borne and other vector-borne diseases control methods is one of the most important ways to understand this system and put into place measures based on practical scientific evidence. Understanding the impacts of climate change on ticks, hosts and tick-borne diseases in Africa is an important and necessary step towards future management of ticks and tick-borne diseases and reduction of their impacts to the health and veterinary industries, economy and welfare of African people.

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