



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

J.M. OLWOCH^{1*}, A.S. VAN JAARSVELD², C.H. SCHOLTZ³ and I.G. HORAK⁴

ABSTRACT

OLWOCH, J.M., VAN JAARSVELD, A.S., SCHOLTZ, C.H. & HORAK, I.G. 2007. Climate change and the genus *Rhipicephalus* (Acari: Ixodidae) in Africa. *Onderstepoort Journal of Veterinary Research*, 74:45–72

The suitability of present and future climates for 30 *Rhipicephalus* species in Africa are predicted using a simple climate envelope model as well as a Division of Atmospheric Research Limited-Area Model (DARLAM). DARLAM's predictions are compared with the mean outcome from two global circulation models. 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. More than 20% of the species experienced range shifts of between 50 and 100%. There is also an increase in tick species richness in the south-western regions of the sub-continent. Actual range alterations due to climate change may be even greater since factors like land degradation and human 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

INTRODUCTION

The realization that species distributions are significantly influenced by climate has placed considerable emphasis on the need to acquire information con-

cerning the ways in which the present distributions of organisms will be affected by climate change. In response to this challenge, the issue of vector distribution has recently received much 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, Ferriera, Grainger, Hannah, Hughes, Huntley, Van Jaarsveld, Midgley, Miles, Ortega-Huerta, Peterson,

* Author to whom correspondence is to be directed. E-mail: jane.olwoch@up.ac.za

¹ Department of Geography, Geo-informatics and Meteorology, University of Pretoria, Pretoria, 0002 South Africa.

² CIB, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, 7160 South Africa

³ Scarab Research Group, Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002 South Africa

⁴ Department of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria, Onderstepoort, 0110 South Africa and Department of Zoology and Entomology, University of the Free State, Bloemfontein, 9300 South Africa

Philips & Williams 2004) have attempted to predict the distribution of species based on the major environmental factors that would influence this.

This approach neither disregards the need for further detailed and comprehensive eco-physiological studies 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 elements are excluded (Sutherst 2003). This paper also accents the necessity of acquiring more detailed information concerning the biology and environmental sensitivities of each species in the light of likely climate change. In the absence of such information, relatively straightforward statistical methods that seek correlations between environmental factors and the presence of animals or plants are likely to remain the best pragmatic approach for exploring the expected future distributions of large numbers of species. This study focuses on climate induced changes likely to occur in the distribution of some species of an economically important African arthropod, namely the tick genus *Rhipicephalus*.

The intimate relationship between climate and the requirements of ticks for survival 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). This has led to several studies using climate as a means of predicting the distributions of African ticks (Rogers & Randolph 1993; Randolph 1993, 2001; Randolph & Rogers 1997; Norval, Sutherst, Kurki, Kerr & Gibson 1997; Cumming 2000a, b; Estrada-Peña 2001; Olwoch *et al.* 2003). Collectively the results obtained from these works, some of which used data garnered mainly from interpolated climate databases at 25 km resolution (Perry *et al.* 1990) or 6 x 6 km resolutions (Cumming 2000b), suggest that accurate predictions of tick distributions at different temporal and spatial scales should be feasible. This approach would be especially useful for predicting the distribution of species in poorly sampled species in poorly sampled regions of Africa.

The genus *Rhipicephalus* is the fourth largest in the Family Ixodidae (Walker, Keirans & Horak 2000), and there are 74 species currently recognized. It is essentially an African genus with approximately 63 species recorded only in the Afro-tropical region and ten species outside the 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 (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 and, as two distribution data sets have been used, the current distribution of these ticks are relatively well plotted. The way 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, 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 (Sutherst & Maywald 1985). The use of CLIMEX in northern Australia was considered a great success for predicting the distribution of the tick *Boophilus microplus* (Canestrini, 1887), and it was anticipated that this initial success could be translated into predicting distributions of African tick species. However, early studies tended to over-estimate the distribution of *B. microplus* across Africa, and the predicted high incidence of *Rhipicephalus appendiculatus* Neumann, 1901 in West Africa was at complete variance with the tick's absence in this region.

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 regions for *Amblyomma hebraeum* Koch and *Amblyomma variegatum* Fabricius, 1794, is almost the opposite of the actual distribution of these ticks, both in Zimbabwe and in the rest of Africa (Norval, Perry, Gebreab & Lessard 1991; Norval *et al.* 1992).

BIOCLIM was the second climate-based approach employed to model tick distributions (Nix 1986; Norval *et al.* 1992). BIOCLIM generates 24 climatic attributes from which annual and seasonal mean conditions, extreme values and intra-year seasonality are derived, for each of a selection of geographic points throughout the distribution range of a tick species. Computer-selected thresholds and limits for each of the indices are matched across a geographical grid to predict 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 unsatisfactory (Norval *et al.* 1992). The climate database used was interpolated at an increased resolution (8 km), and this factor alone may explain the improved 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 with a resolution of 25 km (Hutchinson, Nix, MacMahon & Ord 1996) achieved even better accuracy. Such an approach, however, normally requires the existence of a training data set that includes presence and absence information (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) mounted on the National Oceanic and Atmospheric Administration's (NOAA's) meteorological satellites was given preference in the 1990s. This instrument allowed the direct detection of environmental factors at an 8 km resolution (Lessard *et al.* 1990). The main predictor in this procedure is the satellite-derived maximum mean monthly Normalized Difference Vegetation Index (NDVI). However, this technique was reportedly very complicated when used to predict the distribution of *R. appendiculatus* (Kruska & Perry 1991). There are, however, 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 presence maps for species (Erasmus *et al.* 2000). When used to predict the contemporary potential distribution of African ticks (Olwoch *et al.* 2003) the model achieved positive predictions of more than 70% for the four tick species tested.

Climate data used for predicting African tick distributions

The principal sources of climate data for predictive distribution modelling are climate surfaces, generated by interpolating data sampled at varying inten-

sities across a region. Consequently, differences between these climate surfaces can usually be attributed to spatial and temporal evenness of the 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 Global Circulation Models (GCMs). These are coupled ocean-atmosphere models that provide three-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 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 preclude GCMs being run at meso-scale grid resolutions (10–100 km).

The present study used a Division of Atmospheric Research Limited Area 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 model. 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 datasets for predicting current tick distributions has been assessed by Olwoch *et al.* (2003). In this study, DARLAM's future predictions are compared with those obtained by using mean climates from two GCMs (CGCM and Centre for Climate System Research/National Institute for Environmental Studies [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

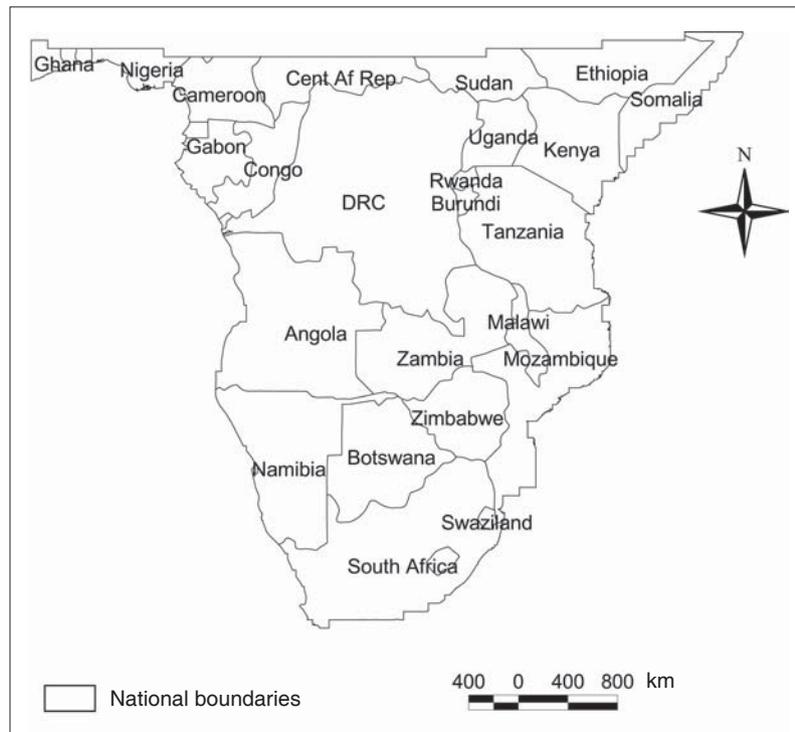


FIG. 1 Study area

resolution. This resolution was determined by the DARLAM climate data.

Tick data

Point localities of tick recoveries were obtained from Cumming (1999), who compiled the data that he used from various collections of ticks, and from recent collections made by one of us (I.G.H.). Combining data sets from different sources frequently 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 tick species selected for this study belong to the ixodid genus *Rhipicephalus*. Species 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. The *Rhipicephalus* species selected are those whose distribution and life history strategies are relatively well known and it is our hope that these re-

sults 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 selected tick species 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 solely by climate. To arrive at a predicted distribution in 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 approach was used as a standardized base for evaluating the relative performances of the DARLAM and the mean GCM climate data sets, and allows the creation 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 separate 10-year periods. The periods selected are the 1990s and 2020. The simulations were performed at a horizontal grid resolution of 60 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 A₂ 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 total rainfall 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.

GCM future climate data

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 CO₂ experiments has ten vertical levels 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 CO₂. 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 current climate predicted by DARLAM. This represents a useful comparison between predicted distributions and known records (see Olwoch *et al.* 2003). To obtain predicted future 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:

- (i) Analysis of species range expansion
- (ii) An analysis of range contraction
- (iii) Change in species richness pattern
- (iv) Species range shifts
- (v) 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 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 carnivorialis* 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 ticks of the *Rhipicephalus capensis* group (*Rhipicephalus capensis* Koch, 1844; *Rhipicephalus follis* Dönitz, 1910 and *Rhipicephalus gertrudae* Feldman-Muhsam, 1960), *Rhipicephalus distinctus* Bedford, 1932, *Rhipicephalus exophthalmos* Keirans & Walker, 1993, *Rhipicephalus oculatus* Neumann, 1901, *Rhipicephalus zambeziensis* Walker, Norval & Corwin, 1981 and the subspecies *Rhipicephalus evertsi mimeticus* Dönitz, 1910.

There are also species that have wide ranging distributions that overlap in various regions of 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 current 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 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 N_c/N_s where N_c is the number of common grid cells between a pair of areas under comparison and N_s is the number of grid cells containing data for both groups or the maximum number of overlapping grid cells possible.

RESULTS

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 it was 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 2020s vs the 1990s 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 be-

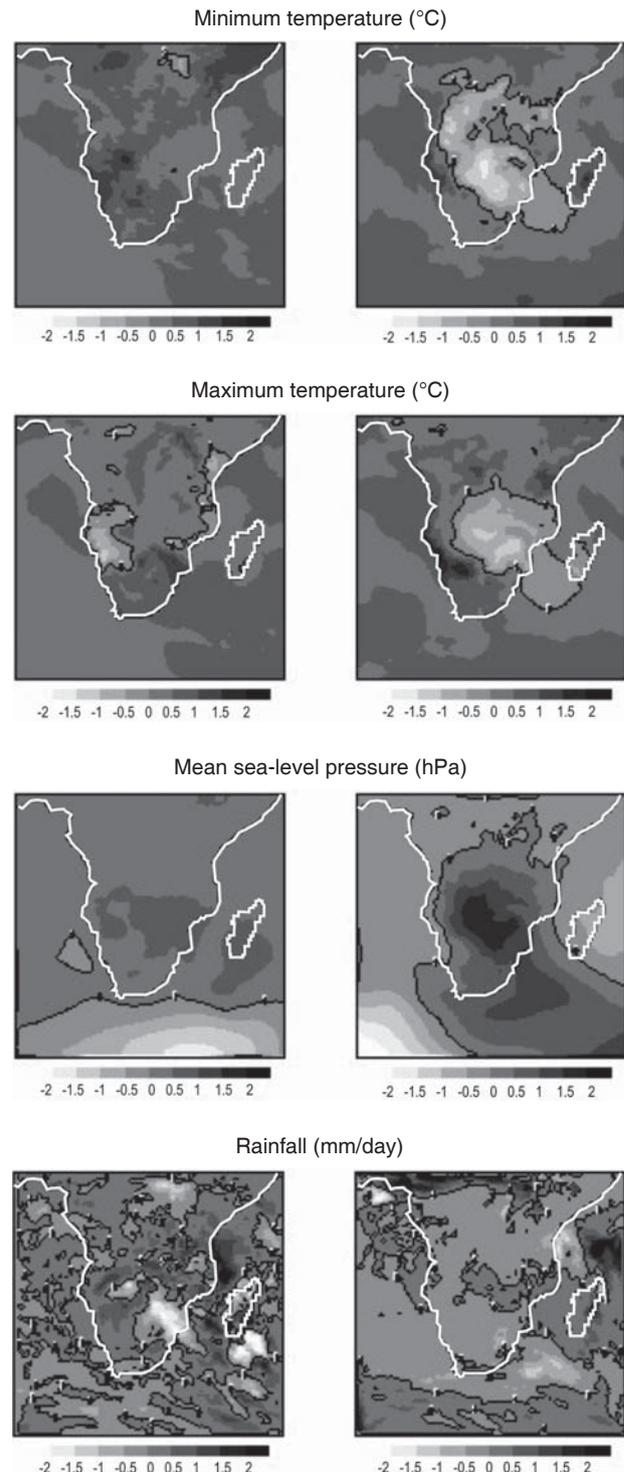


FIG. 2 DARLAM's climatological anomalies for the 2020s v. 1990s

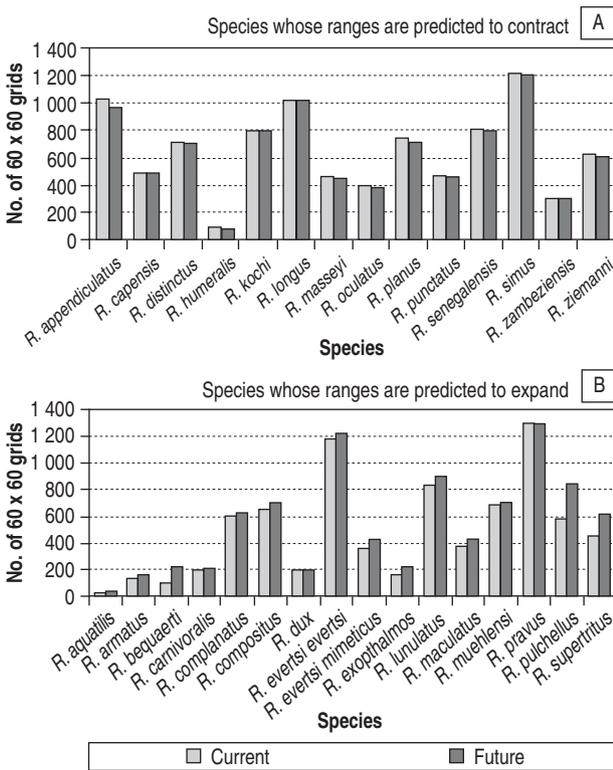


FIG. 3 *Rhipicephalus* species in sub-Saharan Africa that are predicted to show (A) range size contraction and (B) range size expansion

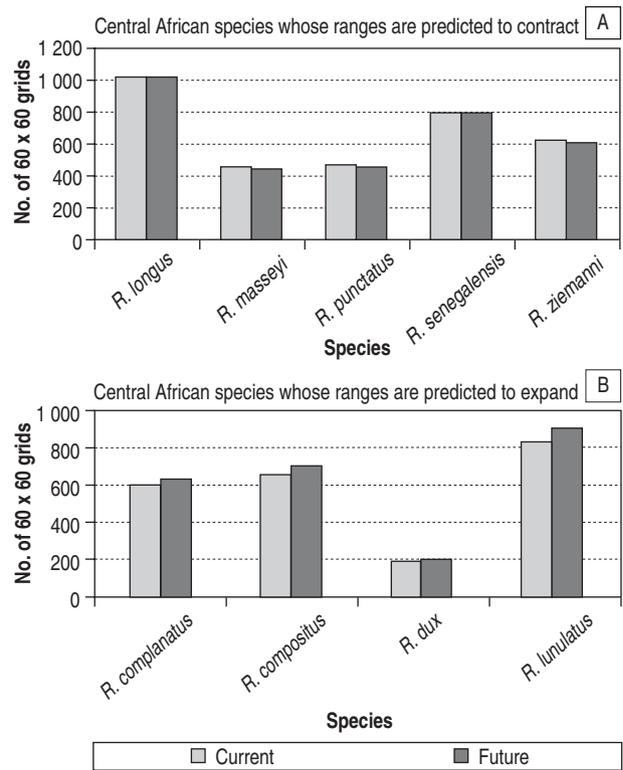


FIG. 4 *Rhipicephalus* species in Central Africa that are predicted to show (A) range size contraction and (B) range size expansion

come 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* group, *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. exophthalmos*, *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 3502800 km² (12%) in total tick range with a total reduction of 640800 km² (2%).

Central African species (Fig. 4A, B, 16,17, 19, 25, 26, 28, 34, 35 and 39)

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. complanatus*, *R. compositus*, *R. dux* and *R. lunulatus*) are predicted to show range expansions. Although the ranges of the majority of tick species are predicted to contract, the total area of contraction is only 19%, while the total area of expansion by the remaining species is 81%. The tick species predicted to expand its range most in this region is *R. lunulatus* with a total expansion of 252000 km².

East African species (Fig. 5A, B, 11, 12, 13, 15, 23, 24, 27, 29, 31 and 33)

In East Africa 30% of the species (*R. humeralis*, *R. kochi* and *R. planus*) are predicted to show range contractions, while 70% (*R. aquatilis*, *R. armatus*, *R. bequaerti*, *R. carnivoralis*, *R. maculatus*, *R. muehlensi* and *R. pulchellus*) are predicted to show range expansions. This translates into a total expansion of 1760400 km² (91%) with a mere 169200 km² (9%) reduction in total area. The predicted greater expansions are mainly attributable to *R. bequaerti* which

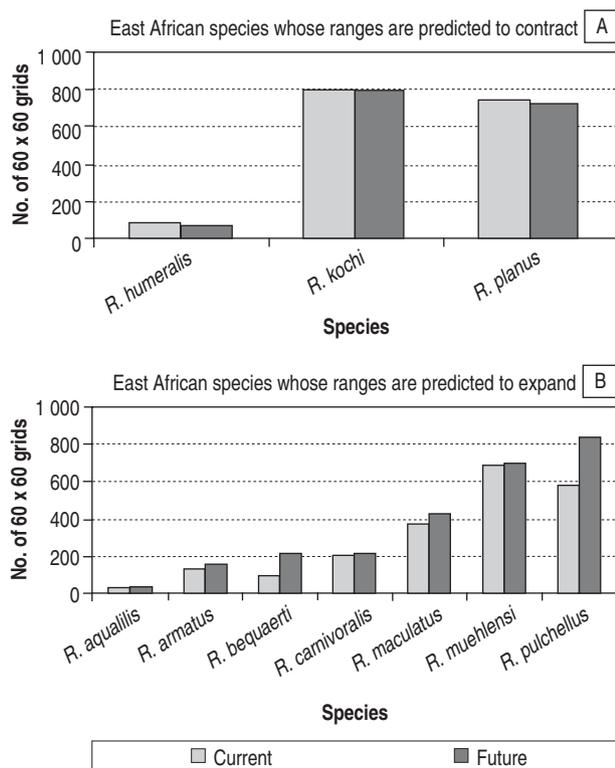


FIG. 5 *Rhipicephalus* species in East Africa that are predicted to show (A) range size contraction and (B) range size expansion

more than doubles its present range and *R. pulchellus*, which is predicted to expand its range by some 921 600 km² (49%).

Southern African species (Fig. 6A, B, 14, 18, 21, 22, 30 and 38)

In southern Africa some 66% (*R. capensis* group, *R. distinctus*, *R. oculatus* and *R. zambeziensis*) of the tick species are predicted to contract their ranges. Although only 33% (*R. evertsi mimeticus* and *R. exophthalmos*) of the ticks are predicted to expand their current ranges, the total range expansion is 439 200 km² (23%) while the total range reduction is only 64 800 km² (1%). Most of the expansion in this region is attributable to *R. evertsi mimeticus*.

“General” tick species (Fig. 7A, B, 10, 20, 32 and 36)

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, e.g. *R. appendiculatus* is confined to parts of eastern, central and south-

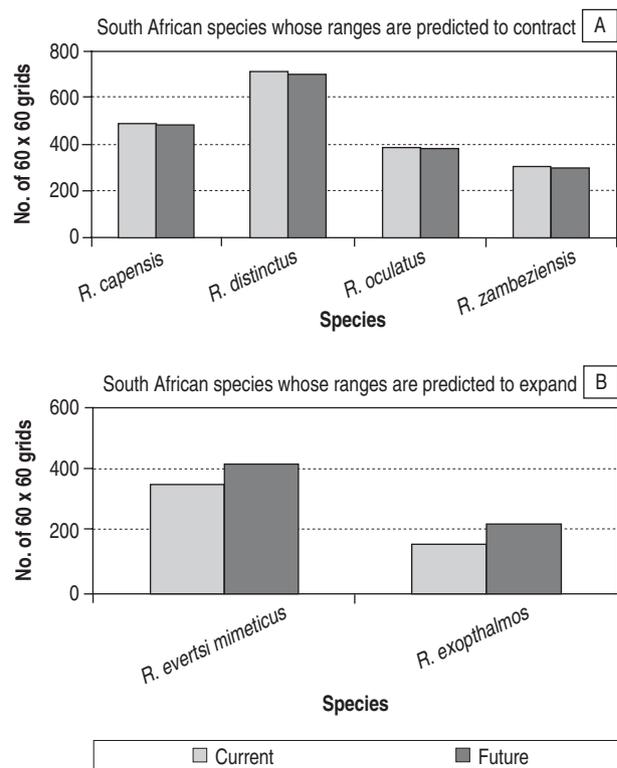


FIG. 6 *Rhipicephalus* species in southern Africa that are predicted to show (A) range size contraction and (B) range size expansion

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 a major cause of cattle mortality and also causes considerable production losses in cattle in most African countries (Okello-Onen *et al.* 1999). 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 km² (5%). The ranges of 75% of the ticks in this category, namely *R. evertsi evertsi*, *R. pravus* and *R. simus* are predicted to expand. The total range expansion in this region is equivalent to 864 000 km² (7%). This expansion is mainly associated with *R. simus*, which is predicted to expand its range by 601 200 km² (70%).

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 pattern (Fig. 8A) the predicted pattern is spatially different and broader (Fig. 8B) with encroachment of ticks into new regions. These regions, which include An-

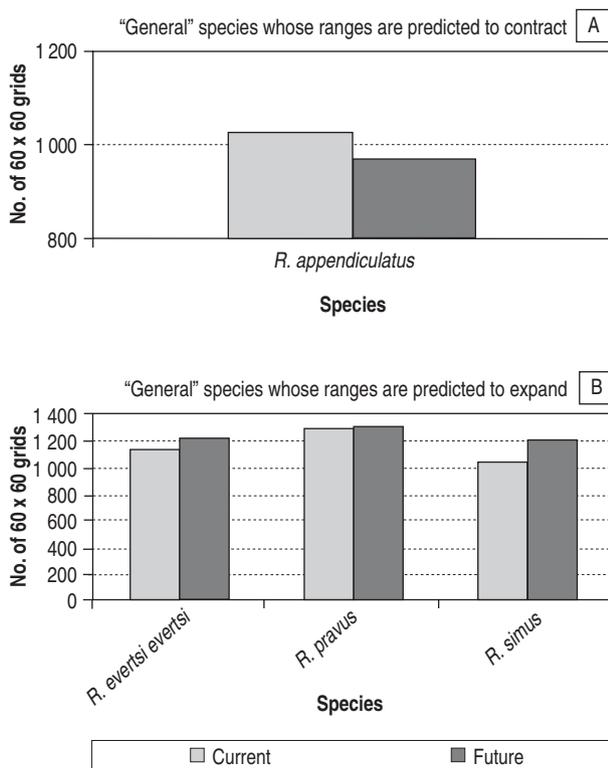


FIG. 7 *Rhipicephalus* species in the "General" ticks that are predicted to show (A) range size contraction and (B) range expansion

gola, Namibia, Botswana and the Northern Cape Province of South Africa, are forecast to experience a more than 50% increase in tick species richness (Fig. 8C). This could be related to increased rainfall in these regions, rendering the south-western regions of sub-Saharan Africa more suitable for ticks. The general west-east shift in species ranges reported by Erasmus *et al.* (2002) is not supported in this study on ticks, in which varying degrees of shift in different directions appears to be the emergent pattern for this taxon. Analysis of range shifts further indicates that 80% of species show less than a 50% range shift, while 20% of species show a range displacement of more than a 100%. The latter species are mainly those that populate the western arid regions of Africa (Fig. 8).

Species range changes and tick-borne disease implications

Thirty percent of the ticks included in this study are classified as economically important because they are vectors of diseases of domestic livestock or other animals (Table 1). Although *R. appendiculatus*, the principal *Rhipicephalus* vector of disease in Africa

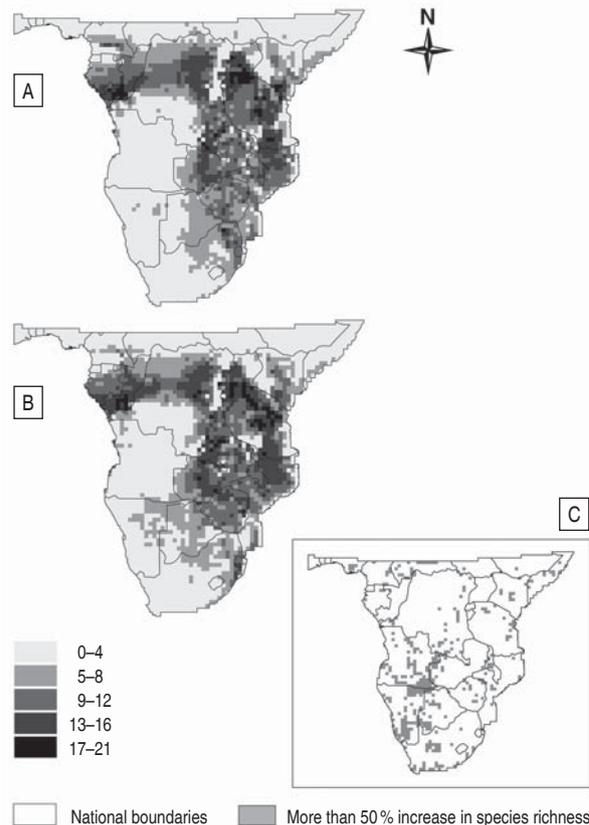


FIG. 8 Species richness pattern of *Rhipicephalus* species in sub-Saharan Africa: (A) current; (B) future; and (C) areas with more than 50% increase

shows range contraction, the remaining vectors are responsible for 52% of the predicted range expansion under future climate conditions. The non-vector species are responsible for 48% of future tick range expansions.

Predicted future distributions using DARLAM and GCM climate data

The predictions of future climate suitability for ticks when DARLAM is used are generally more extensive than those generated when using the combined GCM climates. With the exception of four species (*R. compositus*, *R. evertsi mimeticus*, *R. exophthalmos* and *R. oculatus*), and the *R. capensis* group, 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 511200 km². 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

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

| Disease and causal agents | Animal affected | Vectors |
|---|------------------------|--|
| East Coast fever (<i>Theileria parva</i>) | Cattle | <i>R. appendiculatus</i> <i>R. zambeziensis</i> |
| Tick toxicosis | Cattle | <i>R. appendiculatus</i> |
| Corridor disease or Buffalo disease (<i>Theileria parva</i>) | Cattle, buffalo | <i>R. appendiculatus</i> <i>R. zambeziensis</i> |
| Gall sickness (<i>Anaplasma marginale</i>) | Cattle | <i>R. evertsi evertsi</i> <i>R. simus</i> |
| Equine biliary fever or equine piroplasmiasis (<i>Babesia caballi</i> , <i>Theileria equi</i>) | Horses, mules, donkeys | <i>R. evertsi evertsi</i> |
| Spring lamb paralysis | Lambs, calves | <i>R. evertsi evertsi</i> |
| Canine biliary fever or canine tick fever (<i>Babesia canis</i>), rickettsiosis (<i>Ehlichia canis</i>) | Dogs | <i>R. sanguineus</i> |
| Paralysis | Sheep, lambs, calves | <i>R. lunulatus</i> |
| Nairobi sheep disease (<i>Bunyaviridae</i>) | Sheep | <i>R. pulchellus</i> |

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

| “General” tick species | DARLAM 2030 | GCM 2030 | Common grids | Proportional overlap value (%) |
|-----------------------------|-------------|-------------|--------------|--------------------------------|
| <i>R. appendiculatus</i> | 969 | 858 | 476 | 55 |
| <i>R. evertsi evertsi</i> | 1 220 | 945 | 611 | 65 |
| <i>R. pravus</i> | 1 300 | 868 | 621 | 29 |
| <i>R. simus</i> | 1 209 | 858 | 597 | 60 |
| East Africa | | | | |
| <i>R. aquatilis</i> | 33 | 17 | 5 | 29 |
| <i>R. armatus</i> | 153 | 116 | 29 | 25 |
| <i>R. bequaerti</i> | 215 | 40 | 11 | 28 |
| <i>R. carnivoralis</i> | 205 | 111 | 67 | 60 |
| <i>R. humeralis</i> | 79 | 33 | 12 | 55 |
| <i>R. kochi</i> | 797 | 491 | 326 | 29 |
| <i>R. maculatus</i> | 425 | 173 | 98 | 56 |
| <i>R. muehlensi</i> | 699 | 678 | 315 | 67 |
| <i>R. planus</i> | 719 | 413 | 278 | 55 |
| <i>R. pulchellus</i> | 841 | 217 | 179 | 25 |
| Central Africa | | | | |
| <i>R. complanatus</i> | 626 | 595 | 400 | 67 |
| <i>R. compositus</i> | 699 | 737* | 443 | 60 |
| <i>R. dux</i> | 201 | 192 | 77 | 40 |
| <i>R. longus</i> | 1 020 | 990 | 642 | 25 |
| <i>R. lunulatus</i> | 897 | 518 | 308 | 28 |
| <i>R. masseyi</i> | 450 | 338 | 202 | 60 |
| <i>R. punctatus</i> | 458 | 440 | 262 | 28 |
| <i>R. senegalensis</i> | 803 | 622 | 415 | 56 |
| <i>R. ziemanni</i> | 611 | 558 | 352 | 72 |
| South Africa | | | | |
| <i>R. capensis</i> group | 485 | 547* | 309 | 56 |
| <i>R. distinctus</i> | 707 | 352 | 254 | 72 |
| <i>R. evertsi mimeticus</i> | 423 | 577* | 49 | 49 |
| <i>R. exophthalmos</i> | 212 | 236* | 116 | 15 |
| <i>R. oculatus</i> | 386 | 434* | 293 | 49 |
| <i>R. zambeziensis</i> | 299 | 226 | 169 | 60 |

Bold* = GCM predictions wider than those of DARLAM

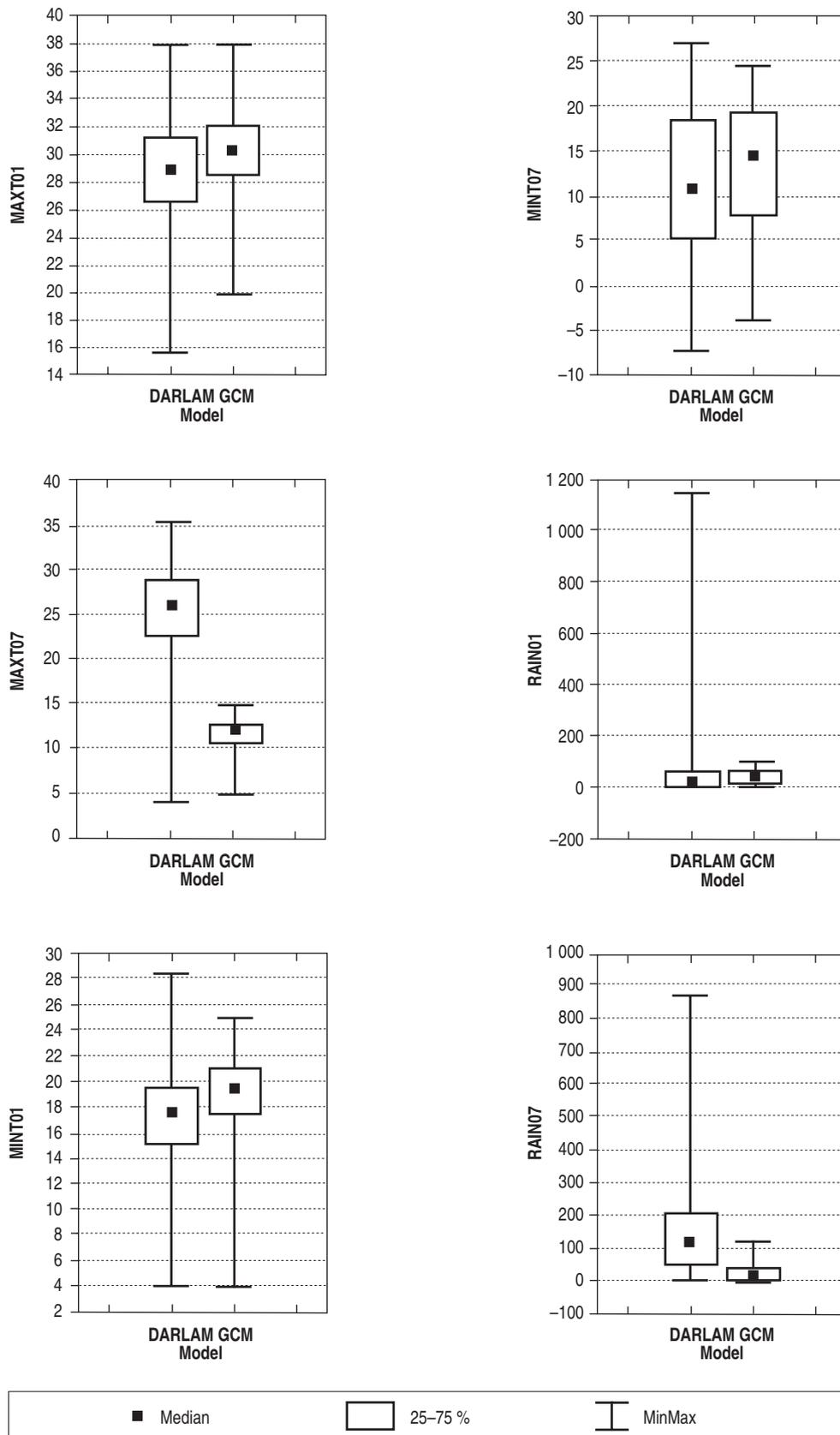


FIG. 9 Box plots based on the Kolmogorov-Smirnov test that compared climate predicted by DARLAM and a combined GCM

FIG. 10–39 Predicted probability distribution of *Rhipicephalus* species using DARLAM and GCM future climates: (A) DARLAM; (B) GCM

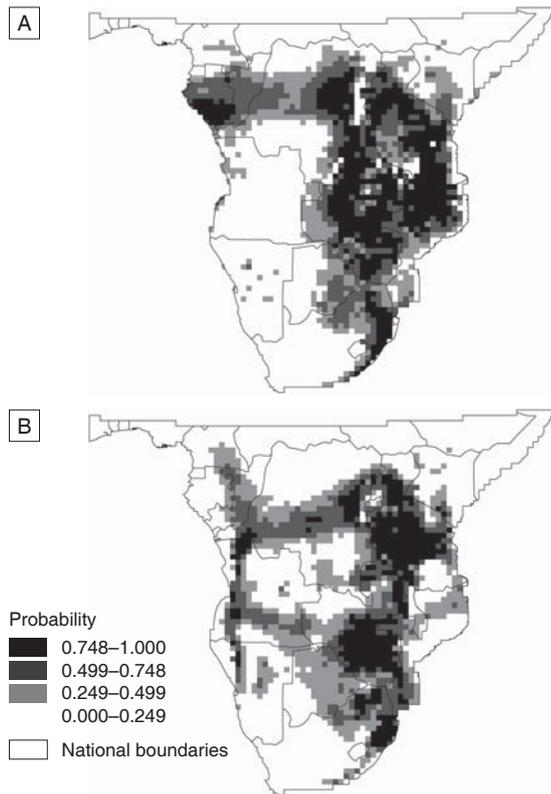


FIG. 10 *R. appendiculatus*

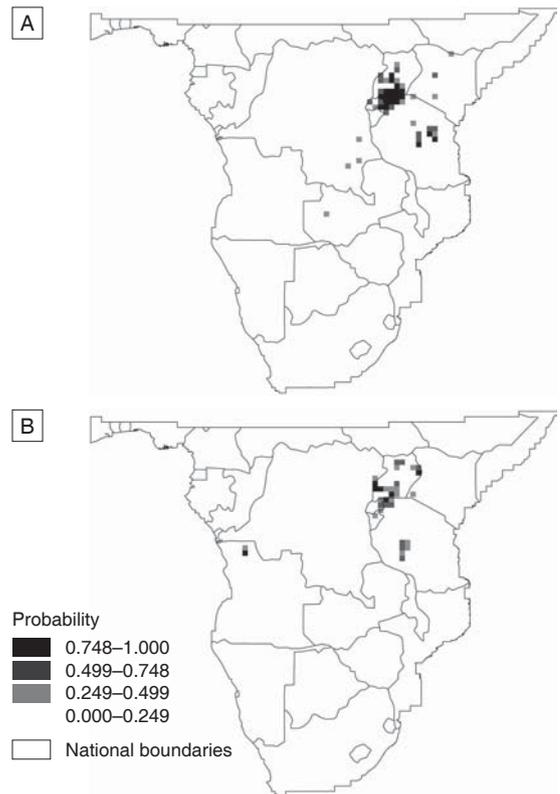


FIG. 11 *R. aquatilis*

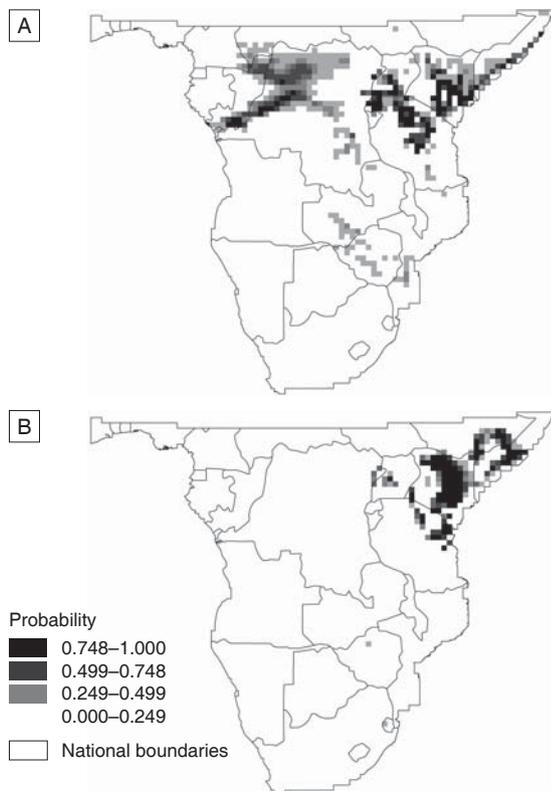


FIG. 12 *R. armatus*

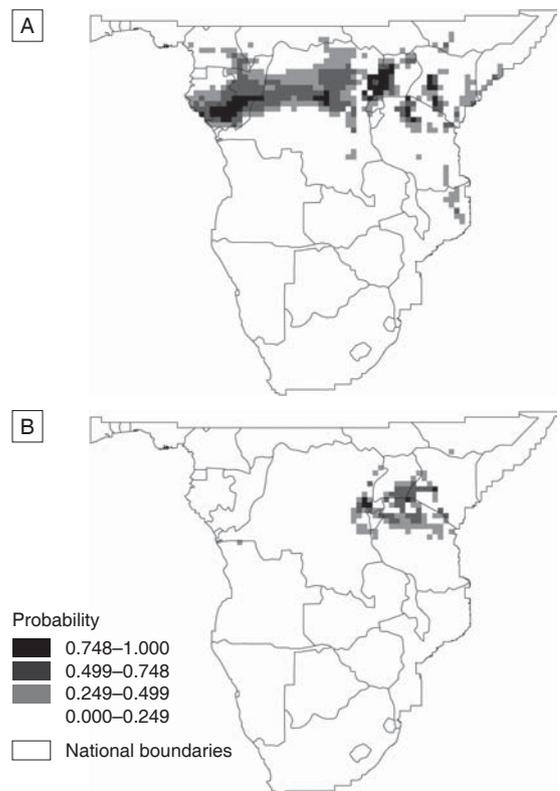


FIG. 13 *R. bequaerti*

FIG. 10–39 *Continued*

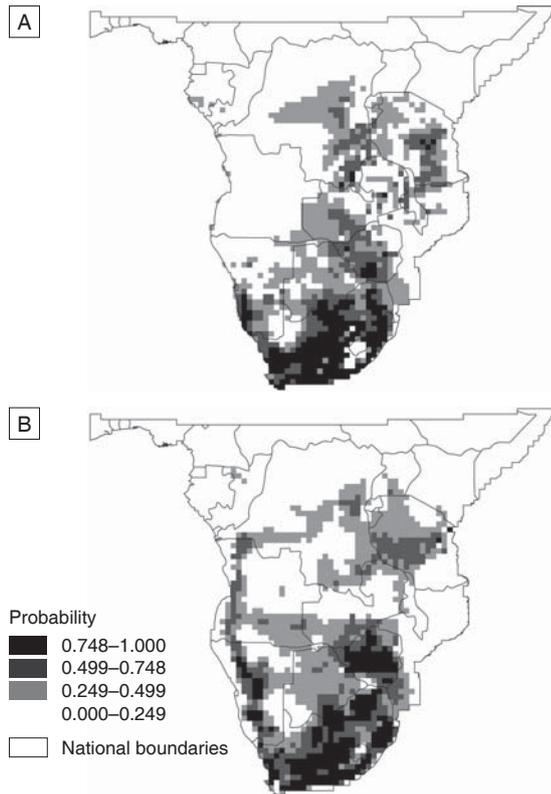


FIG. 14 *R. capensis* group

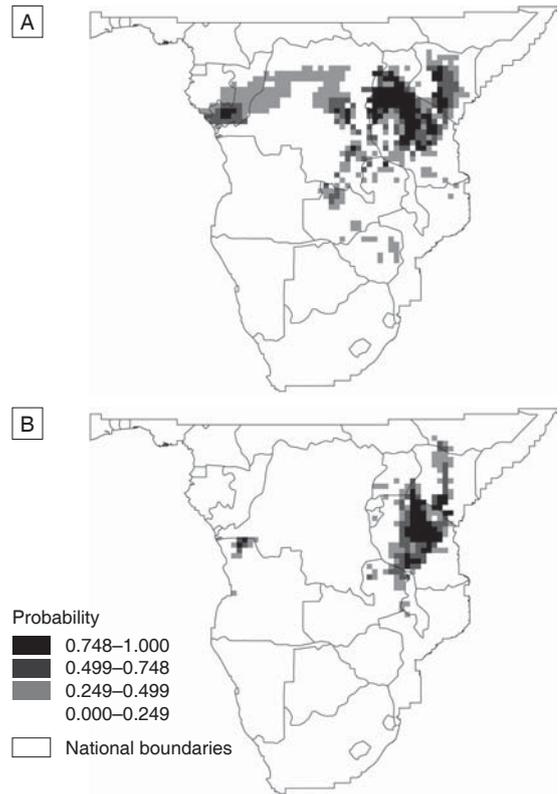


FIG. 15 *R. carnivoralis*

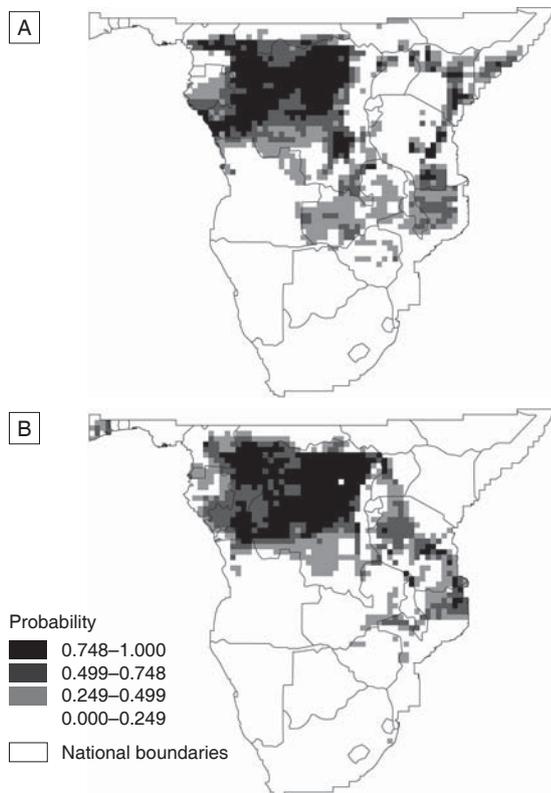


FIG. 16 *R. complanatus*

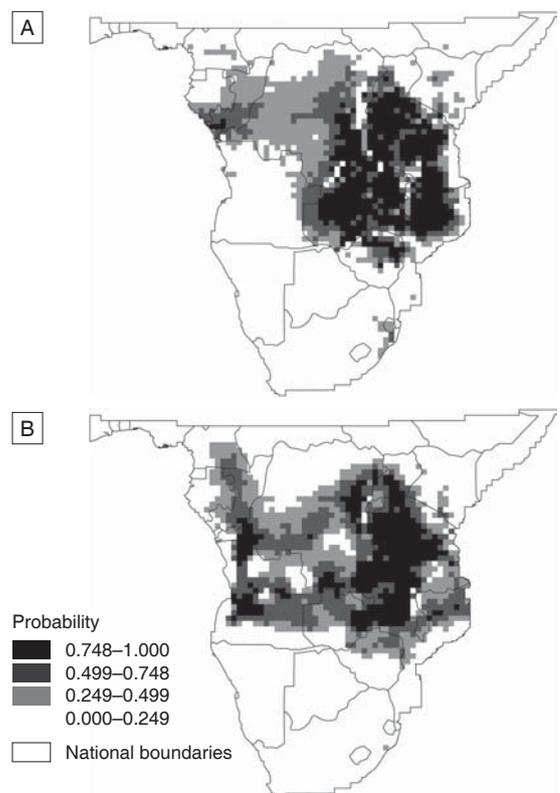


FIG. 17 *R. compositus*

FIG. 10–39 *Continued*

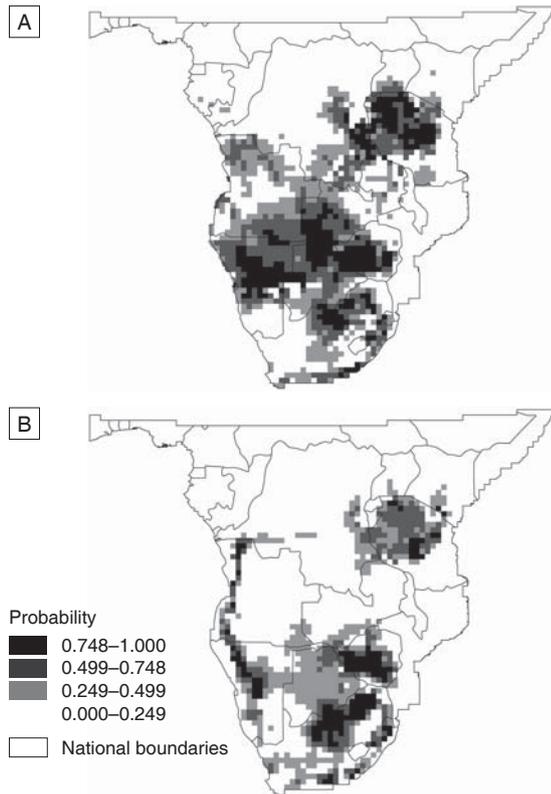


FIG. 18 *R. distinctus*

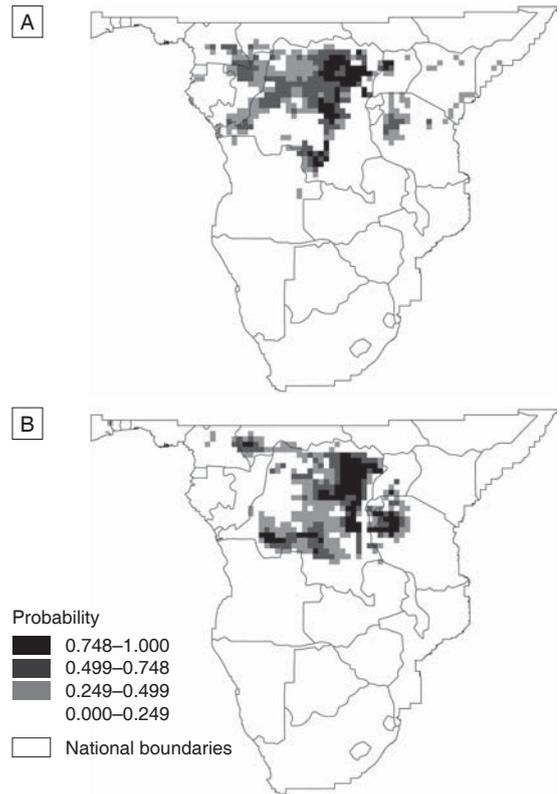


FIG. 19 *R. dux*

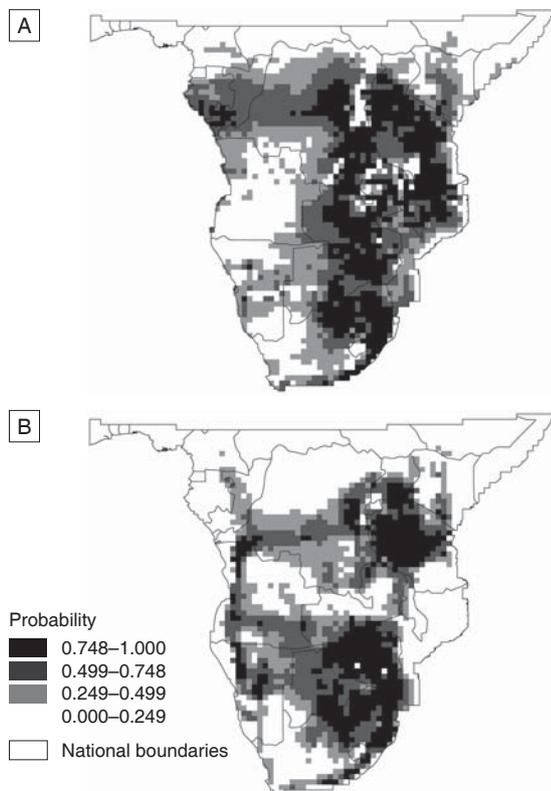


FIG. 20 *R. evertsi evertsi*

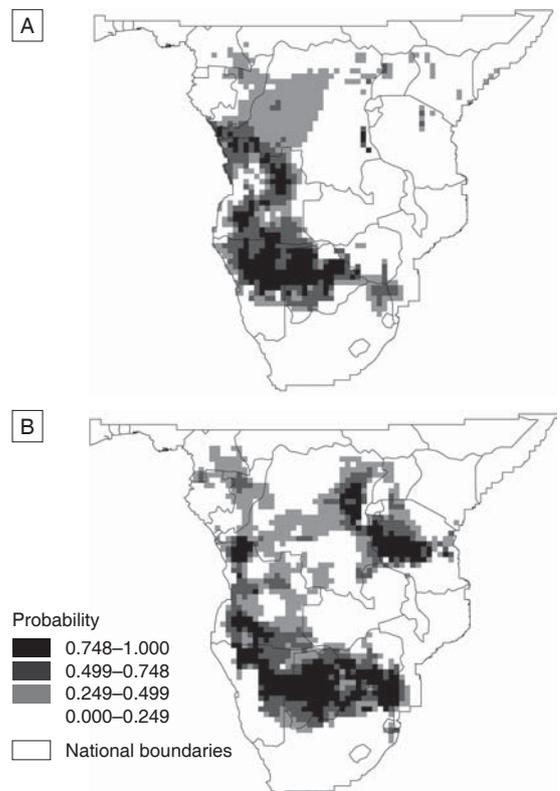


FIG. 21 *R. evertsi mimeticus*

FIG. 10–39 *Continued*

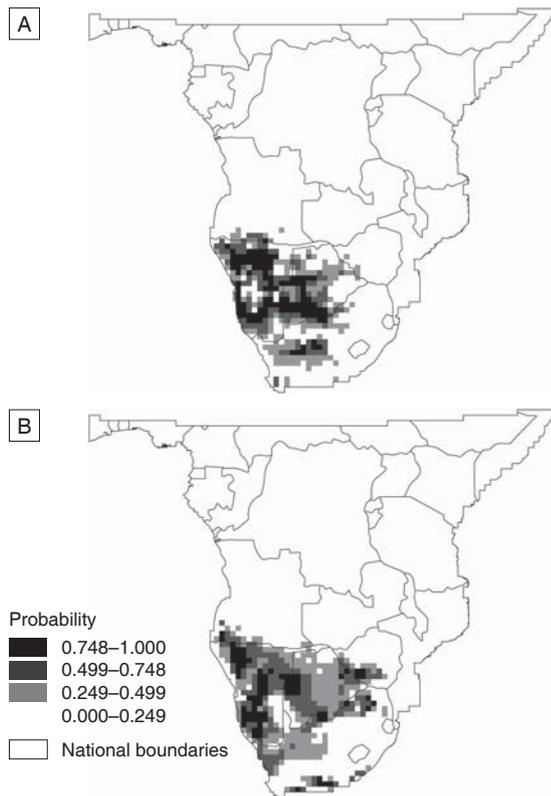


FIG. 22 *R. exophthalmos*

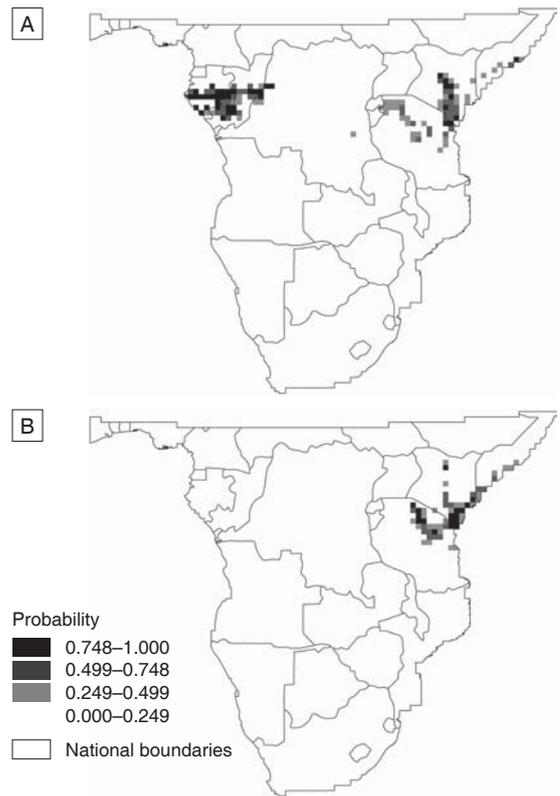


FIG. 23 *R. humeralis*

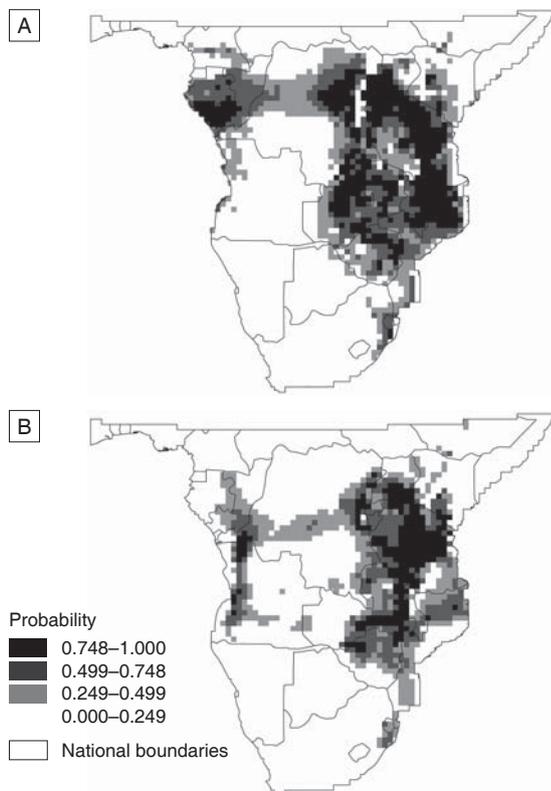


FIG. 24 *R. kochi*

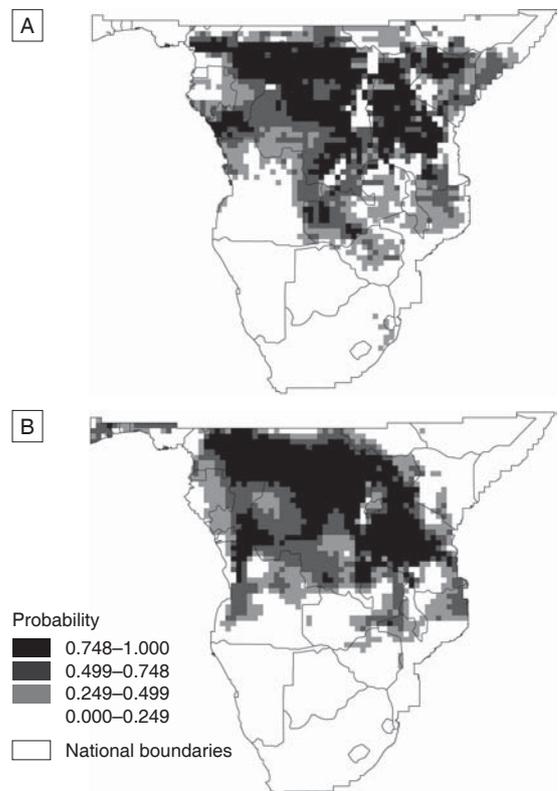


FIG. 25 *R. longus*

FIG. 10–39 *Continued*

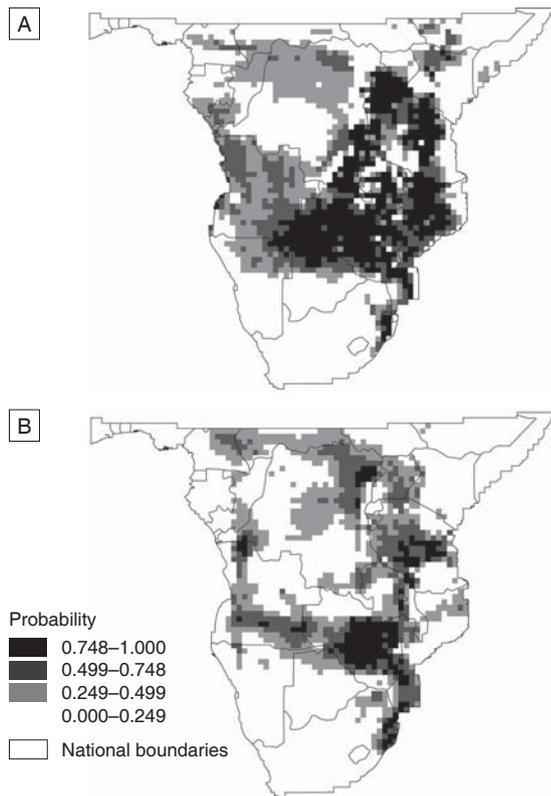


FIG. 26 *R. lunulatus*

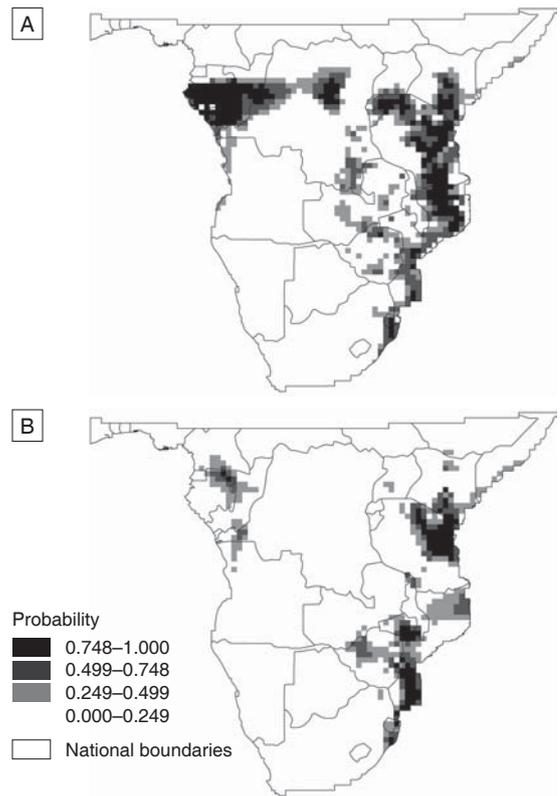


FIG. 27 *R. maculatus*

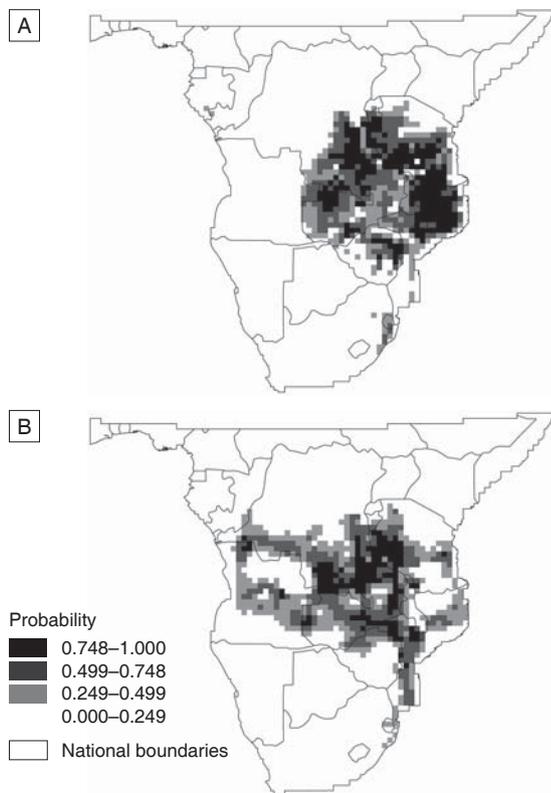


FIG. 28 *R. masseyi*

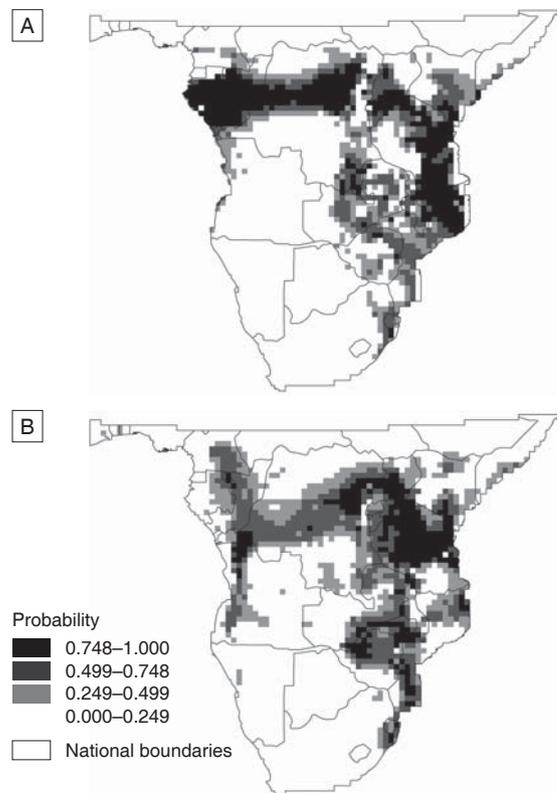


FIG. 29 *R. muehlensi*

FIG. 10–39 *Continued*

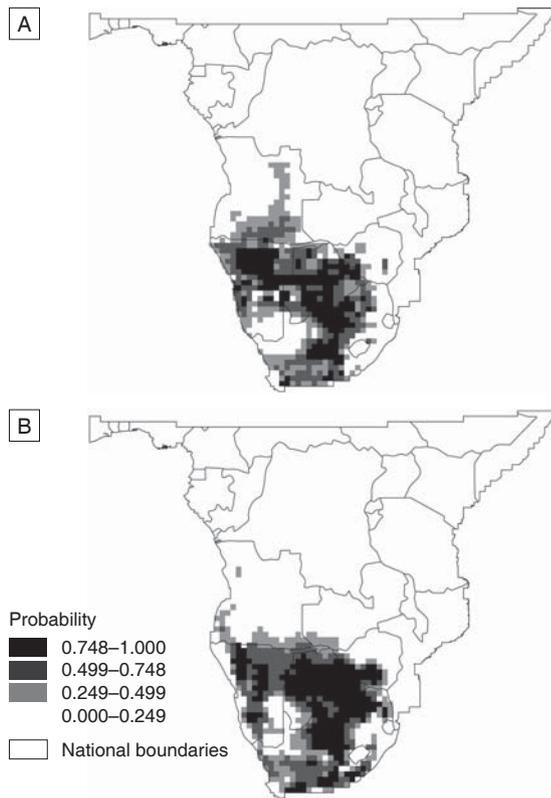


FIG. 30 *R. oculatus*

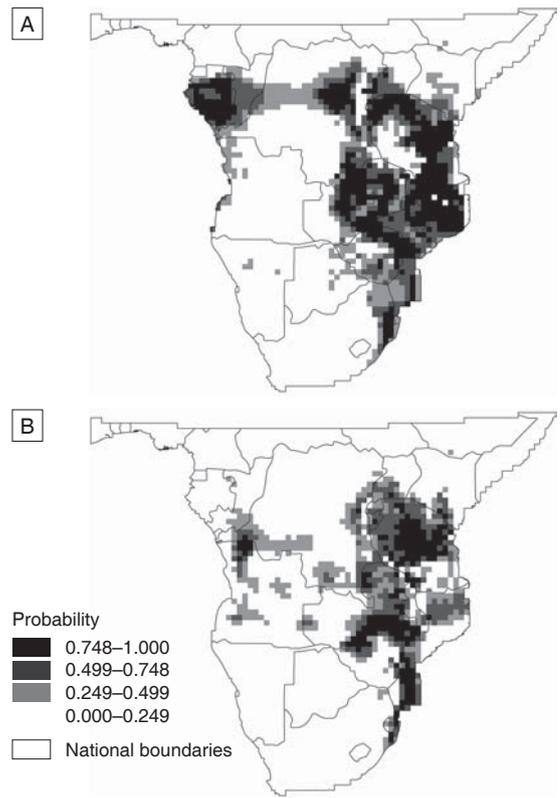


FIG. 31 *R. planus*

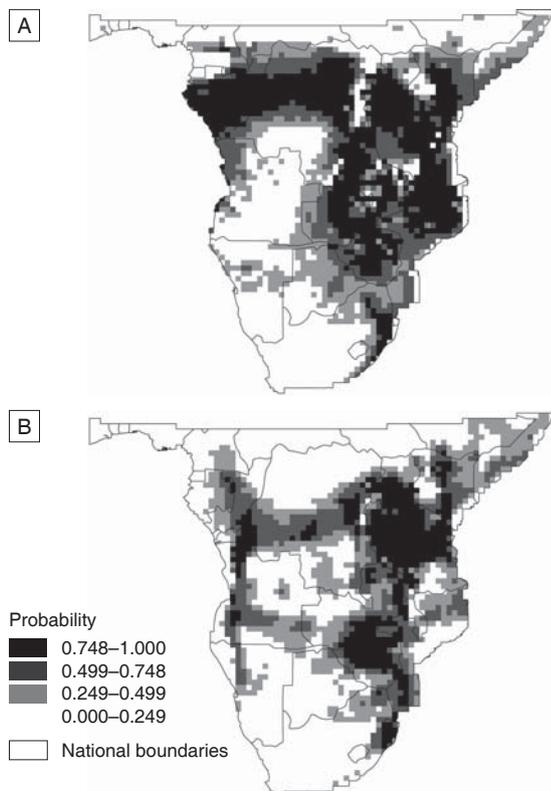


FIG. 32 *R. praeus*

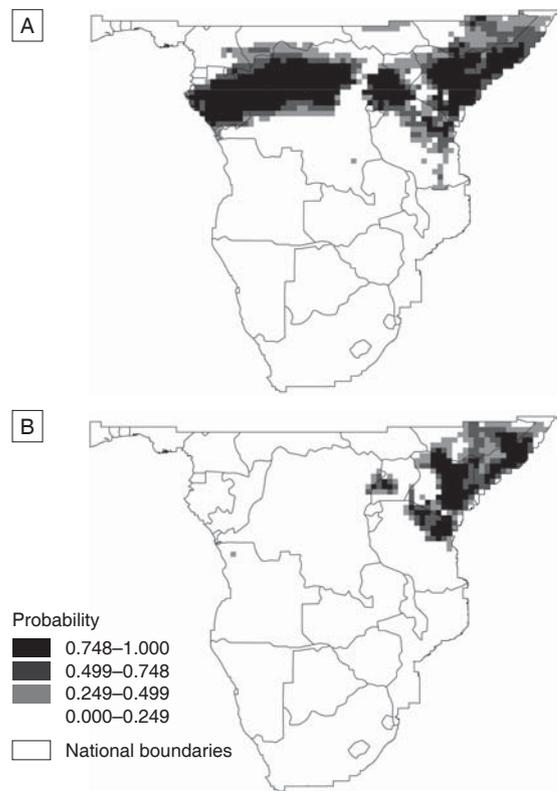


FIG. 33 *R. pulchellus*

FIG. 10–39 *Continued*

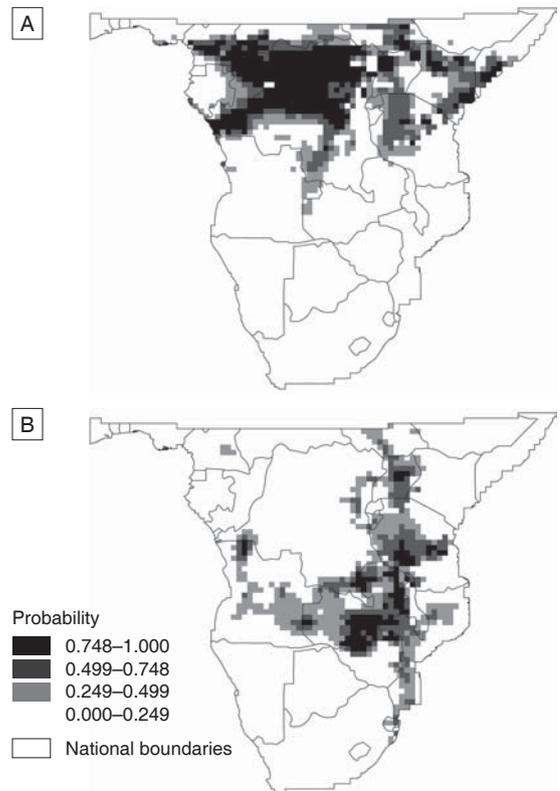
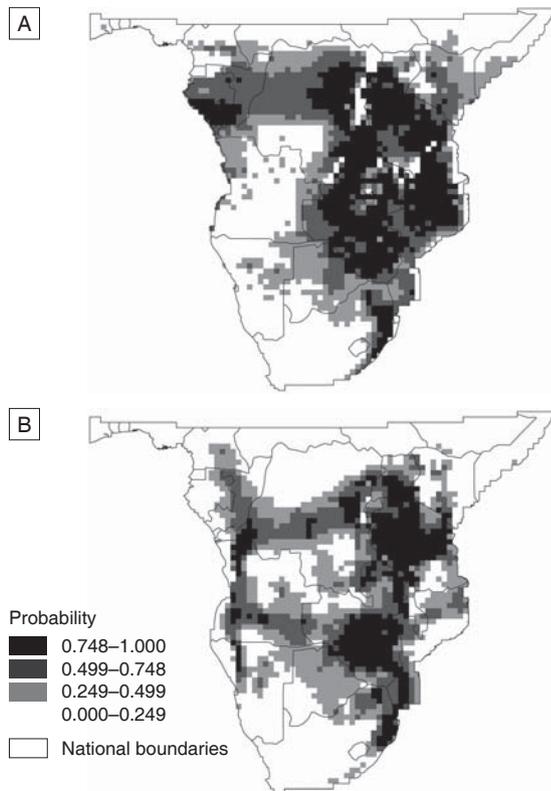
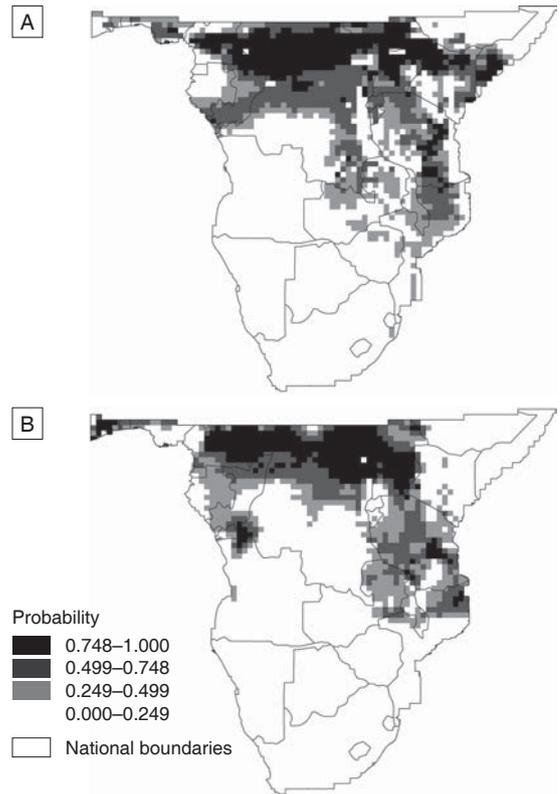
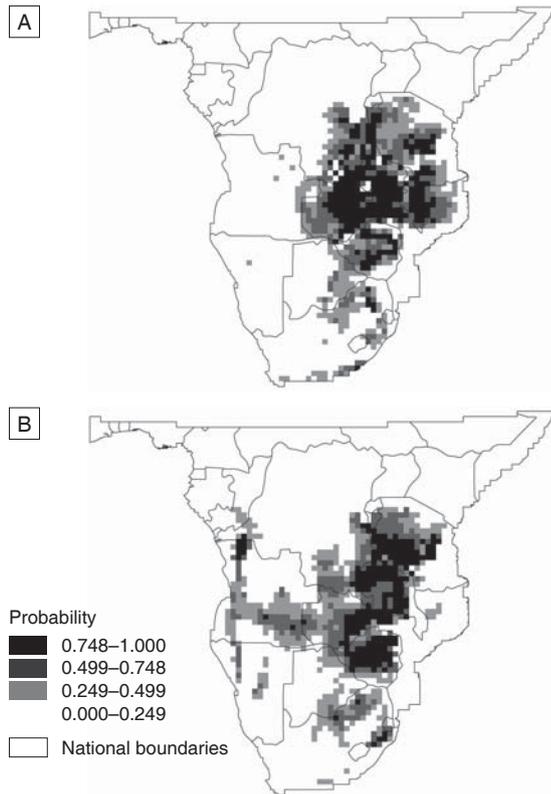
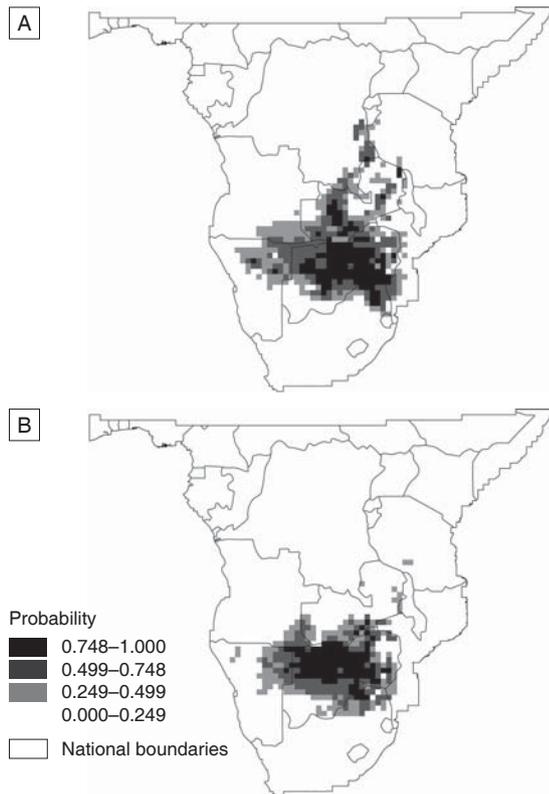
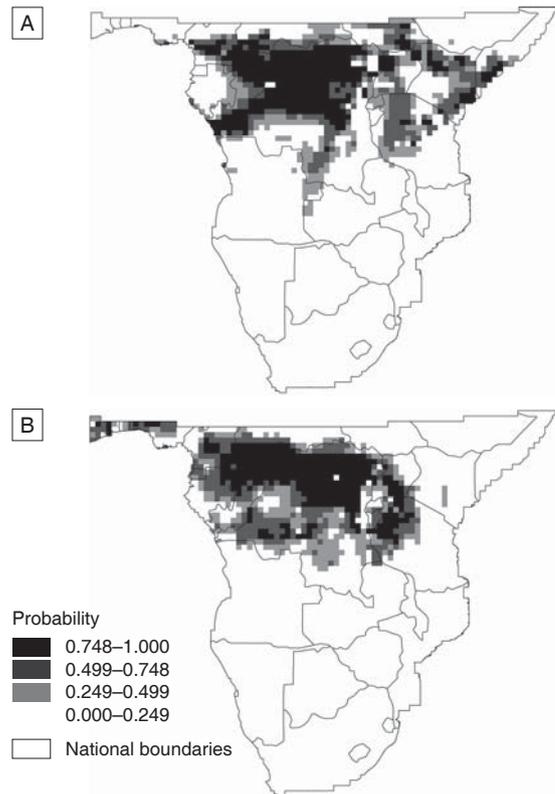


FIG. 10–39 *Continued*FIG. 38 *R. zambeziensis*FIG. 39 *R. ziamanni*

is a highly significant difference 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 January, and mean rainfall for January and July where the GCM data predicted hotter and drier climates than DARLAM.

The regional analysis of predicted tick distributions using DARLAM and GCM 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. Of these species *R. capensis* is present in a winter rainfall region with hot and generally dry summers, whereas *R. evertsi mimeticus*, *R. exophthalmos* and *R. oculatus* are species that occupy arid and semi-arid areas in South Africa with an annual mean rainfall of 100–400 mm. The other two species for which GCM predictions were found to be broader than DARLAM are *R. compositus* and *R. muehlensi*. *Rhipicephalus compositus* is a central African species present in a variety of wooded habitats with rainfall varying between 700 to more than 1 600 mm per annum (Walker *et al.* 2000). On the other hand, *R. muehlensi* is

present in all African countries with an eastern seaboard from Somalia to South Africa. It occurs in coastal mosaic and undifferentiated woodland with the rainfall generally between 500 and 1 100 mm per annum (Walker *et al.* 2000).

Proportional overlap tests between the GCM and DARLAM fields on a sub-Saharan scale yield overlap values ranging from 24–72%. 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 (Table 2).

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 tick genus *Rhipicephalus*. A climate com-

piled 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* group, *R. longus* and *R. zambeziensis* in Africa using DARLAM. With this as background we 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, 8 or 6 km resolution of most long-term interpolated climate data sets gives a false picture because it depends on the original low-resolution point observations (for a comparison of different climate data sets 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 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 limited to those species of *Rhipicephalus* of which one of us (I.G.H) has considerable field experience, namely *R. appendiculatus*, *R. capensis* group, *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 wild ruminant or equine 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 (*Syncerus caffer*), bushpigs (*Potamochoerus larvatus*) and rhinoceroses (*Ceratotherium simum* and *Diceros bicornis*) as hosts, and those of the latter tick tragelaphine antelope species such as kudu (*Tragelaphus* spp.), nyalas (*Tragelaphus angasii*) and bushbuck (*Tragelaphus scriptus*) (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 2005). 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 sensu strictu* 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 spe-

cies 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 general 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 predicted future climate conditions. This has implications for the time ahead, as some of these species 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 pathogens evolve. Because of the number of new 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 a reduction in the desiccation and death of eggs. 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 mimiticus* 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 their 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 *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, Horak *et al.* (2000) recorded a double seasonal peak in tick numbers in 1998 implying that an additional generation of ticks had been completed. 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 distributions of these two ticks could be due to the fact that it is only recently that their specific identities have been resolved; 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 the relatively small scale of contraction found in the species investigated. 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 dominant species, namely *Glossina pallicera* and *Glossina nigrofusca* resulting in the continued transmission of trypanosomiasis (Sutherst 2001). Additionally, the suppression of *B. 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 *B. microplus* (Sutherst 2001). Although the latter 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 *B. microplus*, transmit economically more important diseases than the indigenous *B. 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 rainfall 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 1991/1992 drought (Horak *et al.* 2000). An explanation for these observations appear to be that an increase in the ratio 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. The contraction in the distribution of *R. appendiculatus* may be looked at with relief since it is the most important vector of tick-borne diseases on the African continent, transmitting the pathogen *Theileria parva* that causes East Coast fever and Corridor diseases in cattle. This could imply that areas currently showing Corridor disease as an emerging disease may become vector free in the future. 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 present day features of the global climate (Goodess & Palutikof 1993). Ticks are habitat specialists and spend more than 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 infestation with ticks that act as vectors of disease. With its poor reaction 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 integration 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 tick-borne 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 sev-

eral 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 change 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.

ACKNOWLEDGEMENTS

We thank the CSIRO Atmospheric Research Division in Australia for making DARLAM available to LRAM at the University of Pretoria, thus enabling us to perform model simulations for the SADC region. The study benefited from financial support provided in part by the University of Stellenbosch and the University of Pretoria, while the Global Change System for Analysis, Research and Training (START) (<http://www.start.org>) and the NRF/DST Centre for Invasion Biology (CIB) provided support for ASvJ.

REFERENCES

- BURROWS, R., HOFER, H. & EAST, M.L. 1994. Demography, extinction and intervention in a small population: the case of the Serengeti wild dogs. *Proceedings of the Royal Society, London B*, 256:281–292.
- CARPENTER, J.W., APPEL, M.J.G., ERICKSON, R.C. & NOVILLA, M.N. 1976. Fatal vaccine-induced canine distemper virus infection in black-footed ferrets. *Journal of the American Medical and Veterinary Association*, 169:961–964.
- CUMMING, G.S. 1999. *The evolutionary ecology of African ticks*. Doctoral thesis, University of Oxford.
- CUMMING, G.S. 2000a. Using between model comparisons to fine tune linear models of species ranges. *Journal of Biogeography*, 27:441–455.
- CUMMING, G.S. 2000b. Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). *Journal of Biogeography*, 27:425–440.
- DIPEOLU, O.O. 1989. Research on ticks of livestock in Africa: review of the trends, advances and milestones in tick biology and ecology in the decade 1980–1989. *Insect Science Application*, 10:723–740.
- ENGELBRECHT, F.A., RAUTENBACH, C.J., DEW., MCGREGOR, J.L. & KATZFEY, J.J. 2002. January and July climate simulations over the SADC region using the limited-area model DARLAM. *Water SA*, 28:361–373.
- ERASMUS, B.F.N., KSHATRIYA, M., MANSELL, M.W., CHOWN, S.L. & VAN JAARVELD, A.S. 2000. A modelling approach to antlions (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomology*, 8:157–168.
- ERASMUS, B.F.N., VAN JAARVELD, A.S., CHOWN, S.L., KSHATRIYA, M. & WESSELS, K.J. 2002. Vulnerability of South African animal taxa to climate change. *Global Change Biology*, 8:679–693.
- ESTRADA-PEÑA, A. 1999. Geostatistics as predictive tools to estimate *Ixodes ricinus* (Acari: Ixodidae) habitat suitability in the western Palearctic from AVHRR satellite imagery. *Experimental and Applied Acarology*, 23:337–349.
- ESTRADA-PEÑA, A. 2001. Climate warming and changes in habitat suitability for *Boophilus microplus* (Acari: Ixodidae) in Central America. *Journal of Parasitology*, 87:978–987.
- ESTRADA-PEÑA, A. 2003. Climate change decreases habitat suitability for some tick species (Acari: Ixodidae) in South Africa. *Onderstepoort Journal of Veterinary Research*, 70:79–93.
- FIELDING, A.H. & BELL J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24:38–49.
- FLATO, G.M. & BOER, G.J. 2001. Warming asymmetry in climate change simulations. *Geophysical Research Letters*, 28:195–198.
- FLATO, G.M. & HIBLER, W.D. 1992. Modelling pack ice as a cavitating fluid. *Journal of Physical Oceanography*, 22:626–651.
- FOURIE, L.J., HORAK, I.G. & WOODALL, P. 2005. Elephant shrews as hosts of immature ixodid ticks. *Onderstepoort Journal of Veterinary Research*, 72:293–301.
- GASTON, K.J. 1994. *Rarity*. London: Chapman & Hall.
- GENT, P.R. & MCWILLIAMS, J.C. 1990. Isopycnal mixing in ocean circulation models. *Journal of Physical Oceanography*, 20:150–155.
- GITHEKO, A.K., LINDSAY, W., CONFALONIERI, U.E. & PATZ, J.A. 2000. Climate change and vector-borne diseases: a regional analysis. *Bulletin of the World Health Organisation*, 48:1136–1147.
- GOODESS, C.M. & PALUTIKOF, J.P. 1993. The development of regional climate scenarios and the ecological impact of greenhouse gas warming, in *Global Climate Change: the Ecological consequences*, edited by F.I. Woodward. London: Academic Press.
- GOUTEUX, J. & JARRY, M. 1998. Tsetse flies, biodiversity and the control of sleeping sickness. Structure of a *Glossina* guild in southwest Cote d' Ivoire, *Acta Oncologica*, 19:453–471.
- HORAK, I.G., BOOMKER, J., SPICKETT, A.M. & DE VOS, V. 1992. Parasites of domestic and wild animals in South Africa. XXX. Ectoparasites of kudus in the eastern Transvaal Lowveld and the eastern Cape Province. *Onderstepoort Journal of Veterinary Research*, 59:259–273.
- HORAK, I.G., BOOMKER, J. & FLAMAND, J.R.B. 1995. Parasites of domestic and wild animals in South Africa. XXXIV. Arthropod parasites of nyalas in north-eastern KwaZulu-Natal. *Onderstepoort Journal of Veterinary Research*, 62:171–179.
- HORAK, I.G., SPICKETT, A.M. & BRAACK, L.E.O. 2000. Fluctuation in the abundance of *Boophilus decoloratus* and three *Rhipicephalus* species on vegetation during eleven consecutive years, in *Proceedings of the 3rd International Congress on Ticks and Tick-borne Pathogens: Into the 21st Century*, edited by M. Kazimirova, M. Labuda & P.A. Nuttall: 247–251 [Bratislava, Slovakia].
- HUTCHINSON, M.F. 1989. A new procedure for gridding elevation and streamline data with automatic removal of spurious pits. *Journal of Hydrology*, 106:211–232.
- HUTCHINSON, M.F. 1991. The application of thin plate splines to continent-wide data assimilation, in *Data assimilation systems*, edited by J.D. Jasper, Melbourne: Australia.
- HUTCHINSON, M.F. & GESSLER, P.E. 1994. Splines-more than just a smooth interpolator. *Geoderma*, 62:45–67.
- HUTCHINSON, M.F., NIX, H.A., MACMAHON, J.P. & ORD, K.D. 1996. A topographic and climatic database for Africa, ver. 1.1. Canberra: Australian National University.
- JEFFREE, E.P. & JEFFREE, C.E. 1994. Temperature and the biogeographical distribution of species. *Functional Ecology*, 8:640–650.
- JEFFREE, C.E. & JEFFREE, E.P. 1996. Redistribution of the potential geographical ranges of Mistletoe and Colorado Beetle

- in Europe in response to the temperature component of climate. *Functional Ecology*, 10:562–577.
- KRUSKA, R. & PERRY, B.D. 1991. Evaluation of grazing lands of Zimbabwe using the AVHRR normalized difference vegetation index. *Preventative Veterinary Medicine*, 11:363–365.
- LESSARD, P., L'ÉPLATTENIER, R., NORVAL, R.A.I., KUNDERT, K., DOLAN, T.T., CROZA, H., WALKER, J.B., IRVIN, A.D. & PERRY, B.D. 1990. Geographic information systems for studying the epidemiology of cattle diseases caused by *Theileria parva*. *The Veterinary Record*, 126:255–262.
- LINDGREN, E., TALLEKLINT, L. & POLFELD, T. 1998. Impacts of climate change on the northern latitude limit and population density of the diseases-transmitting European tick *Ixodes ricinus*. *Environmental Health Perspectives*, 108:119–123.
- LONDT, J.G.H. 1977. Oviposition and incubation in *Boophilus decoloratus*. *Onderstepoort Journal of Veterinary Research*, 44:13–20.
- MCGREGOR, J.L. 1997. Regional climate modelling. *Meteorology and Atmospheric Physics*, 63:105–117.
- MINSHULL, J.I. & NORVAL, R.A.I. 1982. Factors influencing the spatial distribution of *Rhipicephalus appendiculatus* in Kyle recreational park, Zimbabwe. *South African Journal of Wildlife Research*, 12:118–123.
- NIX, H. 1986. A biogeographic analysis of Australian elapid snakes, in *Atlas of Elapid snakes of Australia*, edited by R. Longmore. Canberra: Australian Government Publishing Services (Australia Flora and Fauna series, 7:4–15).
- NORVAL, R.A.I., WALKER, JANE B. & COLBORNE, J. 1982. The ecology of *Rhipicephalus zambeziensis* and *Rhipicephalus appendiculatus* (Acarina, Ixodidae) with particular reference to Zimbabwe. *Onderstepoort Journal of Veterinary Research*, 49:181–190.
- NORVAL, R.A.I., PERRY, B.D., GEBREAB, F. & LESSARD, P. 1991. East Coast Fever: a problem of the future for the horn of Africa? *Preventative Veterinary Medicine*, 10:163–172.
- NORVAL, R.A.I., PERRY, B.D. & YOUNG, A.S. 1992. *The Epidemiology of Theileriosis in Africa*. London: Academic Press.
- NORVAL, R.A.I., PERRY, B.D., MELTZER, M.I., KRUSKA, R.L. & BOOTHROYD, T.H. 1994. The factors affecting the distribution of ticks *Amblyomma hebraeum* and *Amblyomma variagatum* in Zimbabwe: implication of reduced acaricide usage. *Experimental and Applied Acarology*, 18:383–407.
- NORVAL, R.A.I., SUTHERST, R.W., KURKI, J., KERR, J.D. & GIBSON, J.D. 1997. The effects of the brown ear tick *Rhipicephalus appendiculatus* on milk production of Sanga cattle. *Medical and Veterinary Entomology*, 11:148–154.
- NOZAWA, T., EMORI, S., NUMAGUTI, A., TSUSHIMA, Y., TAKEMURA, T., NAKAJIMA, T., ABE-OUCHI, A. & KIMOTO, M. 2001. Projections of future climate change in the 21st Century, simulated by the CCSR/NIES CGCM under the IPCC SRES scenarios, in *Present and future of modelling global environmental change: Towards integrated modelling*, edited by T. Matsumo & H. Kida.
- OKELLO-ONEN, TUKAHIRWA, E.M., PERRY, B.D., ROWLANDS, G.J., NAGDA, S.M., MUSISI, G., HEINONEN, R., MWAYI, W. & OPUDA-ASIBO, J. 1999. Population dynamics of ticks on indigenous cattle in pastoral dry to semi-arid rangelands zone of Uganda. *Experimental & Applied Acarology*, 23:79–88.
- OLWOCH, J.M., RAUTENBACH, C.J. DE W., ERASMUS, B.F.N., ENGELBRECHT, F.A. & VAN JAARSVELD, A.S. 2003. Simulating tick distributions over sub-Saharan Africa: the use of observed and simulated climate surfaces. *Journal of Biogeography*, 30:1221–1232.
- PERRY, B.D., LESSARD, P., NORVAL, R.A.I., KUNDERT, K. & KRUSKA, R. 1990. Climate, vegetation and the distribution of *Rhipicephalus appendiculatus* in Africa. *Parasitology Today*, 6:100–104.
- PRENDERGAST, J.R., QUINN, R.M., LAWTON, J.H., EVERSHAM, B.C. & GIBBONS, D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, 365:335–337.
- RANDOLPH, S.E. 1993. Climate, satellite imagery and seasonal abundance of the tick *Rhipicephalus appendiculatus* in southern Africa: a new perspective. *Medical and Veterinary Entomology*, 7:243–258.
- RANDOLPH, S.E. 2001. The shifting landscape of tick-borne zoonoses: tick-borne encephalitis and Lyme borreliosis in Europe. *Philosophical Transactions of the Royal Society, London, B*, 356:1045–1056.
- RANDOLPH, S.E. 2002. Ticks and tick-borne disease systems in space and from space. *Advances in Parasitology*, 47:217–243.
- RANDOLPH, S.E. & ROGERS, D.J. 1997. A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology*, 115:265–279.
- RECHAV, Y. 1981. Ecological factors affecting the seasonal activity of the brown ear tick, *Rhipicephalus appendiculatus*, in *Proceedings of an International Conference on Tick Biology and Control*, edited by G.B. Whitehead & J.D. Gibson. Tick Research Unit, Rhodes University, South Africa.
- RECHAV, Y. 1982. Dynamics of tick populations (Acari: Ixodidae) in Eastern Cape Province of South Africa. *Journal of Medical Entomology*, 19:679–700.
- REYERS, B., VAN JAARSVELD, A.S. & KRÜGER, M. 2000. Complementarity as a biodiversity indicator strategy. *Proceedings of the Royal Society, London, B*, 267:505–513.
- ROBERTSON, W.D. 1981. A four-year study of the seasonal fluctuation in the occurrence of the blue tick *Boophilus decoloratus* in the coastal regions of the eastern Cape, in *Proceedings of an International Conference on Tick Biology and Control*, edited by G.B. Whitehead & J.D. Gibson. Tick Research Unit, Rhodes University, South Africa: 199–204.
- ROGERS, D.J. & RANDOLPH, S.E. 1993. Distribution of tsetse and ticks in Africa: past, present and future. *Parasitology Today*, 9:266–271.
- ROGERS, D.J. & RANDOLPH, S.E. 2000. The global spread of malaria in a future warmer world. *Science*, 289:1763–1766.
- SHORT, N.J. & NORVAL, R.A.I. 1981. The seasonal activity of *Rhipicephalus appendiculatus* Neumann 1901 (Acari: Ixodidae) in the high veld of Zimbabwe Rhodesia. *Journal of Parasitology*, 67:77–84.
- SPICKETT, A.M. & HEYNE, H. 1990. The pre-hatch period and larval survival of *Boophilus decoloratus* under natural conditions in the Transvaal, South Africa. *Onderstepoort Journal of Veterinary Research*, 57:95–98.
- SUTHERST, R.W. (Ed.) 1996. Impacts of climate change on pests, diseases and weeds in Australia. (IGBP-GCTE working document, no. 25).
- SUTHERST, R.W. 2001. The vulnerability of animal and human health to parasites under global change. *International Journal for Parasitology*, 31:933–948.
- SUTHERST, R.W. 2003. Prediction of species geographical ranges. *Journal of Biogeography*, 30:805–816.
- SUTHERST, R.W. & MAYWALD, G.F. 1985. A computerized system for matching climates in ecology. *Agriculture, Ecosystem and Environment*, 13:281–299.

- SUTHERST, R.W., MAYWALD, G.F. & SKARRATT, D.B. 1995. Predicting insect distribution in a changed climate in *Insects in a changing environment*, edited by R. Harrington & N.E. Stork.
- THOMAS, C.D., CAMERON, A., GREEN, R.E., BAKKENES, M., BEAUMONT, L.J., COLLINGHAM, Y.C., ERASMUS, B.F.N., FERRIERRA DE SIQUEIRA, M., GRAINGER, A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A.S., MIDGLEY, G.F., MILES, L., ORTEGA-HUERTA, M.A., PETERSON, A.T., PHILIPS, O. & WILLIAMS, S.E. 2004. Extinction risk from climate change. *Nature*, 427:145–148.
- TUKAHIRWA, M.E. 1976. The effects of temperature and relative humidity on the development of *R. appendiculatus* Neumann (Acari, Ixodidae). *Bulletin of Entomological Research*, 66:301–312.
- VAN STADEN, V., ERASMUS, B.F.N., ROUX, J., WINGFIELD, M.J. & VAN JAARSVELD, A.S. 2004. Modelling the spatial distribution of two important South African plantation forestry pathogens. *Forest Ecology and Management*, 187:61–73.
- VAN JAARSVELD, A.S., CHOWN, S.L., ERASMUS, B.F.N., KSHATRIYA, M. & WESSELS, K.J. 2002. Vulnerability and adaptation assessment of South African animal taxa to climate change. *Report to the Department of Environmental Affairs and Tourism, Pretoria*.
- WALKER, J.B., KEIRANS, J.E. & HORAK, I.G. 2000. *The genus Rhipicephalus (Acari, Ixodidae): a guide to the brown ticks of the world*. Cambridge: Cambridge University Press.
- WALSH, K. & MCGREGOR, J.L. 1995. January and July climate simulations over the Australian region using a limited-area model. *Journal of Climate*, 8:2387–2403.