

FIG. 10–39 *Continued*

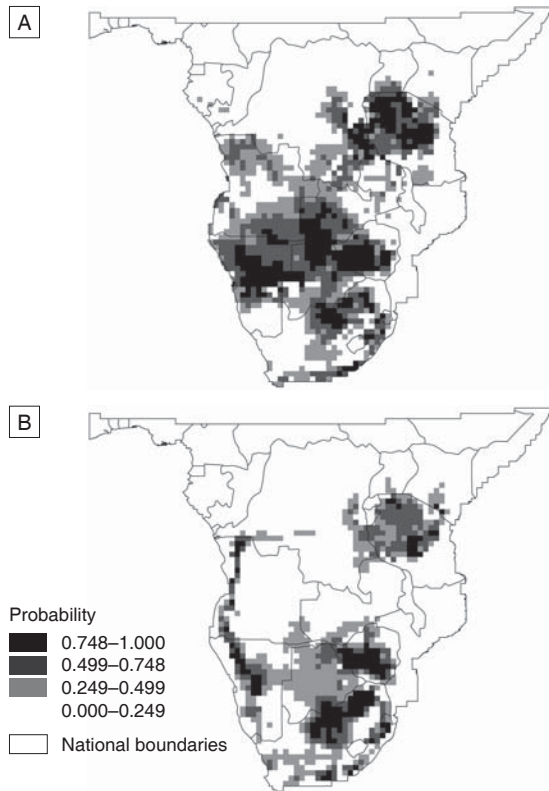


FIG. 18 *R. distinctus*

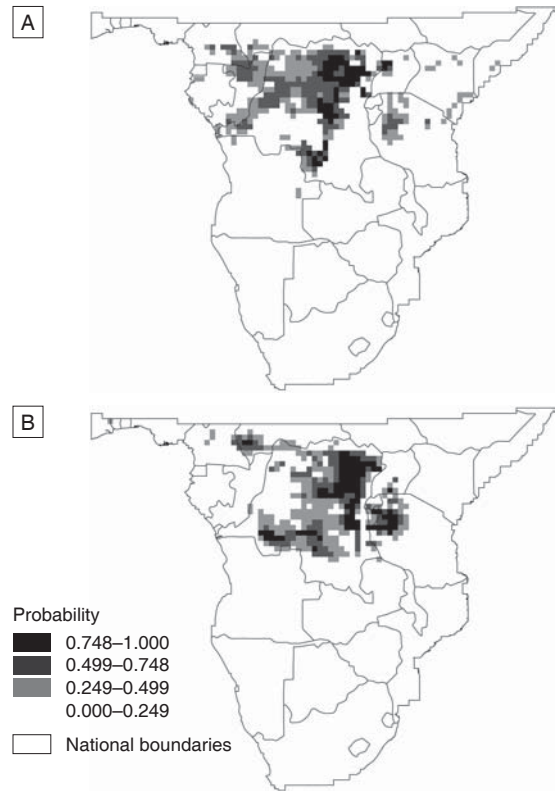


FIG. 19 *R. dux*

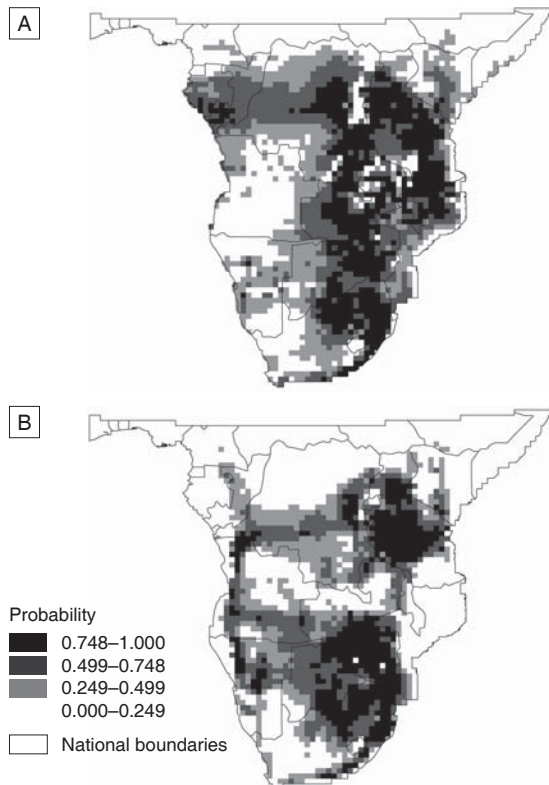


FIG. 20 *R. evertsi evertsi*

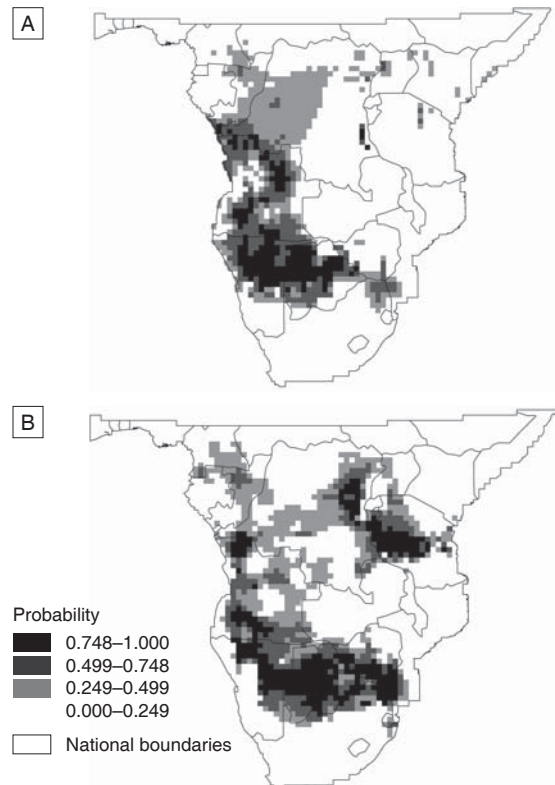


FIG. 21 *R. evertsi mimeticus*

FIG. 10–39 *Continued*

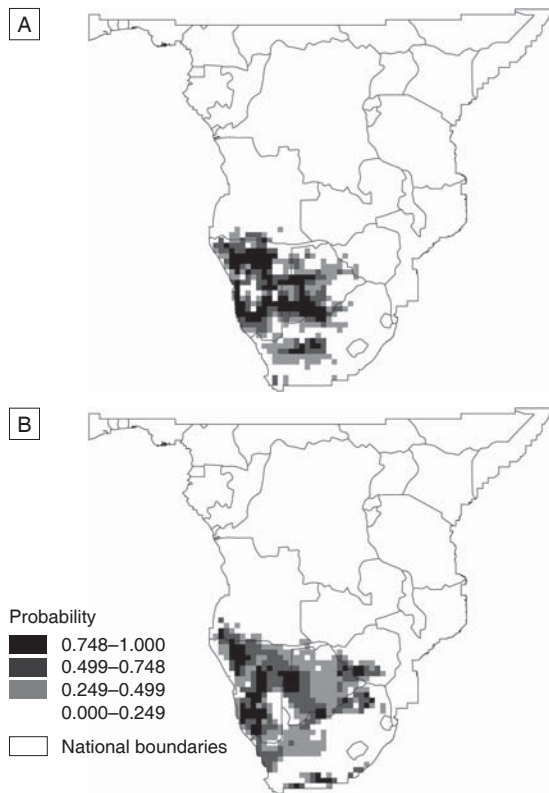


FIG. 22 *R. exophthalmos*

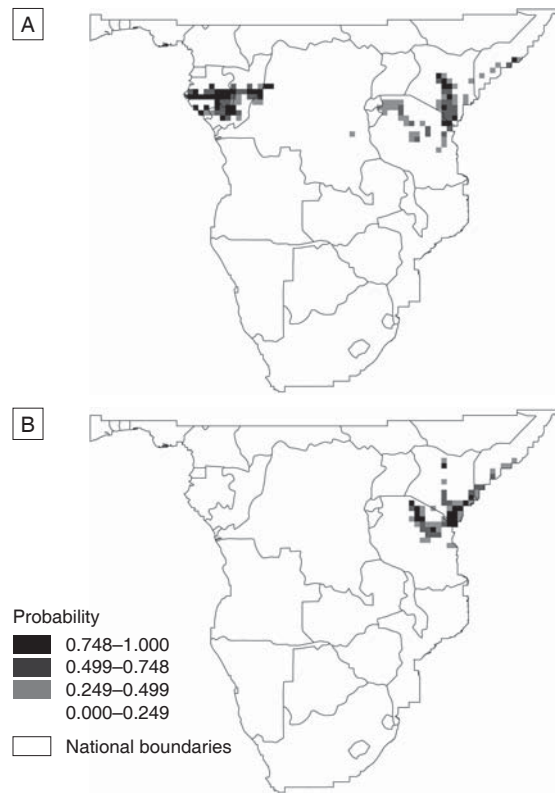


FIG. 23 *R. humeralis*

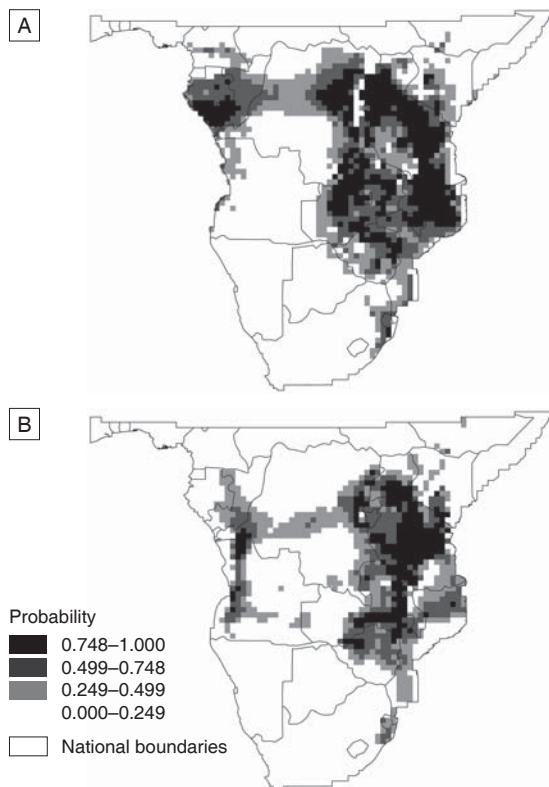


FIG. 24 *R. kochi*

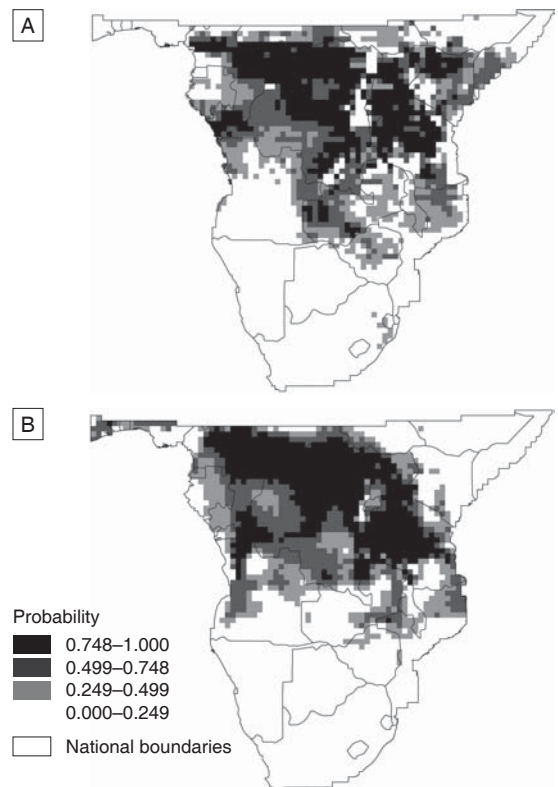


FIG. 25 *R. longus*

FIG. 10–39 *Continued*

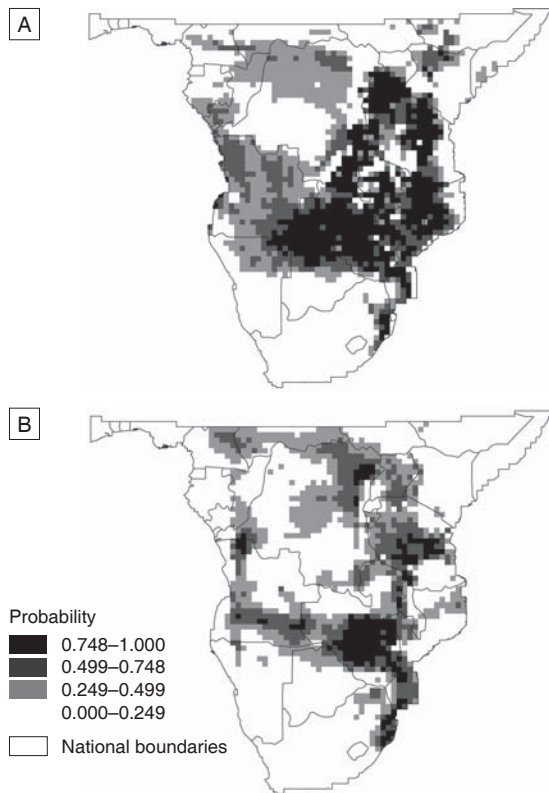


FIG. 26 *R. lunulatus*

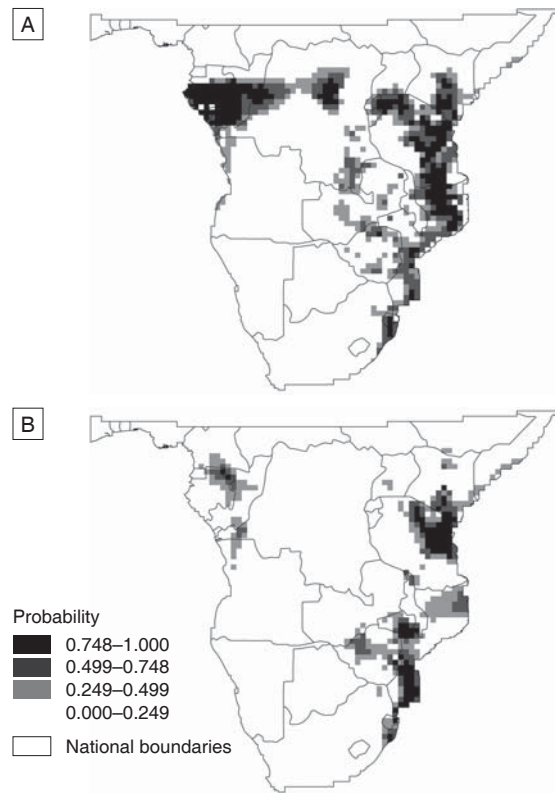


FIG. 27 *R. maculatus*

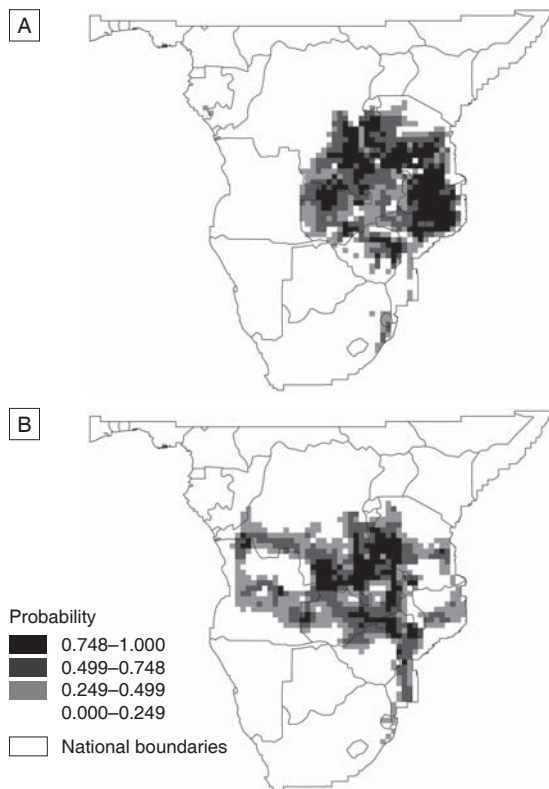


FIG. 28 *R. masseyi*

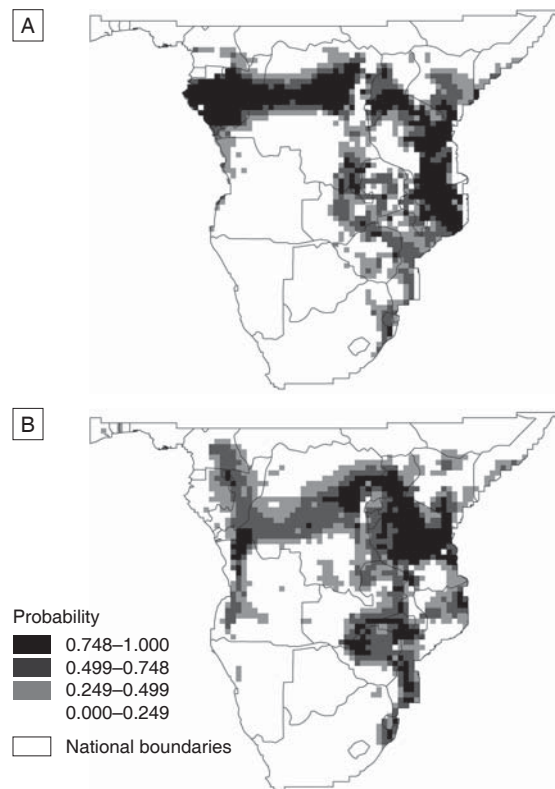


FIG. 29 *R. muehlensi*

FIG. 10–39 *Continued*

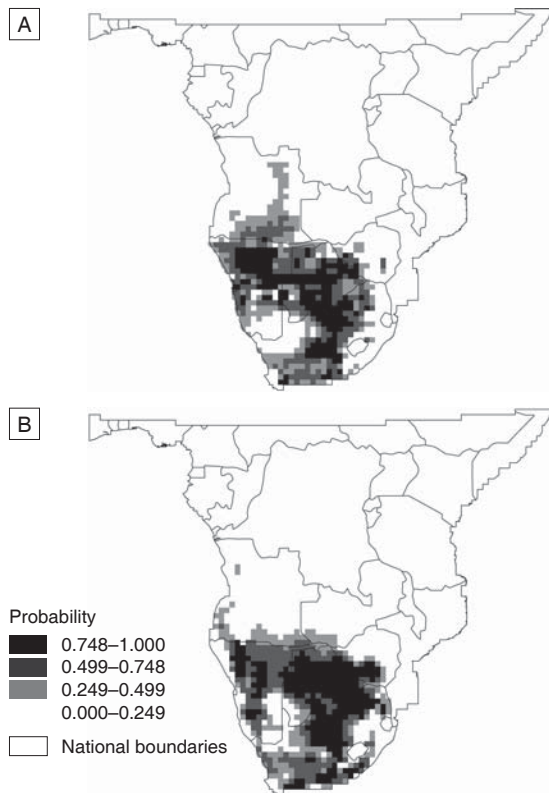


FIG. 30 *R. oculatus*

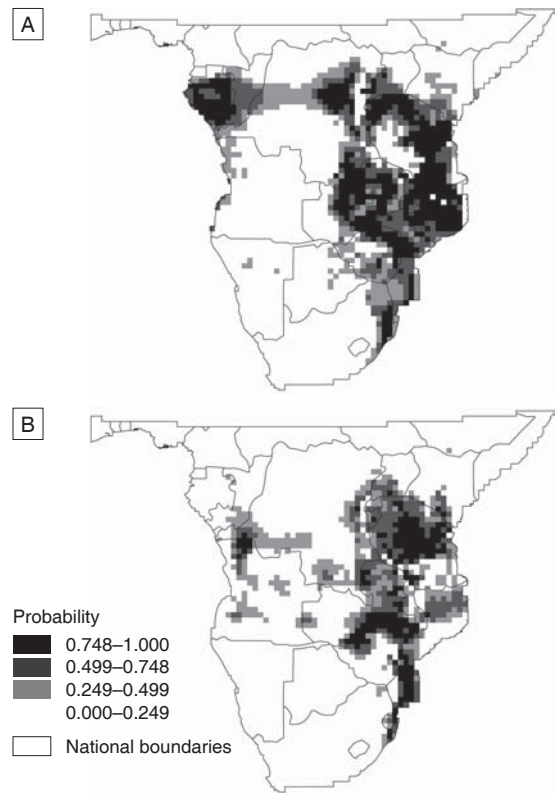


FIG. 31 *R. planus*

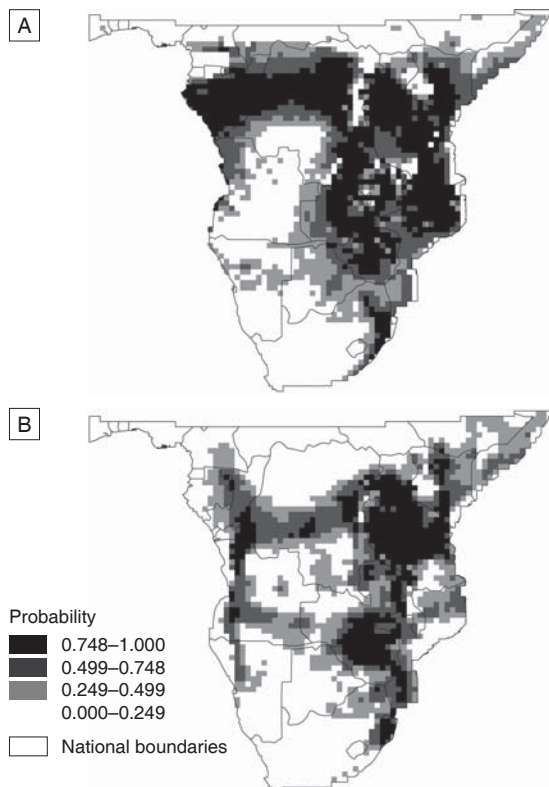


FIG. 32 *R. praeus*

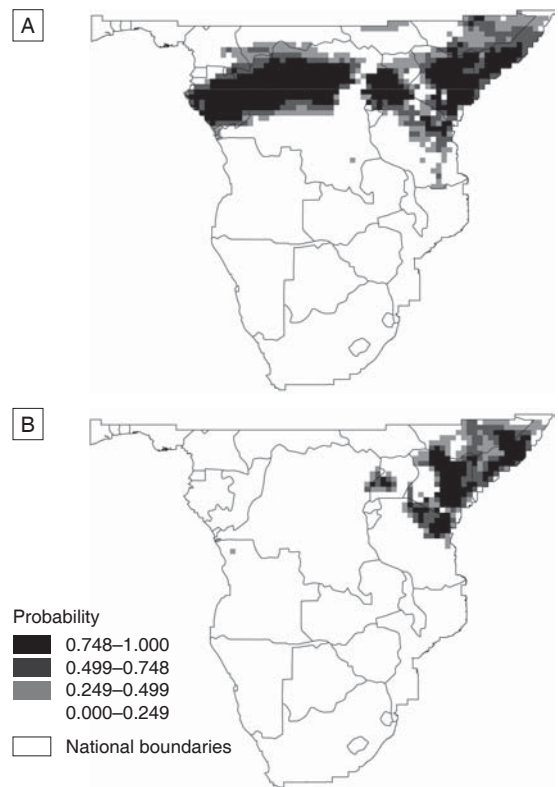


FIG. 33 *R. pulchellus*

FIG. 10–39 *Continued*

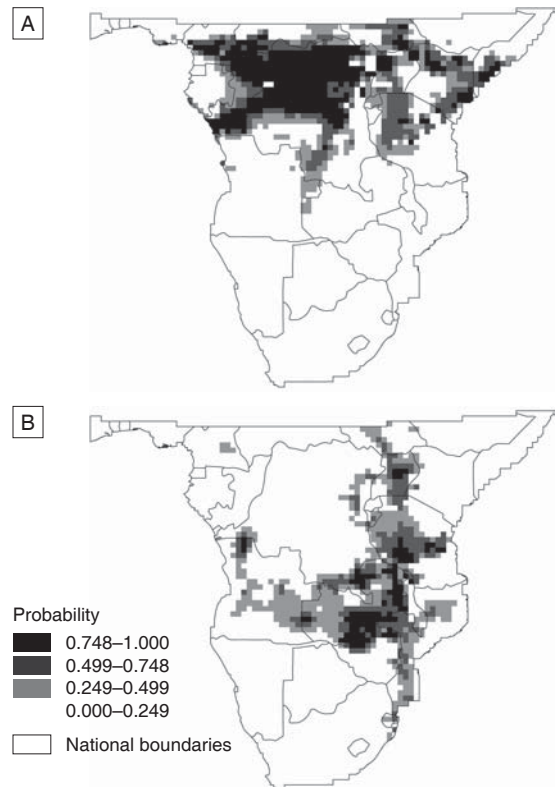
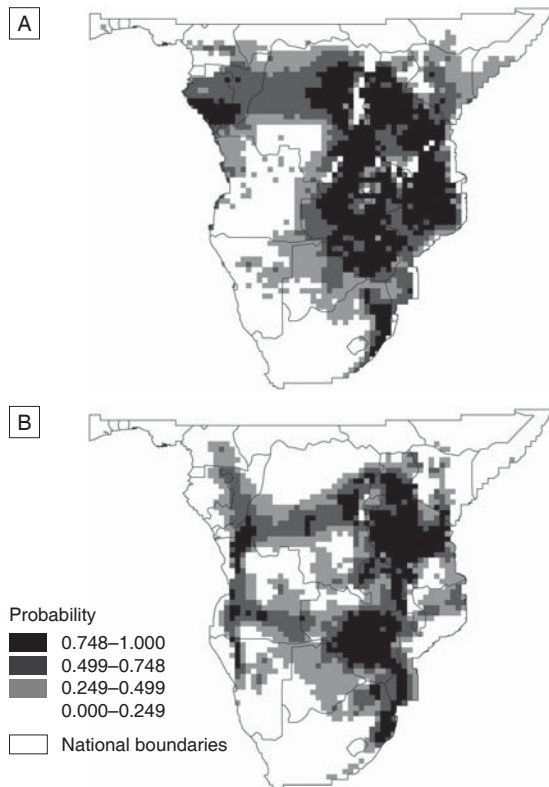
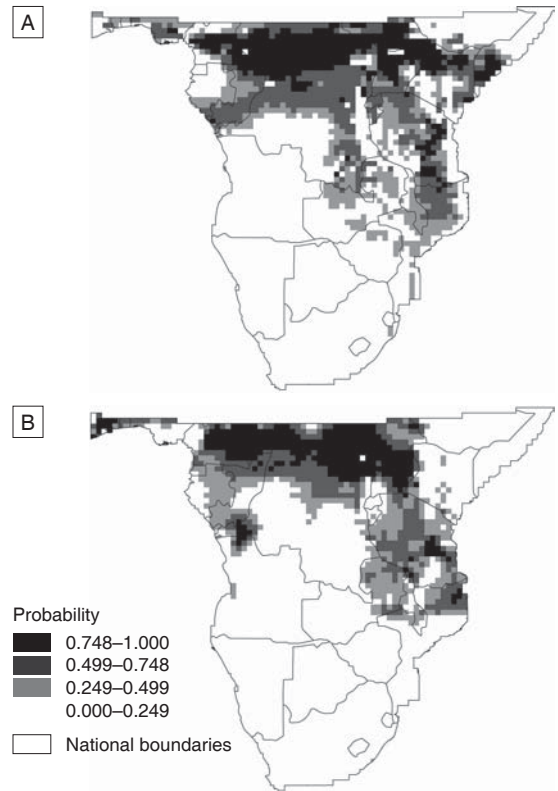
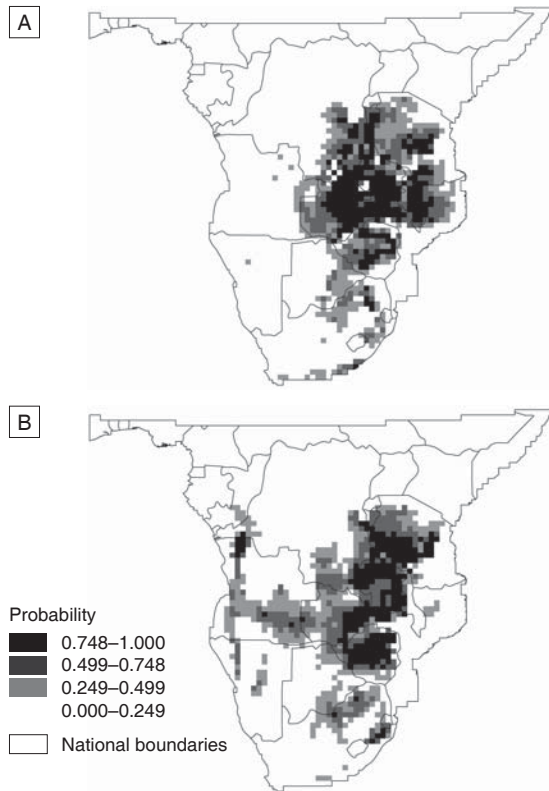
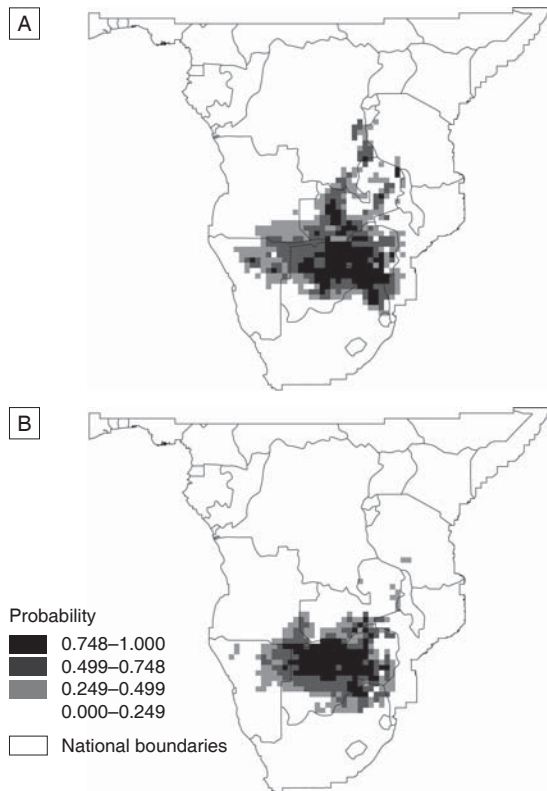
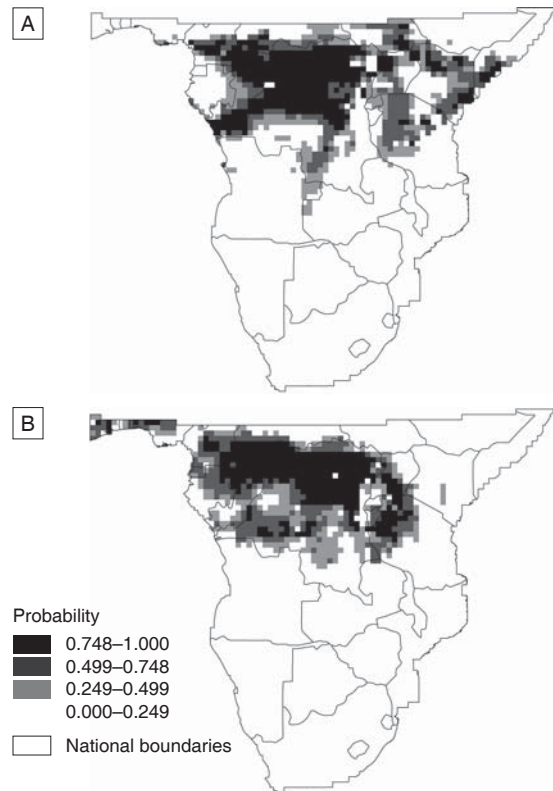


FIG. 10–39 *Continued*FIG. 38 *R. zambeziensis*FIG. 39 *R. ziamanni*

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.

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