CHAPTER FIVE

Host assemblages under climate change conditions

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ABSTRACT

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

INTRODUCTION

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

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

Host species are not only important for ticks because they act as suitable hosts but because biodiversity per se plays an important role in the maintenance of ticks and tick-

borne diseases (Ostfeld & Keesing 2000a; Schmidt & Ostfeld 2001). The phenomenon known as the '*dilution effect*' assumes that communities of hosts characterised by high species richness or evenness are likely to contain a higher proportion of hosts that are inefficient in transmitting the disease agents to a suitable feeding vector. The greater the abundance of weakly competent reservoir species, the stronger the '*dilution effect*' and the lower the probability of disease transmission for any given bite. However, these communities of incompetent reservoirs could increase the density of vectors by providing the vector population with more feeding opportunities than they would have in species poor communities. Thus more diverse communities of incompetent hosts could simultaneously decrease infection prevalence and increase the population density of vectors, with unpredictable net effects on disease risk in humans and livestock (Schmidt & Ostfeld 2001). An understanding of this relationship underpins a more sustainable management basis for these diseases and a better approach towards their epidemics.

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

In Africa, detailed field data regarding the relative importance of hosts and biodiversity in determining the distribution and abundance of ticks and the prevalence of tick-borne diseases remain limited and vague. In this chapter initial modelling attempts are made to

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

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

REVIEW: HOSTS AND BIODIVERSITY IN TICK-BORNE DISEASE TRANSMISSION

Importance of hosts in limiting tick ranges

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

Furthermore, tick life cycles vary from those that require a single host species, in which the ticks develop from larva to adult, to two or three-host species, in which the ticks feed on two or three different host species before they complete their development. This would therefore necessitate studying more than one host species. Throughout the life of a tick suitable hosts are therefore crucial because of the dependence of each tick developmental stage on a blood meal. Hard ticks such as the family Ixodidae, to which *R. appendiculatus* belongs, take very large meals (10-100) times their body weight only once per life cycle stage. This intimate relationship between ticks and hosts characterised by feeding, development, elimination of excess ions and water and the exchange of microorganisms form fundamental and crucial parts of a tick's life cycle (Randolph 2002). Furthermore, the seasonal dynamics of ticks is to a greater degree influenced by

the availability of hosts. Detailed quantitative analysis of published tick datasets summarised by Randolph & Rogers (1997) reported that three of five factors that determine the seasonal dynamics of ticks, were host related. These factors are i) facultative diapause, manifested as a delay in the onset of host-questing behaviour ii) very strong density dependence in the interstadial mortalities caused by hosts' response and iii) tick questing activity characterised by a certain level of daily mortality plus a certain probability of successfully contacting a host.

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

In addition to this, field studies on the importance of hosts elsewhere have reported that at local scales the absence or scarcity of hosts in any part of a region within a tick-permissive environment will cause patchy distributions, so that, for example, ticks may be absent in fields or residential areas but present in adjoining woodlands inhabited by appropriate vertebrate species (Randolph 2001). There is also some compelling evidence (reviewed by Spielman *et al.* 1985; Barbour & Fish 1993), that in the US deforestation and the elimination of deer during the 18th and 19th centuries destroyed the pre-existing conditions suitable for *Ixodes scapularis* populations. These conditions were subsequently re-established from 1926 onwards, first through the reintroduction and

proliferation of deer, and finally by the spread of ticks from their refuges on certain undisturbed islands. The effects of fallow deer (*Dama dama*) on *Ixodes ricinus* abundance has also been documented in Ireland, where tick densities were significantly higher inside than outside a fenced deer park (Gray *et al.* 1992).

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

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

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

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

Biodiversity and the risk of exposure to tick-borne diseases

Ticks and tick-borne diseases have plagued many parts of the world, and Africa in particular, for a very long time. As pointed out by Randolph (2004), "Vector-borne diseases are bad enough in the northern hemisphere, but in Africa they have scarred the entire continent. Diseases carried by ticks and the tsetse fly have made it impossible for Africans to keep livestock successfully, and this has had a devastating impact on the history of the continent" (http://www.anapsid.org/lyme/riseinticks.html). So far no proper control practice has managed to reduce this impact to manageable levels. One of the main reasons for this is that control usually follows an outbreak and in order to alleviate this epidemic the quickest acting methods of control are preferred and these are mainly directed at treating the disease or the eradication of the vector. In most cases farmers are advised to increase dipping to reduce tick numbers. Such a method of control is not successful partly because most ticks that are of economical importance in Africa

are generalists that not only feed on cattle and other domestic animals but also use a number of wild reservoirs. Therefore controlling the disease in cattle only is not sustainable because the infections can be maintained in the reservoir hosts until such a time as they are transferred back to the domestic animals. Taking into account current human population expansions, overexploitation of our natural resources and concurrent climate change, African livestock farmers are likely to move in search of greener pastures. This inevitable movement, which is exacerbated by low levels of law enforcement, means that encroachments into nature reserves or other areas in close proximity to wild animals can be anticipated. In this case the issue of the knowledge and inclusion of reservoir hosts in tick control efforts becomes increasingly important.

It is imperative to understand and identify how the disease flows through the host population and more specifically which host individuals are responsible for the majority of the transmissions (Perkins *et al.* 2003). In the case of tick-borne disease transmission, the key hosts are those that support large numbers of vectors. A particularly important variable in macro parasites-host systems is the observation that the majority of hosts harbour a minority of the parasites and that a minority of hosts support the majority of the macro parasite population (Shawn & Dobson 1995). Woolhouse *et al.* (1997) examined contact rates between vectors and their hosts and showed that not only were these highly variable between individual hosts but also displayed a negative binomial distribution. This has a major impact on the basic reproductive number, R_0 (the ability of a pathogen to invade or persist within a population). An infection can establish if $R_0 > 1$ but if $R_0 < 1$ then an infection cannot invade or persist. The study also identified that 20% of hosts contributed some 80% of the transmission potential, conforming to the '20/80' rule. This pattern has important consequences for the control of parasites and pathogens, since if the 20% of hosts that account for 80% of diseases transmission can be identified and targeted to the extent that R_0 falls below one, the impacts of control efforts would be maximised. Also, it is fundamentally important in vector-borne disease control to identify the reservoir of infection, that is the epidemiologically connected populations or environments in which the pathogen can be permanently maintained and from which infection is transmitted to the target population (Woolhouse *et al.* 1997).

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

Transmission Cycle of ECF

East Coast Fever (ECF) is caused by a protozoan parasite *Theileria parva*. It is an acute, tick-borne disease causing high rates of morbidity and mortality in cattle in 12 countries in sub-Saharan Africa (Norval *et al.* 1992). One million cattle die each year from ECF with an annual economic cost estimated to be $168 million (Dolan 1999). As the livelihood of smallholder farms, often managed by women, depend on one or two cattle, the financial burden due to loss of income and livestock products impacts on the quality

of all aspects of family life. The brown-ear tick, *Rhipicephalus appendiculatus*, transmits the parasite (*T. parva*) through sporozites released in feeding activity (Norval *et al.* 1992). Normally, for transmission to occur, the infected tick must be attached for several days to enable sporozites to mature and be emitted through the tick's saliva (Chen *et al.* 1991). However, under high ambient temperatures, ticks on the ground may develop infective sporozites, which can be transmitted to cattle within a few hours of attachment (Norval *et al.* 1992).

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

The full life cycle of *T. parva* is complex and some stages are poorly understood. It begins when a *R. appendiculatus* tick bites a host and introduces sporozites, which invade lymphocytes where they develop into intracytoplasmic, multinucleated schizonts. The infected animal then develops a lymphoma-like disorder that is rapidly degenerative and usually fatal; many animals die within 3-4 weeks of infection (Norval *et al.* 1992). This disease is not transmitted to ticks transovarily (Harwood & James 1979) and all eggs are therefore free of the diseases. The newly hatched larvae are therefore free of the pathogen but can acquire the pathogen during its first feed. Cattle are the preferred domestic hosts

of all stages of development of *R. appendiculatus* (Norval *et al.* 1982; Okello-Onen *et al.* 1999). The preferred wild hosts of all stages of development are African buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*), sable antelope (*Hippotragus niger)* impala (*Aepyceros melampus*) and waterbuck (*Kobus ellipsiprymnus ellipsiprymnus)* (Horak *et al. 1*983; 1995; Norval *et al.* 1992). The African buffalo (*Syncerus caffer*) is a reservoir of *T. parva* infection, and it has recently been demonstrated that waterbuck (*Kobus* spp.) also act as reservoirs (Norval *et al.* 1992). Buffaloes may suffer clinical symptoms from *T. parva* infection, but its effects on waterbuck are unknown.

MATERIALS AND METHODS

Study area

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

Modelling species distribution

The distribution of *R. appendiculatus,* cattle density layer and climate data used in this chapter were described in the previous chapters. The distribution data of indigenous host species were obtained from a Databank for the Conservation and Management of the African Mammals (AMD) (Boitani *et al.* 1999). The 'original data' about host distributions were obtained from numerous published maps and converted into GIS (Arc/Info, ESRI, USA) polygon coverages. Known extent of occurrence of the "preferred host group" was used in this study (Boitani *et al.* 1999). For comparative purposes, the extent of occurrence of those host species that support the immature tick stages is represented. This was done as it is established that changes in the numbers of hosts will influence tick abundances (Horak *et al.* 2000). This Horak *et al.* (2000) study showed that an increase in the abundance of larvae and nymphs of *R. simus* and *R. turanicus* in 1994 was in response to the rodent population explosion towards the end of 1993. There was however, no concomitant increase in the population of *R. appendiculatus* that does

not feed on rodents. However, smaller antelope species and hares are considered good hosts of immature stages of *R. appendiculatus* (Walker *et al.* 2000). Thus, for this study the following additional host species were considered: *Lepus capensis* (Cape or brown hare), *Lepus saxatilis* (Scrub hare) and *Lepus victoriae* (African Savanna hare). Using the same six-climate variables (chapters 2-4), the known extent of occurrence of the relevant host species were used as input variables into the habitat model (Erasmus *et al.* 2002). These point localities were imported into ArcView GIS and by means of a spatial intersect; each 60 x 60 km grid was assigned a host presence or absence and allocated its relevant climate variables. The modelling was executed in SPLUS. From the known distribution records of the accepted host species, the predicted current distribution was initially obtained using the current climate as described in the previous chapters. To obtain the future distributions of the host species, the grid cells were populated with future climate data (see chapter 3).

Current and future distributions of host species

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

Analysing host distribution range changes

The following analyses were performed to compare the current and future predicted distributions of hosts in response to climate change i) analysis of changes in the overall

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

Host assemblage distribution changes

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

RESULTS

Broad scale range alterations

The predicted current and future host species ranges are visibly different (Figures 1-10). Statistically, a comparison between range sizes (number of 60 x 60 grid cells occupied) between the predicted current and future distributions for host species revealed highly significant differences (Kolmogorov-Smirnov; $p < 0.001$, $N = 3000$) for the following

species: cattle, Burchell's zebra, Waterbuck, Cape shrub hare, African savanna hare and Buffalo. There were no significant differences between the predicted current and future range sizes of the other host species: Eland, Sable antelope, Impala and Scrub hare. Differences in the number of grid cells in different probability classes were also evident in these results revealing increases or decreases in suitability of grid cells for a host species under climate change conditions. These changes, which vary per species and probability class, are presented in table 1 and figure 11.

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

Host assemblage distribution changes

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

assemblages under future climate conditions (Figure 13b). The total area occupied by the probability range (0.4-0.9) visibly decreases.

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

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

DISCUSSION

Modelling host distributions

The precise current and future part played by hosts in determining the abundance, distribution of ticks and the prevalence of tick-borne diseases in Africa is poorly documented. This is as a result of numerous difficulties in studying host distributions over time. In this chapter, the current and predicted future ranges of host species have

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

Implication of the findings

ECF and the "dilution effect"

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

changes in host ranges on tick abundance and ECF prevalence will be explored using the "dilution effect" model.

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

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

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

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

This predicted general decrease in suitable habitat for the suite of host species together with the predicted increase in areas suitable for tick establishment (see chapters 3 & 4) means that a greater tick burden is likely for the available hosts. It can be argued that under these conditions increased tick mortalities will increase due to the unsuccessful

host questing behaviour. But, the realised impacts of these collective changes on the tick-borne disease system will also depend on the unexplored shifts in pathogen geographic ranges, possibly putting them into contact with new host populations or species (Bergot *et al.* 2004) resulting in potential disease outbreaks as severe as those observed following pathogen imports (Harvell *et al.* 2002).

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

Conclusion and recommendations

The importance of biodiversity as a source of medicine or food supply has been well documented (MA 2003). The central role played by species diversity in the performance of ecosystem functions such as primary production and for resource extraction purposes is also rapidly emerging (MA 2005). However, the importance of biodiversity in the ecology of infectious diseases is still poorly understood. The inevitable links between climate change and the emergence of new diseases including HIV/AIDS, Lyme disease, Ebola, SARS and the likely redistribution of old diseases such as Malaria and TB and associated species losses is also poorly documented. Scant information exists regarding the effects of climate change on livestock diseases in Africa and even less information regarding the importance of host species in tick abundance and tick-borne disease prevalence exist. For proper management of ticks and tick-borne disease, field studies looking at the relative importance of these hosts' assemblage are vital and will improve the existing tick-borne disease control methods in Africa. Also the regular monitoring of

the reservoir hosts of infection is useful not only in devising appropriate tick-borne disease control programmes but also for the protection of the threatened wildlife species. This may incorporate managing the disease in reservoir hosts, limiting the size of the reservoir host which in turn would reduce contact rates and therefore lower the probability that the infection could persist. Also managing the diseases reservoir host would contribute significantly towards the effective control of tick borne diseases. Similar programmes were established in the past; vaccinating domestic dogs against rabies to protect lions and wild dogs and vaccinating domestic dogs to protect the Ethiopian Wolf (*Canis simensis*) (Woodroffe 1999). More important to the tick-host-disease system would be to limit the size of the reservoir host population so as to reduce the contact rate between the domestic and wild reservoir hosts.

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

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TABLE 1

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

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

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

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

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

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

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

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

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

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

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

FIGURE LEGENDS

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

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

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

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

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

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

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

Figure 1

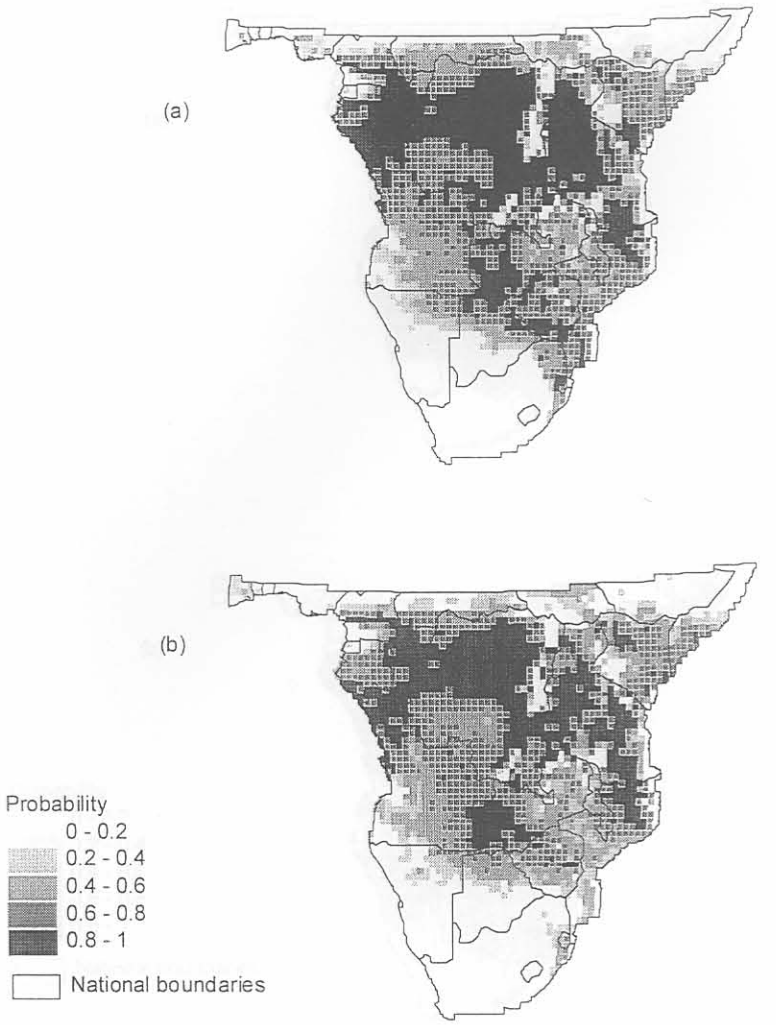


Figure 2

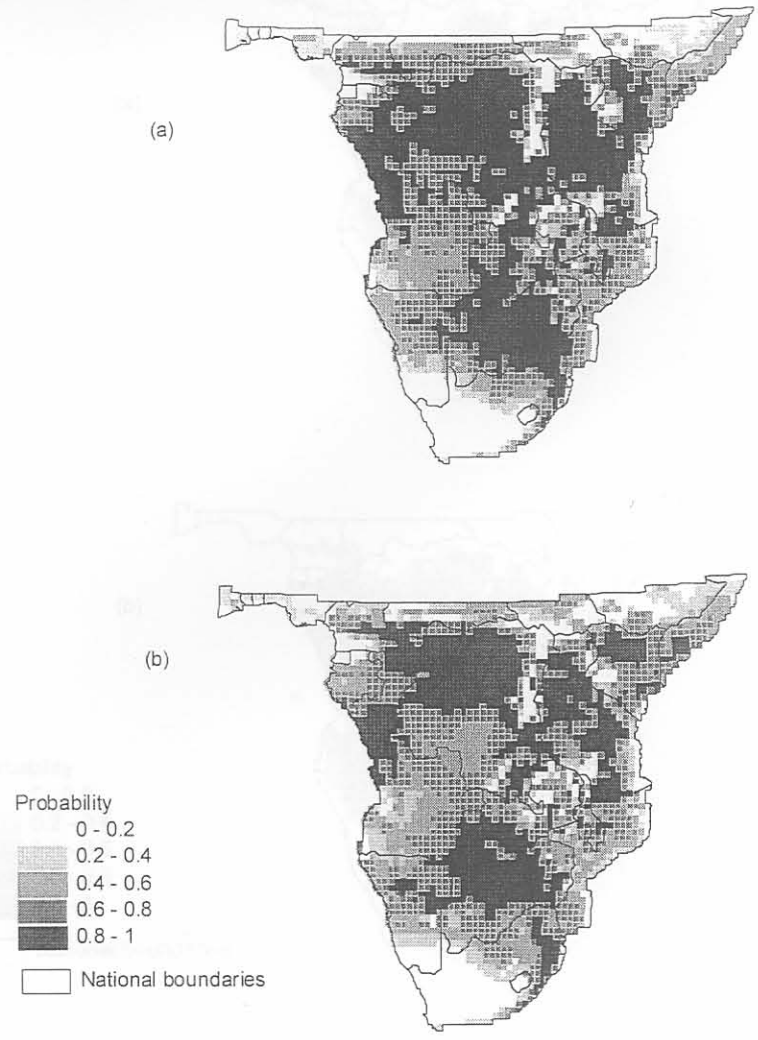


Figure 3

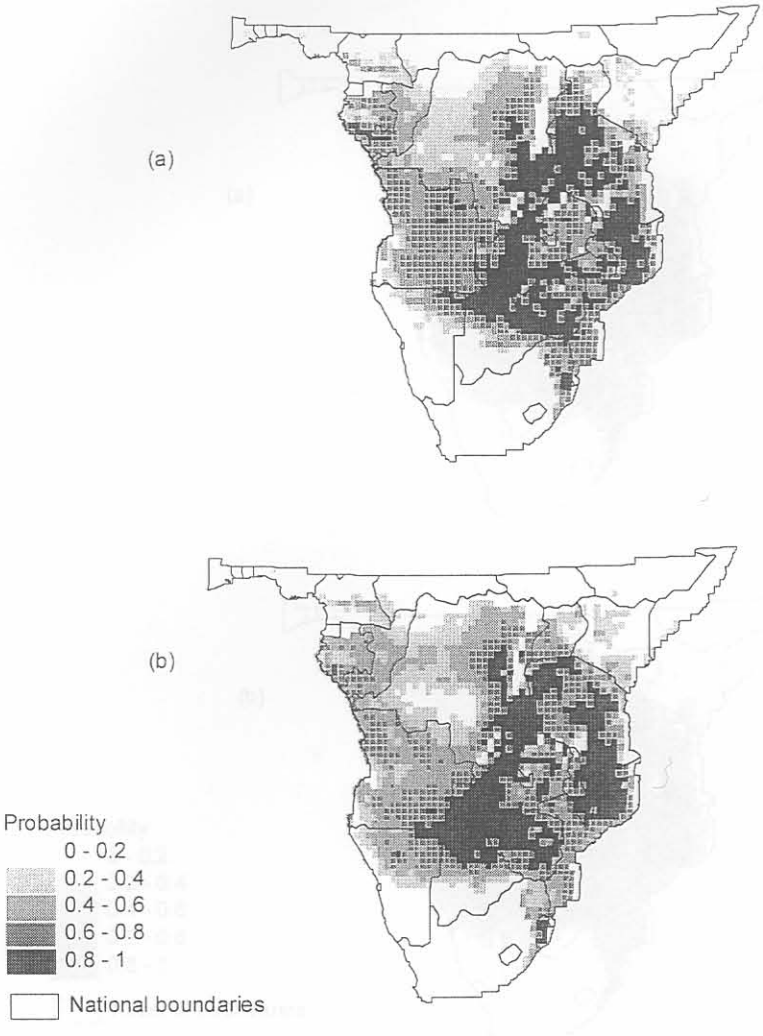


Figure 4

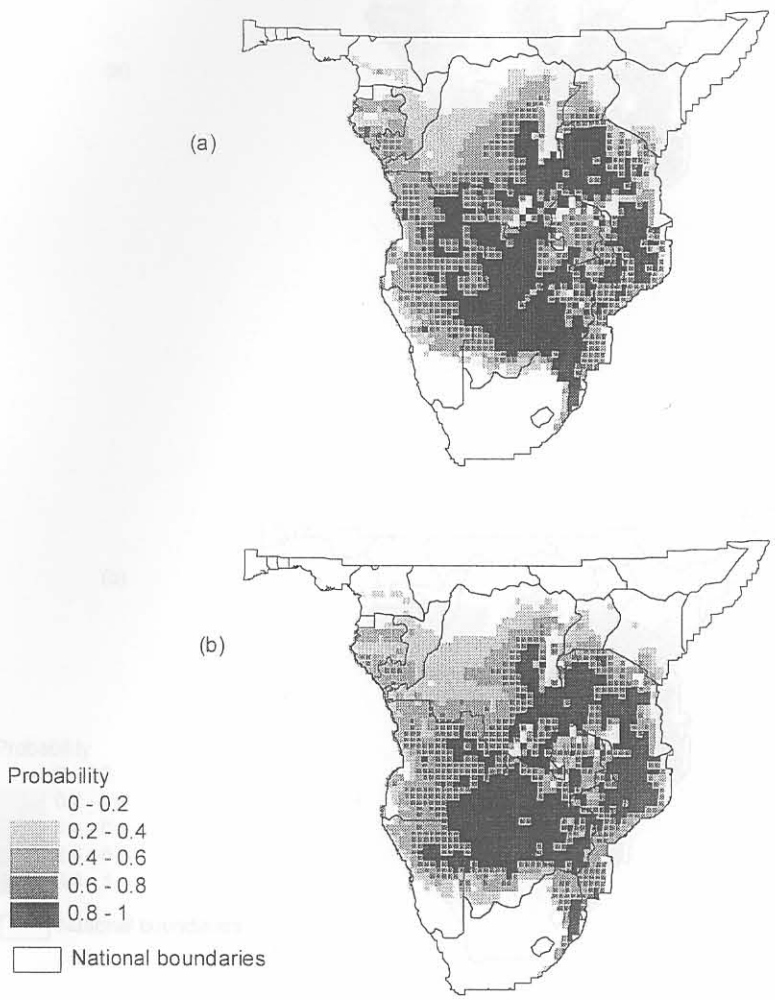


Figure 5

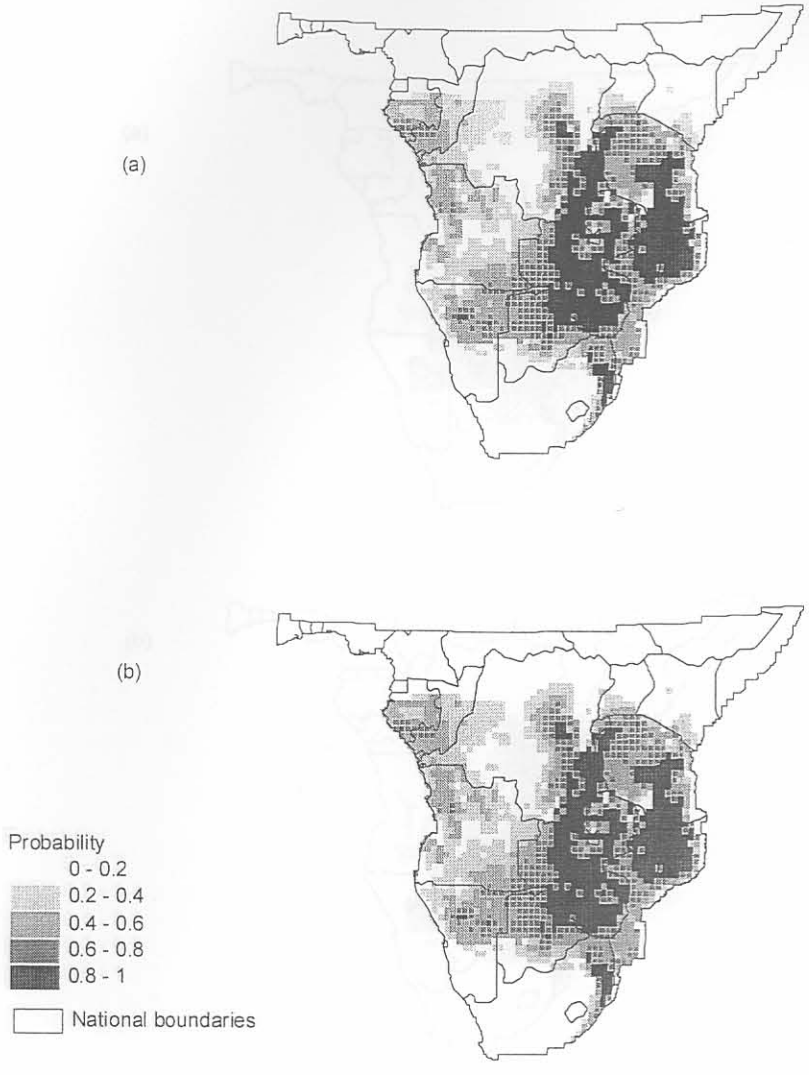


Figure 6

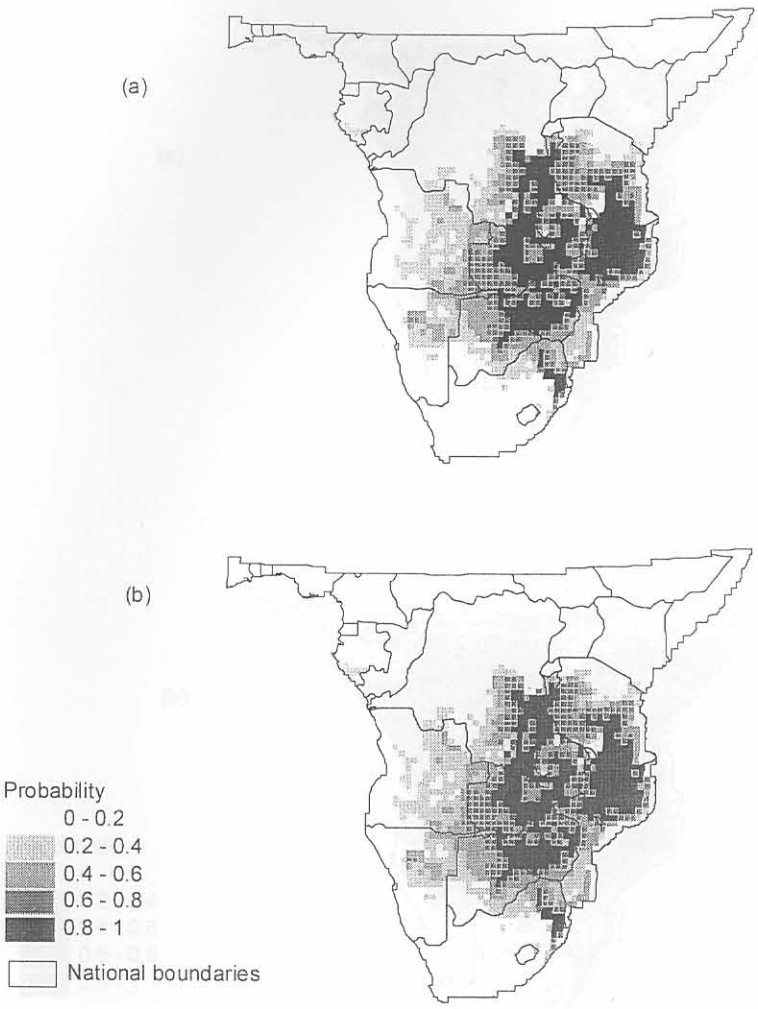


Figure 7

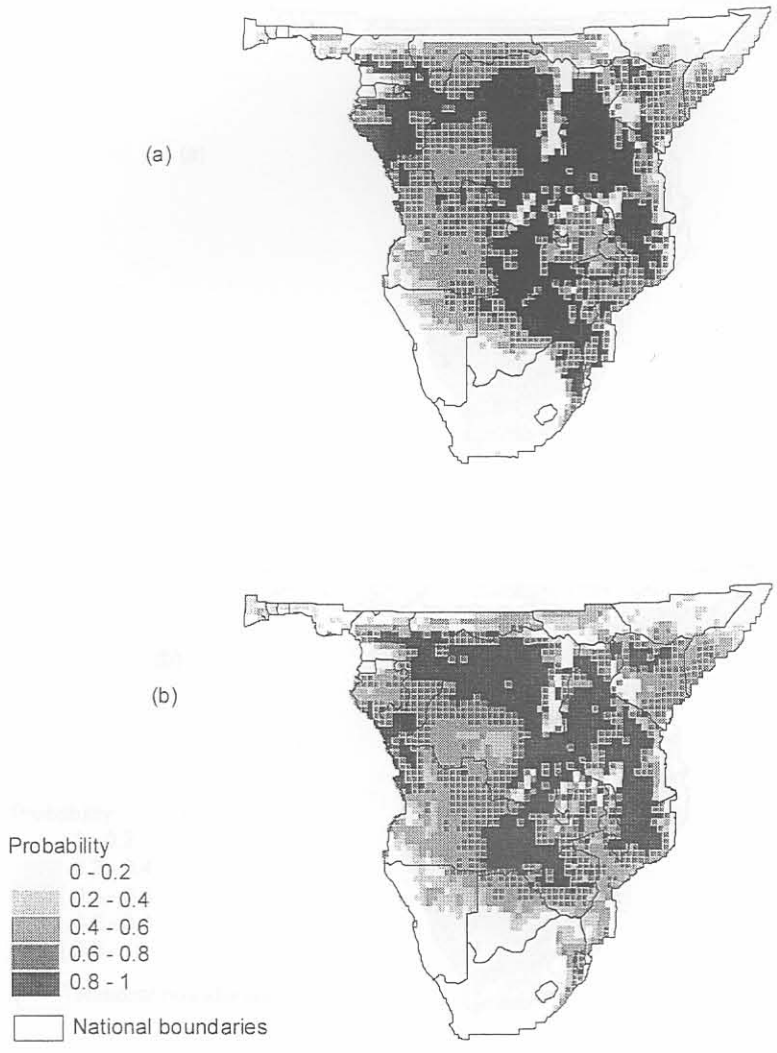


Figure 8

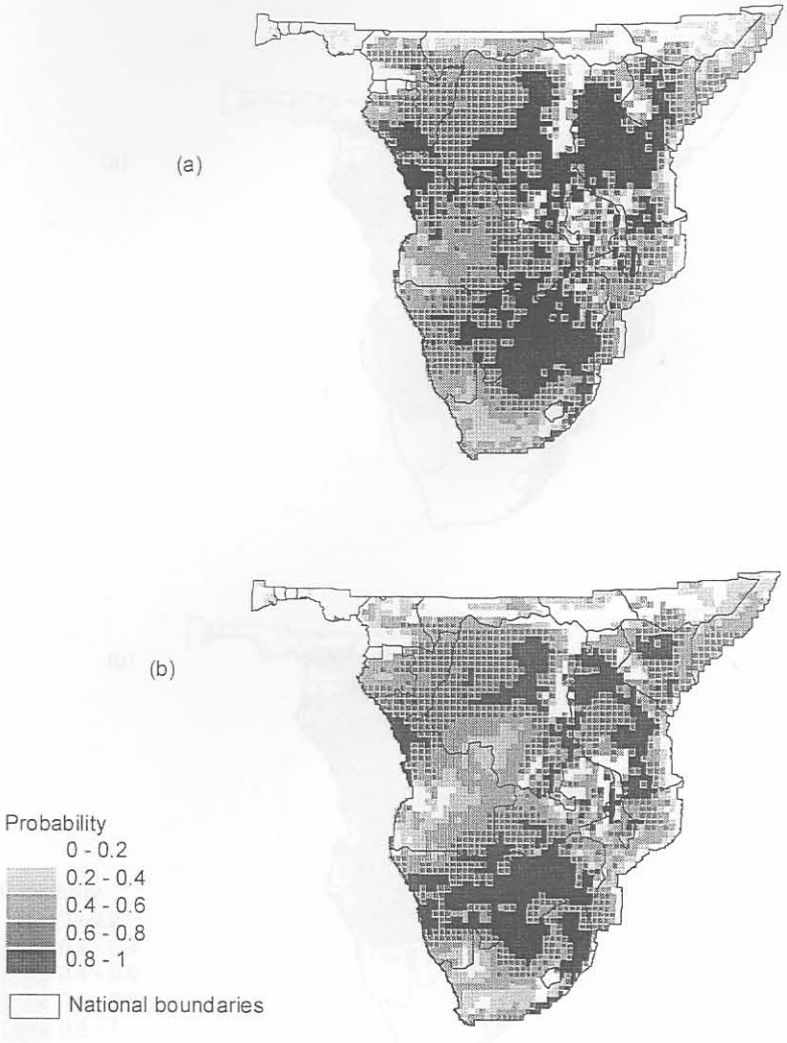


Figure 9

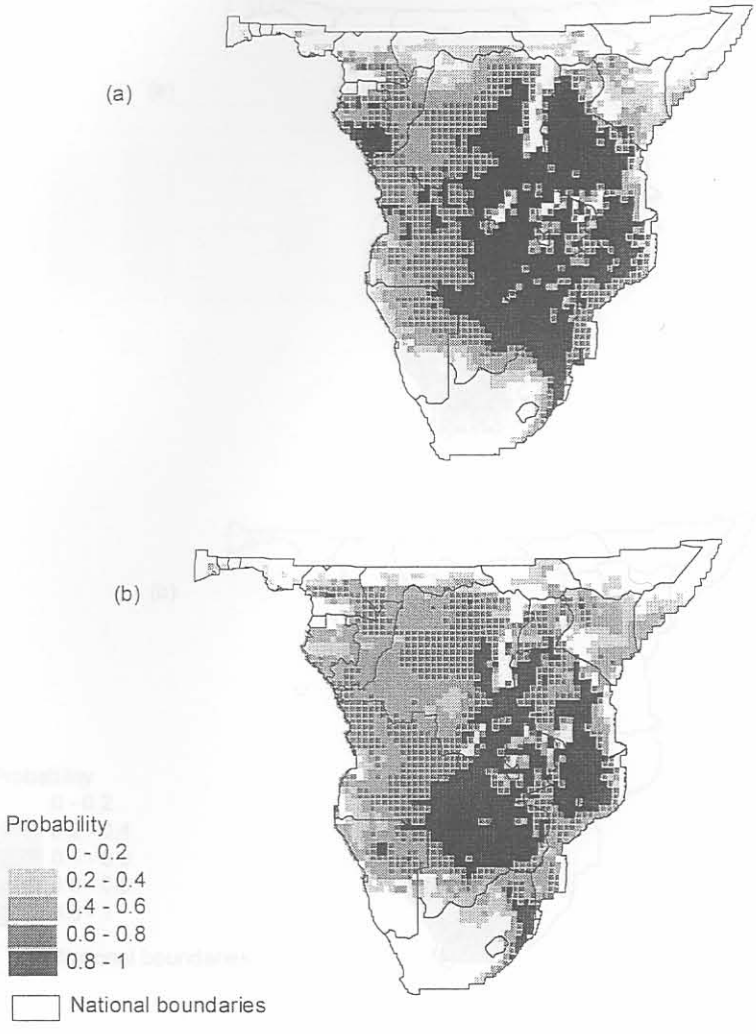


Figure 10

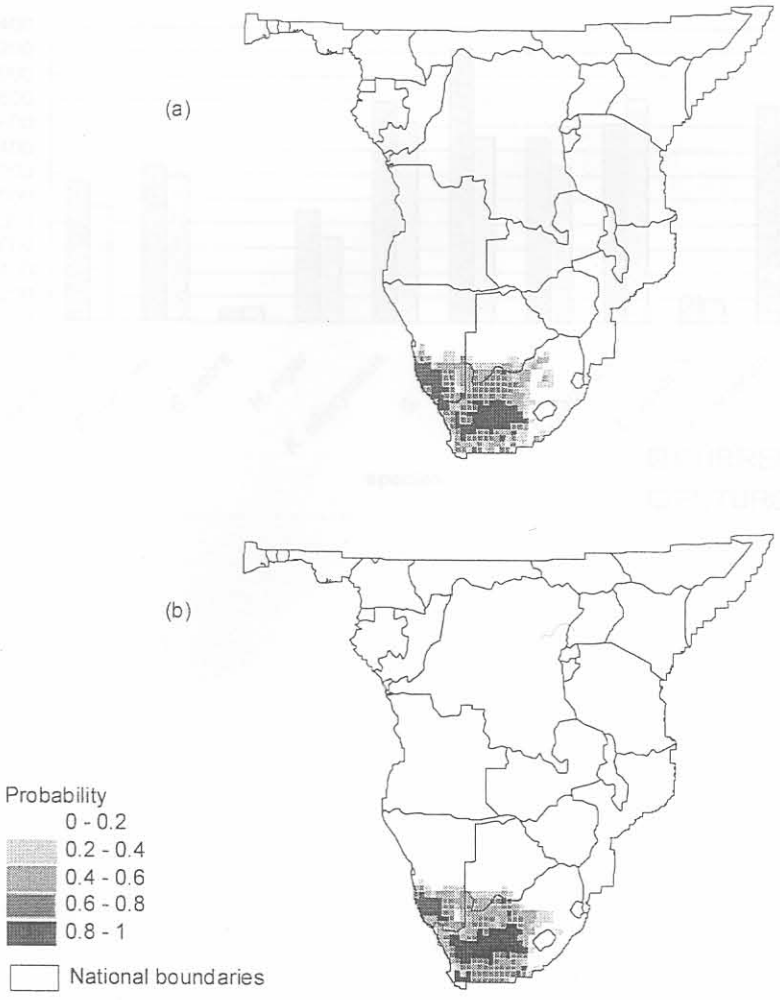


Figure 11

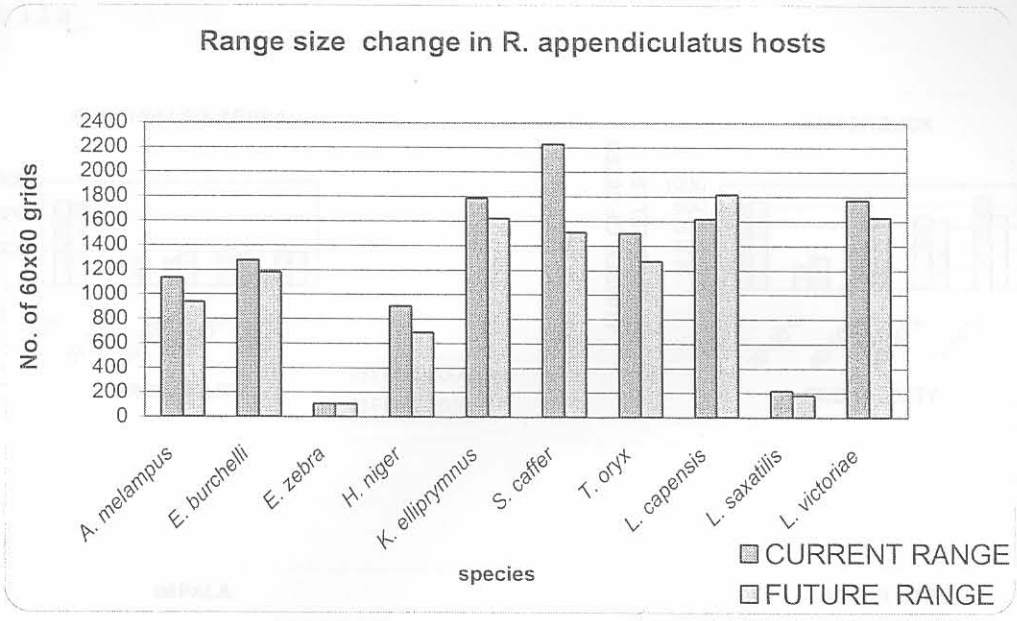
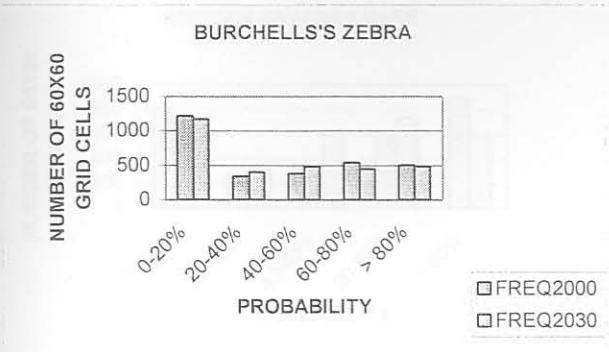
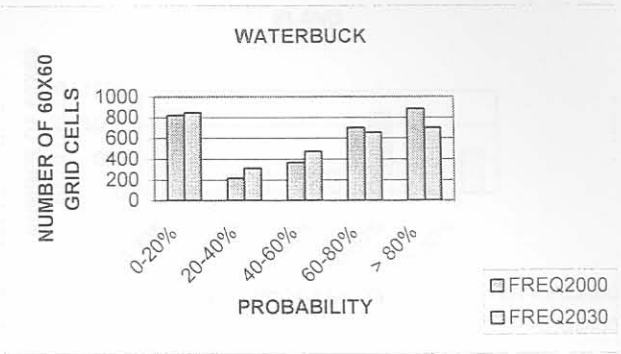
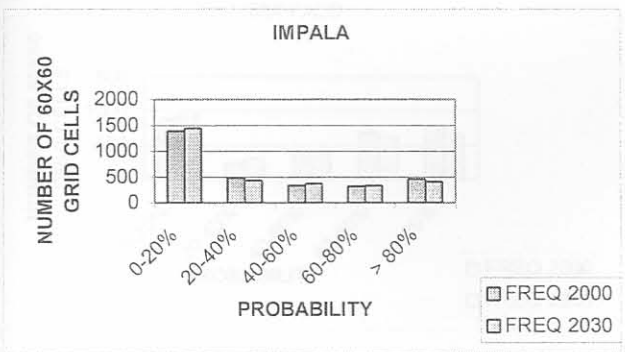
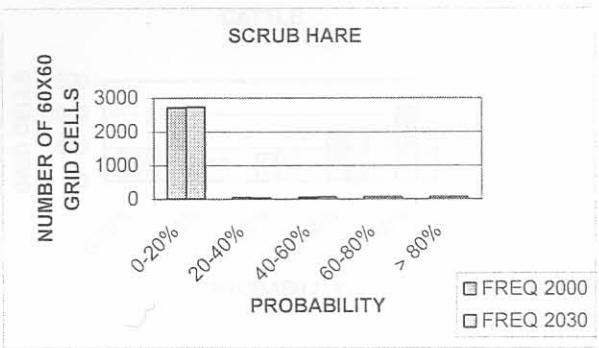


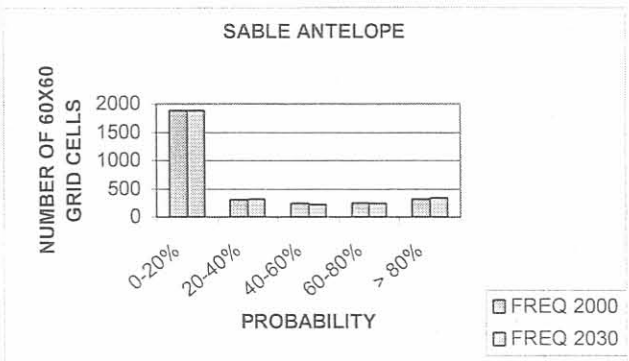
Figure 12 a











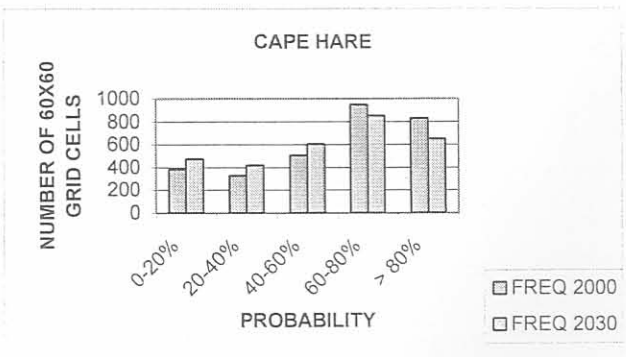
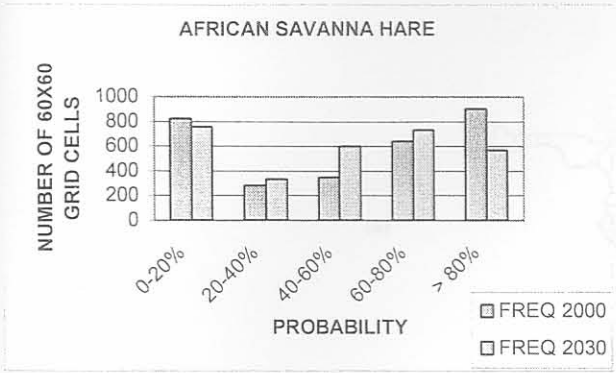
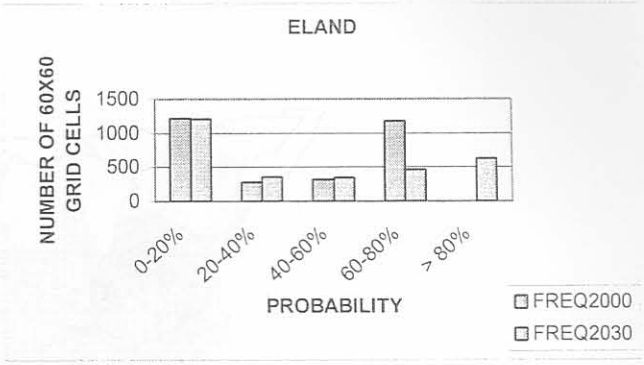
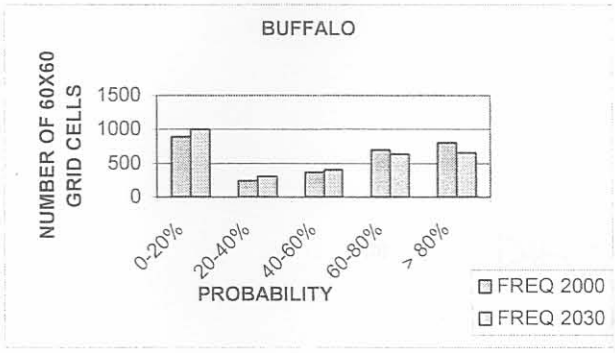


Figure 12 b







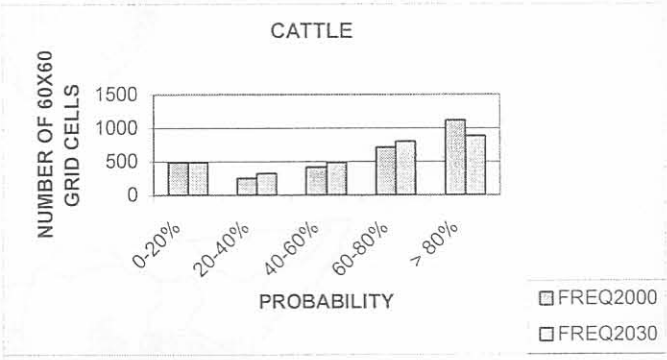


Figure 13

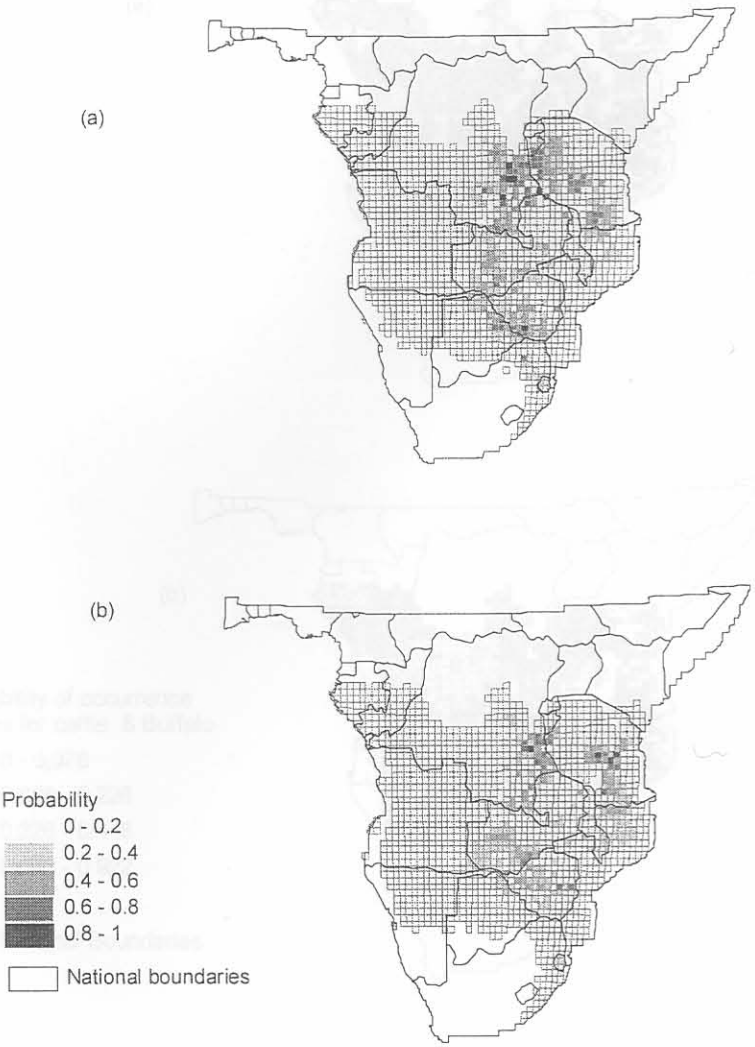


Figure 14

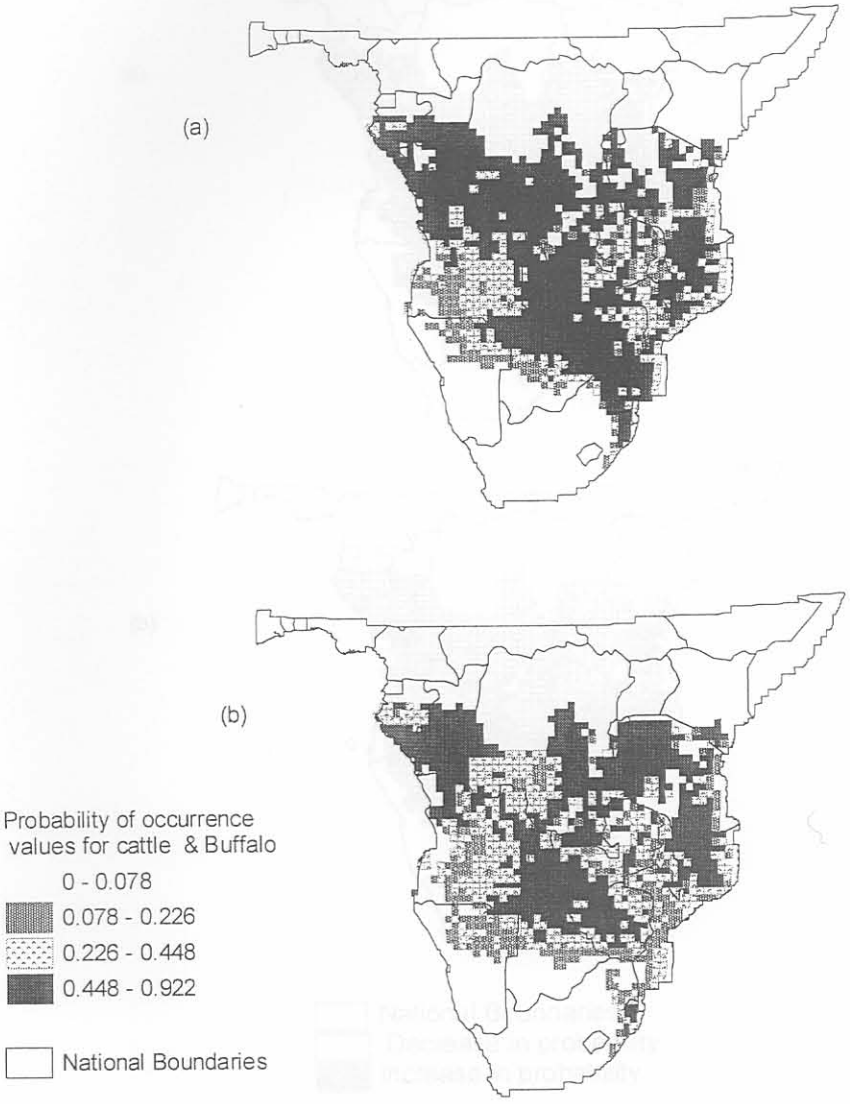


Figure 15