

Climate change decreases habitat suitability for some tick species (Acari: Ixodidae) in South Africa

A. ESTRADA-PEÑA*

Department of Parasitology, Veterinary Faculty, Miguel Servet, 177. 50013-Zaragoza, Spain

ABSTRACT

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

Models predicting current habitat availability for four prominent tick species in Africa (*Boophilus decoloratus*, *Amblyomma hebraeum*, *Rhipicephalus appendiculatus* and *Hyalomma truncatum*) were constructed using remotely sensed information about abiotic variables and a point-to-point similarity metric. Year-to-year variations in the forecasted habitat suitability over the period 1983–2000 show a clear decrease in habitat availability, which is attributed primarily to increasing temperature in the region over this period. Climate variables were projected to the year 2015 using Fourier series analysis of the decadal abiotic data. The simulations show a trend toward the destruction of the habitats of the four tick species. In addition, a sensitivity analysis was developed to probe the changes in the habitat suitability in response to variations in temperature, vegetation availability and water vapour deficit. Four basic scenarios were studied: increasing or decreasing the temperature 1 or 2 °C together with correlated variations in the other abiotic variables. A decrease in temperature was predicted to promote habitat gain for every species except *H. truncatum*, while an increase of 1 °C was forecast to sustain a small but positive response in *A. hebraeum* and *B. decoloratus*. Increasing the temperature by 2 °C was forecast to have damaging effects on the habitat structure of all four species. The effect of climate warming on the habitat range of these ticks is considered in the light of economically sound control measures over an ecological background.

Keywords: Climate change, habitat suitability, South Africa, ticks

INTRODUCTION

Climate is the main factor influencing the geographical distribution of tick species, since host distribution does not limit the range of most African ticks (Cumming 1998). The definition of suitable habitats and how these change over time is also of prime importance in the management and control of pest species. Ticks are major vectors of livestock pathogens. The most widely used methods for controlling

ticks have remained unchanged in recent years. The natural method of limiting the impact of most tick-borne diseases is the establishment of enzootic stability. However, this balance may be broken if the arthropod-vertebrate transmission cycle is disturbed. Thus, ecology plays a central role in the design of tick control and eradication programmes.

Arthropods and the diseases they transmit are exquisitely sensitive to climate. Throughout the past century, researchers have understood that climate circumscribes the distribution of mosquito-borne diseases (Epstein, Diaz, Elias, Grabherr, Graham, Martens, Mosley-Thomson & Suskind 1998). It is often suggested that one of the most important so-

* E-mail: aestrada@posta.unizar.es

cietal consequences of climate change may be an increase in the geographic distribution and transmission intensity of vector-borne disease. The documented rise in global surface temperatures, together with accompanying changes in rainfall (and hence relative humidity) is driving profound changes in major habitats. Global warming will transform wide territories, changing the distribution of most important health-related arthropods. In fact, changes in distribution and abundance have already been reported for *Ixodes ricinus* (Lindgren, Talleklint & Polfeldt 2000) and *Ixodes scapularis* (Dennis, Nekamoto, Victor, Paul & Piesman 1998), and these changes have been associated with long-term variations in climate.

Recently, geographic information systems (GIS) have become a key tool for understanding and targeting areas according to their suitability for different parasites (Hay, Parker & Rogers 1997). In the same way, remotely sensed information about habitat characteristics is useful for developing models to analyze the properties of tick populations and transmitted diseases (Randolph & Rogers 1997; Estrada-Peña 2001a). There is currently concern about how climate change will affect the distribution of arthropods and thus the diseases they carry (Randolph 2001; Sutherst 2001). This concern relates not only to the direct effects of climate change on tick life cycles but also to potential modifications to landscape structure and/or host abundance patterns. Although there is broad agreement that climate change is happening, there are still major uncertainties concerning the rate and regional consequences of this change and how it might impact on tick ecosystems. The effects of long-term climate trends on the habitat structure for the tick *Boophilus microplus* in South America have already been determined (Estrada-Peña 2001b) using remotely sensed information about abiotic variables. This paper combines the use of remote sensing and GIS to monitor the evolution in the habitat suitability (HS) over the period 1983–2000 for four important tick species in South Africa, as well as to forecast the trend in these changes. Special attention is given to long-term climate change and its potential effects on target areas in the near future.

MATERIAL AND METHODS

The purpose of this study was to ascertain the spatial distribution of habitat suitability for four tick species in southern Africa. Additional objectives were to understand the abiotic factors involved in habitat

variation, to establish the time evolution of these variables in recent years, and to use Fourier series analysis to project the behaviour of these variables into the near future. Sensitivity analysis was also performed to determine the way in which the habitat changes in response to variations in the main abiotic variables.

Ticks species and geographical scope

Four tick species were selected for study: *Amblyomma hebraeum*, *Boophilus decoloratus*, *Hyalomma truncatum* and *Rhipicephalus appendiculatus*. These species were selected on the basis of several criteria:

- They are important parasites of livestock in the study region.
- Much is known about their distributions.
- Adequate work on their life cycles has been produced.

Boophilus microplus was not included because its distribution depends not only on climate but also on the presence of *B. decoloratus* (Sutherst 1987), a closely related species with which it competes. Although the entire African continent was used to compile the distributions of the tick species of interest, further analysis is restricted to South Africa. This was done because sensitivity analysis and climate trend forecasting require a relatively small, well-defined area supporting a variety of biotopes.

South Africa lies at the southernmost part of the African continent. It is bordered to the north by Botswana and Zimbabwe, to the northeast by Mozambique and Swaziland and to the northwest by Namibia. South Africa completely surrounds Lesotho. Temperatures (Fig. 1) follow a pattern delineated by the mountain chains in the east and south, and the highest temperatures occur in the northwest of the country. Humidity (and hence vegetation vigour) follows an inverse pattern. Most of South Africa has elevations of over 900 m (Fig. 1) and at least 40% of the land surface is at elevations of over 1 220 m. The land rises steadily from west to east to the Drakensberg mountain series, the highest of which is Mont-aux-Sources at 3 300 m. The coastal belt in the west and south varies from 5–50 km in width and is between 150 and 190 m above sea level. North of the coastal belt lie the Little and the Great Karoo. These areas are bounded by mountains, lie higher than the coastal belt, and are semi-arid to arid, merging into sandy wastes that ultimately join the Kalahari Desert.

From the Drakensberg, the land falls via the rolling hills and valleys of Natal, which are covered with rich vegetation, towards the Indian Ocean.

Data sources

Two sets of data were obtained as baseline for the modelling procedures. The distributions of the target tick species in Africa were recorded primarily from published reports. The main source for tick distribution data was the work by Cumming (1999) including only the records published after 1980. This compilation was complemented with unpublished collections assembled by Ivan Horak (Faculty of Veterinary Science, University of Pretoria, South Africa) and Heloise Heyne (Onderstepoort Veterinary Institute, South Africa) as well as with data from the National Tick Survey in Zimbabwe,

compiled by Trevor Peter. Records were projected into latitude/longitude following coordinates in the Gazetteers of the United States Geological Survey (available on the internet at the following address: <http://164.214.2.59/gns/html/index.html>).

The other source of data was the full set of satellite imagery available from the AVHRR sensor of the NOAA series of satellites. This set extends from 1983 to the present, in 10-day intervals, with a resolution of 8 km per pixel. The imagery provides information about surface temperature (T), the normalized derived vegetation index (NDVI) an indirect measure of vegetation stress, and the water vapour pressure deficit (WVPD). The methodology used to obtain these abiotic variables is described by Estrada-Peña (2001b) for T and NDVI, and Prince & Goward (1995) for WVPD.

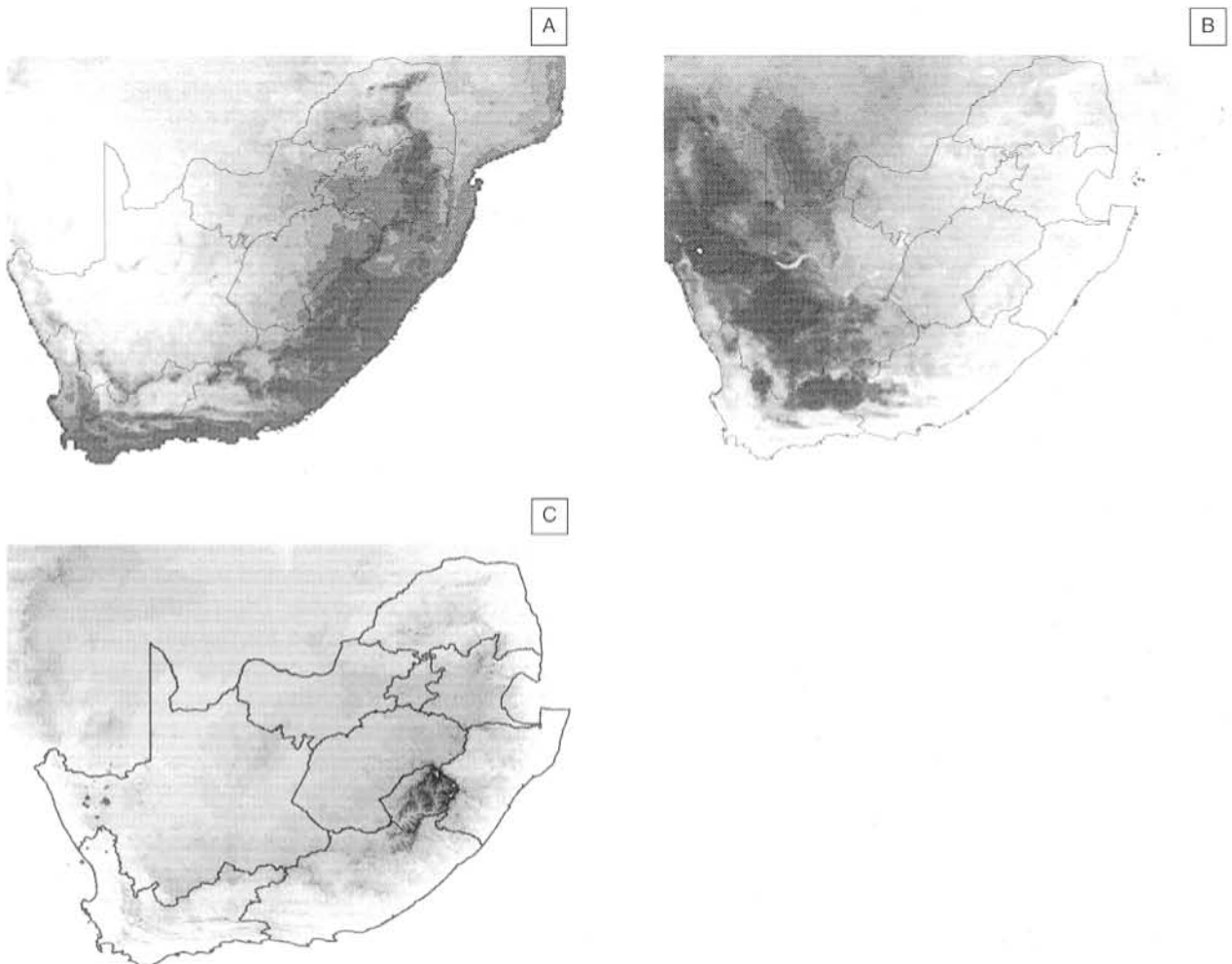


FIG. 1 Major physiogeographical variables of the target area (South Africa and small parts of adjoining countries)

- A: Temperature (lighter is higher)
- B: Normalized Derived Vegetation Index, NDVI (darker is higher)
- C: Elevation (darker is higher)

Modelling procedures

The modelling procedure adopted here uses a point-to-point similarity metric to assign a classification value to a candidate site based on the proximity in environmental space of the most similar record site (Carpenter, Gillison & Winter 1993). The distance (d) between two points A and B in the Euclidean p -dimensional space is defined as:

$$d_{AB} = \frac{1}{p} \sum_{k=1}^p \frac{|AK - BK|}{\text{range}K}$$

This metric uses range standardization to equalize the contribution from each bioclimatic attribute. This method of standardization is preferred over variance standardization in this application because it is less susceptible to bias arising from dense clusters of sample points. The complementary similarity measure R_{AB} is $R_{AB} = 1 - d_{AB}$. R is constrained between 0 and 1 for points within the ranges of the equation, but may yield negative values for points outside this range. The maximum similarity (S_A) between candidate point A and the set of known record sites T_m is defined as:

$$S_A = \max_{j=1}^m R_{TjA}$$

By evaluating S for all grid points in a target area, a matrix of similarity values is generated, considered here as a measure of HS. After calculation of HS for every species from the formula above, both the sensitivity and specificity of the model data as compared with the already known tick distribution were computed. The final calculation of HS was carried out using the set of abiotic variables that gave the maximum sensitivity and specificity, as described previously (Estrada-Peña 2001b).

Two kinds of HS calculations were performed. The first used the averaged abiotic variables for the entire period (1983–2000) to obtain baseline data about the abiotic preferences of each tick species and to compute the geographical extension of the HS averaged over this time period. Table 1 lists the variables computed using the whole 1983–2000 data set, as well as the set of variables providing the best fit between model output and the recorded distribution of the target tick species. These variables were also calculated on a yearly basis to determine the temporal changes of HS, and to build regression models for the sensitivity analysis and Fourier series analysis (see below).

Temporal changes in habitat suitability

The abiotic variables listed in Table 1 were computed for each year in the period 1983–2000. Application of the modelling procedures to this yearly data gave the changes in HS from year to year. The changes in HS were probed by the calculation of several variables that compared the HS values from every two consecutive years, namely the loss of territory covered with positive HS (percentage of territory switching from positive to negative HS in consecutive years), the gain of new suitable territory (percentage switching from negative to positive HS) and the net change of HS values in the entire target territory. Furthermore, the trend in HS in this period was computed under a geographical approach.

Determination of climate trend and calculation of habitat suitability in the near future

Temporal Fourier analysis describes variation through time of the satellite signals as a series of simple sine curves with different frequencies and amplitudes (Rogers 2000). Fourier analysis was used to test for cyclic behaviour in the time evolution of the abiotic variables over the period 1983–2000 and to forecast these variables into the near future (year 2015).

Input data were decadal (10-day) AVHRR values of T, NDVI, and WVPD, measured between 1983 and 2000. After calculation of the series coefficients, the time intervals were substituted with those of the time period to forecast, and new values for every decadal in the year 2015 were derived. Using this new set of forecasted decadal climate values, the complete set of variables (listed in Table 1) was recomputed, and the expected values of HS in the year 2015 were obtained. The results were compared with those obtained for the set of averaged variables (1983–2000) computing the same variables to probe for changes in HS as for the year-to-year analysis before.

Sensitivity analysis

A sensitivity analysis was performed to ascertain the behaviour of the system of each tick species under different sets of abiotic conditions. The first step was to determine how the three basic variables of this study (T, NDVI and WVPD) correlated in the period 1983–2000 on a monthly basis. Both T and WVPD are derived from the thermal channels of the satellite and are therefore directly correlated. However, T and NDVI have no such link. NDVI may

have low values in areas where T is low (zones too cold to support vigorous vegetation) or in areas where T is high (deserts). Thus, an unsupervised classification was carried out over the target area to detect ecologically different zones as a function of the monthly values of T and NDVI, averaged over the period 1983–2000. This unsupervised classification detected a total of 36 ecologically consistent areas based on spectral signatures. Some additional zones were detected, each enclosing only a few pixels (less than 1% of the total image). These spurious zones were rejected and included with the closest spectral category.

Regressions were then performed between T (independent variable) and NDVI or WVPD (dependent variables) for every month and every ecological area detected by the procedure above. This method keeps the residuals at a minimum and ensures better regression performance. Thus, 36 different regression equations (one for each ecological zone) were obtained for each month and each set of data (T + NDVI or T+WVPD).

Four basic scenarios were computed for the sensitivity analysis, which involved changing the yearly mean temperature by +1, +2, -1, or -2 °C, respectively. For each scenario, new temperature conditions were calculated for each month, and WVPD and NDVI were then calculated from regressions as applied for each month and ecological zone. Thus, year variables as in Table 1 were computed and the new abiotic conditions were used to set up the HS values over the whole territory with the new climate conditions. No attempt was made to modify the cattle density as a consequence of climate change pressure.

RESULTS

The abiotic variables providing the best fit are presented in Table 1, together with data about the sensitivity and specificity of the models. It is of interest to see how abiotic variables are involved in the modulation of HS for the various target tick species. The results of the specificity/sensitivity analysis show that absolute minimum temperature and NDVI are marginal variables defining the tick habitat, and that WVPD has a reduced relevance in the determination of suitable areas. However, the NDVI series values are key variables. Both maximum T and NDVI values are essential in the outline of habitat for all species except *H. truncatum*, whereas medium range abiotic variables (T2, V2, T3, V3) are decisive in the delineation of adequate sites for *H. truncatum*. Although these models have adequate values of sensitivity and specificity, the forecasted data for *H. truncatum* are weak as shown by relatively low values of both parameters.

The recorded known distribution of each species is included in Fig. 2. The geographical distribution of the forecasted HS for the target tick species, averaged over the period 1983–2000, is shown in Fig. 3. Areas with positive suitability for *B. decoloratus* (Fig. 3A) cover zones of the Limpopo Province, and all of Gauteng, Mpumalanga and Kwazulu-Natal Provinces, and the northern and eastern parts of the Free State Province. The region of positive suitability for this tick also extends into Lesotho, the eastern and north-eastern parts of the Eastern Cape Province, as well as the coastal belt and the winter rainfall areas of the Western Cape Province. Although the core areas of positive HS for this tick species are restricted to the central part of the

TABLE 1 Abiotic variables used to construct the main model, together with variables providing the best fit between model forecast and recorded tick distribution. Included are the sensitivity (se) and specificity (sp) for each species model

| | |
|--|--|
| - Mean yearly temperature | (T) |
| or Normalized Derived Vegetation Index | NDVI (V) |
| - Absolute maximum yearly temperature | (T4) or NDVI (V4) |
| - Absolute minimum yearly temperature | (T1) or NDVI (V1) |
| - Mean of monthly maximum temperatures | (T3) or NDVI (V3) |
| - Maximum of mean monthly temperatures | (T2) or NDVI (V2) |
| - Mean, minimum and maximum yearly water vapour pressure deficit | (WP, WP1, WP2) |
| - Amplitude of the yearly series for temperature and vegetation | (FT) (FV) |
| - <i>B. decoloratus</i> : | T, V, T4, V4, T3, V3, T2, V2, WP, FT, FV; se: 0.92; sp: 0.84 |
| - <i>A. hebraeum</i> : | T, V, T4, V4, T3, V3, WP, WP2, FT, FV; se: 0.88; sp: 0.86 |
| - <i>R. appendiculatus</i> : | T, V, T4, T3, V3, WP, WP2, FT, FV; se: 0.91; sp: 0.89 |
| - <i>H. truncatum</i> : | T, V, T4, V4, T2, V2, WP1, FT, FV; se: 0.77; sp: 0.81 |

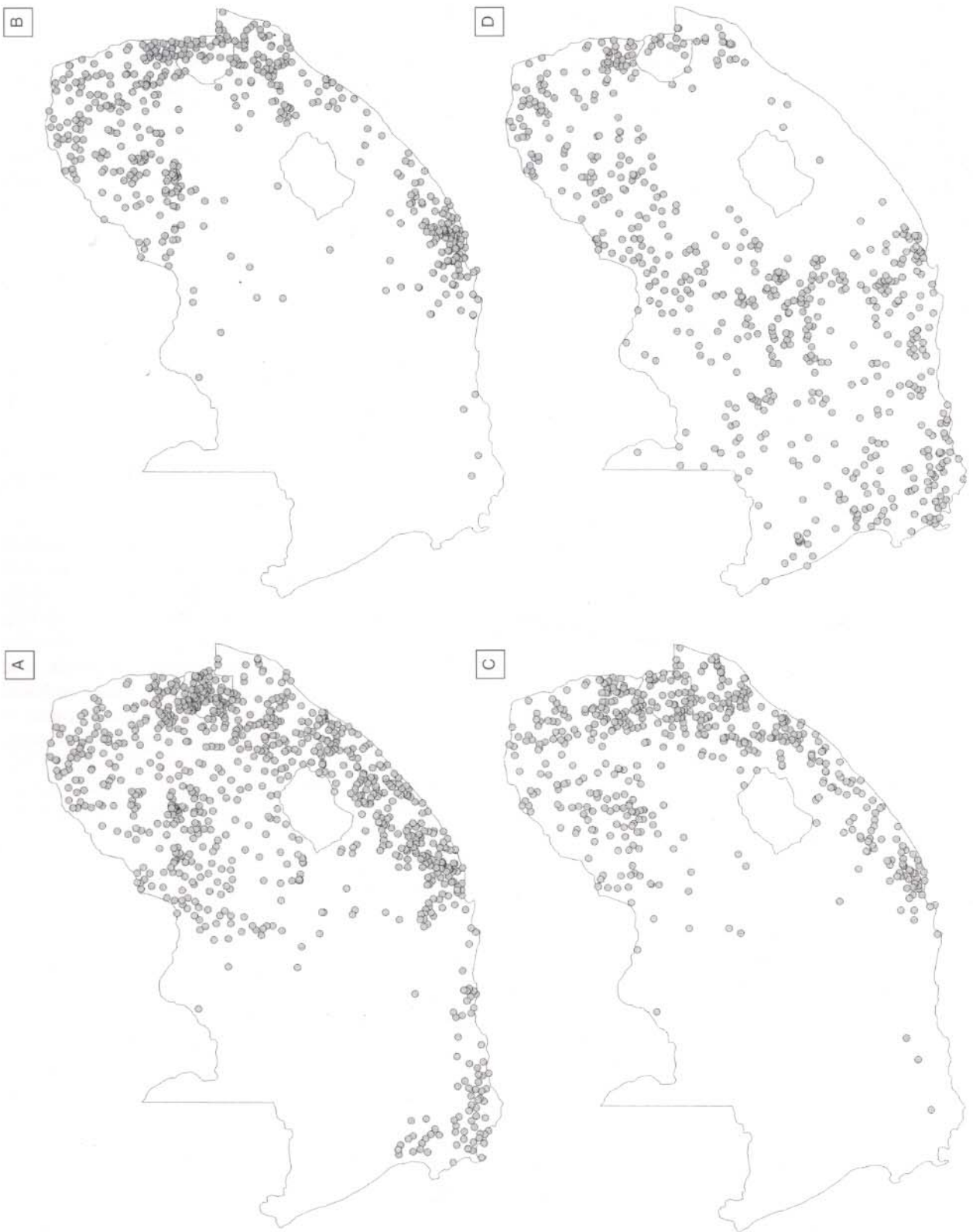


FIG. 2 The recorded distribution of the ticks included in the current study, as obtained from several published records and databases, and updated with unpublished records as mentioned in Material and Methods

A: *B. decoloratus*
C: *R. appendiculatus*

B: *A. hebraeum*
D: *H. truncatum*

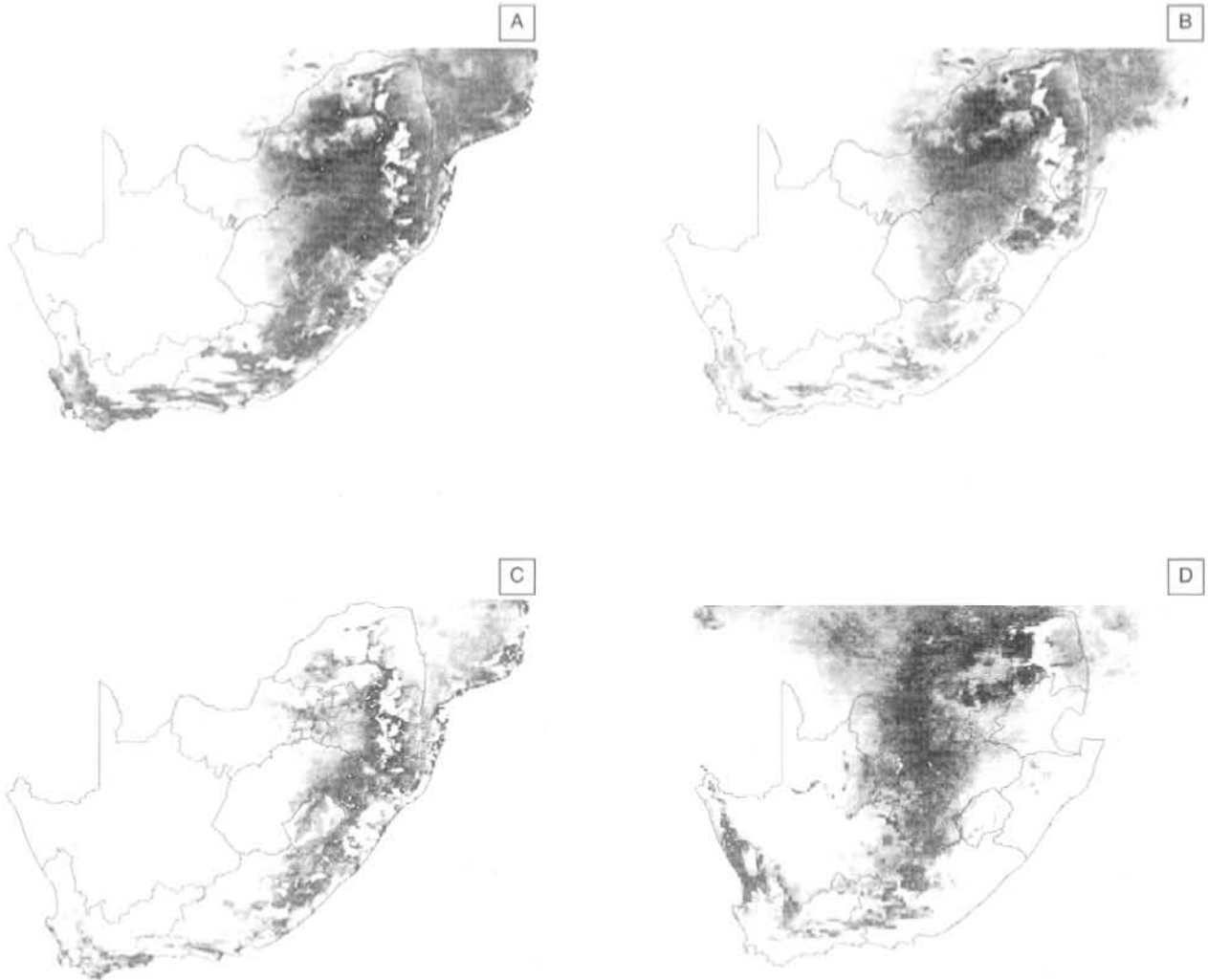


FIG. 3 Predicted habitat suitability of the four tick species (darker is higher)

A: *B. decoloratus*
C: *R. appendiculatus*

B: *A. hebraeum*
D: *H. truncatum*

region outlined above, fluctuations in the climatic conditions may briefly extend the positive suitability into the most eastern parts of Northern Cape Province and into the southern parts of Botswana. The areas of positive suitability forecast for *A. hebraeum* (Fig. 3B) extend largely over the same areas as those forecast for *B. decoloratus*. Higher HS for *A. hebraeum* is forecast around the Limpopo Province, much of Mpumalanga and Gauteng, as well as Kwazulu-Natal and the north-eastern parts of the Eastern Cape (former Transkei). Positive suitability also extends into the coastal areas of South Africa, and some positive suitability is detected in southern Botswana, mostly around the Gaborone area. Zones of positive HS for *R. appendiculatus* (Fig. 3C) extend through parts of the Limpopo Prov-

ince, into Mpumalanga, most parts of Kwazulu-Natal and the Transkei region of the Eastern Cape Province, reaching some sites in the coastal areas. Pockets of positive HS are also detected between Port Elizabeth in the east and Cape Town in the west. In the case of *H. truncatum* (Fig. 3D), the distribution of adequate habitat in South Africa seems to occur north and west of a line drawn from west Mpumalanga to south-western East Cape Province, with the exception of some areas in eastern Limpopo Province and northern Kwazulu-Natal. There is also a large zone in Northern Cape Province without adequate HS for the survival of the species. Positive suitability for *H. truncatum* is additionally detected over wide areas of southern Botswana.

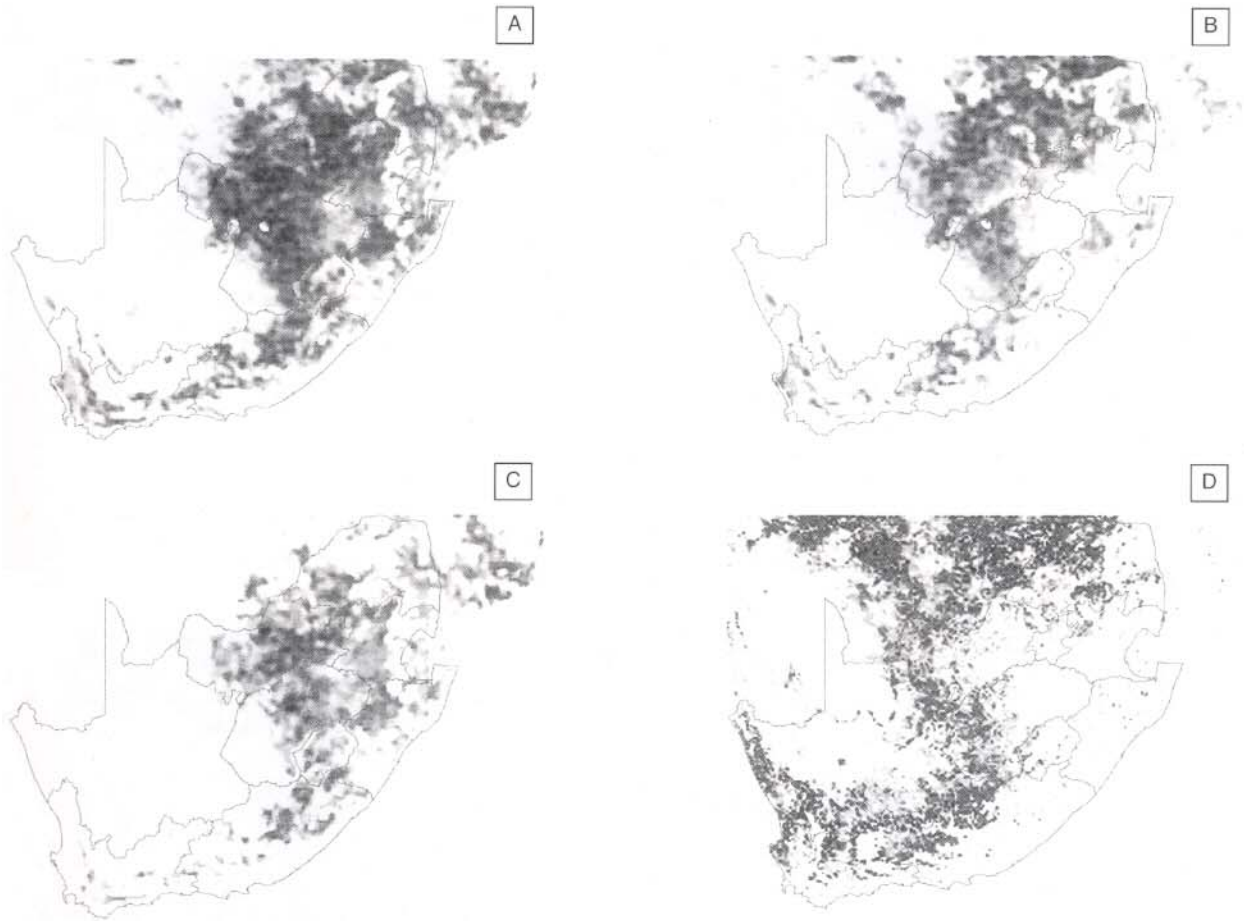


FIG. 4 Predicted habitat suitability of the four tick species as projected to the year 2015 through Fourier series analysis (darker is higher)

A: *B. decoloratus*
C: *R. appendiculatus*

B: *A. hebraeum*
D: *H. truncatum*

Table 2 summarizes the year-to-year changes in the HS for the targeted tick species, including the percentage of habitat newly available and percentage of habitat lost as a consequence of climate change between consecutive years. The data show large variations without a clear trend. However, in the final years of the study period (1995–2000) there is a drift towards the destruction of available habitat at a higher rate than the appearance of new habitat. This tendency towards habitat destruction manifests for all species considered. Fourier series analysis for the year 2015 (Fig. 4) clearly shows a clear decrease in HS. It is of interest to compare the ratio between the amount of habitat gained and lost as a consequence of climate change (Table 3) between the average values of the period 1983–2000 and the forecasted figures for 2015. This ratio is approximately 1:2 for *A. hebraeum* and *B. decoloratus*, approximately 1:2.5 for *H. truncatum*, and remains at 1:1 for *R. appendiculatus*.

The sensitivity analysis of the habitat model to varying temperature scenarios shows varying behaviour for the four tick species (Fig. 5 and 6; Table 3). A temperature increase of 1 °C would produce a weak tendency toward habitat gain for *A. hebraeum* and *R. appendiculatus*, whereas this change would have negative effects on the populations of *B. decoloratus* and *H. truncatum*. An increase of 2 °C is expected to produce the loss of many formerly suitable areas for every species. Decrease of the temperature (Fig. 5) by 1 °C promotes an increase of the geographical extension of adequate HS for *A. hebraeum*, *B. decoloratus* and *R. appendiculatus*, and these species show even greater gains of suitable habitat when the temperature is decreased by 2 °C. In contrast, decreasing the temperature by 1 or 2 °C promotes the loss of habitat for *H. truncatum*. The data for the forecasted change in habitat availability within the framework of the sensitivity

TABLE 2 Expected change in habitat availability including percentage of newly available habitat (HAB+) and percentage of lost habitat (HAB-) as obtained between consecutive years in the period 1983–2000. Species are *A. hebraeum* (Ah), *B. decoloratus* (Bd), *R. appendiculatus* (Ra) and *H. truncatum* (Ht). (*) Data for the year 1994 were lost, therefore changes were calculated between 1993 and 1995

| | Ah | Bd | Ra | Ht |
|-------------|------|------|------|------|
| HAB+ | | | | |
| 1983–84 | 12.6 | 4.9 | 4.6 | 10.9 |
| 1984–85 | 13.1 | 15.4 | 7.7 | 11.1 |
| 1985–86 | 5.6 | 3.4 | 3.8 | 6.5 |
| 1986–87 | 4.9 | 2.6 | 1.7 | 8.0 |
| 1987–88 | 8.6 | 2.4 | 5 | 6.9 |
| 1988–89 | 21.1 | 23.6 | 25.1 | 16.5 |
| 1989–90 | 6.1 | 3.7 | 3 | 6.8 |
| 1990–91 | 1.5 | 0.4 | 1 | 2.9 |
| 1991–92 | 23.8 | 23.1 | 15.4 | 8.3 |
| 1992–93 | 7.5 | 0.6 | 1.6 | 10.6 |
| 1993–95* | 27.7 | 27.9 | 20.5 | 22.6 |
| 1995–96 | 1.2 | 0.6 | 0.9 | 2.7 |
| 1996–97 | 1.6 | 0.8 | 4.5 | 4.4 |
| 1997–98 | 4.7 | 3.6 | 5.2 | 3.8 |
| 1998–99 | 5.9 | 4.3 | 4.4 | 7.8 |
| 1999–2000 | 6.8 | 0.5 | 2.1 | 25.1 |
| HAB- | | | | |
| 1983–84 | 8.8 | 11.1 | 8.7 | 3.8 |
| 1984–85 | 10.5 | 2.3 | 4.7 | 11.5 |
| 1985–86 | 4.6 | 3.8 | 2.2 | 3.6 |
| 1986–87 | 8.3 | 6.9 | 7.0 | 11.2 |
| 1987–88 | 16.5 | 18.3 | 13.6 | 11.7 |
| 1988–89 | 10.6 | 1.1 | 4.0 | 13.3 |
| 1989–90 | 4.9 | 4.9 | 8.9 | 5.6 |
| 1990–91 | 19.1 | 18.2 | 9.5 | 10.5 |
| 1991–92 | 2.3 | 0.5 | 1.2 | 4.7 |
| 1992–93 | 28.3 | 30.1 | 22.6 | 13.8 |
| 1993–95* | 7.1 | 0.4 | 0.8 | 10.2 |
| 1995–96 | 8.1 | 6.4 | 11.3 | 6.6 |
| 1996–97 | 7.9 | 8.2 | 4.3 | 5.1 |
| 1997–98 | 4.6 | 3.5 | 4.7 | 3.4 |
| 1998–99 | 5.8 | 4.9 | 4.3 | 3.1 |
| 1999–2000 | 14.4 | 14.6 | 13.7 | 9.8 |

TABLE 3 Expected change in habitat availability including percentage of newly available habitat (HAB+) and percentage of lost habitat (HAB-) as obtained within the framework of the Fourier series analysis (2015) and the sensitivity analysis. Values for temperature increase in 1 °C and 2 °C (+1, +2) and decrease (-1, -2) are provided in the sensitivity analysis. Species are *A. hebraeum* (Ah), *B. decoloratus* (Bd), *R. appendiculatus* (Ra) and *H. truncatum* (Ht)

| | Ah | Bd | Ra | Ht |
|-------------|------|------|------|------|
| HAB+ | | | | |
| 2015 | 9.3 | 5.0 | 9.8 | 0.8 |
| +1 | 5.2 | 0.4 | 3.7 | 0.0 |
| +2 | 1.8 | 0.1 | 1.7 | 1.1 |
| -1 | 15.2 | 8.0 | 9.6 | 0.1 |
| -2 | 18.8 | 11.8 | 13.4 | 1.1 |
| HAB- | | | | |
| 2015 | 17.1 | 10.6 | 10.7 | 34.4 |
| +1 | 3.3 | 4.4 | 1.9 | 20.8 |
| +2 | 3.6 | 7.9 | 4.0 | 21.3 |
| -1 | 6.1 | 1.7 | 1.2 | 20.1 |
| -2 | 8.5 | 1.9 | 1.3 | 24.3 |

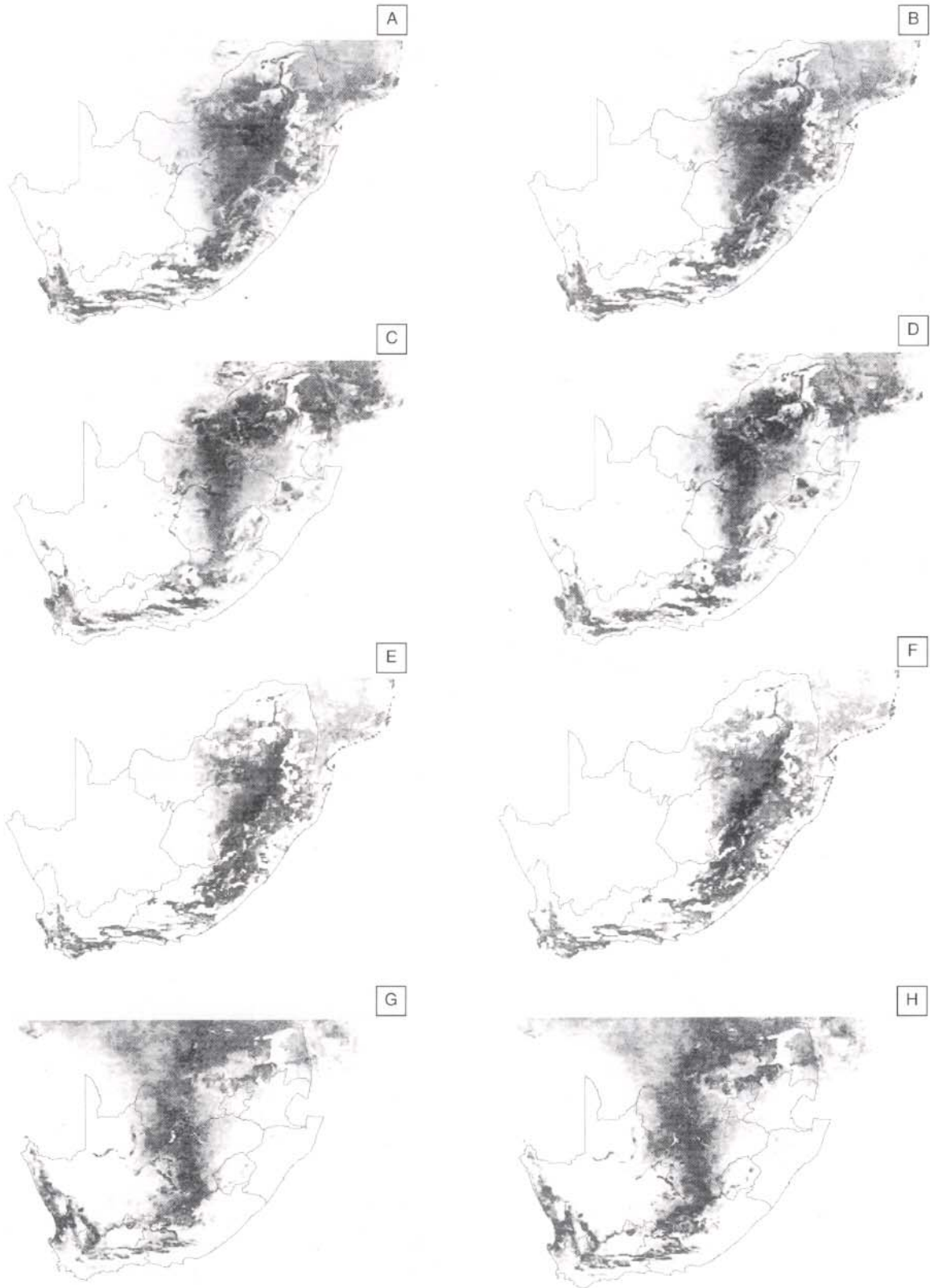


FIG. 5 Sensitivity analysis of the habitat suitability estimation when subjected to a decrease in temperature of 1 °C (left column) or 2 °C (right column). Darker regions indicate for higher habitat suitability

A, B: *B. decoloratus*
E, F: *R. appendiculatus*

C, D: *A. hebraeum*
G, H: *H. truncatum*

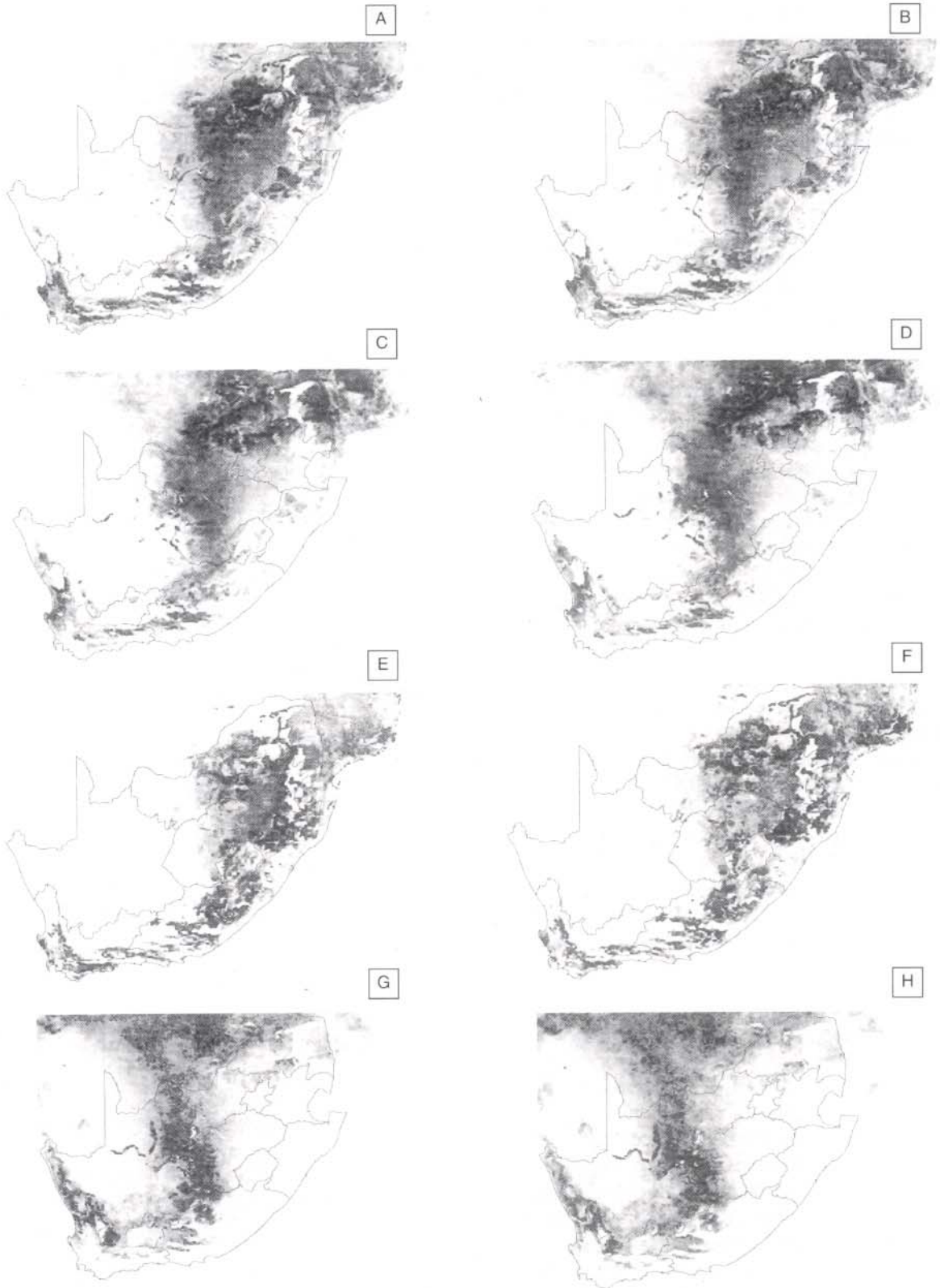


FIG. 6 Sensitivity analysis of the habitat suitability estimation when subjected to an increase in temperature of 1 °C (left column) or 2 °C (right column). Darker regions indicate for higher habitat suitability

A, B: *B. decoloratus*
E, F: *R. appendiculatus*

C, D: *A. hebraeum*
G, H: *H. truncatum*

analysis are included in Table 3, along with the estimated changes in habitat under the four different scenarios.

DISCUSSION

This study focuses on the habitat characteristics of four tick species in South Africa as derived from abiotic variables. The variations in abiotic variables governing the environment were used to analyze changes in habitat during the period 1983–2000. These long-term studies showed no drastic changes in habitat, and consequently no significant changes in tick distribution. Over the period 1995–2000, however, a significant transformation in suitability was observed for all species toward the decrease of areas with climate suitability. This trend in HS seems to be produced by the warming of the territory. The forecasted trend in the year 2015, as predicted by Fourier analysis of abiotic variables, also shows a clear decrease in HS for *A. hebraeum*, *B. decoloratus*, and *H. truncatum*. The results are very different for the distribution of *R. appendiculatus*, for which the rate of habitat destruction is approximately equal to the rate of habitat gain. This study also analysed the sensitivity of the model to increases and decreases in the temperature, with the accompanying change in NDVI and WVPD. A decrease in temperature was forecast to cause an increase in the areas with positive HS for all of the species considered except *H. truncatum*, whereas a temperature increase was forecast to remove wide areas of habitat currently suitable for the target species. However, every climate scenario seems to have a variable but positive response for *R. appendiculatus*, showing different degrees of net habitat gain under every condition.

Linear models of the ranges of species are emerging as valuable tools in biology. Such models quantify the relationship between environmental data and known occurrences of a species. Quantitative comparisons between linear models based on different variables for the same species can be used to make the modelling approach more objective and to compare the habitat characteristics between different species. The approach using logistic regression models (Cumming 2000) requires the existence of a training data set that includes sites both positive and negative for the tick surveyed, against which the forecasts of the model can be compared. Tick surveys citing locations where a given species has been encountered are easily found in the literature. However, it is difficult to

establish the reliability of surveys in which a tick species is cited as not present in a particular area. Consequently, evaluation of habitat characteristics for each species may change the approach if a different set of data is used. Point-to-point habitat similarity, as used here, has been proposed to map potential distributions of plants and animals (Carpenter *et al.* 1993). In comparison to other methods for mapping species ranges, the approach used here has the advantage that it can operate effectively using only presence records and a limited number of biophysical attributes. This can be seen in the modelling results obtained in the present study, which adequately forecast much of the variation in the distribution of the target species in comparison with the known distribution of these ticks, as outlined by Walker, Mehlitz & Jones (1978), Norval & Lightfoot (1982), Paine (1982), Petney, Horak & Rechav (1987), Walker & Olwage (1987) and Walker (1991). The smallest sensitivity and specificity were obtained for *H. truncatum*, with discrepancies between the recorded distribution of *H. truncatum* in Northern Cape Province and the HS forecast for the region. According to the model data, this zone is too warm and dry to provide an adequate habitat for this species. However, the tick was collected in the area between 1937 and 1944 (Theiler 1956), suggesting that either the model data is incorrect or that the abiotic variables changed noticeably between the period in which the tick was collected and the study period considered in the modelling. Moreover, the use of satellite imagery at a different resolution may establish a completely different picture of the habitat relationships of *H. truncatum*, displaying a range of abiotic conditions different from those available for this study and revealing a diverse habitat forecasting. Although the NDVI series of data are better predictors than water vapour deficit data, it remains to be tested if the incorporation of seasonal rainfall patterns into the main model structure would change the model output. It has been demonstrated that rainfall may influence the seasonal abundance of ticks (Mooring, Mazhowu & Scott 1994) but does not seem to be a sufficient definition of habitat suitability. Rainfall was not introduced into the model descriptors because the remotely sensed data did not uniformly cover the study period.

The sensitivity analysis performed can be considered as the response of a tick population to the search for adequate habitat for expansion and survival. Physiogeographic conditions and the requirements of each species are responsible for the variations in the species distribution patterns. The

response of a tick population can be understood only within a framework that includes both arthropod requirements and spatial and long-term temporal changes in abiotic variables. It should be noted that a 2 °C reduction in temperature is predicted to increase the distributions of *A. hebraeum*, *B. decoloratus* and *R. appendiculatus*. Such a temperature drop would cause areas currently too dry and warm to become colder and have adequate NDVI, lending support to the survival of ticks. The change in temperature is also expected to cause a shift in the amount of adequate vegetation. *A. hebraeum* is present in tall grass, well-drained areas with trees or bushes offering shade, but is not present in open savanna, steppe with only short grass, or arid areas (Petney *et al.* 1987). *B. decoloratus* is absent in zones with an average annual rainfall of less than about 380 mm and *R. appendiculatus* is restricted to regions with over 400 mm of rain a year, provided the vegetation cover is adequate (Walker 1991). Therefore, the decrease in temperature commonly accompanied by an increase in NDVI (as a general measurement of higher humidity) is responsible for the expected expansion in the distribution of these species. In the case of *H. truncatum*, all variations in abiotic variables are predicted to promote a loss of habitat greater than the gain from areas that switch to suitable habitat. Therefore, it seems that the current climate variables (and hence the distribution of *H. truncatum*) as obtained from the model data are close to the optimum conditions for this species. It must be noted that the forecasted distributions and their changes are based on abiotic variables.

A number of authors (summarized by Norval & Lightfoot 1982) have noted that the two principal requirements of a tick population are (a) a suitable environment for the survival of the free-living stages and (b) the presence of suitable hosts in sufficient numbers. In a given environment it can thus be assumed that the density of suitable hosts must exceed a certain threshold level before a tick population can become established. Moreover, it follows that this host threshold level must increase as environmental suitability decreases to account for the increased mortality in the free-living stages of the tick (i.e. lower tick survival rates must be counteracted by increasing the probability of host encounters). When host density exceeds the threshold level the size of the tick population is expected to increase with increasing host density. It has been demonstrated that host preferences alone are not adequate indicators of suitable habitat (Cumming 1998). Figures about host suitability

have not been included in the present study, although it has been shown elsewhere that the habitat suitable for *B. decoloratus* is better predicted if cattle density is included in the calculations (Estrada-Peña 2002). However, data about the distribution of wild hosts are coarse for much of the target area and difficult to integrate into the calculation of tick preferences.

A growing number of investigators propose that vector-borne diseases shift their range in response to climate change (McMichael, Haines, Sloff & Kovats 1996). In addition, models incorporating vectorial capacity uniformly indicate that global warming could potentially lead to the spread of the geographic areas that can sustain these diseases to higher elevations and higher latitudes (Carcavallo & De Casas 1996). Some experimental data are in agreement with this hypothesis, for example the spread of the tick *I. ricinus* in northern Europe (Lindgren *et al.* 2000). Data presented here support a similar picture. In the study area the climate is becoming too warm to maintain the foci of suitable habitat formerly available to the tick species considered, and the tick distribution is shifting to areas that were formerly too cold for tick survival. The tendency is toward the destruction of currently suitable habitat at a rate higher than the gain of "new" habitat, i.e. previously unsuitable zones switching to suitable. It should be noted that the figures presented here are not indicative of the presence or absence of the tick concerned in a given area, if targeted as suitable or unsuitable, for the short time periods considered. This is only an indication of the trend of habitat availability, or, in other words, the degree of stress. A similar behaviour has been previously described by Randolph (2001) in regard to the landscape ecology of Lyme borreliosis and tick-borne encephalitis. The prediction of this study was that if the climate continues along the current trend then enzootic cycles of TBE virus may not survive along the southern edge of their present range and will shift to different regions.

In higher rainfall areas of southern Africa, the tick species *B. microplus*, which is of Asian origin, has displaced *B. decoloratus*. This suggests that *B. microplus* has a marked competitive advantage over *B. decoloratus* in these habitats. *B. decoloratus* has been reported by Gothe (1967) to be much more cold tolerant than *B. microplus*, and it has been collected by Howell, Walker & Nevill (1978) in areas considered being too cold for *B. microplus*. However, the broadly similar climatic requirements of the two species suggest that the

competitive advantage of *B. microplus* arises from differences in fecundity caused by different female engorgement weights. *B. microplus* was not included in the present modelling because of the lack of adequate data about competitive competence, other than the dynamics of hybrid zones as provided by Sutherst (1987). Most authors (see, for example, Sutherst 2001) agree that the distribution of *B. microplus* is expanding in parts of Africa, as a consequence of management pressures and, most probably, because it is moving into areas that were formerly too cold for this species and only occupied by *B. decoloratus*. Although this hypothesis has not been tested in the current study, it remains possible that areas converted into unsuitable habitats for *B. decoloratus* may suffer invasive dynamics by *B. microplus*, especially under conditions of low acaricide pressure.

Modern control methods against ticks and tick-borne diseases should be introduced which will allow cattle to be kept successfully in areas endemic or epidemic for tick-borne diseases. The main criteria for these methods are that they be robust, cheap and flexible. Such methods should include an ecological background of the tick species involved integrated into economically sound acaricide measures. This ecological background should include the analysis of medium and long-range climate changes and trends.

REFERENCES

- CARCAVALLO, R.U. & DE CASAS, S.C. 1996. Some health impacts of global warming in South America. *Journal of Epidemiology*, 6:S153–S157.
- CARPENTER, G., GILLISON, A.N. & WINTER, J. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity & Conservation*, 2:667–680.
- CUMMING, G.S. 1998. Host distribution does not limit the species ranges of most African ticks (Acari: Ixodida). *Bulletin of Entomological Research*, 89:303–327.
- CUMMING, G.S. 1999. The evolutionary ecology of African ticks. Doctoral thesis. University of Oxford.
- CUMMING, G.S. 2000. Using habitat models to map diversity: pan-African richness of ticks (Acari: Ixodida). *Journal of Biogeography*, 27:425–440.
- DENNIS, D.T., NEKAMOTO, T.S., VICTOR, J.C., PAUL, W.S., PIESMAN, J. 1998. Reported distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the United States. *Journal of Medical Entomology*, 35:629–638.
- EPSTEIN, P.R., DIAZ, H.F., ELIAS, S., GRABHERR, G., GRAHAM, N.E., MARTENS, W.J.M., MOSLEY-THOMPSON, E. & SUSSKIND, J. 1998. Biological and physical signs of climate change: focus on mosquito-borne diseases. *Bulletin of American Meteorological Society*, 79:409–417.
- ESTRADA-PEÑA, A. 2001a. Forecasting habitat suitability for ticks and prevention of tick-borne diseases. *Veterinary Parasitology*, 98:111–132.
- ESTRADA-PEÑA, A. 2001b. Climate warming and changes in habitat suitability for *Boophilus microplus* (Acari: Ixodidae) in Central America. *Journal of Parasitology*, 87:978–987.
- ESTRADA-PEÑA, A. 2002. A simulation model for environment populations densities, survival rates and prevalence of *Boophilus decoloratus* (Acari: Ixodidae) using remotely sensed information. *Veterinary Parasitology*, 104:51–78.
- GOTHE, R. 1967. Investigations into the cold resistance of the eggs and larvae of *Boophilus decoloratus* (Koch, 1844), *Boophilus microplus* (Canestrini, 1888) and *Margaropus winthemi* Karsch, 1879. *Onderstepoort Journal of Veterinary Research*, 34:109–127.
- HAY, S.I., PARKER, M.J. & ROGERS, D.J. 1997. The impact of remote sensing on the study and control of invertebrate intermediate hosts and vector for diseases. *International Journal of Remote Sensing*, 18:2899–2930.
- HOWELL, C.J., WALKER, J.B. & NEVILL, E.M. 1978. *Ticks, mites and insects infesting domestic animals in South Africa. Part I. Descriptions and Biology* (Science Bulletin Department of Agriculture Technical Services, Republic of South Africa, No. 393).
- LINDGREN, E., TALLEKLINT, L., POLFELD, T. 1998. Impact of climate change on the northern latitude limit and population density of the disease-transmitting European tick *Ixodes ricinus*. *Environmental Health Perspectives*, 108:119–123.
- MOORING, M.S., MAZHOWU, W. & SCOTT, C.A. 1994. The effect of rainfall on tick challenge at Kyle Recreational Park, Zimbabwe. *Experimental and Applied Acarology*, 18:507–529.
- McMICHAEL, A., HAINES, A., SLOFF, R., KOVATS, S. 2000. Climate change and human health. World Health Organization, Geneva.
- NORVAL, R.A.I. & LIGHTFOOT, C.J. 1982. Tick problems in wildlife in Zimbabwe. Factors influencing the occurrence and abundance of *Rhipicephalus appendiculatus*. *Zimbabwe Veterinary Journal*, 13:11–20.
- PAINE, G.D. 1982. Ticks (Acari: Ixodoidea) in Botswana. *Bulletin of Entomological Research*, 72:1–16.
- PETNEY, T.N., HORAK, I.G. & REACHY, Y. 1987. The ecology of the African vectors of Heartwater, with particular reference to *Amblyomma hebraeum* and *Amblyomma variegatum*. *Onderstepoort Journal of Veterinary Research*, 54:381–395.
- PRINCE, S.D. & GOWARD, S.J. 1995. Global primary production: a remote sensing approach. *Journal of Biogeography*, 22:815–835.
- RANDOLPH, S.E. & ROGERS, D.J. 1997. A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology*, 115:265–279.
- 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 of London, B*, 356:1045–1056.
- ROGERS, D.J. 2000. Satellites, Space, Time and the African Trypanosomes. In: *Remote sensing and geographical Information Systems in Epidemiology. Advances in Parasitology*, 47:130–165.
- SUTHERST, R.W. 1987. The dynamics of hybrid zones between tick (Acari) species. *International Journal of Parasitology*, 17:921–926.

- SUTHERST, R.W. 2001. The vulnerability of animal and human health to parasites under global change. *International Journal of Parasitology*, 31:933–948.
- THEILER, G. 1956. Tick survey. IX. Distribution of the three South African *Hyalomma* or bontpoots. *Onderstepoort Journal of Veterinary Research*, 27:239–269.
- WALKER, J.B. 1991. A review of the ixodid ticks (Acari: Ixodidae) occurring in Southern Africa. *Onderstepoort Journal of Veterinary Research*, 58:81–105.
- WALKER, J.B., MEHLITZ, G.E. & JONES, G.E. 1978. *Notes on the ticks of Botswana*. Eschborn: German Agency for Technical Cooperation.
- WALKER, J.B. & OLWAGE, A. 1987. The tick vectors of *Cowdria ruminantium* (Ixodoidea, Ixodidae, genus *Amblyomma*) and their distribution. *Onderstepoort Journal of Veterinary Research*, 54:353–379.