Modelling the distribution of *Rhipicephalus microplus* and *R. decoloratus* in Zimbabwe

*Sungirai M^{1,2}, Moyo D Z³, De Clercq P⁴, Madder M⁵, Vanwambeke S O⁶,

De Clercq E M⁷

¹Sungirai M, Department of Livestock and Wildlife Management, Midlands State
University, Private Bag 9055, Gweru, Zimbabwe. sungiraim@staff.msu.ac.zw
²Sungirai M, Unit of Entomology, Department of Biomedical Sciences, Institute of
Tropical Medicine, Nationalestraat 155, Antwerp 2000, Belgium. msungirai@itg.be
³Doreen Zandile Moyo, Department of Biological Sciences, Midlands State
University, P. Bag 9055, Gweru, Zimbabwe. moyodz@staff.msu.ac.zw
⁴Patrick De Clercq, Department of Plants and Crops, Ghent University, Coupure
Links 653, B-9000 Ghent, Belgium. patrick.declercq@ugent.be
⁵Maxime Madder, Department of Veterinary Tropical Diseases, Faculty of Veterinary
Science, University of Pretoria, Private Bag X04, Onderstepoort 0110, South Africa.
maxime.madder@clinglobal.com

⁶Vanwambeke SO, Georges Lemaître Institute for Earth and Climate Research,
Université catholique de Louvain, Place Louis Pasteur 3, B-1348 Louvain-la-Neuve,
Belgium. sophie.vanwambeke@uclouvain.be

⁷De Clercq EM, Research Fellow FNRS, Georges Lemaître Institute for Earth and Climate Research, Université catholique de Louvain, Place Louis Pasteur 3, B-1348 Louvain-la-Neuve, Belgium, eva.declercq@uclouvain.be,

*Corresponding author

Abstract

Species distribution modelling is a very useful tool in vector management. Ticks are vectors of various pathogens which cause serious problems in livestock production in tropical countries. They have a high dispersal potential which is mainly facilitated by the movement of animals from one area to another. In light of the observed geographic expansion of Rhipicephalus microplus in Zimbabwe, we used species distribution modelling techniques to identify areas which may provide suitable habitats for the occurrence of this invasive tick species as well as the autochthonous Rhipicephalus decoloratus. Our results suggest that, despite the geographic expansion of *R. microplus*, climate will continue to be a limiting factor for the further expansion of this tick species. We expect its distribution to be restricted to the most favourable areas in the eastern and northern parts. The greater part of Zimbabwe is suitable for R. decoloratus, although in areas where R. microplus occurs, displacement of the former by the latter will be expected to occur. A heterogeneous climate, unregulated movement of cattle and episodic droughts are suggested to be possible factors for the continued existence of R. microplus and R. decoloratus in Zimbabwe and the partial displacement.

Keywords: Rhipicephalus (Boophilus), modelling, habitat suitability, Zimbabwe

Highlights

- Widespread occurrence of Rhipicephalus decoloratus in Zimbabwe
- Patchy and discontinuous occurrence of R. microplus in Zimbabwe
- Small areas of co-existence for R. microplus and R. decoloratus

1. Introduction

The invasive tick species *Rhipicephalus microplus* is regarded as the most important cattle tick in the world (Giles et al., 2014). Having originated from South East Asia, *R. microplus* has spread globally, and is now found in most tropical and subtropical countries (Estrada-Peña et al., 2006a). The invasiveness of this tick species has been largely attributed to its high reproductive capacity characterised by a short life cycle, its high adaptability to changing environments, its increasing resistance to chemical acaricides and the fact that it is a one host tick benefitting from cattle movement for spreading efficiently (Barrè and Uilenberg, 2010). The introduction of this species in an area becomes a concern to disease control authorities as not only does it cause production losses in cattle but it transmits the more pathogenic form of bovine babesiosis (*Babesia bovis*) which may be a threat to indigenous non-immune cattle (De Clercq et al., 2012). Even more, the opportunities for keeping the more superior temperate breeds in these areas is jeopardised as these are more susceptible to *B. bovis* infections (Madder et al., 2011).

Control strategies for invasive vector species involve identifying risk areas within which these species can potentially establish upon introduction (Estrada-Peña, 1999). Thereafter, areas deemed suitable for the tick species but not yet invaded may be put under surveillance with constant inspection for the presence of ticks (Hahn et al., 2016). On the other hand, tick eradication programmes may be organised targeting isolated areas where the tick species is currently established and thus preventing its potential spread to areas that may provide the right environmental conditions for survival and proliferation (Wilson, 1996). For tick species, these are climate, vegetation and availability of suitable hosts (De Clercq *et al.*, 2013; Estrada-

Peña, 2008). During the parasitic phase, the host provides all resources required for tick development, but during the pre- and post-parasitic phases, favourable climatic conditions and vegetation patterns are essential. It has been proposed that of these factors, climate is the most limiting factor for tick distribution (Cumming, 2002).

An exhaustive review of the habitat suitability models developed for *Rhipicephalus microplus* ticks has been published by Wang *et al.* (2017). For these and other tick species, a common approach in modelling species distribution is the use of a generalised linear model (GLM) for presence and absence data together with environmental variables as predictors of species occurrence (Hijmans and Elith, 2016). Data on weather and climate are routinely obtained from weather stations around the world or from satellite imagery. For climate data, the WorldClim dataset is often used and sensors like the Moderate Resolution Imaging Spectroradiometer (MODIS) are useful in gathering environmental data (De Clercq *et al.*, 2015). The final output of species modelling is a suitability map which shows a degree of suitability for each pixel, where values close to '1' indicate the areas that are highly suitable and values close to '0' indicate the areas that are unsuitable for the occurrence of a species.

Previous studies in Zimbabwe suggested a complete displacement of *R. decoloratus* by *R. microplus* in eastern Zimbabwe (Mason and Norval, 1980). Other studies suggested that because of the 1981-1984 drought experienced in Zimbabwe, *R. microplus* could have completely disappeared in Zimbabwe (Norval *et al.*, 1992). Later studies however showed that the tick was present in the east and north east parts of the country (Katsande *et al.*, 1996). In other countries *R. microplus* has been

reported to displace *R. decoloratus* (Berkvens *et al.*, 1998; De Clercq *et al.*, 2012; Nyangiwe *et al.*, 2013; Tønnesen *et al.*, 2004). Recently, an expansion in the geographic range of *R. microplus* was reported by Sungirai *et al.* (2017) and in contrast with earlier studies, they observed a partial displacement of the more drought-tolerant *R. decoloratus* by the former.

The expansion in the range of R. microplus and the possible displacement of R. decoloratus raises two questions: (i) Are there other areas in Zimbabwe where climatic conditions are suitable for R. microplus to exist, survive and reproduce and where the species is not presently reported? and (ii) do the two tick species R. microplus and R. decoloratus share the same ecological niche in Zimbabwe? This study therefore seeks to model the habitat suitability of these competing tick species, the autochthonous R. decoloratus and the invasive R. microplus, and to determine whether their niche overlaps. Previous papers have predicted the habitat suitability of these two tick species on a continental scale (Estrada-Peña et al., 2006a) using tick records from 1900 to 1990 (Cumming, 1999). However, as more recent tick occurrence data became available, we felt it necessary to update these species distribution maps. This will be important to understand the ecology of these two tick species and particularly for R. microplus to provide the forecast of its distribution changes. From a management point of view it will also provide a platform to allow animal health authorities to evaluate the control programmes in place (Hahn et al., 2016).

2. Materials and Methods

2.1 Study area and tick data

The country of Zimbabwe is situated in southern Africa, neighbouring Botswana in the west, Zambia in the north, Mozambique in the east and South Africa in the south. The climate is tropical, but can vary locally due to large differences in relief over a short range. The Zambezi valley to the north is hot and arid, and the eastern plateau is rather cool with relatively high annual rainfall. Overall, the main vegetation cover is savannah (miombo woodland), and tropical forests occur where the climate allows (Gambiza and Nyama, 2000). The country is divided into five agro-ecological regions on the basis of temperature and rainfall, ecological regions 1 and 2 being referred to as the Highveld, region 3 as the Middleveld while region 4 and 5 are referred to as the Lowveld (Norval et al., 1994).

This study used data of *R. microplus* and *R. decoloratus* ticks collected in Zimbabwe during a survey conducted on cattle at communal dipping tanks from September 2013 to May 2015. The details on sample collection are described in detail by Sungirai *et al.* (2017). Briefly, using the formula of Thrusfield (2005) whereupon a dip tank prevalence of 50% was assumed, 384 dipping tanks were to be sampled throughout the country. This translated to sampling around 77 dipping tanks per ecological region, although the figure varied depending on the respective size and the total number of dipping tanks in the region. Due to this and other logistical reasons explained by Sungirai et al. (2017), sampling was done at 322 dipping tanks throughout the country. A sampling frame of the dipping tanks in each region was obtained from the department of Veterinary Services of Zimbabwe, random numbers were generated using Microsoft Excel as many as the number of dipping tanks and the order of assigned random numbers was used to select the dipping tanks in each region. Ecological region three had the most dipping tanks sampled

(109), followed by region four (76), region five (65), region two (55) and region one (17). At each dipping tank, at least five heavily tick infested cattle were sampled for ticks targeting all the predilection sites i.e. the base of tail, perianal region, perineum, legs, axillae, hooves, udder, scrotum, belly, dewlap, head and ears. The name of the dipping tank, geographic co-ordinates, date of collection were collected. The ticks and the labels were stored in specimen bottles with 70% ethanol and were identified in the laboratory using morphological keys (Walker et al., 2003). *Rhipicephalus microplus* ticks were found at 32% (103/322) of the dipping tanks while *R. decoloratus* ticks were found at 62% (200/322) of the dipping tanks. *Rhipicephalus decoloratus* showed a nearly uniform presence throughout the country, while *R. microplus*' distribution was limited to sub-regions in the eastern part of the country.

2.2 Environmental variables

The predictor variables used in the study were the 19 bioclimatic variables (Table 1) obtained from the WorldClim dataset which is an interpolated dataset of temperature and precipitation data obtained from weather stations for the period 1950-1990 (Hijmans *et al.*, 2005). Other predictor variables were the mean, minimum and maximum values of the Normalised Difference Vegetation Index (NDVI) for the period January 2013- December 2015 obtained by remote sensing from the MODIS sensor downloaded at a 1 km spatial resolution (Justice *et al.*, 1998). Monthly NDVI values were averaged into mean, maximum and minimum NDVI values for each dip tank. The NDVI is a measure of photosynthetic activity which reflects available moisture on the ground (Randolph, 2010), its values range from – 1 to +1, with negative values indicating water while values close to zero indicate bare soil and values closer to one indicate a lot of greenness.

Table 1. Univariate logistic regression to find the potential predictor variables for *Rhipicephalus microplus* and *R. decoloratus* occurrence in Zimbabwe using bioclimatic and NDVI variables.

Variable	Description of variable	R. microplus		R. decoloratus	
		p-value	Coefficient	p-value	Coefficient
alt	Altitude	0.018 *	-0.001	1.13e-08 ***	0.003
Bio_01	Annual mean temperature	0.528	-0.004	5.80e-05 ***	-0.029
Bio_02	Mean diurnal range	1.04e-05 ***	-0.05	0.119	-0.017
Bio_03	Isothermality	1.36e-05 ***	0.341	3.63e-06 ***	-0.359
Bio_04	Temperature seasonality	2.04e-07 ***	-0.003	0.01 *	-0.001
Bio_05	Maximum temperature of the warmest month	0.00339 **	-0.016	0.03 *	-0.011
Bio_06	Minimum temperature of the coldest month	0.001 ***	0.029	0.001 ***	-0.028
Bio_07	Temperature annual range	4.96e-08 ***	-0.037	0.959	0.0003
Bio_08	Mean temperature of the wettest quarter	0.527	-0.004	7.79e-07 ***	-0.035
Bio_09	Mean temperature of the driest quarter	0.521	0.004	0.005**	-0.019
Bio_10	Mean temperature of the warmest quarter	0.183	-0.008	6.39e-05 ***	-0.026
Bio_11	Mean temperature of the coldest quarter	0.623	0.004	0.000294 ***	-0.027
Bio_12	Annual precipitation	6.21e-06 ***	0.003	0.045 *	0.001
Bio_13	Precipitation of the wettest month	7.48e-07 ***	0.013	0.042*	0.005
Bio_14	Precipitation of the driest month	7.78e-05 ***	0.125	0.253	-0.032
Bio_15	Precipitation seasonality	0.479	0.01	0.0004***	0.051
Bio_16	Precipitation of the wettest quarter	1.80e-06 ***	0.005	0.0136 *	0.002
Bio_17	Precipitation of the driest quarter	2.19e-05 ***	0.042	0.166	-0.011
Bio_18	Precipitation of the warmest quarter	1.72e-06 ***	0.004	0.726	-0.0003
Bio_19	Precipitation of the coldest quarter	9.68e-05 ***	0.037	0.404	-0.007
NDVI.max	NDVI maximum value	0.067 .	2.57	0.203	1.688
NDVI.mean	NDVI mean value	0.039*	3.4	0.244	1.862
NDVI.min	NDVI minimum value	0.009 **	5.54	0.466	1.531

^{*}p≤ 0.05, **p≤0.01, ***p≤0.001, ****p≤0.0001

2.3 Model building

We used the procedure described by Cumming (1999) to develop models to predict the habitat suitability of the two tick species. In this procedure logistic regression is done with the environmental predictor variables and it is realised that the multicollinearity of the variables will not affect the predictive performance of the model (Cumming, 1999). The main effects of autocorrelation are on co-efficient values rather than on predicted probabilities (Cumming, 2002) hence the former will not be interpreted in this paper since there was no correction for collinearity. The presence-absence data for both tick species was divided into a training set (75%) for model calibration and a test set (25%) for model evaluation. First, univariate logistic regression was done using a generalised linear model (GLM) with the "binomial logit" link function to test the association between each variable and tick occurrence. Variables which were significantly correlated (p ≤ 0.05) with tick presence were retained as potential predictors for habitat suitability (Table 1). With these, multivariate logistic regression analyses were done using the stepwise method for model selection (Hirzel et al., 2006), whereby the model with the lowest Akaike Information Criterion (AIC) was selected, the significant variables (p \leq 0.05) were concluded to be the best predictors for habitat suitability.

2.4 Model Evaluation

The test dataset was used to evaluate the predictive power of the model applying the Area Under the ROC-Curve index (AUC) as a criterion (Cumming, 2002; Pearce and Ferrier, 2000). AUC values of 0.5-0.7 indicate low accuracy, 0.7-0.9 useful applications and > 0.9 high accuracy (Manel *et al.*, 2001). Another important feature of the AUC is that it is not affected by collinearity and spatiotemporal autocorrelation

(Cumming,2002). Afterwards, the correlation between the two suitability maps of *R. microplus* and *R. decoloratus* was assessed using the Kendall rank correlation coefficient, a non-parametric test for dependence.

2.5 Environmental requirements for the two tick species

Probability density distributions and bivariate plots were computed to show the range of environmental conditions where the two tick species occurred and to compare their requirements with each other.

2.6 Software used

All statistical analyses were carried out in the R statistical package version 3.2.3 (R Development Core Team, 2013). The following R packages as described by Hijmans and Elith (2016): "raster", "rgdal", "dismo", "sp", "maptools", "RODBC", "caret", "mlbench", were used in the importation of occurrence data (dismo, RODBC), crosschecking co-ordinates of the data points (sp), reading environmental predictor variables which were in raster format (raster and dismo), plotting the raster layers (maptools), splitting the training and test datasets (caret and mlbench) and performing the stepwise logistic regression (MASS). All maps were prepared using QGIS software (QGIS Development Team, 2013).

3. Results

3.1 Univariate analysis

Of the 23 variables, 16 were found to be significantly correlated with the presence of *R. microplus*. These were: altitude, annual mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum

temperature of the coldest month, annual temperature range, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the coldest quarter, precipitation of the warmest quarter, mean monthly NDVI and minimum NDVI values. Fourteen variables were found to be significant predictors (p≤0.05) for *R. decoloratus*: altitude, annual mean temperature, isothermality, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation seasonality and precipitation of the wettest quarter.

3.2 Multivariate Analysis

3.2.1 Rhipicephalus microplus

The best model (AIC = 299.5) for *R. microplus* included the following variables: altitude, annual mean diurnal range, temperature seasonality, minimum temperature of the coldest month, precipitation of the wettest quarter, precipitation of the warmest quarter and the mean NDVI values (Table 2). The AUC of the model was 0.85. Altitude had the highest contribution in terms of variable importance (22.9%) followed by minimum temperature of the coldest month (16.4%), mean diurnal range (15.4%), temperature seasonality (14.3%), mean NDVI (13.4%), precipitation of the wettest quarter (10.6%), and precipitation of the warmest quarter (7.6%).

3.2.2 Rhipicephalus decoloratus

The best model for *R. decoloratus* (AIC=363.3) included the following variables: altitude, mean temperature of the driest quarter, annual precipitation, precipitation of

Table 2. Final variables and their relative contribution to the habitat suitability models for *Rhipicephalus microplus* and *R. decoloratus* occurrence in Zimbabwe.

R. mi	icroplus	R. decoloratus			
Variable in the model	Variable Importance / %	Variable in the model	Variable Importance / %		
Altitude	22.9	Altitude	26.3		
Minimum temperature of the coldest month	16.4	Precipitation of the 21.8 wettest month			
Mean diurnal range	15.4	Annual precipitation 20.1			
Temperature seasonality	14.3	Mean temperature of the driest quarter	16.5		
NDVI_mean	13.4	Precipitation seasonality	15.2		
Precipitation of the warmest quarter	10.6				
Precipitation of the wettest quarter	7.6				

the wettest month and precipitation seasonality (Table 2). The AUC of the model was 0.73. Altitude had the highest relative contribution to the model (26.3%) followed by the precipitation of the wettest month (21.8%), annual precipitation (20.1%), mean temperature of the driest quarter (16.5%), and precipitation seasonality (15.2%).

3.3 Habitat suitability maps

The habitat suitability map of *R. microplus* (Figure 1) showed a patchy distribution being highly suitable in some parts of the east, north-east and north-west parts of the country. These areas correspond to the Highveld, an area characterised by high average annual rainfall (800-1000mm) and a temperature range of 12-24°C. Although R. microplus was collected in the Zambezi Valley (areas adjacent to Lake Kariba) and the Middle-veld, the suitability maps show that these areas are not entirely suitable for this tick species. The habitat suitability map for *R. decoloratus* (Figure 2) shows the tick species occupying almost the entire part of the country with absences in the southern Lowveld and some parts in the east and north east of the country, sites which would be possibly occupied by R. microplus. The two maps were combined (Figure 3), what is clear from this map is that *R. decoloratus* may occupy the greater portion of the country whereas R. microplus will be restricted to some pockets in the east and north eastern parts of the country. There are areas in the eastern parts where there is expected co-existence of the two tick species. The Kendall correlation between the two suitability maps was negative (- 0.18) and highly significant (p \leq 0.001).

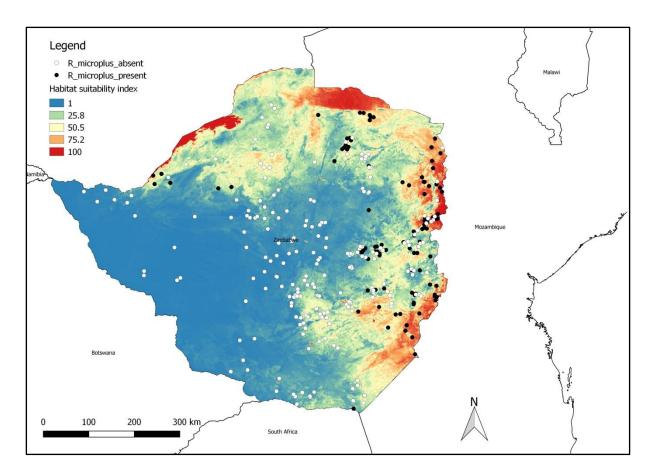


Figure 1. Habitat suitability map for *R. microplus* in Zimbabwe

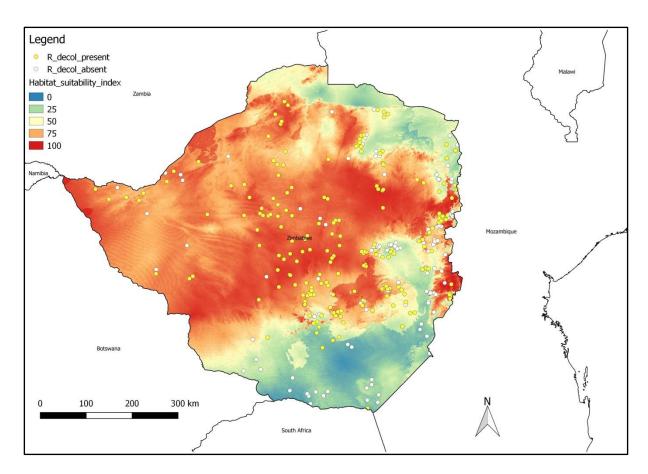


Figure 2. Habitat suitability map for *R. decoloratus* in Zimbabwe

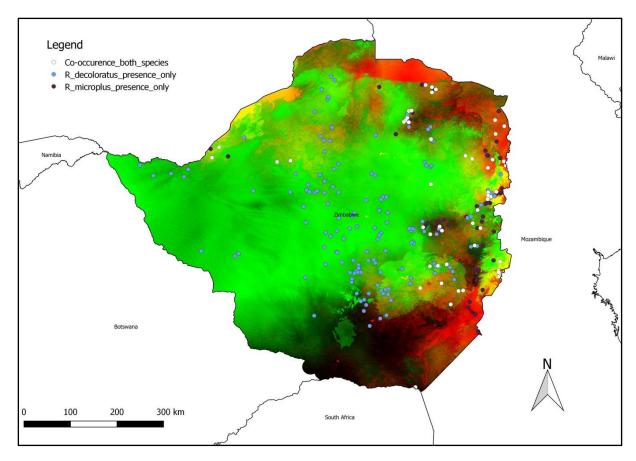


Figure 3. Combined habitat suitability map for *R. microplus* and *R. decoloratus* (areas in green are suitable habitats for *R. decoloratus* while areas in red are suitable for *R. microplus*, those in yellow show possible areas of co-existence)

3.4 Environmental requirements for the two tick species

The average conditions for rainfall and temperature appear to be similar for both species (Figures 4 and 5) with peaks observed at temperatures between $18-20^{\circ}$ C and rainfall of around 750mm. Rainfall of below 500mm appears unfavourable for both species while an increase of rainfall appears to give R. microplus a competitive advantage over R. decoloratus. On the temperature gradient, temperatures above $\approx 23^{\circ}$ C will tend to favour R. microplus at the expense of R. decoloratus. Quite interesting is the influence of altitude on the occurrence of the two tick species. In all the models, altitude had the largest contribution (>22%). For both species peak occurrences will occur at altitudes of 1000m above sea level. However lower altitudes tend to favour the proliferation of R. microplus at the expense of R. decoloratus. On the other hand, the probability of occurrence of R. decoloratus at higher altitudes above 1200m is higher than that of R. microplus.

4. Discussion

This study builds upon the efforts made to model the distribution of boophilid tick species, be it on a global scale (Estrada-Peña *et al.*, 2006a), or on a regional scale in Sub-Saharan Africa (Sutherst and Maywald, 1985), South America (Estrada-Peña *et al.*, 1999) and West Africa (De Clercq *et al.*, 2013). Countrywide modelling for the boophilid ticks has been performed in Mexico (Estrada-Peña *et al.*, 2006b), Benin (De Clercq *et al.*, 2015) and Tanzania (Lynen *et al.*, 2008). Cumming (1999) attempted to map the suitable habitats for African ticks including the boophilids of Zimbabwe using records collected between 1975 and 1980. Since then, major changes have been reported by Sungirai *et al.* (2017) and this has necessitated

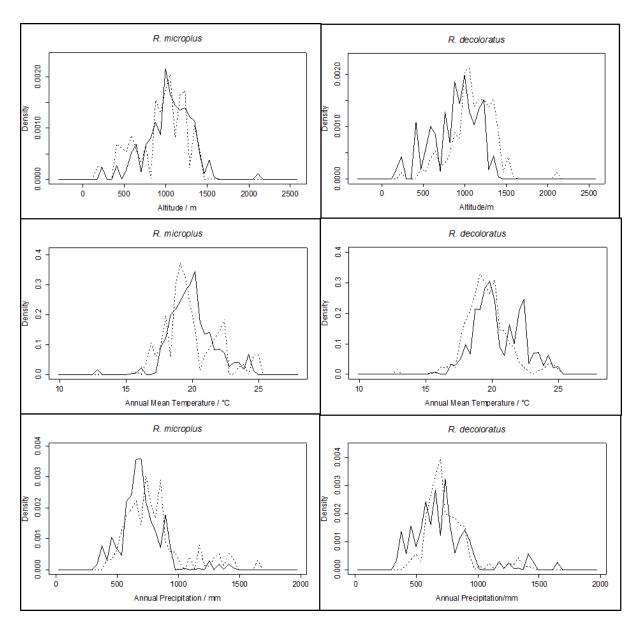


Figure 4. Probability density distributions of altitude, annual mean temperature and annual precipitation with respect to the presence (dashed line) and absence (continuous line) of *R. microplus* and *R. decoloratus* in Zimbabwe.

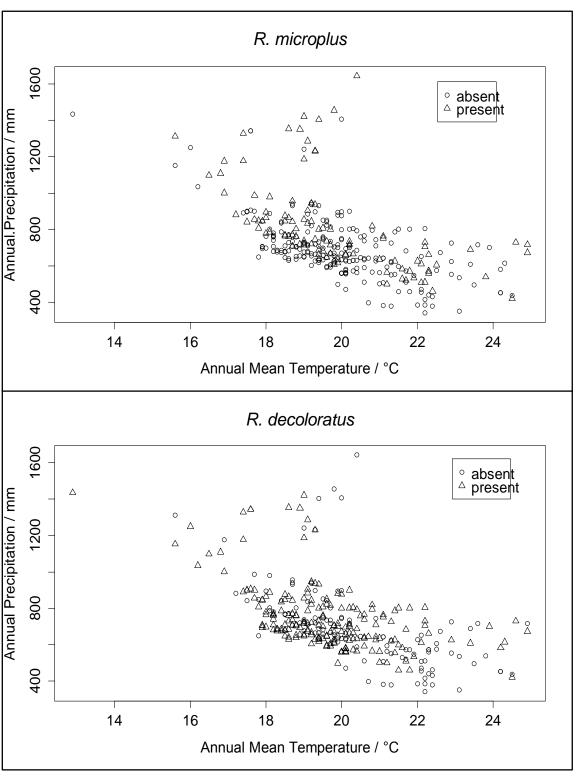


Figure 5. Bi-plot showing annual mean temperature and annual precipitation with respect to presence or absence of *R. microplus* and *R. decoloratus* in Zimbabwe

modelling the distribution of boophilid ticks in Zimbabwe using these recent records. This information is vital to disease control authorities as it will help in the monitoring of the more pathogenic *B. bovis* infections.

In ixodid ticks, development and mortality rates are governed by temperature and water availability, respectively (Estrada-Peña et al., 2015). Correlative modelling, which was used to develop the habitat suitability maps in this study, does not allow examining the specific role played by each climatic variable on the tick developmental stages (Estrada-Peña et al, 2015). However, patterns are observed which relate to the development and survival of the different life cycle stages of these one-host ticks and these will be discussed. R. microplus, as well as R. decoloratus, are one-host ticks with multiple generations in a year (Walker et al., 2003). Temperature and precipitation variability throughout the year have important implications on the survival of off-host stages. Field studies carried out in Zimbabwe indicated that all developmental stages of both ticks varied, being short, intermediate and longest during the hot, wet and cool seasons, respectively (Short et al., 1989b). Diurnal temperature range refers to fluctuations in temperature which will affect tick development and activity on a regional basis with day length accentuating the effects of temperature (James et al., 2015). Tick immature stage development and seasonal activity are influenced by stability in temperature and moisture while extremes of temperature and moisture will influence egg and larvae survival. In field studies to determine the behaviour and survival of unfed ticks Short et al. (1989a) observed that the survival times of R. microplus, R. decoloratus and R. appendiculatus larvae were influenced by low temperature stress in June/July (winter) and high temperature stress in September/October (hot dry season). Thus minimum temperature of the coldest quarter will have an influence on larval development as it has been observed in South Africa where *R. microplus* larvae were found in vegetation during the winter whilst those of *R. decoloratus* seemed to disappear (Nyangiwe *et al.*, 2011). There is a positive correlation between precipitation and humidity, which is vital for tick survival (Needham and Teel, 1991), especially for ixodid ticks (Randolph and Storey, 1999).

The variables used in this study represent annual trends and seasonality as well as extreme environmental factors of temperature and precipitation (Estrada-Peña et al., 2013). For *R. microplus*, the variables which had the greatest influence on the model were altitude, minimum temperature of the coldest month, mean diurnal range, temperature seasonality, mean NDVI, precipitation of the warmest quarter and precipitation of the wettest quarter. The variables which had the greatest influence on the model for R. decoloratus were altitude, precipitation of the wettest month, annual precipitation, mean temperature of the driest quarter and precipitation seasonality. Variability in temperature and precipitation has been observed to drive the distribution of other Ixodidae tick species studied (Hahn et al., 2016, James et al., 2015, Johnson et al., 2016). Annual mean NDVI seemed not to influence the occurrence of R. decoloratus despite its being considered a proxy for water availability which is key to the survival of ticks. In both species, altitude had the greatest contribution to the models, which confirms earlier studies listing altitude as the best single predictor for use in estimating tick distributions (Cumming, 2002). For illustration purposes, we add a map of altitude in Zimbabwe in Figure 6.

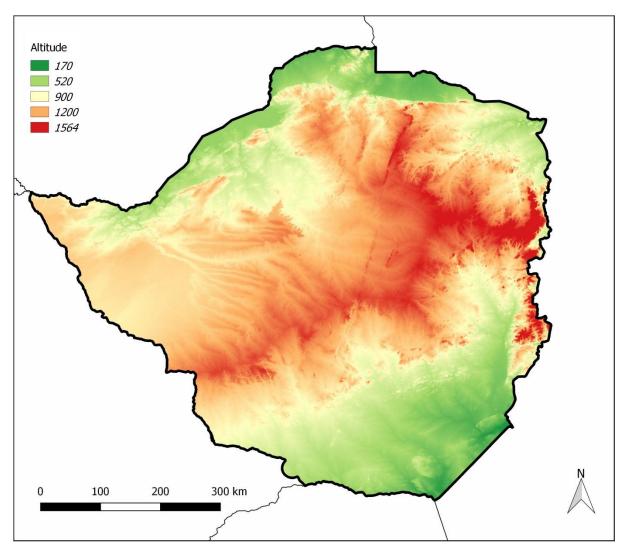


Figure 6. Map of Altitude (m) based on WorldClim data.

Looking at the average conditions of temperature and rainfall (annual trends), they appear largely the same for both species while extremes influenced the occurrence of the two species. High and low temperatures favoured *R. microplus* and *R. decoloratus*, respectively. The same trend was observed for rainfall where high extremes favoured the occurrence of *R. microplus* whilst low extremes favoured the occurrence of *R. decoloratus*. Similar observations were made in Tanzania by Lynen *et al.* (2008) when they compared the distributional ranges of *R. decoloratus* and *R. microplus*.

Comparing with earlier modelling papers, the distribution of *R. microplus* seemed to have expanded with more occurrences of the tick in the Zambezi Valley near Lake Kariba in the north-western parts of the country. The patchy and discontinuous distribution of *R. microplus* shows that this tick species has established in the east, and the north-eastern parts of the country, in the south-east Lowveld region as well as the environment around Lake Kariba. During the nationwide survey described by Sungirai et al. (2017), R. microplus was found for the first time in this area when compared to previous studies (Norval et al., 1983; Katsande et al., 1996). The water from the lake does provide the essential humid conditions for the proliferation of these two tick species in the surrounding environment. From the model, there are areas where it is postulated that R. microplus and R. decoloratus will co-exist. The reasons for the continuous co-existence of R. decoloratus with R. microplus have been described by Sungirai et al. (2017): Persistent droughts may lead to temporary disappearance of R. microplus hindering its permanent establishment and subsequent displacement of R. decoloratus (Norval et al., 1983). Also tick control practises, where R. decoloratus has been found to be more refractive to acaricides (Baker *et al.*, 1981, Mason and Norval, 1980), and adaptability of *R. decoloratus* to wildlife (Sutherst, 1987) may provide *R. decoloratus* with a competitive advantage. The introduction of *R. microplus* as well as the temporary disappearance and emergence may have influence on the epidemiology of *Babesia bovis*. Norval *et al.* (1983) found out that in areas where *R. microplus* had been recently introduced there was no endemic stability for babesiosis, which existed in areas where the tick species appeared to be established.

The model output indicates that the habitat suitability of *R. microplus* in Zimbabwe continues to be restricted, having a patchy and discontinuous distribution. *R. decoloratus* still has a wider distribution in the country with very few areas of coexistence between the two species and possible displacement of *R. decoloratus* in areas highly suitable for *R. microplus*. These results suggest that *R. microplus* is not expected to survive in most parts of the country in the event of spread into new areas, for example by cattle movement. The Zambezi Valley might not entirely be suitable for this tick except for areas close to the lake which might provide appropriate humidity conditions for the survival of the tick species. Surveys in the southern province of Zambia did not confirm the presence of *R. microplus* (Speybroeck *et al.*, 2002). It might be important to resample areas in the southern province of Zambia as well to check if *R. microplus* occurs near the Lake Kariba on the Zambian side.

5. Conclusion

Although other factors could influence the distribution of these two tick species, such as host abundance and tick control practises, models have been produced which seek to explain the limitations in as far as the spread of these ticks is concerned. From the models, the distribution of the invasive tick *R. microplus* is expected to be patchy and discontinuous being found in climatically suitable areas. The tick *R. microplus* was collected in areas which are not environmentally suitable for its development and survival and this may influence the epidemiology of *Babesia bovis* in these areas. There are areas where the two tick species *R. microplus* and *R. decoloratus* are expected to co-exist and there is need to study the population dynamics of these two species in these areas.

Conflict of Interest

Authors declare that there are no conflicts of interest.

Acknowledgements

The authors would like to acknowledge the financial support by the Belgian Department of Development Co-operation (DGD).

Bibliography

Baker, J.A.F., Jordaan, J.O., Robertson, W.D., 1981. Comparison of the resistance spectra to Ixodicides of *Boophilus decoloratus* (Koch) and *Boophilus microplus* (Canestrini) in the Republic of South Africa and Transkei. In Tick biology and control: proceedings of an International Conference January 27-29, 1981/edited by GB Whitehead and JD Gibson. Grahamstown, South Africa: Tick Research Unit, Rhodes University.], 27-29.

- Barrè, N., Uilenberg, G., 2010. Spread of parasites transported with their hosts: case study of two species of cattle tick. Rev Sci Tech 29, 149-47.
- Berkvens, D.L., Geysen, D.M., Chaka, G., Madder, M., Brandt, J.R., 1998. A survey of the ixodid ticks parasitising cattle in the Eastern province of Zambia. Med. Vet. Entomol. 12, 234-240.
- Cumming, G.S., 2002. Comparing climate and vegetation as limiting factors for species ranges of African ticks. Ecology 83, 255-268.
- Cumming, G., 1999. The evolutionary ecology of African ticks. PhD thesis. University of Oxford.
- De Clercq, E.M., Estrada-Peña, A., Adehan, S., Madder, M., Vanwambeke, S.O., 2013. An update on the distribution models for *Rhipicephalus microplus* in West Africa. Geospat Health 8, 301-308.
- De Clercq, E.M., Leta, S., Estrada-Peña, A., Madder, M., Adehan, S., Vanwambeke, S.O., 2015. Species distribution modelling for *Rhipicephalus microplus* (Acari: Ixodidae) in Benin, West Africa: comparing datasets and modelling algorithms. Prev. Vet. Med. 118, 8-21.
- De Clercq, E.M., Vanwambeke, S.O., Sungirai, M., Adehan, S., Lokossou, R., Madder, M., 2012. Geographic distribution of the invasive cattle tick *Rhipicephalus microplus*, a country-wide survey in Benin. Exp. Appl. Acarol 58, 441-452.
- Estrada-Peña, A., 1999. Geostatistics and remote sensing using NOAA-AVHRR satellite imagery as predictive tools in tick distribution and habitat suitability estimations for *Boophilus microplus* (Acari: Ixodidae) in South America. National Oceanographic and Atmosphere Administration-Advanced Very High Resolution Radiometer. Vet. Parasitol. 81, 73-82.

- Estrada-Peña, A., Bouattour, A., Camicas, J.L., Guglielmone, A., Horak, I., Jongejan, F., Latif, A., Pegram, R., Walker, A.R., 2006a. The known distribution and ecological preferences of the tick subgenus *Boophilus* (Acari: Ixodidae) in Africa and Latin America. Exp. Appl. Acarol, 38, 219-235.
- Estrada-Peña, A., García, Z. and Sánchez, H.F., 2006b. The distribution and ecological preferences of *Boophilus microplus* (Acari: Ixodidae) in Mexico. Exp. Appl. Acarol, 38(4), 307-316.
- Estrada-Peña, A., 2008. Climate, niche, ticks, and models: what they are and how we should interpret them. Parasitol. Res. 103, 87-95.
- Estrada-Peña, A., Estrada-Sánchez, A., Estrada-Sánchez, D., de la Fuente, J., 2013. Assessing the effects of variables and background selection on the capture of the tick climate niche. Int J Health Geogr, 12(1).,43-48.
- Estrada-Peña, A., de la Fuente, J., Latapia, T., Ortega, C., 2015. The impact of climate trends on a tick affecting public health: a retrospective modeling approach for *Hyalomma marginatum* (Ixodidae). PLoS ONE, 10(5), p.e0125760.
- Gambiza, J., Nyama, C., 2000. Country pasture/forage resource profiles. Country profiles, Zimbabwe. Food and Agriculture Organization of the United Nations 4.
- Giles, J.R., Peterson, A.T., Busch, J.D., Olafson, P.U., Scoles, G.A., Davey, R.B., Pound, J.M., Kammlah, D.M., Lohmeyer, K.H., Wagner, D.M., 2014. Invasive potential of cattle fever ticks in the southern United States. Parasit Vectors 7.
- Hahn, M.B., Jarnevich, C.S., Monaghan, A.J., Eisen, R.J., 2016. Modeling the Geographic Distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the Contiguous United States. J. Med. Entomol. 53, 1176-1191.

- Hijmans, R.J., Cameron, S., Parra, J., Jones, P., Jarvis, A., Richardson, K., 2005. WorldClim, version 1.3. University of California, Berkeley.
- Hijmans, R.J., Elith, J., 2016. Species distribution modeling with R. In. https://cran.r-project.org/web/packages/dismo/vignettes/sdm.pdf.
- Hirzel, A.H., Le Lay, G.I., Helfer, V.Ã., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199, 142-152.
- James, A.M., Burdett, C., McCool, M.J., Fox, A., Riggs, P., 2015. The geographic distribution and ecological preferences of the American dog tick, *Dermacentor variabilis* (Say), in the USA. Med. Vet. Entomol., 29(2), 178-188.
- Johnson, T.L., Bjork, J.K.H., Neitzel, D.F., Dorr, F.M., Schiffman, E.K., Eisen, R.J., 2016. Habitat suitability model for the distribution of *Ixodes scapularis* (Acari: Ixodidae) in Minnesota. J. Med. Entomol., 53(3)., 598-606.
- Justice, C.O., Vermote, E., Townshend, J.R., Defries, R., Roy, D.P., Hall, D.K., Salomonson, V.V., Privette, J.L., Riggs, G., Strahler, A., 1998. The Moderate Resolution Imaging Spectroradiometer (MODIS): Land remote sensing for global change research. IEEE Trans Geosci Remote Sens 36, 1228-1249.
- Katsande, T.S., Mazhowu Turton, J.A., Munodzana, D., 1996. *Babesia bovis* case reports and the current distribution of *Boophilus microplus* in Zimbabwe. Zim. Vet. Journ. 27, 33-36.
- Lynen, G., Zeman, P., Bakuname, C., Di, G.G., Mtui, P., Sanka, P., Jongejan, F., 2008. Shifts in the distributional ranges of *Boophilus* ticks in Tanzania: evidence that a parapatric boundary between *Boophilus microplus* and *B. decoloratus* follows climate gradients. Exp. Appl. Acarol 44, 147-164.

- Madder M, Thys E, Achi L, Touré A, De Deken R, 2011. *Rhipicephalus (Boophilus) microplus*: a most successful invasive tick species in West-Africa. Exp Appl

 Acar 53, 139-145.
- Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921-931.
- Mason, C.A., Norval, R.A.I., 1980. The ticks of Zimbabwe. I. The genus *Boophilus*. Zim. Vet. Journ. 11, 36-43.
- Needham, G.R., Teel, P.D., 1991. Off-host physiological ecology of ixodid ticks.
- Annu. Rev. Entomol., 36(1), 659-681.
- Norval, R.A., Perry, B.D., Meltzer, M.I., Kruska, R.L., Booth, T.H, 1994. Factors affecting the distributions of the ticks *Amblyomma hebraeum* and *A. variegatum* in Zimbabwe: implications of reduced acaricide usage. Exp. Appl. Acarol 18, 383–407.
- Norval, R.A., Perry, B.D., Hargreaves, S.K., 1992. Tick and tick-borne disease control in Zimbabwe: what might the future hold. Zim. Vet. Journ. 23, 1-15.
- Norval, R.A.I., Fivaz, B.H., Lawrence, J.A., Daillecourt, T., 1983. Epidemiology of tick-borne diseases of cattle in Zimbabwe. I. Babesiosis. Trop Anim Health Prod, 15(2), 87-94.
- Nyangiwe, N., Goni, S., Hervé-Claude, L.P., Ruddat, I., Horak, I.G., 2011. Ticks on pastures and on two breeds of cattle in the Eastern Cape province, South Africa. Onderstepoort J. Vet. Res., 78(1), 1-9.
- Nyangiwe, N., Harrison, A., Horak, I.G., 2013. Displacement of *Rhipicephalus decoloratus* by *Rhipicephalus microplus* (Acari: Ixodidae) in the Eastern Cape Province, South Africa. Exp. Appl. Acarol 61, 371-382.

- Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225-245.
- QGIS Development Team, 2013. QGIS geographic information system. Open Source Geospatial Foundation Project http://qgis. osgeo. org.
- R Development Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. In: Vienna, Austria.
- Randolph, S.E., 2010. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. Parasitology 129, S37-S65.
- Randolph, S.E., Storey, K., 1999. Impact of microclimate on immature tick-rodent host interactions (Acari: Ixodidae): implications for parasite transmission. J. Med. Entomol., 36(6), 741-748.
- Short, N.J., Floyd, R.B., Norval, R.A.I., Sutherst, R.W., 1989a. Development rates, fecundity and survival of developmental stages of the ticks *Rhipicephalus* appendiculatus, *Boophilus decoloratus* and *B. microplus* under field conditions in Zimbabwe. Exp. Appl. Acarol, 6(2), 123-141.
- Short, N.J., Floyd, R.B., Norval, R.A.I., Sutherst, R.W., 1989b. Survival and behaviour of unfed stages of the ticks *Rhipicephalus appendiculatus*, *Boophilus decoloratus* and *B. microplus* under field conditions in Zimbabwe. Exp. Appl. Acarol, 6(3), 215-236.
- Speybroeck, N., Madder, M., Van Den Bossche, P., Mtambo, J., Berkvens, N., Chaka, G., Mulumba, M., Brandt, J., Tirry, L., Berkvens, D., 2002. Distribution and phenology of ixodid ticks in southern Zambia. Med. Vet. Entomol. 16, 430-441.

- Sungirai, M., Abatih, E.N., Moyo, D.Z., De Clercq, P., Madder, M., 2017. Shifts in the distribution of ixodid ticks parasitizing cattle in Zimbabwe. Med. Vet. Entomol. 31, 78-87.
- Sutherst, R.W., Maywald, G.F., 1985. A computerised system for matching climates in ecology. Agriculture, Ecosyst. Environ, 13(3-4), 281-299.
- Sutherst, R.W., 1987. The dynamics of hybrid zones between tick (Acari) species.

 Int. J. Parasitol., 17(4), 921-926.
- Thrusfield, M., 2005. Veterinary Epidemiology, 3rd edn. Blackwell Publishing Company, Oxford, pp 233.
- Tønnesen, M.H., Penzhorn, B.L., Bryson, N.R., Stoltsz, W.H., Masibigiri, T., 2004.

 Displacement of *Boophilus decoloratus* by *Boophilus microplus* in the Soutpansberg region, Limpopo Province, South Africa. Exp. Appl. Acarol., 32, 199-208.
- Walker, A.R., Bouattour, A., Camicas, L., Estrada-Peña, A., Horak, I.G., Latif, A.A., Pegram, P.G., Preston, P.M., 2003. Ticks of Domestic Animals in Africa: a Guide to Identification of Species. Bioscience Reports, Edinburgh, pp 149-161.
- Wang, H.-H., Corson, M. S., W. E. Grant, Teel, P. D., 2017. Quantitative models of *Rhipicephalus (Boophilus)* ticks: historical review and synthesis. Ecosphere 8(9):e01942. 10.1002/ecs2.1942
- Wilson, A., 1996. Appropriate Strategies for the Control or Eradication of Ticks and Tick Borne Diseases. Ann N Y Acad Sci., 791, 54-63.