Changes in climate and habitat suitability for the cattle tick *Boophilus microplus* in its southern Neotropical distribution range

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ABSTRACT: We addressed the possible effects of several climate scenarios on habitat suitability (HS) for the cattle tick *Boophilus microplus* and the probability of producing permanent populations from introduced females of that tick in central parts of Argentina, using both a correlative model (derived from climate predictors) and a mechanistic (life cycle) model. There was high correlation ($R^2 = 0.866$) between HS-derived and life cycle outputs for HS values higher than 0.52, suggesting that HS is a good estimator of the life cycle of the tick above a critical threshold of HS values. Scenarios with increased temperatures increased suitable habitats for the tick in southern parts of the study region, extending below parallel 34º S, but suitable habitats remained limited in the west. A concurrent increase in rainfall produced a further increase of HS in these areas. Results from the life cycle model suggest that in areas of suitable habitat, permanent cattle tick populations are most probable if engorged females are introduced during mid-summer. *Journal of Vector Ecology* 31 (1): 158-167. 2006.

Keyword Index: *Boophilus microplus*, climate scenarios, habitat suitability, Argentina, models.

INTRODUCTION

Approximately 1 billion cattle, most of which live in the tropics, are at risk from various tick species or tick-borne diseases (Pegram et al. 1993) that can cause significant production losses. The cattle tick *Boophilus microplus* is a serious pest of cattle in various tropical and subtropical regions of Africa, Latin America, and Australia. It represents one of the main constraints on cattle production due to its direct parasitic action and its role as a vector of important pathogens. A closely related tick species, *B. annulatus*, also serves in this role but in the New World remains restricted to certain areas of Mexico. Parasitism by cattle ticks, *B. annulatus* and *B. microplus*, results in poor condition, weight loss, reduced meat and milk production, and potential transmission of *Babesia* spp., which causes an often fatal disease.

Studies have been undertaken to understand the factors governing tick distribution. The presence of suitable hosts is a necessary but not sufficient condition for tick presence; rather, climate is the most important factor driving tick presence/absence (Cumming 2002). This reasoning supports the idea that ecological niches of tick species represent long-term stable constraints on geographic distribution potential. Models developed using ecological-niche modelling techniques provide an adequate predictive basis for understanding species’ ecological niches based on climate alone. Thus, the potential of species to disperse to regions other than their native ranges can be predicted by observing the conditions that define the ecological niches of species in those regions. However, ecological-niche models assess only one step of a complex phenomenon that includes introduction and establishment of non-native populations, appropriateness of the landscape for the invader, and population spread across the landscape.

Models used to predict species’ potential distribution have been described as either correlative or mechanistic. Correlative models rely on strong, often indirect, links among species distribution records and environmental predictor variables to make predictions (Beerling et al. 1995). These models use values of a predictor variable (more commonly a set of predictor variables) associated with distribution records to classify the predictor variable hyperspace into presence-absence regions, suitability values, or probabilities (Robertson et al. 2003). Mechanistic models attempt to simulate the mechanisms considered to underlie observed correlations with environmental attributes by using a detailed representation of the physiological responses of the target species, as well as life-history attributes (Stephenson 1998). Predictive models generally have been used to predict the potential distribution of a target species under current climate conditions or various climate change scenarios and to determine the importance of selected climatic variables on the distribution of the target species. Correlative models are particularly well suited to cases where an initial estimate of potential distribution of an organism is required. After this initial estimation, mechanistic models, commonly computer-intensive, often can generate predictions at smaller temporal and spatial scales.

Previous studies have modelled the life cycle of the cattle tick using both methods. Spatial modelling of habitat suitability for *B. microplus* has been performed using remote
sensing (Estrada-Peña 1999), while accurate life-cycle models have been used to understand interactions among habitat type, host cattle, and cattle tick populations (Corson et al. 2004, Teel et al. 1998). A previous, retrospective study about climate change in the Americas and its effects on the ecological niche of the tick emphasized the potential for reintroduction of this parasite into central Argentina (Estrada-Peña et al. 2005). A long-term trend toward warmer winters has been detected in this region, as well as short-term (two to four year) increases in winter temperatures. The area currently remains free of the parasite due to strict chemical control of animals entering the region and its cold climate. However, if chemical control is relaxed or the climate trend continues, the possibility exists of reintroducing the parasite into new sites where the climate was previously too cold to support permanent populations.

This paper focuses on the expected effects of several climate change scenarios on the distribution and probability of producing permanent populations of the tick *B. microplus* in central Argentina. As the main host of the tick is abundant in the target region, it addresses explicitly the response of the tick to several climate scenarios and then produces a realistic overview of the possibilities that permanent populations of the tick could persist. Animal health authorities may then use this output as an additional tool in control of the tick.

**MATERIALS AND METHODS**

**Tick records**

An historical dataset of the distribution of the tick in the Neotropics was previously compiled by one of the authors (A.G.) and published (ICTTD, 2004). Distribution data recorded between 1970 and 2000 were selected from this dataset, and from this subset, 1,484 records could be adequately georeferenced. Although this study is spatially restricted to Argentina, where the tick has been eradicated below 30° S, the selected tick records cover the entire Neotropics (Figure 1).

**Climate data**

The database of tick records has been checked against a spatially and temporally extensive gridded climate dataset that extends from 1960-1999, interpolated at a resolution of 2.5 km (available at http://biogeo.berkeley.edu). This dataset contains monthly records of temperature (mean, minimum, and maximum) and precipitation (monthly total). From this basic set of climate variables, a further set of 19 variables was derived and used for predictive mapping. These variables were 1: Annual Mean Temperature, 2: Mean Diurnal Range (Mean of monthly (max temp - min temp)), 3: Isothermality (2/7*100), 4: Temperature Seasonality (standard deviation *100), 5: Max Temperature of Warmest Month, 6: Min Temperature of Coldest Month, 7: Temperature Annual Range (5-6), 8: Mean Temperature of Wettest Quarter, 9: Mean Temperature of Driest Quarter, 10: Mean Temperature of Warmest Quarter, 11: Mean Temperature of Coldest Quarter, 12: Annual Precipitation, 13: Precipitation of Wettest Quarter, 14: Precipitation of Driest Month, 15: Precipitation Seasonality (Coefficient of Variation), 16: Precipitation of Wettest Quarter, 17: Precipitation of Driest Quarter, 18: Precipitation of Warmest Quarter, 19: Precipitation of Coldest Quarter.

**Model development and testing**

Different methods have been proposed to predict species distributions based on presence data only (correlative models). These methods search for an “environmental envelope” characteristic of the points where the species is present to extrapolate to the remaining area under study (Guisan and Zimmerman 2000). For this study, we used the Gower metric (Carpenter et al. 1993), hereafter referred to as the habitat suitability (HS) model, to estimate habitat (environmental) suitability for the tick species. First, we “trained” the HS model with a randomly selected half (742) of the 1,484 georeferenced records of tick presence in the study region. The HS model correlated each location of tick presence with climate data (i.e., the 19 variables described above) from the nearest location in the climate dataset to estimate an environmental envelope at each point of presence. The predictive accuracy of these envelopes was evaluated with the second half of the dataset. Based on the climate at each location of tick presence in the “evaluation” dataset, the HS model calculated an average multidimensional similarity index between that location and the location in the training dataset with the most similar environmental envelope. The higher the index value (in the range 0-1) the greater the similarity between a point and the set of actual captures in the training set, and thus the greater the suitability of the range of climate values for the tick species. Predictive accuracy of the HS model was estimated with Cohen’s Kappa statistic, a value that indicated the degree by which the HS model correctly predicted tick presence better than that performed by random selection (Segurado and Araújo 2004). The Kappa statistic correlates well with the more computing-intensive Area Under the Receiver Operating Characteristic (AUC) plot (Manel et al. 2001). The value of the Kappa statistic was used as the cut-off threshold for categorizing predictions of habitat suitability into confusion matrices that identified true positives, true negatives, false positives, and false negatives (Segurado and Araújo 2004).

We were interested in obtaining estimates of habitat suitability under different conditions of temperature and rainfall, which in turn produced variations in several of the 19 bioclimatic variables derived. Our approach did not predict environmental conditions for the tick at a given moment in time according to estimates of climate trends. Instead, we prepared different climate scenarios at the same 2.5-km resolution of the original climate dataset and studied their influence on HS for the tick. Thus, we produced new climate datasets by adjusting monthly temperatures by ±1°C and ±2°C and by setting monthly rainfall at 60%, 80%, 120%, and 140% of normal values. This produced a total of 25 scenarios (five temperature and five rainfall patterns, including baselines) to which the HS model was applied.

The correlative model developed using the Gower metric produced an overview of the habitat suitability for the tick. This estimation of HS was a straightforward, quick method...
based on ground estimates of prominent climate predictors. However, this conceptual figure could not adequately predict the probability of a tick population establishing itself permanently at a given point in the study region. To supply an index of tick permanence to compare with values obtained from the HS computation, we also used a mechanistic model describing the dynamics of the tick population to predict if a permanent population could develop from engorged females “imported” to a given site. The life-cycle model of *B. microplus* used herein has been previously published and validated (Corson et al. 2004). It simulates temporal dynamics of populations of the tick species as influenced by factors such as weather, vegetation, and host density (Corson et al. 2004). This model provides greater insight into system processes and their behavior. We explicitly examined the probability of establishing a permanent population of the tick by simulating introduction of a given number of engorged females on different days of the year and correlating this value with the HS rate computed for the same site. Besides providing predictions of population dynamics, this procedure provided good comparison of both modelling strategies, each based on different approaches to the biology of the tick.

We used a grid of 50 x 50 km that covered a region from 57.67° W and 28.5-38.5° S with daily climate interpolated from the previously mentioned datasets. We performed this up-scaling of the climate grid because the mechanistic model required significantly more time to generate predictions than the HS model. Tick dynamics simulated in this model depended greatly not only on climate but also on host density (Corson et al. 2004). To predict the probability of tick permanence we used the following simulation procedure: twenty engorged females were “released” in each cell of the aforementioned grid on day-of-year (DOY) 1 (1 Jan, summer), 90 (31 Mar, autumn), 180 (29 Jun, winter), or 270 (27 Sep, spring) and each cell contained an estimated number of *Bos taurus* cattle. Density of cattle in the region was obtained from the Global Livestock Data Files (available at http://ergodd.zoo.ox.ac.uk/agaagdat/). If a tick population existed at the end of 10 simulated years, it was considered permanent (presence = 1); if not, absent (presence = 0). Due to stochastic cattle movement within a cell, each cell was simulated 10 times for each climate scenario (the same as those used in the HS model). We averaged the 10 presence values for each cell to obtain the final probabilities of establishing permanent tick populations. Under current climate conditions, results obtained for DOY 1 releases were compared with those of the HS model to find the correlation between the two models’ predictions.

**RESULTS**

Figure 1 shows the actual distribution of *B. microplus* in the area of study according to a compilation of published reports. Predictions of the HS (correlative) model derived from this dataset showed a Cohen’s Kappa of 0.86, a very good agreement between observed and predicted distributions. Figures 2 and 3 display the changes in HS for the different scenarios of temperature and rainfall. Under decreased rainfall, two major effects were predicted: an increase in HS in northeastern parts of the study area (southern Brazil) when temperature decreased and an increase in HS in southeastern portions, extending into latitude 34° S, when temperature increased (Figure 2). Decreased rainfall, however, regulated the effects of temperature: expansion of suitable habitat in both portions of the study area decreased greatly when rainfall fell to 60% of normal, even in the highest temperature (+2°C) scenario.

This situation changed considerably when an increase of rainfall was included in computations (Figure 3). Increased rainfall produced a clear decrease in HS in northeastern parts of the study area. High rainfall (140%) and a decrease in temperature reduced suitable habitat for the tick in Uruguay (the eastern portion of the study area). In contrast, a coupled increase in rainfall and temperature (+2°C) produced the biggest predicted increase of HS in central Argentina. It is interesting to note that the growth of suitable habitat for the tick remained limited to the west at every tested condition of temperature and rainfall. Although some patches with adequate HS were predicted west of this line (in Santiago del Estero and Tucumán provinces), they comprised only small, spatially limited islands of suitability in northwestern Argentina.

The correlation between results from the mechanistic model started on DOY 1 and the HS estimates with the Gower metric is shown in Figure 4. Using the complete range of HS values, R² equalled 0.544; however, when only HS values in the range 0.5-1.0 were considered, R² rose to 0.834. Values of HS below 0.52 were consistently associated with non-permanent populations produced by engorged females released on DOY 1. Figure 5 shows the predicted probabilities of establishment of permanent populations of the tick obtained with the mechanistic (life cycle) model. As mentioned, application of this model was intended to estimate the temporal effects of climate on life-cycle dynamics. Figures thus display the probability that a permanent tick population resided in a given cell of the grid when engorged females were introduced into the cell on DOY 1, 90, and 270. Introduction of engorged females on DOY 180 (winter) always produced non-permanent populations; data for that time are not shown. Under current temperature and rainfall conditions, probabilities of establishing permanent populations were high for populations introduced on DOY 1 in many cells of the study area (Figure 5, center top). The provinces of Sante Fe and Entre Ríos marked the southern limit of permanent tick populations, while the western limit was located on the eastern portions of Córdoba and Santiago del Estero provinces. These probabilities decreased for DOY 90 and 270 introductions. As expected, decreased temperatures reduced the area available for production of permanent tick populations; permanent populations that had been introduced on DOY 1 and 90 covered areas barely half of those predicted under current temperature conditions (Figure 5). Under increased temperatures, the model predicted that the area available for permanent tick populations would expand greatly in the south (province of Buenos Aires) and west (Córdoba, but not northwest into Santiago del Estero) (Figure 5). As before, the extent of permanent populations from ticks imported on DOY
Figure 1. The recorded (historical) distribution of *B. microplus* in the Neotropics, as used for the current study. The tick is currently eradicated in Argentina below the parallel 30° S. The grey area marks the zone selected to run the mechanistic model.
Figure 2. Changes in habitat suitability (HS) for *B. microplus* under decreased rainfall and variations in temperature. The central figure in the top row illustrates the HS under current climate conditions. From this figure to the right, temperature increases (+1°C and +2°C, respectively). From the central figure to the left, temperature decreases (-1°C and -2°C, respectively). The top row shows current rainfall conditions, while the second and third rows show rainfall of 80% and 60% of current conditions. Levels of HS are proportional to the shades of grey (darker is higher). Grey lines depict provincial borders of Argentina and national borders of Uruguay, Paraguay, and Brazil.
Figure 3. Changes in habitat suitability (HS) for *B. microplus* under increased rainfall and variations in temperature. The central figure in the top row illustrates the HS under current climate conditions. From this figure to the right, temperature increases (+1°C and +2°C, respectively). From the central figure to the left, temperature decreases (-1°C and -2°C, respectively). The top row shows current rainfall conditions, while the second and third rows show rainfall of 120% and 140% of current conditions. Levels of HS are proportional to the shades of grey (darker is higher). Grey lines depict provincial borders of Argentina and national borders of Uruguay, Paraguay, and Brazil.
Figure 4. Regression plot between HS as estimated from the correlative model and the probability of finding permanent populations as computed from the mechanistic model. Two regression lines are included, one for the whole range of HS values ($R^2: 0.559$), the second for the range $HS>0.52$ ($R^2: 0.869$).

The correlative and mechanistic models provided similar predictions of changes in potential $B.\ microplus$ range in the region around central Argentina in response to climate change. Thus, these models appear to capture the major effects of similar factors on $B.\ microplus$ populations, despite their construction at different scales. This study’s results do not prove that the cattle tick will expand into central Argentina in the future, as the results projected here cannot be evaluated until and unless they occur. Besides the abiotic factors thoroughly represented in this study, the relationships between tick and host populations, as well as the land use and chemical treatment of imported cattle, are important factors involved in the possibility of introducing the tick into the study area.

The potential geographic ranges of tick species may be modified on a local scale by the community structure that gives rise to variations in (i) microhabitats and microclimates in which non-parasitic stages of ticks exist, and (ii) densities of tick hosts. The former influences the survival of ticks during non-parasitic phases of the life cycle (Needham and Teel 1991), while the latter influences tick survival by affecting host-finding success, on-host tick mortality rates, and density-dependent regulation of tick populations (Randolph 1994). This study is the first time that output of both types of models has been compared. While the correlative model is easy to compute, it provides only a conceptual estimate of tick habitat. The mechanistic model is more computer intensive but is well correlated with the previous one above a critical threshold of $HS=0.5$. This result points to a positive and strong correlation between the HS estimates and the probability of permanent tick populations introduced on DOY 1. Below this threshold, no populations of $B.\ microplus$ are predicted to inhabit an area permanently after introduction. Within these considerations, it is then possible to compute a fine-scale estimator of tick persistence and project it into the future using climate change scenarios and habitat suitability estimates as surrogates for tick permanence. One possible drawback of the mechanistic model is the prediction of relatively suitable habitats in parts of northern Argentina, where no adequate climate suitability exists. This is likely to be produced by the existence of unambiguous records of the tick in the zone that are not reflecting permanent populations (i.e. moving animals). Because the model looks for the environmental envelope of the set of records, the existence of these few records may bias...
Figure 5. Probabilities of finding permanent populations of *B. microplus* as computed from the mechanistic model under conditions of temperature change. From top to bottom, females are introduced on days 1, 90, and 270 (negative results were obtained always for day 180). Each central figure shows predictions under current temperatures. From these figures to the right, a progressive increase in temperature (+1°C and +2°C, respectively) was simulated. From the central figure to the left, a progressive decrease in temperature (-1°C and -2°C, respectively) was simulated. The probabilities are proportional to the shades of grey (darker is higher).
the preferences of the tick as calculated by the model. The existence of endemic populations of *B. microplus* ticks and the establishment of new populations is constrained by biotic factors (host densities and habitat) and abiotic factors such as climate (Teel et al. 1997). Each of these factors affects tick survival rates, influencing the densities of endemic tick populations and the threshold number of immigrating ticks needed to establish a tick population in a new location. Climate impacts tick survival mostly during non-parasitic periods of the life cycle. Outside certain temperature and rainfall ranges, tick populations cannot survive because these conditions directly kill individual ticks (Ivancovich 1975). Invasion involves two essential stages: transport of organisms to a new locality and establishment and population increase in the invaded locality. A third stage, not considered herein, is regional spread from initial successful populations. There is much evidence that the probability of establishment increases markedly with the arrival rate of a species at a potential invasion site. In the case of the cattle tick and central Argentina, the real danger is introduction of the tick by animals travelling from the endemic region (northern part of the study area) to zones where adequate habitat suitability exists. Under current climate conditions, the chemically-free area (the zone of the country where the tick was eradicated through chemical control) is still susceptible to reinfection. Under adequate conditions of host density, this risk of reintroduction may extend south into latitudes 33-34° S.

Results from the simulations are clear: increasing both temperature and rainfall in central Argentina would shift areas of suitable habitat for *B. microplus* to the south of their current distribution. Decreasing temperature and rainfall would shift them to the north. Results obtained from the HS model agree well with the probabilities of producing permanent tick populations from the mechanistic model. However, the risk of producing permanent populations of the tick changes with the season that engorged females are introduced into an area. Risk is highest in the middle of the summer and clearly smaller in spring and autumn, given the same host density and landscape use. Risk of introduction in winter is null even under the highest temperature (+2° C) and rainfall (140% of current average) conditions tested. Under these extreme conditions, risk of reintroduction may extend south into approximately 34° S if adequate host availability exists.

REFERENCES CITED


