

# Maximum Entropy-Based Ecological Niche Model and Bio-Climatic Determinants of Lone Star Tick (*Amblyomma americanum*) Niche

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## Abstract

The potential distribution of *Amblyomma americanum* ticks in Kansas was modeled using maximum entropy (MaxEnt) approaches based on museum and field-collected species occurrence data. Various bioclimatic variables were used in the model as potentially influential factors affecting the *A. americanum* niche. Following reduction of dimensionality among predictor variables using principal components analysis, which revealed that the first two principal axes explain over 87% of the variance, the model indicated that suitable conditions for this medically important tick species cover a larger area in Kansas than currently believed. Soil moisture, temperature, and precipitation were highly correlated with the first two principal components and were influential factors in the *A. americanum* ecological niche. Assuming that the niche estimated in this study covers the occupied distribution, which needs to be further confirmed by systematic surveys, human exposure to this known disease vector may be considerably under-appreciated in the state.

**Key Words:** Lone star tick—*Amblyomma americanum*—MaxEnt—Climate—Soil moisture—Temperature—Precipitation.

## Introduction

**A**MBLYOMMA AMERICANUM (LINN.) (Acari: Ixodidae), or the lone star tick, is a vector for multiple human and animal pathogens in the United States. The best-known diseases resulting from pathogens transmitted by this tick species include human monocytic ehrlichiosis and human ewingii ehrlichiosis (Centers for Disease Control and Prevention 2015a), tularemia (Centers for Disease Control and Prevention 2015b), southern tick-associated rash illness (STARI) (Centers for Disease Control and Prevention 2015c), and feline cytauxzoonosis (Reichard et al. 2010). Recent studies also identified yet another *A. americanum*-transmitted viral pathogen, Heartland virus from northwestern Missouri, causing a novel emerging disease in people (Savage et al. 2013, Centers for Disease Control and Prevention 2015d). The biology of *A. americanum* and the pathogens that it vectors have been reviewed by Childs and Paddock (2003) and Goddard and Varela-Stokes (2009). *A. americanum*-vectored diseases in humans are mostly endemic to regions where the ticks are known to occur, but the

status of these diseases elsewhere in the United States remain poorly understood. The current geographic extent of *A. americanum* distribution estimated by the United States Centers for Disease Control and Prevention (CDC) covers all of the southeastern and eastern United States, including areas covering a large portion of eastern Kansas ([www.cdc.gov/ticks/maps/lone\\_star\\_tick.html](http://www.cdc.gov/ticks/maps/lone_star_tick.html)). However, a recent article by Springer and colleagues (Springer et al. 2014) indicated a wider but discontinuous distribution pattern for the state and noted some western counties in Kansas that have reported this species over the last century.

Some evidence suggests that the disease agents transmitted by *A. americanum* ticks in Kansas may be increasing (Raghavan et al. 2013, 2014). The spatio-temporal pattern of human monocytic ehrlichiosis, vectored by *A. americanum*, used to be concentrated in the southeastern counties in the state but is now reported commonly from most eastern and many central Kansas counties (Raghavan et al. 2014). Although other factors could influence this trend, such as human or animal movements, better awareness among physicians and patients of tick-borne illnesses, and improved and easy access to

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diagnostic techniques, the potential for *A. americanum*-vectored transmission from increasing abundance and geographic expansion is a concern. The current spatial distribution pattern estimated by the CDC for *A. americanum* in Kansas is based on acarological surveys conducted around 1945 (Bishopp and Trembley 1945), yet much may have changed in the ensuing years. Knowledge of the spatial extent of a vector species distribution is important for management and prevention of diseases that they transmit. One effective approach to understand species distribution is through correlative modeling (Phillips et al. 2006, Estrada-Peña and Venzal 2007).

Diverse methods have been developed for modeling Grinnellian niches of species and estimating their geographic distributions (Soberón 2007, Soberón and Nakamura 2009). Modeling approaches such as climate envelopes, logistic regression, multivariate regression splines, and boosted regression trees require absence data for modeling, but such data are difficult to obtain and may also be unreliable (Elith et al. 2006, Phillips et al. 2006). Other approaches such as the genetic algorithm for rule-set production (GARP) and maximum entropy (MaxEnt) do not require species absence data and have been used to model ecological niches and estimate potential distributions of a wide variety of species. Inclusion of species absence data, however, yields better information about prevalence than presence-only methods (Elith et al. 2009); such information is incorporated in GARP and MaxEnt methods as background or pseudo-absence data (Phillips and Dudik 2008, Stockwell 2009). The quality of predictions based on different modeling approaches and their interpretation has been discussed previously (Phillips et al. 2004, Peterson et al. 2007). Some studies have shown MaxEnt to produce consistently robust species distribution estimates among presence-only methods (Tsoar et al. 2007, Elith et al. 2009, Fera-Arroyo et al. 2014).

The spatial distribution of most arthropods, including *A. americanum* ticks, are limited for the most part by climatic conditions and physical environment, such as landscape cover and landscape structure. Other influential factors that limit species' distributions include ecological forces such as predator availability and density, competition, and host abundance, which are difficult to incorporate in correlative models (Thuiller et al. 2006, Soberón and Nakamura 2009). In this study, we modeled the ecological niche of *A. americanum* in Kansas using a maximum entropy approach and evaluated important bioclimatic and physical environment determinants of that niche.

## Materials and Methods

### Species distribution data

Lone star ticks are widely present in the eastern, southeastern, and midwestern United States (Childs and Paddock 2003). Species distribution data were obtained from three sources. The Walter Reed Biosystematics Unit (WRBU), based in the Smithsonian Institution, made available historical collection data, which included presence records from across the species' range in North America. The Kansas State University Museum of Entomological and Prairie Arthropod Research (MEPAR) provided tick collection data from 1982 to 1995. Taxonomic label data in this collection were reviewed, and records with discernable textual location information were georeferenced using the MaNIS georeferencing

calculator (<http://manisnet.org/search.shtml>). Only records that had an error radius of  $\leq 1$  km were used in analyses. Finally, we conducted tick surveys in central and eastern Kansas during May through August of 2012–2014. The presence of larval, nymphal, and both sexes of adult stages of *A. americanum* ticks in a given survey location was considered to indicate species presence in this study. In total, there were 461, 107, and 258 unique presence locations obtained from WRBU, MEPAR, and tick surveys, respectively. Counties in which *A. americanum* ticks were positively identified in the three data sources are shown in Figure 1. Duplicate presence locations within 1 km were removed to avoid redundancy; presence records were rarefied whenever clusters of points were noted by removing minimum necessary points until they were  $\geq 2$  km apart. These steps resulted in 682 unique presence records for modeling.

### Environmental variables

Environmental variables summarizing aspects of climate were prepared to summarize important potential drivers of the *A. americanum* ecological niche. That is, summaries of temperature, precipitation, and soil moisture index were obtained from the CliMond archive (Kriticos et al. 2012). CliMond contains gridded historical climate data at 10' or 30' resolution collectively, representing a statistical summary of temperature, precipitation, radiation, and soil moisture, primarily using historical data sourced from WorldClim (Hijmans et al. 2005) and Climate Research Unit datasets ([www.cru.uea.ac.uk/cru/data/hrng/](http://www.cru.uea.ac.uk/cru/data/hrng/)). We used CliMond as our source for climate data instead of WorldClim, which is used more frequently by others, because the latter does not include data on soil moisture estimates that are ecologically relevant in the *A. americanum* life cycle.

High correlations among independent climatic variables are well known and their simultaneous presence in MaxEnt models has been shown to cause problems. To address this concern, *a priori* selection of variables (Medley 2010, Tonini et al. 2014) was carried out using the Band Collection Statistics tool in ArcGIS 10.1 to exclude pairs of highly correlated variables ( $r > 0.8$ ). Dimensionality among independent variables was reduced by conducting principal component analysis using SPSS version 18 (IBM Corporation, Somers, NY), which yields uncorrelated axes of variance, or principal components. Principal components analysis was conducted by extracting climate and habitat data from 10,000 random points across the study area. The corresponding values were standardized such that each variable had a zero mean and standard deviation of 1. Data layers representing principal components were then used for modeling species distribution, and variable loading scores were used to interpret the importance of different variables to each factor, and ultimately *A. americanum* niche.

### Niche modeling

We used the maximum entropy algorithm MaxEnt version 3.3.3k for modeling the ecological niche of *A. americanum*. A statistical explanation of the algorithm is provided in Elith et al. (2011). Briefly, the ecological niche and/or the spatial distribution of a species can be modeled in MaxEnt using correlative algorithms and known point-occurrences of a given species in relation to various environmental constraints.

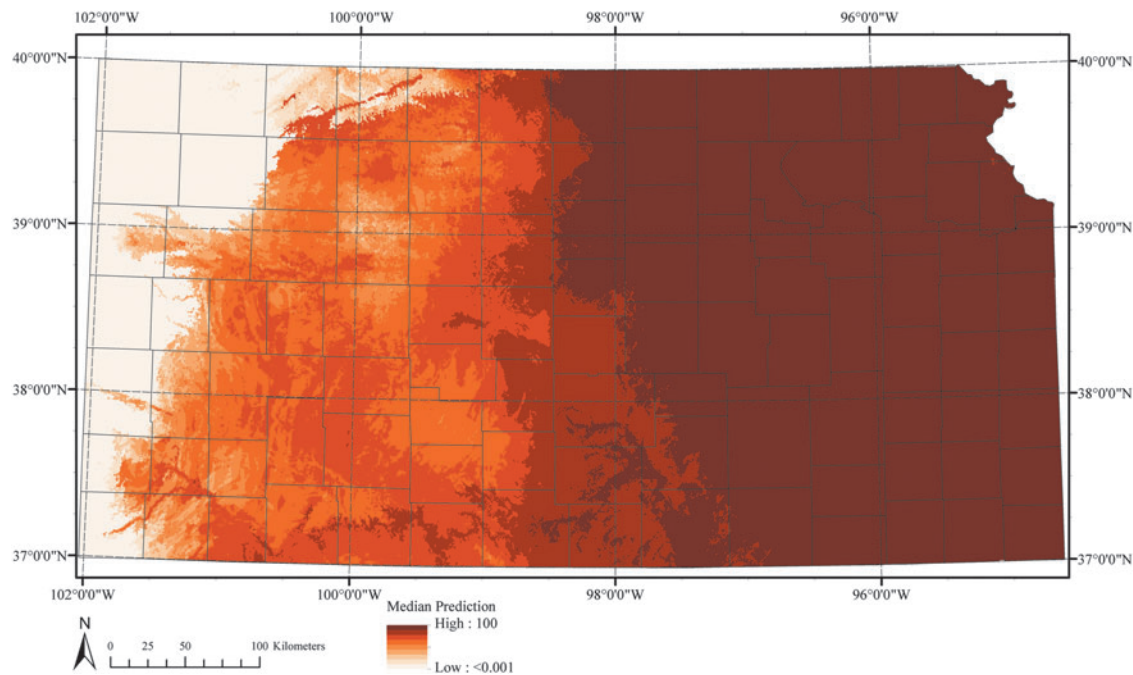


FIG. 1. Abiotically suitable regions for *A. americanum* ticks in Kansas as modeled with MaxEnt.

For this study, models were run mostly with default settings (Phillips et al. 2006), except as following. We set aside 25% of occurrence points for the binary omission rates tests, and the remaining were used to run 20 cross-validation replicates. The advantage of using cross-validation is that it uses all of the data for model building and validation, unlike the single training/test data split. We used the subsampling method in MaxEnt for randomly selecting test data points, and the model was iterated 5000 times to allow sufficient time for model convergence. Two complementary models were run, the first containing climatic variables only and the second with climatic and land cover variables.

We evaluated the model performance using area under the curve (AUC) scores, which is a measure of the area under a receiver operator characteristic curve (ROC) that plots the rate of true positives to false positives. It varies between 0.5 when the result is not better than random and 1.0 when the result is significantly better than random. Another evaluation method based on false negatives (omission error) was also used. MaxEnt calculates the omission error rate for training and test data, which indicates the percentage of test localities that falls into pixels not predicted as suitable for a given species (Phillips et al. 2006). Better models have low or nonsignificant omission rates. The AUC values and standard deviation of the replicated models, and the omission rates at threshold of M10, which have been suggested as an appropriate threshold (Pearson et al. 2006) were used.

## Results

The principal components analysis of independent climatic variables defined an environmental space of reduced dimensionality that allowed modeling the ecological niche of *A. americanum*. The first two axes of the principal components analysis explained 87.9% of the total variance in the data (Table 1) and were significantly different from random

( $p < 0.01$ ). The first principal component, consisting mostly of variables representing soil moisture index and also temperature, explained 61.4% of the variance; the second axis, consisting of variables primarily representing precipitation, explained 26.4% of the variance (Table 1).

The ROC analysis of the resulting MaxEnt models based on all presence data and principal components as predictor variables indicated adequate performance without overfitting to training data (Table 2). When applying the M10 threshold to the cross-validation replicate with highest AUC values (0.84) for the models, they were found to perform significantly better than random ( $p < 0.01$ ), with no records used for modeling falling outside the predicted suitable area. MaxEnt output includes a jackknife analysis of the contribution of each variable to the model (Table 2). Of the two principal components used as predictor variables in the model, the first component contributed most to the model, followed by the second component (Table 2).

On the basis of the average values of the 20 MaxEnt models generated, the median distribution for *A. americanum* using the three principal components as predictor variables is presented in Figure 2. The pixels with highest presence probabilities were concentrated in an east to west gradient, with the eastern region gradually more suitable than the west. Areas predicted to be suitable for this species in the present study covered a visibly larger area in the central and western areas of Kansas than currently estimated by the CDC.

## Discussion

Most attempts to study the distribution and abundance of *A. americanum* and other tick species in Kansas have been made in the more populated eastern and central parts of the state, so few data exist from the western areas. Although MaxEnt and other niche modeling approaches are perhaps capable of predicting species' distributions in unsampled

TABLE 1. VARIABLES AND PRINCIPAL COMPONENT ANALYSIS LOADINGS FOR THE FIRST TWO MAIN AXES

Source	Variable	Factor loadings <sup>a</sup>	
		PC-1	PC-2
CliMond	(Bio01) Annual mean temperature (°C)	<b>-0.75</b>	-0.18
	(Bio02) Mean diurnal temperature range	0.68	-0.24
	(Bio07) Temperature annual range (Bio05-Bio06) (°C)	0.19	0.01
	(Bio11) Mean temperature of coldest quarter (°C)	-0.31	-0.22
	(Bio16) Precipitation of wettest quarter (mm)	0.05	<b>0.82</b>
	(Bio19) Precipitation of coldest quarter	-0.14	<b>0.73</b>
	(Bio28) Annual mean moisture index	-0.51	0.13
	(Bio30) Lowest weekly moisture index	0.48	-0.19
	(Bio32) Mean moisture index of wettest quarter	<b>0.81</b>	0.05
	(Bio35) Mean moisture index of coldest quarter	<b>0.92</b>	-0.01
Eigenvalue		6.24	3.88
% Explained variance		61.42	26.48
Cumulative % variance			87.90

<sup>a</sup>Variables strongly correlated ( $r > 0.7$ ) with the axes are shown in *bold*.

areas, extrapolations based on such spatially biased data should be interpreted with caution (Stockwell and Peterson 2002, Pearson et al. 2007). Presence-only models such as MaxEnt provide a robust and repeatable method for studying species distributions; however, limitations of such methods have been discussed elsewhere (Elith et al. 2011, Karplus 2011, Hijmans 2012). One particular problem with correlative modeling is the accidental introduction of false-positives (localities where species was collected but long-term population establishment is not feasible in such places) and false-negatives (conditions are suitable but the species has not reached due to natural barriers). This issue is also true for other statistical datasets and can be mitigated to a considerable extent through careful evaluation and ground-truthing, which we attempted in this study. The model output for *A. americanum* in this study should not be interpreted as the definitive limits of its range; cell-level occurrence probabilities should be used only as a guide for actual detailed field evaluations of this species' presence and abundance.

Our model indicates that the area suitable for *A. americanum* in Kansas is likely larger than the area currently suggested by the CDC. Particularly, the central and western portions of the state are likely suitable for *A. americanum* (Fig. 2), which is to some extent consistent with Springer et al. (2014), wherein a few western counties in Kansas were highlighted for *A. americanum* presence. That study was based on historic tick collection records covering the entire

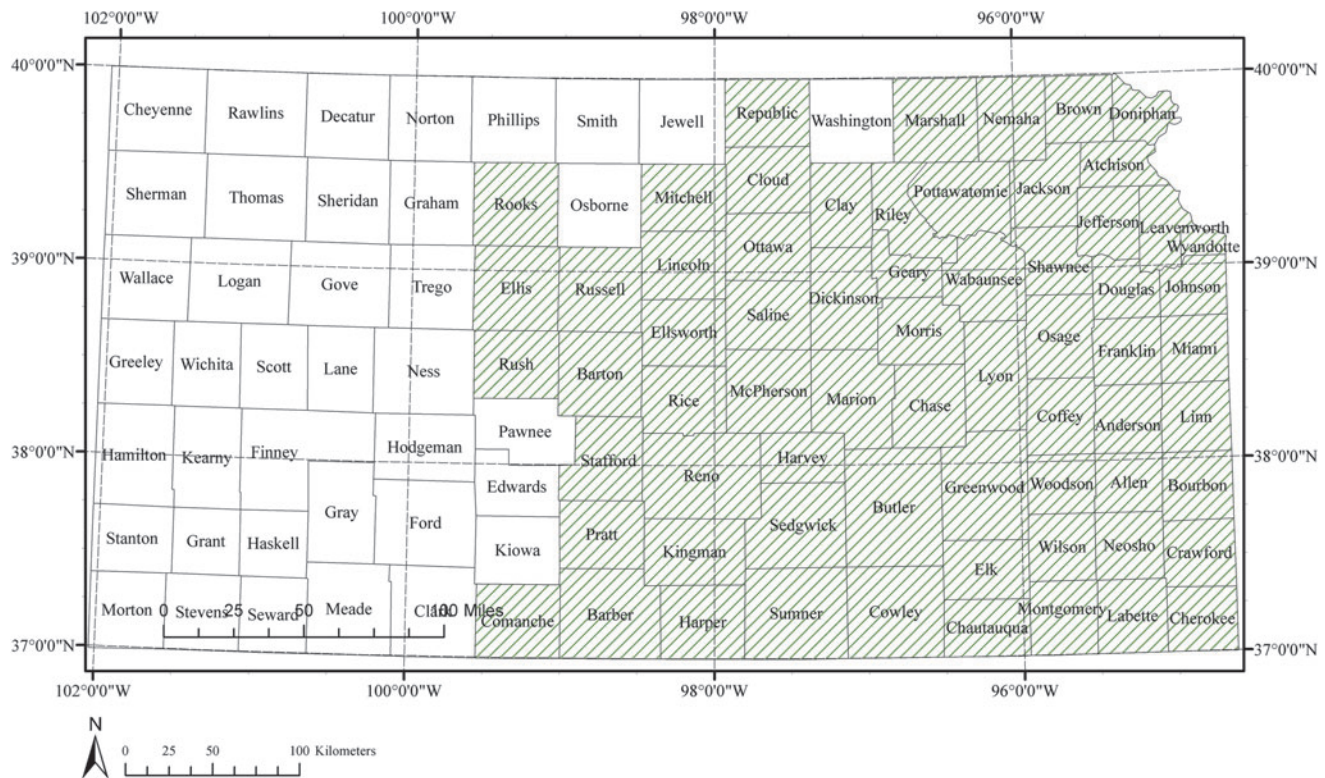
United States for over a century, and although it leaves many central Kansas counties without information, the authors noted that true absence needs confirmation in systematic surveys. The contrast with CDC's distribution map could be a result of many factors, including methods used for distribution modeling and adequacy of presence data used for predictions. The current CDC prediction is based on acarological surveys conducted over a broad region around 1945 (Bishop and Trembley 1945), and the distribution of *A. americanum* has likely changed since that time owing to environmental, climatic, and anthropogenic influences.

The model evaluation criteria used in the study indicated satisfactory performance. Although similar studies evaluating the ecological niche or the spatial distribution for other species have achieved higher AUC values up to and above 0.9, our models consistently performed around 0.8. The significant variables in our models, based on variable associations with the first two axes ( $r > 0.7$ ), were consistent with the biology of *A. americanum* ticks. The first principal component was primarily associated with variables representing soil moisture index and temperature. Soil moisture and temperature are important aspects in tick ecology, and the availability of soil moisture has been suggested as an important factor in characterizing tick habitats (Randolph 2000, Berger et al. 2013). Higher soil moisture content, lower midday temperature, and increased cloud cover are linked to increased questing activity of a similar hard tick, *Ixodes ricinus*

TABLE 2. MODEL RESULTS WITH BIOCLIMATIC DETERMINANTS OF *AMBLYOMMA AMERICANUM* DISTRIBUTION IN KANSAS

Model	Training AUC (mean $\pm$ SD)	Testing AUC (mean $\pm$ SD)	Avg. variable contribution (%)	Jackknife results	
				Avg. AUC without the variable	Avg. AUC with only the variable
Climatic variables	0.87 $\pm$ 0.01	0.82 $\pm$ 0.01			
PC-1			81.81	0.74	0.78
PC-2			19.18	0.79	0.62

AUC, area under the curve; SD, standard deviation; PC, principal component axes.



**FIG. 2.** County-level presence map of *A. americanum* ticks in Kansas. Shaded counties include one or multiple locations where nymph, larvae, and adult stages of *A. americanum* were recorded by one or more presence data source in this study—the Walter Reed Biosystematics Unit, the Prairie Arthropod Research at Kansas State University, and field collections conducted between years 2012 and 2014.

(Medlock et al. 2013). Conditions that negatively affect soil moisture, such as droughts, can result in reduced host-seeking behavior and may increase mortality among quiescent *A. americanum*.

The second component of principal component analysis was associated with precipitation, which could be linked to soil moisture availability, but also may be a proxy for other factors, such as availability of vegetation and host density. Large variations exist in annual rainfall across Kansas, with eastern Kansas receiving up to three times more rainfall than the western portion (Goodin et al. 2004). As a result, climate and vegetation are transitional between the wetter east and semiarid western Kansas, which may explain the relatively higher probability for *A. americanum* habitat suitability in the east versus central and western portions of the state. The normalized difference vegetation index (NDVI) has been suggested, in general, as a better predictor for some tick spatial distributions compared to precipitation variables because it better captures water availability (Randolph 2000, Estrada-Peña et al. 2013). However, precipitation variables may perform adequately for regional studies such as the present one (Estrada-Peña et al. 2013).

The potential for a broader distribution of *A. americanum* ticks in Kansas and the wider region in general is worrisome because of the number of human and animal diseases these ticks are known to vector. A recent study (Raghavan et al. 2014a) has shown a steady spatio-temporal progression of human monocytic ehrlichiosis (HME) in Kansas during years 2005–2012. The spatial distribution noted in that study for a

steady HME spatiotemporal progression has high visible concordance with the predicted distribution for *A. americanum* in the present study. Other diseases vectored by these ticks could also be increasing in the region. The number of cases of feline tularemia (Raghavan et al. 2013) and cytauxzoonosis (Raghavan et al. 2014b) in the region diagnosed at the Kansas State Veterinary Diagnostic Laboratory (KSVDL) have increased steadily over the years, at least partly owing to the wider geographic distribution of *A. americanum*. An important contributing factor for the current distribution of this species in the state and increases in *A. americanum*-vectored diseases could be the almost exponential population increase of their primary host, the white-tailed deer, in Kansas in the past two decades (Paddock and Yabsley 2007, Kansas Department of Wildlife, Parks and Tourism [KDWP] 2015). Studies evaluating nonstationary ecological processes (*e.g.*, changes in climate patterns, landscape fragmentation) that may influence vector–host and as well as vector–human contact rates cannot be found for *A. americanum* ticks and are worthy of consideration.

Finally, ongoing warming of global temperatures will likely influence the ecology and distribution of such medically important ticks. Changes in climatic patterns, including regional increases in temperatures and shifts in precipitation, are altering the structure and function of ecosystems globally (Parmesan and Yohe 2003). These changes can favor emergence of new parasites and new disease agents transmitted by ticks (Epstein 2001, Harvell et al. 2002), and also alter host–parasite relationships (Kutz et al. 2005). Climate conditions

considered typical for the Central Plains region (including Kansas) have already been noted to have changed in noticeable ways (Schoof 2013, Hayhoe et al. 2015), and many such conditions are known to affect tick phenology and spatial distribution either directly or indirectly. For instance, diurnal temperature range, a climate-change index, has been decreasing steadily since the 1950s, particularly in the midwestern United States but also other regions of North America (Karl et al. 1991, 1993). Increased atmospheric humidity during spring and summer months over the Northern Plains was noted for roughly the same time period (Schwartz 1995). Other ixodid ticks (*Ixodes scapularis* and *I. ricinus*) occurring in northern latitudes have already shown shifts in their distribution and abundance that have been linked to warming climate (Daniel et al. 2003, Leighton et al. 2012, Descamps 2013). Any such effect on *A. americanum* distribution in the midwestern United States is yet to be documented and requires further studies.

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### Author Disclosure Statement

No competing financial interests exist.

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