

# Habitat Factors Influencing Distributions of *Anaplasma phagocytophilum* and *Ehrlichia chaffeensis* in the Mississippi Alluvial Valley

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## ABSTRACT

Human monocytotropic ehrlichiosis (HME), caused by the bacterium *Ehrlichia chaffeensis*, and human granulocytic anaplasmosis (HGA), caused by the bacterium *Anaplasma phagocytophilum*, are two emerging tick-borne zoonoses of concern. Factors influencing geographic distributions of these pathogens are not fully understood, especially at varying spatial extents (regional versus landscape) and resolutions (counties versus smaller land units). We used logistic regression to compare influences of physical environment, land cover composition, and landscape heterogeneity on distributions of *A. phagocytophilum* and *E. chaffeensis* at multiple spatial extents. Pathogen presence or absence was determined from white-tailed deer (*Odocoileus virginianus*) serum samples collected from 1981 to 2005. Ecological predictor variables were derived from spatial datasets that represented deer density, elevation, land cover, normalized difference vegetation index (NDVI), hydrology, and soil moisture. We used three strategies (a priori, exploratory, and spatial extent) to develop models. Best fitting models were applied within a geographic information system to create predictive probability surfaces for each bacterium. Ecological predictor variables generally resulted in better fitting models for *E. chaffeensis* than *A. phagocytophilum* (90.5% and 68% sensitivity, respectively), possibly as a result of differences in the natural histories of tick vectors. Although alternative model development strategies produced different models, in all cases bacteria presence or absence was affected by a combination of soil moisture or flooding variables (thought to affect primarily tick vectors) and forest cover or NDVI variables (thought to affect primarily mammalian hosts). This research demonstrates the potential for modeling the distributions of microscopic tick-borne pathogens using coarse regional datasets and emphasizes the importance of forest cover and flooding as environmental constraints, as well as the importance of considering ecological variables at multiple spatial extents. Key words: *Anaplasma phagocytophilum*—*Ehrlichia chaffeensis*—Tick-borne disease—Forest fragmentation—Landscape ecology—Geographic information systems—Mississippi alluvial valley.

## INTRODUCTION

**H**UMAN MONOCYTOTROPIC EHRLICHIOSIS (HME), caused by the bacterium *Ehrlichia chaffeensis*, and human granulocytic anaplasmosis (HGA), caused by the bacterium *Anaplasma phagocytophilum*, are two emerging tick-borne zoonoses of concern. The severity of HME

and HGE varies among individuals and results in the death of 2%–3% of affected patients (McQuiston et al. 2003). Reported HME cases occur mainly in the southeastern and south central United States; HGA cases occur more commonly in the northeastern and upper midwestern United States (Demma et al. 2005).

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The complex zoonotic cycles of bacteria, tick vectors, and mammalian hosts create unique challenges for discerning geographic distributions of these pathogens. The black-legged tick (*Ixodes scapularis*) is a three-host tick and is the primary vector of *A. phagocytophilum* in the eastern United States (Telford et al. 1996). The white-footed mouse (*Peromyscus leucopus*) is its principal host in the eastern United States and is also a competent reservoir for *A. phagocytophilum* (DesVignes and Fish 1997, Magnarelli et al. 1999). The white-tailed deer (*Odocoileus virginianus*) is an important host for adult ticks (Mount et al. 1997). The lone star tick (*Amblyomma americanum*) is the primary vector of *E. chaffeensis* (Anderson et al. 1993). The white-tailed deer is the principal host of the lone star tick and an important reservoir for *E. chaffeensis* (Mount et al. 1993, Dawson et al. 1994). Vector species' distributions are not constant throughout their geographic ranges and are influenced locally by forest fragmentation, temperature, vegetation, and vapor pressure (Estrada-Pena 1998, Schulze et al. 2002, Brownstein et al. 2003, Wilder and Mekle 2004, Ogden et al. 2005). Host availability, host movement, and suitable habitat affect the ability of ticks to establish successful populations at new sites (Wilson 1998, Thomson and Connor 2000, Guerra et al. 2002). Size, shape, isolation, and connectivity of habitat patches also influence host movements and infection rates of ticks and hosts (Allan et al. 2003, Estrada-Pena 2003, Brinkman et al. 2005, Ostfeld et al. 2005).

White-tailed deer are an effective sentinel species for defining geographic distributions of *E. chaffeensis* and *A. phagocytophilum* (Yabsley et al. 2003, Dugan et al. 2006). Spatial analyses of each bacterium based on white-tailed deer serum samples across 18 states predicted pathogen distributions at a county level that had strong correlations with reported human cases of HME and HGA (Dugan 2005, Yabsley et al. 2005). Our study built on existing knowledge of the distributions of *A. phagocytophilum* and *E. chaffeensis* by performing spatial analyses at an increased data resolution (land management units rather than counties) and focusing on a smaller geographical area than previously used (the Mississippi alluvial valley).

The primary objective of our exploratory analysis was to determine the influences of physical environment, land cover composition, and landscape heterogeneity on distributions of *A. phagocytophilum* and *E. chaffeensis*; and to assess how these influences varied at multiple spatial extents. A secondary objective was to assess the potential for mapping risk of exposure to each bacterium for the Mississippi alluvial valley. To accomplish these objectives, we developed several models using logistic regression, and we applied the final models within a geographic information system (GIS) to generate predicted probability surfaces for each pathogen. Multiple hypotheses were developed to consider the effects of ecological predictor variables on pathogen distributions:

- Land cover variables are correlated with pathogen presence through their influence on habitat for tick vectors and mammalian hosts.
- Landscape connectivity is correlated with pathogen presence through its influence on movements of mammalian hosts.
- Soil moisture and flooding are correlated with pathogen presence through their influence on habitat for tick vectors and mammalian hosts.
- The influences of ecological predictor variables vary with the spatial extent used to measure them.

## MATERIALS AND METHODS

### *Study location*

The Mississippi alluvial valley (MAV) encompasses the area bordering the lower Mississippi River that historically received alluvial deposits from frequent flooding (Stanturf et al. 2000, LMVJV 2001). Although the MAV was historically covered by bottomland forests, it is now dominated by agriculture, and the remaining forests are highly fragmented (Rudis 1995). Past studies based on serology of white-tailed deer have found lower prevalences of *A. phagocytophilum* and *E. chaffeensis* within the MAV than in surrounding ecoregions (Yabsley et al. 2003, Dugan et al. 2006). In some instances, deer sampled outside the MAV tested

positive for both bacteria, but neighboring areas of the MAV tested negative, suggesting an isolation effect (Yabsley et al. 2005, Dugan et al. 2006).

#### *Anaplasma phagocytophilum* and *Ehrlichia chaffeensis* database

A surveillance database of serum samples from white-tailed deer in wildlife management areas, national wildlife refuges, national forests, and private lands throughout the MAV was developed for the period 1981–2002 by the Southeastern Cooperative Wildlife Disease Study, University of Georgia, Athens (Yabsley et al. 2003, Dugan et al. 2006). The database consisted of results of an indirect immunofluorescent antibody test of serum for the presence of antibodies reactive to *E. chaffeensis* and *A. phagocytophilum* for each deer population (Lockhart et al. 1996, Yabsley et al. 2003, Dugan et al. 2006). We conducted additional tests of archived serum samples to expand the existing database to include the serostatuses of a total of 65 white-tailed deer populations tested for both *A. phagocytophilum* and *E. chaffeensis*. An additional three populations were tested for *E. chaffeensis*, for a total of 68 populations. Populations were classified as positive if  $\geq 1$  seropositive deer was detected and negative if  $\geq 5$  deer were seronegative according to previously established criteria (Yabsley et al. 2003, Dugan et al. 2006). Sample collection sites (latitude and longitude) were used if available; otherwise, centroids of public land polygons were designated as deer population locations within a GIS.

#### *Logistic regression modeling*

*Explanatory variables.* Ecological predictor variables for logistic regression modeling are described in Table 1. Soil drainage and deer density variables were developed previously (Yabsley et al. 2005). From the spatial analyst extension of ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, CA), a cost distance surface was calculated as a cost-weighted distance from the boundary of the MAV to the sample collection location based on a MAV border from the Lower Mississippi Valley Joint Venture (LMVJV 2001). A forest and non-forest map derived from the 1992 Na-

tional Land Cover Dataset (NLCD) (Vogelmann et al. 1998) was used as the cost raster; each pixel of non-forest represented a greater cost for movement across the landscape, with a score of 1, and each pixel of forest represented no cost for movement across the landscape, with a score of 0. Deer density data from 1999 were obtained from the Quality Deer Management Association (Yabsley et al. 2005). Elevation data were obtained from the 30-m USGS National Elevation Dataset. A circular moving window with a 1.6-km radius was used to smooth the elevation dataset to represent local average elevations for a second elevation index. Mean and maximum seasonal and annual normalized difference vegetation indices (NDVI) were calculated by averaging 2002 16-day composites from a 250-m MODIS dataset obtained from the Global Land Cover Facility (Carroll et al. 2002). Seasons were classified as spring (March–May), summer (June–August), fall (September–November), and winter (December–February). Land cover values for agriculture, deciduous forest, total forest, and wooded wetlands were calculated as percentages from the NLCD. A percent forest edge variable was developed based on forest and non-forest areas derived from the NLCD. Boundaries of wildlife management areas, national forests, and national wildlife refuge locations were obtained from the LMVJV. A measure of distance from major rivers and lakes within the MAV was developed from vector hydrography data (1:100,000) obtained from the LMVJV. Buffers of 3, 5, and 7 km were identified around the same major rivers dataset. Flooding frequency, hydric soils, and soil drainage indices were calculated from the State Soil Geographic (STATSGO) database (1:250,000) to produce a composite value associated with each soil polygon. The flood probability dataset represented a relative flood frequency index obtained from Ducks Unlimited and was developed from 23 years of historic stream gauge data and Landsat thematic imagery (Shankle 2004).

*Spatial extents.* Five spatial extents were created for each white-tailed deer population location (circles of 1.5-, 5-, 10-, 15-, and 20-km radii) to consider the effects of spatial scale. Small spatial extents were loosely based on

TABLE 1. DESCRIPTION OF VARIABLES USED IN LOGISTIC REGRESSION MODELING

Variable	Variable description	Units	Range
Cost distance	Cost distance from edge of MAV as a function of forest cover and minimum distance	Meters	0–23,409
Deer density	Categories of deer density for each county based on 2000 QDMA image	No. of deer/km <sup>2</sup>	5 categories for densities of 0 to $\geq 45$
Distance to major	Shortest straight line distance to major rivers and lakes of the MAV	Meters	0–41,527
Elevation	Average elevation	Meters	0.20–168.41
Smoothed elevation	Average elevation after smoothing elevation dataset	Meters	0.18–15.17
Flood frequency	Frequency of flooding in any year	None	0–98.33
Flood probability	Probability of flooding based on stream gauge data and Landsat imagery	Probability	0–98.83
Hydric soils	Soils that are saturated, flooded, or ponded during the growing season	None	0–96
Soil drainage	Natural drainage condition of the soil, based on frequency and duration of periods when the soil is free of saturation	None	0–71
River corridors	Indicator variable for presence within 3-, 5-, and 7-km buffers surrounding major river corridors	None	0 or 1
Normalized difference Vegetation index	Spectral index of vegetation cover, computed as seasonal and annual means and maxima	NDVI 200 $\pm$ 50	0–237
Land cover	Percentage of agricultural fields	% cover	0–87
	Percentage of forest edge	% cover	0–27
	Percentage of deciduous forest	% cover	0–98
	Percentage of all forest types	% cover	0–100
	Percentage of wooded wetlands	% cover	0–100

QDMA Quality Deer Management Association.

MAV: Mississippi alluvial valley.

NDVI: Normalized difference vegetation index.

white-tailed deer home ranges, and large spatial extents represented dispersal distances of yearling males within an area of highly fragmented forests, which can vary by age, gender, and habitat quality (Nixon et al. 1994, Long et al. 2005, McCoy et al. 2005). The ecological predictor variables were summarized at each spatial extent, resulting in five measurements of each variable for each deer population. Cost distance, distance to lakes/rivers, elevation, flood frequency and probability, hydric soils, NDVI, and soil drainage were each calculated as a mean value per spatial extent. The deer density class occupying the majority of each spatial extent was calculated to represent the deer population locations. The percentage of each land cover class was also calculated for each spatial extent.

*Logistic regression models.* Four categories of logistic regression models were developed with JMP 6 (SAS Institute, Inc., Cary, NC) and Minitab Statistical Software 13.32 (Minitab Inc., State College, PA). In all cases, serostatus of white-tailed deer populations was the dependent variable. Separate univariate logistic regression analyses were completed for each predictor variable at each of the five spatial extents to consider the influence of scale on predicting each bacterium, and to reduce the number of independent variables in subsequent exploratory models.

*Spatial Extent Models:* Multivariate models for each spatial extent (i.e., circular buffers of 1.5-, 5-, 10-, 15-, and 20-km radii) were developed using stepwise logistic regression with a  $p < 0.05$  cutoff value for *E. chaffeensis* and a  $p < 0.15$  cutoff value for *A. phagocytophilum*.

Exploratory models: To reduce the initial list of variables,  $p$  values and area under the receiver operating characteristic curve (AUC) values from univariate models were used to select the most significant spatial extent for each variable. Multivariate exploratory models were developed from this subset of variables using multiple spatial extents and stepwise logistic regression with a  $p < 0.05$  cutoff value for *E. chaffeensis* and a  $p < 0.15$  cutoff value for *A. phagocytophilum*.

*A priori* models were constructed with one soil moisture or flood probability variable (hypothesized to influence tick populations) and one land cover or cost distance variable (hypothesized to influence host populations).

Evaluation of models: Univariate models were evaluated by AUC and model  $p$  values as indices of predictive power and model fit. Multivariate models were evaluated by AUC and pseudo- $R^2$  values. The AUC provides a measure of the models' ability to discriminate between the presence and absence of the bacteria (Hosmer and Lemshow 2000). Pseudo- $R^2$  mea-

asures improvement in the fit of the model due to the independent variables (Hosmer and Lemshow 2000). The logistic regression models were applied in ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, CA) with ecological predictor variables throughout the MAV. A map of predicted probabilities of *A. phagocytophilum* and *E. chaffeensis* occurrence was developed, with bacteria classified as present if the calculated predicted probability was = 0.5. Predicted values were compared to observed values for white-tailed deer populations by calculating percent accuracy, sensitivity, and specificity (Yabsley et al. 2005).

## RESULTS

White-tailed deer populations were sampled throughout the MAV (Fig. 1). Of the 68 populations tested for the presence of antibodies to *E. chaffeensis*, 25 tested negative and 43 tested positive. Of the 65 populations tested for the presence of antibodies to *A. phagocytophilum*, 39

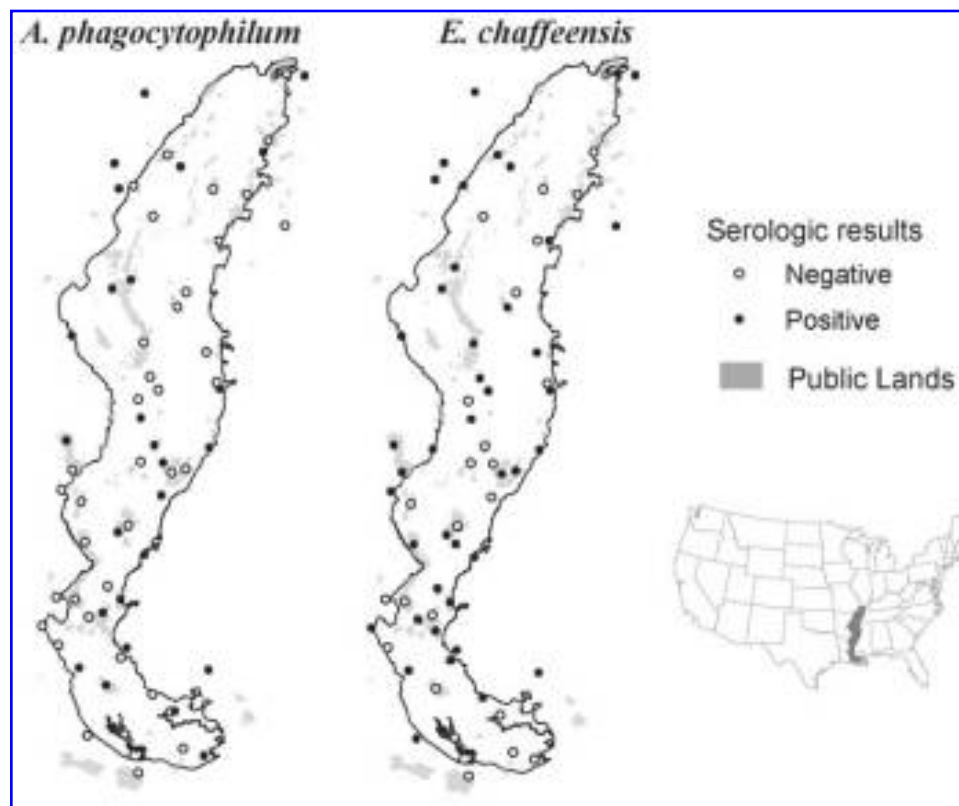


FIG. 1. Indirect immunofluorescent antibody results for white-tailed deer populations in the Mississippi Alluvial Valley.

TABLE 2. LOGISTIC REGRESSION MODELS FOR PREDICTING THE DISTRIBUTIONS OF *ANAPLASMA PHAGOCYTOPHILUM* AND *EHRlichia CHAFFEENSIS*

Model	Variable	Coefficient	$\chi^2$	p Value	
<i>A. phagocytophilum</i>	<i>A priori</i>	Intercept	1.28	4.04	0.0445
		Agriculture (20 km)	-1.85	1.99	0.1585
		Hydric soils (1.5 km)	-0.02	6.67	0.0098
	Exploratory*	Intercept	-8.04	4.54	0.033
		Presence in 3 km river corridor	-1.33	5	0.0253
		Spring maximum NDVI (15 km)	0.04	4.85	0.0277
Spatial extent**	Intercept	-0.51	1.1	0.2953	
	Smoothed elevation (15 km)	0.29	3.36	0.0665	
	Presence in 3 km river corridor	-1.45	6.11	0.0135	
<i>E. chaffeensis</i>	<i>A priori</i>	Intercept	-1.75	2.62	0.1055
		Wooded wetlands (20 km)	-5.22	2.83	0.0927
		Soil drainage (1.5 km)	0.09	7.47	0.0063
	Exploratory**	Intercept	-8.12	3.98	0.0462
		Percent edge (5 km)	16.52	4.26	0.039
		Flood frequency (20 km)	-0.07	8.31	0.0039
		Fall mean NDVI (1.5 km)	0.05	6.28	0.0122
	Spatial extent**	Intercept	-10.85	7.76	0.0053
		Soil drainage (1.5 km)	0.10	7.41	0.0065
		Fall mean NDVI (1.5 km)	0.05	5.47	0.0194

\*Stepwise cut-off value of  $p < 0.15$ .

\*\*Stepwise cut-off value of  $p < 0.05$ .

NDVI: Normalized difference vegetation indices.

tested negative and 26 tested positive. Of the 65 populations tested for both bacteria, 17 populations were seropositive for both bacteria, and 21 populations were seronegative for both bacteria.

Several of the final models contained ecological variables measured at multiple spatial extents (Table 2). Overall, ecological predictor variables resulted in better fitting logistic regression models for *E. chaffeensis* than for *A. phagocytophilum*. The best fitting model for *E. chaffeensis* had an AUC value of 0.82, and a sen-

sitivity of 90.5% as compared to 0.77 and 68% for *A. phagocytophilum* (Table 3).

#### Univariate logistic regression models

Univariate analyses revealed that relationships between environmental variables and the two bacteria varied with spatial extent. Although some variables had similar predictive abilities across the five spatial extents, univariate models for *E. chaffeensis* consistently had higher AUC values than *A. phagocytophilum* for

TABLE 3. COMPARISON OF LOGISTIC REGRESSION MODELS FOR PREDICTING THE DISTRIBUTIONS OF *ANAPLASMA PHAGOCYTOPHILUM* AND *EHRlichia CHAFFEENSIS* IN THE MISSISSIPPI ALLUVIAL VALLEY (1981–2005)

Model	AUC ROC	Pseudo-R <sup>2</sup>	Accuracy (%)	Sensitivity (%)	Specificity (%)	
<i>A. phagocytophilum</i>	<i>A priori</i>	0.721	0.119	66.13	40.00	83.78
	Exploratory	0.766	0.16	69.35	68.00	70.27
	Spatial extent	0.747	0.157	67.70	44.00	83.80
<i>E. chaffeensis</i>	<i>A priori</i>	0.793	0.188	57.58	55.81	60.87
	Exploratory	0.823	0.258	76.92	90.48	52.17
	Spatial extent	0.81	0.229	76.92	85.71	60.87

several variables (cost distance, elevation, percent deciduous, soil drainage, flood frequency, and hydric soils). As spatial extents for *E. chaffeensis* increased, predictive ability also increased for the flood frequency and hydric soil variables (Fig. 2).

#### Spatial extent models

The best fitting spatial extent model for *A. phagocytophilum* and *E. chaffeensis* included variables measured at the 15-km and 1.5-km extents, respectively (Table 2). The predicted probability of *E. chaffeensis* presence increased with STATSGO soil drainage and fall NDVI measured at a 1.5-km extent. The predicted probability of *A. phagocytophilum* presence increased with smoothed elevation values measured at a 15-km extent, and it decreased with presence in the 3-km river corridor.

#### Exploratory logistic regression models

Exploratory models resulted in higher accuracy and sensitivity than spatial extent and *a priori* models when used to create predictive

probability maps (Fig. 3). The presence of *E. chaffeensis* was positively related to percent edge at the 5-km extent and fall mean NDVI at the 1.5-km extent, and it was negatively related to flood frequency at the 20-km extent. The presence of *A. phagocytophilum* was negatively related to presence of a location within the 3-km major rivers buffer, and it was positively related to spring maximum NDVI at the 15-km extent. Maximum predicted probability values derived from predicted probability maps for *E. chaffeensis* (0.99) were greater than those for *A. phagocytophilum* (0.82) in areas both within and outside the MAV (Fig. 3). The high predicted probability values also occurred more frequently with a patchier distribution throughout the valley for *E. chaffeensis*. Large areas along the eastern side of the MAV appeared negative for both bacteria, coinciding with areas of low forest cover and low deer density.

#### *A priori* models

The presence of *E. chaffeensis* was negatively related to percent wooded wetlands at a 20-km

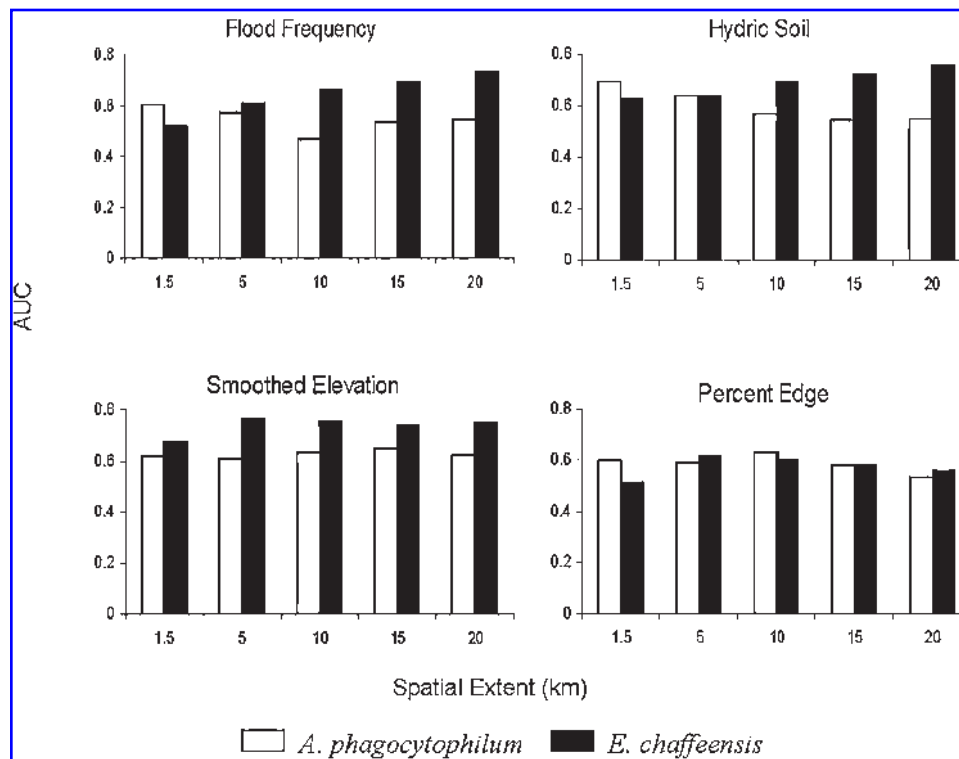


FIG. 2. Comparison of area under the receiver operating characteristic curve (AUC) values for univariate logistic regression models developed for five spatial extents.

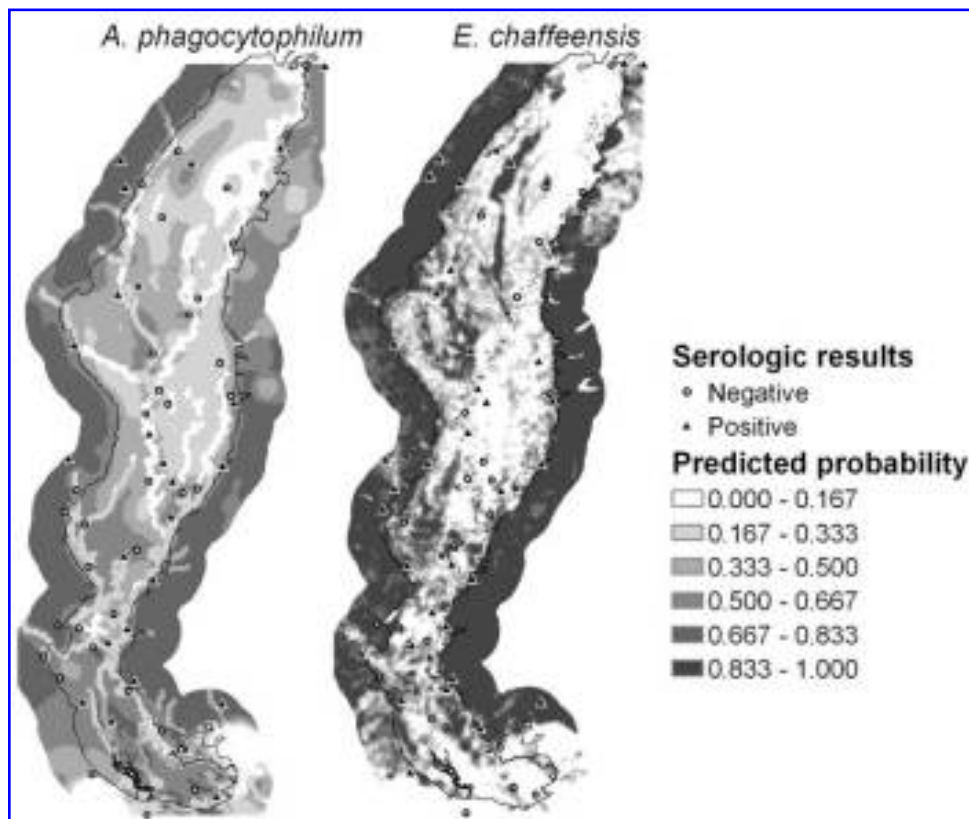


FIG. 3. Probability of occurrences of *E. chaffeensis* and *A. phagocytophilum* predicted by logistic regression models based on white-tailed deer serology and ecological predictor variables for the Mississippi Alluvial Valley.

extent and positively related to soil drainage at a 1.5-km extent in the model with the highest AUC value. The presence of *A. phagocytophilum* was negatively related to percent agriculture at a 20-km extent and soil drainage at a 5-km extent in the model with the highest AUC value.

## DISCUSSION

On the basis of white-tailed deer serum samples, we used logistic regression modeling in an exploratory analysis (1) to determine the influences of ecological predictor variables on the presence of *A. phagocytophilum* and *E. chaffeensis*, and (2) to create predicted probability surfaces for each bacterium throughout the MAV. It has been suggested that white-tailed deer do not harbor the variant of *A. phagocytophilum* that is the causative agent of HGA (Massung et al. 2005). Our study is based solely on serologic results; therefore our predicted probability surface for *A. phagocytophilum* and the implied risk to human health must be viewed

with caution. Nevertheless, serologic results are sufficient for considering the use of GIS to examine the relationships between pathogens and ecological variables.

Our exploratory study into the types of GIS datasets that would provide the strongest associations with infected deer populations involved screening a large number of explanatory variables, many of which were correlated with one another. Explanatory models were composed of different ecological predictor variables depending on the model type (*a priori*, exploratory, or spatial extent). However, ecological relationships were consistent across these models and for both bacteria, supporting the ecological validity of our models. There were positive associations between pathogen presence and indicators of forested landscapes (low agricultural cover, high edge, and high NDVI) and negative associations between pathogen presence and indicators of flooding (high flood probability, low soil drainage, and wooded wetlands).

An advantage of examining multiple spatial extents (e.g., local, intermediate, and landscape

levels) rather than county-level averages, is an enhanced ability to detect ecological relationships. Measuring ecological variables at smaller spatial extents should provide a more precise characterization of factors affecting ticks and hosts at a local (or home range) level, and the use of larger spatial extents should provide an estimate of landscape variables more important to broader movements of vertebrate host species. Most ecological predictor variables (land cover type, soil drainage, flood frequency, hydric soils, cost distance, and NDVI) varied in their influence at different spatial extents. The inclusion of multiple spatial extents in the final models emphasized the importance of considering multiscale spatial analyses for predictive mapping of tick-borne pathogens rather than relying on the use of one spatial extent or several arbitrary spatial units for ecological variable measurements (Table 2).

Overall, the modeling process resulted in better fitting models for *E. chaffeensis* than for *A. phagocytophilum*, regardless of the type of model developed. The better fit and increased sensitivity of *E. chaffeensis* models may be influenced by differences between primary reservoir host species of the two vectors of *E. chaffeensis* and *A. phagocytophilum*. Lone star ticks, vectors of *E. chaffeensis*, rely on white-tailed deer as important hosts for larval, nymphal, and adult life stages, whereas black-legged ticks rely on white-tailed deer as important hosts only for adult ticks (Fish and Dowler 1989, Dawson et al. 1994, Childs and Paddock 2003). Because black-legged ticks depend on multiple host species, it is more difficult to develop a single predictive model that can incorporate multiple habitat relationships.

The negative correlations with moisture-related variables (Table 2) correspond to previous research that suggested a positive association for *I. scapularis* with increasing distance to water, and negative associations for *I. scapularis*, *A. americanum*, and small mammals with wetter soils, increased precipitation, and increased flooding (Bunnell et al. 2003, Chamberlain and Leopold 2003, Dugan 2005, Yabsley et al. 2005). At both the regional and the local level, positive associations have been found between tick distributions and relative humidity (Schulze et al. 2001, Dugan 2005, Yab-

sley et al. 2005) or characteristics that contribute to increased humidity for host-seeking ticks (e.g., increased shrub density and leaf litter) (Schulze et al. 2002). However, excessive moisture at a local level can be detrimental to tick survival (Bunnell et al. 2003). The negative relationships between moisture-related variables and the presence of *E. chaffeensis* and *A. phagocytophilum* are probably indicators of the unfavorable influence of widespread seasonal flooding on the presence of vectors of these pathogens within the MAV, which corresponds to previous research that demonstrated a negative correlation between precipitation and the two pathogens (Dugan 2005, Yabsley et al. 2005).

The positive association between pathogen presence and forest cover variables (spring max NDVI, percent edge, and fall mean NDVI) correspond with previous research about the use of forest cover as habitat by white-tailed deer and ticks in a fragmented area (Nixon et al. 1991, Ostfeld et al. 1995, Miranda and Porter 2003). The lack of significance of the cost distance variable in our final models suggested that the current existence of land management units in remnant forest patches isolated by extensive agricultural fields was not an important factor influencing the distributions of these pathogens. However, the percent edge variable was significant for predicting the distribution of *E. chaffeensis*, possibly by detecting dispersal routes for white-tailed deer throughout the MAV. Dispersal routes may be represented by forest corridors that would be composed primarily of forest edge, which could also be providing favorable tick habitat (Bunnell et al. 2003). Over the last two decades, the MAV has become the focus of extensive bottomland hardwood reforestation efforts driven by concerns for maintaining wildlife habitats and good water quality (Stanturf et al. 2000). The changing landscape of the MAV, as well as the tendency for human populations to expand into rural areas, may increase the potential for exposure to tick-borne zoonoses in the future (Childs and Paddock 2003).

The problem of selecting spatial datasets relevant to vector or host ecology (i.e., selecting the appropriate soil moisture variable from a group that includes, for example, hydric soils,

soil drainage, and flood probability, among others) will become increasingly important as GIS becomes more widely used for mapping tick-borne disease risks. Local tick habitat consists of only a few square meters, and currently available spatial datasets cannot accurately reflect ecological characteristics at this fine scale. However, our research demonstrates that relationships based on coarser predictors, such as soils and land cover maps, are still useful for making ecological inferences and developing predictive maps. Multiple spatial extents must be considered when measuring ecological predictor variables for tick-borne bacteria, because their complex zoonotic cycles encompass processes operating over a wide range of scales, ranging from tick-environment relationships within a few meters to deer movements over many kilometers. We concluded that habitat availability and connectivity for vector and host species (as measured by land cover composition and configuration) and soil moisture for vector species (as measured by water-related variables) influence distributions of *E. chaffeensis* and *A. phagocytophilum* in the MAV. To improve our predictive maps, we must continue to refine our environmental measurements and make them more directly relevant to the complex pathogen-vector-host relationships that exist for vector-borne zoonoses.

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#### REFERENCES

- Allan BF, Keesing F, Ostfield RS. Effect of forest fragmentation on Lyme disease risk. *Conservation Biol* 2003; 17:267–272.
- Anderson BE, Sims KG, Olson JG, et al. *Amblyomma americanum*: a potential vector of human ehrlichioses. *Am J Trop Med Hyg* 1993; 49:239–244.
- Brinkman TJ, Deperno CS, Jenks JA, et al. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *J Wildlife Manage* 2005; 69: 1099–1111.
- Brownstein JS, Holford TR, Fish D. A climate-based model predicts the spatial distribution of the Lyme disease vector *Ixodes scapularis* in the United States. *Environ Health Perspect* 2003; 111:1152–1157.
- Bunnell JE, Price SD, Das A, et al. Geographic information systems and spatial analysis of adult *Ixodes scapularis* (Acari: Ixodidae) in the Middle Atlantic Region of the United States. *J Med Entomol* 2003; 40:570–576.
- Carroll ML, DiMiceli CM, Sohlberg RA, et al. *250m MODIS Normalized Difference Vegetation Index*. College Park, MD: The Global Land Cover Facility 2002.
- Chamberlain MJ, Leopold BD. Effects of flood on relative abundance and diversity of small mammals in a regenerating bottomland hardwood forest. *Southwestern Naturalist* 2003; 48:306–309.
- Childs JE, Paddock CD. The ascendancy of *Amblyomma americanum* as a vector of pathogens affecting humans in the United States. *Annu Rev Entomol* 2003; 48:307–337.
- Dawson JE, Childs JE, Biggie KL, et al. White-tailed deer as a potential reservoir of Ehrlichia spp. *J Wildlife Dis* 1994; 30:162–168.
- Demma LJ, Holman RC, McQuiston JH, et al. Epidemiology of human ehrlichiosis and anaplasmosis in the United States, 2001–2002. *Am J Trop Med Hyg* 2005; 73:400–409.
- DesVignes F, Fish D. Transmission of the agent of human granulocytic ehrlichiosis by host-seeking *Ixodes scapularis* (Acari: Ixodidae) in southern New York State. *J Med Entomol* 1997; 34:379–382.
- Dugan V. *White-tailed Deer and Raccoons as Hosts for Selected Zoonotic Tick-borne Rickettsiae*. Athens, GA: Ph.D. Thesis; University of Georgia, 2005:172 pp.
- Dugan V, Yabsley M, Tate C, et al. Evaluation of white-tailed deer (*Odocoileus virginianus*) as natural sentinels for *Anaplasma phagocytophilum*. *Vector-Borne Zoonotic Dis* 2006; 6:192–207.
- Estrada-Pena A. Geostatistics and remote sensing as predictive tools of tick distribution: a Cokriging system to estimate *Ixodes scapularis* (Acari: Ixodidae) habitat suitability in the United States and Canada from Advanced Very High Resolution Radiometer Satellite Imagery. *J Med Entomol* 1998; 35:989–995.
- Estrada-Pena A. The relationships between habitat topology, critical scales of connectivity and tick abundance *Ixodes ricinus* in a heterogeneous landscape in northern Spain. *Ecography* 2003; 26:661–671.

- Fish D, Dowler RC. Host associations of ticks (Acari: Ixodidae) parasitizing medium-sized mammals in a Lyme disease endemic area of southern New York. *J Med Entomol* 1989; 26:200–209.
- Guerra M, Walker E, Jones C, et al. Predicting the risk of Lyme disease: habitat suitability for *Ixodes scapularis* in the north central United States. *Emerg Infect Dis* 2002; 8:289–297.
- Hosmer DW, Lemshow S. *Applied Logistic Regression*. New York: John Wiley & Sons, Inc., 2000.
- LMVJV (Lower Mississippi Valley Joint Venture). Mississippi Alluvial Valley Conservation Planning Atlas Volume 1, 2001. ([http://lmvjv.org/gis\\_data.htm](http://lmvjv.org/gis_data.htm)).
- Lockhart JM, Davidson WR, Stallknecht DE, et al. Site-specific geographic association between *Amblyomma americanum* (Acari: Ixodidae) infestations and *Ehrlichia chaffeensis*-reactive (Rickettsiales: Ehrlichieae) antibodies in white-tailed deer. *J Med Entomol* 1996; 33:153–158.
- Long ES, Diefenbach DR, Rosenberry CS, et al. Forest cover influences dispersal of white-tailed deer. *J Mammal* 2005; 86:623–629.
- Magnarelli LA, Stafford K, Ijido JW, et al. Antibodies to granulocytic ehrlichiae in white-footed and cotton-mice in eastern United States. *J Wildlife Dis* 1999; 35: 259–265.
- Massung RF, Courtney JW, Hiratzka SL, et al. *Anaplasma phagocytophilum* in white-tailed deer. *Emerg Infect Dis* 2005; 11:1604–1606.
- McCoy JE, Hewitt DG, Bryant FC. Dispersal by yearling male white-tailed deer and implications for management. *J W M* 2005; 69:366–376.
- McQuiston JH, McCall CL, Nicholson WL. Ehrlichiosis and related infections. *J Am Vet Med Assoc* 2003; 223: 1750–1756.
- Miranda BR, Porter WF. Statewide habitat assessment for white-tailed deer in Arkansas using satellite imagery. *Wildlife Soc Bull* 2003; 31:715–726.
- Mount GA, Haile DG, Barnard DR, et al. New version of LSTSIM for computer simulation of *Amblyomma americanum* (Acari: Ixodidae) population dynamics. *J Med Entomol* 1993; 30:843–857.
- Mount GA, Haile DG, Daniels E. Simulation of management strategies for the blacklegged tick (Acari: Ixodidae) and the Lyme disease spirochete, *Borrelia burgdorferi*. *J Med Entomol* 1997; 90:672–683.
- Nixon CM, Hansen LP, Brewer PA, et al. Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife Monogr* 1991; 118.
- Nixon CM, Hansen LP, Brewer PA, et al. Behavior, dispersal, and survival of male white-tailed deer in Illinois. *Illinois Nat Hist Surv Biol Notes* 1994; 139:30 pp.
- Ogden NH, Bigras-Poulin M, O'Callaghan CJ, et al. A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int J Parasitol* 2005; 35:375–389.
- Ostfeld RS, Cepeda OM, Hazler KR, et al. Ecology of lyme disease: habitat associations of ticks (*Ixodes scapularis*) in a rural landscape. *Ecol Appl* 1995; 5:353–361.
- Ostfeld RS, Glass GE, Keesing F. Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends Ecol Evol* 2005; 20:328–336.
- Rudis VA. Regional forest fragmentation effects on bottomland hardwood community types and resource values. *Landscape Ecol* 1995; 10:291–307.
- Schulze TL, Jordan RA, Hung RW. Effects of microscale habitat physiognomy on the focal distribution of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae) nymphs. *Environ Entomol* 2002; 31:1085–1090.
- Schulze TL, Jordan RA, Hung RW. Effects of selected meteorological factors on diurnal questing of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *J Med Entomol* 2001; 38:318–324.
- Shankle S. Flood probability and wetland restoration suitability modeling. Unpublished final report submitted to the USDA Forest Service. Agreement # 00-CS-11083150-030 2004.
- Stanturf JA, Gardiner ES, Hamel PB, et al. Restoring bottomland hardwood ecosystems in the lower Mississippi alluvial valley. *J For* 2000; 98:10–16.
- Telford SR, Dawson JE, Katavolos P, et al. Perpetuation of the agent of human granulocytic ehrlichiosis in a deer tick-rodent cycle. *Proc Natl Acad Sci USA* 1996; 93: 6209–6214.
- Thomson MC, Connor SJ. Environmental information systems for the control of arthropod vectors of disease. *Med Vet Entomol* 2000; 14:227–244.
- Vogelmann JE, Sohl TL, Campbell PV, et al. Regional land cover characterization using Landsat Thematic Mapper data and ancillary data sources. *Environ Monit Assess* 1998; 51:415–428.
- Wilder SM, Mekle DB. Prevalence of deer ticks (*Ixodes scapularis*) on white-footed mice (*Peromyscus leucopus*) in forest fragments. *J Mammal* 2004; 85:1015–1018.
- Wilson ML. Distribution and abundance of *Ixodes scapularis* (Acari: Ixodidae) in North America: ecological processes and spatial analysis. *J Med Entomol* 1998; 35:446–457.
- Yabsley MJ, Dugan VG, Stallknecht DE, et al. Evaluation of a prototype *Ehrlichia chaffeensis* surveillance system using white-tailed deer (*Odocoileus virginianus*) as natural sentinels. *Vector-Borne Zoonotic Dis* 2003; 3:195–207.
- Yabsley MJ, Wimberly MC, Stallknecht DE, et al. Spatial analysis of the distribution of *Ehrlichia chaffeensis*, causative agent of human monocytotropic ehrlichiosis, across a multi-state region. *Am J Trop Med Hyg* 2005; 72:840–850.

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