Site-Specific Geographic Association Between *Amblyomma americanum* (Acari: Ixodidae) Infestations and *Ehrlichia chaffeensis*-Reactive (Rickettsiales: Ehrlichieae) Antibodies in White-Tailed Deer

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ABSTRACT Serum samples from white-tailed deer, *Odocoileus virginianus* Zimmermann, collected from 1982 through 1992 from the southeastern United States were tested for antibodies reactive to *Ehrlichia chaffeensis* Anderson, Dawson, Jones, & Wilson, the causative agent of human ehrlichiosis. Results were compared between areas based on known infestations of the lone star tick, *Amblyomma americanum* L., a suspected vector of *E. chaffeensis*. One hundred and twenty-five of 300 (41.7%) deer tested positive (≥1:128) for *E. chaffeensis*-reactive antibodies by fluorescent antibody analysis. Thirty of 30 (100%) collection areas known to be lone star tick infested contained deer that tested positive for *E. chaffeensis*-reactive antibodies, corresponding to 121/150 (80.7%) of deer examined. A few deer, 4/150 (2.7%) of those examined, from 2 of 30 (6.7%) areas where lone star ticks were not detected were positive for *E. chaffeensis*-reactive antibodies. This site-specific geographic association between *A. americanum* and the presence of *E. chaffeensis*-reactive antibodies in deer provides strong evidence that *A. americanum* is a natural vector of *E. chaffeensis* or a closely related species among white-tailed deer.

KEY WORDS *Ehrlichia chaffeensis, Amblyomma americanum,* white-tailed deer, serology, epidemiology

HUMAN EHRLICHIOSIS IS a recently recognized human illness caused by *Ehrlichia chaffeensis* (Anderson et al. 1991). Since being described in 1986 (Maeda et al. 1987), >400 cases of human ehrlichiosis have been reported from 30 states, with most cases occurring in the southeastern, mid-Atlantic, and south-central United States (Eng et al. 1990, Dawson et al. 1994a).

Current evidence suggests that human ehrlichiosis is a tick-borne zoonosis with *Amblyomma americanum* (L.) and white-tailed deer, *Odocoileus virginianus* Zimmermann, as the primary suspected vector and reservoir host, respectively. Most human ehrlichiosis patients have a history of tick exposure or bites (Fishbein et al. 1989, Harkess et al. 1989) and human ehrlichiosis cases exhibit a seasonality of occurrence that coincides with peak tick activity during warmer months (Eng et al. 1990). Eng et al. (1990) noted the similarity of geographic distribution between human ehrlichiosis cases and the range of *A. americanum*. Polymerase chain reaction (PCR) analysis has demonstrated *E. chaffeensis* DNA sequences from adult *A. americanum* from Arkansas, Kentucky, Mississippi, New Jersey, and North Carolina and from a single American dog tick, *Dermacentor variabilis* (Say) from Arkansas (Anderson et al. 1992, 1993). A temporal relationship has been demonstrated between establishment of *A. americanum* at a site in Georgia and the appearance of *E. chaffeensis*-reactive antibodies in white-tailed deer (Lockhart et al. 1995).

Vertebrate reservoir hosts for *E. chaffeensis* have not been established definitively; however, a survey of white-tailed deer in the eastern United States disclosed that 43% of 1,269 deer were positive for *E. chaffeensis*-reactive antibodies (Dawson et al. 1994a). Seropositive deer were restricted to a geographic area generally corresponding to the distribution of *A. americanum*. Deer have been shown to be susceptible to experimental infection with *E.*

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chaffeensis but not *E. canis* Donatien & Lestoquard, the causative agent of canine ehrlichiosis (Dawson et al. 1994b). When infected with *E. chaffeensis*, deer seroconverted and remained rickettsemic through postinoculation day 24 (Dawson et al. 1994b). No seroconversions were detected in *E. canis*-inoculated deer. White-tailed deer also are well documented to be important hosts for all 3 life stages of *A. americanum* (Patrick and Hair 1978; Bloemer et al. 1986, 1988).

Since the 1960s, personnel of the Southeastern Cooperative Wildlife Disease Study (SCWDS) have monitored health status of white-tailed deer from areas throughout the southeastern United States. This work routinely included collection and identification of ticks and retention of frozen serum samples. These circumstances offered a unique opportunity to retrospectively evaluate the potential geographic relationship between *A. americanum* infestations and *E. chaffeensis*-reactive antibodies among white-tailed deer in the southeastern United States on a site-specific basis.

Fig. 1. Location of counties in the southeastern United States surveyed for *E. chaffeensis*-reactive antibodies in white-tailed deer with classification as *A. americanum*-positive or -negative. ■, *A. americanum* positive. □, *A. americanum* negative.

Materials and Methods

Sample Collection. Data representing 300 deer from 60 populations studied during SCWDS deer herd health monitoring activities were included in this retrospective study. For each deer population studied, samples of 5 deer were collected by shooting during June through September (1982–1992). Whole blood, collected from each deer by cardiac puncture, was allowed to clot. Serum was harvested, placed in 1.5-ml cryovials, and stored at −30°C. Each animal was visually examined for ticks and a subjective estimate of tick infestation intensity was determined for each animal according to the following criteria: 0, no ticks observed; 1, <20 ticks observed; 2, between ≈20 and ≈100 ticks observed, and 3, >100 ticks observed. Representative specimens of ticks were collected, stored in 70% ethanol, and submitted to the National Veterinary Services Laboratories, USDA, Ames, IA, for identification.

Herd health data sets were selected based on the primary criterion of identifying 30 areas where deer populations were infested with *A. americanum* and 30 areas where deer populations did not harbor *A. americanum*. A secondary selection criterion was achieving a broad geographic representation of the southeastern United States. On 19 of 60 areas, tick infestation data from an additional 5–25 deer from different years were available and were used to substantiate status of these areas in regard to tick infestation. Populations classified as *A. americanum*-negative had no lone star ticks during any SCWDS herd health monitoring activities; populations classified as positive had infestation prevalences of ≈100% and mean subjective intensities of >1. Serum samples from 5 deer at each site were analyzed by indirect fluorescent antibody test (IFA).

Using the above criteria, deer populations that had been surveyed between 1982 and 1992 were selected for study. These included populations at the following locations (Fig. 1): Alabama—Choctaw National Wildlife Refuge, Choctaw County; Eufaula National Wildlife Refuge, Barbour County; Fort Rucker, Dale County and Coffee County; G. E. Property, Lowndes County; Lee Haven Property, Sumter County; Solomon Farm, Houston County; Arkansas—Bayou DeView Wildlife Management Area, Poinsett County; Big Lake National Wildlife Refuge, Mississippi County; Caney Creek Wildlife Management Area, Polk County; Fort Chaffee, Sebastian County; Private tract, Fulton County; Pine Bluff Arsenal, Jefferson County; Florida—Everglades National Park, Broward County; St. Marks National Wildlife Refuge, Wakulla County; Georgia—Chickamauga National Battlefield, Walker County and Catoosa County; Dixon Memorial Forest, Ware County; Eufaula National Wildlife Refuge, Stewart County; Fort Benning, Muscogee County and Chattahoochee County; Fort Gordon, Richmond County; King's Bay Submarine Base, Camden County; Piedmont National Wildlife Refuge, Jasper County and Jones County; Kentucky—Land-Between-the-Lakes, Lyon County and Trigg County; Mammoth Cave National Park, Edmonson County; Louisiana—Big Lake Wildlife Management Area, Madison Parish; Delta National Wildlife Refuge, Plaquemines Parish; Lake Ophelia National Wildlife Refuge, Avoyelles Parish; Oak Grove Wildlife Management Area, East Carroll Parish; Red River Wildlife Management Area, Concordia Parish; Saline Wildlife Management Area, LaSalle Parish; Weldon Property, Claiborne Parish; Maryland—Blackwater Na-

tional Wildlife Refuge, Dorchester County; Catoctin Mountain National Park, Frederick County; White Oak Naval Weapons Center, Montgomery County and Prince Georges County; Mississippi—Dahomey National Wildlife Refuge, Bolivar County; Mississippi Sandhill Crane National Wildlife Refuge, Jackson County; Noxubee National Wildlife Refuge, Noxubee County; Panther Swamp National Wildlife Refuge, Yazoo County; Yazoo National Wildlife Refuge, Washington County; Missouri—Knob Noster State Park, Johnson County; Squaw Creek National Wildlife Refuge, Holt County; North Carolina—Alligator River National Wildlife Refuge, Dare County; Cameron Property, Hyde County; Mackay Island National Wildlife Refuge, Currituck County; Pee Dee National Wildlife Refuge, Anson County; South Carolina—Cape Romain National Wildlife Refuge, Charleston County; Croft State Park, Spartanburg County; Santee National Wildlife Refuge, Clarendon County; Savannah National Wildlife Refuge, Jasper County; Tenneesee—Big Sandy National Wildlife Refuge, Henry County; Carter Mountain Wildlife Management Area, Franklin County; Chickasaw National Wildlife Refuge, Lauderdale County; Hatchie National Wildlife Refuge, Haywood County; Reelfoot National Wildlife Refuge, Obion County; Virginia—Chincoteague National Wildlife Refuge, Accomack County; Mason Neck National Wildlife Refuge, Fairfax County; Prince William Forest National Park, Prince William County; Smithsonian National Zoological Park, Warren County; West Virginia—Bluestone Farm, Monroe County; French Creek, Upshur County; and Somerville Fork, Wirt County.

Serology. An IFA test (Dawson et al. 1991) was used to test for the presence of *E. chaffeensis*-reactive antibodies. Antigen, consisting of *E. chaffeensis*-infected DH82 canine macrophages, was obtained from the Centers for Disease Control and Prevention (CDC) in Atlanta, GA, and acetone-fixed to slides for the IFA procedure. Samples, tested without knowledge of the collection site, were screened at a dilution of 1:128 in 0.01 M phosphate buffered saline (PBS). Fluorescein isothiocyanate-labeled rabbit antideer immunoglobulin G (Kirkegaard and Perry Laboratories, Gaithersburg, MD) diluted 1:100 in 0.01 M PBS, was used as the antibody conjugate.

A positive control serum sample was obtained from an experimentally *E. chaffeensis*-infected white-tailed deer (Dawson et al. 1994b) that exhibited a titer of 1:512. A negative control serum sample was obtained from a hunter-killed fawn from Lake Russell Wildlife Management Area, Stephens County, Georgia, collected as part of a program monitoring for hemorrhagic disease. Serum from this animal tested negative for antibodies to *E. chaffeensis*.

Statistical Analyses. The chi-square test using Yates correction factor (Ott 1993) was used in testing differences in prevalence of *E. chaffeensis*-reactive antibodies between the 30 *A. americanum*-positive and 30 *A. americanum*-negative populations. The same procedure was used to compare the percentage of seropositive deer pooled for tick-positive and tick-negative populations. Statistical significance was determined at $P < 0.05$.

Results

One hundred and twenty-five of 300 deer (41.7%) tested were positive (≥1:128) for *E. chaffeensis*-reactive antibodies (Table 1). Thirty of 30 (100%) *A. americanum*-positive areas contained deer that were positive for *E. chaffeensis*-reactive antibodies, corresponding to 121 of 150 deer (80.7%). Two of 30 (6.7%) *A. americanum*-negative areas contained deer that were positive, corresponding to 4 of 150 deer (2.7%). The prevalence of reactive antibodies was significantly higher among *A. americanum* infested populations (100%) than *A. americanum*-negative populations (6.7%, $\chi^2 = 48.82$, df = 1, $P < 0.001$). The percentage of seropositive deer also was significantly higher for *A. americanum*-positive areas (80.7%) than negative areas (2.7%, $\chi^2 = 184.54$, df = 1, $P < 0.001$).

Two areas (Choctaw National Wildlife Refuge, AL, and Dahomey National Wildlife Refuge, MS) that were classified as *A. americanum*-negative contained deer that were positive for *E. chaffeensis*-reactive antibodies. No ticks were reported on any of the deer collected from these areas. Five *A. americanum*-negative populations had *A. maculatum* infestations present during herd health evaluations (Table 1). All deer tested from these populations were seronegative. The prevalence of the *A. maculatum* infestations ranged from 40 to 80% with mean subjective intensities of 0.4–0.8.

Discussion

Field evidence of an association between a suspected vector with an appropriate host is 1 of 4 criteria outlined for confirmation of arthropod vector competency (WHO 1967). Our data strengthen the field evidence supporting the concept that *A. americanum* is an important vector of *E. chaffeensis* or a closely related species among white-tailed deer. *A. americanum* was identified as a potential *E. chaffeensis* vector by Eng et al. (1990) who reported a general geographic relationship between lone star ticks and human ehrlichiosis cases. Dawson et al. (1994a) later noted a general geographic concordance between seropositive deer and the distribution of the lone star tick. Although no isolates have been obtained from ticks, PCR reactions performed with primers presumed to be specific for *E. chaffeensis* resulted in products of the expected size (Anderson et al. 1993). We have previously confirmed a temporal relationship between the establishment of *A. americanum* and the appearance of *E. chaffeensis*-reactive antibodies in a

Table 1. Tick infestations and antibodies reactive to *E. chaffeensis* in white-tailed deer collected from the southeastern United States, 1982–1992

Area	Collection date	Positive test[a]	Intensity of ticks[b]	Other ticks
	A. americanum positive areas			
Fort Rucker, AL	July 1982	3/5	1.6	
Lee Haven Property, AL	July 1988	5/5	1.4	A.m.
Solomon Farm, AL	Aug. 1990	3/5	1.0	
Caney Creek WMA, AR	July 1991	4/5	1.8	I.a.
Fort Chaffee, AR	Aug. 1983	5/5	2.0	
Fulton County, AR	Sept. 1987	4/5	1.6	I.s.
Pine Bluff Arsenal, AR	Sept. 1987	4/5	2.8	
St. Marks NWR, FL	Sept. 1987	4/5	3.0	A.m.
Dixon Mem. Forest, GA	Aug. 1989	5/5	1.6	A.m.
Fort Benning, GA	Aug. 1990	4/5	1.4	
Fort Gordon, GA	June 1985	4/5	1.2	
King's Bay Sub. Base, GA	Aug. 1988	5/5	1.6	
Piedmont NWR, GA	Aug. 1989	4/5	2.6	
Land-Between-Lakes, KY	Aug. 1983	5/5	2.0	
Mammoth Cave NP, KY	Sept. 1984	4/5	1.0	
Big Lake WMA, LA	Aug. 1984	3/5	1.4	
Oak Grove WMA, LA	July 1991	3/5	0.8	
Weldon Property, LA	Sept. 1987	3/5	1.6	
Blackwater NWR, MD	Aug. 1988	3/5	1.4	
Noxubee NWR, MS	July 1991	5/5	1.0	A.m.
Knob Noster SP, MO	Sept. 1992	5/5	2.0	
Alligator River NWR, NC	Sept. 1985	5/5	1.8	
Cameron Property, NC	July 1987	5/5	2.0	I.a.
Mackay Island NWR, NC	Aug. 1988	4/5	1.6	
Cape Romain NWR, SC	July 1987	3/5	1.8	
Big Sandy NWR, TN	Aug. 1991	4/5	1.2	
Carter Mountain WMA, TN	July 1988	4/5	1.0	
Chincoteague NWR, VA	Aug 1990	5/5	2.0	
Mason Neck NWR, VA	July 1992	2/5	2.6	A.m.
Prince William NP, VA	Aug. 1988	4/5	2.0	
	A. americanum negative areas			
G. E. Property, AL	Aug. 1990	0/5	0.6	A.m.
Eufaula NWR, AL	July 1986	0/5	0.4	A.m.
Choctaw NWR, AL	July 1985	1/5	0.0	
Bayou DeView WMA, AR	Sept. 1984	0/5	0.0	
Big Lake NWR, AR	Sept. 1992	0/5	0.0	
Everglades NP, FL	July 1982	0/5	0.0	
Chickamauga NB, GA	Aug. 1991	0/5	0.0	
Eufaula NWR, GA	July 1986	0/5	0.4	A.m.
Delta NWR, LA	July 1985	0/5	0.0	
Lake Ophelia NWR, LA	Sept. 1992	0/5	0.0	
Saline WMA, LA	Sept. 1991	0/5	0.0	
Red River WMA, LA	Sept. 1986	0/5	0.0	
Catoctin Mountain NP, MD	Aug. 1988	0/5	0.0	
White Oak, MD	Aug. 1988	0/5	0.0	
Dahomey NWR, MS	Sept. 1992	3/5	0.0	
Yazoo NWR, MS	Sept. 1986	0/5	0.0	
MS Sandhill NWR, MS	Sept. 1992	0/5	0.8	A.m.
Panther Swamp NWR, MS	Sept. 1986	0/5	0.0	
Squaw Creek NWR, MO	Sept. 1992	0/5	0.0	
Pee Dee NWR, NC	July 1987	0/5	0.0	
Croft SP, SC	Aug. 1989	0/5	0.0	
Savannah NWR, SC	Sept. 1993	0/5	0.0	
Santee NWR, SC	July 1986	0/5	0.4	A.m.
Chickasaw NWR, TN	Sept. 1992	0/5	0.0	
Hatchie NWR, TN	Sept. 1989	0/5	0.0	
Reelfoot NWR, TN	Sept. 1989	0/5	0.0	
Smithsonian, VA	Sept. 1985	0/5	0.0	
Bluestone Farm, WV	Aug. 1987	0/5	0.0	
French Creek, WV	Aug. 1989	0/5	0.0	
Somerville Fork, WV	Aug. 1989	0/5	0.0	

A.m., *A. maculatum;* I.a., *I. affinis;* I.s., *I. scapularis.* NWR, National Wildlife Refuge; NP, National Park; NB, National Battlefield; SP, State Park; WMA, Wildlife Management Area.

[a] Number of deer testing positive (≥1:128) for *E. chaffeensis*-reactive antibodies per number of deer tested.

[b] Mean tick infestation for the collection rated by subjective category scale: 0, no ticks; 1, <20 ticks; 2, ~20–100 ticks; 3, >100 ticks.

white-tailed deer population in Georgia (Lockhart et al. 1995). Subsequent to the current study, experimental deer to deer transmission of *E. chaffeensis* by *A. americanum* was accomplished (Ewing et al. 1995)

Although lone star ticks were generally abundant, widely distributed, and found on deer in most southeastern states surveyed during herd health monitoring, analysis at the site-specific level indicates that lone star ticks were not present on deer in all areas of each state. These findings are consistent with the concept that the distribution of the lone star tick in the southeastern United States is discontinuous (Smith 1977), with nearby areas often showing vast differences in tick populations.

Major factors vital to sustaining lone star tick populations include abundance of large mammals as principal hosts for the adult stage (Bishopp and Trembley 1945; Patrick and Hair 1977, 1978), and wooded habitat necessary for survival of free living stages (Semtner et al. 1971a, b; Koch 1984). Haile and Mount (1987) have proposed that in addition to the above factors, population dynamics of *A. americanum* are influenced by habitat, temperature, and relative humidity. These variables, in conjunction with the history of deer restoration (restocking) in the southeast, may help explain the current discontinuous distribution of *A. americanum.*

In addition to their role as a major host of *A. americanum,* recent studies have implicated white-tailed deer as possible reservoir hosts of *E. chaffeensis.* In a study of 1,269 deer from the eastern United States, 43% were positive for antibodies reactive to *Ehrlichia* spp. (Dawson et al. 1994a). This compares favorably with the finding of 41.7% seroreactive deer in this study. However, caution has been advised in interpreting serologic results because cross-reactions can occur between antibody to different species of *Ehrlichia* in the IFA test (Dawson et al. 1994a). Experimental infection trials have indicated that deer are susceptible to *E. chaffeensis,* but not to *E. canis* (Dawson et al. 1994b), a species known to cross react with *E. chaffeensis.* These experimental data suggest that *E. chaffeensis*-reactive antibodies in wild deer are probably not due to *E. canis* cross-reactions, but the possibility of currently unknown cross-reacting Ehrlichiae cannot be ruled out.

If *A. americanum* is shown to be the major vector of *E. chaffeensis,* the risk of human ehrlichiosis should prove to be discontinuous and probably similar to the density and distribution of *A. americanum* on a local scale. Dawson et al. (1994a) suggested that white-tailed deer might serve as sensitive natural sentinels of *E. chaffeensis,* and our data indicate that it may be possible to apply this concept on a finer scale than previously anticipated.

Of the other tick species found on deer during this study, only *A. maculatum* was present at several collection sites. The absence of seropositive deer from 5 *A. maculatum*-positive populations suggests that this tick may not be involved in transmission of *E. chaffeensis.* Past PCR evidence has implicated *D. variabilis* as a potential carrier of *E. chaffeensis* (Anderson et al. 1992) but this species is rare on white-tailed deer (Bishopp and Trembley 1945, Smith 1977).

Several potential reasons exist for the detection of *E. chaffeensis*-reactive antibodies in deer from areas classified as *A. americanum*-negative. The most probable explanation is that either lone star ticks occurred at low prevalences on these areas but were not present on the deer examined or that field personnel did not detect some low intensity infestations. Other factors to consider include the possibility that other tick species may be capable of transmitting *E. chaffeensis* or that other unknown ehrlichial organisms may be present, causing serologic cross-reactions.

Although *E. chaffeensis* has not been isolated from naturally-infested ticks or white-tailed deer, evidence is accumulating that the lone star tick is a primary vector for *E. chaffeensis.* This site-specific geographic retrospective analysis, combined with past studies, provides strong indications that *E. chaffeensis* may be transmitted primarily by the lone star tick.

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