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Prevalence of *Borrelia burgdorferi* Sensu Lato Infection Among Rodents and Host-Seeking Ticks in South Carolina

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ABSTRACT Tissues of rodents and host-seeking adult ticks collected in the Piedmont, Sandhills, Coastal Plain, and Coastal Zone of South Carolina were cultured in attempts to isolate *Borrelia burgdorferi* (Johnson, Schmid, Hyde, Steigerwalt & Brenner), the etiologic agent of Lyme disease. An exploratory, tree-based statistical analysis was used to identify ecological variables that were associated with spirochete infection among rodents and ticks. Spirochetes were isolated from tissues of 71 rodents: 22 (69%) of 32 eastern woodrats, 39 (53%) of 74 cotton mice, and 11 (25%) of 44 hispid cotton rats. Rodent infection prevalences were significantly higher in the Coastal Zone than in other regions. Spirochetes were also cultured from 31 (2.6%) of 1,193 questing ticks. Prevalence of spirochetes in *Ixodes affinis* Neumann (19/74, 26%) was significantly higher than in *I. scapularis* Say (12/864, 1.3%) and other species (0/255) of ticks tested. In addition, two (9%) of 23 adult *I. minor* Neumann removed from woodrats contained spirochetes. Isolates from rodents and ticks were analyzed immunologically by indirect immunofluorescence and Western blots, and further characterized by polymerase chain reaction assays and sodium dodecyl sulfate-polyacrylamide gel electrophoresis. All were determined to be *B. burgdorferi* sensu lato. Results of this study confirmed that *B. burgdorferi* is endemic in South Carolina, and that enzootic transmission cycles exist at foci in the Coastal Zone. These findings add additional evidence that *I. affinis* and *I. minor* are potentially significant maintenance vectors of the spirochete.

KEY WORDS *Borrelia burgdorferi*, Lyme disease, rodents, ticks, South Carolina

LYME DISEASE IS the most commonly reported arthropod-associated disease of humans in the United States. The etiologic agent of Lyme disease, *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt & Brenner, is maintained in transmission cycles involving various species of mammals, birds, and ticks in the genus *Ixodes* (Anderson 1989, Lane et al. 1991, Anderson and Magnarelli 1994). Although the majority of human Lyme disease cases in the United States have been reported from the Northeast, hundreds of indigenous cases have also been recognized in the Southeast (Ciesielski et al. 1989; CDC 1989, 1991, 2001; Mullen and Piesman 1987; Levine et al. 1991b). From 1990 through 1999, the South Carolina State Department of Health and Environmental Control reported an average of approximately eight cases of Lyme disease per year (79 cases total) to the Centers for Disease Control and Prevention (CDC 2001). A review of Lyme borreliosis in the southern United States has been published (Oliver 1996).

The cotton mouse, *Peromyscus gossypinus* (LeConte); hispid cotton rat, *Sigmodon hispidus* Say & Ord; marsh rice rat, *Oryzomys palustris* (Harlan); and eastern woodrat, *Neotoma floridana* (Ord) are all common hosts for immature ticks in the Southeast (Bishopp and Trembley 1945, Rogers 1953, Levine et al. 1991a, Luckhart et al. 1991, Tedders 1994, Lavender and Oliver 1996, Durden et al. 1997a, Clark et al. 1998). The susceptibility of the cotton mouse (Oliver et al. 1993a), cotton rat (Burgdorfer and Gage 1987), and rice rat (Levin et al. 1995) to infection by Lyme disease spirochetes has been confirmed. Prevalence of antibodies to *B. burgdorferi* among cotton mice was 22% in North Carolina, 38% in South Carolina, 37% in Georgia, and 35% in Florida (Magnarelli et al. 1992). *Borrelia burgdorferi* has been isolated from naturally infected cotton mice, cotton rats, rice rats, and woodrats from the same southeastern states (Oliver et al. 1993a, 1995; Oliver et al. 2000; Ryan et al. 2000).

In the southeastern United States, three tick species frequently bite humans: the lone star tick, *Amblyomma americanum* (L.); the American dog tick, *Dermacentor variabilis* (Say); and the blacklegged tick,

All animals sampled during this study were collected and handled in accordance with scientific collecting permits from the Department of Natural Resources and Department of Parks, Recreation, and Tourism of the state of South Carolina, and approved institutional care and use guidelines.

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Ixodes scapularis Say (Piesman and Sinsky 1988), all of which are common in South Carolina and have been removed from humans in the state (DiSalvo 1989, Clark et al. 1996, Felz et al. 1996). Borreliae have been detected in host-attached *A. americanum* (from raccoons) and *D. variabilis* (from rodents and raccoons) in coastal Virginia (Levine et al. 1991a), and from host-attached and questing *A. americanum* in Alabama (Luckhart et al. 1991, Burkot et al. 2001). *Borrelia* spirochetes have also been found in host-seeking *A. americanum* in Michigan (Walker et al. 1994), New Jersey (Schulze et al. 1984), Florida (K.L.C., unpublished data), Georgia (J.H.O., unpublished data), and Texas (Rawlings and Teltow 1994). *Dermacentor variabilis* and *A. americanum* appear to be incompetent laboratory vectors of *B. burgdorferi* (Piesman and Sinsky 1988, Mather and Mather 1990, Mukolwe et al. 1992, Sanders and Oliver 1995). Nevertheless, questions regarding the ability of *A. americanum* to transmit a different spirochete more closely related to relapsing fever *Borrelia* spp. (Barbour et al. 1996, Rich et al. 2001) to humans remain.

Southern *I. scapularis* are efficient vectors of *B. burgdorferi* (Burgdorfer and Gage 1986, Piesman and Sinsky 1988, Oliver et al. 1993b, Sanders and Oliver 1995). Spirochetes have been detected in *I. scapularis* removed from hosts in Alabama (Luckhart et al. 1991), specimens from vegetation in coastal Virginia (Levine et al. 1991a), and host-attached (Magnarelli et al. 1986) and questing (Levine et al. 1989) specimens from coastal North Carolina at sites associated with human cases. *Borrelia burgdorferi* has been isolated from host-seeking *I. scapularis* from Georgia (Oliver et al. 1993a, 1995) and South Carolina (Oliver et al. 2000). Additionally, Scoles et al. (2001) reported a previously unrecognized spirochete in blacklegged ticks from four northeastern states. Although data exist, the primary reservoir hosts and tick vectors involved in both natural maintenance and transmission of *Borrelia* to humans in the Southeast have not been determined unequivocally. Specific objectives of our study were to sample and identify rodents and ticks at several sites in South Carolina, screen them for *B. burgdorferi* infection, estimate the prevalence of *B. burgdorferi* infection in rodents and ticks from endemic sites, and analyze variation in infection prevalences among rodents and ticks with respect to several ecological variables.

Materials and Methods

Study Sites. Rodents and host-seeking adult ticks were collected at 10 sites in four regions of South Carolina (Clark et al. 1998, 2002). Sampling was focused at five sites in the Piedmont (Worthy's Ferry in Chester County), Sandhills (Poinsett State Park in Sumter County), and Coastal Zone (Hobcaw Barony in Georgetown County, and Wedge Plantation and Mt. Pleasant in Charleston County). Physiographic regions, habitats, and dominant vegetation at study sites have been previously described (Kovacik and Winberry 1987, Clark et al. 1998).

Rodent Collection and Maintenance. A combination of Sherman live-traps (Sherman Traps, Tallahassee, FL) and Tomahawk traps (Tomahawk Live Trap, Tomahawk, WI) were set in promising habitats at various sites and times during each month from July 1994 through December 1995. Collection methods were not standardized because the main purpose of rodent collection was to collect as many rodents as possible and examine them for presence of *B. burgdorferi.* Traps were usually baited with whole oats, and occasionally with dry dog food. Captured rodents were identified to species, anesthetized with ketamine hydrochloride (100 mg/ml, Ketaset, Bristol, Syracuse, NY) at a dosage of 0.2 ml/kg body weight, and examined for ticks. Rodents were maintained in the laboratory at the University of South Carolina's former International Center for Public Health Research, McClellanville, SC, for several days before being transported to the Institute of Arthropodology and Parasitology, Georgia Southern University, Statesboro, GA, where they were euthanized, and various tissues cultured for *Borrelia* isolation.

Tick Collection. Ticks were removed from hosts and stored in 70% ethanol. Host-seeking adult ticks were collected from May 1994 through December 1995 by flagging/dragging a 1-m square flag made of yellow flannel cloth over vegetation. Live adult ticks destined for *B. burgdorferi* culture were maintained in transport vials containing a few blades of grass until they could be tested. Voucher tick specimens from this study are deposited in the U.S. National Tick Collection, Institute of Arthropodology and Parasitology, Georgia Southern University with accession numbers RML 121717 and RML 122303 through RML 122321.

Spirochete Isolation and Characterization. Culture procedures were the same as previously reported by Oliver et al. (1993a, 1998). Briefly, rodent tissues (urinary bladder and ear clips) were cultured in Barbour-Stoenner-Kelly medium (Barbour 1984) and incubated at 34°C. Cultures were examined for spirochetes by darkfield microscopy twice weekly for 2 wk and, if spirochetes were not detected, weekly thereafter for 6 wk. Our methods for screening and characterizing spirochetal isolates by indirect fluorescent antibody (IFA) analysis, Western blot, polymerase chain reaction (PCR), and sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) have been published previously (Oliver et al. 1993a, 1995, 1996).

Statistical Analysis. Spirochetal infection prevalence data were analyzed using a tree-based classification system in SPSS AnswerTree (SPSS 1999) as an exploratory method to investigate ecological variables that were most strongly associated with *B. burgdorferi* infection in rodents and ticks. Specifically, we used the chi-squared automatic interaction detection (CHAID) algorithm as the tree growing method. CHAID is a highly efficient technique for segmentation, or tree growing (Kass 1980). The statistical test used by the program depends on the measurement level of the target variable. For a continuous target variable, an *F*-test is used to identify optimal splits for tree growth, and if the target variable is categorical, a

Table 1. Prevalence of *B. burgdorferi* sensu lato infection in rodents from South Carolina, 1994–1995

Physiographic Region	County	Locality	No. of positive rodents/no. tested (%) of each species								
			N. f.	*O. n.*	*O. p.*	*P. g.*	*P. l.*	*R. h.*	*R. r.*	*S. h.*	Total
Piedmont	Chester	Worthy's Ferry	—	0/1	0/6	—	0/2	0/1	—	1/23 (4.3)	1/33 (3.0)
Sandhills	Sumter	Poinsett State Park	0/1	—	—	2/25 (8.0)	—	—	0/1	0/1	2/28 (7.1)
Coastal plain	Orangeburg	Biser Farm	—	—	—	—	—	—	—	0/3	0/3
	Berkeley	Naval Weapons Station	—	—	—	0/1	—	—	—	0/3	0/4
Coastal zone	Georgetown	Hobcaw Barony	8/13 (61.5)	—	—	10/14 (71.4)	—	—	—	—	18/27 (66.7)
	Charleston	Wedge Plantation	7/10 (80.0)	—	0/7	16/18 (88.9)	—	0/1	—	2/4 (50.0)	25/40 (62.5)
		Mt. Pleasant	7/8 (87.5)	—	—	11/16 (68.7)	—	—	—	8/10 (80.0)	26/34 (76.5)
Total			22/32 (68.8)	0/1	0/13	39/74 (52.7)	0/2	0/2	0/1	11/44 (25.0)	72/169 (42.6)

N. f., Neotoma floridana; O. n., Ochrotomys nuttalli; O. p., Oryzomys palustris; P. g., Peromyscus gossypinus; P. l., Peromyscus leucopus; R. h., Reithrodontomys humulis; R. r., Rattus rattus; S. h., Sigmodon hispidus.

chi-squared test is used. The target variable for our tree-based analyses was the presence/absence of *B. burgdorferi* infection. Predictor variables for the rodent classification tree included rodent species, place of collection (county and site as separate variables), collection date (month and year separately), number of larvae, nymphs, adults (where applicable), and total number of each tick species for all tick species found parasitizing the rodents collected. The only predictor variables for the tick classification tree were tick species, collection site, and county.

Accuracy (predictive validity) of the trees was estimated by both resubstitution, whereby the tree is both built and tested on the entire set of data, and cross-validation. The significance level (alpha) for splitting tree nodes and merging categories of data was 0.05. Bonferroni adjustment, activated by default in AnswerTree, was used to correct alpha levels for multiple comparisons. Tree growth was limited to a maximum depth (number of levels below the root node) of five. Other tree growth stopping rules we specified were related to the minimum number of cases for nodes to be split. Parent nodes with fewer than 10 cases would not be split, and if splitting a node would result in a child node with less than five cases, that node would not be split.

Results

Rodent and Tick Collection. The species, numbers, and distribution of rodents captured, and the geographic distribution, abundance, and seasonal activities of the ticks recovered from those rodents and from vegetation have been described (Clark et al. 1998). Briefly, a total of 237 rodents representing seven genera and eight species were captured at nine sites in six counties and four geographic regions of South Carolina. Host associations of ticks collected from those rodents are reported in another paper (Clark et al. 2002). A total of 3,535 host-seeking adult ticks was collected from vegetation (Clark et al. 1998). Collections represented three genera and six species from eight sites in the state.

Spirochete Isolation. Spirochetes were isolated from cultured tissues of 72 (43%) of 169 rodents tested (Table 1). This included 22 (69%) of 32 woodrats, 39 (53%) of 74 cotton mice, and 11 (25%) of 44 cotton rats. All isolates were *B. burgdorferi* sensu lato based on results of IFA, Western Blot, PCR, and SDS-PAGE analyses. Of these, 25 isolates from rodents and ticks from the Mt. Pleasant site (Charleston area) were further characterized as *B. burgdorferi* sensu stricto (Oliver et al. 2000). Overall, infection prevalence was highest in the Coastal Zone, with similar prevalences recorded at individual sites in this region (Table 1). Prevalence of infection in rodents was 77% at Mt. Pleasant, 63% at Wedge Plantation (both in Charleston County), and 67% at Hobcaw Barony (Georgetown County). By contrast, infection prevalences of rodents at Poinsett State Park (7%) in the Sandhills, and Worthy's Ferry (3%) in the Piedmont, were much lower.

Infection prevalences of cotton mice (37/48, 77%), cotton rats (10/14, 71%), and woodrats (22/31, 71%) tested from the Coastal Zone were similar, as noted above. At Poinsett State Park in the Sandhills and Worthy's Ferry in the Piedmont, only two (8%) of 25 cotton mice and one (4%) of 23 cotton rats, respectively, were infected. Seasonal prevalence of *B. burgdorferi* infection in cotton mice, cotton rats, and woodrats captured at coastal zone sites was ≈46% in winter (December–February), 63% in spring (March–May), 71% in summer (June–August), and 81% in autumn (September–November). Although few tick specimens from rodents were tested, one (7%) of 14 adult *I. minor* recovered from woodrats trapped at Hobcaw Barony, and one (11%) of nine adult *I. minor* from woodrats at Wedge Plantation contained *B. burgdorferi* spirochetes.

Isolations were also made from 31 (2.6%) of 1,193 host-seeking adult ticks (Table 2). Only two species, *I. affinis* and *I. scapularis*, were found to harbor *B. burgdorferi.* The prevalence of spirochetes in *I. scapularis* (12/864, 1.3%) was low compared with that in *I. affinis* (19/74, 25.7%). Infected *I. scapularis* were collected only at the three Coastal Zone sites, whereas positive *I. affinis* originated from two sites in the Coastal Zone (Hobcaw Barony and Wedge Plantation), and one site in the Sandhills, Poinsett State Park (Table 2). Five isolates from adult *I. scapularis* from the Mt. Pleasant site were identified as *B. burgdorferi* sensu stricto (Oliver et al. 2000).

Statistical Analysis. The CHAID analysis of *B. burgdorferi* infection in rodents produced a fitted tree

Table 2. Prevalence of *B. burgdorferi* sensu lato infection in host-seeking adult ticks from South Carolina, 1994–1995

Physiographic Region	County	Locality	No. of culture positive ticks/no. tested (%) of each species					
			A. a.	*A. m.*	*D. v.*	*I. a.*	*I. s.*	Total
Piedmont	Chester	Worthy's Ferry	—	—	0/1	—	—	0/1
Sandhills	Sumter	Poinsett State Park	0/10	—	—	4/10 (40.0)	0/256	4/276 (1.4)
Coastal zone	Georgetown	Hobcaw Barony	0/127	—	—	1/6 (16.6)	2/120 (1.6)	3/249 (1.2)
	Charleston	Wedge Plantation	0/73	0/15	0/10	14/39 (35.9)	5/242 (2.0)	19/379 (5.0)
		Mt. Pleasant	—	0/19	—	0/19	5/246 (2.0)	5/284 (1.8)
Total			0/210	0/34	0/11	19/74 (25.7)	12/864 (1.3)	31/1193 (2.6)

A. a., Amblyomma americanum; A. m., Amblyomma maculatum; D. v., Dermacentor variabilis; I. a., Ixodes affinis; I. s., Ixodes scapularis.

consisting of nine nodes (Fig. 1). The initial split on "*county*" partitioned the 169 observations into groups of 68 and 101 individuals (nodes 2 and 3). This split showed that rodents collected at sites in the Coastal Zone counties of Charleston and Georgetown were infected at significantly higher prevalences (68.3%) than those from sites in other counties (4.4%) not in the Coastal Zone region ($\chi^2 = 79.84$, df = 1, P value = 0.0000). The first group (node 2) represented a terminal node and was not split further.

The second group (node 3) of rodents was then split based on the variable *species.* This split showed a significant difference in infection prevalence between harvest mice and rice rats (node 4, n = 8, 0%) and

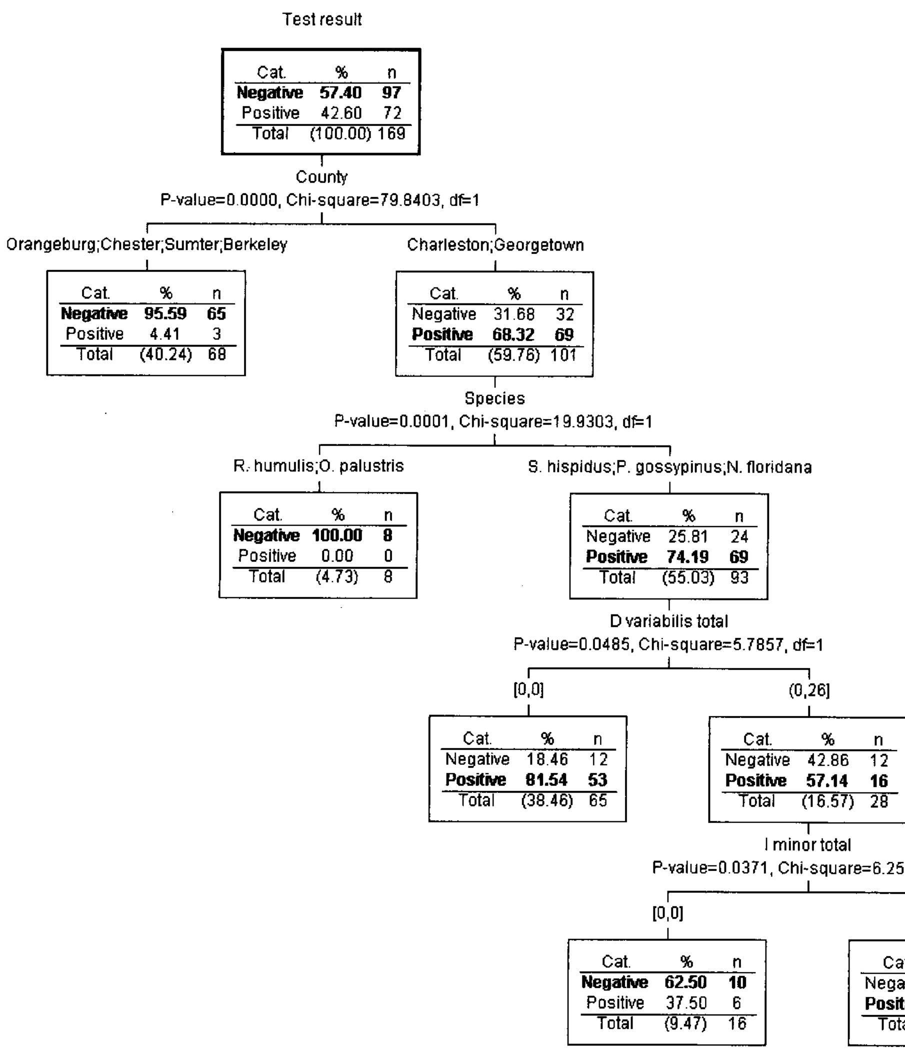

Fig. 1. Classification tree created from CHAID analysis of *B. burgdorferi* infection among rodents in South Carolina.

cotton rats, cotton mice, and woodrats (node 5, $n = 93$, 74.2%) from Coastal Zone sites ($\chi^2 = 19.93$, df = 1, $P = 0.0001$). Node five was then split on the basis of the total number of *D. variabilis* ticks (larvae and nymphs) found parasitizing these rodents. Infection was significantly higher among cotton rats, cotton mice, and woodrats that were not parasitized by this species of tick (node 6, $n = 65$, 81.5%, $\chi^2 = 5.78$, df = 1, $P = 0.0485$) compared with those parasitized by up to 26 ticks (node 7, $n = 28$, 57.1%).

Finally, the latter group was split based on the total number of *I. minor* parasitizing those rodents. This showed that, among the aforementioned rodents parasitized by *D. variabilis*, spirochete prevalence (node 9, $n = 12$, 83.3%) was significantly higher ($\chi^2 = 6.25$, df = 1, $P = 0.0371$) among those parasitized by *I. minor* (up to 53 larvae, nymphs, and/or adults) than among those from which no *I. minor* were recovered (node 8, $n = 16$, 37.5%). The tree misclassified or incorrectly predicted individual rodents' infection status 14% or 18% of the time with a standard error of the risk estimate of 0.026 or 0.030 based on whether the risk estimate and standard error were calculated via resubstitution or cross-validation, respectively.

CHAID analysis of *B. burgdorferi* infection in ticks produced a fitted tree consisting of eight nodes (Fig. 2). The split on *species* partitioned the 1,193 observations into three groups of 255, 864, and 74 individual ticks (nodes 2, 3, and 4), respectively. This split showed that *I. scapularis* ticks were infected at a significantly higher rate (1.39%) than *A. americanum, A. maculatum,* or *D. variabilis* (all 3, 0%) ($\chi^2 = 76.72$, df = 2, P value = 0.0000). The second group (node 3) of *I. scapularis* was then split on the variable *county*, showing a significant difference ($\chi^2 = 8.50$, df = 1, P value = 0.0106) in infection prevalence between ticks collected from Charleston and Georgetown counties in the Coastal Zone (1.97%, node 5) and those from Sumter County in the Sandhills (0%, node 6). The *I. affinis* ticks (node 4) were split on the statistically significant variable *site* ($\chi^2 = 13.40$, df = 1, P value = 0.0018), which separated ticks from Hobcaw Barony, Wedge Plantation, and Poinsett State Park, with a combined infection prevalence of 34.6% (node 7) from those from Mt. Pleasant (0%, node 8). This tree misclassified tick infection status an estimated 2% of the time (SE = 0.005), whether calculated using resubstitution or cross-validation.

Discussion

Infected rodents and ticks collected at sites in Sumter, Charleston, and Georgetown counties in the centrally located Sandhills, and Coastal Zone of South Carolina confirm that *B. burgdorferi* is endemic at several locations in different regions. Although no infections were detected in rodents or ticks from the Coastal Plain, *B. burgdorferi* may occur there also. However, we tested no ticks and only seven rodents from that region. Because no ticks and only one cotton rat from the Worthy's Ferry site in the Piedmont were found to be infected, more research is necessary to determine if *B. burgdorferi* is established in that region of the state.

Infection prevalences of cotton mice, cotton rats, and woodrats captured in the Coastal Zone (50–89%) were comparable to those reported for *Peromyscus leucopus* in northeastern states (Anderson et al. 1985, 1987; Levine et al. 1985; Mather et al. 1989), and much higher than those reported for rodents collected in southeastern states during previous investigations (Luckhart et al. 1991, Magnarelli et al. 1992). Prevalence of spirochetes in rodents from Coastal Zone sites was also much higher than in those from sites located further inland (4–8%). This agrees with findings from investigations conducted in some other southeastern states, where isolations of Lyme disease spirochetes from rodents and ticks have been most commonly reported from coastal areas (Levine et al. 1991a, 1993; Oliver et al. 1993a; Oliver et al. 1995). Thus, we believe that the intensity of *B. burgdorferi* transmission involving rodents in South Carolina is greatest in the Coastal Zone, and that prevalence of infection in rodents (and presumably ticks) probably decreases with increasing distance inland from this region. This geographic difference in prevalence of infection in rodents is most likely due to the differences in distribution and abundance of the ticks involved in endemic maintenance of the spirochete.

Spirochete infection prevalences were similar in all three infected rodent species collected in the Coastal Zone (Charleston and Georgetown counties). Cotton mice and cotton rats are suspected reservoirs of *B. burgdorferi* (Oliver et al. 1993a), and naturally infected specimens have been collected in Georgia and Florida (Oliver et al. 1993a, 1995). Our findings demonstrate the first isolation of the Lyme disease spirochete from the eastern woodrat (Oliver et al. 2000) and from *I. minor* adults attached to this host. Endemic maintenance cycles of *B. burgdorferi* involving *Ixodes spinipalpis* Hadwin & Nuttall (synonym: *I. neotomae* Cooley) and dusky-footed woodrats, *Neotoma fuscipes* Baird in California (Brown and Lane 1992), and Mexican woodrats, *Neotoma mexicana* Baird in Colorado (Maupin et al. 1994) have been reported. *Borrelia burgdorferi* sensu lato has been previously isolated from *I. minor* attached to birds collected at the Wedge Plantation (Durden et al. 1997b). We are currently conducting laboratory transmission studies with *I. minor* and eastern woodrats (*N. floridana*) to test our hypothesis that a similar endemic maintenance cycle exists in coastal South Carolina.

Although the rice rat is a competent reservoir for *B. burgdorferi* (Levin et al. 1995), none of the specimens collected during this study tested positive for spirochetes. However, isolates of *B. burgdorferi* have been obtained from rice rats collected in North Carolina (Levine et al. 1993) and Virginia (Sonenshine et al. 1993). We examined low numbers of rice rats ($n = 13$) in this study, which may partially explain our findings. Lack of infection in rice rats from the Coastal Zone of South Carolina, where overall prevalence of spirochetes in several other species was high, may be further explained by habitat-associated factors. Most

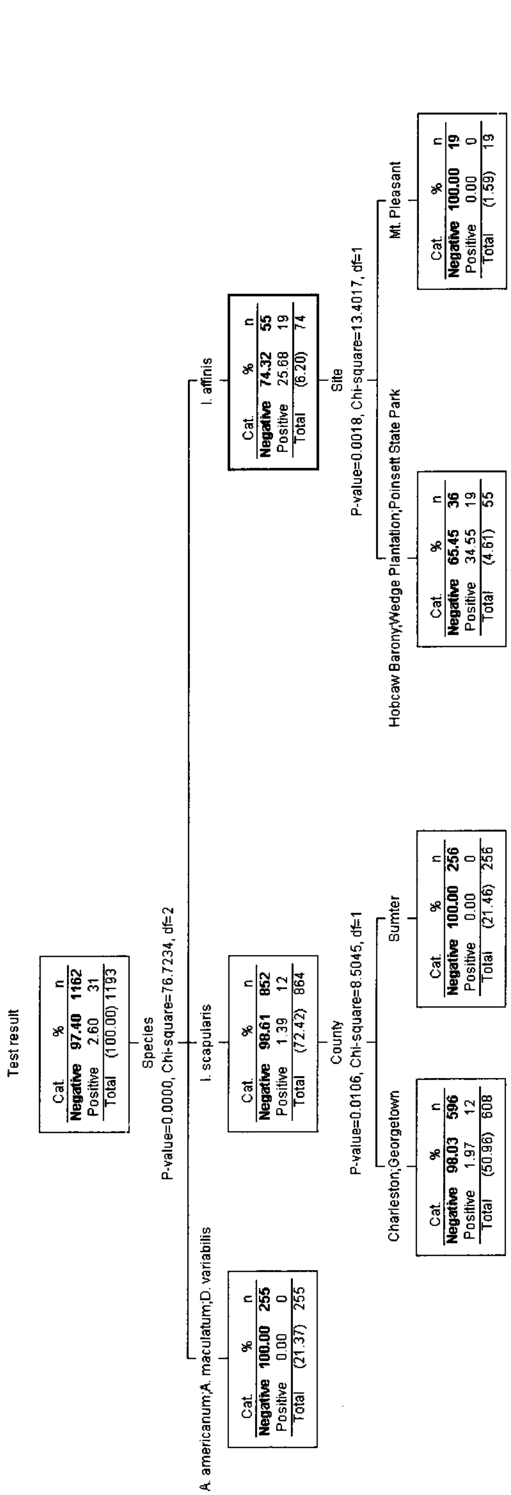

Fig. 2. Classification tree created from CHAID analysis of *B. burgdorferi* infection among ticks collected in South Carolina.

(6/8, 75%) of the rice rats we collected in this region came from a marsh habitat, where tick populations are usually low. Also, rice rats are known to forage underwater for plants (Whitaker 1980), which may reduce the duration of tick attachment, and perhaps minimize probability of spirochete transmission to these hosts in wetland areas.

We isolated spirochetes from rodents captured during all seasons, but the highest prevalence of infection was in rodents collected during autumn months. This differs from reported seroprevalences for white-footed mice, *Peromyscus leucopus* (Rafinesque), in the northeastern United States, which are highest in spring and summer when nymphal *I. scapularis* are most active (Anderson et al. 1987, Magnarelli et al. 1988). Our data also contrast with reported seroprevalence data for deer mice, *Peromyscus maniculatus* (Wagner), and piñon mice, *Peromyscus truei* (Shufeldt), in northern California, which were highest in spring (Lane 1990a).

Our results document the first isolations of *B. burgdorferi* from host-seeking *I. affinis* (Oliver 1996). Prevalence of infection in adults of this species was surprisingly high (26%) in comparison to that recorded for *I. scapularis* (1.4%). Immature stages of *I. affinis* commonly feed on rodents (Oliver et al. 1987, Durden and Keirans 1996, Lavender and Oliver 1996, Clark et al. 1998). Therefore, the high prevalence of spirochetes in adult *I. affinis* from Hobcaw Barony (17%) and Wedge Plantation (36%), both sites in the Coastal Zone where rodent infection levels were high, was not surprising. However, no isolates were obtained from *I. affinis* collected at Mt. Pleasant, the Coastal Zone site where the overall prevalence of spirochetal infection in rodents was highest. More puzzling was the finding that the prevalence of spirochetes in *I. affinis* was highest (40%) in those collected from Poinsett State Park in the Sandhills, where only two (8%) of 25 cotton mice were found to be infected with *B. burgdorferi*.

The numbers of questing adult *I. affinis* recovered by drag sampling is generally low (Clark et al. 1998). Because relatively few specimens were tested for spirochetal infection, sampling variability alone may be the reason for the apparently confusing results. Another possible reason may be lack of knowledge of host associations for this tick. Immatures have been recovered from a variety of hosts including *N. floridana; P. gossypinus; S. hispidus;* southern short-tailed shrew, *Blarina carolinensis* (Bachman); eastern gray squirrel, *Sciurus carolinensis* Gmelin; Virginia opossum, *Didelphis virginiana* Kerr; raccoon, *Procyon lotor* (L.); and Carolina wren, *Thryothorus ludovicianus* (Latham) (Oliver et al. 1987, Durden and Keirans 1996, Lavender and Oliver 1996). Serologic surveys have demonstrated antibodies to *Borrelia* in gray squirrels and opossums (Magnarelli et al. 1984, Godsey et al. 1987). Also, *B. burgdorferi* has been isolated from raccoons (Anderson et al. 1983), although this mammal apparently is an inefficient reservoir of the spirochete (Norris et al. 1993, Ouellette et al. 1993). Spirochete-infected *I. dentatus* Marx and *I. scapularis* have been removed from Carolina wrens (Levine et al. 1991a, Stafford et al. 1995, Durden et al. 1997b), and a high proportion of larval *I. scapularis* removed from this host in one study were infected with *B. burgdorferi* (Stafford et al. 1995). Therefore, it may be that immature *I. affinis* in South Carolina commonly parasitize, in addition to rodents, other host species whose involvement in the ecology of the Lyme disease spirochete is not yet understood.

The low *B. burgdorferi* isolation prevalence from *I. scapularis* in our study agrees with reported findings in other southeastern states (Levine et al. 1989, Levine et al. 1991a, Teltow et al. 1991, Oliver et al. 1993a). Southern *I. scapularis* immatures frequently feed on certain lizards (especially skinks) under natural conditions (Rogers 1953, Apperson et al. 1993, Oliver et al. 1993b), and this habit may act to divert some ticks from feeding on reservoir-competent rodents (Apperson et al. 1993, Oliver et al. 1993b). Studies in California (Lane and Loye 1989, Lane 1990b) showed that the western fence lizard, *Sceloporus occidentalis* Baird & Girard, is not a competent reservoir for *B. burgdorferi.* If this is also true for skinks in the southeastern United States, it might explain the low number of isolates recovered from adult *I. scapularis* during this study and those conducted in other southern states. However, a report by Levin et al. (1996) concluded that two lizard species common to this area, the southeastern five-lined skink, *Eumeces inexpectatus* Taylor, and the green anole, *Anolis carolinensis* (Voigt), were both susceptible to infection with *B. burgdorferi* and capable of infecting attached *I. scapularis* under laboratory conditions. Due to its arboreal habits, the green anole is not often parasitized by ticks, but southeastern five-lined skinks; five-lined skinks, *Eumeces fasciatus* (L.); broadhead skinks, *Eumeces laticeps* (Schneider); and eastern glass lizards, *Ophisaurus ventralis* (L.), are commonly parasitized by immature *I. scapularis* (Apperson et al. 1993, Oliver et al. 1993b; K.L.C., unpublished data). It is not known if lizards in South Carolina or other southern states are capable of naturally acquiring and maintaining *B. burgdorferi* infections that are infective to ticks.

No spirochetes were detected in *A. americanum* or *D. variabilis* adults tested during this study. Despite reports of spirochetes in host-seeking specimens (Teltow et al. 1991, Walker et al. 1994, Burkot et al. 2001), laboratory experiments have shown that neither species is a competent vector of Lyme disease spirochetes (Piesman and Sinsky 1988, Sanders and Oliver 1995). Those same experiments, and others (Mather and Mather 1990, Mukolwe et al. 1992, Oliver et al. 1993a), have confirmed the efficiency with which *I. scapularis* transmits *B. burgdorferi,* and *I. scapularis* is considered the primary vector of this spirochete to humans in the southeastern United States (Oliver 1996). Therefore, if the low infection prevalence recorded in *I. scapularis* during this study is representative of actual conditions, it may at least partially explain the low number of reported cases of Lyme disease in South Carolina (CDC 2001).

Ixodes scapularis is also considered the primary natural maintenance vector of *B. burgdorferi* in the eastern United States (Brown and Lane 1996). However, that may not be true in some areas, particularly the extreme Southeast. Our data suggest that *I. scapularis* may be only minimally involved in the endemic maintenance of *B. burgdorferi* in coastal South Carolina, and that *I. affinis* and *I. minor* may play more significant roles in maintaining and amplifying the frequency of infection among populations of reservoir competent rodent hosts.

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