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PRECIPITATING ANTIBODIES TO EPIZOOTIC HEMORRHAGIC DISEASE AND BLUETONGUE VIRUSES IN WHITE-TAILED DEER IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT: From 1981 to 1989, sera were collected from 3,077 white-tailed deer (*Odocoileus virginianus*) in Georgia and from 1,749 deer from 12 additional states in the southeastern United States. In Georgia, prevalence of precipitating antibodies to epizootic hemorrhagic disease virus (EHDV) and bluetongue virus (BTV), as determined by agar gel immunodiffusion tests, was dependent on physiographic region, age, and year. Overall prevalence of antibodies to EHDV and/or BTV was 11, 33, 48, and 14% for the Mountain, Piedmont, Coastal Plain, and Barrier Island regions, respectively. Results suggested varying patterns of EHDV and BTV activity throughout the state. Serologic results from other southeastern states were consistent with the Georgia sample; prevalence estimates (EHDV and/or BTV) for corresponding physiographic regions deviated by <10%. Over this larger geographical area, antibody prevalence in deer appeared to increase with decreasing latitude.

Key words: Epizootic hemorrhagic disease virus, bluetongue virus, white-tailed deer, *Odocoileus virginianus*, antibodies, prevalence, serosurvey.

INTRODUCTION

Epizootic hemorrhagic disease virus (EHDV) and bluetongue virus (BTV) (Reoviridae: Orbivirus) infections in white-tailed deer (*Odocoileus virginianus*) may be inapparent (Kocan et al., 1982) or may produce a clinical syndrome collectively referred to as hemorrhagic disease (HD) (Thomas et al., 1974). Although there is much clinical, virological and serological evidence of EHDV and BTV in white-tailed deer (Stair et al., 1968; Thomas and Trainer, 1970; Prestwood et al., 1974; Thomas et al., 1974; Foster et al., 1980; Couvillion et al., 1981; Feldner and Smith, 1981; Brannian et al., 1983), many epizootiological aspects of these viruses in wild populations remain undefined.

Hemorrhagic disease was first documented in white-tailed deer of the southeastern United States in 1971 during an epizootic in which both EHDV and BTV were isolated (Prestwood et al., 1974; Thomas et al., 1974). These viruses were believed to be responsible for unexplained deer mortality in this region as early as

1949 (Prestwood et al., 1974). In a subsequent serological survey of 455 white-tailed deer sampled from 12 southeastern states from 1973 to 1981, precipitating antibodies to EHDV and BTV were detected in 34% and 24% of deer, respectively (Couvillion et al., 1981). Of 414 white-tailed deer sampled in 1980 in Georgia, 34% and 36% were seropositive to EHDV and BTV, respectively (Odiawa et al., 1985).

We report data from an 8-yr serological survey of white-tailed deer in Georgia. Objectives of this study were to serologically determine the prevalence and annual pattern of EHDV and BTV infection in the state and to test for potential effects associated with physiographic region and age structure of the sample. Supplemental serological data from white-tailed deer in 12 additional states in the southeastern United States also are presented.

METHODS

From 1981 to 1989, sera were collected from hunter-killed deer harvested from October to January on wildlife management areas administered by the Georgia Department of Natural

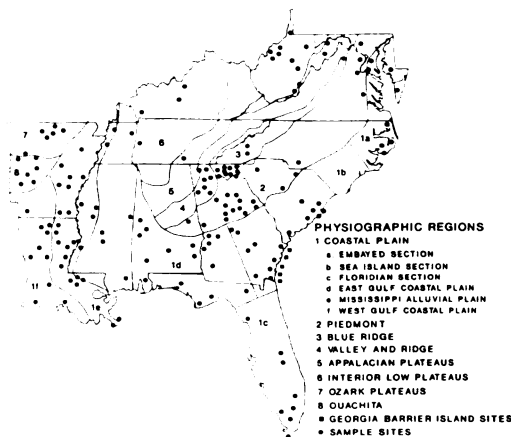


FIGURE 1. Sample locations for white-tailed deer in the southeastern United States by physiographic regions.

Resources. Additional samples from Georgia were obtained from deer collected under permit during herd health checks and other unrelated studies. Statewide, deer were collected from 49 areas (Fig. 1); however, areas sampled varied by year. Sera also were collected during 1981 to 1989 from 118 locations in 12 additional southeastern states, primarily during routine herd health checks in summer and early fall (Fig. 1).

When possible, age was determined based on tooth eruption and wear patterns (Severinghaus, 1949). Physiographic regions from which deer were sampled were delineated by Fenneman (1946). Two exceptions were made for data analysis. The Georgia barrier islands, which are a part of the Sea Island section of the Coastal Plain physiographic region, were treated as an

individual region. Due to sample size restraints, data from the Blue Ridge region and the Ridge and Valley region of Georgia were pooled and were collectively referred to as the Mountain region.

Sera were tested for EHDV and BTV antibodies by agar gel immunodiffusion (AGID) (Pearson and Jochim, 1979) at the Georgia Diagnostic Assistance Laboratory (College of Veterinary Medicine, The University of Georgia, Athens, Georgia 30602, USA) or at the National Veterinary Services Laboratories, Science and Technology (Animal and Plant Health Inspection Service, USDA, Ames, Iowa 50010, USA). Annual data for Georgia white-tailed deer were compiled based on observations that clinical epizootic hemorrhagic disease and bluetongue in deer tend to occur during late summer and early fall (Couvillion et al., 1981). Therefore, the calendar year was not used; rather data for a given annual period included animals sampled from August 1 through July 31 of the succeeding year.

Prevalence data from Georgia by physiographic province and age class were tested for independence using the G-statistic (Sokal and Rohlf, 1981).

RESULTS

Prevalence of precipitating antibodies to EHDV and BTV for 3,077 white-tailed deer sampled in Georgia are given in Tables 1 and 2, respectively. Of these, 3,077 samples, all but 323 were collected from hunter-killed deer. Except for the Barrier Islands, prevalence of antibodies to EHDV exceeded those for BTV in all physiographic regions.

TABLE 1. Precipitating antibodies to epizootic hemorrhagic disease virus in white-tailed deer from Georgia, 1981 to 1989.

Sample period ^a	Physiographic region				Total
	Mountain ^b	Piedmont	Coastal Plain ^c	Barrier Island	
1981–82	6/33 (18%) ^d	27/68 (40%)	39/68 (57%)	25/75 (33%)	97/244 (40%)
1982–83	1/36 (3%)	33/71 (46%)	44/60 (73%)	33/94 (35%)	111/261 (43%)
1983–84	2/112 (2%)	7/36 (19%)	14/41 (34%)	14/101 (14%)	37/290 (13%)
1984–85	5/126 (4%)	18/63 (28%)	21/51 (41%)	10/167 (6%)	54/407 (13%)
1985–86	8/86 (9%)	19/93 (20%)	38/72 (53%)	10/198 (5%)	75/449 (17%)
1986–87	10/127 (8%)	16/85 (19%)	21/42 (50%)	7/236 (3%)	54/490 (11%)
1987–88	4/101 (4%)	11/65 (17%)	21/70 (30%)	4/179 (2%)	40/415 (10%)
1988–89	51/163 (31%)	47/97 (48%)	42/114 (37%)	4/147 (3%)	144/521 (28%)
Totals	87/784 (11%)	178/578 (31%)	240/518 (46%)	107/1,197 (9%)	612/3,077 (20%)

^a August 1 to July 31.

^b Includes the Blue Ridge and Ridge and Valley Regions.

^c Includes the Sea Island Section and East Gulf Coast Section of the Coastal Plain.

^d Number seropositive/number tested (% positive).

TABLE 2. Precipitating antibodies to bluetongue virus in white-tailed deer from Georgia, 1981 to 1989.

Sample period ^a	Physiographic region				Total
	Mountain ^b	Piedmont	Coastal Plain ^c	Barrier Island	
1981–82	1/33 (3%) ^d	27/68 (40%)	35/68 (51%)	51/75 (68%)	114/244 (47%)
1982–83	1/36 (3%)	29/71 (41%)	39/60 (65%)	42/94 (45%)	111/261 (43%)
1983–84	1/112 (1%)	5/36 (14%)	13/41 (32%)	24/101 (24%)	43/290 (15%)
1984–85	2/126 (2%)	3/63 (5%)	19/51 (37%)	15/167 (9%)	39/407 (10%)
1985–86	2/86 (2%)	6/93 (6%)	28/72 (39%)	7/198 (4%)	43/449 (10%)
1986–87	1/127 (1%)	10/85 (12%)	8/42 (19%)	0/236 (0%)	19/490 (4%)
1987–88	0/101 (0%)	12/65 (18%)	14/70 (20%)	1/179 (1%)	27/415 (7%)
1988–89	28/163 (17%)	26/97 (27%)	22/114 (19%)	5/147 (3%)	81/521 (16%)
Totals	36/784 (5%)	118/578 (20%)	178/518 (34%)	145/1,197 (12%)	477/3,077 (16%)

^a August 1 to July 31.^b Includes the Blue Ridge and Ridge and Valley Regions.^c Includes the Sea Island Section and East Gulf Coast Section of the Coastal Plain.^d Number seropositive/number tested (% positive).

For all years combined, prevalence of deer seropositive to EHDV differed ($P < 0.001$) among physiographic regions and was highest in deer from the Coastal Plain (Table 1). Differences ($P < 0.001$) were apparent in all pairwise comparisons between physiographic regions except for the Mountain (11%) versus Barrier Island (9%) comparison ($P > 0.3$). Differences in annual prevalence of EHDV antibodies were detected among years ($P < 0.001$), with the statewide peak prevalence of EHDV precipitating antibodies occurring during 1981–1982 and 1982–1983. However, periods of peak prevalence did not correlate among physiographic regions. For the Mountain regions and Piedmont, EHDV antibody prevalence was highest during 1988–1989, at which time antibodies were observed in 31 and 48% of these populations, respectively. An additional period of high EHDV antibody prevalence was apparent in the Piedmont during 1981 to 1983. A general decline in annual prevalence from 1981 to 1989 was observed in deer from the Barrier Islands, whereas only slight annual variation was evident in the Coastal Plain.

Evidence of recent EHDV activity, as determined by presence of EHDV precipitating antibodies in the 0.5-yr age class, was apparent throughout the 1981–1989 period in all physiographic regions except

the Barrier Islands (Table 3). This age class included 138, 112, 85, and 146 animals from the Mountains, Piedmont, Coastal Plain, and Barrier Islands, respectively.

Results for BTV (Table 2) were similar to observations for EHDV. Prevalence of seropositive deer differed ($P < 0.001$) among physiographic regions and was highest in the Coastal Plain. Differences also were apparent in all pairwise comparisons between physiographic regions ($P < 0.01$).

Except for the Mountain regions, a general decrease in BTV antibody prevalence with time was observed in all physiographic regions. This was most apparent in the Barrier Island deer populations where prevalence decreased from 68% in 1981–1982 to 3% in 1988–1989. All BTV-seropositive deer observed from the Barrier Islands from 1981–1982 to 1984–1985 were sampled from Ossabaw Island. In this single population, which represented 63% of the total Barrier Island sample, prevalence of BTV antibodies decreased from 80% during 1981–1982 to 2% during 1988–1989. Similar results were observed with EHDV antibodies in this population; their prevalence decreased from 34% to 1% during this time period.

Variation in prevalence of BTV antibodies was detected between years ($P < 0.001$). Antibodies to BTV in the 0.5-yr

TABLE 3. Precipitating antibodies to epizootic hemorrhagic disease virus (EHDV) and bluetongue virus (BTV) in 0.5-yr old white-tailed deer from Georgia, 1981 to 1989.

Sample period ^a	Physiographic region				Total
	Mountain ^b	Piedmont	Coastal Plain ^c	Barrier Island	
1981–82	5 ^d	8 (2B, 1X)	13 (1B)	12 (4B, 6X)	38 (7B, 7X)
1982–83	13	21 (1E, 1B, 3X)	6 (1X)	19 (1E, 1B, 1X)	59 (2E, 2B, 5X)
1983–84	26 (1E)	10 (1B)	20 (1B)	23 (1E, 1B)	79 (2E, 3B)
1984–85	25 (2E)	15 (4E)	9	17	66 (6E)
1985–86	9 (1X)	24 (4E)	11 (1X) ^f	19	63 (4E, 2X)
1986–87	18 (3E)	15 (1X) ^e	7 (1E)	16	56 (4E, 1X)
1987–88	15	10 (1E) ^f	10 (1E)	13	48 (2E)
1988–89	27 (2B, 1E)	9 (1E) ^f	9 (1E, 1X)	27	72 (3E, 2B, 1X)

^a August 1 to July 31.^b Includes the Blue Ridge and Ridge and Valley Regions.^c Includes the Sea Island Section and East Gulf Coast Section of the Coastal Plain.^d Number sampled (E, number seropositive to EHDV alone; B, number seropositive to BTV alone; X, number seropositive to both EHDV and BTV). Unless otherwise noted, all seropositive deer were sampled during November through January.^e Detected 30 March 1987.^f Detected from 14 October to 30 October.

age class were clustered in the 1981–1982, 1982–1983, and 1983–1984 sample periods when they were detected in the Piedmont, Coastal Plain, and Barrier Islands (Table 3).

Age data were available for 2,424 of the 3,077 deer sampled in Georgia. Prevalence of antibodies to EHDV and/or BTV increased with age ($P < 0.001$) in the Piedmont, Coastal Plain, and Barrier Island samples (Fig. 2). Age class differences ($P > 0.4$) were not detected among deer from the Mountain regions.

A high frequency of sera from all physiographic regions tested positive on both the EHDV and BTV AGID tests (Table 4). The pattern of seropositive results, how-

ever, varied by region ($P < 0.005$). The highest percentage of dual reactivity occurred in those regions (Coastal Plain and Piedmont) with the highest prevalence of antibodies to EHDV (Table 1) or BTV (Table 2).

The percentage of seropositive animals which tested positive to both the EHDV and BTV AGID tests also varied among age classes (Fig. 3). However, this variation was not statistically significant ($P > 0.1$). Sera with antibodies to both EHDV and BTV represented 31% (16 of 52) of seropositive samples in the 0.5-yr age class and 53% (73 of 138) of seropositive results in the >4.5-yr age class. The percentage of seropositive samples which were positive for EHDV antibodies alone demonstrated an inverse trend and decreased with age. No trend with age was apparent in the observed frequency of sera which tested positive to the BTV AGID alone.

Overall, the prevalence of antibodies to either EHDV, BTV, or both in Georgia white-tailed deer from 1981–1989 was 11, 33, 48 and 14%, for the Mountain, Piedmont, Coastal Plain and Barrier Island regions, respectively (Table 4). Results from 1,148 deer samples from Alabama ($n = 140$), Arkansas ($n = 164$), Florida ($n = 189$), Kentucky ($n = 21$), Louisiana ($n =$

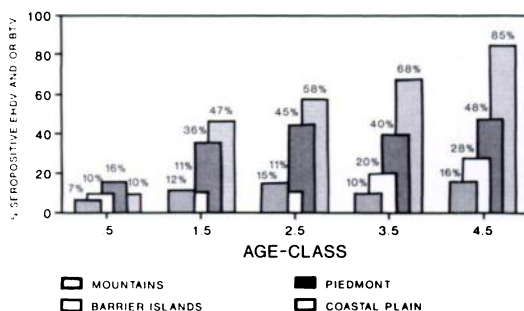


FIGURE 2. Prevalence of precipitating antibodies to epizootic hemorrhagic disease virus and/or bluetongue virus by age class and physiographic region in Georgia white-tailed deer, 1981 to 1989.

TABLE 4. Agar gel immunodiffusion (AGID) test results for antibodies to epizootic hemorrhagic disease virus (EHDV) and bluetongue virus (BTV) on sera from Georgia white-tailed deer by physiographic region.

Region	Positive AGID test results to:			Total seropositive ^a
	EHDV only	BTV only	EHDV + BTV	
Mountain	50 (59%) ^b	4 (5%)	30 (36%)	84/784 (11%)
Piedmont	74 (38%)	15 (8%)	104 (54%)	193/578 (33%)
Coastal Plain	79 (32%)	17 (7%)	154 (62%)	250/518 (48%)
Barrier Islands	35 (20%)	65 (38%)	72 (42%)	172/1,197 (14%)
Total	238 (34%)	101 (14%)	360 (51%)	699/3,077 (23%)

^a Number with antibodies to EHDV or BTV/number samples (% seropositive).^b Number seropositive (% of seropositive results).

164), Maryland ($n = 68$), Mississippi ($n = 57$), North Carolina ($n = 44$), South Carolina ($n = 112$), Tennessee ($n = 29$), Virginia ($n = 25$), and West Virginia ($n = 125$) are presented by physiographic region and section in Table 5. As with the Georgia data, prevalence of antibodies to EHDV and/or BTV in these physiographic regions was extremely variable and ranged from 7 to 48%. Prevalence of antibodies to EHDV exceeded those to BTV in all areas except for the Blue Ridge and Interior Highlands. Results from southeastern deer were consistent with preva-

lence estimates for the corresponding physiographic regions in Georgia, and in no case deviated by more than 10%. State-wide prevalence estimates for antibodies to EHDV, BTV, or both for Alabama (50%), Arkansas (34%), Florida (50%), Kentucky (19%), Louisiana (37%), Maryland (9%), Mississippi (47%), North Carolina (9%), South Carolina (58%), Tennessee (38%), Virginia (8%), and West Virginia (25%) showed a decreasing trend with increasing latitude.

The extent of dual reactivity in these samples, as in the Georgia sample, increased with antibody prevalence. For 77 seropositive results observed in regions with an antibody prevalence (EHDV or BTV) of less than 30% (Table 5), 42 (55%) tested positive for EHDV antibodies only, 22 (29%) were positive for BTV antibodies only, and 13 (17%) tested positive on both tests. Of the 303 seropositive samples from those regions where overall prevalence exceeded 30% (Table 5); 115 (38%) serums were positive for EHDV antibodies only, 24 (8%) were positive for BTV antibodies only, and 164 (54%) tested positive in both AGID tests.

DISCUSSION

The high frequency of deer with positive reactions to both the EHDV and BTV AGID tests limits reliability of individual prevalence estimates for these viruses, since cross reactions could not be differentiated from actual dual infection. Prevalence estimates for precipitating antibodies to

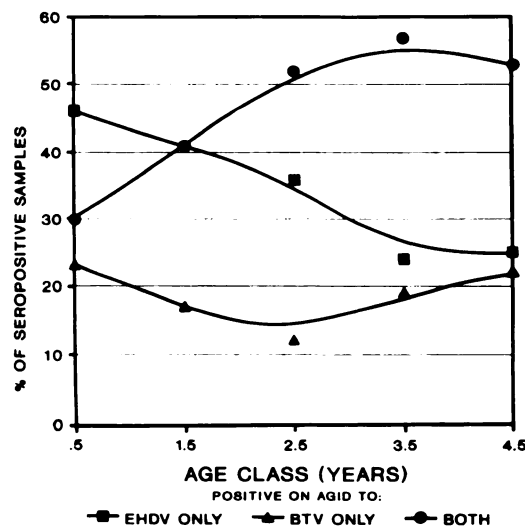


FIGURE 3. Frequency of seropositive white-tailed deer with precipitating antibodies to epizootic hemorrhagic disease virus (EHDV) alone, bluetongue virus (BTV) alone, and EHDV and BTV by age class, 1981 to 1989.

TABLE 5. Precipitating antibodies to epizootic hemorrhagic disease virus (EHDV) and bluetongue virus (BTV) in white-tailed deer of the southern United States by physiographic region (1981 to 1989).

Physiographic region	States	n	EHDV	BTV	Total sero-positive*
Blue Ridge	NC, VA	18	1 (5%) ^b	2 (11%)	3 (17%)
Ridge and Valley	WV	31	4 (13%)	1 (3%)	5 (16%)
Appalachian Plateau	TN, WV	99	21 (21%)	5 (5%)	26 (26%)
Piedmont	AL, MD, NC, SC, VA	43	6 (14%)	5 (12%)	10 (23%)
Interior Low Plateaus	KY, TN	27	4 (15%)	2 (7%)	4 (15%)
Interior Highlands ^c	AR	102	15 (15%)	17 (17%)	23 (23%)
Coastal Plain					
(Embayed Section)	NC, VA, MD	99	4 (4%)	3 (3%)	7 (7%)
(Sea Island Section)	SC	99	46 (46%)	29 (29%)	47 (47%)
(Floridian Section)	FL	115	44 (38%)	43 (37%)	51 (44%)
(East Gulf Coast Section)	AL, FL, MS	242	112 (46%)	57 (23%)	116 (48%)
(Mississippi Alluvial Section)	AR, LA, MS, TN	201	52 (26%)	36 (18%)	63 (31%)
(West Gulf Coast Section)	AR, LA	62	25 (40%)	23 (37%)	25 (40%)
Totals		1,138	334 (29%)	223 (20%)	380 (33%)

* Number with antibodies to EHDV or BTV.

^b Number seropositive (% positive).^c Includes Ozark Plateaus and Ouchita Provinces.

EHDV (Table 1) and BTV (Table 2) therefore should be interpreted as maximum values. Although these prevalence estimates provide little information relating to exposure to specific viruses or serotypes and may not adequately describe herd immunity, they do provide a basis for comparing broad patterns of EHDV and/or BTV exposure over time and between populations and regions.

Antibodies to both EHDV and BTV in individual white-tailed deer have been previously reported (Couvillion et al., 1981; Odiawa et al., 1985) and may result from cross reactivity between shared minor antigenic determinants (Campbell, 1985) or through actual dual infections, as reported in cattle (Foster et al., 1980). In sheep, complement-fixing antibodies developed against both EHDV and BTV following inoculation with either virus (Tomori, 1980). A broadening of the host's antibody response to these viruses also may follow repeated antigenic stimulation even with a homologous virus. In sheep, this has been observed with complement-fixing antibodies at a serotype specific level (Tomori, 1980). This has also been reported at a group specific level in cattle tested by

AGID (Bowen, 1987). The observed increase in frequency of dual positive animals with increased antibody prevalence and age in white-tailed deer is consistent with a pattern of repeated virus exposure. The extent to which these dual positive results have resulted from multiple infections with different viruses or from repeated infections with homologous viruses is unknown.

Due to the lower frequency of antibodies to both EHDV and BTV in the 0.5-yr age class, young deer may provide clearer serological evidence of group-specific viral activity than older animals. The 0.5-yr age class also can be utilized as serological indicators of recent viral activity, provided that the sample period is late enough to eliminate or greatly reduce the possibility of detecting maternal antibody. In Georgia, peak rut occurs from mid-October through mid-December and varies throughout the state (Kammermeyer, 1987). With a gestation period of 200 days, fawning on the Barrier Islands and the adjacent eastern portion of the Coastal Plain, starts in May. It occurs latest in the Mountains and southwestern Coastal Plain where peak fawning occurs in June and

July. Fawns born in Texas during June maintained maternal antibodies to BTV until the 4th week of August (<3 mo) (Hoff et al., 1974). Assuming a 3-mo duration for maternal antibodies to EHDV and BTV in Georgia deer, detection of antibodies in the 0.5-yr age class during November, December, and January would be indicative of actual infection rather than maternal transfer. However, in areas of late fawning antibody prevalence estimates for the fawn age class may not reliably estimate annual incidence due to maternal antibody protection during all or a portion of the late summer/early fall transmission period.

Statewide prevalence estimates of EHDV (20%) and BTV (16%) precipitating antibodies in Georgia white-tailed deer are lower than estimates reported by Couvillion et al. (1981) (EHDV = 44%, BTV = 20%) and Odiawa et al. (1985) (EHDV = 34%, BTV = 36%). As annual prevalence of EHDV and BTV antibodies varied greatly in this study, this discrepancy may be related to an extended sample period. Our statewide prevalence estimates may also be biased by the large proportion of the sample (64%) collected from the Mountain regions and Barrier Islands.

Differences in prevalence of precipitating antibodies to EHDV and BTV among the physiographic regions of Georgia were more extreme than regional differences reported for cattle and white-tailed deer by Odiawa et al. (1985). The bases for regional divisions utilized by Odiawa et al. (1985) were not explained and the inclusion of several physiographic regions in each division may have served to reduce variation. It is interesting, however, that the highest prevalence of antibodies to EHDV and BTV in white-tailed deer were associated with regions in the southern half of Georgia (Odiawa et al., 1985), which included the Coastal Plain physiographic region.

Regional variation in the prevalence of precipitating antibodies in deer, the distribution of antibodies among age classes, and the extent of dual reactivity in EHDV

and BTV AGID tests all suggest that different patterns of EHDV and/or BTV activity occur throughout Georgia. In the Mountain region (Blue Ridge and Ridge and Valley physiographic regions), an overall low antibody prevalence with abrupt annual changes suggests a pattern of low annual incidence and sporadic epizootic virus transmission. Nevertheless, seropositive results to EHDV and/or BTV in the 0.5-yr age class during all but 3 yr suggest that these viruses are present in these regions on an annual basis. In most years, however, only a small percentage of the population is infected.

The weak relationship between antibody prevalence and age class observed in the Mountain regions also is consistent with a sporadic activity pattern. With little or no prior exposure to these viruses, all age classes would be equally affected in the event of an outbreak. Such an event occurred between the 1987–1988 and 1988–1989 sample periods when prevalence of deer seropositive to EHDV and BTV increased from 4 to 31% and 0 to 17%, respectively. This rise in antibody prevalence was preceded by a clinical hemorrhagic disease outbreak in deer during late summer in which a type 2 EHDV was isolated (NVSL, unpubl. data). During 1988–1989, seropositive deer in the Mountain regions were detected at five of 13 sampled areas. Of the 111 deer sampled from these five areas, 51 (46%) were seropositive to EHDV and 28 (25%) had antibodies to BTV. During the previous year (1987–1988), 68 deer were sampled from these same five locations with only three animals testing positive on the EHDV AGID test.

It is impossible from these data to determine which viruses were present in the Mountain region populations during 1988–1989. It is interesting, however, that animals which tested positive for antibodies to EHDV and BTV alone were detected in the 0.5-yr age class. The possibility that both EHDV and BTV were present is supported by a high frequency of dual reac-

tivity (45%) during this single year. During the seven preceding years in this region, 37 seropositive deer were detected with only 7 (19%) testing positive on both the EHDV and BTV AGID tests.

In the Piedmont and Coastal Plain, a large percentage of the white-tailed deer population is infected with EHDV and/or BTV annually or on a short term cycle (2 to 3 yr). A similar pattern has been reported for BTV in white-tailed deer in the Coastal Plain of Texas (Hoff et al., 1974). In both the Piedmont and Coastal Plain regions, antibody prevalence increased with age. This increase with age is characteristic of a cumulative effect associated with annual infection of these populations. In the Coastal Plain of Georgia, an average of 85% of the >4.5-yr age class has been previously exposed to one or more of these viruses. An increase in antibody prevalence to BTV with age has also been reported for cattle in Louisiana (Hugh-Jones et al., 1989). Similar results with EHDV and BTV antibody prevalence and age have been reported for white-tailed deer (Swenson et al., 1979; Couvillion et al., 1981; Feldner and Smith, 1981). Annual or short-term viral transmission or multiple exposures to one or more of these viruses in these regions is also suggested by the high frequency of animals with antibodies to both EHDV and BTV (Table 3).

The observed serological patterns for the Barrier Island deer population appear similar to those observed in the Mountain region with a low annual incidence with sporadic outbreaks. In the Barrier Island, high antibody prevalence was restricted to Osabaw Island during 1981–1982 and 1982–1983. This was the only area in Georgia where a high percentage of animals tested positive on BTV AGID alone. Deer testing positive on the EHDV AGID test alone, however, were also detected in the 0.5-yr age class during 1982–1983 and 1983–1984 and may indicate that both viruses were present. Differences in serological results observed in the Barrier Island and Coastal Plain populations indicate that variation is

present not only between but within physiographic regions.

In relation to herd susceptibility, it appears that deer from the Mountain regions and Barrier Islands of Georgia have limited population immunity to both of these viruses and are at risk should conditions for EHDV or BTV transmission occur. However, for the Piedmont and Coastal Plain populations herd susceptibility cannot be assessed without more detailed information on immunity to specific viruses and serotypes. In Georgia, EHDV-1, EHDV-2, BTV-11, and BTV-17 have been isolated from ruminants (Odiawa et al., 1985). In the western United States, geographic variation and temporal shifts in dominant serotypes were observed over a 3-yr period (Stott et al., 1981). Whether such shifts occur naturally in white-tailed deer populations in the southeastern United States is unknown.

Serological results from other areas in the Southeast were consistent with those from the Georgia sample. Over this larger area, however, prevalence appeared to be related to latitude as well as to physiographic region. This was apparent among statewide prevalence estimates and within physiographic regions. Among the sectional divisions of the Coastal Plain, antibody prevalence increased from 7% from the northernmost Embayed section (NC, VA, MD) to 47 and 44% for the southernmost Sea Island (SC) and Floridian (FL) sections, respectively. Prevalence of antibodies to EHDV or BTV in the Floridian section was actually higher (59%) when a sample of 32 isolated Key deer (*Odocoileus virginianus clavium*) was removed from the data. A similar north-to-south increase in prevalence was apparent within the Piedmont deer populations, with a 10% antibody prevalence to EHDV or BTV in Maryland, Virginia, and North Carolina and 33% prevalence of antibodies in South Carolina and Georgia. This relationship is also apparent from statewide serological data reported by Couvillion et al. (1981).

In summary, the high frequency of deer

with precipitating antibodies to both EHDV and BTV limits reliability of antibody prevalence estimates for these viruses. In addition, without serologic data for specific EHDV and BTV serotypes, only negative data can be related to herd immunity. A lower frequency of dual positive AGID results in the 0.5-yr age class suggests that these animals may provide clearer serological evidence of group specific activity as well as evidence of recent viral transmission.

Serological data from white-tailed deer in Georgia indicate different patterns of virus activity throughout the state. These range from a pattern of annual enzootic activity in the Coastal Plain and Piedmont to a pattern of low annual incidence with sporadic epizootic activity in the Barrier Islands and Mountains. Local variation also is apparent within physiographic regions. The detection of antibodies in the 0.5-yr age class throughout the state on an almost annual basis suggests that EHDV and/or BTV are enzootic in all physiographic regions. Differences in viral activity patterns therefore may relate to local variations in host and/or vector conditions which regulate transmission.

Serologic results from deer sampled throughout the southeastern United States are consistent with the Georgia data. However, variation relative to latitude greatly influences results within broad physiographic regions.

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LITERATURE CITED

- BOWEN, R. A. 1987. Serologic responses to calves to sequential infections with epizootic hemorrhagic disease virus serotypes. *American Journal of Veterinary Research* 48: 1449-1452.
- BRANNIAN, R. E., N. GIESSMAN, W. PORATH, AND G. L. HOFF. 1983. Epizootic hemorrhagic disease in white-tailed deer from Missouri. *Journal of Wildlife Diseases* 19: 357-358.
- CAMPBELL, C. H. 1985. Bluetongue: Diagnostic/antigenic interpretation. *Progress in Clinical and Biological Research* 178: 435-444.
- COUVILLION, C. E., V. F. NETTLES, W. R. DAVIDSON, J. E. PEARSON, AND G. A. GUSTAFSON. 1981. Hemorrhagic disease among white-tailed deer in the Southeast from 1971 through 1980. *Proceedings of the United States Animal Health Association* 85: 522-537.
- FELDNER, T. J., AND M. H. SMITH. 1981. Epizootic hemorrhagic disease virus in Montana: Isolation and serologic survey. *American Journal of Veterinary Research* 42: 1198-1202.
- FENNEMAN, N. M. 1946. Physical divisions of the United States. United States Department of the Interior, Geologic Survey, Washington, D.C., 1 pp. (Map.)
- FOSTER, N. M., H. E. METCALF, T. L. BARBER, R. H. JONES, AND A. J. LUEDKE. 1980. Bluetongue and epizootic hemorrhagic disease virus isolations from vertebrate and invertebrate hosts at a common geographic site. *Journal of the American Veterinary Medical Association* 176: 126-129.
- HOFF, G. L., D. O. TRAINER, AND M. M. JOCHIM. 1974. Bluetongue virus and white-tailed deer in an enzootic area of Texas. *Journal of Wildlife Diseases* 10: 158-163.
- HUGH-JONES, M. E., W. P. TAYLOR, F. JONES, G. LUTHER, J. MILLER, P. KARNS, AND P. HOYT. 1989. Serological observations on the epidemiology of bluetongue infections in Louisiana cattle. *Preventative Veterinary Medicine* 7: 11-18.
- KAMMERMEYER, K. 1987. Why Georgia's rut varies. *Georgia Outdoor News* 1: 16-12.
- KOCAN, A., A. E. CASTRO, B. ESPE, R. T. DOYLE, AND S. K. OLSEN. 1982. Inapparent bluetongue in free-ranging white-tailed deer. *Journal of the American Veterinary Medical Association* 181: 1415-1417.
- ODIAWA, G., J. L. BLUE, D. E. TYLER, AND E. B. SHOTTS. 1985. Bluetongue and epizootic hemorrhagic disease in ruminants in Georgia: Survey by serotest and virologic isolation. *American Journal of Veterinary Research* 46: 2193-2196.

- PEARSON, J. E., AND M. M. JOCHIM. 1979. Protocol for the immunodiffusion test for bluetongue. *Proceedings of the American Association of Veterinary Laboratory Diagnosticians* 22: 463–475.
- PRESTWOOD, A. K., T. P. KISTNER, F. E. KELLOGG, AND F. A. HAYES. 1974. The 1971 outbreak of hemorrhagic disease among white-tailed deer of the southeastern United States. *Journal of Wildlife Diseases* 10: 217–224.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as a criteria of age in white-tailed deer. *The Journal of Wildlife Management* 13: 195–216.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W.H. Freeman and Company, New York, New York, 859 pp.
- STAIR, E. L., R. M. ROBINSON, AND L. P. JONES. 1968. Spontaneous bluetongue in Texas white-tailed deer. *Pathologia Veterinaria* 5: 164–173.
- STOTT, J. L., K. C. ELSE, B. MCGOWAN, L. K. WILSON, AND B. I. OSBORN. 1981. Epizootiology of bluetongue virus in the western United States. *Proceedings of the United States Animal Health Association* 85: 170–180.
- SWENSON, J. E. 1979. Effects of a hemorrhagic disease epizootic on a white-tailed deer population in eastern Montana. *Proceedings of the Montana Academy of Science* 38: 25–32.
- TOMORI, O. 1980. Bluetongue and related viruses in Nigeria: Experimental infection of West African dwarf sheep with Nigerian strains of the viruses of epizootic hemorrhagic disease of deer and bluetongue. *Veterinary Microbiology* 5: 177–185.
- THOMAS, F. C., AND D. O. TRAINER. 1970. Bluetongue virus in white-tailed deer. *American Journal of Veterinary Research* 2: 271–278.
- , N. WILLIS, AND G. RUCKERBAUER. 1974. Identification of viruses involved in the 1971 outbreak of hemorrhagic disease in southeastern United States white-tailed deer. *Journal of Wildlife Diseases* 10: 187–189.

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