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EXPERIMENTAL STUDIES OF ST. LOUIS ENCEPHALITIS VIRUS IN VERTEBRATES

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ABSTRACT: Serologically negative birds and mammals of species, known from other studies to be exposed naturally to St. Louis encephalitis (SLE) virus in Memphis, Tennessee, and other selected species were inoculated experimentally with strains of SLE virus to determine their potential as natural hosts. Mosquitoes (*Culex* sp.) were allowed to feed on some of the inoculated vertebrate species, held for 14 days, and tested for SLE infection. The cardinals (*Richmondena cardinalis*), robins (*Turdus migratorius*), and baby chicks (*Gallus gallus*) all became viremic; 97% of the bobwhites (*Colinus virginianus*) and 20% of the Japanese quail (*Coturnix coturnix*) became viremic. No viremia was detected in raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), or adult cotton rats (*Sigmodon hispidus*). Only 20% of cottontail rabbits (*Sylvilagus audubonii*), 50% of wood rats (*Neotoma mexicana*), and 75% of hamsters (*Mesocricetus auratus*) but all the young cotton rats and least chipmunks (*Eutamias minimus*) were susceptible. Robins had the highest titered viremia but were viremic for the shortest period of time. Bobwhites had lower peak viremia titers but for a longer duration. Biologic differences in the response of some vertebrates to different SLE strains were noted. *Culex pipiens quinquefasciatus* mosquitoes readily became infected after feeding on viremic cardinals. Comparisons of the experimental data with information obtained from field investigations provided a better understanding of the contributions of the various vertebrate species to the transmission and maintenance of SLE virus in nature.

INTRODUCTION

St. Louis encephalitis (SLE) virus is found throughout the Americas and periodically causes epidemics among humans in North America. Natural SLE infections are most common in avian hosts and aviaphilic mosquitoes, although SLE virus isolations have been obtained from mammalian hosts (McLean and Bowen, 1980), non-aviaphilic mosquitoes (Mitchell et al., 1980), and even other types of vectors (McLean et al., 1985). Field investigations conducted during epidemic and endemic periods of transmission have identified a number of avian species as the primary hosts for SLE virus (McLean and Scott, 1979) and a few species of culicine mosquitoes as the principal vectors (Mitchell et al., 1980) in North America. However, there are regional differences in the species of birds that serve as the important reservoir and amplifying hosts and in the species of *Culex* responsible for transmission of SLE virus. Also, differences in the effectiveness of vertebrate species serving as hosts for mosquito-borne viruses such as SLE are caused by a number of factors. Some of the factors include intrinsic host susceptibility, viremia of sufficient titer and duration to infect mosquito vectors, attractiveness to vector mosquitoes, and tolerance of mosquito feeding. Some aspects of these factors were investigated in this study. Of course, biologic characteristics of the host, vector, and virus and ecologic factors influencing their interactions are equally important. Studies of these complex interactions were beyond the scope of this study.

Field studies were conducted in rural-suburban habitats of Memphis, Tennessee, by the staff of the Division of Vector-Borne Viral Diseases (DVBVD), Centers for Dis-

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ease Control, to determine the important vertebrate hosts for and the factors affecting vertebrate involvement in the enzootic transmission of SLE virus in that metropolitan area. Information on SLE transmission within peridomestic avian populations in urban habitats was available from the arbovirus surveillance system of the Memphis-Shelby County Health Department (McLean et al., 1983). Some species of birds with higher SLE antibody titers and prevalences compared with the house sparrow (*Passer domesticus*) were present in relatively high densities in selected rural-suburban habitats and appeared to be important maintenance hosts for SLE virus in Memphis. These field data allowed us to concentrate the laboratory studies on a few selected avian species and further examine their potential as enzootic hosts. In addition, several species of mammals were found to have SLE antibody in an area in Memphis from which an SLE virus strain was isolated from ticks [*Dermacentor variabilis* (Say)] (McLean et al., 1985); these mammals were included in the study to determine their suitability as hosts for SLE virus. We also used selected avian and mammalian laboratory animals to compare them with the sylvatic species and to investigate their capability to serve as a source of virus for future transmission studies with the tick strain.

MATERIALS AND METHODS

Birds

Cardinals (*Richmondena cardinalis*) were captured with Potter traps in Memphis, Tennessee, in February 1980, and shipped to Fort Collins, Colorado, for the study. Robins (*Turdus migratorius*) and house sparrows were captured with mist nets in Fort Collins during July. Bobwhites (*Colinus virginianus*), Japanese quail (*Coturnix coturnix*), and white leghorn chickens (*Gallus gallus*) were all obtained in July as newly hatched chicks from commercial sources in Fort Collins. Only birds negative for SLE virus neutralizing (Nt) antibody were used in the study. The birds were maintained in the laboratory during the acute infection phase (August 1980) and in an aviary before and after the 30-day experimental period under conditions similar to those described elsewhere (McLean et al., 1983). Uninoculated controls of each species were housed with the inoculated birds and were handled similarly.

Mammals

Raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*) were captured with National traps in Memphis in February 1980, and shipped to Fort Collins for the study. Additional raccoons trapped in Larimer County, Colorado, were also used. These mammals were kept in monkey cages (0.8 × 0.8 × 1.0 m) during the experiment. Cotton rats (*Sigmodon hispidus*) were obtained from a laboratory colony in Lawrenceville, Georgia, and maintained as described elsewhere (McLean, 1982). Wood rats (*Neotoma mexicana*), least chipmunks (*Eutamias minimus*), and cottontail rabbits (*Sylvilagus audubonii*) were all captured in the foothills region of Larimer County, Colorado, during June and were maintained as described by Bowen et al. (1981). Hamsters (*Mesocricetus auratus*) were obtained from a colony maintained at the DVBVD laboratory for more than 15 yr. Only seronegative mammals were used in the experiment.

Virus

Three strains of SLE virus were used. Strain MSI-7 was isolated from a nestling house sparrow in Mississippi (Bowen et al., 1980) and passed twice in suckling mice (SM). Strain 69M-1143 was isolated from a raccoon in Florida (Wellings et al., 1972) and passed four times in SM. Strain 79V-10028 was isolated from ticks (*D. variabilis*) removed from a raccoon in Memphis, Tennessee (McLean et al., 1985), and passed twice in SM. Approximately 2,000 to 4,000 plaque-forming units (PFU) of each strain of virus were inoculated subcutaneously (sc) into all the animals except one group of bobwhites, which received 25,000 PFU.

Feeding of mosquitoes

Three-day-old adult female mosquitoes, *Culex nigripalpus* (Florida strain) and *Cx. p. quinquefasciatus* (Missouri strain), were obtained from established laboratory colonies maintained at the DVBVD laboratory at 24 C and 80% relative humidity in chambers with a 16-hr light and 8-hr dark cycle. The mosquitoes were provided with 5% sucrose, except for 12 hr before they were used in feeding trials, which were conducted inside the controlled chambers. Birds and mammals were placed in wire cages

small enough to restrict some of their movement and to prevent them from pursuing the mosquitoes. The mesh of the wire cages was large enough for mosquitoes to have easy access to the animals. The animal cages were placed into larger cages covered with mosquito-proof netting with a sleeve through which mosquitoes could be introduced each night at 1900 hr and extracted the next morning at 0800 hr by aspirator. Engorged mosquitoes were placed into ½-pint cartons and held in the controlled chamber for 14 days. The surviving mosquitoes were placed into screw-capped vials and kept at −70 C until tested for virus. The vertebrate hosts for the mosquitoes were bled immediately before the mosquitoes were introduced.

Laboratory procedures

Birds were bled from the jugular vein with a 1-ml syringe and 26-gauge needle. Large mammals were bled from the femoral artery with a 5-ml syringe and 20-gauge needle after being immobilized with ketamine hydrochloride and acepromazine. Small mammals were bled from the suborbital sinus with a capillary pipet after being anesthetized with ether. Blood specimens were obtained daily from all animals for days 1–7 and on days 10, 15, 21, and 30 postinoculation (PI). Blood (0.2 ml) from the birds and small mammals was mixed with 0.9 ml of diluent; blood from large mammals was left undiluted. The procedures for handling blood specimens and inoculating sera into cell culture have been described (Scott et al., 1983). Vero cell cultures grown in 25-cm² flasks were used for initial viral screening, and six-well plastic plates were used for virus titrations. The presence of Nt antibody in heat-inactivated sera was determined by the plaque-reduction neutralization test in Vero cell cultures in six-well plates as described by McLean et al. (1983). Single mosquitoes were ground in a mortar and pestle with 1.0 ml diluent, the suspension was centrifuged at 2,500 RPM for 20 min, the supernatant was separated, and 0.2 ml was inoculated onto monolayers of primary Pekin duck embryo cells grown in 25-cm² flasks. Identities of some of the virus isolations were confirmed by the complement fixation test (Calisher and Poland, 1980) to ensure that no other viruses were infecting the vertebrates or mosquitoes.

RESULTS

All of the five avian species inoculated were susceptible to SLE virus infection, although not equally. All cardinals, robins, and baby chickens, 97% of the bobwhites, and 20% of the Japanese quail became viremic (Table 1). The bobwhites, robins, and chickens had the highest viremia titers, and the bobwhites and chickens had the longest duration of viremia. Viremia titers of the cardinals were intermediate, and their total viremic response was quite similar to the response of house sparrows infected during a previous study (McLean et al., 1983). At the lower virus dosage, all the viremic birds tested for SLE Nt antibody developed it by 30 days PI, and all but one of the nonviremic Japanese quail produced antibody.

The viremic response of bobwhites receiving the lower virus dosage was significantly less ($P < 0.01$) in 6-wk-old than in 3-wk-old birds for both peak mean titers (3.03 ± 0.23 vs. 4.41 ± 0.27 $\log_{10}$ PFU/ml) and overall mean titers (2.81 ± 0.16 vs. 3.53 ± 0.14 $\log_{10}$ PFU/ml). Furthermore, the eight 3-wk-old bobwhites were viremic for a total of 42 days PI (average of 5.3 days per bird), and the eight 6-wk-olds were viremic for a total of only 16 days (average of 2.0 days per bird) for the same time period and for the lower virus dosage. In addition, 71% of the 42 viremic days for the 3-wk-olds were at or above 3.0 $\log_{10}$ PFU/ml, and 50% of the 16 viremic days for the 6-wk-olds were at this level. A single adult bobwhite inoculated with the 79V-10028 strain only produced a peak titer of 3.0 $\log_{10}$ PFU/ml and was viremic for 3 days. The response of 3-wk-old bobwhites to the two different concentrations of virus inoculated was also significantly different for both peak ($P < 0.05$) and overall mean titers ($P < 0.01$), with the lower viremia titers occurring in birds inoculated with the higher dosage. The mean peak titers of viremias in 6-wk-old bobwhites inoculated with the 79V-10028 strain were significantly higher ($P < 0.05$) than in bobwhites inoculated with the MSI-7 strain. The combined viremia results for the 24 bobwhites inoculated with the MSI-7 strain demonstrated that some daily viremia titers exceeded 4.0 $\log_{10}$

TABLE 1. Response of birds inoculated with strains of St. Louis encephalitis virus.

Species	Age	SLE virus strain used[a]	No. tested	Percent viremic	Mean viremia (PFU/ml)[b]			Mean duration (days)	Percent Nt Ab positive
					Peak titer[c]	Range of peak titer	Overall titer[d]		
Bobwhite (*Colinus virginianus*)	6 wk	79V-10028	8	100	4.1 ± 0.3	3.0–5.1	3.1 ± 0.1	4.3	NT
	3 wk	MSI-7	8	100	4.4 ± 0.3	3.4–5.3	3.5 ± 0.1	5.3	100
	6 wk	MSI-7	8	88	3.0 ± 0.2	2.0–3.8	2.8 ± 0.2	2.3	88
	3 wk	MSI-7[e]	8	100	3.7 ± 0.1	3.3–4.6	2.9 ± 0.1	4.9	88
Robin (*Turdus migratorius*)	2–3 mo	MSI-7	9	100	4.6 ± 0.4	2.0–6.0	4.2 ± 0.3	1.9	100
Japanese quail (*Coturnix coturnix*)	3 wk	MSI-7	10	20	3.2 ± 0.6	2.6–3.7	2.6 ± 0.3	3.0	89 (9)
Chicken (*Gallus gallus*)	3 day	79V-10028	6	100	4.8 ± 0.4	3.6–5.6	3.5 ± 0.2	4.7	NT
Cardinal (*Richmondena cardinalis*)	Adult	MSI-7	5	100	3.5 ± 0.5	2.0–5.3	3.0 ± 0.3	3.2	100
House sparrow[f] (*Passer domesticus*)	Adult	MSI-7	21	100	3.5 ± 0.1	2.6–5.1	3.0 ± 0.1	2.9	100

[a] MSI-7 = SM_4 passage of nestling house sparrow isolate; 79V-10028 = SM_2 passage of *Dermacentor variabilis* isolate.
[b] Titers expressed as the mean ± standard error $\log_{10}$ plaque-forming units (PFU) per ml of viremic blood.
[c] Peak titer includes only the highest titer for each bird.
[d] Overall titer includes all of the daily titers for all birds.
[e] 25,000 PFU/ml in Vero cell culture of SLE virus inoculated subcutaneously in this group and 2,000–4,000 PFU/ml in all other groups.
[f] These results are from a previous study (McLean et al., 1983).
Nt Ab = neutralizing antibody; NT = not tested; ( ) = number of animals tested.

PFU/ml on 6 consecutive days PI (Fig. 1). Also, the daily percentage of viremic bobwhites was greater than 50% for 5 days PI. Three bobwhites had delayed onsets of viremia (day 7 PI for two birds and day 10 PI for one bird); however, because of the bleeding schedule, only one virus-positive blood was obtained from each of these birds.

Mammals were less susceptible to SLE virus, and no viremia could be demonstrated in inoculated raccoons or opossums (Table 2). Females of *Cx. nigripalpus* readily fed on raccoons and opossums, but none became infected. Cotton rats were quite resistant to the two strains of SLE virus inoculated, although very young cotton rats developed intermediate viremia of short duration. Wood rats and cottontail rabbits were intermediate in susceptibility; chipmunks and hamsters were quite susceptible. Hamsters produced the highest titers and were viremic the longest of the mammalian species tested. The viremic response was similar in hamsters inoculated with the 79V-10028 strain and the MSI-7 strain. There were striking differences, however, in the viremia profile and the overall and daily percentage of hamsters viremic (Fig. 2). Even though many of the experimental mammals were not tested for Nt antibody, there was an obvious difference in the antibody response of cotton rats inoculated with dif-

ferent strains of SLE virus (0% positive with the MSI-7 strain vs. 100% positive with the 79V-10028 strain).

Cardinals were tolerant of *Cx. p. quinquefasciatus* mosquitoes feeding on them; 74% of the mosquitoes became fully engorged, and 13% of all the engorged mosquitoes became infected (Table 3). The SLE infection rate was significantly higher ($P < 0.01$) when the blood titer of the viremic cardinals on which the mosquitoes fed was greater than 3.0 $\log_{10}$ PFU/ml. The highest infection rate occurred when the blood titer was greater than 5.0 $\log_{10}$ PFU/ml. Some mosquitoes even became infected by feeding on viremic cardinals with titers between 2.3 and 2.6 $\log_{10}$ PFU/ml.

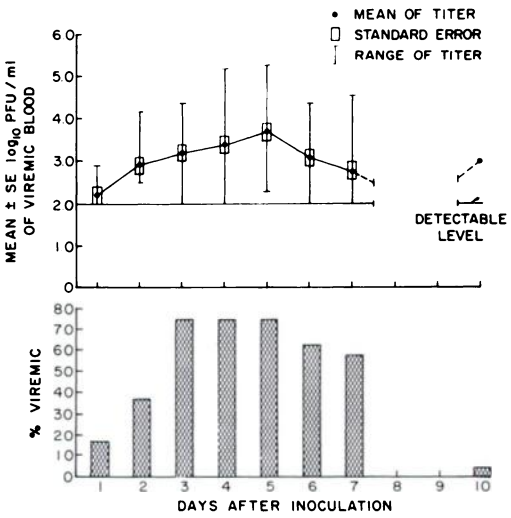

FIGURE 1. Viremia in 24 bobwhites (*Colinus virginianus*) after inoculation with St. Louis encephalitis virus (MSI-7 strain).

DISCUSSION

Experimental infection studies of vertebrate species found naturally exposed to SLE virus are necessary to determine their involvement in the epidemiology of SLE. Field studies conducted in Memphis identified species of birds and mammals that could be important natural hosts for SLE; however, the results from this study suggest that only three of the avian species studied are effective hosts. The three mammal species from Memphis appeared to be resistant to the SLE virus strains used. These results are consistent with those of previous experiments (McLean and Bowen, 1980).

The least chipmunk and the hamster were exceptions to the low susceptibility and poor viremic response of the mammalian species tested in this study and in previous studies. The available data suggest that some rodents, particularly sciurids including the least chipmunk, cricetids, and heteromyids, develop viremia adequate to infect mosquitoes (McLean and Bowen, 1980). There are a few species of sciurids present in sufficient densities and habitats in many midwestern urban areas to serve as natural hosts for SLE virus, although there is no evidence that SLE mosquito vectors feed on them.

The hamsters were quite susceptible to sc inoculation with the 79V-10028 strain of SLE virus used in this study, which is in contrast to previous studies where they were not susceptible by this route of inoculation but were susceptible by other routes of inoculation only (Karabatsos, 1980). With at least some SLE strains, hamsters can serve as a good source of virus in the laboratory and should provide the opportunity for further laboratory studies of virus, vector, and host.

The striking difference in the susceptibility, magnitude and duration of viremia in hamsters inoculated with the two different strains suggests significant biologic differences between the strains. Bobwhites also produced a greater viremic response to the 79V-10028 strain than to the MSI-7 strain, and cotton rats responded with a significantly greater serologic response when inoculated with this strain. In previous studies, the 79V-10028 strain was shown to be somewhat attenuated for 3-wk-old mice compared with the fully

TABLE 2. Response of mammals inoculated with strains of St. Louis encephalitis virus.

Species	Age	SLE virus strain used[a]	No. tested	Percent viremic	Mean viremia (PFU/ml)[b]			Mean duration (days)	Percent Nt Ab positive
					Peak titer	Range of peak titer	Overall titer		
Raccoon (*Procyon lotor*)	Adult	MSI-7 79V-10028 69M-1143	11	0	—	—	—	—	18
Opossum (*Didelphis marsupialis*)	Adult	69M-1143	3	0	—	—	—	—	100
Cotton rat (*Sigmodon hispidus*)	5 day	MSI-7	9	100	3.4 ± 0.2	2.8–4.5	3.1 ± 0.1	1.7	NT
	3 mo	MSI-7	12	0	—	—	—	—	0 (8)
	3 mo	79V-10028	8	0	—	—	—	—	100 (6)
Wood rat (*Neotoma mexicana*)	Adult	79V-10028	2	50	2.5	—	2.4 ± 0.1	3.0	NT
Least chipmunk (*Eutamias minimus*)	Adult	79V-10028	2	100	3.4 ± 0.9	2.5–4.3	2.9 ± 0.3	4.5	NT
Cottontail rabbit (*Sylvilagus audubonii*)	Adult	79V-10028	5	20	2.8	—	2.8 ± 0.1	2.0	100 (3)
Hamster (*Mesocricetus auratus*)	3 wk	MSI-7	6	50	3.6 ± 0.9	2.6–5.3	3.9 ± 0.5	2.0	NT
	3 wk	79V-10028	6	100	4.9 ± 0.2	4.4–5.6	3.8 ± 0.2	4.8	NT

[a] MSI-7 = SM_2 passage of nestling house sparrow isolate; 79V-10028 = SM_2 passage of *Dermacentor variabilis* isolate; 69M-1143 = SM_4 passage of raccoon isolate; 2,000–4,000 PFU/ml in Vero cell culture of SLE virus inoculated subcutaneously.
[b] Titers expressed as the mean ± standard error $\log_{10}$ plaque-forming units (PFU) per ml of viremic blood.
Nt Ab = neutralizing antibody; NT = not tested; ( ) = number of animals tested.

virulent MSI-7 strain in the same host (McLean et al., 1985). Both strains, however, had similar RNA oligonucleotide patterns (Trent and Naeve, 1980). SLE strains previously isolated from culicine mosquitoes in Memphis were similar to the MSI-7 strain in their virulence for 3-wk-old mice (Monath et al., 1980) and not like the intermediate virulence of the 79V-10028 tick strain. The bird and mammals species used in these experiments appeared to be more susceptible to and responded with a greater viremia to the 79V-10028 strain, despite its partial attenuation in 3-wk-old mice. The higher viremogenic capacity of the 79V-10028 strain does not coincide with the lower virulence of this strain, because these biologic markers were positively correlated with the MSI-7 and other SLE strains used in other studies (Bowen et al., 1980; Monath et al., 1980). The uniqueness of this strain from ticks and the possibility of cocirculation of two biologically distinct SLE strains within a single locality needs further investigation.

Of the three avian species found susceptible to SLE virus, the robin produced the highest viremia titers, higher than the baby chicks used in this study and higher than those reported for baby chicks in other studies (McLean and Bowen, 1980). They were also viremic for the shortest period of time. However, the response of the robins in this study may not reflect natural infections as they were stressed by

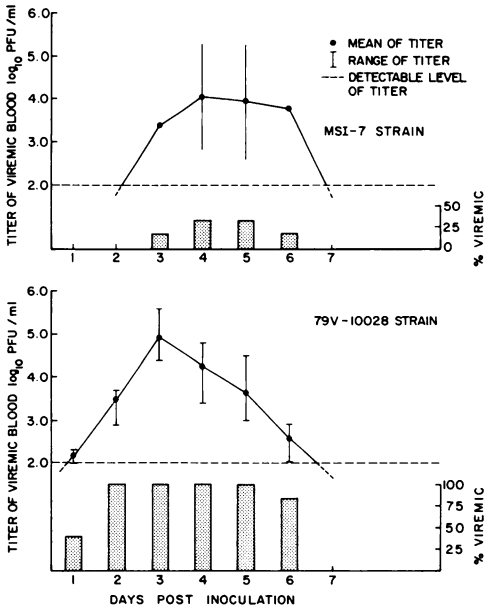

FIGURE 2. Viremia in hamsters (*Mesocricetus auratus*) after inoculation with two strains of St. Louis encephalitis virus.

lack of adequate diet, and half of them died during the first 10 days PI. Robins had the highest prevalence of SLE Nt antibody of any bird species tested during the 1975 SLE epidemic in Chicago (McLean and Bowen, 1980), and SLE virus was isolated from a robin during an epidemic in St. Louis in 1966 (Kokernot et al., 1969). Their seasonal presence in high densities in many urban areas, such as Chicago, St. Louis, and Memphis, combined with their susceptibility to SLE virus, as documented by the high titers of circulating virus demonstrated in this study, confirm their potential as an important amplifying host for SLE virus.

The cardinal was equally as susceptible to SLE virus as the robin but produced moderate titers and duration of viremia. However, even these lower levels of viremia were sufficient to infect vector mosquitoes on 4 of the 5 days that cardinals were viremic, and four of the five viremic cardinals provided an infective source of virus to mosquitoes. No minimum threshold of blood titer necessary to infect *Cx. p. quinquefasciatus* could be established, because a few mosquitoes became infected even on viremias of very low titers. Nevertheless, mosquito infectivity greatly increased when the titer was above 3.0 $\log_{10}$ PFU/ml and was greatest when the titer was above 5.0 $\log_{10}$ PFU/ml. Viremic cardinals, on the average, had titers of circulating virus above 3.0 $\log_{10}$ PFU/ml for 1.2 days and thus were capable of infecting at least 50% of the mosquitoes that fed upon them during that time. This probably represents the minimum viremic response for cardinals, since adult birds were used in this study; younger birds, particularly nestlings, usually produce higher viremic responses (Bowen et al., 1980). Generally, hosts that have greater amounts of virus in their peripheral blood should infect more mosquitoes if, as shown for cardinals in this study, they are attractive to mosquitoes and tolerant of their feeding.

The cardinal has been implicated as an amplifying host of SLE virus during several urban epidemics in Texas (Lord et al., 1974), and SLE virus was isolated also from a cardinal in St. Louis in 1966 (Ko-

TABLE 3. *Culex pipiens quinquefasciatus* mosquitoes exposed to SLE virus-inoculated cardinals (*Richmondena cardinalis*); percent engorged and infected with SLE virus.

Day PI[a]	Blood titer (PFU/ml)[b]	No. birds	No. mosquitoes fed	Percent engorged	Percent infected
1 & 2	2.0	3	106	86	0
5	2.0	1	35	17	0
4 & 5	2.3–2.4	3	80	84	10
2 & 4	2.6	2	62	68	5
3	3.0	1	32	85	0
3	3.3	1	24	100	21
2	3.9	1	37	60	55
3	5.2	1	21	71	80

[a] PI = postinoculation.
[b] Titers expressed as $\log_{10}$ plaque-forming units (PFU) per ml in Vero cell culture.

kernot et al., 1969); their population densities in urban areas in Texas, however, were too low for them to have contributed greatly to those epidemics. Cardinals could be an important enzootic maintenance host for SLE throughout the eastern part of the United States, where their densities are higher, because of their susceptibility, attractiveness to mosquitoes, tolerance of mosquito feeding, and ability to infect mosquitoes, as well as their temporal, spatial, and ecologic association with the mosquitoes which serve as vectors.

The bobwhites were investigated more intensively, i.e., inoculated with different strains, dosages, and at different ages, because of their very high prevalence of SLE antibody in Memphis and because little information was available on their susceptibility and natural exposure to SLE virus. As was found with chickens in other studies (Sudia and Chamberlain, 1959; Bowen et al., 1980), bobwhites were quite susceptible, and their viremic responses decreased with increased age and dosage of virus inoculated. Since young bobwhites had higher and longer viremias, they should be capable of infecting three to four times more mosquitoes than older bobwhites. The seasonal presence of young bobwhites in July in Memphis (McLean, unpubl. data), their susceptibility and adequate viremia of long duration discovered in this study, and the high prevalence of SLE antibody in Memphis all strongly suggest that this species is an important enzootic maintenance host for SLE virus in Memphis and possibly other areas. This species could also be used as an effective sentinel for SLE; it was successfully used for eastern and western (now Highlands J virus) encephalitis viruses in Maryland (Williams et al., 1971, 1972).

Three other sylvatic avian species, the blue jay (*Cyanocitta cristata*), the mockingbird (*Mimus polyglottos*), and the mourning dove (*Zenaidura macroura*), which could also be important hosts for SLE in Memphis because of their antibody prevalences, densities, and distributions, were studied previously in the laboratory (Jennings, 1969). All three species were quite susceptible to inoculation with SLE virus, although the blue jay was more susceptible to lower dosages. This information, combined with the laboratory results obtained from this study, has confirmed some of the field data on the important enzootic avian hosts of SLE and the incidental role of at least some of the mammalian species. A synthesis of these data should provide a more complete understanding of the epidemiology of SLE and should enable us to better design our future research efforts to fill in some of the gaps and enlarge upon undefined aspects.

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