



160865

FORUM

Potential Effect of Global Warming on Mosquito-Borne Arboviruses

WILLIAM C. REEVES, JAMES L. HARDY, WILLIAM K. REISEN, AND MARILYN M. MILBY

School of Public Health, University of California, Berkeley, CA

J. Med. Entomol. 31(3): 323-332 (1994)

ABSTRACT If global warming occurs in California, daily mean temperatures may increase by 3 to 5°C, precipitation patterns will change, and sea level may rise 1 m. Studies were done on effect of temperature changes on survival of *Culex tarsalis* Coquillett, the primary vector of western equine encephalomyelitis (WEE) and St. Louis encephalitis (SLE) viruses, in two regions where temperatures differed by 5°C. Daily mortality of adult vectors increased by 1% for each 1°C increase in temperature. At 25°C, only 5% of *Cx. tarsalis* survived for 8 or more days, the time required for extrinsic incubation of these viruses. Extrinsic incubation times for these viruses shortened when temperatures were increased from 18 to 25°C. WEE virus infection was modulated and transmission decreased at 32°C. If temperatures in the warmer region increase by 5°C, WEE virus may disappear and SLE virus may persist. In the cooler region, a 5°C increase would decrease vector survivorship and virus activity in midsummer. In North America, epidemics of WEE have prevailed above a 21°C isotherm and those of SLE below this isotherm. With global warming, epidemics of these viruses could extend into currently unresponsive northern areas. WEE virus would disappear from more southern regions. Geographic distribution of vector, human, and animal populations could be altered. North America could become more receptive to invasion by tropical vectors and diseases.

KEY WORDS global warming, mosquito, arbovirus

IN NOVEMBER 1987, the U.S. Environmental Protection Agency convened a workshop to consider "The Potential Impact of Climate Changes on Patterns of Infectious Disease in the United States" (Smith & Tirpak 1989). This meeting provided a background on meteorological changes expected to occur in the twenty-first century. It also stimulated us to reexamine existing data and develop research studies to determine how such environmental changes might affect the future prevalence of arbovirus infections and their vectors in California. We now believe it is feasible to predict some of the public health consequences of such events.

The majority of publications and organizations concerned with the effects of global warming have focused their attention on economic, industrial, general ecological, and demographic interests and not on public health outcomes. A review of the rapidly growing literature on the effect of global warming during the twenty-first century has provided a basis to formulate the following three simplified assumptions regarding its future impact in California (Smith & Tirpak 1989, Anonymous 1991): (1) daily mean temperatures will increase by 3-5°C; (2) patterns of precipitation will change and alter seasonal and regional water availability; (3) coastal sea levels may rise as much as 1 m. If these three events occur, we

believe there could be major changes in the prevalence of endemic arboviruses and in the distribution of their vertebrate hosts and vectors. To simplify this presentation, we will focus our attention on the impact of temperature changes on two mosquito-borne arboviruses, western equine encephalomyelitis (WEE), an alphavirus, and St. Louis encephalitis (SLE), a flavivirus, and their primary vector in California, *Culex tarsalis* Coquillett.

Background

WEE and SLE viruses have been active in California and recognized as important health problems since the 1930s. We have considerable knowledge of factors, particularly temperature, that affect the life table of the vector and interrelationships of the vector and viruses (Reeves 1990). These viruses spend most of their existence in the summer in the vector, where they are subject to major temperature variations. However, the viruses also are dependent upon serial transmission between the poikilothermic vector and homeothermic avian hosts. The transmission cycle for WEE virus is representative of many arboviruses (Fig. 1). The feral vertebrate hosts have viremias that are infectious to the vector for only a few days (Hardy & Reeves

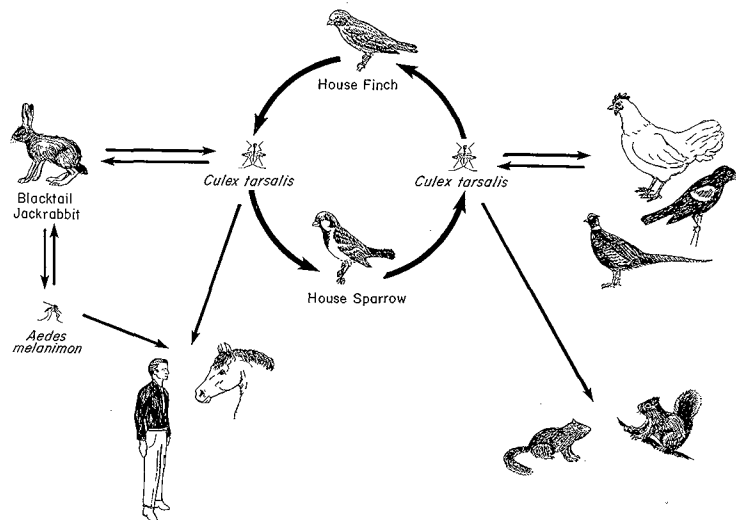


Fig. 1. Current concept of the summer transmission cycle of WEE virus in the Central Valley of California (from Hardy [1987], with permission of the *American Journal of Tropical Medicine and Hygiene*).

1990). Therefore, the vector-virus interrelationships provide an excellent model in which to study the impact of environmental stresses on the survival of both the vector and the virus. *Cx. tarsalis* also is the primary vector of three other viruses in this region, Turlock (a bunyavirus), Llano Seco (an orbivirus), and Hart Park (a rhabdovirus). Future studies could be extended to include these agents. This would provide a unique opportunity to evaluate the impact of climatological changes on five widely disparate infectious agents in a single vector species and its range of vertebrate hosts.

Our approach has been to initiate studies in the twentieth century to provide a data base that will allow us to describe probable events that may evolve in the twenty-first century. Two approaches have been taken. First, the Imperial and Coachella valleys in southern California currently experience the extremes of temperature anticipated to occur in the future in the more northern San Joaquin and Sacramento valleys. We have compared biological and virological findings from these regions to make predictions and used this information to design further field and laboratory studies that will expand the data base. The laboratory studies utilized programmable environmental chambers to determine the

effects of a broad range of temperatures on diapause, life tables, gonotrophic cycles, and vector competence of *Cx. tarsalis*. DATAPOD probes (OmniData International, Logan, UT) that continuously record temperatures are placed in representative microhabitats in the Coachella and San Joaquin valleys where *Cx. tarsalis* rests during the day and in the open spaces where the mosquitoes move after sunset and remain until they reenter resting sites in the morning (Meyer et al. 1990, Reisen et al. 1992a). Thus, realistic temperature data are obtained that can be programmed into the environmental chambers where vectors are held to study vector competence and survival.

Field Observations

Our primary attention has been concentrated on temperature because it is an environmental factor that can be measured and has a major influence on virus-vector-host interactions, vector survival, and generation time. A summary of average daily temperatures over a 30-yr period in the two regions revealed that there has been an amazingly consistent 5°C difference between the southern and northern regions throughout the year (Fig. 2). These differences in temperature

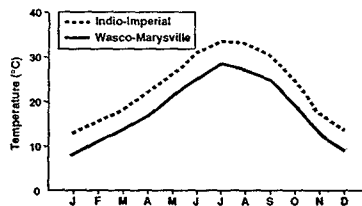


Fig. 2. Average daily temperatures in southern (Indio-Imperial, Coachella-Imperial valleys) and northern (Wasco-Marysville, San Joaquin-Sacramento valleys) California.

and accompanying ecological effects have provided us with a unique natural laboratory in which to investigate the potential impact of global warming on the transmission of arboviruses. These extremes occur within 350 km of each other.

The average monthly abundance patterns of adult female *Cx. tarsalis* in the two regions, based on New Jersey light trap collections, are consistently different (Fig. 3). In the north, the populations are very low in winter and early spring because the females diapause and are gonotrophically inactive in winter (Reisen & Reeves 1990). As a result, the annual buildup to high populations is delayed until midsummer. In contrast, high temperatures block the induction of diapause in southern California (Nelson 1971) and in Texas (Eads 1965). Thus, the vector remains reproductively active, and populations increase rapidly in the spring. Current studies indicate that the southern population is genetically competent to diapause if placed under proper light and temperature conditions. It is fortunate that daily photoperiods are essentially the same in the Coachella and southern San Joaquin valleys, so day length is not a variable that influences diapause differently in the two regions. The absence of diapause and the availability of temperatures compatible with the extrinsic incubation of viruses allows rapid and early buildup of vector populations and an increase in the number of virus cycles that can be completed in a year in the southern region (Reisen et al. 1986, 1993).

A second major difference between the northern and southern regions is that vector populations crash during midsummer in the south when mean daily temperatures exceed 30°C from June into September. This population crash represents, in part, a decrease in the daily survivorship of *Cx. tarsalis*. Data from field studies in Kern County on adult female *Cx. tarsalis* populations indicate that for every 1°C increase in temperature, there is a 1% decrease in mean daily survivorship (Fig. 4). The impact of this

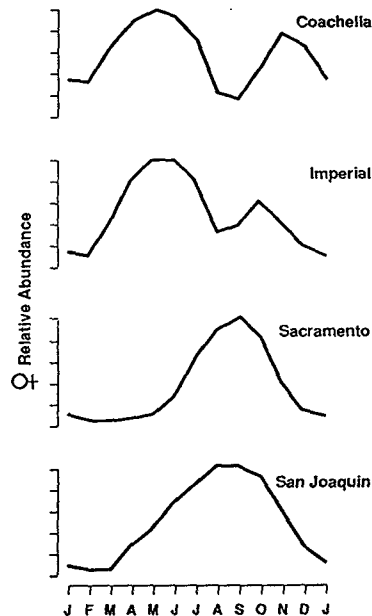


Fig. 3. Adult *Cx. tarsalis* abundance measured by New Jersey light trap collections in southern and northern California (from Reisen & Reeves [1990], with permission from the California Mosquito and Vector Control Association).

decrease on successful transmission of WEE or SLE viruses can be very important at higher temperatures because the majority of the vector population will not survive to complete more than one gonotrophic cycle, thus horizontal transmission of virus would not occur because infected mosquitoes would not refeed (Reisen & Reeves 1990).

Another factor influencing the abundance of *Cx. tarsalis* is autogeny. This is a genetic trait that allows ovarian development without a blood meal. When larvae from a genetically autogenous strain were provided with ample food and a water temperature of >22°C, they expressed a high autogeny rate regardless of the length of photoperiod. However, when the temperature was reduced to 18°C and the daily period of dark was increased from 8 to 14 h, autogeny was not expressed (Reisen et al. 1989). Thus, warmer environmental temperatures probably will increase the period of the year when autogeny is ex-

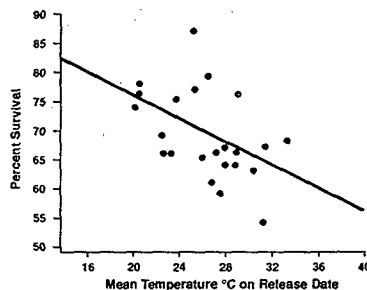


Fig. 4. Environmental temperature effects on adult female *Cx. tarsalis* survival, Kern County, 1976–1981.

pressed. Autogenous females typically are older when taking their first blood meal, and as compared with anautogenous females, fewer will survive to acquire and transmit viruses (Reisen & Reeves 1990). There is no evidence that WEE or SLE viruses are transovarially transmitted by *Cx. tarsalis* (Hardy & Reeves 1990). A high expression of autogeny theoretically could lead to development of large *Cx. tarsalis* populations without efficient virus transmission (Lyness 1970). Regardless of autogeny status, these southern California populations do not enter diapause for an extended time regardless of photoperiod.

To extend this finding further, the effects of 30 and 35% daily loss from an adult female *Cx. tarsalis* population are illustrated in Fig. 5 (Reisen & Reeves 1990). The 70% survivorship curve approximates data from field studies on a population in the northern region exposed to 26°C average daily temperatures. The 65% survivorship takes into account that for every 1°C increase in temperature there is a 1% decrease in daily survival and thus models exposure to an average of 31°C. This temperature is representative of temperatures during midsummer in the southern region. At the higher levels of mortality, a population will decrease rapidly if it is not compensated by an elevated recruitment rate. High mortality in a cohort of vectors also increases the risk that extrinsic incubation of WEE or SLE viruses will not be completed or that competent females will not refeed. As the arrows in Fig. 5 indicate, at these temperatures it requires at least 8 d from emergence for an adult to become infected with and complete extrinsic incubation for WEE virus, and at least 11 d for SLE virus (Reisen et al. 1983). By referring to Fig. 5, it can be seen that 5% or less of the population will survive at those temperatures and complete the extrinsic incubation period for either virus.

As a further factor in the population crash, a 5°C increase in temperature from 26 to 31°C in

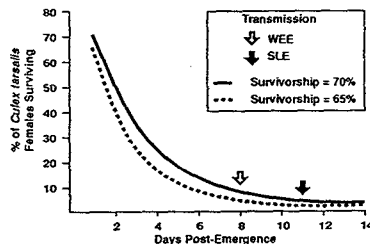


Fig. 5. Influence of environmental temperature on daily survivorship of adult female *Cx. tarsalis* and their transmission of WEE and SLE viruses (adapted from Reisen & Reeves [1990], with permission from the California Mosquito and Vector Control Association).

the aquatic environment caused a 50% decrease in adult production under controlled laboratory conditions (Reisen et al. 1984). Maximal larval survival was observed at 18°C. These studies were done with a laboratory colony of *Cx. tarsalis*.

We have no evidence that a heat-stressed *Cx. tarsalis* population will develop a modified genetic capacity for heat tolerance, and this is a subject for future study.

Data from DATAPODs collected during August in the southern and northern environments revealed that major differences in temperature are experienced by adult vectors each day while resting in refuges during the day and when they move into the open after sundown, at which time they mate, feed on hosts or nectar, and oviposit (Meyer et al. 1990). We have selected August as an example because it is a critical month for virus activity. Again, the temperatures in the Coachella Valley were much higher than in Kern County and will be even higher if global warming occurs (Fig. 6). Note that the vertical line marked "I" is the time of ingress when mosquitoes enter shelters to spend the daylight period and the line marked "E" is the time of egress in the evening. Again, the southern region experiences much higher temperatures, especially at the time of egress in the evening, and extreme differences in daily temperature are experienced by the vector in both areas in the summer.

Laboratory Observations

We will now consider some effects of increased temperature on the vector competence of *Cx. tarsalis* for WEE and SLE viruses. Data from laboratory studies allow us to predict that increased ambient temperatures will have both positive and negative effects on vector competence. As ambient temperatures increase, the

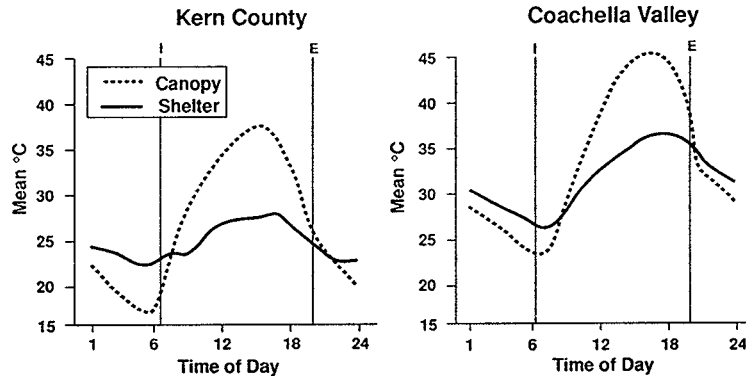


Fig. 6. Daily temperature in diurnal resting and nocturnal vegetation canopy microhabitats of female *Cx. tarsalis* related to extrinsic incubation of viruses (adapted, in part, from Meyer et al. [1990], with permission of the *Journal of Medical Entomology*).

time required for the completion of the extrinsic incubation period of the virus in the vector decreases. Cohorts of a laboratory strain of *Cx. tarsalis* females were fed on WEE or SLE virus, then divided into three groups and incubated at constant temperatures of 18, 25, or 32°C (Hardy & Reeves 1990). Virus transmission rates were determined at various times after infection when vectors were fed individually on chickens (Fig. 7). Both viruses, and particularly SLE virus, were transmitted more efficiently by infected females when incubated at 32°C than when held at lower temperatures. The shortening of the extrinsic incubation period in this instance would

compensate, in part, for the increased mortality of females at the higher temperature, and would ensure continued virus transmission. However, this would not be the case for WEE virus, because *Cx. tarsalis* has an enhanced ability to control or modulate WEE virus multiplication and transmission at higher extrinsic incubation temperatures (Kramer et al. 1983, Hardy 1988, Reitsen et al. 1993).

Virus modulation is illustrated by data from an experiment where infection rates were determined with WEE-infected *Cx. tarsalis* held over time at 18, 25, and 32°C (Kramer et al. 1983). Infection rates remained high for 21 d when fe-

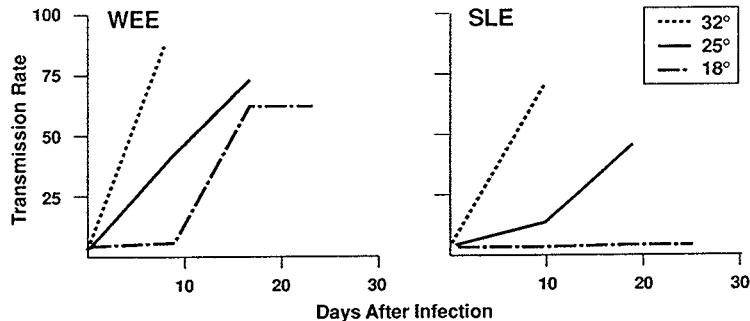


Fig. 7. Effect of temperature on transmission of WEE and SLE viruses by *Cx. tarsalis* (SLE data adapted from Hardy & Reeves [1990], with permission from the California Mosquito and Vector Control Association).

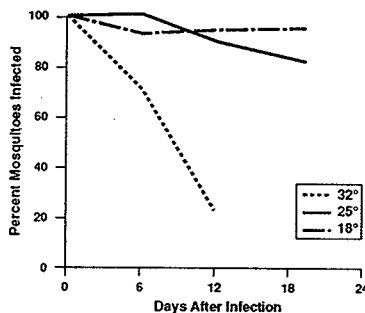


Fig. 8. Effect of temperature on modulation of WEE virus infection in infected *Cx. tarsalis* (from Hardy [1988], with permission from CRC Press, Boca Raton, FL).

males were incubated at 18 and 25°C; however, at 32°C infection rates decreased to 75% by day 6 after infection and to only 22% by day 12 (Fig. 8). This precipitous decrease in WEE virus infection rates at the higher temperature as they grow older may negate the potential enhanced ability of infected females to transmit WEE virus at the higher temperature after short periods of incubation (Fig. 7). Thus, one would expect WEE virus transmission cycles to be dampened as ambient air temperatures increase to the highest levels, where only a small proportion of females survives. It was surprising to find that WEE virus is modulated by the vector at 32°C because this virus experiences temperatures above 40°C for a period of several days during intrinsic incubation in its avian hosts. Subsequent studies dem-

onstrated that WEE virus modulation was a genetically controlled trait of the mosquito (Hardy & Reeves 1990). There is little or no indication that *Cx. tarsalis* can modulate SLE virus multiplication at any temperature (Hardy & Reeves 1990).

During a period of global warming, one expects temperatures to increase in the aquatic environments where the preimaginal mosquitoes develop. As was described above, this could increase larval mortality and the rate of autogeny. Our data also indicate that increased water temperature may affect virus transmission by *Cx. tarsalis*. For example, we demonstrated low levels of vertical transmission of SLE virus by *Cx. tarsalis* when the progeny of infected females were reared at 18°C, but none when the progeny were reared at 27°C (Hardy et al. 1984). Thus, higher temperatures even for a short time may eliminate vertical transmission as a mechanism for the overwintering of SLE virus.

Furthermore, over a 5- to 7-yr period of observation, yearly and intraseasonal changes occurred in the susceptibility of an isolated population of *Cx. tarsalis* to infection with WEE and SLE viruses (Hardy et al. 1990). In this study, late instars and pupae were collected monthly during the breeding season, transported to the laboratory, and newly emerged adult females were fed a dilution series of virus, held for 14 d at a constant temperature of 25°C, and then tested for infection (Fig. 9). The mosquito population was highly refractory to infection with WEE virus in 1976 when spring temperatures were unseasonably warm for a long period. In contrast, this population was highly susceptible to infection during the summer of 1980 following an unusually cool spring. The short period of high temperature in midsummer in 1980 had no

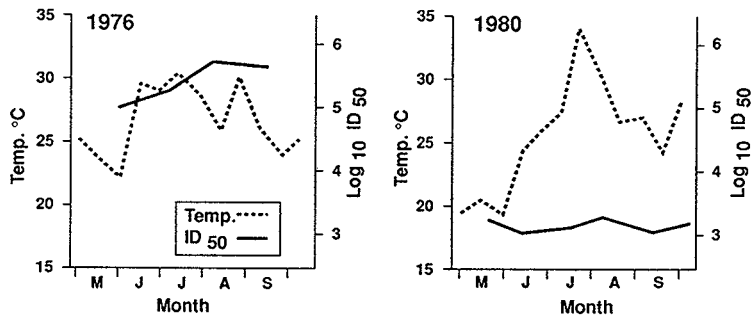


Fig. 9. Effect of seasonal temperatures on the susceptibility of *Cx. tarsalis* for WEE virus (ID_{50} = virus dose that infected 50% of the population (adapted, in part, from Hardy et al. [1990], with permission of the American Journal of Tropical Medicine and Hygiene).

obvious effect on susceptibility. A degree-day analysis indicated that increases in virus resistance correlated significantly with the number of days over 27 or 32°C accrued from April through June. These results indicated that temperature may induce changes during preadult development that affect the susceptibility of adult females to WEE virus (Hardy et al. 1990). However, further analyses indicated that temperature most likely acts indirectly on unidentified factors in the aquatic environment that affect the vector competence of emergent adult females. This is the subject of current studies. Yearly and intraseasonal changes in vector competence for SLE virus also occurred in the same population of *Cx. tarsalis*, but these changes did not correlate with changes in ambient air temperature (Hardy et al. 1990).

No evidence has been found that SLE viruses isolated from the high-temperature southern California region have enhanced ability to infect or be transmitted by vectors (Meyer et al. 1983). Similar studies have not been done with WEE virus.

Discussion

The preceding observations, and our basic knowledge of the epidemiology of arboviruses and the biology of their vectors, allow us to make the following predictions regarding the probable impact of global warming on these two arboviruses in California.

If temperatures increase a further 3–5°C in areas of southern California, some dramatic changes are anticipated. *Culex tarsalis* will become a less-competent vector for WEE virus in midsummer because it modulates this infection when temperatures exceed 30°C. This may eradicate the virus from a large enzootic area. The temperature change should not affect SLE virus to the same extent, because it is not modulated. In the south, *Cx. tarsalis* may become primarily a winter and spring species, as happens in the lower Rio Grande Valley of Texas (Eads 1965). If outdoor temperatures rise to an average of over 35°C for at least 3 mo, vector populations may be forced into estivation if they are to survive. A finding that supported this is that the rate of ovarian maturation after blood ingestion increased as a function of temperature (Fig. 10). However, the rate of oviposition actually decreased at 30°C (Reisen et al. 1992b). Females could quiesce as gravids at high temperatures and possibly delay oviposition.

We do not know the full effect of increased temperature on the vertical transmission of arboviruses. The study with SLE virus indicated that the efficiency of vertical transmission was greater at 18°C than at 27°C (Hardy et al. 1984). If this finding is generally true, then global warming

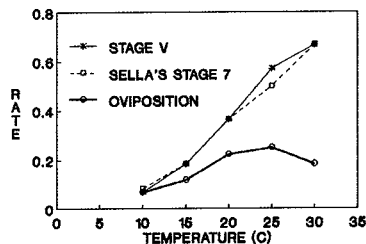


Fig. 10. The rate (inverse of time to achievement by 50% of population) of follicle development in *Cx. tarsalis* to Christophers' Stage V, blood digestion to Sella's Stage 7, and oviposition, plotted as a function of temperature (from Reisen et al. [1992b], with permission from the *Journal of Medical Entomology*).

could be detrimental to survival of viruses that depend on this mechanism for survival.

In the northern areas of California, the peak of *Cx. tarsalis* populations could shift from midsummer and become biphasic with peaks in the spring and fall. The periods of WEE and SLE virus activity should follow the population trend, and cases of encephalitis should no longer peak in midsummer for WEE or early fall for SLE as they have for a period of >40 yr (Reeves 1990) but may occur in a biphasic pattern, reflecting changes in the abundance and vector capacity of *Cx. tarsalis*.

It is tempting to predict what will happen to the distribution of WEE and SLE viruses in a broader area than California. Hess et al. (1963) did an interesting evaluation on the relationship of the 70°F (21°C) June isotherm to the geographical distribution of WEE and SLE epidemics in the period 1933 to 1962 (Fig. 11). It is interesting that the occurrence of epidemics in the ensuing period, 1963–1992, has followed this same pattern. If global warming occurs, we can predict that epidemics of SLE will move northward, and WEE virus may not be able to remain epidemic in some of its current southern distributions. In fact, WEE virus could disappear from much of its current endemic area and become a more common infection in the northern states and Canada. We do not know what will happen to other alphaviruses or to the receptivity of extensive areas of North America to the introduction of alphaviruses such as Venezuelan equine encephalitis, Ross River, and Chikungunya, which seem to prevail currently in areas of the world with high temperatures.

Three assumptions were made originally regarding changes that will occur as a result of global warming, and we have concentrated our studies on temperature. The other assumptions were that there will be major changes in the

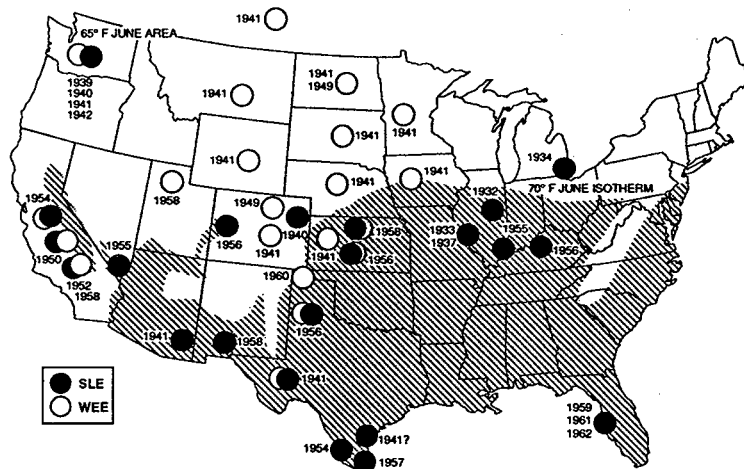


Fig. 11. Distribution of recorded human outbreaks of St. Louis and western encephalitis in the United States in relation to the 70°F (21°C) June isotherm (from Hess et al. [1963] with permission of the *American Journal of Tropical Medicine and Hygiene*).

pattern of precipitation and a rise in sea level. The principal changes in precipitation predicted for California will be a decrease in winter snowfall and an increase in rainfall (Smith & Tirpak 1989). An increase in summer rainfall and temperature could make California more receptive to the introduction of exotic vectors such as *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) and flaviviruses, such as dengue and yellow fever, that they transmit. It may be more important that major changes will occur in the availability of water for domestic and agricultural purposes. The current system of flood control and water storage dams in California was developed largely to redistribute water from snowfall in the mountains of northern California to southern areas needing additional water for agricultural, domestic, and industrial use (Kramer 1975, Kahl 1978). With global warming, snowfall is predicted to decrease and there will be a recession of at least 150 m in the elevation of the snow line (Anonymous 1991). This recession will have a major effect on water availability, on the abundance of *Aedes* mosquitoes that use snow-water pools for breeding, and on the bunyaviruses they transmit (Campbell et al. 1991). The long-term effect this change will have on the geographical relocation of the human population and their exposure to arboviruses has been a topic of speculation (Reeves & Milby 1989, Reeves 1991). It is antic-

ipated that an extensive change will be made in agricultural practices as a result of decreased water availability and that this will decrease mosquito populations that are dependent on such water usage (Reisen & Reeves 1990).

The seasonal patterns of future agricultural practices and changes in distribution of the current vectors also are unknown. We believe that there will be substantial changes in the distribution of mosquitoes that currently occur in California. Species that are now restricted to the warmer southern areas, where freezing temperatures are rare, may extend into and become common in the Central Valley and northern coastal areas. Examples are *Psorophora columbiana* (Dyar & Knab) and *Aedes taeniorhynchus* (Wiedemann).

Most current coastal salt-marsh habitats will be inundated by a predicted rise of up to 1 m in sea level. This change will decrease or eliminate the habitat of current populations of salt-marsh mosquitoes. Species of birds and mammals that are dependent on this habitat, and that are now considered to be endangered, probably will become extinct, and viruses that are now endemic in this environment could disappear (Eldridge et al. 1991). At the same time, salt-water intrusions will occur at great distances inland into current freshwater habitats (Smith & Tirpak 1989). In time, some of these areas may develop into salt

marshes that will be populated by salt-marsh mosquito species, which can be pests and carry viruses.

Very few current publications have drawn attention to the national and international importance of global warming with reference to human health problems. A report from the Institute of Medicine of the National Academy of Sciences (Lederberg et al. 1992) briefly described the problem and stated, "It is thus disturbing to note the apparent lack of interest in global warming as a possible contributor to public health crises on the part of funding agencies and environmental groups." A symposium of the British Society of Parasitology (Hominick & Chapell 1993) covered a wide variety of biological problems associated with global changes but did not focus attention on the wide variety of arthropod-borne diseases that cause major human health problems in tropical regions.

It remains to be seen if more detailed and focused research of the type we describe here will be forthcoming. We believe that global warming and associated ecological changes could result in extreme changes in pathogen distribution. The studies reported here demonstrated that relatively small increases in temperature, such as are expected from global warming, will cause decreases in vector survival, will alter vector competence to transmit pathogens, and could modify the geographical distribution of virus, vector, human, and animal populations. These changes can be studied today and deserve such attention. The concepts and methods developed in the current studies are applicable to a wide variety of vector-borne pathogens that now occur or may emerge as health problems in both temperate and tropical regions of the world.

Acknowledgments

Substantial contributions to this research were made by L. D. Kramer, R. P. Meyer, S. B. Presser, and R. Chiles (University of California, Berkeley). This research was sponsored in part by grants AI3028, AI26154, and AI32939 from the National Institute of Allergy and Infectious Diseases, grant M1435 from the Coachella Valley Mosquito Abatement District, annual grants from the University of California Mosquito Research Program, and continuing logistic support from the Kern Mosquito and Vector Control District.

References Cited

- Anonymous. 1991. Potential impacts of global warming in California, pp. 2-1 to 2-21. In *Global climate changes: potential impact and policy recommendations*. Draft Report, California Energy Commission. March 1991.
- Campbell, G. L., B. F. Eldridge, W. C. Reeves & J. L. Hardy. 1991. Isolation of Jamestown Canyon virus from boreal *Aedes* mosquitoes from the Sierra Nevada of California. *Am. J. Trop. Med. Hyg.* 44: 244-249.
- Eads, R. B. 1965. Biological notes on *Culex tarsalis* in the lower Rio Grande Valley of Texas. *Mosq. News* 25: 61-63.
- Eldridge, B. F., G. C. Lanzaro, G. L. Campbell, W. C. Reeves & J. L. Hardy. 1991. Occurrence and evolutionary significance of a California encephalitis-like virus in *Aedes squamiger* (Diptera: Culicidae). *J. Med. Entomol.* 28: 645-651.
- Hardy, J. L. 1987. The ecology of western equine encephalomyelitis virus in the Central Valley of California, 1945-1985. *Am. J. Trop. Med. Hyg.* 35 (Suppl.): 188-328.
1988. Susceptibility and resistance of vector mosquitoes, pp. 87-126. In T. P. Monath [ed.], *The arboviruses: epidemiology and ecology*, vol. 1. CRC, Boca Raton, FL.
- Hardy, J. L. & W. C. Reeves. 1990. Experimental studies on infection in vectors, pp. 145-253. In W. C. Reeves, *Epidemiology and control of mosquito-borne arboviruses in California, 1943-1987*. California Mosquito and Vector Control Association, Inc., Sacramento, CA.
- Hardy, J. L., L. Rosen, W. C. Reeves, R. P. Scrivani & S. B. Presser. 1984. Experimental transovarial transmission of St. Louis encephalitis virus by *Culex* and *Aedes* mosquitoes. *Am. J. Trop. Med. Hyg.* 33: 166-175.
- Hardy, J. L., R. P. Meyer, S. B. Presser & M. M. Milby. 1990. Temporal variation in the susceptibility of a semi-isolated population of *Culex tarsalis* to peroral infection with western equine encephalomyelitis and St. Louis encephalitis viruses. *Am. J. Trop. Med. Hyg.* 42: 500-511.
- Hess, A. D., C. E. Cherubin & L. C. LaMotte. 1963. Relation of temperature to activity of western and St. Louis encephalitis viruses. *Am. J. Trop. Med. Hyg.* 12: 657-667.
- Hominick, W. & L. H. Chapell. 1993. The impact of global changes on disease. *Parasitology* 106 (Suppl.): 5-95.
- Kahl, W. L. 1978. The California water atlas. California Department of Water Resources, Sacramento, CA.
- Kramer, L. D., J. L. Hardy & S. B. Presser. 1983. Effect of temperature of extrinsic incubation on the vector competence of *Culex tarsalis* for western equine encephalomyelitis virus. *Am. J. Trop. Med. Hyg.* 32: 130-139.
- Kramer, M. C. 1975. The Great Western Basin, pp. 165-178. In M. F. Stanley & M. P. Alpers [eds.], *Man-made lakes and human health*. Academic, London.
- Lederberg, J., R. E. Shope & S. C. Oaks [eds.]. 1992. Emerging infections: understanding the human dimensions. National Academy, Washington, DC.
- Lyness, R. N. 1970. Mosquito vector and arboviral surveillance in Kern County, 1969. *Proc. Calif. Mosq. Control Assoc.* 38: 104-108.
- Meyer, R. P., J. L. Hardy & S. B. Presser. 1983. Comparative vector competence of *Culex tarsalis* and *Culex quinquefasciatus* from the Coachella, Imperial and San Joaquin Valleys of California for St. Louis encephalitis virus. *Am. J. Trop. Med. Hyg.* 32: 305-311.
- Meyer, R. P., J. L. Hardy & W. K. Reisen. 1990. Diel changes in adult mosquito microhabitat tem-

- peratures and their relationship to the extrinsic incubation of arboviruses in Kern County, California. *J. Med. Entomol.* 27: 607-614.
- Nelson, M. J. 1971. Mosquito studies (Diptera: Culicidae). XXVI, Winter biology of *Culex tarsalis* in Imperial Valley, California. *Contrib. Am. Entomol. Inst. (Ann Arbor)* 7: 1-56.
- Reeves, W. C. 1990. Epidemiology and control of mosquito-borne arboviruses in California, 1943-1987. California Mosquito and Vector Control Association, Sacramento, CA.
1991. Population growths in California and their impacts on disease transmission. *Proc. Calif. Mosq. Vector Control Assoc.* 59: 1-4.
- Reeves, W. C. & M. M. Milby. 1989. Changes in transmission patterns of mosquito-borne viruses in the USA, pp. 121-141. In M. W. Service [ed.], *Demography and vector-borne diseases*. CRC, Boca Raton, FL.
- Reisen, W. K. & W. C. Reeves. 1990. Bionomics and ecology of *Culex tarsalis* and other potential mosquito vector species, pp. 254-329. In W. C. Reeves, *Epidemiology and control of mosquito-borne arboviruses in California, 1943-1987*. California Mosquito and Vector Control Association, Sacramento, CA.
- Reisen, W. K., M. M. Milby, W. C. Reeves, R. P. Meyer & M. E. Bock. 1983. Population ecology of *Culex tarsalis* (Diptera: Culicidae) in a foothill environment of Kern County, California: temporal changes in female relative abundance, reproductive status and survivorship. *Ann. Entomol. Soc. Am.* 76: 800-808.
- Reisen, W. K., M. M. Milby & M. E. Bock. 1984. The effects of immature stress on selected events in the life history of *Culex tarsalis*. *Mosq. News* 44: 385-395.
- Reisen, W. K., R. P. Meyer & M. M. Milby. 1986. Overwintering studies on *Culex tarsalis* (Diptera: Culicidae) in Kern County, California: survival and the experimental induction and termination of diapause. *Ann. Entomol. Soc. Am.* 79: 664-673.
1989. Studies on the seasonality of *Culiseta inornata* in Kern County, California. *J. Am. Mosq. Control Assoc.* 5: 183-195.
- Reisen, W. K., J. L. Hardy, S. B. Presser, M. M. Milby, R. P. Meyer, S. L. Durso, M. J. Wargo & E. Gordon. 1992a. Mosquito and arbovirus ecology in south-eastern California, 1986-1990. *J. Med. Entomol.* 29: 512-524.
- Reisen, W. K., M. M. Milby, S. B. Presser & J. L. Hardy. 1992b. Ecology of mosquitoes and St. Louis encephalitis virus in the Los Angeles Basin of California, 1987-1990. *J. Med. Entomol.* 29: 582-598.
- Reisen, W. K., R. P. Meyer, S. B. Presser & J. L. Hardy. 1993. Effect of temperature on the transmission of western equine encephalomyelitis and St. Louis encephalitis viruses by *Culex tarsalis* (Diptera: Culicidae). *J. Med. Entomol.* 30: 151-160.
- Smith, J. B. & D. A. Tirpak [eds.]. 1989. The potential effects of global climate change in the United States. U.S. Environmental Protection Agency, Washington, DC.

Received for publication 16 August 1993; accepted 22 December 1993.