

The impact of drought on mosquito-borne diseases in the Colorado River Basin states

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Background & Introduction

Mosquito-borne diseases enact a heavy economic burden across society. Costs resulting from these diseases include acute and chronic healthcare treatment, lost worker productivity due to illness or caregiving, and funding for proactive or reactive vector control activities.^{1,2} In the United States from 2004-2016, the reported annual number of mosquito-borne disease cases have increased almost 10-fold, from 4,858 to 47,461,³ and will likely continue to increase due to the interplay of climatological and anthropological conditions. During this period, a total of 19,018 cases were reported in the western states with California, Arizona, and Colorado, states in the Colorado River Basin, among the states with the highest burden in the nation.³

Mosquitoes in two genera, *Culex* and *Aedes*, are responsible for the maintenance and transmission of the vast majority of mosquito-borne illnesses occurring in the Western United States. Each genus differs in type of breeding habitat, host preference, and ability to transmit different diseases, but they all undergo the same water-dependent life cycle⁴ (Fig 1). A mated adult female mosquito will lay a batch of eggs in or around a source of water after taking a bloodmeal from an animal or human host. The eggs will hatch into larva which undergo successive molts until they acquire the requisite nutritional stores to transition into the next developmental stage, the pupa. An adult, the only non-aquatic life stage, will emerge from the pupal case after completing metamorphosis. A female mosquito will take multiple bloodmeals during her life, generally 14 days in length, and lay multiple egg batches. Each bite holds the opportunity for disease transmission in either direction between host and mosquito.

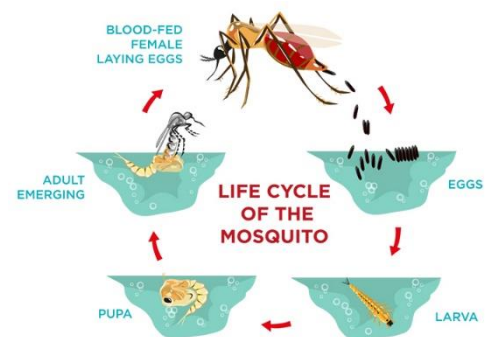


Figure 1. Mosquito life cycle. An adult female lays eggs in a water source. Larva hatch from eggs and develop into pupa. An adult emerges from the pupal case.

Source: <https://www.gptx.org/>

The rise in mosquito-borne disease cases has occurred against a backdrop of heterogeneous drought severity across the Western United States, especially in the Colorado River Basin (Fig 2). During the annual peak of mosquito-borne disease transmission (Jul-Aug), on average of

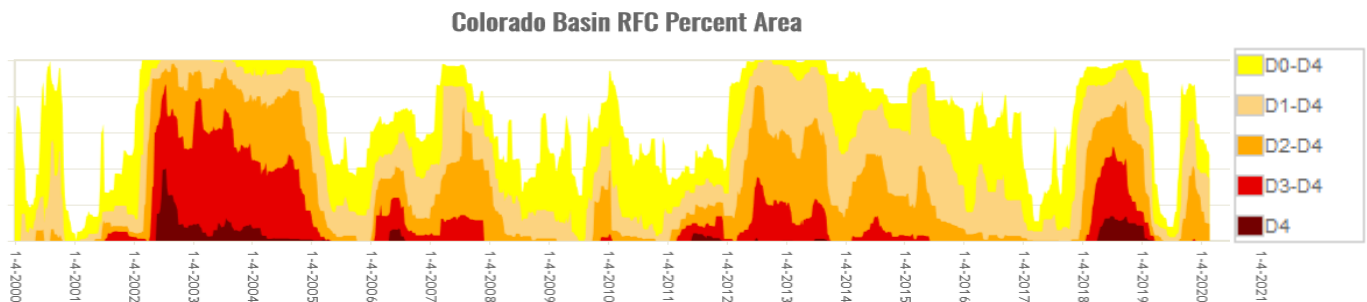


Figure 2. Percent area in Colorado River Basin River Forecast Center under varying levels of drought classifications, 2000-2020. D0: Abnormally Dry; D1: Moderate Drought; D2: Severe Drought; D3: Extreme Drought; D4: Exceptional Drought

Source: <https://droughtmonitor.unl.edu/Data/Timeseries.aspx>

33.03% (range: 0.0-81.07%) of the area in the Colorado River Basin experienced severe to exceptional drought in 2004-2016.^{5,6} The Colorado River Basin includes areas of California, Nevada, Utah, Arizona, Wyoming, Colorado, and New Mexico and provides water for 1 in 10 Americans as well as habitat for a myriad of wildlife and plant species.⁷ Drought in the Colorado River Basin has large impacts across society and the environment. Under the simplest definition, drought is a period of time with low water availability.⁸ Therefore, while not the only factor contributing to the expansion of mosquito-borne diseases in these Western states, drought plays a large, complex role due to the dependence of mosquitoes on the presence of water for successful reproduction and development⁹ and human behavior in response to reductions in water supply.

The interplay of drought and human cases of mosquito-borne diseases in the Colorado River Basin states of the Western United States is exemplified in two representative disease systems, West Nile virus and dengue virus. The incidence of West Nile virus disease, an endemic *Culex*-borne disease in the United States, tends to increase during droughts, illustrating the complex and unintuitive relationships of drought on mosquito biology, viral dynamics, and host distributions. The dengue virus system, an *Aedes*-borne disease, highlights the interconnected climate-, drought-, and human behavior-related conditions that facilitate the expansion and establishment of a disease into a new area.

Drought

While intrinsically tied to a lack of moisture, the phenomenon defined as drought encompasses the interplay of meteorological conditions (i.e. reductions in precipitation, increased wind, high temperatures, and low humidity) with human and agricultural demands for water.⁸ These conditions are amorphous in their geographic and temporal extent, as well as having far-reaching and complex impacts across different sectors of society and the environment.¹⁰ Therefore, no single unified definition of drought exists. Depending on the context of conditions and impacts, drought can be categorized into four main groups: meteorological, agricultural, hydrological, and socioeconomic.^{8,11,12} Meteorological drought focuses on climatic conditions resulting in a sustained period of reduction in precipitation below normal levels.¹³ Agricultural drought occurs when the amount of moisture in the root-zone layer of soil is insufficient for proper growth and production of a particular crop. Subsurface soil layers may still be saturated. Hydrological drought refers to the reduction in surface and subsurface water supplies below normal. Socioeconomic drought involves the imbalance of supply and demand of economic goods and aspects of meteorological, agricultural, and hydrological drought.

Hydrological drought conditions most directly impact mosquitoes and therefore is the lens through which to identify the relationship between drought and mosquito-borne disease. During periods of hydrological drought, sustained reductions in precipitation result in reduced streamflow and groundwater across the landscape, leading to reduced water levels in streams, reservoirs, lakes, and ponds.¹² Increased evapotranspiration due to high temperature, wind, and low humidity often coincide with and exacerbate this reduction in precipitation, increasing the severity of hydrological drought.

Projected climatological models predict an increase in temperatures paired with a decrease in annual precipitation in the Western United States.⁶ Thus, the frequency and intensity of both

short- and long-term droughts are expected to increase, likely leading to water shortages in many areas due to reduced surface and groundwater.¹⁴

Drought & West Nile virus

West Nile virus (WNV) and *Culex* mosquitoes

West Nile virus (WNV) causes a potentially fatal, mosquito-borne neuroinvasive disease.¹⁵ It is maintained in an enzootic cycle between birds and bird-biting mosquitoes (predominantly *Culex* genus), but can spillover to infect horses and humans.¹⁶ Both hosts are dead-ends to the disease as neither develop sufficiently high viremias to re-infect biting mosquitoes.

WNV is endemic in the United States with the highest incidence in the West and Midwestern states, especially across the Colorado River Basin.¹⁷ While 80% of human infections are asymptomatic, 20% result in a febrile illness and <1% in a neuroinvasive disease characterized by encephalitis, meningitis, and acute flaccid paralysis.¹⁸ The severe form of the disease has ~12% fatality rate and often results in long-term physical and mental sequelae.¹⁹ No human vaccine exists so prevention relies heavily on mosquito control and personal protective measures (i.e. wearing long sleeves, avoiding dawn/dusk periods when *Culex* mosquitoes are active, using insect repellent, and removing standing water in which mosquitoes could lay their eggs).¹⁶

Culex (Cx.) tarsalis and *Cx. pipiens* are the predominant mosquito vectors for WNV in both the enzootic maintenance and zoonotic transmission cycles in North America because, while both species prefers to bite birds, they will also feed on mammals and humans.²⁰ Both species are abundant in areas in close proximity to humans across the United States. *Cx. tarsalis* females breed in recently created and relatively clean rural water sources like recently flooded wetlands and rice fields,^{21,22} but also have recently begun exploiting urban locations like abandoned swimming pools.²³ Upon emergence, *Cx. tarsalis* adults may fly into urban areas seeking bloodmeals. In contrast, *Cx. pipiens* typically breed in eutrophic man-made water sources like peridomestic containers, dairy lagoons, and storm drain systems^{22,24,25}, and are often most abundant in urban and suburban areas.

Impacts of drought on WNV dynamics

The incidence of human WNV cases in the Colorado River Basin, and the Western states as a whole, increases during periods of hydrological drought due to the interplay of the effects of drought conditions on mosquito habitats and bionomics coupled with the impacts on avian hosts.^{26,27}

Reduced water levels in streams and lakes characteristic of hydrological drought alters the distribution and quality of *Culex* mosquito breeding habitats, generally resulting in an increase in the abundance of vector mosquitoes present. While some breeding habitat is lost due to complete drying of previous inundated locations, reduced flow of surface water in streams and ponds results in increased numbers of small, stationary water sources that tend to stagnate.²⁶ This increases the quality of larval habitat for *Cx. pipiens*,²² increasing the total size of the adult cohorts emerging. In urban areas, the reduced precipitation of hydrological drought results in water stagnation in storm drain systems because of reduced flushing activity of rainwater through these systems.²⁴ Therefore, larger *Cx. pipiens* cohorts can emerge in close proximity to

humans. While *Cx. tarsalis* are adapted to exploit transient water sources for breeding, sustained reductions in water quantities may alter the spatial extent of breeding sites in non-urban areas. Thus, female mosquitoes may fly into urban areas to find adequate breeding habitats in inadequately maintained swimming pools, ornamental ponds, and water features.²³ Additionally, in some areas during periods of drought, continued use of agricultural flood irrigation techniques and maintenance of managed wetlands create a wealth of larval breeding sites for *Cx. tarsalis*,²⁸ increasing the local population size and number of adults that may fly into neighboring urban areas to breed and find a bloodmeal host.

The reduction in surface water levels during drought also reduce predators and competitors for the mosquito aquatic life stages. Predators like dragonflies and fish have slower generation times and less mobility between water sources than mosquitoes and are thus unable to exploit transient water sources as efficiently as mosquitoes.⁹ Without this regulation, mosquito populations are able to increase rapidly.

The scarcity of water sources across the landscape increases bird-mosquito interactions, increasing enzootic WNV transmission.^{26,27} A ‘watering hole’ phenomenon occurs where both birds and mosquitoes congregate around the limited number of water sources instead of being more dispersed across the landscape. Therefore, the large number of mosquitoes emerging from these generally higher quality larval habitats have more opportunity to feed on potentially WNV-infected or naïve birds. Thus, increased interaction leads to sustained maintenance and amplification of WNV in the system, increasing the total number of *Culex* mosquitoes infected with WNV.

Stress induced during drought situations can impair the immune system of birds, increasing the duration and level of WNV virus present in their blood.²⁹ Thus, a higher number of mosquito bites occur during the period of time when the bird is infectious, also leading to higher infection rates in the mosquito population.

The high temperatures often a contributing factor to hydrological drought enhance *Culex* mosquito development and viral transmission dynamics. Mosquito developmental rates at each stage are temperature dependent, speeding up with increasing temperature.^{30,31} Thus, faster population growth occurs at higher temperatures, up to the thermal upper limit of sustained temperatures above 35°C where death rates exceed population growth rates. Increased temperatures also facilitate rapid disease transmission by increasing mosquito biting rates and reducing the extrinsic incubation period, the time from which a mosquito ingests WNV in a bloodmeal to when it can transmit it.^{32,33} Overall, higher temperatures increase the number of infectious bites a mosquito takes during its lifespan, increasing the total number of new hosts it can infect.

Drought reduces the availability of water sources across the landscape while increasing the quality of many locations as mosquito breeding locations. Changes in water distribution results in congregation of multiple species at the few sources present, increasing host-vector interactions, a large proportion of which result in successful WNV infections due to depressed immunity in birds and increased viral dynamics in mosquitoes.

Drought & dengue virus

Dengue virus and *Aedes* mosquitoes

Dengue virus causes a potentially fatal mosquito-borne hemorrhagic disease and has four unique strains that do not confer cross-immunity.³⁴ It is transmitted from human to human by *Aedes* mosquitoes without the need of an intermediate amplifying host. Infection with any of the strains can be asymptomatic, a febrile illness, or a severe disease with hemorrhage, plasma leakage, and organ impairment. The majority of first time infections are asymptomatic or febrile with the probability of severe disease increases following infection with a different strain than the first infection. No specific treatments for dengue exist. Prevention relies on vector control and personal protective measures like removing standing water, maintaining window and door screening, and using insect repellent.

Aedes (Ae) aegypti is the predominant vector for dengue worldwide and is highly adapted to living with humans. They preferentially feed upon humans.³⁵ They breed in natural and artificial containers that hold water, like tree holes, leaf axils, flower pots, tires, and buckets.³⁶ *Aedes* mosquitoes lay desiccation-resistant eggs in the moist substrate above the waterline that are able to survive up to a year of dry conditions, hatching following re-flooding of the container.³⁷

The highest burden of disease occurs in tropical regions worldwide where *Ae aegypti* are endemic.³⁸ Annually, ~1,000 cases are reported in the United States with around 1/3 of cases reported in the states of the Colorado River Basin; the majority of all dengue cases are travel-associated.³⁹ No local transmission has been reported in the Western United States but, local transmission could occur if local populations of *Ae. aegypti* successfully infect local populations with virus picked up from a returning traveler.

Impacts of drought on dengue virus dynamics

The interplay of hydrological drought with changing climate conditions and human behavior can facilitate the expansion and establishment of dengue across the Colorado River Basin states, highlighting the complex interactions of climate, human behavior, and public health.

The increasing temperatures predicted during the next century can expand the suitability of available habitat for *Ae. aegypti* mosquitoes, increasing the opportunity for local transmission of dengue throughout the Western United States. Currently, suitable conditions for *Ae. aegypti* mosquito populations are confined to the southwestern part of California and Arizona and then only for a few months of the year.⁴⁰ But, populations are spreading north. By 2080, suitable conditions are predicted to extend across the entirety of the Western United States, from Mexico to Canada, with areas conducive for population persistence over half a year. This habitat expansion is already becoming apparent. In September 2019, *Ae. aegypti* were detected for the first time as far north as Moab, Utah⁴¹ and the Sacramento area in California.⁴² With increasing climate suitability, *Ae. aegypti* invade new locations, increasing the spatial and temporal range in which they could potentially pick up dengue from a returning traveler and initiate local transmission cycles.

Human behavior, especially during periods of drought, provide sustained breeding habitats for these invading populations of *Ae. aegypti*, increasing the potential persistence of populations in

close proximity to humans. In response to reduced water supply during drought conditions, people often increase the number of water storage containers around their homes in an effort to conserve water. If not properly maintained, these storage containers provide excellent breeding habitat for *Aedes*, allowing for the establishment of breeding populations in close proximity to human habitation. Surges in dengue transmission during periods of drought driven by large-scale expansion of personal water storage around homes have already been observed in Australia and Brazil, countries with endemic *Ae. aegypti* populations.^{10,43} Domestic water storage containers represent only a proportion of all containers found around humans that *Ae. aegypti* can exploit for breeding habitat. Common items include bottles, watering cans, bird baths, and buckets, but includes anything natural or artificial that holds water.^{36,40} Additionally, desiccation-resistant *Aedes* eggs are able to remain viable during drought periods when containers dry up or are dumped out.³⁶ Following re-wetting of containers by precipitation or sprinklers, larva hatch, leading to rapid local population growth. This mechanism also allows for population continuance across unsuitable climatic conditions. The high prevalence of breeding habitats combined with desiccation-resistance eggs facilitates the establishment of invading populations in close proximity to humans, increasing vector-host interactions and further increasing the potential for local spread of dengue.

The introduction of dengue into expanding populations of *Ae. aegypti* can result in explosive human epidemics due to the high proportion of immunologically naïve people in those areas. The establishment of *Ae. aegypti* in close proximity to humans in a wide spread area allows for the effective maintenance of dengue transmission.

Drought, in concert with climate change and human behavior, can facilitate the establishment of local *Ae. aegypti* mosquito populations across the Colorado River Basin, increasing the probability of local dengue outbreaks. Increased temperatures with climate change open up suitable habitats further north for *Ae. aegypti*. Artificial containers associated with human habitation provide breeding habitat for these invading mosquitoes. Drought augments the number of suitable breeding habitats with increased domestic water storage containers, thus increasing the potential for human-mosquito interactions and local dengue transmission.

Conclusions

The impacts of drought on mosquito-borne disease are multifaceted with many interacting mechanisms and levels of effect. While not the sole driver, hydrological drought conditions can enhance zoonotic transmission of both endemic and invasive mosquito-borne diseases in the states of the Colorado River Basin.

The change in surface water availability in drought conditions changes the availability of mosquito habitats, causing shifts in the distribution and quality of mosquito breeding sites. The stressors of drought reduce host immune systems, increasing their duration and level of viral load. Reduced water availability increases host-vector interactions as hosts and mosquitoes congregate at water sources. More mosquitoes also exploit urban breeding sites like domestic water storage containers, stagnated storm drains, and unmaintained water features, increasing human contact rates and the potential for successful infections with endemic or novel diseases.

The increased temperature concurrent with lower precipitation characteristic of hydrological drought enhances mosquito development rates, viral transmission, and mosquito invasion into new areas. Infection of naïve human hosts in these new areas can lead to explosive epidemics.

Drought alone is unable to explain the dramatic increase in mosquito-borne cases of the previous decade, but it plays an important role alongside human behavior, changing temperatures, and proximity of infectious mosquitoes to humans in facilitating disease transmission. The projected increase in drought in the future could further increase the incidence of mosquito-borne diseases in the West. However, human behavior, like removing standing water, maintaining window and door screening, and using insect repellent, can reduce the potential for disease transmission. In the face of a myriad of factors facilitating transmission, human vigilance and personal responsibility are required to reduce the risk and burden of mosquito-borne diseases on an individual and community level.

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