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Vectors of Change: Ticks and Mosquitoes as Indicators of Coupled Climate and Land-Use
Pressures in a Changing California

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution, and Marine Biology

by

Stephanie Joyce Copeland

Committee in charge:

Professor Hillary Young, Chair

Professor Cherie Briggs

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June 2026

The dissertation of Stephanie Joyce Copeland is approved.

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June 2026

Vectors of Change: Ticks and Mosquitoes as Indicators of Coupled Climate and Land-Use
Pressures in a Changing California

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by

Stephanie Joyce Copeland

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immediate family, mom, dad, Will, and Merry, I truly wouldn't be here if it weren't for all of you. You've traveled thousands of miles to see me, sometimes driving across the U.S. to support me. I can't express how much your love has meant to me and how much it's made me who I am. All I can say is that I love you and thank you.

My dissertation is in honor of my grandmother Joyce Egan and my great-great-aunt Anita Whitney, both of whom would've excelled in higher education had they lived in a time when their gender did not limit their opportunities.

Lastly, this work is dedicated to the being that, through these five years, never left my side, hiked hundreds of miles with me, and sat next to me through the late nights. They were the first thing I said good morning to and the last thing I'd kiss before going to bed at night. Hugo, my Huggy Bear, you'll never read these words, so I can only give you towel rubbies, bully sticks, and walks for sniffs whenever you want them. Thank you for being my light, my guidance, and my companion, through it all.

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2023	Schmidt Mentorship Fellowship (x2), Schmidt Family Foundation. Graduate Student Grant, VESR, UCSB. Faculty Senate Grant (with H.S. Young), UCSB.
2022	Summer Block Grant, EEMB, UCSB.
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ABSTRACT

Vectors of Change: Ticks and Mosquitoes as Indicators of Coupled Climate and Land-Use Pressures in a Changing California

by

Stephanie Joyce Copeland

Human-induced landscape change and climate change are reshaping ecosystems globally, yet their interactive effects remain in need of further understanding. Arthropod vectors, particularly ticks and mosquitoes, depend on both biotic and abiotic environmental conditions throughout their life cycles, making them uniquely sensitive indicators of concurrent anthropogenic pressures and an informative lens for studying ecosystem responses to multiple interacting stressors. My dissertation investigates how the combined and interacting effects of climate variability and land-use alteration shape vector populations and vector-borne disease risk across three distinct systems. In my first study, a replicated exclosure experiment along a topoclimatic gradient revealed that both large-herbivore identity and climate mediate tick population dynamics. My second study examined mosquito density across alpine lakes in the Sierra Nevada, finding that seasonal ice-off timing and human recreational activity were the primary drivers of mosquito abundance, while introduced, nonnative trout had no detectable effect on adult populations. My final study investigated how climate whiplash, the abrupt alteration between drought and extreme

precipitation, shifted the distribution of West Nile Virus hosts across the heavily human-modified landscapes of the San Joaquin Valley. Bird abundance was concentrated in irrigated perennial agricultural landscapes during drought, and the spatial overlap between host aggregations and positive West Nile Virus mosquito pools in Kern County identified agricultural and urban land cover as a key driver of elevated transmission risk.

Together, my studies demonstrated that neither climate change nor landscape alteration alone captures the full scope of change occurring in vector systems. Climate mediates the consequences of large herbivore loss and livestock addition for tick populations; anthropogenic recreation reshapes mosquito host availability even in remote wilderness areas; and precipitation extremes interact with human-created landscapes to concentrate disease transmission risk in space and time. Understanding these interactive effects is essential for predicting and managing arthropod vectors and vector-borne disease in an era of accelerating global change.

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INTRODUCTION

Background

Since the Industrial Revolution, human impacts on the environment have become a significant issue (Candelone et al., 1995; Mitchell, 1989). Over 75% of the world's landscapes are human-managed (Venter et al., 2016) and, therefore, subjected to human-induced changes (Crutzen, 2002) (Figure 0.1a). Additionally, climate change and the predicted drastic increase in global temperatures (Arnell et al., 2019; Hitz & Smith, 2004) have been attributed primarily to anthropogenic reasons, such as fossil fuel use for energy (Judkins et al., 1993), deforestation (Karl & Trenberth, 2003), and urbanization (Dodman et al., 2019). Alongside rising mean temperatures, climate change is intensifying the frequency and severity of extreme weather events, including prolonged droughts, intense precipitation events (Figure 0.1b), heat waves, and large-scale wildfires, which further destabilize ecosystem processes (Diffenbaugh & Field, 2013; Mason-Delmotte et al., 2021; Trenberth et al., 2015). Therefore, most ecosystems on our planet undergo both direct human landscape changes and the indirect human-induced effects of climate change, and understanding how these changes may interact and alter ecosystems is imperative as these threats continue to grow.

Climate and landscape change do not occur in isolation; instead, they likely interact in ways that can produce effects that differ from or are more significant than those caused individually. For example, nitrogen runoff from human infrastructure into coastal freshwaters, along with climate change, has created an interactive response to nitrogen cycling that affects both the retention and reduction rates of nitrogen compounds in the water

(Baron et al., 2013). The interaction between landscape disturbance and climate change has been shown to drive bark beetle (*Dendroctonus* spp.; family: Curculionidae) outbreaks in pine forests far beyond what either stressor causes independently, with warming temperatures reducing overwinter beetle mortality while simultaneously weakening host tree defenses already stressed by drought and habitat fragmentation (Bentz et al., 2010; Raffa et al., 2008) (Figure 0.2).

Similarly, Guo et al., (2018) demonstrated that species range shifts driven by warming temperatures are exacerbated in landscapes already fragmented by human land use, compounding extinction risks and disrupting communities globally. At the ecosystem level, Hautier et al. (2015) found that climate variability and elevated nutrient loading interact to reduce plant diversity and productivity in grasslands beyond what either stressor alone would cause. The interactive effects of climate and land-use change are global and span ecosystem types and boundaries (Didham et al., 2007). Determining interactions among these issues can be difficult and remains an area for investigation (Keane et al., 2015; Moe et al., 2013).

One way to understand these interactions is through organisms that are sensitive to both. Arthropod vectors, such as ticks and mosquitoes, are responsive to both landscape-level and climate changes (Altizer et al., 2013; Diuk-Wasser et al., 2021) and require biotic and abiotic components for their life cycles (Reeves et al., 2018; Bouchard et al., 2019). Arthropod vectors require ample host availability for blood meals; this blood intake supports life-stage development and reproduction (Swei et al., 2011; Lafferty et al., 2018). However, as ectotherms, arthropod vectors spend the majority of their life cycle off or away from hosts and are affected by the surrounding environment (Culler et al., 2015; Needham & Teel,

1991). Environmental conditions must remain ambient and beneficial to maintain their populations.

Arthropod vectors are most commonly studied in the context of the zoonotic diseases they can transmit to human populations, known as vector-borne diseases (VBDs) (Altizer et al., 2013; Bartlow et al., 2019; Elbers et al., 2015; Gage et al., 2008; Swei et al., 2020). Examples of diseases spread by mosquitoes and ticks include Zika, Dengue, Yellow Fever, West Nile Virus, Malaria, Ehrlichiosis, Anaplasmosis, and Lyme Disease. Tick-borne diseases are the most common vector-borne diseases in the Northern Hemisphere. The Centers for Disease Control (CDC) in the United States estimates that slightly less than half a million people contract Lyme Disease per year (Rosenberg et al., 2018; Schwartz et al., 2021). The mosquito-borne disease Malaria has been a deadly disease for at least the past few centuries, if not longer (Talapko et al., 2019). In areas of poor social and economic development, 4 out of 5 mortality cases due to malaria appear in children under 5 years old (The Editors of Nature, 2023). Vector-borne disease incidence has been increasing, and their ranges are fluctuating into new naïve locations due to landscape and climate changes; they will remain, if not increase, a public health risk (Chala & Hamde, 2021; Morand & Lajaunie, 2021; Rocklöv & Dubrow, 2020).

The interactive effects of climate change and human land-use change have produced measurable, often synergistic alterations in tick and mosquito populations across multiple regions. Warming temperatures associated with climate change have extended the seasonal activity windows and geographic ranges of both *Ixodes scapularis* (the black-legged tick) and *Aedes albopictus* (the Asian tiger mosquito) into higher latitudes and elevations previously unsuitable for their survival (Ogden & Lindsay, 2016; Rochlin et al., 2013). Concurrently,

land-use changes, particularly deforestation, agricultural expansion, and suburban sprawl, alter host community composition and density, thereby independently increasing vector abundance and infection prevalence (Allan et al., 2009; Ostfeld & Keesing, 2000). When these pressures occur together, their effects can be compounding: habitat fragmentation reduces biodiversity and elevates the relative abundance of competent reservoir hosts, while warming temperatures simultaneously accelerate vector development and extend transmission seasons (Brownstein et al., 2005; LoGiudice et al., 2003). Drought and heavy precipitation events, both intensified by climate change, further modulate the availability of mosquito breeding habitats and the movement of reservoir hosts, creating dynamic and spatially heterogeneous patterns of transmission risk (Shaman et al., 2011; Wheeler et al., 2009). Together, these findings underscore that neither climate change nor land-use change alone captures the full scope of shifts occurring in vector populations and VBD risk.

Arthropod vectors' reliance on an ecosystem's biotic and abiotic factors – both of which are being altered by concurrent landscape and climate change – makes them a uniquely informative lens for studying human-induced changes in ecosystems. Their populations may provide a way not only to monitor infectious disease risk but also to detect ecosystem responses to multiple interacting human impacts. In my Ph.D., I conducted investigations of interactive effects across three distinct studies.

1. In my first chapter, I examined changes to tick abundance using an experiment that alters large herbivore presence via exclosures and climate via an elevational gradient.
2. In my second chapter, I used adult female mosquito populations in the Eastern Sierra Nevada to monitor the seasonality and anthropogenic change in sensitive alpine regions.

3. Finally, in my third chapter, I investigated how extreme variations between drought and heavy precipitation periods affect the movement of avian reservoir hosts and identified hotspot risk areas for West Nile Virus.

The San Joaquin Valley

The Central Valley of California covers approximately 20,000 square miles, ranging from 400 miles long to an average width of 50 miles (California Climate Commons, n.d.). It is one of the most notable geological depressions in the world, with most of its area lying below sea level. The Central Valley can be split into two regions: the northern Sacramento Valley and the southern San Joaquin Valley. The Cascade Range binds it to the north, the Sierra Nevada to the east, and the Tehachapi Mountains to the south (U.S. Geological Survey, n.d.).

The entire Central Valley has a rich, culturally diverse, and sometimes unfortunate history. The valley is the unceded land of ~25 indigenous tribes. It is thought to have been settled initially by the Yokuts people some 50,000 to 7,000 years ago. Spanish colonialism through missionary and conflict incursions and then by settlers of European descent, brought by the Gold Rush of 1849, dwindled indigenous populations down 80-95% below their original numbers (Castillo, n.d.). The Central Valley is considered the location of John Steinbeck's Pulitzer and Nobel Prize-winning fictional, Depression-era novel, *The Grapes of Wrath* (Paulsen, 2014). Additionally, the Central Valley was a defining area of the Chicano Rights movement through the activism of Dolores Huerta, who co-founded the United Farm Workers union and organized the landmark Delano Grape Strike, securing improved wages and conditions for migrant farm workers throughout the region (Dolores Huerta Foundation, n.d.).

Agriculture is the predominant land cover in the valley, followed by urbanization and fragments of the remaining natural area. Approximately 250 different crops are grown here with an estimated economic value of \$17 billion. The Central Valley contains 75% of California's irrigated land and 17% of the United States's irrigated land, producing ¼ of the nation's food (U.S. Geological Survey, n.d.). The work in Chapters 1 and 3 occurs in the southern portion, the San Joaquin Valley (SJV), where the predominant crops are nuts, grains, and cereals (USGS - CA Water Science Center). Its remaining natural areas of the SJV include annual grassland, oak woodland, mixed woodland, riparian, and chaparral habitats (DiPietro, 2017; Defenders of Wildlife, n.d.). The SJV receives relatively little rainfall, ranging from 127 to 400 millimeters per year, and has a distinctive Mediterranean climate with hot, dry summers and cool, wet winters (Null et al., 2010).

The Eastern Sierra Nevada

The Sierra Nevada range sits between the Central Valley of California and the Great Basin of Nevada. It is part of the American Cordillera, an almost continuous interhemispheric mountain range that forms the western “backbone” of the Americas. The Sierra Nevada runs some 400 miles long with ranges of 50-80 miles wide. It spans a massive elevation range, from 500 feet in its lower areas to above 14,000 feet at the peaks in its northern and middle sections (Burd, n.d.).

The first detectable trace of human residence or travel through the Sierra is that of paleo-Indians dating back to 3,000 to 500 B.C.E. The Sierra is the unceded land of the Northern Paiute, Mono, Sierra Miwok, Kawaiisu, and Tubatulabal tribes (CA Office of Tribal Affairs, n.d.; Hoffman, C., 1868). In 1855, approximately 300,000 European-descendant migrants arrived in the Sierra due to the California Gold Rush of 1849, which led to the displacement

of indigenous peoples from their traditional homelands and hunting grounds (Starr, K. 2005). The Sierra Nevada is represented in historical folklore through the story of the Donner Party. A group following the Oregon Trail that became stuck in the snow-bound Sierra during the winter and had to resort to cannibalism to survive (Worrall, S. 2017).

The Sierra receives relatively little rainfall (17.8-35.6 cm per year), and much of its freshwater supply originates as snow due to orographic lift. The sudden rise in elevation causes rapid cooling, condensation, and deposition of moisture (Lundquist & Loheide II, 2011). The western aqueous drainages of the Sierra feed the central valley and funnel all the way to the San Francisco Bay. The eastern drainages are smaller than the western drainages and do not reach the ocean. Eastern drainage from Mono Lake has been diverted southward into the Los Angeles Aqueduct, supplying water to Southern California and the Los Angeles Basin. The Sierra Nevada contains five biotic zones. This dissertation work occurs in three of them: the Alpine Zone (areas over 11,500 feet), the Subalpine Zone (areas between 10,500 and 11,500 feet), and the Upper Montane Forest (9,000 to 10,500 feet) (Schoenherr, A.A., 1995).

Study Systems Importance:

Together, the San Joaquin Valley and the Eastern Sierra Nevada represent complementary, ecologically distinct natural study systems well suited to investigating the interactive effects of climate and land-use change on arthropod vector populations. The SJV is a heavily human-modified landscape where intensive agriculture, urban expansion, and altered hydrology have fragmented remaining natural habitats and restructured wildlife communities – conditions that have made it one of the most imperiled ecosystems in North America (Ricketts et al., 1999). These landscape pressures, interacting with the region's

pronounced drought-flood precipitation cycles and accelerated warming trajectory (Diffenbaugh et al., 2015), create dynamic and shifting risk landscapes for mosquito-borne diseases such as West Nile Virus (MacDonald et al., 2025). The Eastern Sierra, by contrast, represents a largely intact but climatically and environmentally sensitive system, in which steep elevational gradients compress multiple biotic zones over short distances (Körner, 2007). It also experiences sporadic yet substantial human presence for recreation and is the site of intentional introductions of nonnative species, such as trout stocking, in alpine lakes and streams (Knapp et al., 2001; Owens et al., 2023).

Both regions are experiencing accelerating change: the SJV faces increasing temperatures and more severe drought, and an expanding agricultural footprint, while the Eastern Sierra is undergoing significant shifts in snowpack timing, recreational and nonnative species presence that cascades through its aquatic and terrestrial ecosystems (Knapp et al., 2001; Mote et al., 2018). By examining arthropod vector populations across these two ecosystems, both uniquely defined by human modification and climatic sensitivity, this dissertation captures a breadth of interactive human impacts and contributes to a broader understanding of how coupled landscape and climate pressures reshape vector dynamics, disease risk, and ecosystem function.

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Figures:

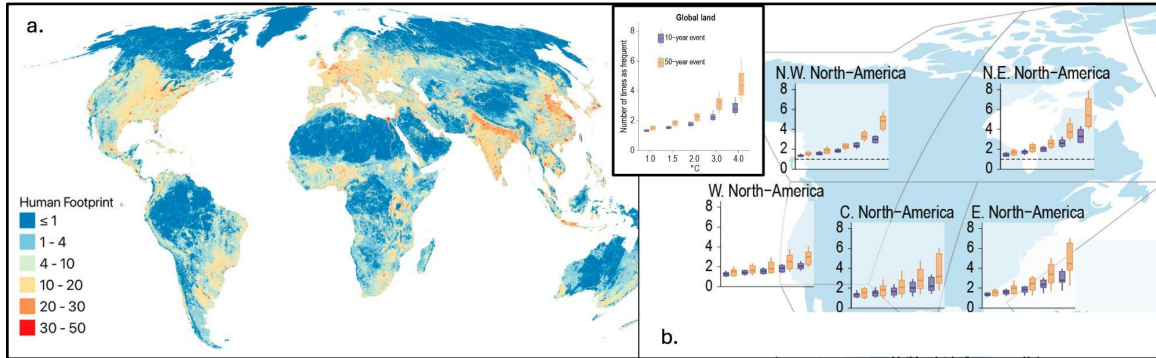


Figure 0.1: (a) The global terrestrial human footprint map from the year 2020, which includes land cover change, population density, electric infrastructure, roadways, railways, and navigable waterways. Figure and analysis completed by Gassert et al. (2023). (b) The IPCC Projected changes in the frequency of extreme precipitation events under 1°C, 1.5°C, 2°C, 3°C, and 4°C global warming levels (Figure 11.7; AR6, Mason-Delmotte et al., 2021).

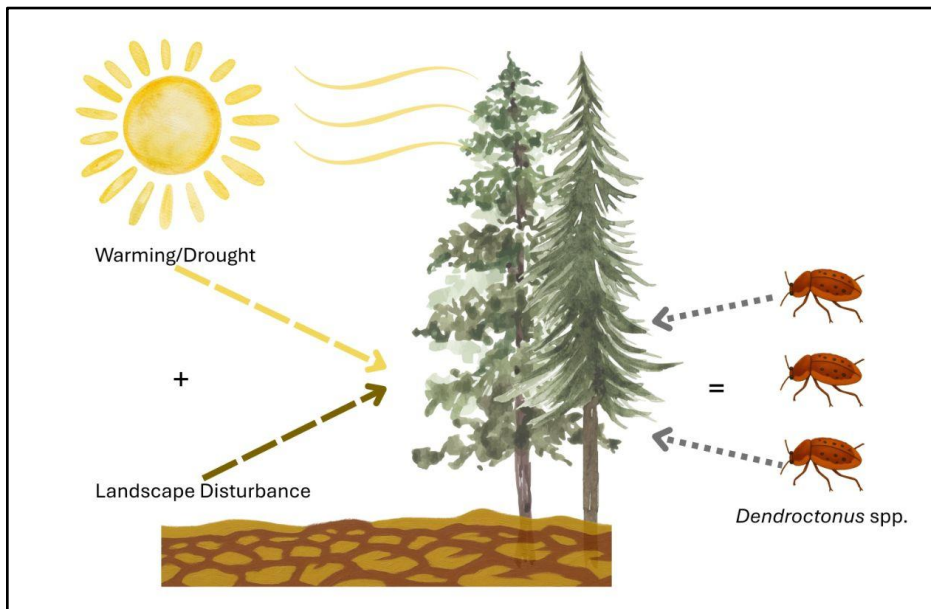


Figure 0.2: Pictorial schematic illustrating the interactive effects of warming temperatures and landscape disturbance on bark beetle (*Dendroctonus* spp.) outbreaks in pine forests (Bentz et al., 2010; Raffa et al., 2008)—figure created in Canva Pro.

CHAPTER 1 – Variable effects of wildlife and livestock on questing tick abundance across a topographical-climatic gradient.

Co-authors: Samantha Sambado, Devyn Orr, An Bui, Andrea Swei, and Hillary S. Young

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Abstract:

Large-bodied wild ungulates are declining worldwide, while domestic livestock continues to increase in abundance. Such changes in large herbivore communities should have strong effects on tick and tick-borne disease control, as they can indirectly modify habitats and directly serve as final hosts in ticks’ life cycles. Numerous studies have now linked changing ungulate communities to changes in tick populations and disease risk. However, the effects of changes in large herbivore communities are variable across studies, and the role of climate as a mediating factor in this variation remains poorly understood. Also, studies to date have largely focused on wildlife loss without considering the extent to which livestock additions may alter tick populations, even though livestock replacement of wildlife is the global norm. In this study, we used a large-scale exclosure experiment, replicated along a topoclimatic gradient, to examine the effects of both large-herbivore removal and livestock additions on

tick populations. We found that while questing ticks increased modestly by 21% when large herbivores were removed from a system, they decreased more substantially by 50% when livestock (cattle) were added. Importantly, in addition to the direct effects of climate on tick populations, climate also mediates the effect of ungulates on questing tick density. In particular, the addition of livestock under the most arid conditions reduced tick presence, likely due to changes in ground-level microclimates that shifted away from conditions favorable to ticks. Overall, the work contributes to our understanding of tick population responses to globally common human-induced rangeland alterations under the concurrent effects of climate change.

Introduction:

Wild ungulate herbivores are disappearing from many ecosystems worldwide through land-use changes and overexploitation, and ~60% of species are at risk of extinction (Ripple et al., 2015). However, defaunation is not occurring in isolation; it typically occurs simultaneously with the introduction of domestic herbivores such as cattle (Barnosky 2008; Orr et al. 2022; Young et al. 2013) and concurrently with climate change (Dirzo et al. 2014; Young et al. 2016). Domestic livestock biomass is presently over fourteen times that of large vertebrate wild animals (Bar-On, Phillips, and Milo 2018). Cattle grazing impacts on vegetation have created immense and cascading effects on ecosystems, including changes in soil carbon storage (Forbes et al. 2019; Sitters et al. 2020) and landscape productivity (Charles et al. 2017; Travers et al. 2018), but these effects can differ based on environmental context, stocking density, and behavior among other factors (Veblen and Young 2010; Young et al. 2013).

Notably, landscape effects of shifting herbivore communities can be altered by aridity and climate change. Grasslands, shrublands, and savannas are the predominant rangelands for many wild ungulates and most cattle. These dryland ecosystems (systems with aridity indices <0.65) cover 41% of the land surface and are inherently water-stressed (Gaur and Squires 2018). As such, they are already predisposed to respond strongly to climate warming or drought conditions. Aridity has been well established to strongly mediate the cascading impact of large ungulate herbivores on plant communities by magnifying the effects of grazing stress on plant biomass, density, and diversity (Goheen et al. 2013; Orr et al. 2022; Pringle et al. 2007; Young et al. 2013).

Ungulate communities also strongly influence arthropod disease vectors, such as ticks (family Ixodidae; subclass Acari) (Goheen et al. 2018; Keesing et al. 2013; Young et al. 2014). Many tick species rely on large herbivores, mammals, and reptiles as blood-meal hosts and require a blood meal at each life-cycle stage. Host population size strongly affected tick population abundance in the tick species *Ixodes ricinus* and *Ixodes pacificus* (Randolph 2004; Swei et al. 2011). Ungulate herbivores – both wild and domestic – serve as final hosts for many tick species and can be necessary for certain tick species like *Ixodes scapularis*, *Amblyomma americanum*, *Rhipicephalus annulatus*, and *Haemaphysalis longicornis*, to reproduce and complete their life cycle (Tsao et al. 2021). Without their final hosts, ticks may not reproduce, and for *Ixodes pacificus*, loss of such hosts typically decreased population sizes (Gilbert et al. 2012; H. J. Kilpatrick, Labonte, and Stafford 2014). However, the removal of large hosts can also increase tick abundance through the competitive release of their juvenile hosts, typically small vertebrates. In the Kenyan Long-term Exclosure Experiment (KLEE), plots with large herbivores removed showed a significant increase in

small mammalian hosts, as reported by Young et al. (2014). This was postulated to enable the response observed in Titcomb et al. 2017, in which the same plots showed significant increases in the abundance of ticks *Rhipicephalus pravus*, *praetextatus*, and *pulchellus*. This variability in tick responses to changes in host communities highlights the complexity of tick-to-host dynamics across landscapes and how multiple factors may interactively affect their landscape-level abundances.

Tick populations are also strongly affected by environmental conditions, notably aridity, which is expected to intensify under climate change. The timing of host-seeking behavior and abundance of *Ixodes pacificus* varied with increasing aridity across different landscapes (A. M. Kilpatrick et al. 2017; MacDonald 2018). In the southwestern United States, increasingly hotter and drier summers have truncated their activity (MacDonald et al. 2020; MacDonald and Briggs 2016). Local climatic conditions shape tick presence and survival, given that ticks spend ~90% of their life cycle off-host and are sensitive to changes in temperature and humidity (Needham and Teel 1991). In especially arid conditions, *Ixodes* spp. ticks escape to nearby moist microclimates, a defense from desiccation-related mortalities (Gray et al. 2016; Padgett and Lane 2001). Herbivores themselves affected the microclimates available to *I. pacificus* and *Dermacentor variabilis* larvae at ground level through the grazing and trampling of vegetation and the grazing and compaction of soils (Copeland & Orr et al., *in review*).

Reported tick-borne diseases accounted for 77% of all reported vector-borne disease cases in the United States and are likely even underrepresented in this statistic, as many cases go undiagnosed (Rosenberg 2018). The Pacific coast tick (*Dermacentor occidentalis*) is a regionally common tick in the southwestern US and a vector of human pathogens *Rickettsia*

rickettsii (Rocky Mountain spotted fever) and *Rickettsia* 364D. Additionally, they are vectors of the livestock diseases *Anaplasmosis bovis* and *Ehrlichia chaffeensis* in both humans and livestock (Holden et al. 2003; Lane et al. 2010; Padgett et al. 2016). Given that ticks affect both human and livestock health, it is crucial to understand fluctuations in tick populations and tick-borne diseases that may occur as rangeland large herbivore communities change.

Studies of tick responses to climatic context (Dantas-Torres 2015; L. Eisen, Eisen, and Lane 2002; R. J. Eisen et al. 2016; Levi et al. 2015; MacDonald et al. 2020), native ungulate community alteration (Bloemer et al. 1986; Daniels, Fish, and Schwartz 1993; Gilbert et al. 2012), and in fewer cases, domestic livestock or cattle additions (Keesing et al. 2013; Mutizhe et al. 2021) have increased our understanding of tick populations in these anthropogenic rangeland landscapes. However, much more work is needed to investigate how these factors interact, as there is strong evidence that this interaction can dampen or amplify tick responses (Keesing et al. 2018; Titcomb et al. 2017).

We address this challenge using a tightly controlled herbivore exclosure experiment in southern California, replicated across a climatic gradient. The study addresses three questions for this system: 1) What are the effects of total large herbivore removal and cattle addition on tick abundance? 2) How does tick abundance vary across climatic contexts? 3) Is there an interactive effect between either large herbivore loss or cattle addition and climate conditions? First, we hypothesized that large-herbivore removal (simulating total defaunation) would increase tick abundance by reducing grazing pressure and increasing vegetative biomass, thereby creating tick-beneficial microhabitats. We expect cattle additions would decrease abundance, with the loss of vegetation increasing the risk of desiccation for ticks across the landscape. Additionally, we anticipate that the increasing aridity of our

climate levels would decrease tick abundance. Further, we expect an interaction between climate and the herbivore-exclusion treatment to predict tick abundance. This interaction will make the effects of cattle addition strongest under more arid conditions. Lastly, it's likely that tick responses to climate level and herbivore treatment will change over the years of our study due to ticks' multi-year lifespan and the time required for landscape vegetation to respond to our exclosure treatments.

Materials and Methods:

Study Area:

We conducted this study on Tejon Ranch in Kern Co., CA (34°59'N, 118°43'W). Tejon Ranch is a mixed cattle ranch and wildlife conservation property containing 97,124 hectares of conserved land. Wild ungulates on the ranch include populations of mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus canadensis nelsoni*), feral pig (*Sus scrofa*), and pronghorn (*Antilocapra americana*), as well as livestock (black angus beef cattle) at an average stocking density of 0.13 head/ha, which falls within the range of recommended stocking density for Sierra foothill and coast-range oak woodland landscapes (George, Frost, and McDougald 2020). All plots were established in a mixed oak savannah-woodland. The study area is characterized by rugged topography that creates steep aridity gradients, resulting in strong local climate variation, and is projected to experience increased aridification under climate change over the next century (McCullough et al. 2016). The regional climate is Mediterranean, with hot, dry summers and cooler, wetter winters. Field collections for this study occurred between 2016 and 2019, during and directly after the California drought (~2011-2017), the driest period recorded in state history (Griffin and Anchukaitis 2014; Mount, Escriva-Bou, and Sencan 2021).

We detected three tick species in this study: *Dermacentor occidentalis* (Pacific coast tick, most collected), *Ixodes pacificus* (black-legged tick), and *Dermacentor variabilis* (American dog tick). In southern California, *D. occidentalis* has been found to be tolerant of open, arid habitats (MacDonald 2018), whereas *I. pacificus* is less tolerant and occurs more often in denser, cooler, forested habitats (L. Eisen, Eisen, and Lane 2006; MacDonald 2018).

Dermacentor variabilis shows aridity tolerance and a preference for more open habitats similar to *D. occidentalis*, but it is found in greater abundance along the California coast and is collected less frequently in the central/eastern parts of the state (Furman and Loomis 1984; Minigan et al. 2018).

In addition to the diseases of concern for human and animal health vectored by *D. occidentalis* (Rocky Mountain spotted fever, Ehrlichiosis, and Anaplasmosis), *I. pacificus* and *D. variabilis* are also known vectors of diseases. *Ixodes pacificus* is the vector for the most common tick-borne disease, Lyme disease (*Borrelia burgdorferi*) (Lane et al. 2010; MacDonald et al. 2017), and another disease, tick-borne relapsing fever (*Borrelia miyamotoi*) (Sambado et al. 2020). *Dermacentor variabilis* is an additional vector of Rocky Mountain spotted fever (*Rickettsia rickettsii*) and tularemia (*Francisella tularensis*) (Minigan et al. 2018).

Experimental Design:

This work was conducted within the Tejon Ranch Exclosure Experiment (TREE), an ongoing study using a replicated system of three exclosure types to alter the presence of cattle and wild ungulates across three climate levels distinguished by topography (increasing elevation) and slope direction (southern- and northern-facing). TREE consists of 27 1-ha. plots spanning these three climatic aridity levels, with nine plots at each level, grouped into

three replicate blocks, each containing one of each herbivory-treatment exclosures (Figure 1.1a).

Categorization of Climate Levels:

The climate levels for our experiment were established using available climate grids, downscaled to thirty meters (Davis and Sweet 2012; McCullough et al. 2016). Each climate level is separated by approximately 2°C average temperature and 200-300mm annual precipitation (Orr et al. 2022). Additionally, all climate levels differed significantly in daily maximum and daily minimum temperatures (Klope 2021). The three climate levels in TREE are Arid, Intermediate, and Mesic. Arid is the hottest and driest level, followed by Intermediate, and Mesic is the coolest and wettest level (Figure 1.1a). The locations were selected to approximate present-, near-future, and far-future climate scenarios (Orr et al. 2022).

Herbivory Treatments:

The three herbivore exclusion treatments consist of *wildlife* (W) (simulating conserved conditions for the landscape), *cattle and wildlife* (CW) (simulating typical ranching conditions in the area), and *minus cattle and wildlife* (-CW) (simulating defaunation) (Figure 1.1b). *Wildlife* exclosures use semi-permeable barbed-wire fencing to exclude livestock while allowing wildlife access. *Cattle and wildlife* exclosures have no fencing and t-posts demarcating plot corners. *Minus cattle and wildlife* exclosures were constructed with complete barriers of barbed wire fencing, which functionally excluded large herbivores over 40 kg in body mass (Figure 1.1b). Exclosure fencing for the herbivory treatments was established in November 2016, and monitoring of dung counts across all plots confirmed that treatments operated as intended (Orr et al. 2022).

Tick Sampling:

We evaluated tick populations by sampling questing ticks in the plots before the herbivore exclusion treatments were applied (April – December 2016) and during the first three years of the experiment following implementation of the exclusion treatments (2017-2019). Each plot was sampled for ticks by dragging a 1 m² white flannel cloth through the understory for one hour, with the drag cloth being checked by the sampler for attached ticks every 80 meters, or approximately every 1-3 minutes. All herbivore treatment plots were sampled at least monthly from 2017 to 2019 (except for October 2019). In 2017 and 2018, during April, the treatment plots were dragged for two additional sixty-minute periods, and in May, for an additional sixty-minute period. In 2019, all treatment plots were sampled for an additional sixty-minute drag in April and in June. In May, the herbivore treatments at the Intermediate and Mesic climate levels were sampled an additional time, whereas the plots at the Arid climate level were sampled only once. The data from each sixty-minute drag were not aggregated by month and remained a separate sampling period within the dataset and subsequent analyses. This metric, adult ticks/hour, establishes enclosure-level relative tick abundance, with the collection rate serving as a proxy for the true abundance of adult ticks within the plot. The herbivore enclosures were sampled only on days when the temperature was above 10°C, and there was no rain, low fog, strong wind, or snow. Any ticks found on the cloth during the 60-minute sampling period were collected with tweezers and stored in 70% ethanol. Ticks were identified to species in the field, and if further confirmation was needed, they were taken back to the lab for further examination under a dissection microscope.

Data Analyses:

Questing Tick Density:

Statistical analyses focused on questing *D. occidentalis* collected during monthly hour-long cloth drag efforts from 2017 through 2019, encompassing the three-year period post-exclosure construction. Since the relative abundance of *I. pacificus* and *D. variabilis* was low, tick totals of all species (*I. pacificus*, *D. occidentalis*, *D. variabilis*) were combined in the summary analysis, but only *D. occidentalis*, the species most collected within our study, was used for the effect and regression analyses. Despite extensive efforts to collect juvenile life stages of all tick species, we had limited success; therefore, only adult life stages were included in the analysis. Our collected data were non-normal and therefore necessitated the use of nonparametric tests and a generalized linear mixed model with a negative binomial distribution for model analysis. All analyses were performed within various statistical packages in RStudio (v 4.4.1).

Tick Density Relationships with Herbivores and Climate:

Effect Size:

To measure the strength of the relationship between herbivore treatment and climate levels on relative *D. occidentalis* abundance, we calculated the effect size using a non-parametric Kruskal-Wallis test followed by a post-hoc Dunn's test with a Bonferroni correction.

Incorporating Interactive Context Between Herbivore Exclusion and Climate:

Model Construction:

Using adult *D. occidentalis*/hour as the response variable, we fit generalized linear mixed models (GLMMs) with a negative binomial distribution. We included the fixed effects of herbivore treatment (-CW, W, CW), climate (Arid, Intermediate, Mesic), and then year

(2017, 2018, 2019). Year serves as a proxy for the number of years that enclosure fences have been constructed. The model intercept was set to W enclosure treatments at the Intermediate climate level, representing mid-level aridity between Mesic (wetter) and Arid (drier). The herbivore enclosure type, W, represents the landscape before the addition of domestic livestock in the CW treatments and represents the landscape not affected by the total defaunation of our -CW treatments. Therefore, as the intermediary enclosure type, it is used as our model intercept. Our models' random effects accounted for the non-independence of repeated sampling of plots over time and tick seasonality. Therefore, we included a unique plot ID to represent each of the 27 plots individually and by month, given the natural seasonal variation in tick populations. All models were constructed using the `'glmmTMB'` package and the `glmmTMB()` function (Brooks et al. 2017).

Model Comparisons & Assessments:

We compared candidate models using AIC values and one-sided likelihood ratio tests with the `anova()` function. For our best-fit model, we compared marginal and conditional R^2 to assess the importance of fixed and random effects in explaining the observed variation in the relative *abundance of D. occidentalis*. Finally, we used k-fold cross-validation with the `'caret'` package and plotted predicted versus observed values to assess the model's overall fit (Kuhn 2008).

Results:

Questing Ticks Varied by Herbivore Enclosure and Topoclimate Level:

Tick sampling from 2016 – 2019 resulted in the collection of 2,692 questing adult ticks. The most common tick species collected via tick drag was *D. occidentalis* (n = 2,420, 89.9%), then *I. pacificus* (n = 206, 7.7%), and lastly *D. variabilis* (n = 68, 2.5%). When

comparing mean tick collection per hour rates of all three tick species collected across herbivory treatments, -CW (*minus cattle and wildlife*) plots had the highest relative abundance ($u = 3.2$ ticks/hour, $SD = \pm 6.4$), followed by W (*wildlife*) ($u = 2.2$ ticks/hour, $SD = \pm 5.1$) and then CW (*cattle and wildlife*) ($u = 1.2$ ticks/hour, $SD = \pm 3.2$). Mean relative abundance of adult ticks by climate level was highest in Intermediate ($u = 3.7$ ticks/hour, $SD = \pm 7.0$), followed by Mesic ($u = 1.3$ ticks/hour, $SD = \pm 2.2$) and Arid ($u = 0.76$ ticks/hour, $SD = \pm 2.8$).

Relative D. occidentalis Abundance was Significantly Different Between Herbivore Exclosure and Climatic Level:

Adult *D. occidentalis*/hour differed significantly between herbivory treatments ($p < 0.001$) and climate levels ($p < 0.001$). For herbivore exclosures, it was significantly different when comparing CW exclosures with W exclosures ($p < 0.001$) or when comparing CW exclosures with -CW exclosures ($p < 0.001$). There was no significant difference in relative *D. occidentalis* abundance between the W and -CW exclosures ($p = 0.36$) (Figure 1.2a). Adult *D. occidentalis*/hour differed significantly among all three climate levels (Figure 1.2b). The effect of climate level on relative *D. occidentalis* abundance based on the Kruskal Effect Size was moderate (H-statistic = 0.060). It was greater than the effect of herbivore treatment on relative *D. occidentalis* abundance, which was small (H-statistic = 0.012).

Significant Interaction Between Herbivore Exclosure and Climate Level:

Our best-fit model included a three-way interactive term between our fixed-effects herbivory treatment, climate level, and year ($df = 30$). The fixed effects accounted for a small proportion of the variance (marginal $R^2 = 0.15$), but including the random effects of month and plot ID improved model fit (conditional $R^2 = 0.90$). Nonetheless, including fixed

effects improved the model fit more than the null model (McFadden's $R^2 = 0.22$). We found that the interaction between CW plots and the Arid climate level was significantly different than the model intercept ($p = 0.02$). The CW plots at Arid were predicted to have approximately two fewer *D. occidentalis* adult ticks per hour collection period ($estimate = -2.1$, $SE = +/-0.9$). Regardless of herbivore treatment, the Arid climate level was predicted to have approximately one less questing *D. occidentalis* adult tick per hour collection period than the model intercept ($p\text{-value} = 0.005$, $estimate = -1.4$, $SE = +/- 0.5$). Except in 2019, when this trend reversed, and it predicted there would be more questing *D. occidentalis* adults at the Arid climate level ($p < 0.001$, $estimate = 1.4$, $SE = +/- 0.4$). The only other predicted significant interannual variation also occurred in 2019, where, during this year, the -CW plots were predicted to have fewer questing *D. occidentalis* adults per hour ($p = 0.05$, $estimate = -0.7$, $SE = +/- 0.3$) (Figure 1.3; Table 1.1).

Model fit was likely affected by the variation in questing *D. occidentalis* within the herbivore treatment plots. 1.74% of the relative *D. occidentalis* abundances we collected fell three standard deviations above the mean (standardized residuals: $u = 0$, $SD = 1$). Yet, a k-fold ($k = 15$) cross-validation showed relatively stable model performance across folds. Additionally, the predicted model means fit well to the observed means of herbivory treatment and climate level; averaging dampened the effect of this variation (Appendix; Chapter 1; Figure S1a & b).

Discussion:

Our study explored the effects of changes in large herbivore communities on questing adult ticks, particularly the tick species *Dermacentor occidentalis*, and how these effects are mediated by topoclimatic context. This was further affected by temporal scales (months

within a year and across 3 years) (Figure 1.3; Appendix; Chapter 1; Figure S2). Both herbivore treatments and climate levels influenced the relative *abundance of D. occidentalis*, but climate had a greater effect. Yet the presence of cattle on the landscape further decreased adult *D. occidentalis* abundance more than climate alone. This was especially pronounced under the most arid conditions of our study.

Our results confirm our hypotheses and supports previous work under similar experimental conditions from Kenya (Titcomb et al. 2017). Titcomb et al., at the Ungulate Herbivory Under Rainfall Uncertainty (UHURU) experiment, found a significant interaction between their experiment's total large herbivore removal (a version of -CW exclosures) and climate level (delineated by differences in mean annual precipitation). Their work found an increase in tick abundances within their -CW exclosures at their most arid location (Titcomb et al. 2017). Our study also found a significant interaction between climate level and herbivore treatment at our most arid study location. In contrast to Titcomb et al., our interaction involved our open CW (*cattle and wildlife*) plots and resulted in a decrease in relative *D. occidentalis* abundance to its lowest level (Table 1.1). In our study, questing adult tick abundance and relative *D. occidentalis* abundance were highest in the -CW plots at the Intermediate climate (Figure 1.2a & Figure 1.2b), differing from results reported in Kenya.

Our similar and differing results to Titcomb et al. (2017) suggest that the way managerial entities of rangelands deal with tick presence and tick-borne disease risk will be highly context-dependent, with the life cycle, life history traits, and climatic resiliency of ticks varying greatly across global rangeland regions even under similar climate aridity regimes. Climate becomes more significant for population success near range limits than at the centers of species ranges (Hampe and Petit 2005; Thomas 2010). This likely explains the significance of the climate level in our system. The climate levels are established by

topography, which creates cooler, moister environments at higher elevations than on the valley floor. The questing ticks at lower elevations experience greater climate-related stress than those at higher elevations, reducing their overall relative abundance (Figure 1.2a). Under climate change scenarios, higher-elevation areas are projected to experience increased temperatures (Pepin et al. 2015). *D. occidentalis* abundance may decrease in this landscape with continued temperature rise and increased aridity under current climate change projections for the area.

Tick populations are protected from climatic stress by seeking microclimatic refugia within the landscape. Within our herbivore exclosure treatments, the mechanism most likely related to tick population success is changes in microhabitat conditions that improved tick survival. Microclimate refugia have been found to protect tick populations from otherwise fatal climatic conditions (e.g., soil protecting from wildfire and snow insulating from below-freezing temperatures) (MacDonald 2018; Padgett et al. 2009; Volk et al. 2022). All tick stages are particularly sensitive to aridity and to the risk of desiccation when off a host (Bouchard et al. 2019; Needham and Teel 1991).

In 2019, Orr et al. (2022) at TREE evaluated the impact of climate and herbivore treatments on plant community structure by sampling thirty-six $1\text{ m} \times 1\text{ m}$ subplots in each exclosure. Surveys of these $1\text{ m} \times 1\text{ m}$ subplots included measurements of total vegetation cover, litter volume, and bare ground. Additionally, ΔPAR (photosynthetically active radiation) was used to determine the percent of light reaching the soil surface at 10 subplots per exclosure. Finally, $0.25\text{ m} \times 0.25\text{ m}$ of residual dry matter (RDM) biomass was collected, dried, and weighed from each of the 36 subplots within each exclosure. Orr et al. found significant differences in all metrics between the -CW plots and the W and CW plots, except for total cover at the Intermediate climate level and total bare ground at the Mesic climate

level. The addition of cattle also decreased shading in the CW plots, allowing more sunlight to reach the soil surface. These results indicate that the herbivore treatments, -CW and W, had significantly more vegetation cover than the CW plots. This additional vegetation likely provided the in-exclosure tick populations with the microclimate refugia needed for their survival within our study system.

Increased vegetation density from decreased grazing pressure in this system and in others increases plant biomass, lowers soil and above-ground temperatures, and increases humidity levels, all of which are beneficial to tick questing activity by lowering the risk of desiccation (Diuk-Wasser, VanAcker, and Fernandez 2021; R. J. Eisen et al. 2016; MacDonald 2018). Tick abundance has increased in more temperate and moister areas (R. J. Eisen et al. 2016; MacDonald 2018; Ogden and Lindsay 2016). Cattle additions to the landscape increased herbivore biomass and grazing pressure, thereby decreasing these tick-advantageous conditions.

Also at TREE, Copeland & Orr et al. (*in review*) completed an in-situ survivorship study on juvenile *I. pacificus* and *D. variabilis* ticks. For this work, they additionally measured daytime soil temperature and relative surface humidity. They found that soil surface temperature was significantly higher in the less-vegetation-dense CW plots and that soil humidity differed significantly between the CW and W, -CW plots at the Arid climate level. Copeland & Orr et al. concluded that large herbivores, particularly the addition of cattle, were drivers of microclimate change and best explained the results of their study on survivorship. They found that aridity, both directly in climate and indirectly through grazing pressure, decreased the survival of juvenile tick life stages (larvae and nymphs) (Copeland & Orr et al., *in review*). The findings of Copeland & Orr et al., which report the lowest survival rates in the CW treatments at the Arid climate level, help confirm our results. The fewer

juveniles that survive on the landscape, the fewer questing adult ticks there will be. The loss of microhabitat within this treatment likely limited tick survival and, therefore, abundance.

It is likely that our study, in sampling three years post-exclosure treatment installation, captured residual pre-exclosure ticks in our plots because of their approximately three-year life cycle (Padgett and Lane 2001), and the removal of final hosts with exclosure construction kept them questing on the landscape and therefore collected by our drag cloths (Rand et al. 2004). In the last year of the study (2019), there was a change in the relative abundance of adult ticks between exclosure types. In 2017 and 2018, the -CW exclosures contained the highest numbers of adult ticks, and in 2019, the greatest numbers of adult *D. occidentalis* collected via one-hour cloth drags were inside the W exclosures (Figure 1.3). Our model also predicted this change, with 2019 indicating significantly fewer questing *D. occidentalis* adults in the -CW than in the W exclosures (Table 1.1). This change in relative abundance between exclosure type and the predicted significance of this treatment type highlights the importance of large herbivores as hosts for the continuation of tick populations. Large herbivores are typically parasitized by adult ticks and are also where the adult ticks breed (Bouchard et al. 2019; A. M. Kilpatrick et al. 2017). The complete loss of critical final hosts results in a decrease in subsequent generations when questing adults cannot parasitize a final host and successfully mate. Further sampling within TREE is needed to confirm that the change in relative *D. occidentalis* abundance from -CW to W exclosures is the result of wild herbivore presence perpetuating plot-level tick populations, not just an effect of inter-annual variation or another factor not included in this study.

Another mechanism suggested by Esser et al., 2018, as well as Buck and Perkins, 2018, postulated that tick increases might be an artifact of experimental plot sizes and that in the absence of reproductive (large mammal) hosts, ticks might have dispersed in the exclosure

plots via rodent populations (Buck and Perkins 2018; Esser, Hartemink, and de Boer 2018).

These mechanisms and their impacts on tick abundance inside experimental plots do not fully explain our results. They would require very large numbers of plot-crossing or existing rodents and/or very high tick densities per animal. We sampled lizard and small mammal populations across all our plots and obtained overall low capture rates (see Appendix S1). However, our study did not account for plot-crossing medium-sized mammals such as hares, sciurids, and small carnivores. *D. occidentalis* will parasitize mammals other than large herbivores as a final reproductive host (Lane et al. 2010; Padgett et al. 2016). We believe part of the remaining tick proliferation in -CW exclosures was due to present and passing medium mammalian wildlife that could still access these plots. To understand such impacts, focused sampling on these species is still needed within our system.

Other mechanisms have been proposed to explain the effects of large herbivores on ticks. In another study, the presence of cattle directly decreased tick populations. In Keesing et al. (2013), cattle acted as a final host sink for tick populations resulting from the routine application of acaricide to the cattle present (Keesing et al. 2013). The cattle present in our landscape are treated once a year with an acaricide in winter or early spring, before the peak tick questing season. In our study, this is likely a compounding effect of cattle reducing vegetation cover and limiting off-host survival. Acaricide treatment would decrease on-host survival, killing attached adult ticks during the period the treatment is active (Petney and Horak 1987; Walker, Klein, and Levin 2014). With the cattle treated once a year, it was undetermined how long the acaricide lasts and whether it would protect the cattle from tick attachment for the duration of the spring tick questing season or from the fall questing season, a smaller but nonetheless peak in tick host-searching activity that occurs before the winter months (Appendix; Chapter 1; Figure S2). The cattle of the Tejon Ranch are very

free-range, so regular application of acaricide is likely logistically infeasible for the livestock managers. Therefore, while this is likely a component of our study results, its significance remains unclear.

Conclusion:

Our work demonstrates the significant potential of increasing climate aridity to alter tick populations, an effect notably exacerbated by landscape-level herbivory. While herbivore treatment was consistently incorporated in best-fit models for tick abundance, climate level was a stronger predictor when evaluated independently. Aridity will continue to impact landscape suitability for microclimates conducive to tick populations. Under climate change projections, Southern California and other parts of the globe are likely to experience further reduced moisture and rising temperatures, and to see further reductions in tick populations. However, other geographic areas may experience different climate change effects, and the interactive impact of climate and herbivore biomass may differ notably on tick abundances in these locations. This highlights the need for studies to continue incorporating multiple drivers of tick abundance into analyses to further our understanding of the variability of tick populations in response to landscape alteration and climate change.

Figures:

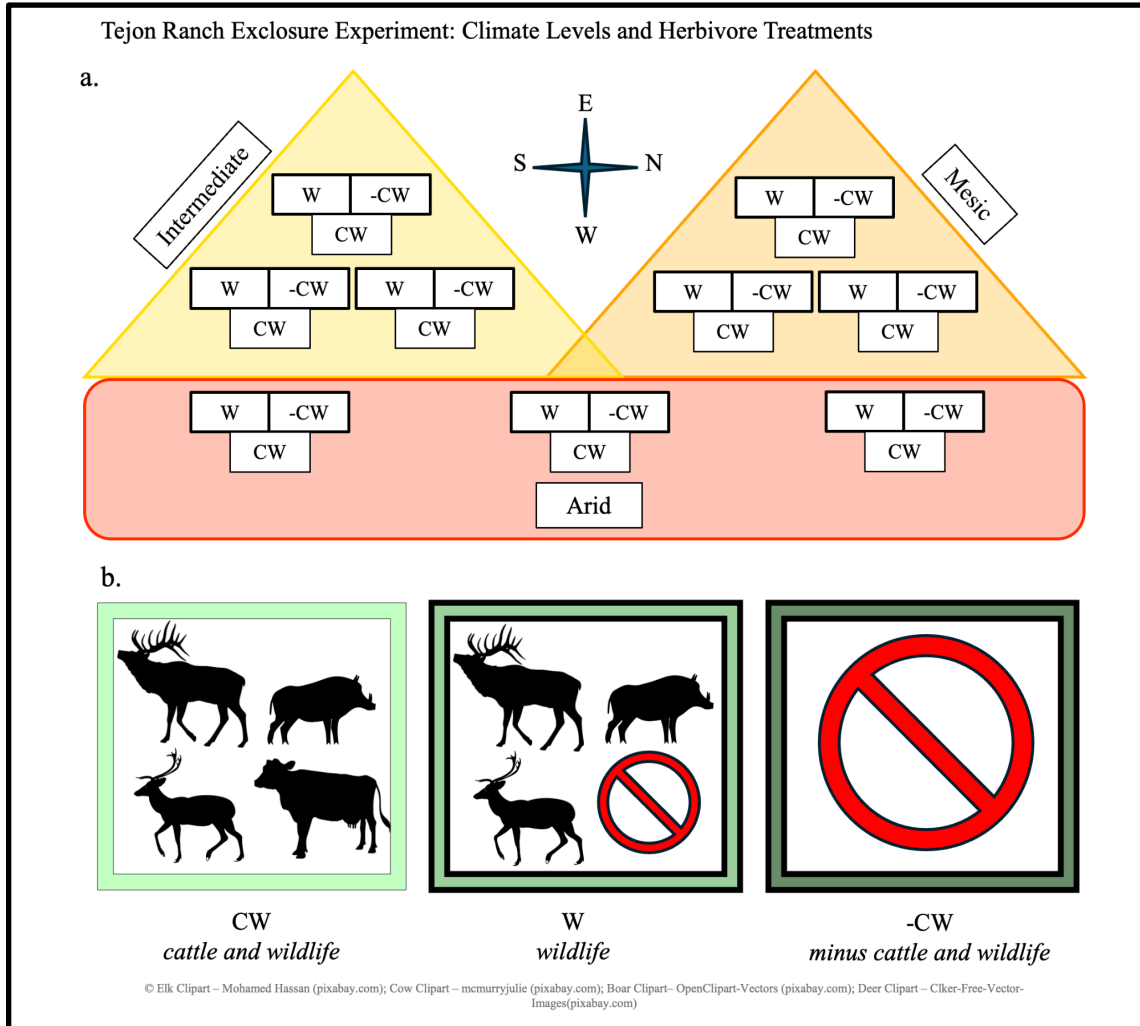


Figure 1.1 a & b: (a) The experimental design of the Tejon Ranch Exclosure Experiment (TREE). TREE consists of three distinct climate levels: Arid, Intermediate, and Mesic. The Arid-climate herbivore exclosures are at ~580m in elevation. Intermediate and Mesic are at the same elevation, ~1,650m, but are located on opposite-facing slopes, with Intermediate-level exclosures on the south (S)–facing slope and the Mesic-level exclosures on the north (N)–facing slope (East – E, West – W). At each climate level, a triplicate array of large-herbivore exclosure treatments was constructed. (b) Each replicate at a climate level includes one exclosure treatment that functionally removes access by all large herbivores to the plot, called the minus cattle and wildlife (-CW) plot. A second exclosure treatment limits plot access to large wildlife herbivores only while preventing domestic herbivores' access, called *wildlife* (W) plot. Finally, the *cattle and wildlife* (CW) plot has no exclusionary fencing and permits the access of both wild and domestic large herbivores. Both plots, W (*wildlife*) and -CW (*minus cattle and wildlife*), were created with barbed wire fencing and, in the figure, have bolded black borders, whereas the non-fenced herbivore treatment, CW (*cattle and wildlife*), has a non-bolded black border.

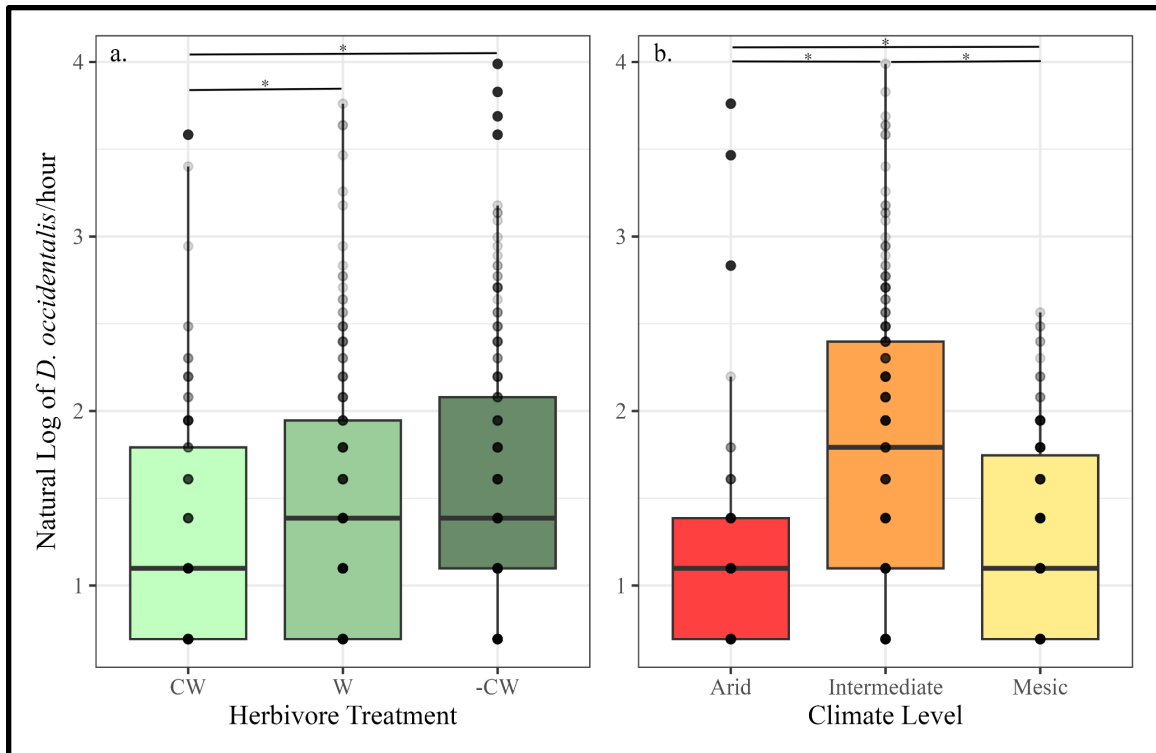


Figure 1.2 a & b: (a) The log-transformed relative abundance of adult *D. occidentalis* across the experimental herbivore treatments. There was a significant difference in relative abundance between the CW (*cattle and wildlife*) plots and the -CW (*minus cattle and wildlife*) plots. Additionally, there was a significant difference in *D. occidentalis* abundance between the CW and the W (*wildlife*) plots. There were no significant differences in relative *D. occidentalis* abundance between the W and -CW exclosure treatments. (b) Relative *D. occidentalis* abundance was significantly different across all three climate levels. The Intermediate climate level had the highest relative abundance of questing *D. occidentalis*, whereas the Arid climate level had the lowest abundance.

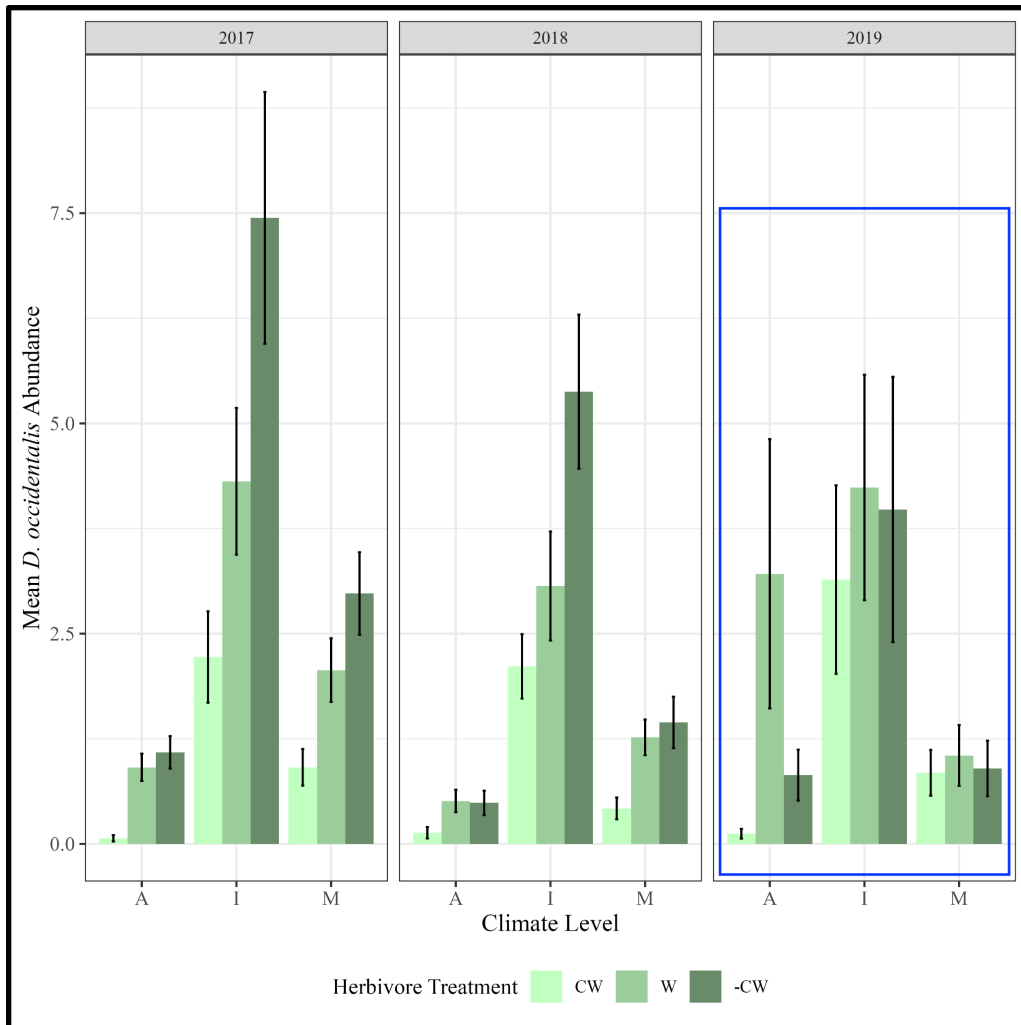


Figure 1.3: Yearly average of relative *D. occidentalis* abundance for the years post-exclosure installation, 2017-2019. For climate level: Arid (A), Intermediate (I), and Mesic (M), and herbivore treatment type: CW (*cattle and wildlife*), W (*wildlife*), and -CW (*minus cattle and wildlife*). In 2017 and 2018, the average *D. occidentalis*/hour was highest in the -CW (*minus cattle and wildlife*) exclosures. In 2019, the highest average relative abundance shifted to the W (*wildlife*) exclosures, as indicated by the blue box in the figure. There was a particularly large change in relative abundance between exclosure treatments at the Arid climate level.

Tables:

Table 1.1:

The significant results from the best-fit generalized mixed linear model – *D. occidentalis* ~ herbivory treatment*climate level*year + (1|Month) (1|PlotID) – with a negative binomial transformation.

<i>Intercept</i>	<i>Estimate</i>	<i>Standard Error</i>	<i>z-value</i>	<i>p-value</i>
<i>Model Intercept</i>	-0.27	0.78	-0.34	0.73
Arid	-1.38	0.49	-2.80	0.005 **
CW:Arid	-2.08	0.90	-2.31	0.02 *
-CW:2019	-0.66	0.33	-1.99	0.05 *
Arid:2019	1.35	0.39	3.42	0.0004 ***

**The model resulted in an AIC value of 3088.4, BIC of 3239.9, and a Log Likelihood value of -1514.2. The conditional R^2 for the model was 0.90, whereas the Marginal R^2 and McFadden's R^2 were lower at 0.15 and 0.22, respectively. There was a predicted interactive effect of herbivory treatment and climate level at the Arid climate and separately within the CW (*cattle and wildlife*) treatment plots at the Arid climate across experiment years. Additionally, there was a predicted significant change in *D. occidentalis* responses within the -CW (*minus cattle and wildlife*) exclosure plots as well as at the Arid climate level in the year 2019.

CHAPTER 2 – Hikers as Hosts: Human recreational activity is a primary driver of relative mosquito abundance at alpine lakes

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Abstract:

Human-driven global change is reshaping ecological communities, driving declines across many taxa while creating opportunities for synanthropic species. Mosquitoes may be particularly well-suited to benefit from certain anthropogenic impacts, with consequences for both ecosystems and public health. However, little is known about how these dynamics unfold in remote alpine ecosystems, which have historically supported low mosquito abundance but are now experiencing increased recreation, invasive species introductions, and climate change – all of which may facilitate mosquito persistence and expansion. Here, we examined the roles of invasive species, human recreation, and seasonal climate dynamics in shaping mosquito populations across alpine lakes in the Sierra Nevada of California, using two years of surveys spanning 27 lakes. Mosquito emergence was tightly linked to lake ice-off timing, with abundance peaking 15-20 days post-ice-off and varying across years in response to snowpack conditions. After accounting for seasonality, human recreational activity was the next strongest predictor of mosquito abundance. Relative abundance is predicted to double with a 25-50% increase in visitor use, and human DNA dominated mosquito blood meals even at the most remote survey sites, suggesting that even modest levels of recreation may substantially elevate mosquito populations. By contrast, the

presence of nonnative trout, another widespread change in lakes, had no detectable effect on adult mosquito abundance despite their known suppression of larval mosquito predators. Together, these results suggest that alpine mosquito populations are more limited by host availability than by aquatic food-web structure, and that human recreation is already reshaping mosquito ecology in wilderness contexts.

Introduction:

Anthropogenic change is reshaping ecological communities worldwide, though not all taxa respond equally to these pressures (Bar-On et al., 2018; Dirzo et al., 2014; Hardesty-Moore et al., 2018). In general, insect populations are experiencing steep declines largely due to habitat loss, pesticide use, and climate change (Hallmann et al., 2021; Wagner et al., 2021; Warren et al., 2021). However, some insect species appear to contradict these trends. Mosquitoes, particularly those that transmit vector-borne diseases, are notable for their persistence and even proliferation in highly human-modified landscapes (Chala & Hamde, 2021; Duval et al., 2023; Kalitsilo et al., 2025). A review by Chala & Hamde (2021) found that human activities, including urbanization and agricultural expansion, have altered ecosystems in ways that favor the persistence and spread of mosquito populations, leading to the resurgence of vector-borne diseases. Human-altered environments across the agricultural-to-urban spectrum may facilitate mosquito persistence by providing both suitable larval habitats and reliable host communities (Goodman et al., 2018; Lafferty et al., 2018). Thus, mosquitoes represent an important case of disturbance-adapted taxa that may benefit from global change.

While mosquito responses to anthropogenic pressures are well documented in highly modified, human-dense landscapes, the effects of global change on their ecology in more

remote and ostensibly “natural” environments remain less well understood. As reliance on protected and remote areas to preserve and maintain species and ecosystem functions increases, this is a critical knowledge gap (Le Saout et al., 2013; Pacifici et al., 2020; Zeng et al., 2022). Few ecosystems remain truly untouched by anthropogenic pressures such as biological invasions, increasing human access and use, and climate change, even when designated as protected or wilderness areas (Grantham et al., 2022; Plumptre et al., 2021). Alpine wilderness systems are especially informative case studies in this context: they are among the most remote and protected ecosystems globally yet are increasingly shaped by the introduction of invasive species, intensifying recreational visitation, and climate change (Aycrigg et al., 2022; Monz et al., 2013; Shackleton et al., 2020). Alpine mosquitoes are likely sensitive to anthropogenic drivers that impact alpine wilderness and could therefore serve as good sentinels of change in these systems. Climate change is expected to shift mosquito development, survival, and seasonal activity (Brady et al., 2013; Culler et al., 2015; Robert et al., 2019), with projections suggesting range shifts under future warming (Colón-González et al., 2021; Mordecai et al., 2017). Invasions can reshape mosquito habitats and host communities, from invasive plants that enhance larval productivity (Stone et al., 2018) to vertebrate introductions that alter host availability and pathogen dynamics (Burkett-Cadena et al., 2021). Human recreation also influences mosquito persistence by altering host communities and providing opportunities for blood meals (Halofsky et al., 2021; Mittelbach & Wambem, 2002). In alpine systems, these pressures can overlap, underscoring the need to study them together rather than in isolation. Crucially, these dynamics are not merely ecological in the conventional sense; they are fundamentally relational: human presence

physically restructures wild communities, whether through disease risk, nuisance biting, or altered ecosystem function. Alpine mosquitoes sit precisely at this interface.

The Sierra Nevada of California provides an ideal natural laboratory to investigate the relationship between anthropogenic pressures and changes in wilderness habitats, with mosquitoes as a focal point. Although much of the region is protected within designated wilderness areas, it remains subject to heavy recreational use and a long history of ecological manipulation. Historic fish stocking for recreation, a globally pervasive challenge in alpine ecosystems (Knapp et al., 2001; Tiberti et al., 2013; Wright, 1999), has introduced nonnative trout to the majority of high-elevation lakes (> 2743 m) in the Sierras, where originally there were no aquatic vertebrates within these lakes (except for some small populations of aquatic-terrestrial amphibians such as *Rana sierrae*). These introductions, in many cases, led to self-sustaining trout populations that restructured aquatic food webs and reduced native invertebrate predators, including mosquito larvae (Epanchin et al., 2010; Knapp et al., 2001; Matthews et al., 2002). Alongside these other stressors, alpine protected areas in the Sierra are visited by millions of people each year, likely reshaping host communities and ecosystem processes (USDA Forest Service, 2022). Human recreation likely deters wildlife presence to some extent and likely occurs—even within protected areas—at greater density than the local wildlife population, which likely impacts both mosquito populations and host preferences (Larson et al., 2016). Furthermore, the highly seasonal Sierra Nevada alpine wilderness is subject to the impacts of climate change. Climate projections indicate this region now faces particularly acute warming, increasingly variable snowpack, and, like much of the western U.S., a reduction in the annual snowpack period (Hubbart & Bradford, 2024; Reich et al.,

2018). Synergistic interactions among various anthropogenic stressors could result in catastrophic shifts to a stable state in the Sierra Nevada alpine ecosystem.

Mosquitoes provide a particularly powerful lens for studying ecological change under anthropogenic pressure. Their tight dependence on aquatic larval habitats, ectothermic physiology, and reliance on vertebrate hosts mean that their abundance and community composition integrate signals from multiple interacting stressors, including climate, food web structure, and host availability. Studies across a range of modified landscapes demonstrate that mosquito communities respond rapidly and detectably to land-use change, species introductions, and warming, often in ways that reflect broader ecosystem-level shifts (Bucciarelli et al., 2019; Fletcher et al., 2023; Lyberger et al., 2025; Perrin et al., 2022). Crucially, these responses are species-specific and context-dependent, meaning that patterns of mosquito abundance and host-use behavior can reveal not just the presence of anthropogenic stressors, but their relative magnitude and mechanistic pathways (Duval et al., 2023; Fletcher et al., 2023). In remote alpine systems where direct ecological monitoring is logistically difficult and long-term data are scarce, this sensitivity makes mosquitoes an especially valuable sentinel taxon for detecting how even ostensibly wild landscapes are being reorganized by human activity. Understanding what drives mosquito abundance in these systems, therefore, has direct relevance to alpine management, informing how protected-area agencies assess the ecological footprint of recreation under climate change. In this study, we use mosquito populations as a sentinel species to assess the current state of the Sierra Nevada amid synergistic anthropogenic stressors, particularly those associated with human recreation and the presence of introduced nonnative species.

Specifically, we ask:

- (1) How does the intense seasonality of the alpine region impact mosquito population peaks and the timing of host seeking?
- (2) Do introduced trout alter relative mosquito abundance around alpine lakes?
- (3) Is human recreation activity associated with increased relative mosquito abundance?
- (3a) To what extent are alpine mosquitoes dependent on humans as blood meal hosts?

Firstly, we expected mosquito populations' host-seeking timing and population peaks to be tightly controlled by seasonality, particularly around annual snowmelt in the region; thus, all analyses of human recreation and trout effects on mosquitoes included a metric for seasonality. Next, we predicted that the presence of nonnative trout would be associated with increased mosquito abundance due to their indirect disruption of aquatic food webs. Specifically, as trout are known predators of native aquatic insect predators such as dragonfly and beetle larvae (Knapp et al., 2001; Knight et al., 2005; Owens et al., 2023), we expected that trout would reduce top-down control on mosquito larvae, thereby facilitating greater emergence of adult mosquitoes and thus higher abundance of mosquitoes in the landscape. Finally, we also hypothesized that humans may serve as important additional hosts for blood meals, such that areas with higher levels of recreational human activity would support greater mosquito abundance. Related, we expected to find more blood meals, and more from humans and their domestic animal companions, at lakes with higher human activity, but fewer blood meals and more wildlife hosts at lakes with less human activity.

We addressed these questions through a two-year survey of adult female mosquitoes across 27 lakes in eight hydrogeologic drainage basins that varied independently in elevation, invasive species status, and levels of human recreation. Across ~20,000 adult female mosquitoes captured, we also conducted blood meal analyses on all fed female mosquitoes to

identify blood meal sources and assess the relative importance of wild vs. human/domestic hosts. Together, we anticipated that these anthropogenic drivers would produce substantial differences in female mosquito abundance across lake sites, potentially leading to increased relative mosquito abundance in response to the presence of trout and human activity levels. By addressing these questions, we also shed light on a broader question about whether adult female mosquitoes in alpine wilderness are constrained primarily by food web structure or host availability and evaluate how global change processes are reshaping their ecology even in remote landscapes. In doing so, we treat the human-mosquito encounter not as incidental to the alpine ecosystem but as a constitutive part of it, one that is intensifying as recreation and climate change converge in alpine systems.

Methods:

Study System & Design:

Inyo National Forest spans nearly two million acres, of which approximately one million acres are further protected by nine wilderness areas, the United States' most highly restricted protection. On average, Inyo National Forest is categorized as only "moderately accessible" (based on access from roads and trails). It holds a few high-remoteness patches, concentrated in its rugged or high-alpine elevation zones. Remoteness in Inyo National Forest is not evenly distributed; instead, proximity to infrastructure heavily determines access (Appendix, Section S2.1). Other factors, such as elevation, slope, and land cover, may also affect landscape access and remoteness. Mosquito species within the Sierra Nevada include *Aedes sierrensis* (Tree Hole Mosquito), *Aedes ventrovittis* (Black Snow Mosquito), *Aedes tahoensis* (Common Snow Mosquito), *Culex tarsalis* (Western Encephalitis Mosquito), *Culiseta incidens* (Cool Weather Mosquito), and *Anopheles freeborni* (Western Malaria Mosquito).

However, only two species, *Aedes sierrensis* and *Aedes ventrovittis*, are known to occur within the altitudinal range of our study sites (2952.0-3361.9 m) (Laws, 2007). Study sites within the Inyo National Forest were chosen to represent the subalpine-to-alpine transitional zone, spanning elevations of approximately 3,050-3,350 m, where continuous subalpine forest gives way to the open, treeless terrain characteristic of true alpine ecosystems. The tree line boundary is defined ecologically by thermal thresholds that limit tree growth and is known as the alpine tree line ecotone (Dandan et al., 2022; Millar et al., 2020). The average lake elevation of the study sites is 3,186 m, where air temperature fluctuates widely, with winter minimums falling below 0 °C and summer maximums averaging 21 °C. Annual precipitation in the Sierra Nevada is relatively low (approximately 17.8-35.6 cm per year), and much of the freshwater supply in Inyo National Forest originates from winter snowpack that accumulates at higher elevations and melts through spring and summer, providing critical water input to lakes and streams (WMRC; LADWP; Lundquist & Loheide II, 2011; USGS–CAWSC).

Potential hosts for mosquitoes in this region include the American Black Bear (*Ursus americanus*), Mule Deer (*Odocoileus hemionus*), Mountain Lion (*Puma concolor*), Coyote (*Canis latrans*), and the federally endangered Sierra Bighorn Sheep (*Ovis canadensis sierrae*). Additionally, there are many smaller mammal hosts, including, but not limited to, several rodent genera (e.g., *Dipodomys* spp., *Peromyscus* spp., *Sorex* spp., and *Tamias* spp.), and more specifically, yellow-bellied marmots (*Marmota flaviventris*), American pika (*Ochotona princeps*), and white-tailed jackrabbit (*Lepus townsendii*), as well as a few small vertebrate passerine genera residing in alpine locations (Abercrombie et al., 2024; Devictor et al., 2012; Laws, 2007). In addition to these wild hosts, there are also ample human and

human commensal hosts, most commonly domestic dogs (*Canis lupus familiaris*), as well as pack animals such as horses (*Equus caballus*), mules (*Equus mulus*), donkeys (*Equus asinus*), and goats (*Capra aegagrus hircus*). There are also managed cattle herds (*Bos taurus*) grazing within the non-wilderness regions of Inyo National Forest. The region is popular, hosting nearly 4 million visitors annually, and offers a plethora of recreational opportunities, including hiking, backpacking, and fishing (Inyo NF, 2025).

General Study Design:

To address our questions, we surveyed adult female mosquitoes across 27 lakes spanning eight lake basins over two years (2023-2024). Given the phenology of mosquitoes in this area, we sampled only in a short window of summer when mosquitoes are typically active (15-60 days post-lake ice-off) (Owens et al., 2023).

2023 Sampling:

The first year of our study (2023) focused primarily on exploring the potential effects of introduced trout on adult female mosquito communities. Thus, the sampling design for this year was paired, comprising six trout- and troutless-lake pairs (12 total lakes), with minimal variation in elevation (all lakes were between 3141.9 m and 3290.9 m). The two lakes in each pair were in close physical proximity and matched in size and elevation as closely as possible. However, in each pair, one lake contained nonnative trout, and the other was naturally fishless (Figure 2.1a). Due to the exceptionally high snowfall during the preceding winter (Figure 2.1b), field work in 2023 began post-ice-off on July 15th and continued until August 26th. One lake pair (two lakes) was sampled each day for adult female mosquitoes between 15:00 and 19:00, targeting dusk as closely as possible, when mosquitoes are most

active (Murdock et al., 2010). All lake pairs were sampled every six to ten days during the field effort for a total of three to five sampling days per lake.

2024 Sampling:

The second year of mosquito sampling focused on exploring the effects of variation in human activity and its interaction with environmental factors. To answer these questions, we needed a larger sample of lakes with greater variation in human activity, so we expanded sampling to 19 lakes (only four of which had also been sampled in 2023). This included seven hydrological basins with a much broader range of elevations - from 2952.0 m to 3361.9 m - and lake distances from trailheads spanning 0.2 km to 21.2 km (Figure 2.1a). While there was no explicit paired design in 2024, lakes were still sampled in pairs, or, in some cases, in threes, for efficiency. Each lake was sampled every 15-20 days in 2024, for a total of 2-3 sampling events per lake, all between 15:00 and 19:00. Nearly all 2024 lakes contained nonnative trout populations established through historical stocking, and fish presence/absence was not systematically incorporated into the 2024 study design. Nonnative trout are present in at least 85% of lakes on Sierra Nevada national forest lands, leaving only 7% of such lakes confirmed fishless, requiring balanced fish presence/absence replications would have been logistically prohibitive (Knapp, 1996). Given earlier ice-off dates and lower snowpack levels (Figure 2.1b), sampling took place between June 18th and August 3rd, 2024. Despite differences in calendar dates across years, sampling occurred at a similar time after ice off.

Mosquito & Blood Meal Collection:

In both years, to survey relative mosquito abundance, we used custom-built, portable, aspirator traps that moved air at a rate of 7 m/s to collect adult mosquitoes and other similarly

sized dipterans, which is comparable in magnitude to the intake velocities for other commonly used mosquito aspirators (John W. Hock Company, Gainesville, FL). During each sampling event, researchers circumnavigated a lake while operating the aspirator through the air column and adjacent vegetation (Figure 2.1c). Sampling duration varied with lake size, and all metrics were thus calculated as catch per unit effort. Following collection, nets were sealed in plastic bags containing acetone-moistened paper towels to euthanize the collected insects.

Immediately after the sampling effort (except when delayed by adverse conditions, in which case no more than 18 hours after sampling), all female mosquitoes were counted and visually inspected for the presence of a blood meal in their abdomens. Abdomens of engorged females were punctured using sterile pipette tips and forceps, and abdomen contents were blotted onto Whatman Flinders Technology Associates (FTA) cards (Sigma-Aldrich, St. Louis, MO) for long-term DNA preservation. Blood meal digestion was visually scored using the criteria of Reeves et al. (2018), adapted from Detinova (1962), to exclude blood meals that could have come from the samplers themselves (Appendix, Section S2.2). No vertebrate animals were captured or manipulated during this study, and no human subjects were enrolled; institutional ethical approval was therefore not required.

Blood Meal Sequencing:

We amplified an approximately 470 base pair region of the vertebrate mitochondrial cytochrome *b* gene using universal primers developed by Verma & Singh (2006), (U.S. Patent No 7,141,364 B1 - expired 2021). Primers were modified to include 16S overhang adapters. Final libraries were sequenced on an Illumina MiSeq (see Appendix, Section S2.3 for full details) (Illumina Inc., San Diego, CA).

Human Activity:

We used data from the social and outdoor recreation app AllTrails ([alltrails.com](https://www.alltrails.com)) to estimate human activity across hydrogeological basins (lakes within the same watershed were naturally binned into the same basin). Reviews from AllTrails were counted between the sampled dates each year and for the two weeks preceding each year's sampling effort. Human activity was grouped into 21-day totals per basin, summing the number of reviews from the two weeks prior to the sampling week. We also measured the distance (km) from the trailhead start to each lake using CalTopo ([caltopo.com](https://www.caltopo.com)) (Appendix, Section S2.4). We assumed lakes farther from trailheads would experience less human activity than those closer to trailheads. These two metrics, review-based activity and trailhead distance, were treated as alternative proxies for human activity and evaluated separately in statistical models to determine which better explained variation in relative mosquito abundance.

Additional Environmental Variables:

Environmental variables of interest were also collected from various open-data sources and included in the model selection process to determine whether any were significant predictors of relative mosquito abundance (see below). From PRISM (PRISM Climate Group, 2023), we downloaded daily maximum and minimum temperature data at 800 m resolution for each hydrogeological basin. We separately averaged them for the 20 days preceding each sampling event within that basin. Additionally, individual lake ice-off dates were determined from satellite imagery as the date when no surface ice was visible (Planet Labs PBC, 2025). Lastly, NDVI (Normalized Difference Vegetation Index) was calculated for a 500 m radius surrounding each lake as an index for wetland/marshland

(potential larval mosquito habitat) using Landsat 9 satellite imagery (USGS, 2024) (Appendix, Section S2.5).

Data Analyses:

Fish vs. Fishless:

We examined variation in the relative abundance of adult female mosquitoes in relation to fish presence and seasonal timing using linear and linear mixed-effects modeling approaches. For relative mosquito abundance (mosquitoes per minute), a $\log(x + 1)$ transformation was applied to improve normality, stabilize variance, and account for zero values. All analyses were conducted in R version 4.4.1 using the 'lme4' and 'lmerTest' packages (Bates et al., 2015). We initially fit a linear mixed-effects model with fish status (presence/absence), the number of days from lake ice-off to the sampling event, and their interaction as fixed effects. To account for repeated sampling at paired lakes, we evaluated alternative random-effects structures, including lake pair and individual lake as random intercepts. Because these random-effects terms resulted in singular fits and did not improve model performance, we proceeded with a series of nested fixed-effects linear models for inference.

Candidate models included: (1) a null model with no predictors, (2) a model including additive effects of fish status and days since lake ice-off, and (3) a model including their interaction. Models were compared using ANOVA (Analysis of Variance) and to evaluate whether additional environmental terms: 20-day average temperature, maximum or minimums, and 500m around-lake NDVI wetland surface area improved explanatory power. Model assumptions were assessed using residual-versus-fitted (assess whether model errors are randomly distributed across predicted values) and Q–Q plots (assess whether model

residuals approximate a normal distribution) and were reasonably met. Finally, for visualization purposes, predicted mosquito abundance was generated across the observed range of days since lake ice-off for lakes with and without fish, with 95% confidence intervals calculated on the log scale and back-transformed for interpretation.

Human Activity:

Next, we evaluated whether human recreational activity modified season trajectories of adult female mosquito abundance by modeling two distinct proxies of anthropogenic exposure: (1) distance to nearest trailhead (km) as a static measure of remoteness and (2) human activity quantified as the number of trip reports posted to the AllTrails platform within each hydrogeologic basin during the two weeks preceding and the week of the sampling event for a 21 day total (reports*basin⁻¹*21d⁻¹). Relative mosquito abundance (mosquitoes per minute) was again log(x+1) transformed to improve normality and heteroskedasticity prior to analysis. Distance to the trailhead was available for all lakes and reflects potential accessibility, whereas AllTrails reports capture realized activity during the relevant period of mosquito presence.

We initially fit parallel linear models of each human metric as a function of days since ice-off. All predictors were z-standardized prior to analysis (rescaled to a mean of 0 and a standard deviation of 1), allowing effect sizes to be compared directly across variables measured in different units. Models were compared using adjusted R² (the proportion of variation in abundance explained by the model, corrected for the number of predictors included) and residual diagnostics to assess relative explanatory power. Because human activity consistently explained more variation in relative mosquito abundance than distance

to the trailhead, and more directly reflects recent host availability, subsequent analyses focused on the activity-based metric.

We then fit linear and linear mixed-effects models to assess robustness, including basin as a random intercept to account for spatial grouping and repeated sampling. Model support was evaluated using likelihood ratio tests and ANOVA comparisons. Next, to assess whether the influence of human activity varied across the seasonal progression, we fit a segmented regression (which fits separate slopes before and after an estimated breakpoint), allowing the slope of mosquito abundance with respect to days since ice-off to change. Model assumptions were evaluated using residual-versus-fitted plots and Q–Q plots, and they were reasonably satisfied. For visualization purposes, predicted mosquito abundance was generated across the observed range of days since ice-off and human activity. Predictions were calculated on the log scale and back-transformed for interpretation, with 95% confidence intervals derived from the standard errors of the fitted values.

Additional Environmental Variables:

To evaluate whether broader environmental factors influenced female mosquito abundance, we constructed additional candidate model sets to examine the effects of fish status or human activity on seasonal trajectories, incorporating other environmental covariates. These analyses focused on identifying independent and interactive drivers of relative mosquito abundance. Environmental variables considered in the model selection process included daily maximum or minimum air temperatures, averaged over the 20 days preceding each sampling event date for each hydrogeological basin. Additionally evaluated was vegetation wetland surface area (NDVI) within a 500m buffer surrounding each lake,

calculated from Landsat imagery as an index of potential larval habitat (Appendix, Section S2.4).

All continuous predictors were z-standardized, and basin was included as a random intercept to account for the non-independence among lakes sampled within the same hydrogeological basin. We began with a full linear mixed-effects model that included all candidate predictors and sequentially simplified it by removing non-influential variables. Competing models were compared using AIC and likelihood-ratio tests (ANOVA) to assess whether the inclusion of specific predictors improved model performance. Diagnostic plots were used to verify model assumptions.

This model selection process revealed that human activity and days since lake ice-off were the strongest predictors of relative female mosquito abundance. In contrast, temperature and vegetation metrics did not improve model fit and were therefore excluded from final models.

Bloodmeal Bioinformatics:

The sequences from the blood meal samples were demultiplexed in the Illumina interface. Read quality for each sample was analyzed using the Galaxy web interface (The Galaxy Community, 2024) with the tools 'FastQC' and 'MultiQC' (Andrews, 2010; Ewels et al., 2016).

Reference mitochondrial genome sequences were retrieved from the National Center for Biotechnology Information (NCBI, 1988) nucleotide database. We simulated *in silico* PCR results using the primer set used for amplification. We created a reference database from these simulated sequences. We used the NCBI BLASTn tool (Altschul et al., 1990) to

compare them with our unknown blood meal samples to identify the host (Appendix, Section S2.3).

Data Caveats:

Relative adult female mosquito abundance (mosquitoes per minute, noted as mos/min) was measured directly at the lake level for each sampling event. However, some predictor variables were available only at coarser spatial or temporal resolutions—for example, lakes within the same basin share certain predictors (e.g., human activity and temperature). In addition, these variables were summarized into 20–21-day intervals to align with the coverage of our sampling frequency (Appendix, Section S2.4), resulting in approximate rather than continuous measurements of these drivers at the study lakes. While these differences may limit the very fine-scale resolution of the study's analysis, our analyses remain appropriate for identifying patterns of relative mosquito abundance in this landscape.

Results:

We collected a total of 21,313 female adult mosquitoes. Nearly all belonged to the genus *Aedes* and were visually estimated to be species *Aedes ventrovittis* (Black Snow Mosquito), with fewer than ten *Culex* specimens, including one *Culex tarsalis* identified in 2023. Of all mosquitoes, 0.06% percent (n=139) were gravid/had a blood meal. We successfully amplified 123 blood meals for host identification.

Fish vs. Fishless

We initially evaluated whether introduced fish influenced relative mosquito abundance, given their evidenced potential to alter aquatic-terrestrial alpine communities (Knapp et al., 2001; Lee, 2023; Matthews et al., 2002; Owens et al., 2023). The best-fitting model included days since lake ice-off and fish presence/absence explaining modest variation in relative

mosquito abundance (adjusted $R^2 = 0.13$). Days since ice-off was a statistically significant predictor of relative mosquito abundance, although the effect was small (slope = $0.034 \log \text{mos/min} + 1$, $p < 0.05$). While the effect of fish was included in the model, the effect was near zero with wide uncertainty, suggesting that it did not significantly affect relative mosquito abundance ($p = 0.99$). Including the interaction between timing and fish presence did not improve model fit or achieve significance ($p = 0.55$; adjusted $R^2 = 0.12$; Figure 2.2a), indicating that introduced trout were not a primary driver of relative mosquito abundance across lakes.

Given the absence of trout effects, we next assessed whether spatial variation in human accessibility to the lakes could better explain patterns in relative mosquito abundance using the same 2023 dataset. In this analysis, relative adult mosquito abundance declined with increasing distance (km) from trailheads (slope = $-0.93 \log \text{mos/min} + 1$; $p < 0.001$; Figure 2.2b), indicating higher mosquito abundance at lakes closer to recreational access points.

The model incorporating fish status, days since ice-off, and distance from the trailhead, including a days-since-ice-off $\times$ distance interaction, revealed that the effect of accessibility varied seasonally. Shortly after lake ice-off, mosquito abundances were greatest at lakes near trailheads; however, relative mosquito abundances increased more rapidly through the season at more remote lakes, as evidenced by a significant positive interaction between days since ice-off and distance from trailhead (slope = $0.024 \log \text{mos/min}$, $p < 0.001$). Consequently, differences between remote and more accessible alpine lakes diminished later in the season. Fish presence again had no detectable effect ($p = 0.4$). Together, these results suggested that human presence, rather than invasive trout, was a potentially dominant predictor of relative

mosquito abundance across alpine lakes, motivating a more explicit examination of recreational activity metrics.

Human Activity

To further explore the effect of human activity, we sampled additional lakes in 2024 that were located at distances (0.2 km - 21.2 km) from trailhead locations to capture a broader range of remoteness from human presence and activity. A linear model including days since lake ice-off, human activity, and their interaction explained significantly more variation in mosquito abundance than a null model (adjusted $R^2 = 0.17$; ANOVA, $p < 0.001$). Both days since ice-off (slope = 0.31, $p = 0.02$) and human activity (slope = 0.37, $p = 0.03$) were positively associated with log-transformed relative mosquito abundance, with a strong negative interaction indicating that the effect of human activity weakened as the season progressed (slope = -0.45, $p < 0.001$; Figure 2.3a; Table 2.1). Because predictors were standardized, these coefficients indicated that a one-standard-deviation increase in human activity, equivalent to approximately 55 additional AllTrails reports in 21 days, was associated with an increase of 13,608 mosquitoes.

In contrast, the parallel model that replaced human activity with distance to the nearest trailhead showed weaker support (adjusted $R^2 = 0.07$). Distance to the trailhead was not a significant predictor of relative mosquito abundance (slope = -0.20, $p = 0.21$), nor did it significantly interact with time since ice-off ($p = 0.32$). Model comparison indicated that the activity-based model provided substantially better explanatory power than the distance-based model.

A segmented regression applied to the activity-based model identified a single seasonal breakpoint at approximately 15 days post-ice-off, separating early- and late-season dynamics.

Prior to this breakpoint, mosquito abundance increased rapidly following ice-off and was positively associated with relative abundance (slope = 0.31, $p = 0.05$). After the breakpoint, the influence of human activity persisted, but declined through time, as indicated by a negative interaction between activity and days since ice-off (slope = -0.37, $p = 0.001$; Figure 2.3b; Table 2.2). Together, these results suggest that human activity strongly predicts variation in relative mosquito abundance.

Other Environmental Variables:

Air temperature and wetland area within 500 m of the lake were not significant predictors of mosquito catch per unit effort and reduced model fit (Appendix, Section 2.6).

Blood Meals

Human blood was the most frequent source of mosquito blood meals across lakes. Humans and domestic animals comprised greater than 50% of meals at 17 of 19 lakes from which blood-fed females were collected. Mule deer (*Odocoileus hemionus*) were the only wildlife host detected. These results underscore the importance of humans as a key blood source even in remote locations, as mosquitoes ~15km from trailheads still primarily fed on humans (Figure 2.4).

Discussion:

Our study demonstrates that human presence is a primary driver of mosquito abundance even in high-elevation wilderness areas of the Eastern Sierra Nevada. Relative mosquito abundances were strongly and consistently linked to human activity, with increases in recreation reports via the AllTrails app for 21 days associated with approximately two- to three-fold higher predicted mosquito abundance (Figure 2.5).

This pattern suggests that in remote ecosystems, human recreation can directly sustain and amplify mosquito communities. Unsurprisingly, seasonality also tightly controls mosquito activity, as expected in a system with such short windows of mild weather. More unexpectedly, there was no detectable effect of nonnative trout, despite robust evidence that trout transform invertebrate communities, including mosquito-larvae predators, in these systems (Knapp et al., 2001). Considering our findings that mosquito abundance is tightly linked to human activity and that those mosquitoes primarily feed on human hosts, this suggests that the mosquito populations are controlled more by host availability than by larval predation. Our findings illustrate how seemingly pristine wilderness areas are shaped by global change drivers, including not only climate and invasive species but also the growing human footprint.

Notably, the effect of human activity on relative adult female mosquito abundance was strongest early in the season, shortly after lake ice-off, and weakened as the season progressed. This pattern emerged from the piecewise regression, which identified a breakpoint approximately 15 days post-ice-off, separating early- and late-season dynamics. During the early-season period, human activity was positively associated with relative mosquito abundance despite relatively low contemporaneous human presence at many sites; later, the influence of human activity declined as seasonality became the stronger effect. Indeed, if solely host availability drove patterns in mosquito abundance, we would expect effects to intensify later in the summer season as recreational use increases (Appendix, Section S2.7). Instead, the early-season signal is likely driven by a legacy effect whereby higher human activity during the prior season increased blood-feeding opportunities, egg

production, and the abundance of overwintering larvae that then emerged early the following year (Culler et al., 2018; Takken & Verhulst, 2013; Vavassori et al., 2022).

Seasonality is a strong, climate-sensitive control.

While human activity is central, seasonality strongly structured mosquito abundance across our study period. Mosquito populations rose sharply 15-20 days post-ice-off (Figure 2.3b), producing a short but intense window of activity that differed by ~30 calendar days between years, depending on snowpack. These results are consistent with alpine mosquitoes operating near their lower thermal limits (Reich et al., 2018; Russel & Brust, 1996; West & Black IV, 1998). Climate change is expected to lengthen this window in many regions by reducing snowpack, hastening ice-off, and elevating summer temperatures (Reisen et al., 2008; Rocklöv & Dubrow, 2020). Such changes could increase mosquito reproductive opportunities and shift phenology, altering both nuisance levels and disease risk. However, outcomes may not be uniformly amplifying (Ludwig et al., 2019; Reisen et al., 2008). Drought conditions that reduce larval habitat availability (Sambado et al., 2025), or extreme snow years that delay emergence (Montini et al., 2021; Reinhold et al., 2018), could suppress populations in some years. Thus, the net effects of climate change on alpine mosquitoes are likely to be heterogeneous, underscoring the need for site and year-specific monitoring.

Limited role of nonnative trout in adult mosquito abundance.

Contrary to expectations, we found no evidence that nonnative trout influenced adult mosquito abundances. While trout are known to suppress larval mosquito predators, such as dragonfly larvae and aquatic beetles (Cobbaert et al., 2010; Knapp et al., 2001; Knight et al., 2005), several lines of evidence suggest that this pathway may be weak or decoupled from adult mosquito abundance in alpine systems. In Sierra Nevada lakes, mosquitoes oviposit and

develop in shallow, warm pools and ephemeral wetlands that are hydrologically disconnected from lakes and therefore largely inaccessible to trout (Knapp et al., 2001). Under this spatial separation, fish-mediated effects on aquatic food webs within lakes would be less likely to translate into changes in mosquito emergence. Consistent with this mechanism, we directly observed large numbers of dipteran larvae in shallow, often tannin-rich pools adjacent to lakes during our 2023 sampling effort, while larval mosquitoes were rarely encountered within lake habitats themselves, suggesting that primary mosquito production occurs outside of trout-occupied waters. Future exploration of the location and abundance of larval mosquitoes may shed further light on the drivers of adult relative abundance or emergence and would benefit from additional field studies.

Our adult-focused sampling may also have limited sensitivity to localized larval effects, as adult mosquitoes can disperse among nearby aquatic habitats, potentially obscuring site-specific differences in larval survivorship (Verdonshot & Besse-Lototskaya, 2014). More broadly, previous studies demonstrate that fish impacts on mosquito populations are highly context dependent, ranging from suppression (Howard et al., 2007; Matias & Adrias, 2010; Walshe et al., 2017) to neutral and even positive effects depending on habitat structure and connectivity (Azevedo-Santos et al., 2017; Kumar et al., 2015; Pyke, 2008). To our knowledge, no prior published studies have explicitly evaluated adult mosquito abundance around fish and fishless alpine lakes in the Eastern Sierra (but see Appendix, Section 2.8). Together, these results suggest that in this system, the spatial separation between mosquito breeding habitats and fish-occupied lakes limits the capacity of nonnative trout to influence adult mosquito abundance, whereas human presence exerts a strong effect. However, because we did not measure larval survival, our findings do not imply that trout do not affect larval

mosquito survival per se, but rather that such effects may not propagate to adult mosquito populations in these alpine landscapes.

Ecological and conservation dimensions.

Shifts in mosquito abundance may have broader implications for community food webs in alpine ecosystems (Bhattacharya et al., 2016; Prudêncio, 2020). In these systems, nonnative trout introductions are known to substantially reduce the biomass of emergent aquatic insects, thereby altering energy subsidies to terrestrial consumers (Owens et al., 2023; Pope et al., 2009; Romero et al., 2021). Against this backdrop, mosquitoes have been hypothesized to function as a compensatory prey resource for insectivorous birds and bats when other emerging aquatic insects are suppressed (Bonds et al., 2022; Gonsalves et al., 2013; Wray et al., 2018). For example, little brown bats in the Eastern Sierra Nevada have been observed to forage more intensively around certain lakes, a pattern that Gruenstein et al. (2021) hypothesized may reflect compensatory foraging in systems where nonnative trout reduce the availability of larger emergent aquatic insects. Under this hypothesis, bats may increasingly exploit lakes with higher mosquito availability. However, that study did not directly quantify mosquito abundance or bat diet composition at these sites and thus cannot independently assess the contribution of mosquitoes to bat foraging activity.

Our results suggest that such an interpretation should be made cautiously. We found no evidence that introduced trout increased adult female mosquito abundance and observed mosquito production was largely decoupled from lake habitats. Instead, relative mosquito abundances increased with both time since lake ice-off and human presence, regardless of fish status, with an approximately 50% increase in adult female mosquito abundance associated with human activity (Figure 2.5). Although mosquitoes are generally smaller-

bodied than many other emergent aquatic insects (Gratton & Zanden, 2009; Jackson & Fisher, 1986), these patterns raise the possibility that human-mediated increases in mosquito abundance could partially—but likely incompletely—offset trout-driven losses in emergent insect biomass. Taken together, these findings underscore the difficulty of predicting community outcomes where nonnative species introductions and human activity interact and highlight a previously underappreciated human-mediated pathway shaping alpine food webs under global change (Epanchin et al., 2010; Owens et al., 2023).

Human Recreation as a Limiting Factor

Our blood meal data reinforce the central role of humans as hosts: at 17 of the 19 lakes from which blood meal samples were taken, at least 50% of the blood meals were identified as human-derived. Overall, 66% of all sampled blood meals had human or domestic commensals—dog and cattle—as hosts. This dominance occurred even at lakes more than 12 km from trailheads (Figure 2.4), where female mosquitoes might otherwise have been expected to rely on wildlife hosts; indeed, 90% of blood meals in our five most remote sites were from humans or commensals. Human visitation thus creates a form of reliable host availability that can sustain mosquito populations where they would otherwise be much more limited (Burkett-Cadena et al., 2011, 2013; Dahlin et al., 2024).

While native large ungulates are present in the Sierra Nevada, their population densities are low compared to the number of human visitors. Recent California Department of Fish & Wildlife estimates suggest only ~380-400 Sierra Nevada bighorn sheep remain in the entire mountain range (CDFW, 2025). Their preferred habitats within the Sierra Nevada are along steep, cavernous inclines, far from lakebeds (USFWS, 2007; Whiting et al., 2023). Although modeled deer abundance within hunt zones encompassing Inyo and Mono counties was

estimated at approximately 19,400 individuals in 2017 (CDFW, 2017), this value reflects total population size across a large and heterogeneous landscape and does not directly capture host availability at high-elevation lake margins during the brief period of mosquito activity. In contrast, recreational visitation to the Inyo peaks during summer months (Appendix, Section 2.7) coincides with mosquito emergence.

Importantly, mule deer use of alpine and subalpine habitats in the Eastern Sierra is seasonally and altitudinally constrained, with densities declining at higher elevations, where many study lakes are located, and deer presence is often transient rather than continuous (Monteith et al., 2011, 2014). As a result, while deer represent an important regional host, human presence likely exceeds ungulate host availability at mosquito-active sites on a per-area and per-day basis, particularly during peak recreation periods. From the perspective of host-seeking mosquitoes, humans may represent a more predictable host not in terms of annual presence, but rather in their short-term spatial and temporal consistency during peak mosquito activity. Recreational use likely concentrates people in lake areas during daylight and crepuscular periods, often for extended periods, increasing the probability of encounters (Cummins et al., 2012; Duffield, 2024; Perkins et al., 2013). In contrast, deer move widely across the landscape and may pass briefly through high-elevation basins without prolonged use of near-lake habitats (Kauffman et al., 2020; Stewart et al., 2002).

We did not detect evidence of mosquito feeding on small mammals or avian hosts. This pattern could reflect limitations of the broad-range primers used for blood meal metabarcoding, including reduced amplification efficiency for degraded or low-template DNA and potential taxonomic bias among vertebrate groups (Verma & Singh, 2006). However, we note that our reference database was customized to include all likely vertebrate

hosts in the Eastern Sierra, reducing the risk of systematic alignment (Appendix, Section S2.3). Alternatively, the absence of small-mammal and avian blood meals may reflect behavioral and ecological differences that reduce exposure to mosquito bites, such as nesting or burrowing, nocturnality, or limited use of near-lake habitats during peak mosquito activity. Distinguishing between methodological limitations and true host-use patterns will require targeted sampling with taxon-specific primers and higher temporal resolution of blood meal degradation dynamics.

Implications for vector-borne disease risk.

The link between recreation and mosquito abundance has direct implications for vector-borne disease (VBD) risk. Increasing human use of alpine areas may elevate the likelihood of human-mosquito encounters (Mertens, 2025; Roveri et al., 2024; Zhang et al., 2025), even in regions where VBDs have not yet been reported. Although no human cases have been documented in Inyo or Mono Counties, West Nile virus-positive mosquitoes have been detected locally (CDPH, 2017-2024). Warming temperatures may also facilitate the expansion of new vector species such as *Culex tarsalis*, *Aedes aegypti*, and *Aedes albopictus* into high-elevation habitats (Chen et al., 2013; Khan et al., 2020; Lozano-Fuentes et al., 2012; Romiti et al., 2022). Similar elevational shifts have been observed worldwide (Escobar et al., 2016), highlighting that alpine ecosystems are not insulated from these dynamics (Caminade et al., 2019; Mordecai et al., 2019). In California, where the dengue virus was recently detected circulating locally in Los Angeles County (Los Angeles County DPH), the potential for novel pathogen introductions into mountain regions is imminent rather than hypothetical. County-level CDC risk maps already classify the Sierra Nevada as “very likely” for *A. aegypti* and *A. albopictus* to persist and reproduce (CDC, 2024). Global climate

models also project rising suitability for these vectors and their pathogens across the Sierra Nevada under future warming (Kamal et al., 2018; Nakase et al., 2024; Ryan et al., 2019).

Monitoring mosquito populations will therefore be critical in alpine regions where climate-driven changes in seasonality and host community composition may interact with recreation to amplify disease risk (Carney et al., 2022; Maia et al., 2024). This study, which uniquely focused on sampling adult female mosquitoes in the Sierra Nevada, establishes the “baseline” conditions against which future monitoring can be compared. Wilderness areas often function as early-warning systems for ecological change because they are relatively insulated from urban or agricultural confounders (Buřivalová et al., 2021; Cumming & Allen, 2017; Graumlich, 2000); they allow us to detect novel dynamics before they emerge more broadly. In this context, our findings note that global change pressures in alpine ecosystems extend beyond temperature and snowpack to include direct anthropogenic presence as a disease-relevant driver.

Conclusion:

Wilderness under pressure:

Our findings demonstrate that host abundance is likely a limiting factor for alpine female mosquito abundance, and that human recreation directly fuels higher relative abundances because humans are important food sources (Figure 2.3a; Figure 2.5). Nonnative trout did not alter adult mosquito abundances in our study (Figure 2.2b). Seasonality tightly constrains alpine mosquitoes (Figure 2.3b), so climate change is likely to extend their activity windows and increase variability. In total, these findings highlight how even remote alpine ecosystems are not insulated from global change and, in fact, may be especially vulnerable as climate warming, invasive species, and recreation converge. Wilderness areas like the Eastern Sierra

remain rare opportunities to detect, disentangle, and anticipate the multiple forces driving adult mosquito populations under global change. As recreational use and climate pressures intensify, these ecosystems will increasingly serve as sentinel landscapes for both ecological and public health consequences. Recognizing human presence as an ecological driver in its own right is essential to managing not only disease risk, but also the broader integrity of alpine wilderness under global change.

Figures:

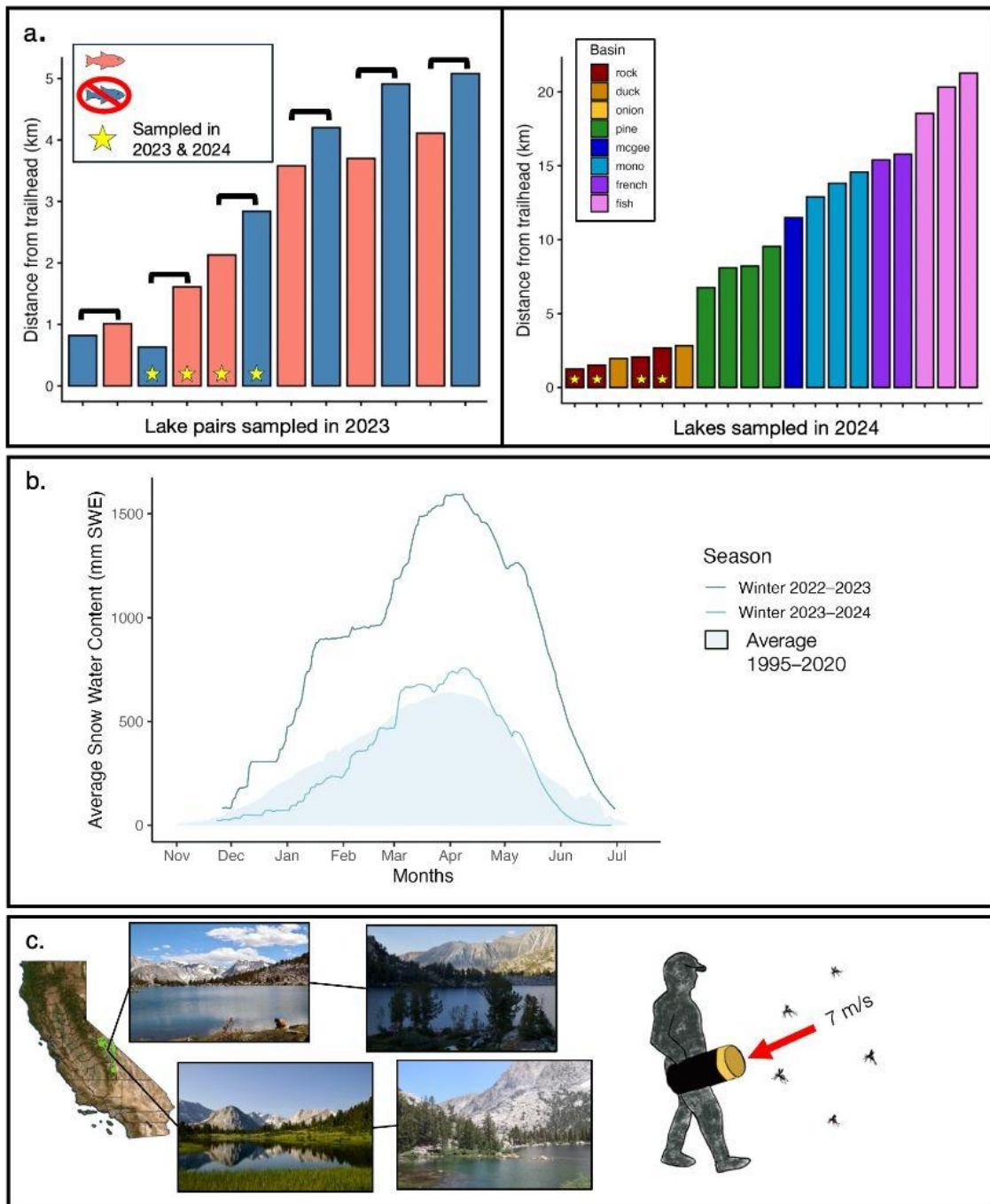


Figure 2.1: Overview of study sites, methods, and field seasons. **(a)** A bar graph where each column represents a lake that was the location of sampling efforts in 2023 or 2024. In the first panel, column colors indicate whether the lake contained fish (pink) or was fishless (blue). In the second panel, column colors indicate which hydrogeological basin each lake was assigned to. The y-axes in both panels show how far (km) each lake was from a respective trailhead. **(b)** Difference in average snow water content, December–July, for 2022–2023 vs. 2023–2024; 2022–2023 set historical snowpack records (CDWR, 2023;

Cassidy, 2023; Mutch, 2023). (c) Inyo National Forest (green) in the Sierra Nevada (left), photos of lake locations sampled in Inyo National Forest (center; courtesy of KJ), and an illustration of the field-aspirator trap used to collect female mosquitoes and similar insects (right).

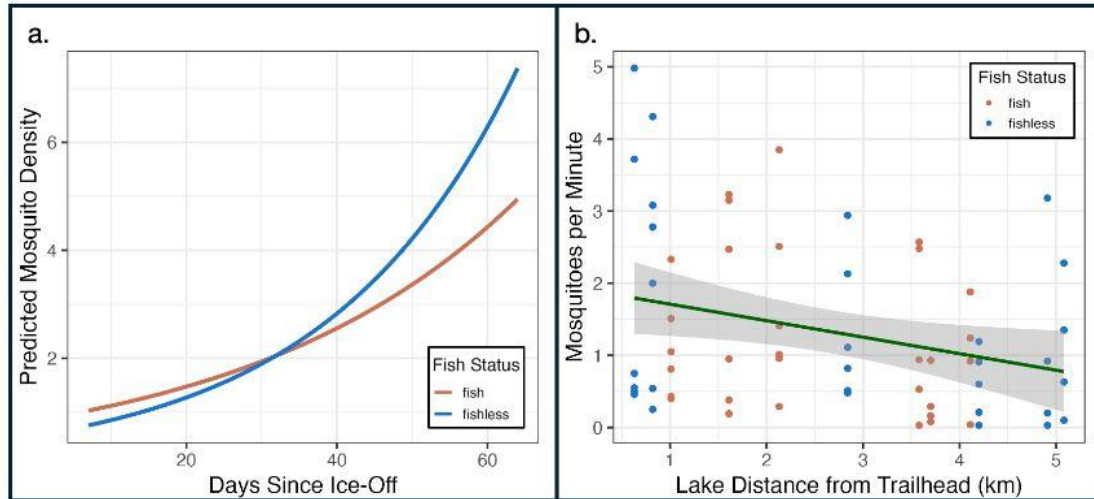


Figure 2.2: (a) Model-predicted relative female mosquito abundance as a function of days since lake ice-off for lakes with fish (salmon pink) and without fish (blue). Predicted values are from the best-supported linear model; fish presence did not significantly influence mosquito abundance. (b) Observed relative mosquito abundance (mosquitoes per minute) in relation to lake distance from trailheads (km). Mosquito data declined with increasing distance from trailheads, consistent with high mosquito activity near areas of human use. Points represent individual sampling events and are colored by fish presence or absence. The green line indicates the fitted linear relationship, with the shaded region representing ± 1 standard error.

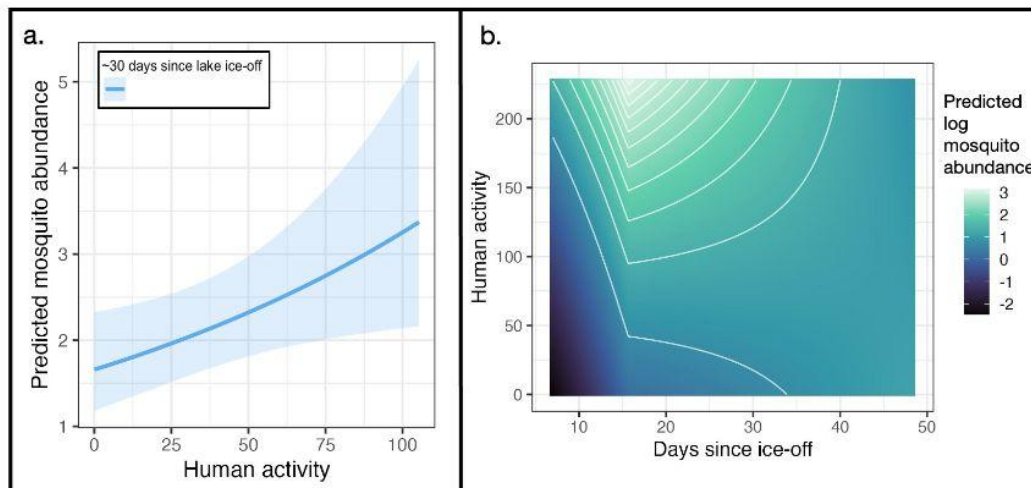


Figure 2.3: (a) The back-transformed model predictions of relative mosquito abundances (mosquitoes per minute) increasing by a function of increasing human activity at approximately 30 days after lake ice-off, when initial seasonally driven spikes in mosquito abundance begin to level off. (b) The best-fitting piecewise regression model predicted that

human activity significantly increased mosquito abundance at the beginning of the season. However, later in the season, the effect of human activity was nullified by seasonally driven declines.

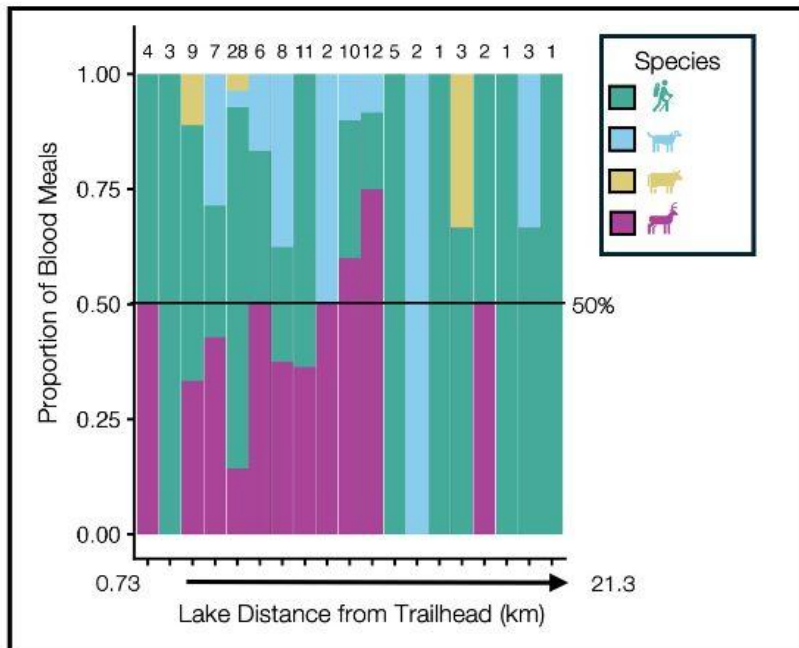


Figure 2.4: Proportional composition of mosquito blood-meal hosts across 19 lakes sampled during 2023–2024, ordered by increasing distance from the nearest trailhead (km). Stacked bars show the proportion of blood meals attributed to each host species (colors), with the total number of blood meals successfully identified per lake indicated above each bar. Across all lakes, humans accounted for 53% of identified blood meals (turquoise). Although fewer blood meals were recovered at lakes farther away from trailheads, humans were the dominant hosts at 17 of 19 lakes, including the most distant and remote lakes.

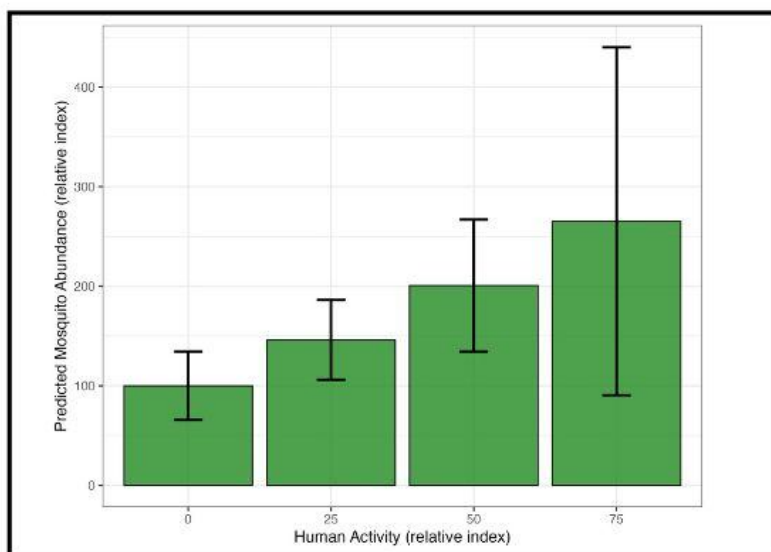


Figure 2.5: Effects plot of model-predicted mosquito abundance across increasing levels of human activity. Predictions were generated from the best-supported model while holding the time since lake ice-off constant. Human activity is represented as a relative, unitless index, evaluated at 0, 25, 50, and 75. Predicted mosquito abundance was back-transformed to the original count scale and rescaled so that abundance at zero human activity equals 100. Bars show predicted means, and error bars indicate ± 1 standard error. Mosquito abundance was predicted to increase monotonically with human activity, reaching approximately 2.6 times the baseline at the highest activity level, with uncertainty increasing at higher activity levels.

Tables:

Table 2.1: Best-fit Linear Model

Coefficients	Estimate	Standard Error	<i>p</i>-value
Days since ice-off	0.31	0.13	0.02
Human activity	0.37	0.16	0.02
Ice-off:human activity	-0.45	0.11	< 0.0001
Res. Stand. Error = 1.2		Degrees of Freedom = 98	
Adj. R ² = 0.17			
F-statistic = 7.9	<i>p</i> -value < 0.0001		

Table 2.2: Regression Model with Segmented Relationship

Coefficients	Estimate	Standard Error	<i>p</i>-value
Days since ice-off (break 1)	4.22	1.6	0.01
Human activity	0.31	0.16	0.05
Day since ice-off (break 2)	-4.1	1.6	NA
Ice-off:human activity	-0.37	0.11	0.001
Res. Stand. Error = 1.1		Degrees of Freedom = 96	
Adj. R ² = 0.23			

CHAPTER 3 – Drought-driven aggregation of avian West Nile Virus hosts in the San Joaquin Valley of California

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MacDonald

Abstract:

In the San Joaquin Valley (SJV) of California, West Nile Virus (WNV) transmission risk paradoxically increases during drought despite drought conditions reducing overall mosquito abundance, a pattern that implicates avian host redistribution as a key mediating mechanism. The SJV's extensive irrigated agricultural infrastructure may partially decouple local water availability from precipitation and potentially concentrate both avian hosts and mosquito vectors in the same focal habitats. However, the degree to which drought-driven shifts in host communities align spatially with confirmed transmission has not been systematically evaluated. Here, we integrated species-level bird abundance modeling, hydroclimatic scenario analysis, and WNV mosquito surveillance data to test whether irrigated agricultural land cover mediates the relationship between drought-driven changes in avian abundance and WNV transmission risk in Kern County. Using eBird checklists from 2010-2024, we fit negative binomial generalized linear mixed models for forty bird species present in the SJV, generating counterfactual abundance predictions under drought and wet conditions across a 1 km² prediction grid. Drought was associated with a predicted redistribution of birds toward irrigated perennial crop lands. Extremely high WNV-competency “superspreader” bird species showed drought-driven concentration specifically in row and field crop habitats, a

pattern not shared by lower-competency species. WNV-positive mosquito sample counts were significantly elevated in perennial crop and urban/developed land settings, the same habitats where predicted drought-driven increases in host abundance were strongest. Explicitly modeled predicted host abundance metrics did not independently improve WNV-positive sample predictions beyond a static landcover baseline, a result attributable to near-perfect spatial collinearity between the variables.

These findings reframe the drought-WNV relationship, indicating that the primary mechanism is not drought but the human-created hydrological stability of irrigated agriculture, which restructures host-vector contact under climatic extremes. As hydroclimatic variability intensifies across the American West, integrating land cover, avian host dynamics, and climate monitoring into unified surveillance frameworks will be essential for protecting both rural agricultural communities and broader public health.

Introduction:

Climate change is altering human health risk globally in spatially heterogeneous and often compounding ways (Romanello et al., 2024; Semenza, 2014; Yu et al., 2021). Among the most consequential emerging patterns is increasing climate variability, for example, the abrupt transition between hydroclimatic extremes, in which severe multi-year droughts are punctuated by intense precipitation events driven by atmospheric rivers. These swings between moisture deficits and surpluses are projected to intensify across many regions globally (Corringham et al., 2022; Mullens & Engström, 2025; Swain et al., 2018, 2025). Vector-borne diseases are among the health outcomes most sensitive to such climatic variability, and the incidence of reported vector-borne diseases in North America has increased substantially over the past half-century (Ogden & Lindsay, 2016; Petersen et al.,

2022; Rocklöv & Dubrow, 2020; Rosenberg et al., 2018). Accurately predicting and managing this risk requires understanding not only how vectors respond to environmental change, but how their vertebrate hosts do as well.

Mosquitoes are ectothermic insect vectors whose population dynamics depend on environmental conditions, particularly temperature and the availability of standing water, as well as biotic factors, including host presence and density (Burkett-Cadena et al., 2013; Campbell et al., 2023; Mordecai et al., 2019). Changes in precipitation exert particularly strong, opposing effects on mosquito populations. Drought reduces standing water and constrains oviposition (egg-laying) habitat but may simultaneously concentrate mosquitoes and their hosts around remaining water sources, increasing contact rates and potentially elevating transmission intensity (Chapoterera et al., 2025; Russell et al., 2025; Sambado et al., 2025). Conversely, intense precipitation can greatly expand mosquito egg-laying habitats and increase abundance, but the broader distribution of water across the landscape may dilute host-vector contact (Colón-González et al., 2021; MacDonald et al., 2025; Nosrat et al., 2021; Seidahmed & Eltahir, 2016; Trebski et al., 2025). These non-linear dynamics mean that neither drought nor flooding straightforwardly reduces disease risk, and that the net effect on transmission depends on how hosts redistribute across the landscape in response to the same conditions.

Birds are primary reservoirs and amplifying hosts for numerous arboviruses, including West Nile Virus (WNV), avian malaria, and avian pox, and their responses to hydroclimatic variability are highly species- and habitat-dependent (LaPointe et al., 2012; MacDonald, E. et al., 2021; Royan et al., 2013). Drought generally reduces avian community abundance and species richness, though the magnitude varies substantially (Albright et al., 2010; van den

Bosch et al., 2025). In the southwestern United States, severe drought was associated with declines of 18-34% in abundance in nearly a quarter of surveyed species (van den Bosch et al., 2025). However, outright declines are not universal: habitat shifts, rather than population losses, can occur when drought desiccates natural habitats while irrigation-supported agricultural and urban areas maintain moisture through artificial water inputs (Goldstein et al., 2024; Pascoe et al., 2021). Reproductive output is also impaired under drought, with suppressed renesting attempts and reduced clutch success documented across multiple systems (Carleton et al., 2019). Functional group analyses indicate that insectivores and omnivores are particularly vulnerable (Zhang et al., 2024). Flooding poses distinct yet equally significant challenges, including the abandonment of territory, food scarcity, and mass mortality during migration (Bateman et al., 2020; McPherson et al., 2025; Reiley et al., 2017; Soriano-Redondo et al., 2016). Wetland-dependent species, by contrast, often benefit from elevated water levels, with rising Great Lakes water levels associated with increases in abundance across 18 marsh bird species (Tozer et al., 2024). The variable, sometimes opposing, responses of bird communities to drought and precipitation highlight that host dynamics must be explicitly incorporated into frameworks for predicting mosquito-borne disease risk.

The San Joaquin Valley (SJV) of California provides a compelling natural study system at the intersection of these environmental and public health pressures. The SJV comprises the eight southernmost counties of California's Central Valley (Westerling et al., 2018), one of the most intensively managed and agriculturally productive landscapes in the world, generating over \$17 billion in annual revenue, with the majority of crops in the SJV used for nut, grain, and cereal production (U.S. Geological Survey, n.d.). The productivity is sustained

by extensive artificial irrigation infrastructure that partially decouples local hydroclimatic conditions from precipitation (Escriva-Bao et al., 2020). The region receives ~127-400 mm of rainfall annually (Galloway & Riley, 1999), and its hydroclimatic record over the past two decades has been defined by the whiplash dynamics of concern: two severe multi-year droughts, in 2012-2016 and 2020-2022, each punctuated by abrupt single-year recoveries to wet or near-normal conditions (Facincani Dourado et al., 2024). In addition to direct precipitation, two major rivers – the San Joaquin and Kern Rivers – deliver snowmelt from the eastern Sierra Nevada into the valley systems, providing spatially constrained supplementary water that sustains riparian corridors and feeds agricultural irrigation canals, but surface flow does not extend uniformly across the valley (National Park Service, 2022).

WNV is the primary mosquito-borne disease of public health concern in this system (MacDonald, E. et al., 2021). First detected in New York City, United States, in 1999, WNV has since spread across the continental US (Kramer et al., 2019), with passerine birds implicated as key hosts in its westward expansion along migratory routes (Reed et al., 2003; Swetnam et al., 2018). California accounts for ~15% of all reported human WNV cases nationally, and the Central Valley reports disease incidence roughly double the state average (Danforth et al., 2021; Snyder et al., 2020). While most human WNV infections are asymptomatic or produce mild febrile illnesses, approximately 1% of cases progress to severe neuroinvasive disease, which can be fatal (Gould et al., 2025); clinical underreporting means true incidence is likely substantially higher than surveillance records indicate (Lindsey et al., 2016). In the SJV, transmission is mediated by two *Culex* mosquito species: the urban-associated *Culex quinquefasciatus* and the rural-associated *Culex tarsalis* (Hernandez et al., 2019; Thiemann et al., 2012). Birds amplify the virus to titers sufficient for mosquito

infection during a blood meal, and humans and horses are dead-end hosts that do not contribute to onward transmission (Reisen et al., 2009).

Despite this public health burden, predicting WNV transmission risk across the SJV remains difficult because the drivers of transmission – land cover, drought, host abundance and distribution, and vector behavior – operate simultaneously across spatial and temporal scales and interact in ways that are difficult to characterize (Bayles et al., 2023; Kala et al., 2017; Parker, 2024). Advances in spatial modeling, community science-driven data collection, and robust public health vector surveillance programs now make it increasingly feasible to evaluate these interactions across large, heterogeneous landscapes (Abbasi, 2025; Heidecke et al., 2023; Holcomb et al., 2023; Humphreys et al., 2021; Mencattelli et al., 2023; Tran et al., 2017). Here, we leverage these tools to address a key knowledge gap. *How do drought and extreme precipitation alter the abundances of WNV-competent avian hosts across land-cover types in the SJV?*

We focus on two primary questions: first, how do abundance and habitat associations of SJV bird species vary across SJV land cover types during drought versus wet conditions within the spring and early summer viral amplification season? Second, do modeled host abundance patterns under drought conditions align in space or time with confirmed WNV-positive mosquito pool detections in Kern County, the southernmost county in the SJV? We hypothesize that during drought, WNV-competent birds shift away from natural habitats that dry out and lose vegetation structure and concentrate in irrigated agricultural fields and urban green spaces that provide artificial water inputs. We further predict that these drought-aggregated hosts in human-modified habitats will overlap spatially and temporally with positive WNV mosquito pool detections. These findings would provide a mechanistic

explanation for the counterintuitive pattern, documented in prior studies, in which WNV incidence rates increase during drought and decrease during wetter years – a pattern with direct implications for disease surveillance and vector control prioritization.

Methods:

Data Collection & Curation:

The study region comprised the eight counties of the San Joaquin Valley (SJV): Fresno, Kern, Kings, Madera, Merced, San Joaquin, Stanislaus, and Tulare. The region was partitioned into a grid of approximately 1,100 1 km² cells, which served as the primary spatial unit of analysis. All analyses were restricted to March through July across a 15-year window (2010-2024), corresponding to the West Nile Virus (WNV) transmission and avian breeding season in the SJV. Analyses were conducted using full county extents rather than clipping to the valley floor ecoregion boundary for two reasons. First, retaining full county extents maximized the number of available eBird checklists for modeling, particularly for less-sampled counties. Second, including foothill and montane areas ensured that eBird observations were not disproportionately drawn from a narrow set of natural-area hotspots, such as wildlife refuges or reserves. Land cover covariates explicitly account for this compositional heterogeneity across grid cells.

Land cover was characterized using two complementary sources harmonized following the methods of Goldstein et al. (2024). Agricultural land cover was derived from the California Department of Water Resources (DWR) Statewide Crop Mapping dataset (2023), and non-agricultural areas were classified using the LANDFIRE Existing Vegetation Type (EVT) layer (2022). Together, these sources were reclassified into six mutually exclusive categories: row and field crops, perennial crops, grassland and pasture, riparian and natural

wetlands, other natural and semi-natural vegetation, and developed or urban land. Bird occurrence data were obtained from the eBird Basic Dataset (EBD; Cornell Lab of Ornithology), with county-level downloads for all eight SJV counties processed using the `auk` package. Checklists were filtered to the March-July study window, traveling protocol only, durations of 180 minutes or fewer, and groups of eight or fewer observers. Each species was matched to the AVONET Supplementary Dataset 1 (Tobias et al., 2022) to collect species trophic niche and migratory strategy as trait covariates.

Two environmental covariates were incorporated to characterize hydrological and climatic conditions across the study period. Monthly Palmer Drought Severity Index (PDSI) values were obtained from gridMET, ~4 km resolution (Abatzoglou, 2013), via the `climateR` package (Johnson et al., 2023), downloaded for 2010-2024 (data available through March 14, 2024), and aggregated from daily rasters to monthly means per pixel. Monthly river discharge data from the San Joaquin and Kern Rivers were retrieved from the USGS as JSON time series, parsed to extract discharge in cubic feet per second, and filtered to the same seasonal and temporal window. River flowlines for the SJV bounding box were obtained from the National Hydrography Dataset, filtered to the mainstems and dissolved into a single multilinestring geometry, and projected to EPSG:3310 for use in subsequent distance calculations.

Analysis Grid Assembly:

A unified analytical panel was constructed by cross-joining the ~1,100 1 km² grid cells with all 75 month-year combinations (March-July x 2010-2024), yielding one row per cell-month-year. Each 1 km² cell contained a static proportion of each of the six land cover categories. PDSI values were extracted at each cell centroid from the 4 km gridMET rasters,

assigning each 1 km cell the value of its containing 4 km pixel. River discharge was incorporated only for cells within a 2,500 m corridor along each river's centerline, a threshold selected to ensure adequate spatial replication across the 1 km² grid while remaining ecologically plausible. Riparian corridors in arid agricultural landscapes disproportionately support bird diversity and serve as movement pathways well beyond the immediate streambank (Fischer et al., 1999), and the SJV's highly modified landscape makes these riparian zones particularly important. Non-corridor cells were assigned a discharge value of 0. All eBird checklists, including those with no target-species detections, were extracted and filtered using the effort criteria described above, while retaining zero-detection checklists to support zero-filling and detection-probability modeling. Time of day was converted from HH:MM:SS to decimal hours (e.g., 6:30 AM = 6.5) and then standardized to a [0,1] scale by dividing each checklist's start time by 24, such that midnight = 0 and 11.59 PM $\approx$ 1. Checklist duration was similarly standardized by dividing each checklist's duration in minutes by 180, the maximum allowable effort under the filtering criteria, yielding 0 for an instantaneous observation and 1 for a full 180-minute checklist. Each checklist was then spatially assigned to its corresponding 1 km² grid cell and merged with the panel, attaching the appropriate PDSI and river discharge values for that cell's location and time step.

Species Abundance Modeling:

Species abundance was modeled using generalized linear mixed models (GLMMs) with a negative binomial distribution, implemented in the `glmmTMB` package (Brooks et al., 2017). This framework follows a hierarchical observation model in which observed counts per checklist are modeled as a function of latent abundance, modulated by detection

probability, with effort covariates included as noise controls and environmental covariates informing the ecological signal. Models were fit independently for forty-one target species.

Prior to modeling, zero-filling was applied using only complete checklists. Every complete checklist was crossed with all 41 target species, with species not detected on a given checklist assigned a count of zero. All continuous covariates were then z-scored using means and standard deviations computed from the full zero-filled dataset; this standardization was applied consistently across all species and downstream prediction grids. Discharge covariates for the San Joaquin and Kern Rivers were first transformed by replacing NA values (indicating non-corridor cells) with zero, then $\log(x+1)$ -transformed to compress right skew, prior to z-scoring. Rows with missing values in any of PDSI, time of day, duration, or with duration ≤ 0 minutes were excluded. A cell-year grouping variable was created for use as a random intercept term.

Model Structure:

Three model structures were evaluated for each species. The null model included a log-transformed effort offset (checklist duration), a quadratic term for time of day, observer count, and cell-year random intercept, serving as a baseline for AIC comparison. The full model extended the null by adding five land cover main effects (with riparian + natural wetlands omitted as the reference category to avoid rank deficiency), a PDSI main effect, five PDSI x land cover interactions, San Joaquin and Kern River discharge main effects, and five discharge x land cover interactions per river (10 discharge interaction terms in total), yielding 15 interaction terms and 26 fixed-effect terms overall. The spatial model further extended the full model by adding a second random intercept for spatial blocking, in which a

spatial block was defined as a ~10 km geographic bin to capture broad-scale geographic gradients in abundance that were not explained by covariates.

Because the six land-cover proportions sum to approximately 1 per cell, including all six simultaneously induces perfect multicollinearity. The riparian + natural wetlands category was therefore omitted from the main effects and from all three interaction groups (PDSI, San Joaquin, and Kern River discharge), serving as the implicit reference throughout. Raw variance inflation factors for main-effect terms that also appear in interactions are expected to be inflated as an artifact of the interaction structure rather than an indicator of true collinearity; adjusted VIFs were all ≤ 9.3 , confirming the absence of problematic multicollinearity. Of the 41 target species, 40 models converged successfully and were retained for downstream prediction.

Gridded Prediction Abundance:

The 40 converged spatial models were applied to a standardized prediction grid, covering every 1 km² cell across the entire San Joaquin Valley, for each month-year combination in the study window. A cross-joined grid of all 72,105 cells x 5 months (March-July) x 15 years (2010-2024) yielded ~5.4 million rows per species. Cell coordinates used true geometric centroids rather than eBird checklist points. Land cover proportions were treated as static and drawn from the same reclassified sources described above. PDSI and river discharge values were the observed spatially varying values. To standardize detection effort across the prediction grid and produce effort-independent abundance surfaces, all predictions used a reference effort of 60 minutes duration, one observer, and the median time of day from the training data. Spatial block bins were assigned using the same floor-division rule as during model fitting.

Predictions were generated at the population level using fixed effects only (`re.form = NA` in `glmmTMB``), excluding both the cell-year and spatial block random intercepts. This approach is appropriate for two reasons. First, the `glmmTMB`` package does not support partial `re.form`` subset formulas. Secondly, eBird checklists are spatially sparse relative to the exhaustive prediction grid: the training data represent only a small, unevenly distributed subset of all cell x month-year combinations, meaning the cell-year random effect would be zero for virtually all prediction rows. To manage memory demands across 40 species and ~5.4 million rows per species, predictions were computed in chunks of 300,000 rows. A dominant habitat class was assigned to each cell as the land-cover category with the highest proportion for use in subsequent grouping analyses.

Drought & Atmospheric River Counterfactual Scenarios:

To quantify the effects of drought and atmospheric rivers on bird abundance across the SJV, the 40 fitted spatial models were used to generate counterfactual predictions under two fixed PDSI scenarios that represent contrasting hydroclimatic conditions observed in the historical record. A drought scenario assigned a uniform PDSI of -2.5 to all cells corresponding to conditions observed during the 2012-2015 and 2020-2022 drought periods. An atmospheric river scenario assigned a uniform PDSI of +2.5, corresponding to wet conditions observed during 2017 and 2022-2023. Both values were z-scored using the same PDSI mean and standard deviation from the training data prior to model entry, ensuring predictions remained on the same covariate axis as the fitted models. River discharge was held at climatological means for all scenarios, isolating the effect of PDSI from hydrological variation.

For each species, two summary metrics were derived from the scenario predictions. Community host abundance under drought (H^{drought}) was defined as the mean predicted abundance per cell under the drought scenario (PDSI = -2.5), averaged across all month-year combinations within the study window, and summed across the 40 host species to produce a spatially explicit index of baseline host presence during dry conditions. The drought-induced host abundance shift (ΔH) was defined as the difference in predicted abundance between the wet and drought scenarios (predicted wet - predicted drought), with positive values indicating greater abundance under atmospheric river conditions and negative values indicating greater abundance under drought conditions. ΔH was likewise summed across species to produce a community-level index of hydroclimatic sensitivity. Together, H^{drought} and ΔH characterize both the magnitude of host abundance under drought stress and the direction and degree of the host community's response to shifts between drought and wet conditions.

Overlap with WNV Positive Mosquito Samples in Kern County:

We modeled counts of WNV+ mosquito samples across 4,032 site-month-year observations from 204 trap sites in Kern County (2010–2023), using negative binomial mixed models with a log-transformed count of the total number of pools tested as an offset. All models included random intercepts for month, trap site, and surveillance year to account for repeated sampling and seasonal and interannual variation in transmission intensity.

Given that 72.6% of observations recorded zero positive pools, we evaluated whether a zero-inflated negative binomial or hurdle negative binomial provided better fit than the standard negative binomial. DHARMA simulation-based diagnostics indicated that the zero-inflated model (intercept-only zero-inflation) produced acceptable residual behavior (dispersion test $p = 0.69$), while the hurdle model showed severe underprediction of high-

count pools. However, the zero-inflation intercept converged to -17 ($p \approx 1.0$) across all model formulations, indicating that the negative binomial count distribution, aided by the random effects structure, already accommodated the zero-heavy outcome without a separate structural-zero component. The zero-inflated and negative binomial models produced nearly identical AIC values ($\Delta\text{AIC} < 2$), and we proceeded with the negative binomial family on parsimony grounds.

The three nested NB models were compared using AIC, BIC, and log-likelihood to evaluate the incremental contribution of each host abundance metric beyond environmental conditions alone. The second model added drought-induced community host abundance to test whether the spatial distribution of WNV hosts under dry conditions explained additional variation in positive pool counts beyond climate and land cover. The third model added ΔH , the drought-induced shift in host abundance, to test whether the sensitivity of the host community to hydroclimatic extremes, rather than its predicted absolute abundance, provided additional predictive value. This sequential structure allows the contribution of predicted host abundance magnitude and host community responsiveness to be evaluated independently and compared against a purely environmental baseline.

Results:

Data Exploration:

The filtered eBird dataset contained 70,517 unique checklists distributed across the eight SJV counties during the March-July study window from 2010 to 2024. In raw counts, Kern County contributed the greatest number of checklists (~20,800; 29.4%), followed by Stanislaus, Fresno, and Tulare (~9,400-11,600 each), while Kings County contributed the fewest (~1850; 2.6%). However, raw counts reflect county size, not county observer effort.

When scaled by county area, Stanislaus (296 checklists per 100 km²) and San Joaquin (242 per 100 km²) emerge as the most densely sampled counties. Kern County, despite its high raw count, ranks third in area-adjusted density (98 per 100 km²) due to its large geographic extent (~21,100 km²). Kings County remained the most sparsely sampled in both absolute and area-adjusted terms (51 per 100 km²) (Figure 3.1). Observation counts varied substantially across species: Mourning Dove and House Finch were the most frequently observed (~38,000 records), while the Swainson's Thrush, Ring-billed Gull, and Western Screech-Owl were the least detected (~2,000 records, each), reflecting a combination of true rarity, habitat specificity, and differences in detectability (Figure 3.2).

The merged land-cover product, derived from the DWR Crop Mapping and LANDFIRE EVT layers, classified the SJV into six mutually exclusive categories. By pixel area, semi-natural vegetation and developed or urban land were the two most extensive classes. The large footprint of semi-natural vegetation partly reflects that inclusion of foothill and montane terrain within full county boundaries, particularly Kern, Fresno, and Tulare counties, which extend eastward into the Sierra Nevada region of the state, rather than the valley floor alone. The riparian and natural wetlands class had the smallest extent among the categories. The distribution of eBird checklists across land cover classes largely mirrored this pixel-area pattern, with developed or urban land hosting the greatest checklist density, followed by semi-natural vegetation (Figure 3.3).

Hydroclimatic conditions varied substantially across the 15-year study period. A severe and prolonged drought from 2012-2016, during which monthly PDSI values reached below -4, and a second drought period from 2020-2022 of comparable intensity. Brief recoveries to positive PDSI occurred in 2017 and again in 2023. River discharge tracked these

hydroclimate swings closely. Both the San Joaquin and Kern Rivers showed peak flows in 2011 and 2023, and near-zero flows during drought years such as 2021. The Kern River exhibited the same seasonal and interannual structure as the San Joaquin but with substantially lower absolute discharge values, consistent with its smaller watershed area. On the San Joaquin, peak discharge typically occurred in April or May across most years, while the Kern River exhibited a sharper snowmelt-driven pulse centered on May. During drought years, discharge on both rivers during the June-July window was effectively negligible (Figure 3.4).

Bird Abundance Shifts Under Drought:

We modeled drought-induced changes in predicted abundance (Δ abundance = wet – drought) for 40 bird species across 72,091 grid cells in the San Joaquin Valley from March to July 2010–2024. Across species, drought was associated with a redistribution of birds away from row/field crops (mean Δ = +0.018 expected individuals per cell) and developed land (mean Δ = +0.006), and toward riparian/natural habitats (mean Δ = –0.052), perennial crops (mean Δ = –0.045), and grass/pasture (mean Δ = –0.025), where negative values indicate greater abundance under drought than under wet conditions (Figure 3.5).

Species-level regressions of ΔH abundance on habitat proportions confirmed that perennial crop area was the strongest habitat-level predictor of drought concentration: across 40 species, the mean regression coefficient for perennial crops was –0.085 (SE across species = 0.095), and 55% of species showed a significant negative relationship, indicating that cells with greater perennial crop cover had substantially higher bird abundance under drought. Riparian/natural area showed a similar directional pattern (mean coefficient = –0.078, SE = 0.060). Row/field crops had the only positive mean coefficient (0.015), though this was

highly variable across species and included nearly equal proportions of significant positive (47.5%) and significant negative (37.5%) individual-species relationships, suggesting heterogeneous habitat use in agricultural row-crop settings (Figure 3.6). These patterns were broadly consistent across WNV competency; however, those classified as superspreader species (American Crow, American Robin, California Scrub Jay, House Finch, and House Sparrow) were the only group indicated to have drought-driven rather than wet-period-driven concentration in row/field crop habitats (Figure 3.7).

WNV+ Samples Model:

All three models were within $\Delta AIC = 1.7$ of each other (Table 3.1), providing no support for either host variable improving fit beyond the environmental baseline. The environmental model (PDSI + habitat class) was selected as the most parsimonious. In the best-supported model (PDSI + habitat class), WNV-positive pool counts were significantly higher in areas with greater perennial crop cover (IRR = 1.65, 95% CI [1.13, 2.41], $p = 0.008$) and developed land cover (IRR = 2.10, 95% CI [1.29, 3.43], $p = 0.003$). Row field crop cover was marginally associated with higher counts (IRR = 1.36, $p = 0.032$). Drought severity (PDSI), grassland/pasture, and other natural/semi-natural cover were not significant predictors. The month random effect accounted for the largest share of variance ($\sigma^2 = 1.55$), consistent with strong seasonality in WNV transmission (Snyder et al., 2020); site-level ($\sigma^2 = 0.09$) and year-level ($\sigma^2 = 0.23$) variance components were smaller but retained in all models.

Neither the absolute host abundance under drought (H^{drought} : estimate = -0.023 , SE = 0.046 , $p = 0.62$) nor the drought-induced host shift (ΔH : estimate = 0.135 , SE = 0.120 , $p = 0.26$) was a significant predictor of WNV pool positivity. Variance inflation factor (VIF) diagnostics on (+ ΔH) revealed substantial multicollinearity among the habitat predictors

(VIF range: 10–44), consistent with the compositional structure of proportional land cover data, and between ΔH and perennial crop cover in particular ($r = -0.88$). To assess whether collinearity was suppressing the ΔH effect, we fit two sensitivity models: one omitting the most collinear habitat variable (developed; $\Delta AIC = +4.5$) and one applying an isometric log-ratio transformation of the habitat block to produce orthogonal predictors ($\Delta AIC = +20.3$). Across these formulations, the ΔH estimate ranged from 0.069 to 0.230 and remained non-significant or, at best, marginal ($p = 0.053 - 0.14$), and the best-fitting model remained the $+\Delta H$ negative binomial model despite its collinearity. We conclude that the non-significance of the host variables is not purely a collinearity artifact, though the high spatial correlation between the modeled host shift surface and perennial crop area ($r = -0.88$) limits the ability to independently identify their contributions.

Discussion:

Bird Redistribution in the SJV:

The findings presented here suggest that irrigated agricultural infrastructure fundamentally mediates the translation of hydroclimatic variability into West Nile Virus transmission risk in the San Joaquin Valley. Rather than drought simply increasing or decreasing risk, the human-created hydrological stability of perennial crop systems buffers against precipitation deficits while simultaneously concentrating avian hosts and mosquito vectors in the same focal habitats, restructuring spatial transmission in ways that a climate-only or vector-only framework would not predict (MacDonald et al., 2025; Paull et al., 2017; Reisen et al., 2009; Sambado et al., 2025). Our species-level abundance modeling across 40 bird species that vary in their competence for WNV reveals drought does not uniformly suppress avian hosts across the SJV landscape but instead redistributes them, drawing birds

away from natural habitats that desiccate under moisture deficit and concentrating them in irrigated perennial crop lands and riparian corridors that retain surface water through artificial water input or, often controlled via dams, snow-melt flows (Null et al., 2010; Stanislaus County Public Works, (n.d.); Gilkeson, 2022). Superspreader species, the American Crow, American Robin, California Scrub-Jay, House Finch, and House Sparrow (Kilpatrick et al., 2006a; Komar et al., 2003; Reisen et al., 2005; 2006), showed drought-driven aggregation in row and field crop habitats, a pattern not shared by lower-competency species.

The apparent paradox of drought-associated WNV amplification is resolved, at least partially, when transmission risk is understood not as a simple function of mosquito abundance but as the product of vector density, vector infection rate, and host availability in shared space (Kilpatrick, Daszak, et al., 2006; McMillan et al., 2019; Mordecai et al., 2019; Sambado et al., 2025). Although drought constrains oviposition habitat and reduces the total number of mosquitoes, it also concentrates surviving mosquitoes around residual water sources and channels host-seeking behavior toward the same focal habitats where birds are aggregating (Caldwell et al., 2025; Hagan et al., 2018; Holmes et al., 2024; Russell et al., 2025). The net effect on transmission intensity, therefore, depends on whether the increase in contact rate between infected vectors and competent hosts outweighs the decrease in overall vector abundance (Colón-González et al., 2021; Paull et al., 2017; Smith et al., 2012). A threshold relationship may explain why our PDSI metric, while directionally consistent with the expected drought-transmission association, was not a significant independent predictor of positive WNV mosquito pools in Kern County. The high interannual variability of the SJV hydroclimatic record, in which severe multi-year droughts alternate with anomalously wet

years, may further complicate the statistical isolation of drought effect, dampening the signal by introducing interannual heterogeneity that obscures the cumulative consequences of prolonged dryness. An alternative but complementary mechanism concerns the age structure of mosquito populations under drought conditions: reduced recruitment of nulliparous females from contracted aquatic habitats may shift the surviving population toward older, more parous females with a higher gonotrophic cycling rate and greater completion of extrinsic incubation, increasing infection prevalence even as abundance declines (Barker et al., 2010; Kramer and Ciota, 2015; Reisen, 1995). These two mechanisms, spatial concentration of hosts and vectors in shared irrigated habitats, and drought-induced shifts in vector age structure, are not mutually exclusive, and their relative contributions to interannual WNV risk in the SJV remain open to empirical inquiry.

Divergent Agricultural Land Responses:

Among the most informative findings is the divergent response of two agricultural land-cover types in the SJV. Perennial crops, primarily orchards and vineyards, showed the strongest and most consistent drought aggregation signal across species, with 55% of modeled species exhibiting significantly higher predicted abundance in perennial crop cells under drought conditions (Figure 3.5). Row and field crops showed a more heterogeneous response: nearly equal proportions of species exhibited significantly positive and significantly negative drought associations with this habitat (Figure 3.6), although the superspreader species of WNV specifically showed drought-driven concentration in this habitat (Figure 3.7). This contrast likely reflects multiple interacting factors.

Perennial crops maintain more continuous canopy cover, structural complexity, and subsurface irrigation even when surface precipitation is absent (Goldstein et al., 2024;

Helalia et al., 2021; Mall and Herman, 2019; Medellín-Azuara et al., 2024; Peria and Francis, 2025), providing stable foraging and refuge habitat across drought years. Row and field crop lands, by contrast, are more frequently left fallow or subject to crop rotation under drought conditions when water allocations are reduced, or fallowing agreements are triggered (Cole et al., 2024; Gebremichael et al., 2021; Medellín-Azuara et al., 2022), rendering them effectively uninhabitable for birds and mosquitoes alike in the driest years. The persistence of resources in perennial crop settings may thus create refugia that attract a broad suite of species, while the variable management and moisture status of annual crop fields produce the heterogeneous species-level responses we observe (Barbaree et al., 2020; Borges et al., 2017; Goldstein et al., 2024; Priyadarshana et al., 2024; Redlich et al., 2018). That superspreader hosts nevertheless appear to aggregate in row-crop areas during drought suggests these species may be tracking residual agricultural water sources, such as irrigation tailwater, stock ponds, and drainage ditches, that persist even when crops are not actively growing (Hsuan Hsu et al., 2019; Hu et al., 2025; Kovach and Kilpatrick, 2024; López-Pomares et al., 2015; Pascoe et al., 2021; Vest et al., 2023).

Urban Land & eBird Limitations:

Developed and urban land showed only marginal drought-associated host movement, which may reflect that urban landscapes sustain artificial irrigation and relatively consistent moisture in green spaces across hydroclimatic conditions (Allen et al., 2021; Miller et al., 2022; Quesnel-Siepp et al., 2019; Torres et al., 2024), reducing the magnitude of drought-driven redistribution compared to natural and agrarian habitats.

eBird data provide unparalleled spatial and temporal coverage across the SJV, but checklist density was uneven and concentrated around urban centers and road corridors.

Critically, the bird abundance surfaces used here are modeled predicted values rather than raw detection counts, generated from models that explicitly account for detection probability through effort covariates, partially mitigating spatial bias, though predictions data-sparse agricultural interiors carry greater uncertainty than those in well-sampled urban areas.

Collinearity of Host Abundance Responses & Land Cover:

Despite clear spatial correspondence between drought-aggregated bird hosts and predicted positive WNV pool locations in both perennial crop and irrigated agricultural settings, the explicitly modeled host-shift metrics, H^{drought} and ΔH , did not significantly improve predictions of WNV pool positivity beyond the environmental baseline in Kern County. The primary statistical explanation is multicollinearity: the drought-induced host abundance shift surface was strongly and negatively correlated with perennial crop cover across trap sites ($r = -0.88$), indicating that static land-cover classification and dynamic host redistribution encode essentially the same spatial signal from different analytical directions. Cells dominated by perennial crops are precisely where birds concentrate under drought, so a model containing both predictors cannot independently assign variance to each. Sensitivity analyses are instructive here: removing the most collinear habitat predictor increased the ΔH estimate from 0.135 to 0.230, approaching conventional significance ($p = 0.053$), and orthogonalizing the habitat block via an isometric log-ratio transformation yielded a ΔH estimate of 0.069 ($p = 0.14$). The ΔH signal is directionally consistent across all formulations and increases as collinearity decreases; the data do not contradict the host redistribution hypothesis but rather cannot statistically distinguish it from the static landscape feature it tracks.

This collinearity is not merely a statistical inconvenience; it is itself a meaningful result. Land cover is functioning here as an integrated proxy for hydrology, vector habitat, host redistribution, and human water management simultaneously. At the surveillance scale available in Kern County, these processes are spatially inseparable, and that inseparability has direct implications for public health monitoring. The static maps of perennial agriculture are, in this landscape, also a reasonable first approximation of where drought concentrates transmission risk. The distinction between these two explanations – stable infrastructure as risk predictor versus dynamic host redistribution as the mechanism – matters enormously for the type of public health response required. If perennial crop infrastructure is the primary driver, risk is predictable and mappable in advance. If drought-driven host concentration is the dominant mechanism, risk is dynamic and would require early-warning systems tracking both climate conditions and avian movements. The current surveillance network cannot resolve this distinction, and expanding trap coverage into rural, riparian, and agricultural settings is both a research and public health priority.

Public Health Implications:

The public health implications of drought-driven host aggregation in irrigated agricultural settings are distinct from, and in some respects more concerning than, those associated with urban transmission dynamics. Agricultural workers represent a high-exposure population during drought periods: those who work in close quarters with perennial crops and orchard environments where WNV-competent hosts and *Culex tarsalis*, the rural-associated vector, are simultaneously predicted to be concentrated (Odigie et al., 2024; Russell et al., 2025). This population faces well-documented structural barriers to accessing health care and may receive less targeted public health messaging than urban residents, despite elevated

occupational exposure risk (Harrigan et al., 2010; Hernandez et al., 2019). The urban transmission pathway – concentrated year-round between *Culex quinquefasciatus* and generalist bird hosts in developed areas – appears relatively insensitive to hydroclimatic variability and thus represents a more temporally stable baseline risk (Bhattachan et al., 2021; Reisen et al., 2009; Sambado et al., 2025). The agricultural pathway, by contrast, may be highly sensitive to drought severity and duration, suggesting that surveillance and vector control resources should be prioritized for deployment in rural and agricultural areas during extended drought years (DeGroote and Sugumaran, 2012; Eisen et al., 2010; Sambado et al., 2025).

Conclusion:

Future Directions:

This study provides evidence that irrigated agricultural landscapes restructure how hydroclimatic variability drives WNV transmission risk in the SJV, not by uniformly amplifying drought effects, but by creating stable refugia that concentrate both avian hosts and mosquito vectors independently of precipitation. Superspreader species, including the American Crow, American Robin, House Sparrow, House Finch, and the California Scrub Jay, showed strong drought-driven concentration in precisely these irrigated habitats. The inability to statistically separate the host redistribution signal from static perennial crop cover reflects the deep ecological coupling between these two variables – not an absence of the mechanism – and points to the need for spatially targeted surveillance in agricultural settings and broader geographic coverage in future analyses. As hydroclimatic variability intensifies across the SJV and the broader western United States, the frequency and severity of hydroclimatic swings that drive this redistribution will likely increase (Gupta et al., 2023;

Swain et al., 2018, 2025; Williams et al., 2022). Resolving whether static agricultural infrastructure or dynamic host redistribution is the dominant risk driver, and which communities that distinction matters most for, requires surveillance systems designed to detect both. Expanding trap coverage into rural and riparian settings, tracking avian movements in real time, and applying this framework across all eight SJV counties are the next logical steps towards a public health infrastructure that matches the spatial complexity of transmission risk in an increasingly variable hydroclimatic system.

Figures:

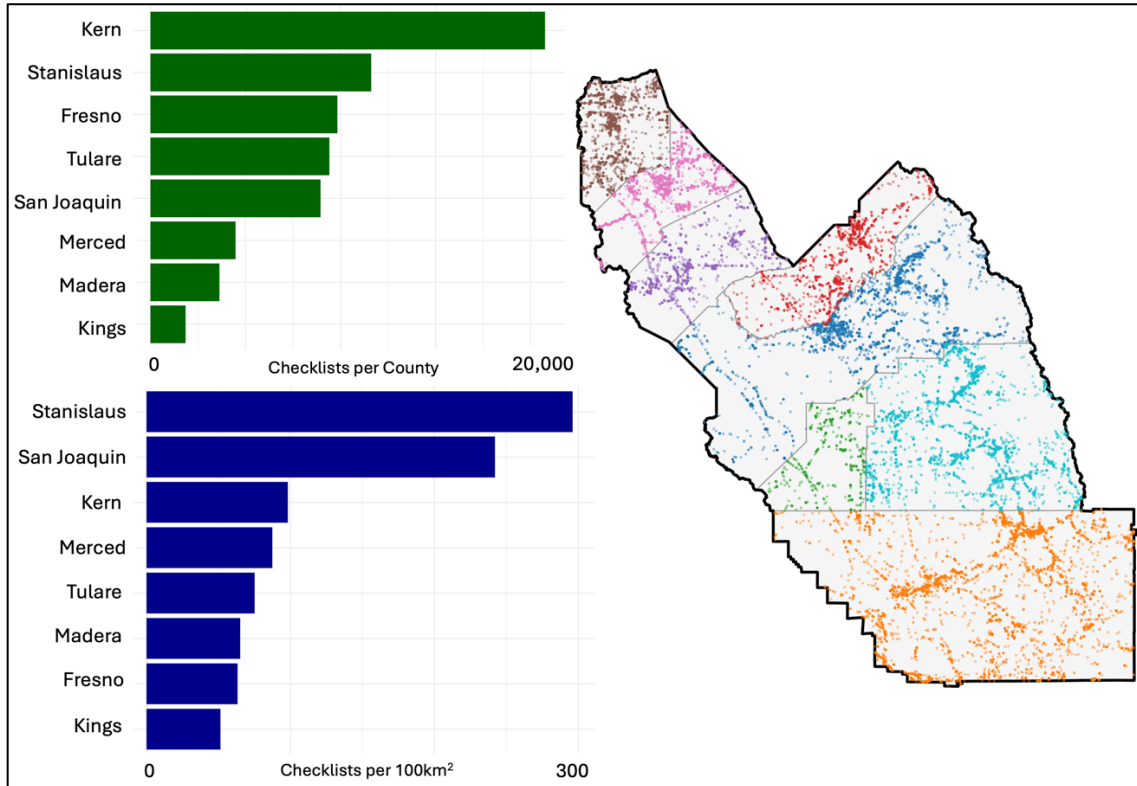


Figure 3.1: Distribution of filtered eBird checklists across the eight San Joaquin Valley counties during the March–July study window (2010-2024). Top left: raw checklist counts by county, with Kern County contributing the largest share. Bottom left: area-adjusted sampled density (checklists per 100 km²). Counties most intensively sampled relative to their size were Stanislaus County and San Joaquin County. Right: spatial distribution of all 70,517 checklist locations across the SJV, colored by county.

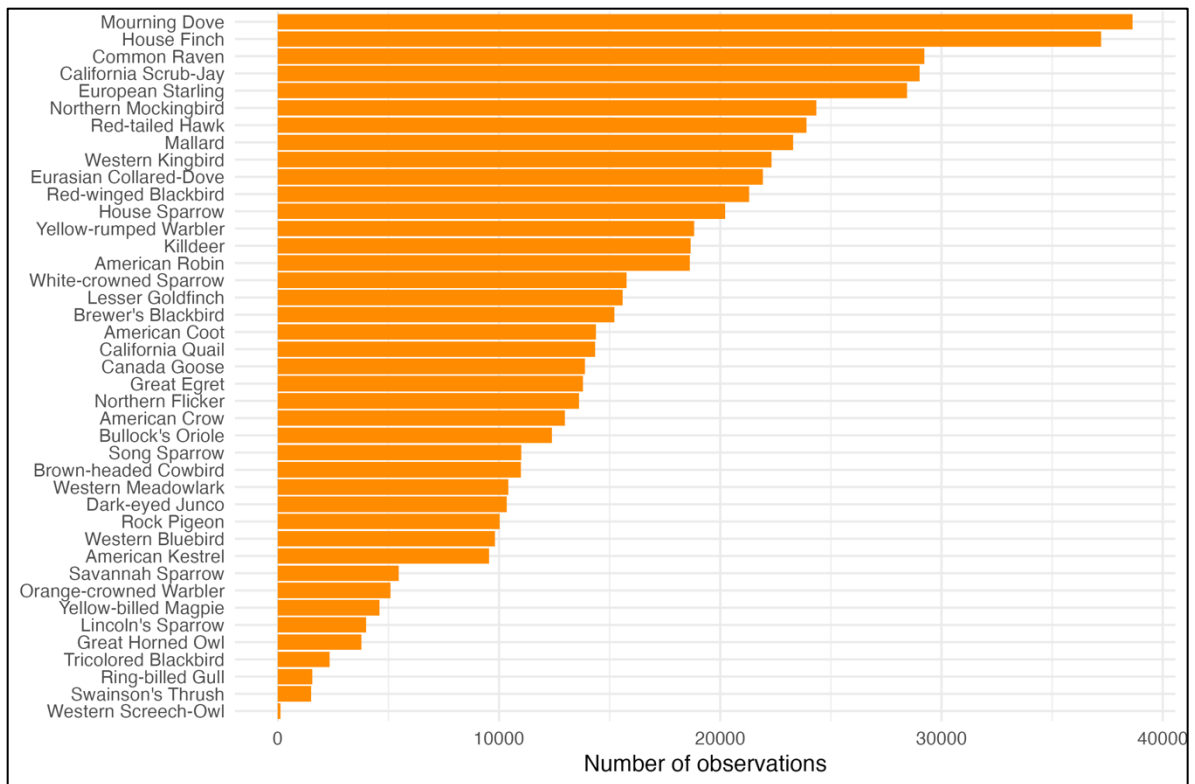


Figure 3.2: Number of checklists in the SJV containing the selected bird species common in the SJV or highly competent for WNV.

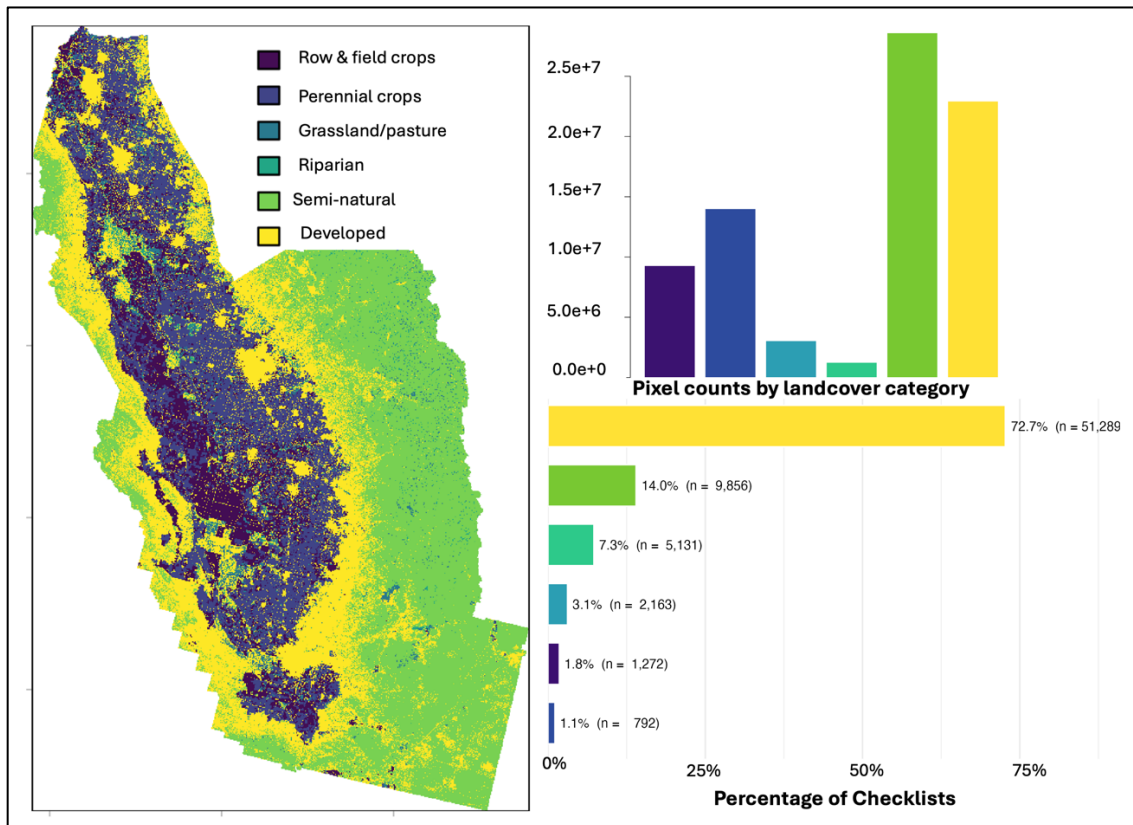


Figure 3.3: The six land cover classes across the SJV, by pixel. The categories semi-natural and developed had the highest pixel coverage in the SJV. They were also the location of the most eBird checklists, except that developed was the top pixel for eBird checklists, and semi-natural was the second-highest.

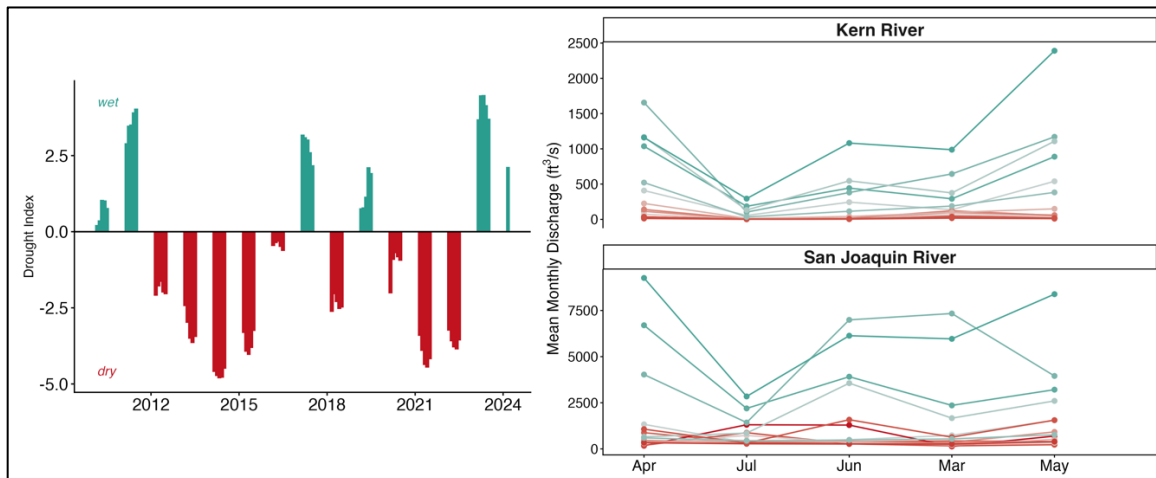


Figure 3.4: From monthly PDSI values, there are two major multi-year drought periods in the SJV from 2012–2016 and 2020–2022, with single-year rebounds to wet conditions in 2017 and 2023. There’s a large year-to-year variation in river discharge. The Kern River shows the same flow patterns as the San Joaquin but at lower values, reflecting its smaller watershed.



Figure 3.5: Habitat standardized Δ abundance (wet-drought) for each modeled bird species (left). Spatial distribution of mean Δ abundance averaged across all 40 species for March to July 2010 to 2024, covering the SJV (top). Mean Δ abundance by habitat class. Blue = positive, more birds under wet. Red = negative, more birds under drought conditions.

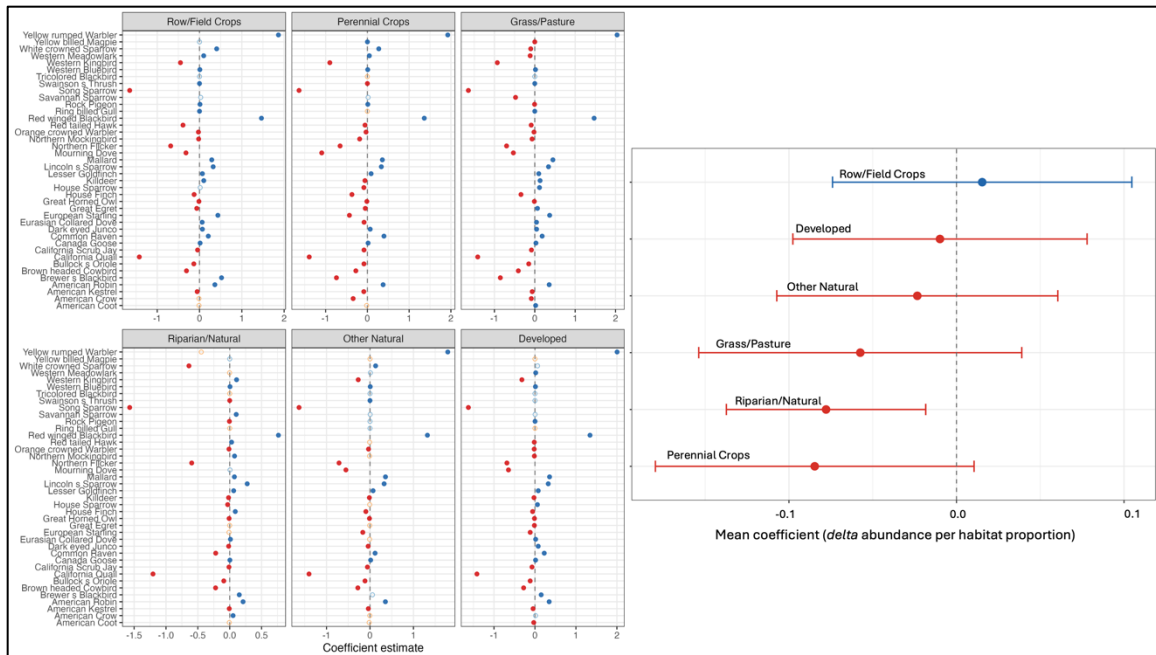


Figure 3.6: Per-species regression coefficients (left) and mean regression coefficient (right) for the change in avian abundance across SJV habitat proportions. For regression coefficients, blue-filled indicate significant aggregation during wet periods, and red-filled indicate significant aggregation during drought periods.

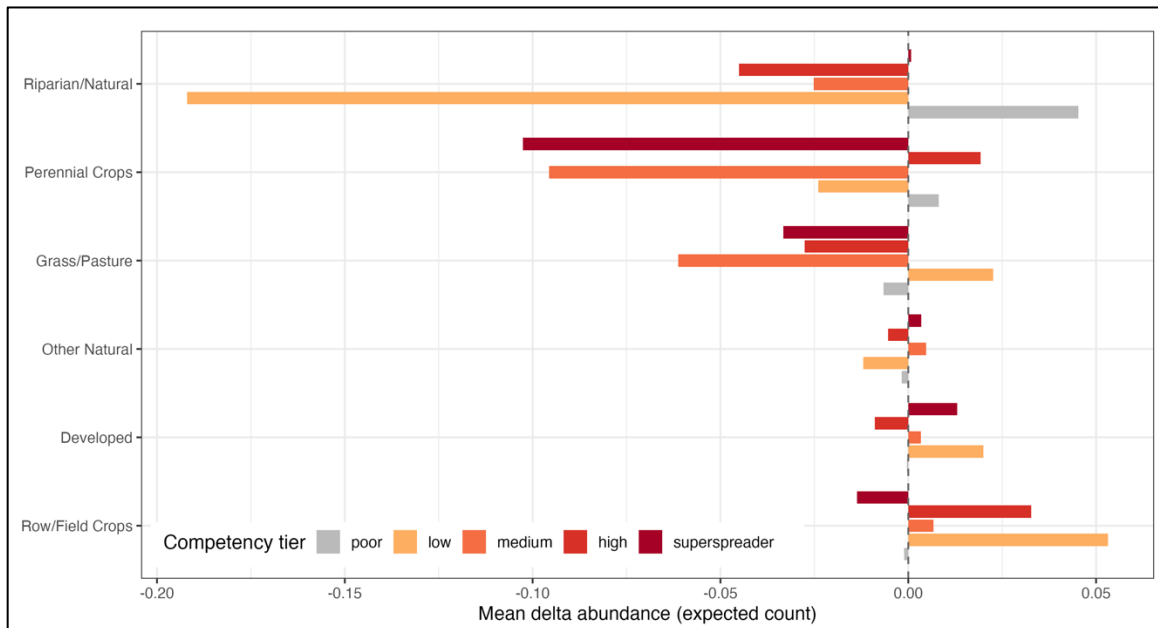


Figure 3.7: Mean Δ abundance by avian species competency tier for WNV transmission (poor, low, medium, high, superspreader) and by habitat classification. Negative = more birds under drought; each bar is the mean across species in that tier.

Tables:

Table 3.1: AIC Diagnostics of Model Fit (family: Negative Binomial)

Model	AIC	df	Δ AIC
PDSI + habitat class	5666.2	11	0.0
+ H^{drought}	5666.9	12	0.7
+ ΔH	5667.9	12	1.7

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APPENDICES

Chapter 1

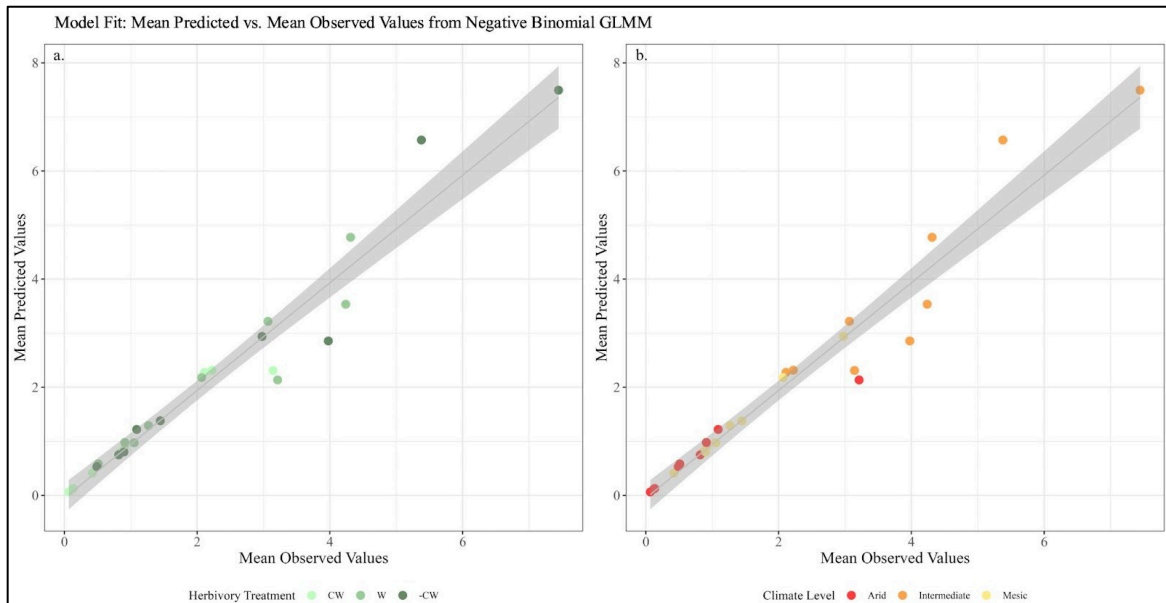


Figure S1.1(a & b): Model fit of *D. occidentalis* abundance by herbivore treatment (a) and climate level (b). Model fit improves when *D. occidentalis* abundance is lower than when it is higher, as the model may under- or overpredict these higher values. The positive slope of the relationship between observed and predicted values indicates that the model captures overall trends in *D. occidentalis* abundance. The negative binomial distribution of our data indicates that most *D. occidentalis* abundance per drag collection was low (between 0 and 5). The data also showed considerable variability, with several outliers showing very high counts of *D. occidentalis* collected during the drag session. The lower reliability in predicting *D. occidentalis* at higher abundances may be due in part to these large outliers.

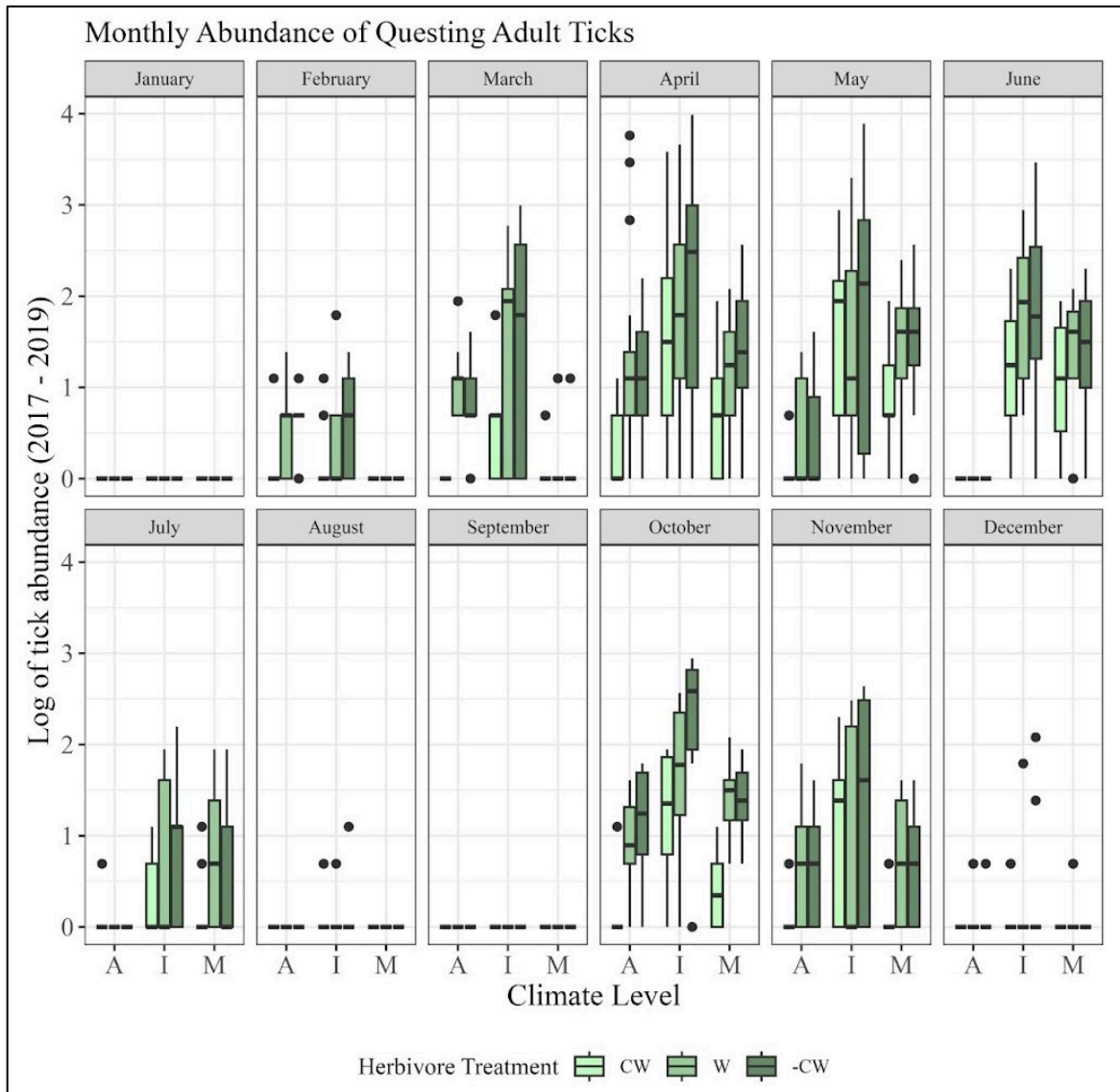


Figure S1.2: Monthly log abundance of questing adult *D. occidentalis*. There is a seasonal fluctuation in questing tick abundance in Southern California. The major peak in abundance occurs in spring, with a smaller peak in early winter. Prior studies on tick populations in Southern California have found similar seasonal questing activity patterns (MacDonald and Briggs 2016; MacDonald et al. 2017).

Small Mammal & Lizard Responses to Climate Level + Herbivore Treatment:

Lizard visual mark-recapture surveys:

Western fence lizard populations were surveyed using a mark-recapture approach at all treatment locations with the Arid and Intermediate climate levels in July of 2016 (pre-exclosure installation) and in June of 2017 & 2018 (post-exclosure installation). The

treatment plots at the Mesic climate level were sampled as well but yielded few to no marked lizards and were therefore not included in the analysis. The survey timing encompasses the decline from peak juvenile tick questing activity in this region, which typically occurs from April through mid-June (MacDonald, 2018). At each herbivore treatment, we visually surveyed lizards along six 50-meter transect lines, 10 meters apart. Sighted lizards were sprayed on their dorsum with a latex paint mixture. This marking was temporary, lasting only until the lizard's next molt (Swei et al., 2011). We surveyed lizards in each treatment on three consecutive days, using a different paint color each day to determine a lizard's encounter history (IACUC protocol #908.1).

Small Mammal Density & Burden:

We sampled small mammal populations annually at all treatment plots from April to December in 2016 and January to December in 2017 & 2018. In 2019, due to the previous year's low capture rates across plots, we focused efforts on only one block in Mesic and one block in Arid, where past trapping efforts had yielded the greatest number of mammals from April to June and then again in November. Small mammals were trapped for three consecutive nights with five rows of ten traps, yielding fifty traps per exclosure plot. All captured animals were given an individually numbered fingerling ear tag (National Band and Tag Co., Newport, KY, USA), identified by species and sex, and weighed. All ticks were removed from the ears and head of each animal before release on-site (IACUC protocol #908.1).

Vertebrate Abundance Estimates:

To quantify the impacts of large herbivores and climate on lizard and small mammal population estimates, we used the Wilcoxon rank-sum test and the Kruskal-Wallis test with a

post-hoc Dunn test with a Bonferroni correction. Vertebrate population abundances were estimated for each experimental plot when sampling over three consecutive days occurred in 2017 and 2018 using the 'R capture' package (Baillargeon and Rivest 2007).

Tick Density & Vertebrate Population Estimates:

To measure the experimental design impacts on vertebrate populations and indirectly on ticks, we correlated tick abundance and vertebrate population estimates and conducted a Spearman's rank correlation test between tick abundance and a) lizard or b) mammal population estimates with the 'cor.test()' function.

Lizard & Small Mammal Population Estimates Fluctuated with Climate & Herbivore

Treatment:

There was a significant difference in lizard population estimates between the Arid and Intermediate climate levels ($p < 0.0$), with Intermediate having more lizards than Arid. For mammal population estimates, there was a significant difference across all climate levels ($p < 0.0$), with the Mesic climate level estimated to have the highest small-mammal population. Lizard population estimates varied significantly between the W and -CW exclosures ($p < 0.005$). There were no significant differences in estimates between the CW and W exclosures and the CW and -CW exclosures. There was a significant difference in mammal population estimates between CW and W exclosures as well as CW and -CW exclosures ($p < 0.0$). W and -CW exclosures were estimated to have higher numbers of mammals than the CW exclosures.

Lizard Populations were Slightly Correlated with Tick Abundance:

There was a statistically significant, weak positive correlation between lizard population estimates and questing tick abundance ($p < 0.0$). As lizard populations increase, questing

ticks increase slightly as well ($\rho = 0.3$). There is no significant correlation between mammal population estimates and questing tick abundance.

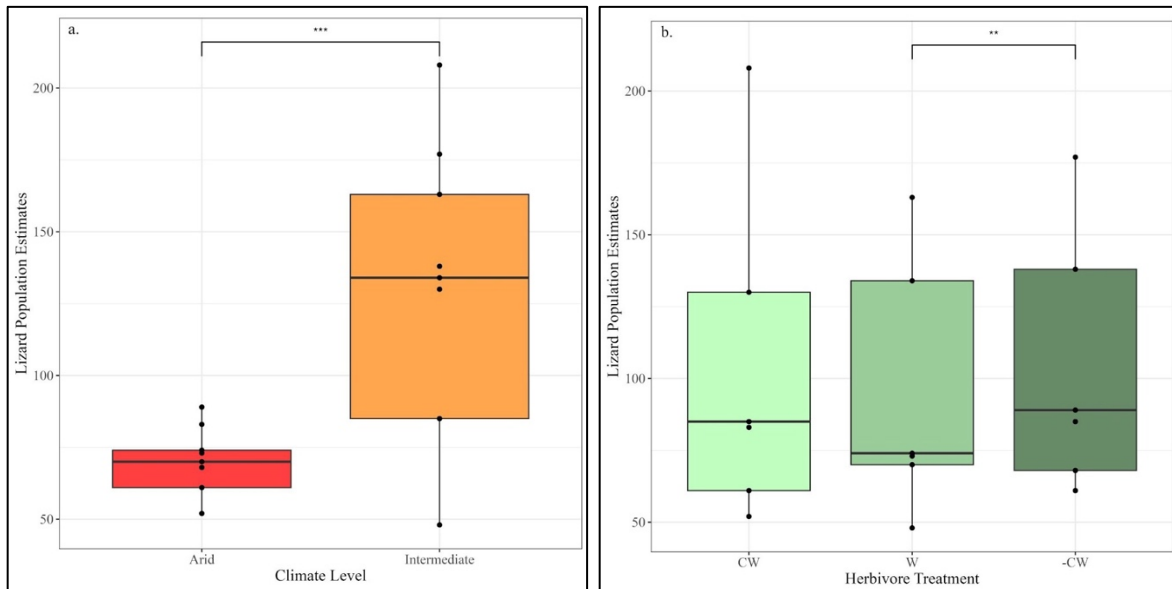


Figure S1.3: Lizard population estimates from mark-recapture sampling done at Tejon Ranch Enclosure Experiment (TREE) by climate level (a.) and herbivore treatment (b.). Mark-recapture sampling for lizards was conducted at the Intermediate and Arid climate levels, but not at the Mesic climate level. There was a significant difference in lizard populations between the two climate levels. For herbivore treatment, there was a significant difference between fenced enclosure plots W (*wildlife*) and -CW (*minus cattle and wildlife*).

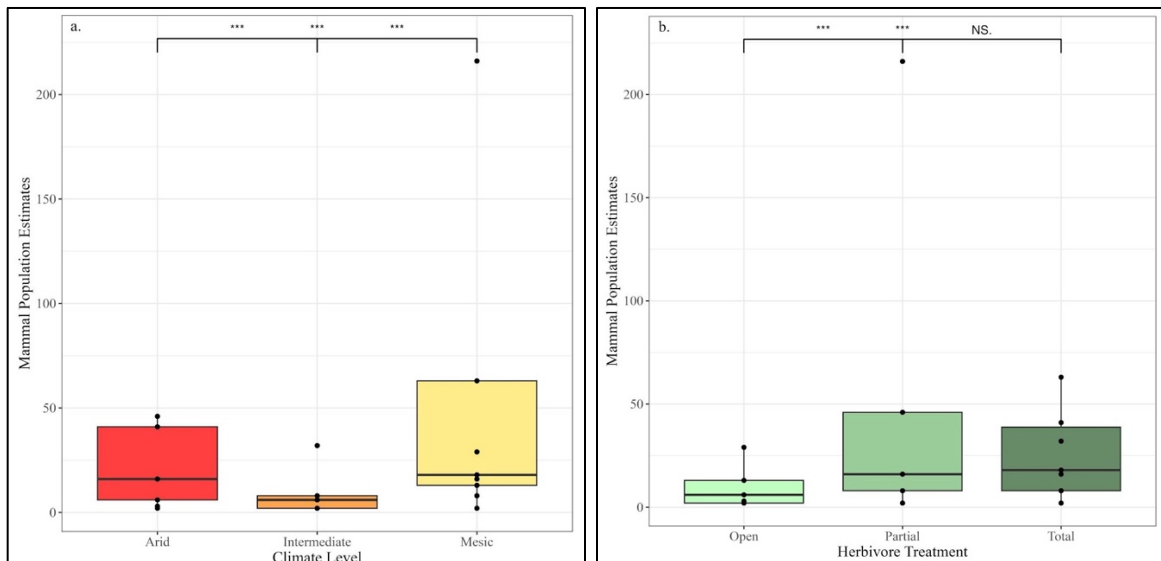


Figure S1.4: Small mammal population estimates based on trap-grid sampling by climate level (a.) and herbivore treatment (b.). There was a significant difference in small-mammal estimates across climate levels. Additionally, there was a significant difference between the CW (*cattle and wildlife*) enclosures and the W (*wildlife*) and -CW (*minus cattle and wildlife*)

exclosures. The W herbivore treatments had the highest small-mammal population estimates, but there were no significant differences between the W and -CW exclosures.

Table S1.1: Totals of lizards and small mammals surveyed and sampled at the Tejon Ranch Exclosure Experiment (TREE). A mark-recapture survey of lizards within treatment plots was conducted from 2016 to 2018. The only lizard species surveyed was *Sceloporus occidentalis* (western fence lizard), so the data are not separated by species. Small-mammal grid trapping took place in 2016, 2017, 2018, and 2019. The numbers represent all species, and the total number of small mammals caught per climate level for all grid-trapping efforts.

Lizards	Arid	Intermediate
2016	258	549
2017	222	483
2018	367	484

Small Mammals	<i>Peromyscus maniculatus</i>	<i>Peromyscus boylii</i>	<i>Peromyscus californicus</i>	<i>Peromyscus spp.</i>	<i>Chaetodipus californicus</i>
Arid	42	23	0	0	3
Intermediate	33	10	0	0	0
Mesic	53	29	62	1	0

<i>Neotoma fuscipes</i>	Unknown	Total:
0	11	84
0	0	43
3	34	182

Chapter 2:

S2.1 - Inyo National Forest Remoteness:

We quantified landscape remoteness in the Inyo National Forest using Euclidean distance to roads and trails. Forest boundaries were obtained from USFS administrative datasets and projected to NAD83 / California Albers (EPSG:3310). Road and trail layers were downloaded from USFS Feature Services, cropped to the forest boundary, and converted into Terra SpatVector objects. Each network was rasterized at 90 m resolution, and cell-wise distances to the nearest road and trail were calculated. Distances were standardized (z-scores) and averaged to create a composite remoteness index, with higher values indicating locations farther from infrastructure. The index was masked to the forest extent and visualized as a continuous raster surface.

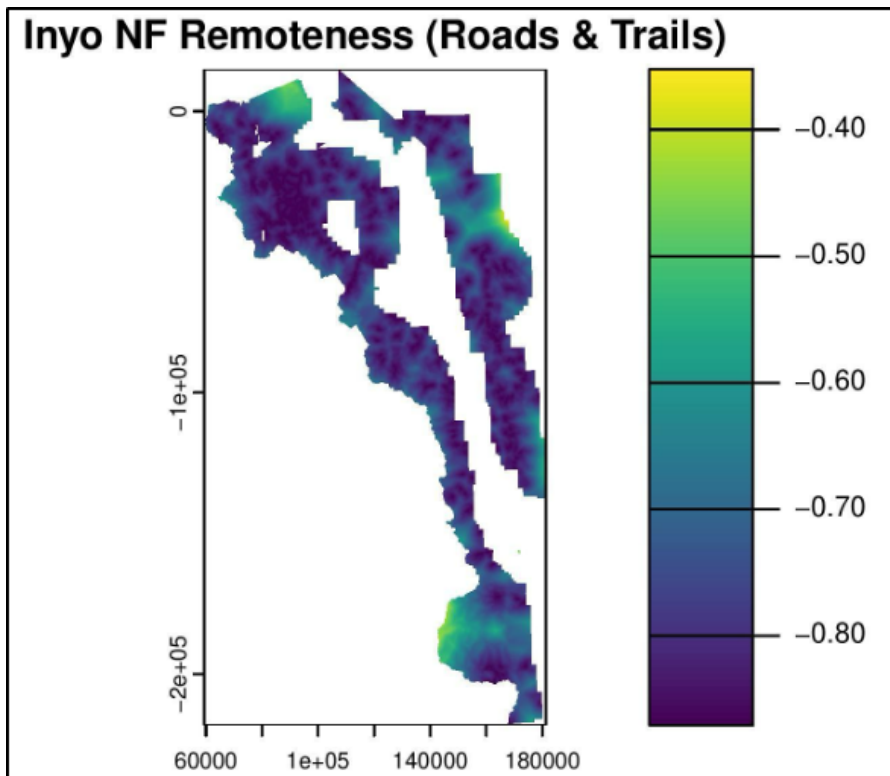


Figure S2.1: Remoteness index for Inyo National Forest, California, based on standardized Euclidean distances to the nearest road and trail. Higher values indicate locations farther from infrastructure (i.e., more remote), whereas lower values reflect closer proximity to roads

and trails. The raster surface was generated at 90 m resolution and masked to the forest boundary.

S2.2 – Blood Meal Digestion Scoring:

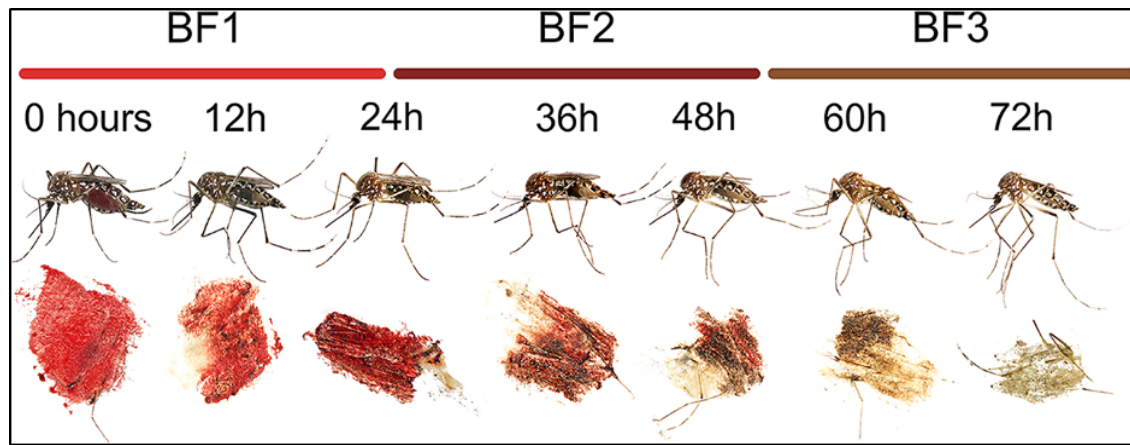


Figure S2.2: From Reeves et al., 2018, a visual scoring chart of mosquito abdomen appearance and blood spot color that estimates approximately how long ago the blood meal was taken. We did not sequence any blood meals noted to be in the ~0 hours range to avoid potential sampler contamination, or any blood meals post the ~60 hours range, as these are typically too digested for sequencing. To avoid sampler contamination in the field, samplers wore full-length shirts, pants, and hoods or head nets to prevent mosquito bites.

S2.3 – Blood Meal Sequencing Details:

For mosquitoes in which bloodmeal was found, a subsample from each blood spot on the FTA cards was excised using sterile scissors and forceps. DNA was extracted using the Qiagen DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. Extraction success was verified using a Qubit Fluorometer (Thermo Fisher Scientific, Waltham, MA).

We amplified an approximately 470 bp region of the vertebrate mitochondrial cytochrome *b* gene. Primers were modified to include 16S overhang adapters (Illumina Inc., San Diego, CA) (Table S3.1). Each 25 uL reaction included: 2.5 uL of template DNA (or negative control), 5.0 uL of forward primer, 5.0 uL of reverse primer, and 12.5 uL of NEB Master Mix (New England Biolabs, Ipswich, MA).

Table S2.1: Primer Information.

Target	Primer Name	Sequence 5' – 3'	Reference
Mitochondrial cyt-b	F-MCB398	TACCATGAGGACAAATATCATTC	Verma & Singh (2006)
	R-MCB869	TG CCTCCTAGTTTGTAGGGATTGA TCG	
Illumina 16s adapter	F-Overhang	TCGTCGGCAGCGTCAGATGTGGT	Illumina
	R-Overhang	ATAAAGACAG GTCTCGTGGGCTCGGAGATGTGT ATAAAGACAG	

Thermal cycling conditions included: an initial denaturation at 95°C for 10 minutes; 35 cycles of 95°C for 45 seconds, 51°C for 1 minute, and 72°C for 2 minutes; and a final extension at 72°C for 10 minutes (Verma & Singh, 2006).

PCR products were purified using AMPure XP beads (Beckman Coulter, Brea, CA). A second PCR was performed according to Illumina's protocol to attach dual indices and Nextera XT adapter sequences, thereby assigning a unique barcode to each blood meal sample. Final libraries were cleaned using AMPure XP beads—once in 2023, and twice in 2024—then normalized, pooled, and sequenced on an Illumina MiSeq using a 600-cycle kit.

Bioinformatics processing was performed in Python (3.12.9) using the packages 'cutadapt', 'trimmomatic', and 'biopython' (Bolger et al., 2014; Chapman & Chang, 2000; Martin, 2011).

Due to the high digestion levels of the blood meal samples (Bellekom et al., 2023; Martínez-de la Puente et al., 2013) and the lower reliability of MiSeq in sequencing reverse reads (Ramakodi, 2021; Schirmer et al., 2015), our resulting R2 reads were often of poor quality. Therefore, only R1 reads were used in sequence analysis. The few 2023 samples that produced high-quality R1 and R2 reads, using 'vsearch' (Rognes et al., 2016), were merged

and analyzed against the reference database to confirm the reliability of the BLASTn results for the R1 reads.

The BLASTn output was a .txt file for each blood meal sample, containing an NCBI reference code for each unique sequence found in that sample. Using RStudio (4.4.1), we selected the top five sequences in each file based on the highest number of occurrences, the lowest error value, and the highest percent identity. If more than one distinct identification for different species were tied in the top five for error value, percent identity, length, and mismatch, then both unique species were recorded. Whether this results from a mixed host blood meal or the universality of the cyt-b amplicon, which prevented NCBI BLASTn from determining which species were present, cannot be confirmed. Otherwise, in the top five, the reference code identifying the sequence with the lowest error value and the highest percent identity was designated as the host from which the blood meal originated. We looked up the reference ID code in NCBI to determine the species name for the sequence.

S2.4 – Variable Grouping Information:

Table S2.2: Variables analyzed in the modeling analyses.

Variable	Grouping	Further Information
Relative Mosquito Abundance	Lake	Response variable. The number of female mosquitoes captured per minute of an individual sampling effort. Used to adjust for differences in total lake sampling minutes between lakes due to lake size or logistical constraints that limited sampling effort. Log-transformed in model analyses to improve normality
Days Since Ice-off	Lake	Z-score standardized. The number of days passed between the date of total lake melt-off and the date sampling efforts occurred.
Fish Status	Lake	Categorical: presence/absence
Human Activity	Basin	Z-score standardized. The number of visitor reports to the basin for the two weeks prior to the sampling effort date and the week of sampling date.
Around-Lake NDVI	Lake	Z-score standardized. Surface area of wetland habitat within a 500m buffer around the sampled lake.

Maximum and Minimum Temperature	Basin	Z-score standardized. Average encompassing the temperatures in the 20-days prior to the date sampling efforts began in the basin. All lakes within a basin were sampled 48-80 hours apart so averages were taken from the starting date of those sampling trips.
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The variables included in our stepwise model comparisons, the grouping level, and further information on how these variables were incorporated into the model analyses.

Section 2.5 – Around Lake NDVI:

Landsat 9 imagery for 2023 and 2024 was acquired after the total snowmelt in both years.

In QGIS, we calculated NDVI (Normalized Difference Vegetation Index) for the region using the Near-Infrared (NIR; Band 5) and Red (Band 4) bands (equation below).

$$\text{NDVI} = \frac{\text{NIR (Band 5)} - \text{Red (Band 4)}}{\text{NIR (Band 5)} + \text{Red (Band 4)}}$$

We then created a binary raster layer that differentiated wetland ($\text{NDVI} \geq 0.25$ AND $\text{NDVI} \leq 0.4$; = 1) from other types of vegetation (= 0). This binary raster was then clipped to a 500m vector buffer around each lake. We used 'Zonal Statistics' to calculate the number of wetland pixels for each 500m buffer. Each Landsat pixel is $30\text{m} \times 30\text{m}$, or 900m^2 . Therefore, we multiplied the sum of each lake buffer's wetland pixels by 900 to get the around-lake wetland surface area. These values were then extracted to a .csv file that could be read into RStudio for modeling analyses of mosquito density.

S2.6 – Other Tested Models:

Table S2.3: Best-Fit Linear Mixed Model

Random Effects:	Variance	Standard Deviation	
basin	0.07	0.26	
Residual	1.4	1.2	
	Number of Obs = 102	Groups = 8	
Fixed Effects:	Estimate	Standard Error	t-value

Human activity	0.35	0.17	2.1
Days since ice-off	0.28	0.13	2.2
Human activity:ice-off	-0.43	0.11	-3.9
	REML criterion = 329.1		

Table S2.4: Linear Model (+ 20 day average maximum temperature)

Coefficients	Estimate	Standard Error	<i>p</i> -value
Days since ice-off	0.27	0.13	0.04
Human activity	0.40	0.16	0.02
Temperature	-0.15	0.13	0.23
Ice-off:human activity	-0.44	0.11	< 0.0001
Res. Stand. Error = 1.2		Degrees of Freedom = 97	
Adj. R ² = 0.17			
F-statistic = 6.3	<i>p</i> -value < 0.0001		

Table S2.5 Linear Model (+ 2024 wetland surface area of each lake)

Coefficients	Estimate	Standard Error	<i>p</i> -value
Days since ice-off	0.29	0.13	0.03
Human activity	0.32	0.16	0.052
Wetland	0.07	0.12	0.57
Ice-off:human activity	-0.43	0.11	< 0.001

Res. Stand. Error = 1.2		Degrees of Freedom = 96	
Adj. R ² = 0.15			
F-statistic = 5.5	<i>p</i> -value < 0.001		

S2.7 – Seasonal Human Recreation in Inyo National Forest:

We quantified seasonal human recreational activity using publicly available historical reservations for overnight visits to Inyo National Forest from [Recreation.gov](https://www.recreation.gov). Annual datasets from fiscal years 2021–2024 were combined and filtered to include only reservations associated with the Inyo National Forest with trip start dates between April and November. Reservation start dates were aggregated into weekly counts, using the start of each week (Monday), to reduce day-to-day variability and emphasize seasonal patterns in permit purchasing. Weekly reservation totals were visualized across years to facilitate interannual comparison of season use patterns.

Weekly wilderness reservation counts in Inyo National Forest exhibited a pronounced seasonal increase beginning in late May to early June, followed by peak use in mid-summer and a steady decline through September–October (Figure S6.1). In 2023 and 2024, increases in recreational activity occurred shortly after the earliest observed lake ice-off dates. In contrast, peak recreational use consistently occurred several weeks later, coinciding with the lake's June through August period. Notably, early-season increases in reservations preceded the seasonal maximum in human activity. At the same time, the steepest declines in mosquito abundance observed in the main analyses occurred during periods of high or declining recreational use. This temporal mismatch may indicate that the strongest statistical associations between human activity and mosquito density occurred early in the season,

when human presence remained relatively low compared to peak summer use, supporting a possible temporal decoupling between immediate recreational intensity and mosquito abundance patterns.

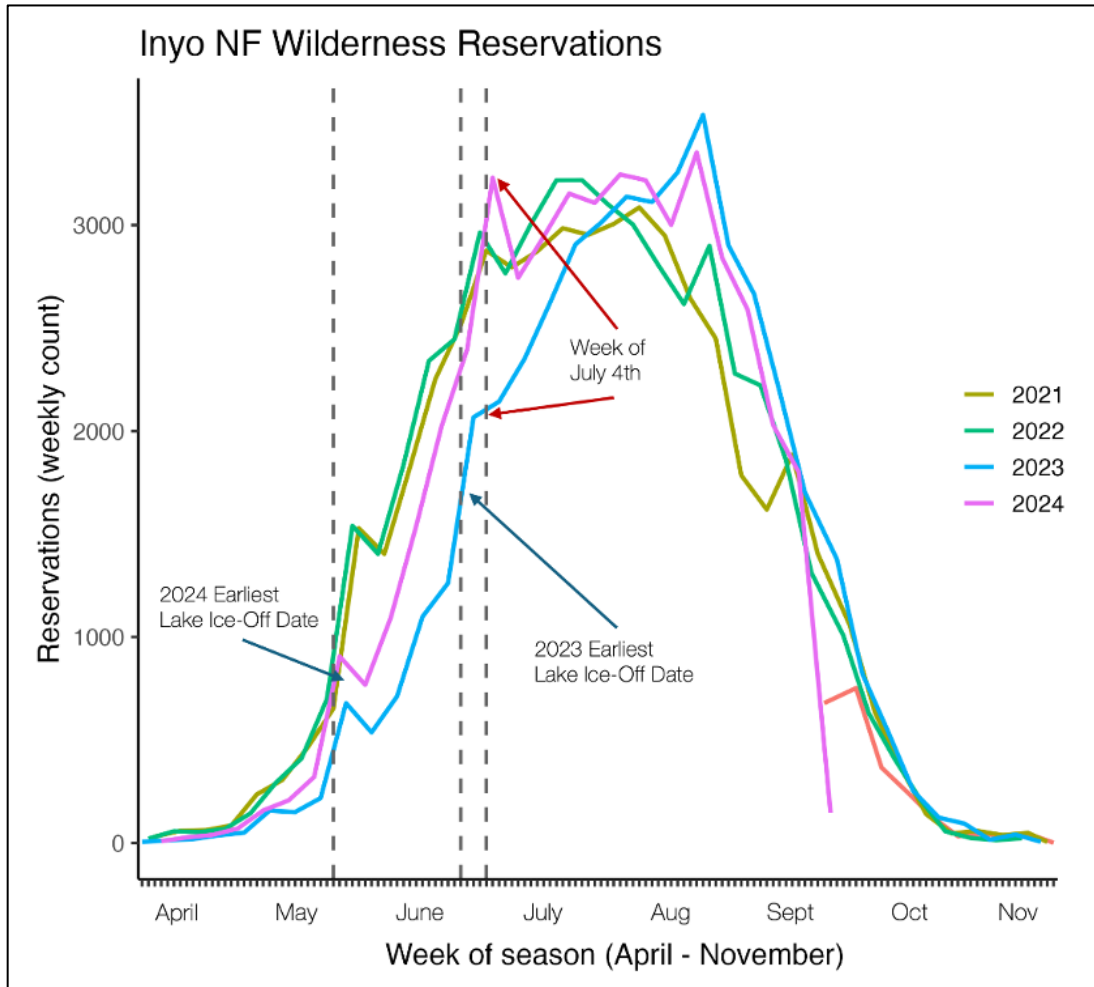


Figure S3: Weekly counts of wilderness permit reservations for Inyo National Forest from April-November across 2021-2024. Vertical dashed lines indicate the calendar weeks containing May 22, June 22, and July 4th. May and June 22 are the earliest lake ice-off dates we detected for each sampling year. July 4th usually falls on a weekend in the U.S.

S2.8 – Relative Mosquito Abundance around Fish & Fishless Lakes in the Sierra National

Forest:

From July 23, 2019, to August 16, 2019, there was a concentrated adult mosquito sampling effort at three lake pairs (six lakes total) in the Sierra National Forest, ranging in elevation from 3400 to 3650 m. Three lakes contained introduced nonnative trout and were

paired with another lake that remained fishless (see lake information in Owens et al., 2023). Mosquitoes were collected with CDC light traps (Stealth Trap, 2014 Model; John W. Hock Company, Gainesville, FL), supplemented with CO₂ released from a hanging thermos over the trap. Four traps were placed at each lake on the North, South, East, and Western shores. The traps were turned on at sunset and remained active until sunrise the next morning. Each lake was sampled every 5-7 days.

The data were non-normal, necessitating the use of non-parametric tests. A Wilcoxon Rank Sum Test with a continuity correction indicated that there was no significant difference between the number of mosquitoes trapped around lakes with fish versus lakes without fish (Figure S2.4). Additionally, a Kruskal-Wallis Rank-Sum Test found no significant difference in the number of female mosquitoes trapped among low-, middle-, and high-elevation lakes. Lastly, a Wilcoxon Rank-Sum Test comparing the number of mosquitoes collected at fish vs. fishless lakes, paired by elevation (“low”, “medium”, and “high”), found no significant difference (Figure S2.5).

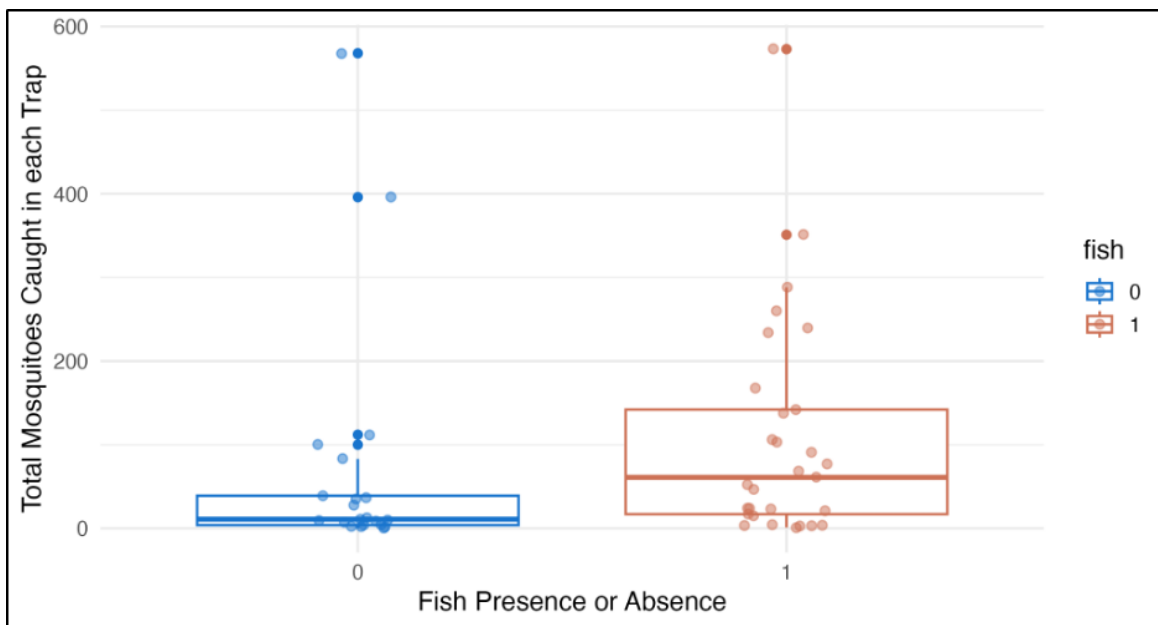


Figure S2.4: The number of mosquitoes collected per each trap set-up around three lakes without fish (blue) and three lakes with fish present (pink).

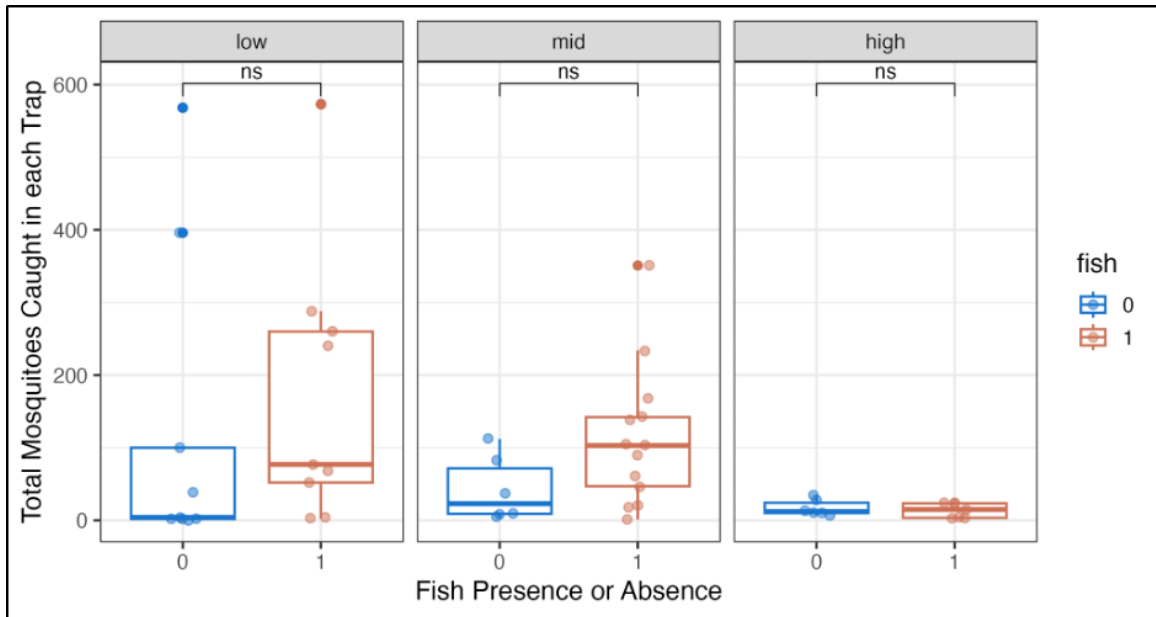


Figure S2.5: Three pairs of six lakes found at low, medium, and high elevations. Wilcoxon tests between pairs of lakes showed no significant differences in the number of mosquitoes collected from traps at fish- or fishless-lakes.