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Original Contribution

Microclimate and Human Factors in the Divergent Ecology of *Aedes aegypti* along the Arizona, U.S./Sonora, MX Border

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Abstract: This study examined the association of human and environmental factors with the presence of *Aedes aegypti*, the vector for dengue fever and yellow fever viruses, in a desert region in the southwest United States and northwest Mexico. Sixty-eight sites were longitudinally surveyed along the United States–Mexico border in Tucson, AZ, Nogales, AZ, and Nogales, Sonora during a 3-year period. *Aedes aegypti* presence or absence at each site was measured three times per year using standard oviposition traps. Maximum and minimum temperature and relative humidity were measured hourly at each site. Field inventories were conducted to measure human housing factors potentially affecting mosquito presence, such as the use of air-conditioning and evaporative coolers, outdoor vegetation cover, and access to piped water. The results showed that *Ae. aegypti* presence was highly variable across space and time. *Aedes aegypti* presence was positively associated with highly vegetated areas. Other significant variables included microclimatic differences and access to piped water. This study demonstrates the importance of microclimate and human factors in predicting *Ae. aegypti* distribution in an arid environment.

Keywords: *Aedes aegypti*, vegetation, microclimate, human ecology, U.S.–Mexico border, dengue fever

INTRODUCTION

Dengue is the most important arthropod-borne virus, and its global resurgence has made it a major public health problem in the tropics and subtropics (Gubler, 2006). Dengue fever (DF) and dengue hemorrhagic fever (DHF) are diseases that are endemic in the tropical world, caused by four closely related viruses of the genus *Flavivirus*. *Aedes aegypti* (Diptera: Culicidae) is the principal vector of the dengue viruses, which result in an estimated 100 million dengue infections annually worldwide with hundreds of thousands of people developing the more

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severe form of the disease: dengue hemorrhagic fever (Gubler, 2006).

Dengue viruses are transmitted by the bite of infected *Aedes* females, in particular *Ae. aegypti*, an urban mosquito with widespread distribution in tropical cities. It is axiomatic that the ecology of a wide-ranging species varies along environmental, including latitudinal gradients, or where conditions change abruptly, such as at ecosystem boundaries (MacArthur, 1972). The phenomenon has received little attention in vector ecology; however, it potentially may explain disease transmission, and thus represents an important dimension of the interplay of ecology, including climate variability, and epidemiology. Moreover, host range expansion has been described as a primary criterion for disease emergence (resurgence in the case of dengue). Thus, understanding vector ecology at the geographic limits of endemic dengue presents an opportunity to better understand emergence mechanisms.

Aedes aegypti is an anthropophilic species that thrives in human modified landscapes, in and around human dwellings. This habit, along with the expansion of global human transport systems facilitating its dispersal, has allowed *Ae. aegypti* to expand its range, contributing to the global resurgence of dengue and other arborviral diseases (Wilder-Smith and Gubler, 2008).

In the United States, endemic dengue's northern limit generally falls several hundred kilometers short of the vector's northern-most extension. In addition to decreasingly suitable ecological conditions for robust, year-round vector populations, demographic, sociocultural, and economic factors, as well as public health infrastructure affect the vector and dengue transmission.

Notably, even without a climatic barrier, endemic dengue declines relatively abruptly at the Mexico–United States border. Although transborder transmission occurs (Reiter et al., 2003; Ramos et al., 2008), and *Ae. aegypti* populations extend well into the United States, the United States is free of significant epidemic activity, whereas Mexico is not.

The abrupt decrease in dengue transmission along the Mexico–United States border likely reflects human-driven ecological factors that distinguish the Mexican and U.S. landscapes. The characteristically different demographic, sociocultural, and land use and land cover attributes may present less favorable conditions for dengue transmission. Moreover, these factors may interact with local climate in ways that influence *Ae. aegypti* ecology.

This study investigates, from a transnational boundary perspective, whether *Ae. aegypti* ecology differs in response to these human ecosystem conditions. As such, the article focuses on an integrative ecosystem approach, i.e., an examination of the multiple factors involved in the ability of this disease vector, typically a tropical/subtropical mosquito, to survive in a seemingly inhospitable region, the Sonoran Desert. We explicitly measure microclimatic characteristics of *Ae. aegypti* habitat, including temperature, relative humidity, and the amount of vegetation. Elevation, vegetation, household irrigation, winds, and cold air drainage are the most important processes that drive microclimatic variability over scales of (100 m to 10 km) (Daly et al., 2002, Comrie, 2000). These physical characteristics respond to and are influenced by human alterations to the landscape. For example, in the study region, arid conditions and/or lack of infrastructure may necessitate irrigation or water storage thus providing ample oviposition sites for *Ae. aegypti*. Such findings should be useful in the design of future studies aimed at understanding the mechanisms influencing transmission dynamics, combining vector ecology and disease incidence.

BACKGROUND

Aedes aegypti is found in tropical and subtropical environments throughout the world where it effectively transmits the dengue and yellow fever viruses. *Aedes aegypti* generally oviposits into artificial containers, such as flowerpots, water storage vessels, and old tires in or around human habitation (Christophers, 1960). After a curing period, the eggs may become completely desiccated but remain viable for weeks or even months (Christophers, 1960; Juliano et al., 2004), thus facilitating the accidental transport of the mosquito to new locations. *Aedes aegypti* predominates in urban settings, in areas where crowded conditions, population movement, and lack of infrastructure, such as piped water and adequate solid waste disposal, contribute to the transmission of dengue viruses (Gubler, 1997, WHO, 2004, Morrison et al., 2008). Human housing factors including screened windows and doors, irrigation, and vegetation play a key role in the presence or absence of *Ae. aegypti* in and around dwellings (Chang et al., 1997; Nagao et al., 2003; WHO, 2004; Kay and Vu, 2005).

Climate is one of the factors limiting the geographic distribution of *Ae. aegypti*. Before eradication efforts undertaken in the middle to late 20th century (PAHO, 2006), the species was found in North America only in regions with a January isotherm of more than 10°C

(Christophers, 1960). The lower temperature threshold for larval development is approximately 15°C (Rueda et al., 1990); however, different strains of *Ae. aegypti* may exhibit slightly different adaptations to temperature (Mattingly, 1957). By influencing human and vector behavior (Peterson et al., 2005; Chakravarti and Kumaria, 2002), climatic factors strongly affect not only the development and survival of the mosquito (Alto and Juliano, 2001; Nagao et al., 2003) but also the transmission dynamics of diseases, such as dengue (Colwell et al., 1998; Patz et al., 2000; Bartley et al., 2002; Ratho et al., 2005; Thammapalo et al., 2005).

Little information is available, however, about *Ae. aegypti* at the northern margins of its distribution, particularly in a desert environment. The presence of *Ae. aegypti* was noted in the Tucson, Arizona region between 1931 and 1946 (Bequaert, 1946; Murphy, 1953), but surveillance to define the extent of regional arbovirus activity in the 1950s and 1960s failed to detect *Ae. aegypti* (Tinker and Hayes, 1959; Hayes and Tinker, 1958; McDonald et al., 1973). Routine surveillance was initiated by the Arizona Department of Health Services in Tucson in 1969, but no evidence of *Ae. aegypti* presence was documented until 1994. Since then, its presence has been documented yearly in the urban and suburban communities of southern Arizona (Engelthaler et al., 1997; Hoeck et al., 2003; Merrill et al., 2005). This longitudinal study is the first of its kind to examine the impact of human and environmental factors on the presence of *Ae. aegypti* in a binational setting in Southern Arizona and Northern Sonora. We also investigated the extent to which human environment and *Ae. aegypti* population associations are contingent upon the prevailing pre-monsoon, monsoon, and post-monsoon time periods.

METHODS

Study Sites

The study region is in the Sonoran Desert, an arid region covering 193,100 square kilometers. This area is characterized by summer midday temperatures that frequently climb above 38°C and infrequent rainfall with 309.2 mm annually in Tucson (NWS, 2006) and 483.4 mm annually in *Ambos Nogales* ("Both" Nogales) with almost half the annual rainfall occurring from July to September (NCDC, 2006).

Tucson, AZ is located in the Southwestern United States (elevation 735 meters) with a population of 907,059 (U.S. Census estimate, 2005). Nogales, AZ is located 100 kilometers south of Tucson on the United States–Mexico border (elevation 1178 meters) and has a population of 40,784 (U.S. Census estimate, 2005). Nogales, Sonora is located directly across the border with an official population of 159,787 (INEGI, 2000) and an estimated population of between 350,000 and 400,000.

Sites were distributed across different urban and suburban ecologies in geographic quadrants of each study city but were not systematically selected. Each quadrant contained three to four sampling sites. The average distance between sampling sites was 10.12 km in Tucson, AZ, followed by Nogales, AZ (5.99 km) and Nogales, MX (3.79 km). Distances between study sites were selected to be larger than *Ae. aegypti's* average dispersal range (Reiter, 2007). Participating sites consisted of a shaded outdoor space on the property of private homes, businesses, or public buildings. On the U.S. side of the border, most of the houses were constructed of wood, brick, or stucco. There was a greater variety to the housing structure in Nogales, Sonora, particularly in the squatter and recently urbanized settlements. Many of the houses in the squatter settlements were semipermanent and constructed of a variety of materials, including, cardboard, plywood, and corrugated metal siding. In the more established neighborhoods, cinderblock and stucco were used as construction materials; however, despite piped water, storage was necessary because of the unpredictable water flow. University of Colorado at Denver Internal Review Board (IRB) approval (#998) was obtained, and all participants were verbally consented before setup of equipment.

Mosquito Sampling

The study used one oviposition trap at each site which consisted of 2 quart jars painted black containing hay infusion and seed germination paper as a removable substrate to determine *Ae. aegypti* presence (Reiter et al., 1991). This method is an economical and sensitive measure of adult presence (Fay and Eliason, 1966), although its accuracy in assessing overall population density in a desert environment is not well-established. Mosquito surveillance was conducted during pre-monsoon (early July), monsoon (August), and post-monsoon (September) seasons from 2002 to 2004. The oviposition traps were collected 4 days after they were placed in the field, and seed germination papers were returned to the University of Arizona where eggs were counted, hatched, and reared to the fourth larval instar for species identification (Darsie and Ward, 2005).

Climate Sampling

Table 1 summarizes the microhabitat characteristics that were related to *Ae. aegypti* presence. Data loggers (HOBO ProTemp 8, Onset Corporation, Bar Harbor, Maine) were colocated with ovipostion traps and situated approximately 2 meters above ground level in a shaded location on the north side of dwellings to ensure relative insensitivity to rapid microclimate changes near the surface. Hourly average, minimum, and maximum temperature, and average relative humidity data were collected continuously during the 3-year study period.

Due to equipment malfunction, climate data were only collected at a subset of stations in Tucson (1) and *Ambos Nogales* (10) for the monsoon and post-monsoon collection periods of 2002. Climatic data for the defunct sites were estimated by developing unique multiple linear regression prediction equations for temperature and relative humidity for each household using weather data from Tucson, AZ or Nogales, AZ. Prediction equations were developed from daily 2003–2004 data logger and weather station (NCDC, 2006) relationships and used to estimate daily 2002 monsoon and post-monsoon climate information. The prediction equations captured a large fraction of the variance and exhibited strong correspondence between predicted and observed values for all variables except minimum temperature. The estimated data tended to underpredict relatively high observed values and over-predict low observed values.

Relative humidity captured by the data loggers is not equivalent to precipitation measurements because relative humidity may also reflect moisture from nearby sources, such as sprinkler/irrigation systems. Local weather stations quantify precipitation and allow precipitation to be directly related to the proportion of positive *Ae. aegypti* traps in each location. Precipitation and temperature data are averaged across four Tucson, AZ weather stations, and the Nogales, AZ station is considered to be representative of Nogales, AZ and Nogales, Sonora (NCDC, 2006).

Human Housing Factors

Inventories were conducted to assess local factors potentially associated with mosquito presence/absence including the following items: access to services (piped water, sewage, solid waster disposal); presence or absence of window and door screens; presence or absence of air conditioners and/or evaporative coolers; and irrigation. We grouped irrigation infrastructure and usage into two categories; 1) irrigation present and utilized, or 2) irrigation present but not utilized or irrigation absent. Irrigation usage was assessed at the beginning of the study.

Vegetation

A visual assessment of vegetation coverage at each site was performed in the dry and monsoon seasons to categorize the vegetation coverage within 50 meters (estimated flight range of *Ae. aegypti* (Harrington et al., 2005)) of the oviposition traps and categorized as 0–25%, 25–50% (inclusive), or 50–100%. The pre-monsoon mosquito collection

Table 1. Predictors of *Ae. aegypti* at Study Sites in Monthly and Longitudinal Regression Analysis

Variable	Character
Vegetation area	
Survey	Ordinal classes: $<$25%, 25–50%, $>$50%
Satellite imagery (m)	Continuous
Maximum, minimum, or average Temperature (F)	Continuous
Relative humidity (%)	Continuous
Running water in household	Presence/absence
Swamp coolers	Presence/absence
Irrigation	Irrigation present and utilized/irrigation present but not utilized or irrigation absent
Location*	Nogales, MX, Nogales, AZ, and Tucson & Tubac
Year*	2002, 2003, 2004

* Predictors only included in the longitudinal data analysis

was best represented by the dry season vegetation survey, whereas the monsoon season survey corresponded to monsoon and post-monsoon collection periods. Two to three researchers assessed each site independently and established a consensus measure. Additionally, for *Ambos Nogales*, an assessment employing Ikonos 1-meter resolution satellite imagery from August 2003 (Space Imaging, Thornton, CO) was used to quantify the number of square meters covered by vegetation within a 50-meter radius of the oviposition traps. For sites in Tucson and Tubac, AZ, 2-foot resolution color aerial photographs were used for September 2002 from the Pima County Department of Transportation. Images were processed using the ArcView 3.3 (ESRI, Redlands, CA) Geographic Information System (GIS). Satellite and aerial photograph measurements were grouped into analogous categories and correlated to the field based vegetation surveys. Remotely sensed vegetation cover is significantly associated with the field-based surveys in the pre-monsoon period (Somer's D, 0.31, 95% confidence interval (CI), 0.13–0.49, $p = 0.001$). The relationship is logically stronger in the monsoon period when the satellite and aerial photograph measurements were acquired (Somer's D, 0.42; 95% CI, 0.2–0.65, $p < 0.001$).

Statistical Analyses

Aedes aegypti prevalence across each location is measured by the proportion of positive sampling sites. The interannual analysis removes seasonal environmental influences (e.g., onset of the monsoon) by converting monthly precipitation and temperature into anomalies from long-term monthly averages calculated for 1982–2004. This analysis explicitly tests if anomalously hot or wet periods are related to more sites with *Ae. aegypti*. For each location, ordinary multiple regression associates the current and the previous month's temperature and precipitation anomalies onto the proportion of positive sites (converted into anomalies from each sampling period).

Two multiple logistic regression models using either the remotely sensed or the field survey-based vegetation measurements were created for the pre-monsoon, monsoon, and post-monsoon collection periods of each year (STATA 9.2). The model that best maximized sensitivity and specificity as measured by the area under the receiver operating characteristic curve is reported. A backwards stepwise variable selection procedure with a stopping criterion of $p < 0.05$ determined the relative association of static human housing factors, microclimatic variables, and *Ae. aegypti* presence from the previous period on *Ae. aegypti* presence/absence in the current period. Microclimate variables were averaged over 7 days preceding each mosquito collection period. All study site samples were pooled in the analysis, and location indicator variables attempted to control for differences among study sites not captured by the explanatory variables. Vegetation by study location interactions was evaluated against a reduced model without the interaction term with a likelihood ratio test. Model diagnostics procedures tested whether the assumptions of logistic regression (e.g., linearity in log odds, no outliers) were fulfilled in the final models.

Generalized Estimating Equation (GEE) covariance pattern models longitudinally assessed *Ae. aegypti* presence/absence across all pre-monsoon, monsoon, or post- monsoon periods. Analysis was conducted on the monsoon and post-monsoon for 2002–2004 and 2003–2004 to determine if the estimated 2002 climate data introduced bias. The population averaged GEE accounted for repeated measurements on study sites by modeling the temporal autocorrelation structure. A logit link GEE function assessed *Ae. aegypti* presence or absence, and exchangeable, unstructured, first order autoregressive, stationary, and first order nonstationary correlation structures were compared. All potential fixed effects were included in the GEE, and best fitting correlation structure with the lowest quasi-likelihood under the independence model criterion (QIC) value was preserved (Pan, 2001, Cui, 2007). A stepwise backwards elimination variable selection with a stopping criterion of $p < 0.05$ produced the final GEE models.

To more accurately characterize binational associations between *Ae. aegypti* and environmental predictors, a stratified analysis separately examined the United States (Tucson, AZ and Nogales, AZ) and Mexico (Nogales, MX). At each time period, separate remotely sensed and field-surveyed vegetation models were created, and the best fitting model with the lowest QIC value was presented. Potentially significant interannual variability not captured by human housing, the local environment, or *Ae. aegypti* persistence was captured by indicator variables representing each sampling year. In the U.S. analysis, an additional binary location predictor variable was included in the GEE analysis to control for unmeasured differences between Tucson and Nogales, AZ. Potential vegetation by location interactions also was tested and accepted if $p < 0.05$.

RESULTS

Aedes aegypti mosquitoes were found to be present throughout Tucson and *Ambos Nogales*. The proportion of households hosting *Ae. aegypti* follows a distinct seasonal pattern. *Aedes aegypti* populations were geographically restricted in the pre-monsoon period, expanded during the monsoon, and tended to stay elevated in the post-monsoon period (Table 2).

Climate

Tucson, AZ was the only location where interannual precipitation variability controlled the proportion of positive containers. Each additional centimeter of precipitation above normal translated into 0.06% more positive containers.

HUMAN HOUSING FACTORS

Infrastructural amenities (piped water, sanitation, sewage) existed at all locations on the U.S. side of the border. On the Mexican side of the border, in Nogales, Sonora, conditions were more variable with some sectors without paved roads, water or waste disposal and little to no drainage. Thirty-nine percent of households had no piped water; water was stored outside the dwelling in 55-gallon drums, which typically had no lid or an ill-fitting cover, or inside the dwelling in smaller containers. Even in the more established neighborhoods with piped water, storage was necessary because of the unpredictable water flow.

Additionally, in the entire study region, 21% (14/68) of the households had no screens on windows or doors, and 25% (17/68) had no cooling mechanism while 47% (32/68) had swamp (evaporative) coolers.

Vegetation coverage varied both spatially and temporally. Locale specific remotely sensed and categorical vegetation coverage are described as follows:

All Nogales, MX households were sparsely vegetated according to both land cover metrics. Remotely sensed mean Nogales, MX vegetation cover (1,328 m; 95% CI, 817–1,839 m) is below Tucson, AZ levels (1,963 m; 95% CI, 1,575–2,351) and significantly lower than bordering Nogales, AZ (2,847 m; 95% CI, 2,248–3,445 m). In Nogales, MX households, 55% of the houses (12/22) had < 25% vegetation coverage, 27% (6/22) had 25–50%, and 18% (4/22) had > 50%. In Nogales, AZ 35% (6/17) had < 25%, 53% (9/17) had 25–50%, and 12% (2/17) had > 50% vegetation. In Tucson, AZ 36% (9/25) had < 25%, 53% had 25–50% (7/25), and 36% (9/25) had > 50% vegetation coverage within a 50-m radius of the oviposition trap (Fig. 1).

Monthly Multiple Logistic Regression

The monthly multiple regression results showed that the strength of human housing and environmental factors' influence on the distribution of *Ae. aegypti* presence/absence varied from year to year (Table 3). *Aedes aegypti* presence in the preceding pre-monsoon period strongly influenced *Ae. aegypti* distribution in the 2004 monsoon period. Greater vegetation cover favored *Ae. aegypti* pres-

Table 2. Oviposition Trap Summary Statistics. Ratio of Traps Containing *Aedes aegypti* Eggs to the Total Number of Traps; Average Number of Eggs Per Oviposition Trap and Range of Counted Eggs for Each Analysis Period and Study City for 2002–2004

	Tucson, AZ	Nogales, AZ	Nogales, SO
2002			
Pre-monsoon	3/19; 5.7 (0–53)	3/18; 14.6 (0–150)	2/18; 6.6 (0–63)
Monsoon	8/19; 42.1 (0–204)	9/18; 37.7 (0–248)	8/18; 89.6 (0–525)
Post-monsoon	9/19; 14.5 (0–131)	9/18; 16.9 (0–67)	9/18; 33.8 (0–249)
2003			
Pre-monsoon	1/20; 4.3 (0–85)	2/18; 6.1 (0–78)	2/20; 3.9 (0–61)
Monsoon	13/21; 26.3 (0–85)	9/18; 17.7 (0–86)	11/22; 20.0 (0–137)
Post-monsoon	10/25; 22.4 (0–131)	7/18; 11.6 (0–100)	12/22; 52.1 (0–183)
2004			
Pre-monsoon	8/26; 20.5 (0–173)	4/16; 8.7 (0–76)	5/22; 8.1 (0–55)
Monsoon	10/26; 24.7 (0–205)	4/16; 4.8 (0–45)	13/22; 29.4 (0–133)
Post-monsoon	9/22; 2.9 (0–59)	2/16; 1.7 (0–23)	9/22; 8.6 (0–53)

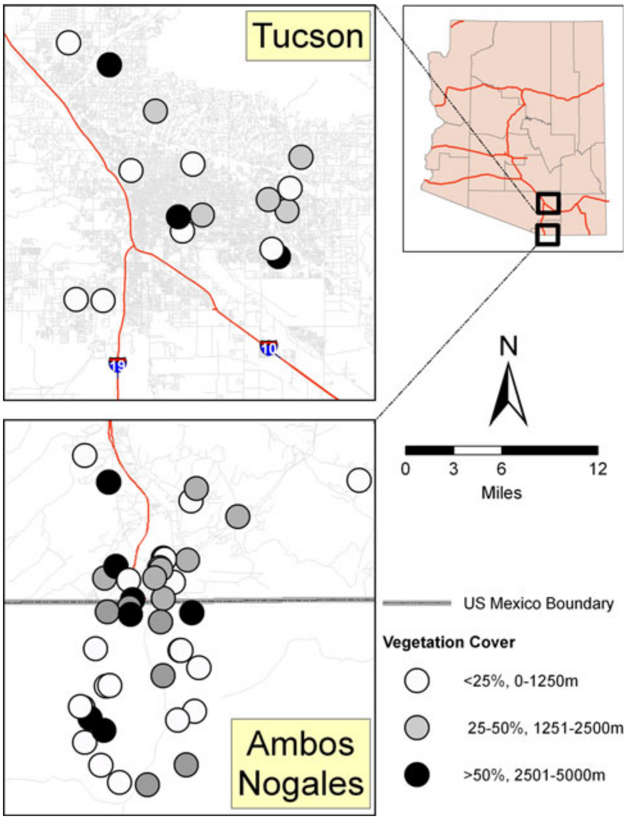

Figure 1. Map illustrates the amount of vegetation at each study site. The field based survey categorized vegetation into <25, 25–50, and >50% of the 50 m area around each study site. Vegetation also was separately quantified from remote sensing (aerial photographs, satellite) images. For illustration purposes, the remote sensing measurements were grouped into three analogous categories. The field based survey vegetation information is shown for the United States locations and the remote sensing based measurements for Mexico.

ence before, during and after the monsoon, but the strength of this effect exhibited interannual variability. Pre- and post-monsoon, there were significant differences in the proportion of study sites positive for *Ae. aegypti* among the three study cities. In 2003, Tucson, AZ sites with low vegetation, low temperatures, and/or air conditioners provided poor *Ae. aegypti* habitat compared to Nogales, MX. *Ae. aegypti's* geographic distribution is limited more by moisture in Tucson, AZ than in Nogales, MX. One possible explanation for this binational difference is that household behaviors more strongly influence *Ae. aegypti* population dynamics in Nogales, MX. Nogales, AZ sites, similarly, had significantly fewer *Ae. aegypti* in the 2003 post-monsoon period compared with Nogales, MX. Household amenities also provided favorable habitats for *Ae. aegypti*. Swamp coolers and dwellings without piped water were positively associated with *Ae. aegypti* in the post-monsoon period.

Longitudinal Data Analysis

The U.S. monsoon and post-monsoon analysis spanning the period of 2002–2004 produced very similar results to 2003–2004 analysis; as a result, the models from the longer analysis period are presented. Temperature and relative humidity were not significant predictors of Mexican monsoon or post-monsoon *Ae. aegypti* oviposition, and the 2002–2004 results are reported (Table 4). Controlling for potential confounders related to inter-annual variability, study location, and human housing, vegetation, and microclimate strongly influenced the distribution of U.S. *Ae. aegypti*. Moisture stress and low relative humidity before the monsoon limited the prevalence of the mosquito in the U.S. study sites dominated by vegetation (odds ratio (OR), 22.41, 95% CI, 5.46–92.00) and/or with higher relative humidity values (OR, 1.32, 95% CI, 1.08–1.62) were more likely to be positive for *Ae. aegypti*. Relative humidity was, interestingly, not associated with either the categorical or continuous vegetation metric (Kendall's tau-b; 0.06, Pearson's correlation; 0.02), suggesting an additional moisture effect beyond vegetation that favored *Ae. aegypti* presence. In other words, highly vegetated sites with high relative humidity were more likely to be positive than highly vegetated sites with low–moderate relative humidity. Elevated minimum temperature may partially reflect vegetation's microclimatic influence (Kendall's tau-b; −0.17, Pearson's correlation; −0.29). Figure 2 highlights the strong correspondence between modeled probabilities of *Ae. aegypti* presence to observed North America pre-monsoon presence/absence patterns. Microclimate variables flexibly model *Ae. aegypti* presence in years with both constrained and widespread geographic distributions. Highly vegetated households consistently hosted *Ae. aegypti* and appeared to be an important refuge during the abnormally dry 2003 pre-monsoon period.

Aedes aegypti presence during the pre-monsoon period logically was strongly predictive of U.S. *Ae. aegypti* during the monsoon (OR, 4.69, 95% CI, 1.53–14.39). Housing and environmental features in the United States only indirectly influenced the monsoon distribution of *Ae. aegypti* by fostering *Ae. aegypti* persistence from the preceding pre-monsoon period. This is reflected in the lower correspondence between modeled and observed *Ae. aegypti* distributions (Fig. 3). Modeled 2002 USA and 2003 Tucson

Table 3. Statistically Significant Monthly Logistic Regression Results for July, August, and September 2002–2004

Analysis period	Odds ratio	Standard deviation	*p* value	95% CI	ROC	N
August 2002 categorical vegetation						
July *Ae. aegypti* presence	11.53	12.83	0.028	1.30–102.02	0.63	53
September 2002 categorical vegetation						
25–50% Area covered by vegetation	9.03	7.76	0.010	1.68–48.67	0.78	53
Tucson and Tubac, Arizona	0.11	0.11	0.029	0.02–0.79		
Swamp cooler	7.32	6.29	0.021	1.36–39.47		
September minimum temperature (°C)	2.10	0.56	0.006	1.24–3.56		
September 2003 continuous vegetation						
Vegetation area (1,000 m)	1.99	0.54	0.011	1.17–3.41	0.74	54
Nogales, Arizona	0.20	0.16	0.045	0.04–0.96		
July 2004 Categorical vegetation						
>50% area covered by vegetation	9.80	7.59	0.003	2.15–44.75	0.67	62
August 2004 continuous vegetation						
Tucson and Tubac, Arizona	0.07	0.08	0.024	0.01–0.71	0.77	56
Relative humidity (%)	0.86	0.05	0.010	0.77–0.97		
September 2004 categorical vegetation[a]						
Running water	0.12	0.11	0.021	0.02–0.73	0.62	59

The percent of the area covered by vegetation in a 50 m radius around each study site (categorical) was derived from field surveys. This metric is divided into three categories: <25% area (which is the reference odds ratio category); 25–50%; and >50% of the area. The Receiver-Operating-Characteristic (ROC) measures the improvement in mosquito prediction above predictive accuracy expected by random chance (0.5). Area vegetation (continuous) was quantified from high resolution remote sensing imagery

[a] Human environment risk factor presence compared to risk factor absence

Table 4. Longitudinal Data Analysis for July (Pre-Monsoon), August (Monsoon), September (Post-Monsoon) for 2002–2004

Analysis period	Odds ratio	Standard error	*p* Value	95% CI	QIC	Correlation structure	*N*
US July categorical vegetation					81.95	Exchangeable	113
2003	0.01	0.02	0.001	0.00–0.15			
2004	0.05	0.07	0.044	0.00–0.92			
>50% area covered by vegetation	22.41	16.15	<0.001	5.46–91.99			
Minimum temperature (°C)	2.60	0.56	<0.001	1.70–3.97			
Relative humidity (%)	1.32	0.14	0.007	1.08–1.62			
Tucson, AZ	0.16	0.14	0.037	0.03–0.89			
U.S. August categorical and continuous vegetation					238.20	Unstructured	113
2004	0.32	0.16	0.026	0.12–0.87			
July *Ae. aegypti* presence/absence	4.69	2.68	0.007	1.53–14.39			
U.S. September continuous vegetation							
2004	0.20	0.10	0.001	0.08–0.52	241.21	Unstructured	122
Mexico September continuous vegetation					276.65	Exchangeable	62
August *Ae. aegypti* presence/absence	5.57	3.92	0.015	1.40–22.17			
Vegetation area (1,000 m)	2.04	0.66	0.027	1.09–3.84			

The 2003 and 2004 odds ratios are relative to the 2002 reference year while Nogales, MX is the reference group for the Nogales, AZ and Tucson and Tubac, AZ odds ratios. The percentage of the 50 m area around each study site covered by vegetation is divided into three categories: <25% of the area as the reference odds ratio category; 25–50%; and >50% of the area. The quasi-likelihood under the independence model criterion (QIC) measures how well the model fits the data. Lower QIC values denote better fitting models. The best fitting correlation structure for repeated measurements at study sites is listed in the correlation structure column.

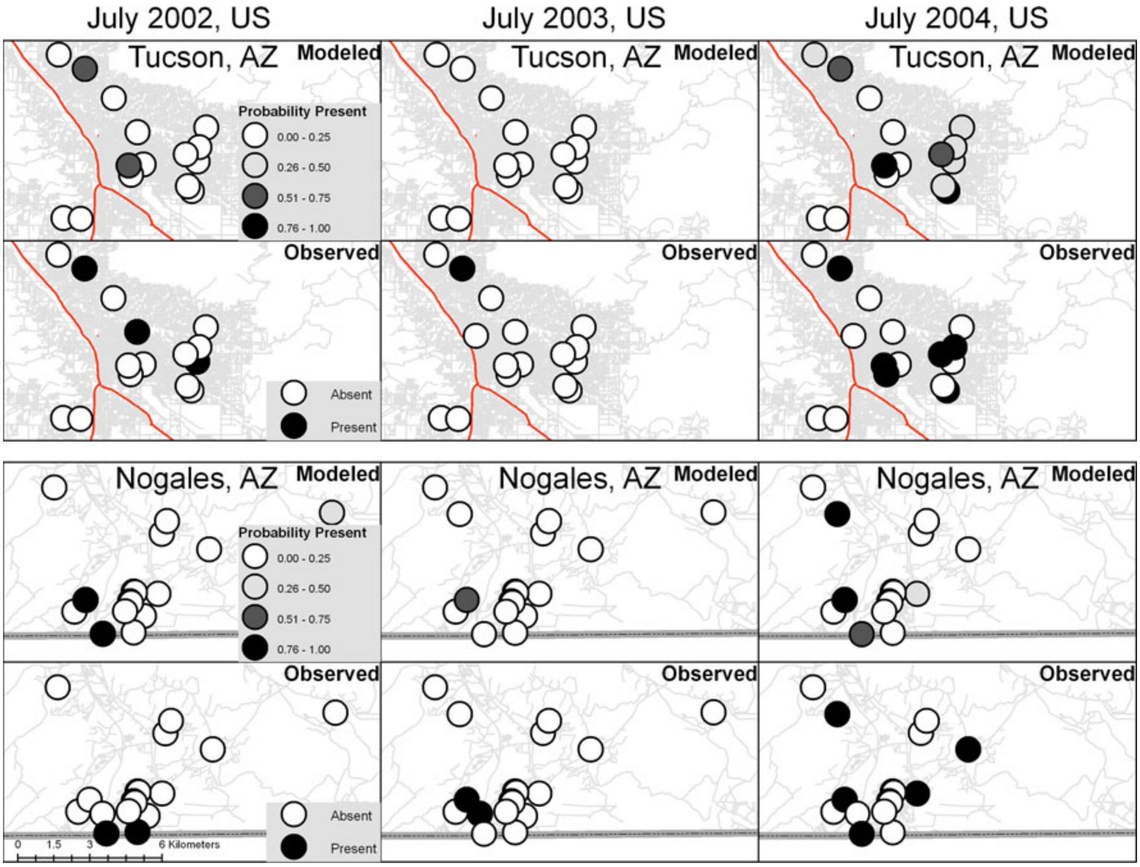

Figure 2. Compares pre-monsoon modeled probabilities of *Ae. aegypti* presence versus observed *Ae. aegypti* presence/absence in the United States (Tubac, AZ not shown). The amount of vegetation cover, minimum temperature, relative humidity, study year, and study location influence *Ae. aegypti*'s geographic distribution (Table 3). Each column contains the results of each study year (2002–2004). The *upper box* in each column compares Tucson, AZ and the *lower box* compares Nogales, AZ modeled versus observed probabilities. There is a strong correspondence between predicted and observed *Ae. aegypti* presence/absence, particularly in 2003 and 2004.

probabilities systematically under predict *Ae. aegypti* observations. Most of Nogales, AZ is considered likely habitat in 2003, which overestimates *Ae. aegypti's* geographic extent. Modeled and observed monsoon *Ae. aegypti* patterns exhibit generally good agreement in 2004.

Significant interannual variability continued to characterize the U.S. monsoon and post-monsoon periods as the extremely dry 2004 monsoon depressed *Ae. aegypti* populations relative to 2002. In Mexico, the post-monsoon period was the only time where study risk factors corresponded with *Ae. aegypti* distribution. Greater vegetation cover (per 1000 m) was still conducive to *Ae. aegypti* even though Mexican households generally had less vegetation compared with the U.S. (OR, 2.04, 95% CI, 1.09–3.84). Positive *Ae. aegypti* Mexican study sites in the monsoon period were conducive to post-monsoon *Ae. aegypti* presence. The observed September 2002 and 2004 distributions are intriguingly similar with *Ae. aegypti* inhabiting sites in the south and near the border (Fig. 4). In September 2002, the analysis assigns higher probabilities of mosquito occurrence at almost all the observed *Ae. aegypti* sites. *Aedes aegypti's* widespread distribution in the preceding monsoon period leads to overestimating its extent in September 2004. The September 2003 pattern is entirely different and the *Ae. aegypti* presence is understated in the northern and southern portions of Nogales, Sonora.

DISCUSSION

We highlight the season specific influence of vegetation on the geographic distribution of *Ae. aegypti* along the northern edges of its global distribution. Vegetation provides well recognized dietary and microclimatic conditions

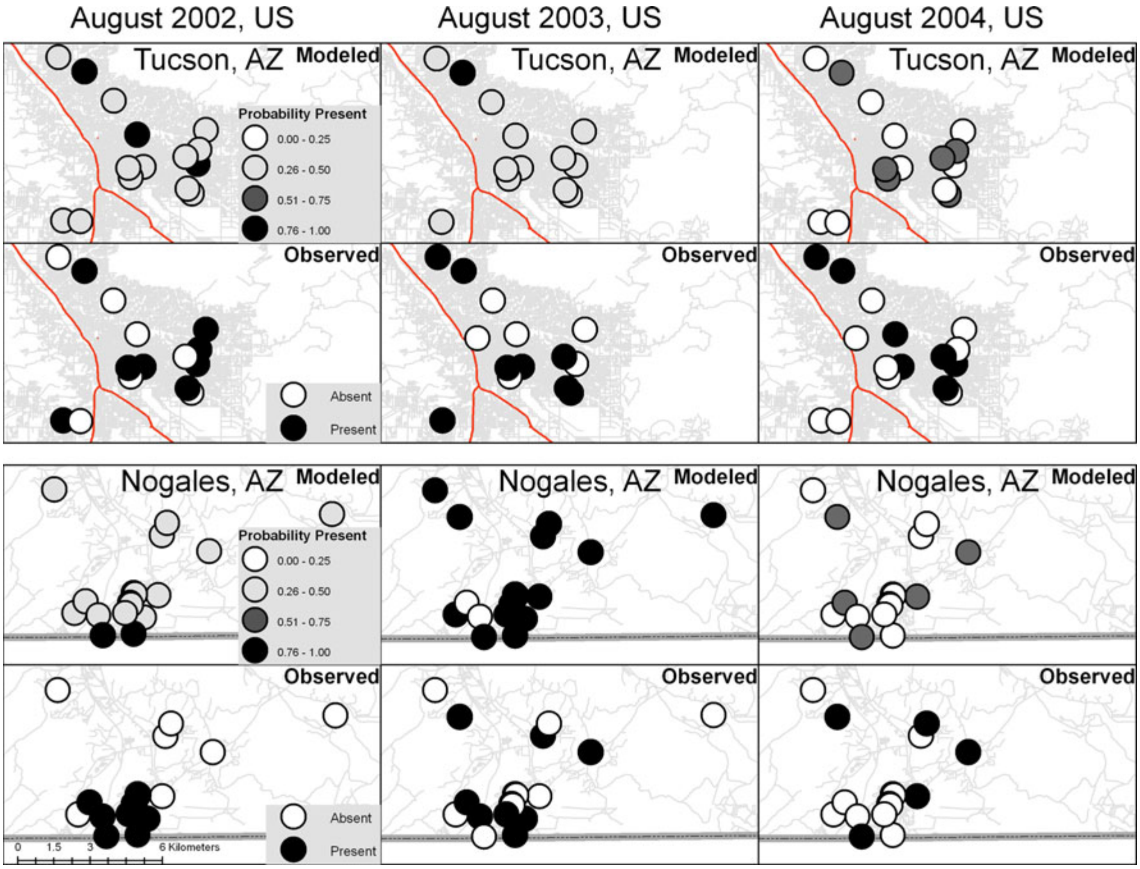

Figure 3. Compares monsoon modeled probabilities of *Ae. aegypti* presence versus observed *Ae. aegypti* presence/absence in the United States (Tubac, AZ not shown). Monsoon *Ae. aegypti* presence is related to *Ae. aegypti* presence/absence in the previous (pre-monsoon) collection period and the study year (Table 3). Each column contains the results of each study year (2002–2004). The *upper box* in each column compares Tucson, AZ and the *lower box* compares Nogales, AZ modeled versus observed probabilities. *Aedes aegypti* presence tends to be underestimated in both cities in 2002 and in Tucson in 2003, but over-estimated in Nogales in 2003.

favorable for *Ae. aegypti*, but the time-contingent nature of these relationships has only recently been quantified. (e.g. Peterson et al., 2005) The binational study design expands upon previous studies to explicitly examine how vegetation and *Ae. aegypti* population relationships are modified by different human socioeconomic and behavioral contexts. For example, irrigated vegetation's mitigation of water stress is expected to be most pronounced during the arid pre-monsoon period as reflected in U.S. vegetation, microclimate and *Ae. aegypti* relationships. No human-environment habitat characteristics are, however, predictive of Mexican pre-monsoon *Ae. aegypti* populations. Although beyond the scope of this study, uncaptured water storage practices, human behaviors, and cultural artifacts may instead account for pre-monsoon adult *Ae. aegypti* oviposition patterns in Mexico. The positive U.S. vegetation and *Ae. aegypti* relationship becomes insignificant during the monsoon and post-monsoon periods. In contrast, vegetation exerts the strongest influence on Nogales, Sonora's *Ae. aegypti* populations in the post-monsoon period. However, this study could not identify a clear mechanism to account for important post-monsoon vegetation relationships in Nogales, Sonora, but not the United States.

Multiple hypotheses attempt to explain the positive vegetation and *Ae. aegypti* oviposition relationship. Young adult female *Ae. aegypti* may preferentially feed on carbohydrates from flowering vegetation before host seeking, or vegetation litter and/or detritus may replenish larval food sources (Magnarelli, 1978, Martinez-Ibarra et al., 1997, Carpenter, 1982, Barrera et al., 2006). The pre-monsoon collection period was after the spring and before the summer flowering seasons suggesting that vegetation provided minimal food benefits to adult *Ae. aegypti*. Shade and evapotranspiration from vegetation provide a favorable mosquito microclimate by decreasing adult mosquito water

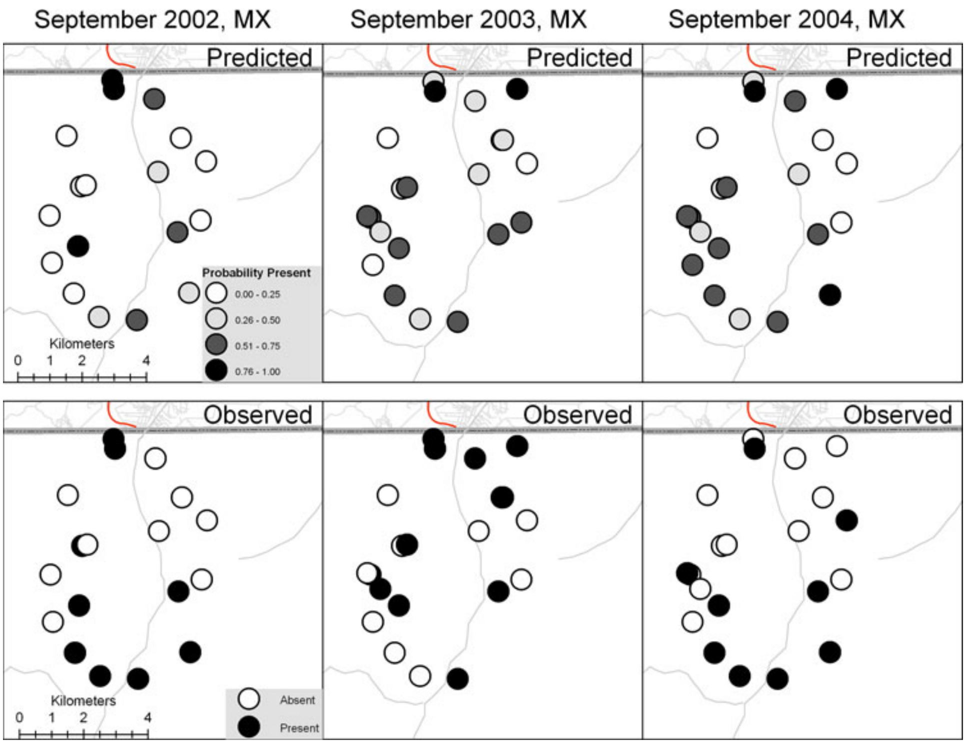

Figure 4. Compares post-monsoon modeled probabilities of *Ae. aegypti* presence versus observed *Ae. aegypti* presence/absence in Nogales, Mexico. *Aedes aegypti's* geographic distribution is related to the amount of vegetation cover and *Ae. aegypti* presence/absence in the previous (monsoon) period (Table 3). Each column contains the results of each study year (2002–2004). The *upper panel* contains the modeled probabilities and the *lower panel* plots the actual observed. There is a stronger correspondence between estimated probabilities of *Ae. aegypti* presence in 2004 than in 2002. The 2003 observed *Ae. aegypti* distribution is more diffuse and the statistical analysis generally overestimates suitable habitats.

stress and desiccation of larval habitats (Oke, 1996, Tun-Lin et al., 2000). This study suggests that the alteration of microclimate by vegetation exerts the strongest influence on temperate *Ae. aegypti* presence/absence although the contribution of vegetation to larval food sources may still be important. (Vezzani et al., 2005, Barrera et al., 2006). The positive U.S. pre-monsoon relationship between *Ae. aegypti* presence and relative humidity further underscores the importance of moisture for *Ae. aegypti* populations in an arid environment. Pre-monsoon relative humidity in the United States was, furthermore, not correlated with vegetation pointing to an additional precipitation or lawn irrigation effect on *Ae. aegypti* presence/absence. The relative importance of vegetation compared to ambient moisture conditions was quantified by the study's unique combination of microclimate data loggers and a vegetation survey.

Tucson, AZ was the only location where precipitation exhibited a direct association with the proportion of sites hosting *Ae. aegypti*. This is probably a reflection of 1) the dominant larval breeding sites in Tucson may be located outside of the household and refilled by precipitation, and 2) interannual precipitation variability was more pronounced in Tucson compared with Ambos Nogales during the study period. Many studies point to strong seasonal temperature and moisture controls on the availability of suitable larval habitats, larval development, and the survival of *Ae. aegypti* eggs (Sota and Mogi, 1992, Rueda et al., 1990). A growing literature of longitudinal studies suggest that *Ae. aegypti* exhibits notable interannual population fluctuations linked to climatic variability (Moore et al., 1978, Aiken et al., 1980, Chadee, 1990, Scott et al., 2000). Climate factors have been used in previous models as predictors of regional *Ae. aegypti* presence and density (Focks et al., 1995; Jetten and Focks, 1997). Drought-like conditions may indirectly influence *Ae. aegypti* populations by increasing the number of household water storage containers and larval breeding sites (e.g. Koopman et al., 1991, Herrera-Basto et al., 1992) In 2004 when summer precipitation was 14.8 cm below normal in *Ambos Nogales* and 7.6 cm below normal in Tucson, AZ, lack of piped water was positively associated with mosquito populations in Nogales, Sonora.

This study is limited by the sole use of ovitrapping, information on household breeding sites, and the study site selection. Ovitrapping monitors seasonal *Ae. aegypti* egg laying behavior and is a sensitive measure of *Ae. aegypti* presence over large geographic areas. This study could be strengthened by complimentary information of other mosquito life stages and behaviors. This information would (1) identify lifestages most sensitive to environmental conditions, and (2) provide a more direct measurement of dengue risk (Sanchez et al., 2006). A pupal survey could determine containers that provide the greatest public health risk should dengue be introduced into the area. Ovitrapping, nonetheless, provides consistent, multiple year evidence of *Ae. aegpyti* presence in the region. Study sites were geographically distributed across the city, but a more systematic selection procedure would have increased the generalizability of the results. Enumerating the species of vegetation and associated detritus surrounding study household may further improve the description of suitable *Ae. aegypti* microhabitats. For example, mango, citrus fruit, and Spanish lime tree detritus were linked to fewer *Ae. aegypti* pupae in Puerto Rico (Barrera et al., 2006).

CONCLUSIONS

Our study suggests the importance of environmental factors such as rainfall at a regional level and human ecologic factors such as vegetation at a local level in predicting *Ae aegypti* presence at a household scale. Rainfall is an important component in increased vegetation and in amplified numbers of rain-filled containers, which provide oviposition sites for *Ae. aegypti*.

Vector presence is, however, only one factor that needs to be examined in predicting dengue infection risk, as the transition to a "sealed" indoor lifestyle may be protective in the United States (Reiter et al., 2003). This indoor lifestyle does not completely negate the risk of dengue fever as many activities continue to occur outdoors in the early morning and early evening hours due to choice, necessity, or housing style, increasing the risk of vector/human contact and potential for dengue transmission.

This study has focused on the vector because dengue has not yet "crossed the border" from Sonora into Arizona. Studies from both Laredo, TX in 1999 (Reiter et al., 2003) and Brownsville, TX in 2005 (Ramos et al., 2008) indicate clear potential for importation and local transmission of cases along the border. The possibility of dengue fever transmission in the *Ambos Nogales*/Tucson border region exists given the general similarities to Texas in human movement across the border (Migration News, 2005) and the presence of *Ae. aegypti* throughout the study area.

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