Quantifying the Drivers of Larval Density Patterns in Two Tropical Mosquito Species to Maximize Control Efficiency

SIOBHAN C. DE LITTLE,[1,2] DAVID M.J.S. BOWMAN,[3] PETER I. WHELAN,[4] BARRY W. BROOK,[1] AND COREY J. A. BRADSHAW[1,5]

ABSTRACT Understanding the contributions of environmental variation and density feedbacks to changes in vector populations is essential for designing effective vector control. We analyzed monitoring datasets describing larval densities over 7 yr of the two dominant mosquito species, *Aedes vigilax* (Skuse) and *Culex annulirostris* (Skuse), of the greater Darwin area (Northern Territory, Australia). Using generalized linear and linear mixed-effects models, we tested hypotheses regarding the environmental determinants of spatio-temporal patterns in relative larval abundance in both species. The most important spatial drivers of *Ae. vigilax* and *Cx. annulirostris* larval densities were elevation and water presence. *Ae. vigilax* density correlates negatively with elevation, whereas there was a positive relationship between *Cx. annulirostris* density and elevation. These results show how larval habitats used by the saltwater-influenced breeder *Ae. vigilax* and the obligate freshwater breeder *Cx. annulirostris* are separated in a tidally influenced swamp. The models examining temporal drivers of larval density also identified this discrimination between freshwater and saltwater habitats. *Ae. vigilax* larval densities were positively related to maximum tide height and high tide frequency, whereas *Cx. annulirostris* larval densities were positively related to elevation and rainfall. Adult abundance in the previous month was the most important temporal driver of larval densities in both species, providing a clear dynamical link between the two main life phases in mosquito development. This study shows the importance of considering both spatial and temporal drivers, and intrinsic population dynamics, when planning vector control strategies to reduce larval density, adult population density, and disease transmission effectively.

KEY WORDS *Aedes vigilax, Culex annulirostris*, density dependence, larval habitats, vector control

Mosquito-borne diseases are a major problem for public health worldwide (WHO 1995, Russell and Dwyer 2000). In the absence of vaccines for many zoonotic diseases, we are reliant on vector control to reduce pathogen prevalence and disease expression (Walker and Lynch 2007). Current control programs targeting adult mosquitoes are compromised by the development of resistance to control agents such as pyrethroid-based insecticides (Bass et al. 2007) and the difficulty in successfully targeting highly mobile adult vectors (Killeen et al. 2002). However, larval mosquitoes are exclusively aquatic and thus are restricted to water bodies that are more amenable to environmental management such as the physical reduction of suitable habitat (Whelan 1989; Brogan et al. 2002; Dale

et al. 2002; Kurucz et al. 2002, 2003; Leisnham et al. 2005; Walker and Lynch 2007) or the application of chemical or biological agents to breeding sites (Whelan 1998; Russell et al. 2003; Howard et al. 2007; Whelan 2007a, b). Because of the comparatively small spatial dispersal capacity of mosquito larvae, larval control is the principal and most effective tool for mosquito-borne disease management (Killeen et al. 2002).

Climate change predictions point toward an increasingly warmer and more variable climate, which is likely to increase the range and abundance of many insect vectors (Hay et al. 2002, Chase and Knight 2003). Understanding the relationships between larval vector habitat distribution and structure, environmental conditions that influence vector abundance and vector population dynamics, is therefore important for both the control of the present extent and impact of vector-borne disease and also for shaping control strategies for the future. Mosquito population density and individual survival probability are affected by a suite of environmental conditions such as broad-scale variability in precipitation, tidal patterns, surface wetness, temperature and humidity, topography, and landscape type and use (Dale et al. 1986; Russell 1986,

[1] Environment Institute, School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia.

[2] Corresponding author, e-mail: siobhan.delittle@adelaide.edu.au.

[3] Department of Plant Science, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia.

[4] Medical Entomology Branch, Communicable Diseases Program, Northern Territory Government Department of Health and Families, PO Box 40596, Casuarina, Northern Territory 0811, Australia.

[5] South Australian Research and Development Institute, PO Box 120, Henley Beach, South Australia 5022, Australia.

1987; Dhileepan 1996; de Garin et al. 2000; Shaman et al. 2002; Chase and Knight 2003; Leisnham et al. 2005; Pope et al. 2005; Obsomer et al. 2007). Mosquito populations also exhibit strong intrinsic (density-dependent) regulation (Hawley 1985, Agnew et al. 2002, Reiskind et al. 2004, Yang et al. 2008a), and failing to account for these intrinsic dynamics can lead to overestimation of the effectiveness of control methods (Hawley 1985, Yang et al. 2008b). As such, control effectiveness and efficiency is dictated by knowing how, where and when these intrinsic and extrinsic variables influence larval densities.

To achieve effective and ecologically informed control regimens, the general geographic distribution of many disease vectors is extensively monitored and mapped (Whelan 1989, Rejmankova et al. 1991, Turner and Streever 1997, Jeffery et al. 2002, Leisnham et al. 2005, Pope et al. 2005, Sattler et al. 2005, Grieco et al. 2006, Lindsay et al. 2007, Obsomer et al. 2007, Zeilhofer et al. 2007), and habitat suitability models outlining species ecological requirements are commonly constructed to direct control strategies (Peterson et al. 2005). Unfortunately, such models are often based on either broad temporal averages or snapshots of mosquito occurrence and environmental conditions at particular times (Russell 1986, Rejmankova et al. 1991, Chase and Knight 2003, Leisnham et al. 2005, Pope et al. 2005, Sattler et al. 2005, Vezzani et al. 2005, Barrera et al. 2006, Grieco et al. 2006, Lindsay et al. 2007, Zeilhofer et al. 2007) and therefore cannot accurately represent the long-term availability and quality of ephemeral larval habitats. Studies with longer time series of data permit examination of the long-term spatio-temporal trends in mosquito dynamics and habitats, yet these studies often rely on making inferences between adult occurrence and the suspected drivers of larval abundance (Dhileepan 1996; Shaman et al. 2002; Hachiya et al. 2007; Whelan 2007a; Yang et al. 2008b, 2009). Inferences based on adult dynamics and habitat relationships are largely decoupled from processes driving larval abundance patterns and so alone are generally unreliable tools for maximizing the efficiency of larval control. The relative importance of both the intrinsic (density-dependent) and extrinsic (environmental) conditions driving mosquito population dynamics are rarely, if ever, considered concurrently in studies that seek to determine the optimal timing and spatial configuration of larval control measures.

Mosquito population control constitutes one of the larger recurrent land management programs in the Northern Territory of Australia. The control program, consisting of both larval habitat engineering (Whelan 1989, Brogan et al. 2002) and regular application of larvicides (Whelan 1989, Whelan 2007a, Yang et al. 2008b), focuses on the two most commonly occurring mosquito species in the Northern Territory: the salt-marsh mosquito *Aedes vigilax* (Skuse) and the fresh-water-breeding common banded mosquito *Culex annulirostris* (Skuse). *Cx. annulirostris* is an important vector of Ross River virus and Barmah Forest virus in both rural and urban situations (Merianos et al. 1992,

Whelan et al. 1997), whereas *Ae. vigilax* is a major vector of both viruses in coastal and subcoastal areas (Whelan et al. 1997, 2003; Russell and Dwyer 2000; Jacups et al. 2008). Both Ross River virus and Barmah Forest virus result in substantial human morbidity and economic loss, and therefore, the effective control of their primary vectors is a high priority for Australian public health management (Jacups et al. 2008).

The Leanyer/Holmes Jungle swamp complex that lies to the northeast of Darwin is the major larval habitat for both *Ae. vigilax* and *Cx. annulirostris.* The populations of these two species fluctuate seasonally (Russell and Whelan 1986), in accordance with their breeding ecology: *Ae. vigilax* are predominately salt-water breeders (Lee et al. 1984), and *Cx. annulirostris* are freshwater breeders (Russell and Whelan 1986, Mottram and Kettle 1997). The cycles of high tide flooding on the coastal wetlands in the dry season suit *Ae. vigilax,* where the retreat of a high tide leaves moist mud for oviposition, after which the eggs mature and become drought resistant until the next tidal or rain inundation stimulates the eggs to hatch (Sinclair 1976). Higher tides during the dry season that flood greater areas containing previously laid eggs result in higher numbers and larval densities (eggs can survive for months or possibly years (Lindsay et al. 1993)). The extreme seasonality of the north Australian monsoon results in high rainfall during a relatively short interval of the year (November–April), and wetlands are rapidly inundated after the onset of appreciable rain, remaining underwater for the remainder of the wet season. Rapid inundation of the tidally influenced swamps from heavy rains and freshwater stream run-off reduces the amount of exposed mud available as a breeding habitat for *Ae. vigilax,* and along with the growth of grasses and reeds that provide protection from predators, these coastal wetlands are effectively transformed into suitable habitat for the freshwater breeding *Cx. annulirostris.* Larval control of both species is currently applied through ground and helicopter application of microbial and chemical insecticides: *Bacillus thuringiensis* variety *israelensis,* (microbial larvacide), temephos (organophosphate insecticide), and methoprene (artificial insect growth regulator [IGR]). The timing of control operations is based on larval surveys that are conducted opportunistically according to tide and rainfall breeding initiation parameters, larval habitat ecology, and adult population monitoring from CO_2-baited mosquito traps (see Yang et al. 2008a, b, for data collection details). This is a highly complex system to monitor and manage, and although current control efforts are based on a sound understanding of the ecology of the vectors and their interaction with the environment, the efficacy of the current management regime at suppressing larval densities and adult emergence has not yet been quantified.

Yang et al. (2008b) previously showed that both intrinsic and extrinsic factors mediate the dynamics of adult mosquito populations in this region; however, there is a disconnect between environmental variables (e.g., tidal regimes and rainfall) included in their models predicting adult abundance and the effect of
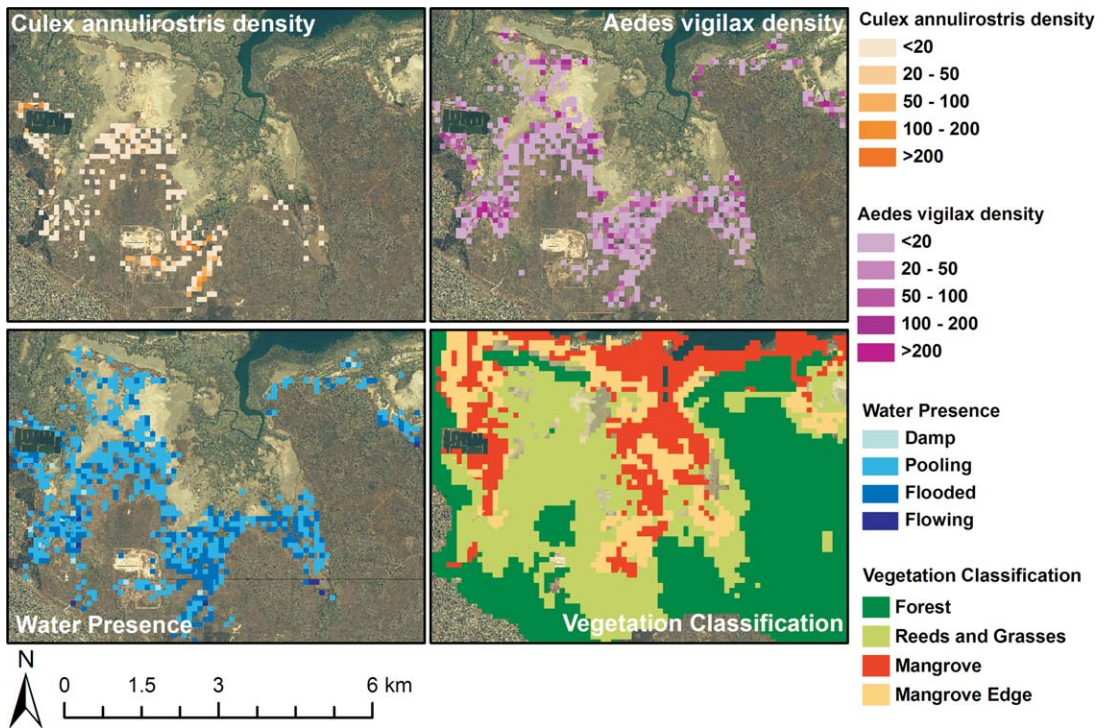
Fig. 1. Study site: Holmes Jungle/Leanyer Swamp complex near Darwin, Northern Territory, Australia showing *Aedes vigilax* and *Culex annulirostris* larval densities, and water presence scores averaged over the entire dataset: November 2000–December 2006, and vegetation types. (Online figure in color.)

these variables on larval survival, abundance, and distribution. Using a long-term (7-yr) dataset of larval surveys, we tested the correlation of different environmental conditions and larval density for saline-breeding *Ae. vigilax* and freshwater-breeding *Cx. annulirostris.* Our tests also considered the effects of density-feedback processes on regulating larval abundance through time given the evidence that intrinsic feedback is a strong modifier of adult population changes (Yang et al. 2008a). The integration of both temporal and spatial environmental variables and intrinsic dynamics in our models provides a powerful system for quantifying larval population dynamics to inform the management of pest mosquito species. We hypothesized that (1) the spatial environmental drivers of larval density (vegetation type, elevation, and tidal range) influence larval densities of the two species differently, and (2) because of the strong density feedback, adult abundance is the most important temporal driver of larval density in both species.

Materials and Methods

Study Area and Data. The Medical Entomology branch (ME) of the Northern Territory Department of Health and Families collected data of larval densities in the Leanyer/Holmes Jungle swamp complex that lies to the northeast of Darwin, Northern Territory, Australia (Fig. 1). ME has divided the swamp complex into a 100-m² grid and visits prospective grid

cells during larval surveys to record species composition and density of larvae. Larval density is recorded by performing a number of dips in any prospective standing water using a standard dipper (190-ml volume) and counting the larvae caught in each of the dips taken within a grid cell. The final estimate of relative larvae densities is the average number of larvae per dip for each mosquito species per grid cell. The completed dataset spans November 2000–December 2006.

Statistical Modeling. We compared weighted-binomial generalized linear models (GLM) and weighted-binomial generalized linear mixed-effects models (GLMM) with logit-link functions using both Akaike's information criterion corrected for small samples (AIC_c) as an estimate of Kullback-Leibler (K-L) information loss (Burnham and Anderson 2002), and the Bayesian information criterion (BIC) (Link and Barker 2006). We calculated the difference between the model's AIC_c or BIC value, the top-ranked model, ΔAIC_c or ΔBIC, and the relative model weights, $wAIC_c$ or $wBIC$ (Burnham and Anderson 2002) to assess relative strength of evidence (for any particular model, weights vary from 0 [no support] to 1 [complete support] relative to the entire model set).

We used both AIC_c and BIC to rank and weight models because they each can provide different rankings based on the size of the dataset and presence/absence of tapering effects (Burnham and Anderson 2004, Link and Barker 2006). AIC_c weighting can favor

more complex models (with many tapering effects) when samples are large, and BIC is considered a better determinant of the principal drivers of complex relationships within larger datasets (Link and Barker 2006). Thus, AIC_c can provide better model-averaged predictions of the response, while BIC identifies the dominant explanatory variables.

The candidate model sets included all possible combinations of the explanatory variables (without interactions). Although we considered the possible importance of various interactions among the terms, we did not model interactions because their inclusion reduces inference when samples are limited and when there are no mechanistic hypotheses underlying their inclusion (Burnham and Anderson 2002). We did all analyses in the R Package V2.6.2 (R Development Core Team 2008). Model sets and variable details follow.

Spatial Drivers of Larval Density. Summed larval density and median larval density across all years per grid square were used as the response variables of weighted-binomial GLMs. We examined both summed and median densities because sums tend to emphasize outliers and extreme values, and medians better reflect central tendency. We summarized environmental data for each grid cell using the geographic information system (GIS) software ArcInfo version 9.1 (ESRI 2008), and the independent predictor variables of spatial larval density we included were as follows: Elevation, topographic elevation above sea level derived from a sub-10-cm resolution digital elevation model of the area; Water, water presence as scored by ME during surveys (0 = dry, 1 = damp, 2 = pooling, 3 = flooding, 4 = flowing); Vegetation, vegetation type derived from a vegetation map of the area produced by manual classification of a QuickBird satellite image (QuickBird 2008). Vegetation was categorized as one of four vegetation types: mangrove, mangrove edge, forest (non-mangrove), or grass/sedge (Fig. 1).

Temporal Drivers of Larval Density. Larval abundance histories did not cover the complete interval of data collection for any single cell (November 2000–December 2006) because ME larval surveys (and the grid cells sampled during any given survey) are done opportunistically. To account for this, we summed the larval survey data across vegetation type for each month, and if that vegetation type was not represented by any grid cells sampled during the month, we set its value to zero. This resulted in a total of 74 monthly estimates of larval density over 7 yr. We used this measure of average larvae per dip summed across vegetation type for each month as the response variable for the GLMM.

The independent predictor variables of temporal larval density we included were as follows: Elevation, topographic elevation above sea level was the most supported spatial driver of larval density determined in the initial analyses (elevations from different grid cells were averaged across vegetation type for each month); Lagged adult abundance, mosquito populations in Darwin predominantly follow the Gompertz-

logistic model of population growth (Yang et al. 2008a). We included a 1-mo lag of the total adult females for each species to account for the effect of previous population density on larval abundance. To represent as accurately as possible the monitored numbers of adult females that emerged from the Holmes Jungle/Leanyer Swamp complex, we used a combination of counts from different numbers of monitoring sites based on the dispersal capacities of the two species under study. *Ae. vigilax* are capable of dispersing >9 km from the emergence site (Chapman et al. 1999); *Cx. annulirostris* commonly travel smaller distances from their emergence sites, with a mean dispersal capacity of ~4 km (Bryan et al. 1992). Therefore, we used an average of the monthly totals of females from the five monitoring sites within 10 km of the swamp complex for *Ae. vigilax*, and the monthly total of female *Cx. annulirostris* for the only monitoring site within 4 km of the swamp complex. We log-transformed lagged adult abundance to linearize the response. Other variables included the following: Spray, to examine the potential effectiveness of past insecticide management interventions at decreasing larval abundance, we included the total number of spraying hours from the previous month; Monthly rainfall, total monthly rainfall (mm); Tide height, maximum monthly tide height (m); Lagged tide frequency, frequency of high tides above 7.4 m from the previous month as a proxy for accumulated tidal water in the swamp (Yang et al. 2009); Lagged monthly rainfall, rainfall (mm) from the previous month to account for accumulated rain water in the swamp.

The Australian Government Bureau of Meteorology provided monthly data for the climatic variables covering the same interval as the larval abundance dataset (BOM 2008). To overcome the possibility of systematic changes in larval density associated with vegetation, we included "vegetation type" as a random factor in the GLMM. We also took 1,000 random subsets of 50% of the larval data to account for any temporal autocorrelation given that both *Cx. annulirostris* and *Ae. vigilax* populations in Darwin show a strong positive temporal autocorrelation in adult mosquito density (Yang et al. 2008a). We calculated the median values of BIC, AIC_c, ΔAIC_c, ΔBIC, $wAIC_c$, $wBIC$, and percent deviance explained for each model across the 1,000 subsets for final model comparisons.

Results

Spatial Drivers of Larval Density. The top-ranked models for the summed densities of *Ae. vigilax* larvae included elevation above sea level and water presence. There was lower support for models including vegetation as a predictor of total *Ae. vigilax* larval density (Table 1). For the median densities of *Ae. vigilax* larvae, two of the most highly ranked models included elevation and water presence, but the null (intercept-only) model ranked highest (Table 1). For summed densities, the most highly ranked model included elevation alone and explained 11.9% of the deviance. On average, drier, low-elevation grid cells

Table 1. Comparison of generalized linear models for the eight models in the full subsets regression used to assess spatial change in summed *Ae. vigilax* larval density, median *Ae. vigilax* larval density, summed *Cx. annulirostris* larval density, and median *Cx. annulirostris* larval density

°Model	%DE	w_i	ΔAIC_c	AIC_c	k
Sum—*Aedes*	°	°	°	°	°
≈elev	11.9	0.587	0.000	124.440	3
≈elev + water	12.0	0.241	1.784	126.220	4
≈elev + veg	13.5	0.122	3.142	127.580	6
≈elev + water + veg	13.6	0.048	5.017	129.45	7
≈1	0.0	0.002	11.724	136.160	2
≈water	0.4	0.001	13.172	137.610	3
≈veg	4.3	0.000	16.273	140.710	5
≈water + veg	4.3	0.000	18.165	142.600	6
Median—*Aedes*					
≈1	0.0	0.503	0.000	17.350	2
≈elev	5.0	0.195	1.892	19.240	3
≈water	0.1	0.184	2.010	19.360	3
≈elev + water	5.0	0.071	3.907	21.260	4
≈veg	1.7	0.025	5.998	23.350	5
≈elev + veg	5.8	0.010	7.909	25.260	6
≈water + veg	1.7	0.009	8.025	25.370	6
≈elev + water + veg	5.8	0.004	9.939	27.290	7
Sum—*Culex*					
≈elev + veg	10.1	0.367	0.000	131.170	6
≈elev	6.4	0.312	0.328	131.500	3
≈elev + water	7.4	0.178	1.448	132.620	4
≈elev + water + veg	10.6	0.143	1.893	133.060	7
≈1	0.0	<0.001	15.099	146.270	2
≈veg	2.8	<0.001	15.556	146.730	5
≈water	0.1	<0.001	17.621	148.790	3
≈water + veg	3.0	<0.001	18.051	149.220	6
Median—*Culex*					
≈elev	6.7	0.543	0.000	88.910	3
≈elev + water	7.5	0.343	0.920	89.830	4
≈elev + veg	9.1	0.075	3.949	92.850	6
≈elev + water + veg	9.5	0.033	5.584	94.490	7
≈1	0.0	0.003	10.166	99.070	2
≈water	0.0	0.001	12.252	101.160	3
≈veg	1.9	<0.001	15.199	104.110	5
≈water + veg	1.9	<0.001	17.274	106.180	6

Explanatory variables are elevation = elevation above sea level in 10-cm increments, water = water presence score (0 = Dry, 1 = Damp, 2 = Pooling, 3 = Flooding, 4 = Flowing), and vegetation = vegetation type (Mangrove, Mangrove Edge, Reeds and Grasses, Forest). *k* indicates the no. of parameters, ΔAIC_c shows the difference between the model AIC_c and the min. AIC_c in the set of models, and AIC_c weights (*wi*) are the relative likelihood of model *i* and %DE is the % deviance explained by the fixed effects of the model.

along the mangrove forest edges had higher densities of *Ae. vigilax* larvae (Table 2).

The top-ranked models of summed densities of *Cx. annulirostris* larvae included elevation above sea level, vegetation, and water presence (Table 1). However, the most supported models for median densities of *Cx. annulirostris* larvae included only elevation and water

presence (Table 1). The deviance explained by the most highly ranked models for both datasets, summed densities and median densities, was relatively low: 10.1 and 6.7%, respectively. On average, high-elevation grid cells with less water and containing reeds and/or grasses had higher densities of *Cx. annulirostris* larvae (Table 2).

Temporal Drivers of Larval Density. According to median *w*BIC derived from the 1,000 resamples, the model of *Ae. vigilax* larvae density with the greatest support included the logarithm of lagged adult abundance and lagged monthly rainfall (Table 3). This was also true based on median *w*AIC_c rankings; however, models including maximum tide height and lagged tide frequency also received substantial support based on AIC_c (median ΔAIC_c of 0.47 and 1.88, respectively). The BIC and AIC_c highest-ranked model described a median deviance of 23.24%. Sensitivity analysis showed that a 10% increase in the number of adult females results in a 4% increase in *Ae. vigilax* larvae densities in the next month, a 10% increase in rainfall results in a 2% decrease in *Ae. vigilax* larvae densities in the next month, and a 10% increase in the height of the maximum tide results in a 30% increase in *Ae. vigilax* larvae densities in the same month.

The median *w*BIC highest-ranked model of *Cx. annulirostris* larvae density included the logarithm of lagged adult abundance and lagged monthly rainfall, and there was also substantial support for the model that also included elevation (median ΔBIC = 1.63). The median *w*AIC_c rankings were similar; the model including lagged adult abundance, lagged monthly rainfall, and elevation received the greatest support (Table 3). The median *w*BIC highest-ranked model explained a median deviance = 5.7%. Once elevation was included, the model explained 22.7% of the deviance. Sensitivity analysis showed that a 10% increase in adult females only results in a 0.4% increase in *Cx. annulirostris* larvae densities in the next month, a 10% increase in rainfall in the previous month results in a 0.3% rise in *Cx. annulirostris* larvae densities, and with a 10% increase in elevation, larvae densities rise by 6%. For both *Ae. vigilax* and *Cx. annulirostris*, the models that included spray hours from the previous month received little support (Table 3).

Discussion

Effective mosquito control requires a detailed understanding of the temporal and spatial variance in larval densities among habitats; otherwise, control by

Table 2. Weighted model coefficients with SEs (in parens) for the relationship between sum of *Ae. vigilax* larvae per dip, median of *Ae. vigilax* larvae per dip, sum of *Cx. annulirostris* larvae per dip, and median of *Cx. annulirostris* larvae per dip and the fixed effects of vegetation type, elevation, and water presence

Response variable	Intercept—Mang edge	Mang	Reeds and grasses	Forest	Elevation	Water
Ae. vigilax sum	6.755 (0.77)	−0.102 (0.07)	−0.021 (0.05)	−0.117 (0.08)	−0.681 (0.10)	−0.027 (0.08)
Ae. vigilax median	3.209 (0.03)	−0.033 (0.37)	−0.018 (0.02)	−0.079 (0.01)	−0.193 (0.02)	−0.090 (0.07)
Cx. annulirostris sum	−3.602 (0.64)	0.183 (0.18)	0.531 (0.13)	−0.307 (0.25)	0.388 (0.08)	−0.180 (0.07)
Cx. annulirostris median	−2.880 (0.58)	0.037 (0.04)	0.102 (0.03)	−0.081 (0.05)	0.343 (0.07)	−0.211 (0.09)

Table 3. Comparison of the 10 top-ranked generalized linear mixed-effects models (32 models considered in total) in the full subsets regression used to assess monthly change from Nov. 2000 to Dec. 2006 in *Ae. vigilax* and *Cx. annulirostris* larval densities

Model	Median BIC	Median wBIC	Median ΔBIC	Median wAIC$_c$	Median ΔAIC$_c$	Median %DE
Aedes vigilax larvae density						
≈logN + rain1 + (1 veg)	67.50	0.524	0.000	0.524	0.000	23.0
≈tide + logN + rain1 + (1 veg)	70.180	0.113	3.020	0.113	3.020	28.8
≈tide.f1 + logN + rain1 + (1 veg)	71.580	0.060	4.315	0.060	4.315	25.4
≈elev + logN + rain1 + (1 veg)	71.930	0.053	4.681	0.053	4.681	24.1
≈spray + logN + rain1 + (1 veg)	72.030	0.050	4.838	0.050	4.838	24.1
≈rain + logN + rain1 + (1 veg)	72.230	0.048	4.909	0.048	4.909	23.6
≈rain + tide + logN + rain1 + (1 veg)	74.570	0.012	7.452	0.012	7.452	30.4
≈elev + tide + logN + rain1 + (1 veg)	74.650	0.012	7.559	0.012	7.559	29.9
≈spray + tide + logN + rain1 + (1 veg)	74.660	0.012	7.531	0.012	7.531	30.0
≈tide.f1 + tide + logN + rain1 + (1 veg)	74.750	0.012	7.563	0.012	7.563	29.6
Culex annulirostris larvae density						
≈logN + rain1 + (1 veg)	54.300	0.464	0.000	0.082	1.176	5.7
≈elev + logN + rain1 + (1 veg)	55.570	0.200	1.717	0.149	0.000	21.7
≈tide + logN + rain1 + (1 veg)	58.700	0.045	4.866	0.036	2.848	7.2
≈rain + logN + rain1 + (1 veg)	58.710	0.045	4.959	0.035	2.968	7.7
≈tide.f1 + logN + rain1 + (1 veg)	58.730	0.048	4.885	0.038	2.890	8.2
≈spray + logN + rain1 + (1 veg)	59.080	0.042	4.937	0.032	3.065	7.0
≈elev + rain + logN + rain1 + (1 veg)	60.150	0.020	6.257	0.065	2.042	24.0
≈elev + tide + logN + rain1 + (1 veg)	60.230	0.020	6.339	0.062	2.098	23.2
≈elev + tide.f1 + logN + rain1 + (1 veg)	60.280	0.020	6.329	0.061	2.087	23.7
≈elev + spray + logN + rain1 + (1 veg)	60.350	0.020	6.370	0.059	2.091	23.1

Explanatory variables are fixed effects: log$N$ = log of adult abundance in the previous month, rain1 = rainfall in the previous month (mm), tide = monthly max tide (m), tide.f1 = frequency of tides above 7.4 m in the previous month, elevation = elevation above sea level at 10-cm resolution, spray = total spraying hours in the previous month, rain = total monthly rainfall (mm), and the random effect: (1 veg) = vegetation type (Mangrove, Mangrove Edge, Reeds and Grasses, Forest). Median ΔBIC shows the median ΔBIC score for each model from 1000 randomizations, (where ΔBIC is the difference between the model BIC and the min. BIC in the set of models), median wBIC is the median BIC wt for each model from 1000 randomizations and median %DE is the median % deviance explained by the fixed effects of the model for each model from 1000 randomizations. The same statistics are shown for AIC$_c$.

insecticides or habitat modifications cannot be targeted efficiently. Here we show that it is important to examine not only the spatial attributes of larval habitats (topography, vegetation type), but also the temporal factors such as adult abundance and rainfall that affect how larvae densities fluctuate within these habitats. To make reliable inference about larval habitat use, vector population dynamics, and the subsequent recommendations for efficient control, long time series over a large spatial scale, such as the datasets we analyzed, are required. Monitoring data that are collected to aid management are imperative for making immediate and informed decisions. However, this type of monitoring data can often fall short of quantifying the variability inherent in ecological systems in sufficient detail. Our larval survey data were collected opportunistically based on information about adult population dynamics, tide and rainfall patterns, and larval habitat ecology. Therefore, the larval dataset lacks the necessary sampling rigor to allow analyses aimed at decoupling the seasonal and environmental variables driving the observed vector population dynamics within these swamp systems. This is show by the low explanatory power of our final models, especially for *Cx. annulirostris.*

Despite drawbacks in data quality, some generalizations can be made from our models. We found the strongest temporal drivers of larval density for both vector species were lagged logarithm of adult density and total rainfall from the previous month. We partially expected this result because adult mosquito populations in tropical north Australia are strongly intrinsically regulated (Yang et al. 2008a, b). Our results take this density relationship one step further by providing a clear mechanistic link between the two main life phases in mosquito development. Yang et al. (2008a) found a negative relationship between the adult mosquito population rate of change (r) and adult population density, and there are several mechanisms by which this dynamic can be realized. Competition during the adult life stage for blood meals, harborage, or oviposition sites can lead to lower larval densities after a peak in adult density. During a population peak, competition at the larval stage for nutrients and/or other stresses in the high density larval habitat will result in mortality at the larval and pupal stages, and the emergence of smaller adults with lower survival and fertility (Agnew et al. 2002). Our results show a positive relationship between adult numbers in the previous month and larval density in the following month, which suggests that the major mechanism of density dependence in these species is not competition during the adult life stage—if this were the case, there would be a negative relationship between lagged adult density and larval density. We hypothesize that the main regulatory mechanism in *Ae. vigilax* and *Cx. annulirostris* occurs during the larval life stage where lower to medium larval densities will result in higher adult emergence, survival, and fertility than would occur at high larval densities. It is therefore important that, during control operations, both low- and high-density larval habitats and seasons are targeted for

control to reduce population size and disease transmission effectively.

For both species studied, we found that elevation was the dominant spatial driver of larval densities. Elevation controls much of the spatial distribution of wetness across the land surface in tidal systems (Shaman et al. 2002), and mosquito larvae are commonly associated with areas of ephemeral water (Chase and Knight 2003). Deeper or more permanent water can allow greater predator access and may subject the larvae to tidal flushing (Dale et al. 2002). Therefore, we expect that, in an extensive and flat, tidally influenced system, small increments in elevation will affect the extent to which the swamp is inundated by tides during the dry season, the extent and depth of retained water between tides, and retained freshwater during the wet season. The suitability and availability of habitat for larval development of different species will fluctuate accordingly. Other environmental conditions being equal, we found that higher densities of saltwater-breeding *Ae. vigilax* larvae are more likely to occur at lower elevations where the swamp complex is more influenced by the tides, and higher larval densities of the freshwater breeder *Cx. annulirostris* were more likely at higher elevations in areas inundated by rainfall and freshwater runoff and not as affected by tidal regimens. The resolution of elevation data included in our analysis (10-cm increments) is much finer than that commonly available in geographic information system analyses (Shaman et al. 2002, Zeilhofer et al. 2007), showing that even subtle changes in elevation are important for differentiating habitat suitability for different species of larvae. This finding is directly useful for larval control strategies because any changes in the topography of the swamp caused by physical engineering, such as runneling (i.e., using shallow channels to link mosquito breeding pools to the tidal source) (Dale et al. 2002), draining (Whelan 1989), or filling (Brogan et al. 2002) will influence larval and therefore adult densities.

The water presence score is in reality a function of many different components: precipitation, temperature, soil properties, vegetation, prior wetness in the catchment, and topography (Shaman et al. 2002). Although water presence was a relatively important spatial driver of larval density in both species, it was better represented in the relationships explored in the temporal analyses using maximum monthly tide height, total monthly rainfall, tidal frequency, and elevation. We found little support for vegetation type as a driver of *Ae. vigilax* larval density and only weak evidence for a relationship between *Cx. annulirostris* larvae and vegetation type, indicating that both species are generalist species that can breed, grow as larvae and emerge from a wide variety of habitats (Lee et al. 1984, 1989). Although vegetation type can influence local population size to some extent (Hearnden and Kay 1997, Turner and Streever 1997), the use of coarse vegetation classes may not have provided sufficient resolution to determine specific vegetation association differences.

As expected, the temporal models showed a positive relationship between *Ae. vigilax* larval abundance and both maximum tides in the same month and high tide frequency in the previous month. Although *Ae. vigilax* is able to breed in ephemeral pools inundated either by tides or early rain, adult females require exposed mud for oviposition (Sinclair 1976). The tidal regimen during the late dry season regularly floods large areas of the swamp complex, and the ephemeral tidal pools allow enough time for larval development and adult emergence before drying to expose mud for oviposition. This pattern continues with early rainfall in the late dry season; however, once rainfall reaches a certain threshold, the swamp complex becomes flooded, and the wetlands become suitable habitat for *Cx. annulirostris.* This observation is supported by the positive relationship we found between *Cx. annulirostris* larvae and lagged rainfall. We also found evidence for a positive relationship between elevation and *Cx. annulirostris* larval abundance. Although rainfall freshens the tidally influenced swamps, the elevation gradient determines the fine-scale depths of larval habitats and the vegetation characteristics in each of the water depth zones (Shaman et al. 2002). Therefore, higher elevations result in shallower and more ephemeral habitats that predators find it harder to access. This finding also introduces serious challenges for analyzing the possible interactions of these drivers of the population dynamics of the system because of the "legacy" effects of the desiccation-resistant egg stocks in the swamp and the retained seasonal tidal and rain inundation.

We found little evidence for a relationship between spraying hours in the previous month and larval densities of either species. Spraying programs aim to reduce the emergence of adults after high-density larval occurrences. Although the spray program can reduce the emergence of adults, our models show that the climatic, landscape, and density-dependent processes that drive population growth rates override any lingering effects the spray program may have on future larval densities. Furthermore, Yang et al. (2008b) found that carrying capacity is largely invariant to landscape modification and spraying, indicating that control measures may only alter the rate at which mosquito populations can fill available niches. Thus, spray operations will generally be required after every high tide or early rain events for *Ae. vigilax*, irrespective of the perceived success of the previous larval control operations. Any reduction in *Cx. annulirostris* emergence by spray operations will only have a temporary effect, and regular and successive spraying will be required until the seasonal aquatic habitat becomes unsuitable. Our results have highlighted the complexity of this system both to manage and model. Even with the extensive datasets presently available, the confounding effects inherent in both the temporal and spatial aspects of this system mean that regular and uniform monitoring is constantly required to be able to tease out the intricacy of these relationships.

Acknowledgments

References Cited

Agnew, P., M. Hide, C. Sidobre, and Y. Michalakis. 2002. A minimalist approach to the effects of density-dependent competition on insect life-history traits. Ecol. Entomol. 27: 396–402.

Barrera, R., M. Amador, and G. G. Clark. 2006. Ecological factors influencing Aedes aegypti (Diptera: Culicidae) productivity in artificial containers in Salinas, Puerto Rico. J. Med. Entomol. 43: 484–492.

Bass, C., D. Nikou, M. J. Donnelly, M. S. Williamson, H. Ranson, A. Ball, J. Vontas, and L. M. Field. 2007. Detection of knockdown resistance (kdr) mutations in Anopheles gambiae: a comparison of two new high-throughput assays with existing methods. Malar. J. 6.

[BOM] Bureau of Meterology. 2008. Australian Government, Bureau of Meteorology. (http://www.bom.gov.au).

Brogan, B., P. I. Whelan, J. Carter, and G. Lamche. 2002. Rectification and control practices in a major salt marsh mosquito breeding site, Darwin, NT. Northern Territory Dis. Control Bull. 9: 16–21.

Bryan, J. H., M. S. O'Donnell, G. Berry, and T. Carvan. 1992. Dispersal of adult female Culex annulirostris in Griffith, New South Wales, Australia: a further study. J. Am. Mosq. Control Assoc. 8: 398–403.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33: 261–304.

Chapman, H. F., J. M. Hughes, C. Jennings, B. H. Kay, and S. A. Ritchie. 1999. Population structure and dispersal of the salt marsh mosquito Aedes vigilax in Queensland, Australia. Med. Vet. Entomol. 13: 423–430.

Chase, J. M., and T. M. Knight. 2003. Drought-induced mosquito outbreaks in wetlands. Ecol. Lett. 6: 1017–1024.

Dale, P.E.R., K. Hulsman, and A. L. Chandica. 1986. Classification of reflectance on colour infrared aerial photographs and subtropical salt marsh vegetation types. Int. J. Remote Sens. 7: 1783–1788.

Dale, P.E.R., H. Chapman, M. D. Brown, S. A. Ritchie, J. Knight, and B. H. Kay. 2002. Does habitat modification affect oviposition by the salt marsh mosquito, Ochlerotatus vigilax (Skuse) (Diptera: Culicidae)? Aust. J. Entomol. 41: 49–54.

de Garin, A. B., R. A. Bejaran, A. E. Carbajo, S. C. de Casas, and N. J. Schweigmann. 2000. Atmospheric control of Aedes aegypti populations in Buenos Aires (Argentina) and its variability. Int. J. Biometeorol. 44: 148–56.

Dhileepan, K. 1996. Mosquito seasonality and arboviral disease incidence in Murray valley, southeast Australia. Med. Vet. Entomol. 10: 375–384.

[ESRI]. Environmental Systems Research Institute. 2008. ArcGIS. (http://www.esri.com/index).

Grieco, J. P., S. Johnson, N. L. Achee, P. Masuoka, K. Pope, E. Rejmankova, E. Vanzie, R. Andre, and D. Roberts. 2006. Distribution of Anopheles albimanus, Anopheles vestitipennis, and Anopheles crucians associated with land use in northern Belize. J. Med. Entomol. 43: 614–622.

Hachiya, M., M. Osborne, C. Stinson, and B. G. Werner. 2007. Human eastern equine encephalitis in Massachusetts: predictive indicators from mosquitoes collected at 10 long-term trap sites, 1979–2004. Am. J. Trop. Med. Hyg. 76: 285–292.

Hawley, W. A. 1985. The effect of larval density on adult longevity of a mosquito, Aedes sierrensis—epidemiological consequences. J. Anim. Ecol. 54: 955–964.

Hay, S. I., J. Cox, D. J. Rogers, S. E. Randolph, D. I. Stern, G. D. Shanks, M. F. Myers, and R. W. Snow. 2002. Climate change and the resurgence of malaria in the East African highlands. Nature (Lond.) 415: 905–909.

Hearnden, M. N., and B. H. Kay. 1997. Importance of Hydrilla verticillata (Hydrocharitaceae) as habitat for immature mosquitoes at the Ross River reservoir, Australia. J. Am. Mosq. Control Assoc. 13: 164–170.

Howard, A. F., G. Zhou, and F. X. Omlin. 2007. Malaria mosquito control using edible fish in western Kenya: preliminary findings of a controlled study. BMC Public Health 7.

Jacups, S. P., P. I. Whelan, and B. J. Currie. 2008. Ross River virus and Barmah Forest virus infections: a review of history, ecology, and predictive models, with implications for tropical northern Australia. Vector Borne Zoonotic Dis. 8: 1–15.

Jeffery, J. A., P. A. Ryan, S. A. Lyons, P. Thomas, and B. H. Kay. 2002. Spatial distribution of vectors of Ross River virus and Barmah Forest virus on Russell Island, Moreton Bay, Queensland. Aust. J. Entomol. 41: 329–338.

Killeen, G., U. Fillinger, and B. Knols. 2002. Advantages of larval control for African malaria vectors: low mobility and behavioural responsiveness of immature mosquito stages allow high effective coverage. Malar. J. 1: 8.

Kurucz, N., P. I. Whelan, and P. Porigneaux. 2002. Mosquito control in Ilparpa Swamp—a big step forward. Northern Territoy Dis. Control Bull. 9: 22–23.

Kurucz, N., P. I. Whelan, and N. D. Daly. 2003. Mosquito control at Hickey's Lake, Katherine, NT. Bull. Mosq. Control Assoc. Austral. 15: 22–25.

Lee, D. J., M. M. Hicks, M. Griffiths, and R. C. Russell. 1989. The Culicidae of the Australasian region. Australian Government Publishing Service, Canberra, Australia.

Lee, D. J., M. M. Hicks, M. Griffiths, R. C. Russell, and E. M. Marks. 1984. The Culicidae of the Australasian region. Australian Government Publishing Service, Canberra, Australia.

Leisnham, P. T., D. P. Slaney, P. J. Lester, and P. Weinstein. 2005. Increased larval mosquito densities from modified landuses in the Kapiti region, New Zealand: vegetation, water quality, and predators as associated environmental factors. EcoHealth 2: 313–322.

Lindsay, M.D.A., A. K. Broom, A. E. Wright, C. A. Johansen, and J. S. Mackenzie. 1993. Ross River virus isolations from mosquitoes in arid regions of Western Australia: implications of vertical transmission as a means of persistence of the virus. Am. J. Trop. Med. Hyg. 49: 686–696.

Lindsay, M.D.A., A. Jardine, C. A. Johansen, A. E. Wright, S. A. Harrington, and P. Weinstein. 2007. Mosquito

5555555555