

ENDOGENOUS AND EXOGENOUS FACTORS CONTROLLING TEMPORAL ABUNDANCE PATTERNS OF TROPICAL MOSQUITOES

GUO-JING YANG,^{1,2,7} BARRY W. BROOK,³ PETER I. WHELAN,⁴ SAM CLELAND,⁵ AND COREY J. A. BRADSHAW^{3,6}

¹*School for Environmental Research, Institute of Advanced Studies, Charles Darwin University, Darwin, Northern Territory 0909 Australia*

²*Jiangsu Institute of Parasitic Diseases, Meiyuan, Yangxiang 117#, Wuxi, 214064, Jiangsu, People's Republic of China*

³*Research Institute for Climate Change and Sustainability, School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005 Australia*

⁴*Medical Entomology Branch, Communicable Diseases Program, Northern Territory Government Department of Health and Community Services, P.O. Box 40596, Casuarina, Northern Territory 0811 Australia*

⁵*Australian Bureau of Meteorology, Northern Territory Regional Office, P.O. Box 40050, Casuarina, Northern Territory 0811 Australia*

⁶*South Australian Research and Development Institute, P.O. Box 120, Henley Beach, South Australia 5022 Australia*

Abstract. The growing demand for efficient and effective mosquito control requires a better understanding of vector population dynamics and how these are modified by endogenous and exogenous factors. A long-term (11-year) monitoring data set describing the relative abundance of the saltmarsh mosquito (*Aedes vigilax*) in the greater Darwin region, northern Australia, was examined in a suite of Gompertz-logistic (GL) models with and without hypothesized environmental correlates (high tide frequency, rainfall, and relative humidity). High tide frequency and humidity were hypothesized to influence saltmarsh mosquito abundance positively, and rainfall was hypothesized to correlate negatively by reducing the availability of suitable habitats (moist substrata) required by ovipositing adult female mosquitoes. We also examined whether environmental correlates explained the variance in seasonal carrying capacity (K) because environmental stochasticity is hypothesized to modify population growth rate (r), carrying capacity, or both. Current and lagged-time effects were tested by comparing alternative population dynamics models using three different information criteria (Akaike's Information Criterion [corrected; AIC_c], Bayesian Information Criterion [BIC], and cross-validation [C-V]). The GL model with a two-month lag without environmental effects explained 31% of the deviance in population growth rate. This increased to >70% under various model combinations of high tide frequency, rainfall, and relative humidity, of which, high tide frequency and rainfall had the highest contributions. Temporal variation in K was explained weakly by high tide frequency, and there was some evidence that the filling of depressions to reduce standing water availability has reduced *Aedes vigilax* carrying capacity over the study period. This study underscores the need to consider simultaneously both types of drivers (endogenous and exogenous) when predicting mosquito abundance and population growth patterns. This work also indicates that climate change, via continued increases in rainfall and higher expected frequencies and intensities of high tide events with sea level rise, will alter mosquito abundance trends in northern Australia.

Key words: *Aedes vigilax*; Australia; density dependence; disease; humidity; mosquito control; rainfall; tidal inundation.

INTRODUCTION

Aside from the irritation and annoyance of mosquitoes to humans and livestock, the threat of pathogens transmitted by mosquitoes is a major public health problem in much of the world (Gubler 1991, World Health Organization 1995, Sharp and Le Sueur 1996). Mosquito-borne diseases such as malaria, dengue, yellow fever, Japanese encephalitis, West Nile virus, and Ross River virus are just a few major representatives of a long list of mosquito-transmitted diseases that have histori-

cally plagued human civilization (Gubler 1998, Gratz 1999). Malaria alone causes a public health problem in over 100 countries worldwide where some 40% of the world's human population resides (World Health Organization 1988). It has been estimated that the incidence of malaria in the world may be 300–500 million clinical cases annually (Breman et al. 2004, Snow et al. 2005, World Health Organization and UNICEF 2005), and there is evidence that the prevalence, morbidity, and mortality induced by zoonotic arboviral diseases worldwide are on the rise (Gubler 2002). Furthermore, global warming is likely to increase the range and abundance of mosquitoes in most countries, resulting in increased frequency of many mosquito-borne diseases (Patz and Reisen 2001, Hay et al. 2002). As such, the mounting

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⁷ E-mail: guojingyang@hotmail.com

quest for efficient and effective mosquito control (Bergquist 2001) requires a better understanding of vector population dynamics and how these are modified by intrinsic and extrinsic processes (de Little et al. 2007, Bradshaw 2008, Chamaillé-Jammes et al. 2008).

The transmission frequency and extent of mosquito-borne diseases depend on a complex set of factors, of which vector distribution, longevity, and abundance are three of the most important (Gubler 1998, Whelan et al. 2003). Mosquitoes require an aquatic environment in which to nurture their larval and pupal stages, with suitable mosquito larval habitats including vegetated margins of lakes and streams, salt marshes, floodplains, man-made wetlands, and physically disturbed environments (Russell and Whelan 1986, Russell 1987, Rejmankova et al. 1991, Norris 2004, Sattler et al. 2005). Environmental factors important for adult mosquito survival and dispersal include optimal humidity, temperature, and wind conditions (Muir 1988, Linthicum et al. 1999), although different species demonstrate distinctly different ecological preferences, such as *Anopheles stephensi* selecting urban areas vs. *A. gambiae* selecting rural habitats (Robert et al. 2003, Scholte et al. 2005). Mosquito numbers also vary extensively over seasons and years, with the amount of rainfall, the physical nature of the habitat, or the height and frequency of tidal inundation (for saltwater-breeding species) accounting for much of the temporal and spatial variation observed (Russell 1986, 1987). In addition, human activities via physical, chemical, and biological control methods can change mosquito population abundance and distribution by modifying breeding habitats and individual survival probability (World Health Organization 1982, 2003).

Most previous studies investigating the factors correlated with mosquito abundance have put particular emphasis on determining the exogenous (environmental) drivers of abundance (Russell 1986, Su et al. 2003, Kunkel et al. 2006); however, mosquito population dynamics can also demonstrate strong intrinsic (density-dependent) regulation (Bradshaw and Holzapfel 1989, Leonard and Juliano 1995, Gimnig et al. 2002, Kiflawi et al. 2003, Yang et al. 2008). Exogenous (extrinsic) processes include stochastic environmental components that affect demographic rates irrespective of population density. Endogenous (intrinsic) population regulation works primarily through negative density feedback on survival or reproductive rates that decline as density increases (Turchin 2003a). Failing to take intrinsic dynamics into account can lead to an overestimation of the medium- to long-term effectiveness of density control methods, such as insecticides or habitat modification. This results from falsely attributing changes in population growth rate resulting exclusively from density feedback in survival and fertility to contemporaneous changes in control effort (Turchin 2003a).

The Gompertz dynamical feedback model describing a negative log-linear relationship between population

growth rate (r) and insect density (Woiwod and Hanski 1992, Zeng et al. 1998, Turchin 2003a, Sibly et al. 2005, Brook and Bradshaw 2006), predicts an exponential decrease in r with greater population size (Turchin 2003b). This functional form tends to promote over-compensatory population responses such as rapid peaks and crashes (oscillations) after successive generations (Hilker and Westerhoff 2007), especially when the rate of decline in r is maximized at a net annual growth of zero (Owen-Smith 2006).

In this study we examine the relative contribution of density feedback mechanisms and environmental stochasticity on the residual variation in population growth rate by incorporating three plausible environmental correlates hypothesized to limit mosquito populations into a suite of density-feedback models. We focus our analysis on the northern saltmarsh mosquito (*Aedes vigilax*) because of its prime importance as a vector of Ross River virus (RRV) disease and Barmah Forest virus (BFV) disease (Whelan et al. 1997, Russell 1998). These human infections are the most commonly reported mosquito-borne diseases in Australia, with RRV accounting for 45% and BFV for 30% of all such cases (Liu et al. 2005). Specifically, we use a long-term monitoring data set (11 years with weekly trapping) for *A. vigilax* in the greater Darwin area, northern Australia to (1) quantify the effects of high tide frequency, rainfall, and relative humidity in controlling r (in addition to intrinsic regulation), using multi-model information-theoretic and Bayesian inference estimates of relative model parsimony, and (2) evaluate the change in seasonal carrying capacities (K) (Bjørnstad and Grenfell 2001) over the 11 years of monitoring as a function of environmental and management correlates. In the greater Darwin region, high tides >7.4 m can generate temporary saltwater habitats ideal for the oviposition and larval development of the saltmarsh mosquito *A. vigilax* (Whelan 1987), similar to other saltwater-breeding mosquito species (Harrington and Harrington 1961, Russell 1998). We therefore hypothesized that the frequency of high tides exceeding 7.4 m would positively influence the abundance of this species. Additional residual variation in abundance was hypothesized to result from average relative humidity and total rainfall over the time intervals investigated (Day et al. 1990, Farid et al. 2000, Lee and Rowley 2000). By taking into account both exogenous and endogenous control of mosquito population dynamics, we aim to provide a quantitative model of sufficient realism to guide the development of optimized control strategies for *A. vigilax* and other tropical saltmarsh mosquito species.

METHODS

Mosquito abundance data

Monitoring data were collected by the Medical Entomology Branch of the Northern Territory Department of Health and Community Services in 11 locations in and around Darwin, Australia for routine vector

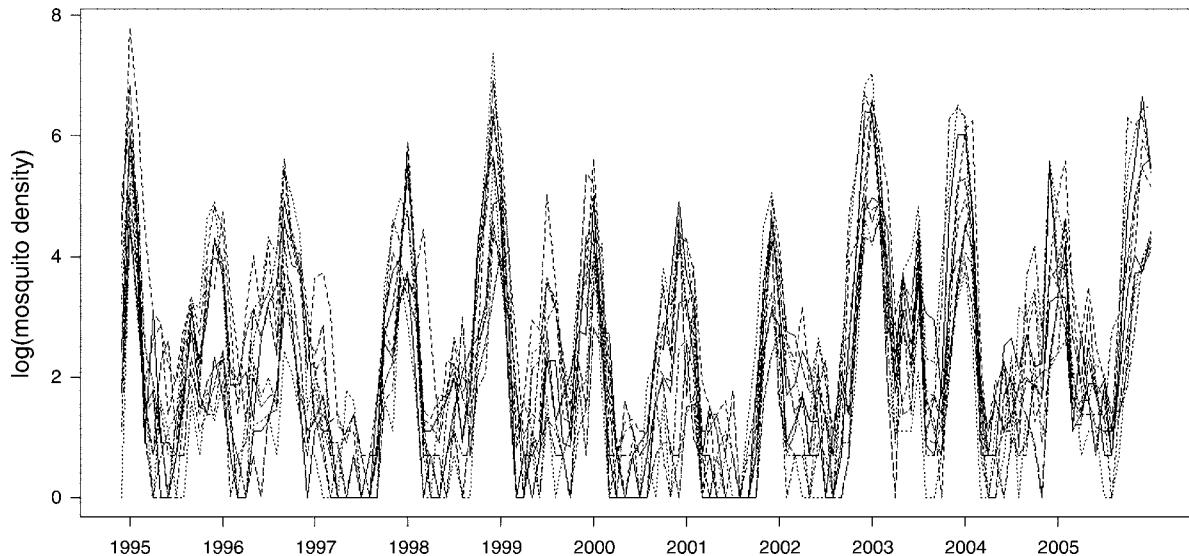


FIG. 1. Time series plot of *Aedes vigilax* monthly abundance from 11 traps (each line represents the time series from a single trap) between 1994 and 2005 (192 months total). Temporal variability overwhelms spatial differences.

surveillance (Whelan 1989, Yang et al. 2008). The mosquito populations were sampled with CO₂-baited mosquito traps (Rohe and Fall 1979), which were operated overnight once per week at locations between adjacent swamp and residential development areas (Whelan 1989). Although human-baited collections have been shown to be effective samplers of other mosquito species such as *A. aegypti*, which feeds specifically on humans (e.g., Schoeler et al. 2004), CO₂-baited light traps offer the advantages of being less labor-intensive, supply all-night collection, offer no bias based on individual attractiveness or skill of the collector, and are particularly effective for many generalist-feeding Australian species such as *A. vigilax* and *C. annulirostris* (Russell 1986, Van Essen et al. 1994, Miller et al. 2005). CO₂-baited traps also tend to target nulliparous females more effectively than other methods, but may not always be as efficient as backpack aspirators or BG-Sentinels (Williams et al. 2006). Regardless, they are effective at registering relative adult abundance and can be used to estimate population rates of change (Whelan et al. 2005). The distance between each pair of traps varied from 1 to 3 km, with the traps covering a total area of 63.2 km². To avoid the possible confounding effects of age structure and overlapping generations on our assessment of density feedback (Turchin 2003a), monthly and every two weeks, female *A. vigilax* population density data were prepared by averaging weekly density data. Only female population density data were used due to this gender's blood-feeding behavior, and resultant importance for disease transmission. Yang et al. (2008) demonstrated that *A. vigilax* exhibited strong spatial homogeneity in the study region. As such, the data for these analyses were pooled among the 11 trap locations as arithmetic mean abundance. The complete data set spans November

1994 to December 2005. The monthly population density of *A. vigilax* was depicted as time series plot and monthly variation over all years (Figs. 1 and 2a).

Environmental data

Frequency of high tides >7.4 m/month, monthly relative humidity (percentage), and total rainfall (millimeters) data covering the same interval as the mosquito abundance data sets were all provided by the Australian Government Bureau of Meteorology ([available online](#)).⁸ The longest-term weather data were available only from the Darwin Airport station (12°25'12" S, 130°53'24" E), which is situated roughly in the center of the 63.2-km² study area bounded by the mosquito trap locations. Monthly variation in the environmental data examined over all years is shown in Fig. 2b–d.

Management data

The physical methods used to reduce the suitable habitats of mosquito larvae in saltmarsh swamps around Darwin included reduction or elimination of mosquito breeding areas via the infilling of depressions that can collect water, maintenance of existing drains, and constructing new drains in breeding stands of water (Whelan 1989). A combination of mosquito larvicides has also been used as a direct control measure to accompany the habitat engineering program. In Darwin, the bacterial insecticide, *Bacillus thuringiensis* var. *israelensis* (B.t.i), and temephos (organophosphorus insecticide) were widely used for larval control, broadcast via both ground and aerial helicopter control operations. Adulticides, which are less specific than larvicides, are generally less effective due to the ability of

⁸ (www.bom.gov.au)

adult mosquitoes to disperse over wide areas (e.g., Chung et al. 2001). To provide a qualitative assessment of the potential effectiveness of physical and chemical management interventions on mosquito carrying capacity, we obtained a yearly summarized time series data set for the >60 km² area describing the number of drains connected, the total area (e.g., depressions) filled, the number of spraying days, and the number of hectares sprayed each year over the entire time interval investigated from the Medical Entomology Branch of the Northern Territory Department of Health and Community Services.

Dynamical models

The Gompertz-logistic (GL) model describes the linear relationship between population growth rates (*r*) and logarithm-transformed density (relative *N_t*) and is characteristic of insect populations (Woiwod and Hanski 1992, Zeng et al. 1998, Turchin 2003a, Sibly et al. 2005, Brook and Bradshaw 2006). Under the GL model, carrying capacity (*K*) is defined as the log(*N*) at which *r* is equal to zero. We expanded the GL model to include time-variant environmental conditions, namely, high tide frequency, rainfall, and relative humidity.

Given our lack of knowledge regarding the potentially complex interaction between density regulation, environmental variation, human control efforts, and modification of carrying capacity, our approach was to modify the GL models in three phases. Model 1 (Eq. 1) relates population growth rate (*r*) to density, with residual variation in *r* explained by stochastic environmental effects; this model assumes carrying capacity (*K*) is invariant over the time series. Model 2 (Eq. 2) is a variant of the GL model in which *K* fluctuates as a function of environmental variability (“*K*-ratio” model) (see Hone and Clutton-Brock 2007). Model 3 (Eq. 3) is the combination of Models 1 and 2, which allows environmental stochasticity to modify *r* and *K* simultaneously:

$$\log_e \left(\frac{N_{t+1}}{N_t} \right) = r_t = r_m \left\{ 1 - \left[\frac{\log(N_t)}{\log(K)} \right] \right\} + \beta \mathbf{E}_t + \varepsilon_t$$

$$\varepsilon_t \sim \mathcal{N}(0, \sigma^2)$$

(1)

$$r_t = r_m \left\{ 1 - \left[\frac{\log(N_t)}{\log(K) \times E_t} \right] \right\} + \varepsilon_t$$

$$\varepsilon_t \sim \mathcal{N}(0, \sigma^2)$$

(2)

$$r_t = r_m \left\{ 1 - \left[\frac{\log(N_t)}{\log(K) \times E_t} \right] \right\} + \beta \mathbf{E}_t + \varepsilon_t$$

$$\varepsilon_t \sim \mathcal{N}(0, \sigma^2)$$

(3)

where *N_t* denotes mosquito population size at time *t*, *r_t* =

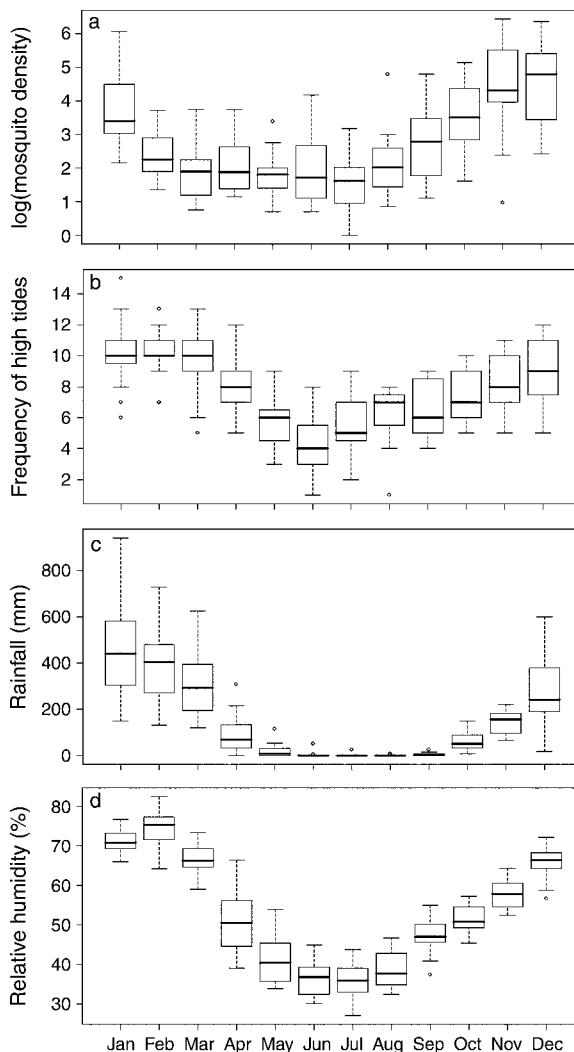


FIG. 2. Box-and-whisker plots showing the monthly variation in (a) population density of *A. vigilax*, (b) frequency of high tide (>7.4 m), (c) rainfall (mm), and (d) relative humidity (%) in the greater Darwin region, Northern Territory, Australia. Box-and-whisker plot indicates the maximum, upper quartile, median, lower quartile, and minimum values. Open diamonds are outliers.

realized population growth rate, *r_m* = maximal intrinsic *r*, *K* = carrying capacity, $\beta = (\beta_0 \beta_1 \dots \beta_n)$, \mathbf{E}_t = vector of environmental factors (*E_{1t}*, *E_{2t}*, ... *E_{nt}*), and ε_t represents unexplained residual error. We also considered lags of two months on the density feedback mechanism (cf. Turchin 1990). All models were fitted using maximum-likelihood estimation.

All analyses were done using the R Package version 2.4.0 (R Development Core Team 2004). Model comparisons were based on multi-model inference (MMI) using three separate methods: (1) Akaike’s Information Criterion corrected for small sample sizes (AIC_c) as an estimate of Kullback-Leibler (K-L) information loss (Akaike 1973, Burnham and Anderson

2002), (2) the dimension-consistent Bayesian (Schwartz) Information Criteria (BIC) as an estimate of the Bayesian odds ratio (Link and Barker 2006), and jack-knifed cross-validation for one-step-ahead prediction (C-V) (Turchin 2003a). For AIC_c and BIC, we calculated the difference between the model's criterion and the top-ranked model (Δ_i) and the relative model weights (w_i) (Link and Barker 2006). Thus, the strength of evidence ($wAIC_c$, $wBIC$, $wC-V$) for any particular model varies from 0 (no support) to 1 (complete support) relative to the entire model set. However, the K-L prior used to justify AIC_c weighting can favor more complex models (with many tapering effects) when sample sizes are large (Link and Barker 2006). Therefore, BIC is generally considered a better procedure for ranking models when sample sizes are large and the goal is to determine the principal drivers of complex relationships (Link and Barker 2006). AIC_c and C-V therefore provide information on the existence of tapering effects necessary to maximize predictive capacity (Link and Barker 2006). As such, we considered BIC weighting to determine mosquito population dynamical model ranking ($n = 134$), and AIC_c and C-V weighting to examine shifts in carrying capacity ($n = 21$).

Carrying capacity

Carrying capacity (K) can be broadly defined as "the theoretical equilibrium population density a given (average) set of environmental conditions (e.g., food availability, breeding habitat) can support" (del Monte-Luna et al. 2004). Under classic negative-feedback density dependence, birth rates often decrease, and death rates typically increase as population density approaches K , with the mathematical definition of K being the point where these two rates are equal (i.e., population growth, $r = 0$). Although variants of the logistic model generally consider K to remain fixed over the time interval investigated, finite resources can still vary with time, causing K to be different at each time point (Bjørnstad and Grenfell 2001, del Monte-Luna et al. 2004).

Temporal variation in K can therefore be explained by adjustments in limiting resources; for example, in the typical monsoon pattern (dry/wet season) in northern Australia, the relative seasonal carrying capacity of mosquitoes will shift according to the availability of water among and within seasons. We therefore tested for correlations between interval-specific carrying capacities and the environmental parameters measured to explain variation in the ecosystem's capacity to support mosquito populations. Carrying capacity here is different from the Models 2 and 3 explained above, which assume K is an instant dynamic variable rather than a relatively constant parameter. The temporal variation in K modeled as a function of these same environmental correlates asks a different, but related question: to what extent can environmental conditions be used to predict

the maximum potential mosquito population size in any given season and year?

To investigate this question, we split the relative abundance time series for *A. vigilax* from 1994 to 2005 by monsoonal (dry/wet) season and used the fortnightly abundance averages to estimate K from the Gompertz-logistic model described previously for each year. This resulted in a total of 22 seasonal estimates of K over 11 years. This K time series was then used as a response variable (log-transformed) in linear models to investigate the correlation with the environmental factors described in the previous analysis (high tide frequency, total rainfall, and average relative humidity):

$$\log_e(K) = \alpha_0 + \boldsymbol{\beta} \times \mathbf{E}_t + \varepsilon_t \quad \varepsilon_t \sim \mathcal{N}(0, \sigma^2) \quad (4)$$

where K = Gompertz-logistic carrying capacity, $\boldsymbol{\beta} = (\beta_0, \beta_1, \dots, \beta_n)$, \mathbf{E}_t = vector of seasonal environmental factors ($E1_t, E2_t, \dots, En_t$), and ε_t represents unexplained error. MMI-ranking procedures were applied to determine relative model support.

RESULTS

Environmental variables (frequency of high tides, rainfall, and relative humidity), when treated as stochastic exogenous forces (Eq. 1), explained more variation in population growth rate (r) than their adjustments to mosquito carrying capacity (Eq. 2; Table 1). Models with K -adjusting environmental components ($\log(K) \times \mathbf{E}_t$) were poorly fitted, demonstrating that carrying capacity is relatively constant over the interval and does not fluctuate markedly depending on environmental conditions (Tables 1 and 2). Rather, environmental stochasticity appears to alter the relative rate at which mosquitoes respond to their own density. As such, the combination approach including environmental forcing of r and K (Eq. 3) does not provide better explanatory power than the simpler Model 1 approach using only stochastic exogenous variables as correlates.

The explanation of deviance in r increased from 31% up to >70% after the Gompertz-logistic model with a two-month lag integrated environmental effects (high-tide frequency, rainfall, and relative humidity; Table 3). Exogenous environmental conditions and endogenous density feedback contributed to explaining the variation in r by ~58% (i.e., 43% of 74%; Table 3) and ~42% (i.e., 31% of 74%; Table 3), respectively. Put more simply, environmental factors explained slightly more than one-half of the total explainable variation in population growth, with the remaining proportion explained by negative density feedback. Thus, negative density feedback is nearly as important as environmental conditions when predicting the abundance of mosquito populations over time.

High tide frequency was the most important determinant of exogenous variation in r , with weaker effects of rainfall and relative humidity. The model with the greatest support ($wBIC = 0.866$) included high-tide frequency and rainfall with a two-month lag (also best

TABLE 1. Ranking of models used to correlate environmental variables with population rate of change (r).

Model	%DE	ΔAIC_c	$wAIC_c$	ΔBIC	$wBIC$	R^2_{pred}	$wC-V$
GL + high tide frequency							
GL.1.2.St _{env}	54.8	0.0	1.000	0.0	1.000	0.673	1.000
GL.1.2	31.4	27.0	<0.001	21.6	<0.001	0.597	<0.001
GL.1	15.1	46.6	<0.001	38.5	<0.001	0.531	<0.001
GL.1.St _{env}	15.1	48.7	<0.001	43.3	<0.001	0.524	<0.001
GL.1.St _{env} .K _{env}	10.7	54.5	<0.001	49.1	<0.001	0.493	<0.001
GL + rainfall							
GL.1.2.St _{env}	43.4	0.0	0.800	2.6	0.212	0.307	1.000
GL.1.St _{env}	38.0	2.8	0.197	0.0	0.779	0.147	<0.001
GL.1.2	31.4	11.7	0.002	8.9	0.009	0.194	<0.001
GL.1	15.1	31.3	<0.001	25.8	<0.001	0.061	<0.001
GL.1.St _{env} .K _{env}	-18.8	78.6	<0.001	75.8	<0.001	-0.160	<0.001
GL + relative humidity							
GL.1.2.St _{env}	40.8	0.0	0.981	0.0	0.778	-0.070	1.000
GL.1.2	31.4	8.2	0.016	2.8	0.191	-0.210	<0.001
GL.1 _{env}	28.6	11.9	0.003	6.5	0.031	-0.270	<0.001
GL.1	15.1	27.8	<0.001	19.7	<0.001	-0.408	<0.001
GL.1.K _{env}	-26.6	83.4	<0.001	75.2	<0.001	-1.099	<0.001

Notes: The Gompertz-logistic (GL) model ($r_t = r_m[1 - \log(N_t)/\log(K)]$, where r_m = maximum r , N_t = abundance at time t , and K = carrying capacity) describing nonlinear reduction in r with N was used as the base density-feedback model that examined the additional contribution of each of three environmental variables in turn: (1) frequency of high tides, (2) rainfall, and (3) relative humidity. Variants of the GL model included (1) lags of interval 1 and 2 without environmental correlates, (2) environmental variables as a stochastic effect on r (St_{env}), (3) environmental correlates modifying carrying capacity (“K-ratio”; K_{env}), and (4) environmental correlates modifying r and K simultaneously (St_{env}.K_{env}). Also shown for each model is the percentage of deviance explained (%DE) as a measure of goodness of fit, and three ranking criteria based on Akaike’s Information Criterion corrected for small samples (AIC_c), Bayesian Information Criterion (BIC), and cross-validation (C-V). The change in information criterion relative to the top-ranked model (ΔAIC_c , ΔBIC), predicted R^2 for the C-V method describing model rank, and model weights ($wAIC_c$, $wBIC$, $wC-V$) are shown for the five most highly ranked models in each analysis. Highest relative strengths of evidence according to each ranking method are shown in boldface. Negative %DE indicates that the model performs worse than the reference model (exponential growth) for explaining variance in r .

supported by $wC-V$; Table 3). The coefficients of high tide frequency in lag 1 and lag 2 are $\beta_1 = 0.18$ (SE = 0.054; Fig. 3a) and $\beta_2 = -0.13$ (SE = 0.051; Fig. 3b), respectively. The relationship between r and rainfall was, in contrast, consistently negative over both lag intervals, albeit much weaker ($\beta_3 = -0.0019$, SE = 0.00052; $\beta_4 =$

-0.0006, SE = 0.00052; Fig. 3c, d). Among the environmental variables considered, high tide frequency with a second-order lag explained a larger component of the variation than rainfall (%DE = 55% vs. 43%, respectively), with an even smaller contribution from relative humidity (%DE = 41; Table 3).

TABLE 2. Ranking of linear regression models examining the hypothesized relationships between carrying capacity (K) and environmental variables: frequency of high tides (Tides), rainfall (Rain), and relative humidity (RH), as well as a temporal sequence (t) to detect trending.

Model	%DE	ΔAIC_c	$wAIC_c$	ΔBIC	$wBIC$	R^2_{pred}	$wC-V$
$K \sim 1$	0.0	0.000	0.229	0.000	0.264	-0.098	0.123
$K \sim Tides$	15.9	0.051	0.223	0.439	0.212	-0.009	0.312
$K \sim Rain$	11.0	0.870	0.148	1.259	0.141	-0.114	0.105
$K \sim RH$	9.8	1.072	0.134	1.460	0.127	-0.109	0.109
$K \sim t$	0.1	2.682	0.060	3.071	0.057	-0.234	0.034
$K \sim Tides + t$	16.7	2.925	0.053	3.385	0.049	-0.137	0.084
$K \sim Rain + t$	12.3	3.671	0.037	4.132	0.034	-0.275	0.024
$K \sim Rain + RH$	11.0	3.889	0.033	4.350	0.030	-0.168	0.062
$K \sim RH + t$	10.6	3.951	0.032	4.411	0.029	-0.270	0.025
$K \sim Rain + Tides$	17.5	6.193	0.010	6.347	0.011	-0.291	0.021
$K \sim Rain + Tides + t$	17.5	6.193	0.010	6.347	0.011	-0.291	0.021
$K \sim RH + Tides$	16.8	6.316	0.010	6.470	0.010	-0.310	0.018
$K \sim RH + Tides + t$	16.8	6.316	0.010	6.470	0.010	-0.310	0.018
$K \sim Rain + RH + t$	12.3	7.068	0.007	7.222	0.007	-0.331	0.015
$K \sim Rain + Tides + RH$	21.7	9.337	0.002	8.732	0.003	-0.318	0.016
$K \sim Rain + Tides + RH + t$	21.7	9.337	0.002	8.732	0.003	-0.318	0.016

Notes: Also shown for each model is the percentage deviance explained (%DE) as a measure of goodness of fit, and three ranking criteria based on Akaike’s Information Criterion corrected for small samples (AIC_c), Bayesian Information Criterion (BIC), and cross-validation (C-V). The change in information criterion relative to the top-ranked model (ΔAIC_c , ΔBIC), predicted R^2 for the C-V method describing model rank, and model weights ($wAIC_c$, $wBIC$, $wC-V$) are shown.

TABLE 3. Ranking of models used to correlate environmental variables (frequency of high tides [Tides], rainfall [Rain], and relative humidity [RH]) with population rate of change (r).

Model	%DE	ΔAIC_c	$wAIC_c$	ΔBIC	$wBIC$	R^2_{pred}	$wC-V$
GL.1.2.Tides.Rain.RH	73.9	0.000	0.684	9.305	0.008	0.713	0.104
GL.1.2.Tides.Rain.RH. t	74.0	2.110	0.238	14.067	0.001	0.709	0.035
GL.1.2.Tides.Rain	73.6	4.959	0.057	0.000	0.866	0.721	0.642
GL.1.2.Tides.Rain. t	73.7	7.169	0.019	4.788	0.079	0.717	0.217
GL.1.2.Tides.RH. t	65.4	13.587	0.001	6.012	0.043	0.692	0.001
GL.1.2.Tides.RH	64.9	16.547	<0.001	11.587	0.003	0.695	0.002
GL.1.2.Tides	54.8	25.457	<0.001	15.231	<0.001	0.673	<0.001
GL.1.2.Rain	43.4	40.736	<0.001	30.51	0.005	0.635	<0.001
GL.1.2.RH	40.8	44.235	<0.001	34.009	<0.001	0.622	<0.001
GL.1.2	31.4	52.454	<0.001	36.819	<0.001	0.597	<0.001
GL.1	15.1	72.079	<0.001	53.689	<0.001	0.531	<0.001

Notes: Ranking is based on the temporally lagged Gompertz-logistic (GL) model ($r_t = r_m[1 - \log(N_t)/\log(K)]$), where r_m = maximum r , N_t = abundance at time t , and K = carrying capacity). Also shown for each model is the percentage of deviance explained (%DE) as a measure of goodness of fit, and three ranking criteria based on Akaike's Information Criterion corrected for small samples (AIC_c), Bayesian Information Criterion (BIC), and cross-validation (C-V). The change in information criterion relative to the top-ranked model (ΔAIC_c , ΔBIC), predicted R^2 for the C-V method describing model rank, and model weights ($wAIC_c$, $wBIC$, $wC-V$) are shown. The highest-ranked model weights according to each information criterion ranking are shown in boldface in columns $wAIC_c$, $wBIC$, and $wC-V$. Highest relative strengths of evidence according to each ranking method are shown in boldface.

There was no evidence for a long-term temporal trend in interval-specific (seasons combined or separated) carrying capacity (Fig. 4a, b). Some of the temporal variation was explained weakly by some of the

environmental variables investigated, with high tide frequency having the relatively highest support (0.22, 0.21, and 0.31 $wAIC_c$, $wBIC$, and $wC-V$, respectively, %DE = 16%), followed by rainfall and relative humidity

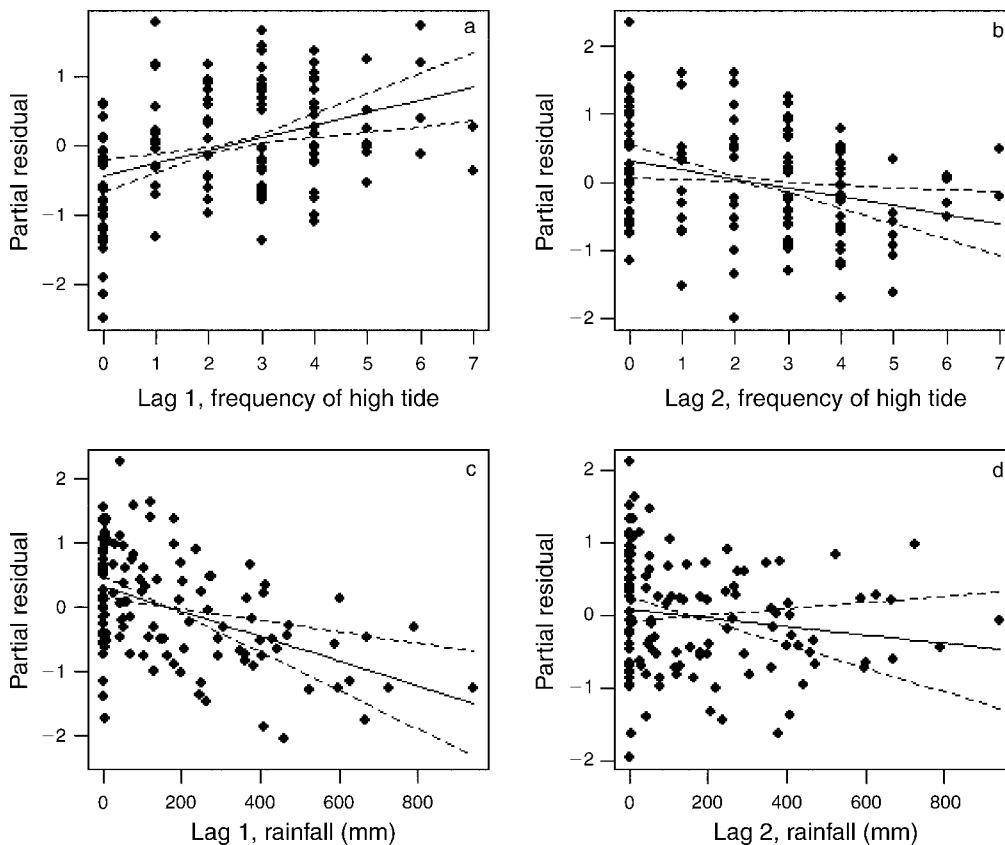


FIG. 3. Partial residual plots derived from the highest-ranked (according to Akaike's Information Criterion corrected for small sample sizes [AIC_c]) Gompertz-logistic model (see Table 3, Model 1: GL.1.2.Tides.Rain.RH) relating population rate of change (r) to frequency of high tides and rainfall at time interval lags of 1 and 2. Dashed lines indicate $\pm SE$ of the mean.

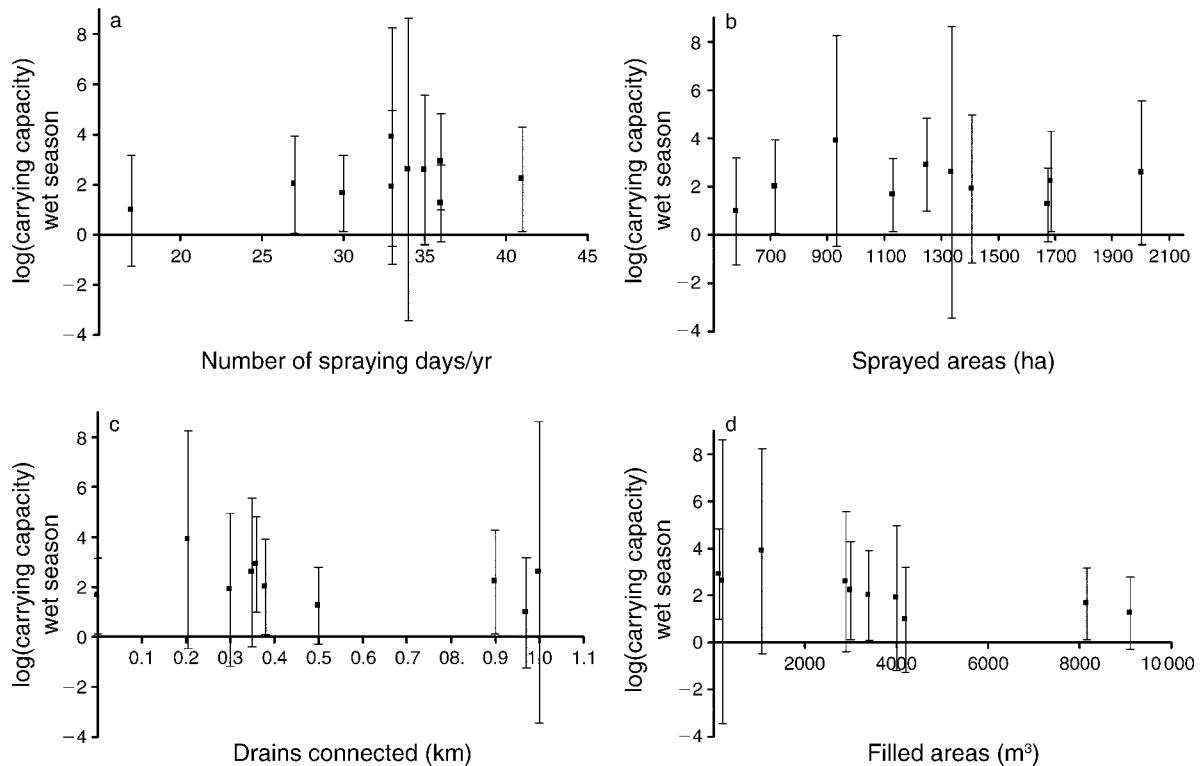


FIG. 4. Scatter plot depicting the relationship between log-transformed carrying capacity estimated from the model-averaged Gompertz-logistic equations for the wet season between 1994 and 2005 and: (a) the number of days per year when larvicide spraying occurred; (b) the extent of area sprayed with larvicide; (c) the length of drains concreted (built) to remove surface water; and (d) the total area filled to reduce standing water accumulation. Error bars show \pm SE.

(Table 2). However, the consistent negative values for R^2_{pred} implies that the correlates of K were fitting noise rather than any underlying signal (Turchin 2003a).

Modification of mosquito breeding habitat over the course of the interval investigated was sporadic (Fig. 4), with generally more engineering construction (new drains, breeding areas filled) in the earlier years (Fig. 4c). Spraying management was also most intensive between 1994 and 1998, followed by relatively lower activity in later years (Fig. 4d). Management activities such as habitat modification focus on reducing mosquito abundance in the wet season, so we examined evidence for their effects on seasonal carrying capacity. There was no strong evidence for a relationship between population control, drains concreted, and carrying capacity in the wet season (Fig. 5).

DISCUSSION

Our study provides an empirical framework for discerning the relative contributions of endogenous and exogenous drivers of mosquito population dynamics. We have demonstrated that it is imperative for both types of drivers to be considered simultaneously when predicting mosquito abundance and population growth patterns. Previous studies of the population dynamics of mosquitoes and other pest insects have focused mainly

on the correlation of environmental variables with abundance (e.g., Shaman et al. 2002, Mondet et al. 2005, Diuk-Wasser et al. 2006), with more studies in the last five years considering density-feedback mechanisms (Gimnig et al. 2002, Kiflawi et al. 2003, Yang et al. 2008). Uniquely, this analysis of the *A. vigilax* dynamics in northern Australia provided a direct confirmation of the higher contribution of environmental drivers relative to density feedback control, but ascertained that endogenous control of mosquito populations represents an important component of the explainable variation in population growth rates. The multi-model inferential support of the two-month density lag suggests that mosquito population growth rate is driven, in part, by elevated survival or fertility in generations following periods of low larval density (Gimnig et al. 2002, Sibly et al. 2005).

High tide frequency contributed the strongest explanatory power to *A. vigilax* population growth rate (Table 3, Fig. 3). Our two-interval lag model provided evidence for a complex, but logical relationship between high tide frequency and growth rate (a positive relationship at lag 1 and a negative relationship at lag 2). *A. vigilax* primarily breeds in saline to brackish wetlands along the coast, where females lay their eggs on moist mud and at the base of plants in high marshlands dominated mainly

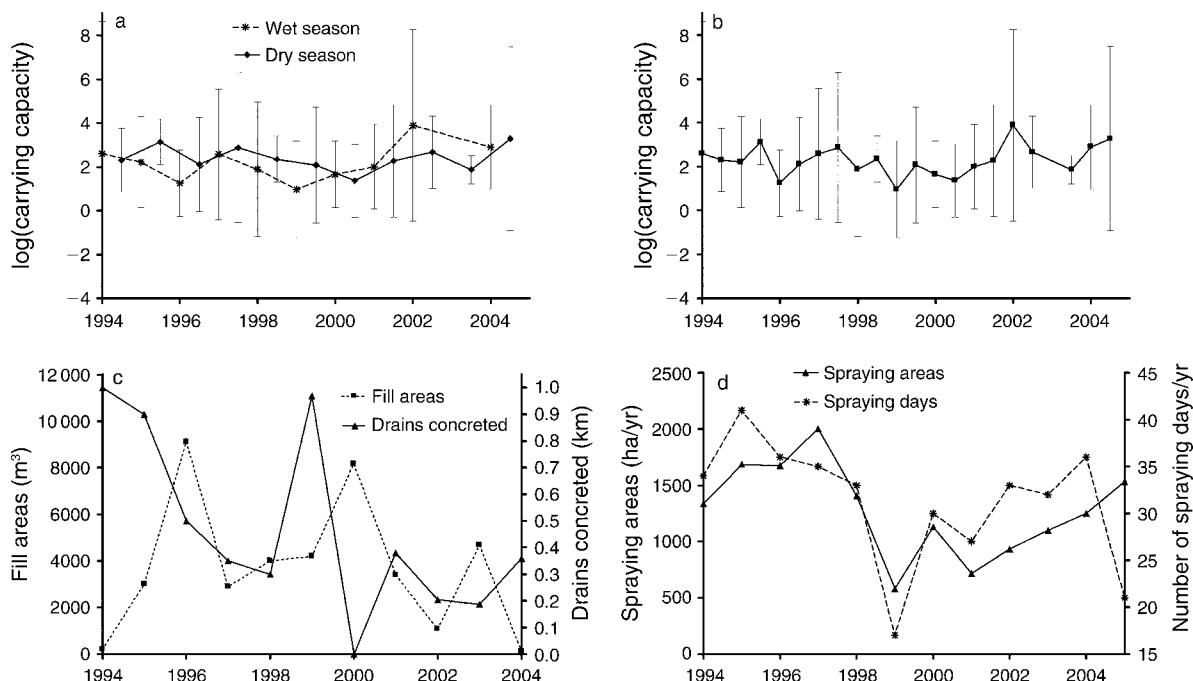


FIG. 5. Temporal trends in the (a) log-transformed *Aedes vigilax* carrying capacity as estimated by the Gompertz-logistic (GL) models in the wet and dry seasons; (b) combined seasonal log-transformed carrying capacity; (c) engineering management (filled areas to reduce water accumulation and drains built to remove excess surface water); and (d) the spatial and temporal extent of larvicide spraying in Darwin between 1994 and 2005. Temporal and seasonal trends were examined based on the following equation: $\log_e(K) = \alpha_0 + \beta \times \text{season} + \varepsilon_t$, where K is the Gompertz-logistic carrying capacity, β is the coefficient of season, and ε_t represents unexplained error. The coefficients of wet season (β_{wet}), dry season (β_{dry}), and combined-season (i.e., entire year; $\beta_{\text{comb.}}$) temporal slopes were 0.004 (SE = 0.03), -0.002 (SE = 0.11), and -0.006 (SE = 0.06), respectively. In other words, long-term carrying capacity fluctuated widely around a relatively stable mean. Error bars show \pm SE.

by brackish water reeds (*Schoenoplectus* spp.) or mangroves (*Avicennia* spp. or *Bruguiera* spp.). As high tides retreat, eggs are laid on moist substrata where they mature quickly and become drought-resistant until the onset of the next high-tide cycle or flood rain. This final process can take weeks to months to re-flood these surfaces and stimulate the eggs to hatch. After the retreat of particularly high tides, substrata suitable for egg laying and development become readily available, so population size generally increases; however, the following time interval generally results in a decrease in population size. The diverging directions of the relationship between r and high-tide frequency at one- and two-interval lags demonstrates the rapid response to high densities typical of the Gompertz-logistic model (i.e., rapid and strong negative density feedback as soon as population size begins to increase).

Rainfall had, in contrast, a consistently negative impact on population growth rate over both lag intervals. The extreme seasonality of the north Australian monsoon (November–April) results in large amounts of rainfall during a relatively short interval of the year (Fig. 2c). This reduces the availability of suitable habitats (moist substrata) required by ovipositing adult female mosquitoes. Despite the drop of reproduction rate in the previous time interval with

increased rainfall, the relatively consistent rainfall patterns within a season in this region negate the probability of a rebound of reproduction rate at the next lag interval.

A fundamental aim in the management of disease-carrying mosquito populations is to reduce overall densities and the probability of large peaks in population size, which enhance the risk of transmission. As such, an underlying but untested assumption of the engineering program has been that modifying drainage patterns reduces the persistence of ephemeral breeding pools. Our explicit modeling of the drivers of temporal variation in environmental carrying capacity (K) investigated this assumption directly. We found that temporal variation in mean *A. vigilax* K was weakly explained by environmental variation. In other words, environmental forcing does not appear to modify greatly the degree to which the available habitats can support mosquito populations; rather, stochastic changes modify the rate at which the population increases or decreases above and below carrying capacity. However, the degree of fit for all K models investigated was low, likely due, in part, to a relatively small sample size, restricting our ability to identify clear trends.

Our qualitative comparison of the physical and chemical management of mosquito habitats over the

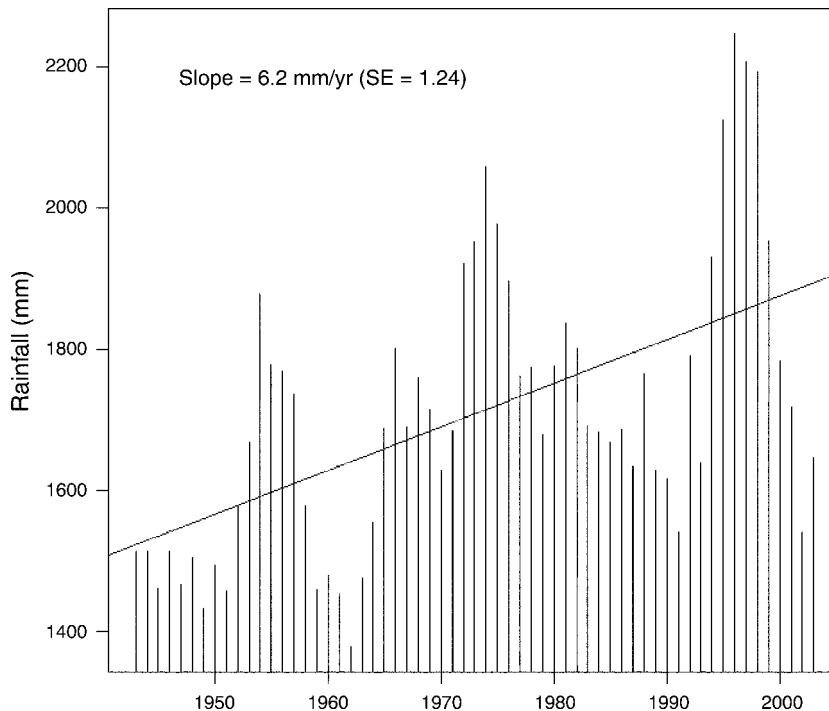


FIG. 6. The 12-month July–June cumulative rainfall between 1943 and 2003 in Darwin, Northern Territory, Australia. The trend line is based on a least-squares linear regression of the five-year running mean ($R^2_{\text{adjust}} = 0.2845$).

same time interval provides some additional insight. For example, recent reductions in drain construction, filling operations, and area sprayed may have contributed to the higher maximum carrying capacities observed in the latter portion of the K time series (Figs. 4 and 5). Indeed, there is the tantalizing suggestion of a weak negative relationship between carrying capacity and the number of drains concreted and areas filled (Fig. 5), but more data are required to verify this hypothesis. However, it appears that the main effects of human modification to mosquito breeding habitats (engineering works) and larval survival (larvicide application) is the reduction in rate of population increase rather than a reduction in the environment's capacity to support high mosquito densities.

In addition to the contribution our results bring to the long-term management of mosquito populations in northern Australia with respect to physical and chemical manipulation of breeding environments, this work offers insight into the hypothesized effects of climate change on mosquito abundance trends. There is a heterogeneous pattern of long-term (50+ years) rainfall change in Australia and globally, with the tropical region of the Northern Territory experiencing clear increases in total annual rainfall since the 1940s (Australian Government Bureau of Meteorology; *available online*).⁸ In the greater Darwin region, 12-month July–June cumulative rainfall increased at an average rate of 6.2 mm/yr (SE = 1.24) between 1943 and 2003 based on a least-squares linear regression of five-year running mean (Fig. 6). Our

models predict that this trend would have an overall effect of reducing the rebound potential of saline-breeding species such as *A. vigilax*. The increased availability of ephemeral freshwater breeding pools implies that freshwater breeding species, such as *Culex annulirostris*, may be exerting greater ecological dominance (Yang et al. 2008). Climate change scenarios also predict that rainfall intensity (frequency of heavier rainfall events) is also likely to increase in areas with increasing rainfall (Goswami et al. 2006).

Recent reports from the Intergovernmental Panel on Climate Change show that the Earth's temperature is most likely to increase by 1.1–6.4°C by 2100, depending on future emission scenarios and climate sensitivity (IPCC 2007). Over Australia in recent decades, observed temperatures have increased in a manner consistent with other areas around the world. The result is that global average sea levels are predicted to rise by up to 59 cm due to the effect of thermal expansion and loss of mountain glaciers, and the possibility of a further, possibly substantial contribution, from polar ice sheet melting (IPCC 2007). These scenarios predict increases in the frequency and intensity of high tide events (Scavia et al. 2002). Our models clearly predict that increases in the frequency of high tide events will provide more suitable breeding habitat for *A. vigilax* and other saline breeding species, which may, by proxy, increase the frequency and transmission of mosquito-borne diseases in northern Australia.

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