

Importance of endogenous feedback controlling the long-term abundance of tropical mosquito species

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Abstract Mosquitoes are a major vector for tropical diseases, so understanding aspects that modify their population dynamics is vital for their control and protecting human health. Maximising the efficiency of control strategies for reducing transmission risk requires as a first step the understanding of the intrinsic population dynamics of vectors. We fitted a set of density-dependent and density-independent models to the long-term time series of six tropical mosquito species from northern Australia. The models' strength of evidence was assessed using Akaike's Information Criterion (AIC_c), Bayesian Information Criterion (BIC) and jack-knifed cross-validation (C-V). Density dependence accounted for more than 99% of the model weight in all model-selection methods, with the Gompertz-logistic (Cushing model) being the best-

supported model for all mosquito species (negative density feedback expressed even at low densities). The second-most abundant species, *Aedes vigilax* (a saline breeder), showed no spatial heterogeneity in its density-dependent response, but the remaining five species had different intrinsic growth rates across 11 study sites. Population densities of saline species were high only during the late dry to early wet season following the highest tides of the month or early flood rains when swamps were mostly saline, whereas those of freshwater species were highest during the mid-wet and mid-dry seasons. These findings demonstrate remarkably strong density dependence in mosquito populations, but also suggest that environmental drivers, such as rainfall and tides, are important in modifying seasonal densities. Neglecting to account for strong density feedback in tropical mosquito populations will clearly result in less effective control.

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Introduction

Mosquito-borne pathogens causing malaria, dengue, yellow fever, filariasis and other well-known conditions, have historically been a major cause of human disease and death (Gubler 1991). However, effective targeted control programmes over the last 50 years have reduced the problem in most regions of the world, except in parts of Africa (Gubler 2001). These programmes emphasised the elimination of mosquito breeding sites through improved environmental hygiene coupled with a limited use of chemical insecticides. Yet, with the increasing rate of

insecticide and drug resistance, changes to public health policy, trends in human demography and society, and climate change, there is a concern that these diseases will once again become a major issue for public health (World Health Organization 1986; Gratz 1999; Sutherst 2004).

Recent work has focused on maximising the efficiency of mosquito control strategies for reducing disease transmission risk (Bergquist 2001) by abating the abundance of pest species. Effective control of these insect populations must take the fundamental first step of understanding their intrinsic population dynamics, because these properties will influence the rate of population recovery and spread following control (Grech et al. 2007). Indeed, there is a general consensus among ecologists that account must be taken of intrinsic (endogenous) and extrinsic (exogenous) population controls (Turchin 1995) when analysing abundance time series, with increasing emphasis placed on determining the degree of interaction between the two (Sæther 1997; Wang et al. 2006; de Little et al. 2007). Endogenous control operates typically via negative density-feedback mechanisms whereby vital rates (e.g., survival, fertility) or individual fitness are reduced as population density increases (Turchin 2003). Exogenous processes include stochastic environmental pressures and human mosquito control activities that affect population density but are not affected by it. Indeed, past mosquito research has placed emphasis on determining the environmental factors that correlate with mosquito abundance (e.g., Russell and Whelan 1986; Su et al. 2003; Kunkel et al. 2006), even though it is known that mosquito populations can also demonstrate strong intrinsic (density-dependent) regulation (Bradshaw and Holzapfel 1989; Leonard and Juliano 1995; Juliano 1998; Gimnig et al. 2002; Kiflawi et al. 2003).

Various population models have been applied to a wide range of species to explore the extent to which density regulation drives fluctuations in abundance time series (e.g., Hanski 1990; Woiwod and Hanski 1992; Gimnig et al. 2002; Yamamura et al. 2006). However, most previous studies have relied on the classic framework of Neyman–Pearson hypothesis testing (NPHT), with the null hypothesis (density-independent model) rejected if the probability is less than the Type I error (usually set arbitrarily at 0.05). It can be difficult to use NPHT to provide answers to complex ecological problems (Burnham and Anderson 2002, 2004; Elliott and Brook 2007; Lukacs et al. 2007) because: (1) a P value is not the probability that the null hypothesis is true—it instead represents the probability that the observed effect, or a more extreme effect, resulted from the null model; (2) large P values are not evidence that the null hypothesis is true—they are confounded by sample size and effect size; (3) small P values do not indicate goodness-of-fit; (4) a priori power tests are

difficult to perform; and (5) alternative hypotheses are encapsulated by a deviation from the null (i.e., only one alternative hypothesis is considered, but not modelled) (McCarthy 2007).

Alternative options have used either Bayesian Information Criterion (BIC) or jack-knifed cross-validation (CV) best-model selection. Zeng et al. (1998) used BIC to select a best model for 31 insect time series. Twenty-three of their 31 cases showed evidence for density regulation, of which 19 included complex density-dependent dynamics. Turchin (2003) used C-V methods to determine the complexity of phenomenological time-series models in the absence of a priori information. He defined the optimal process order (or dimension) of models first and then chose the polynomial degree best describing the realised relationship between population growth and abundance. A more comprehensive approach exploiting the full power of multi-model inference (MMI) has recently been adopted. Models are scaled according to information-theoretic or Bayesian approximation estimates of model parsimony, e.g. Akaike's and Bayesian Information Criteria (Akaike 1973; Burnham and Anderson 2002; Link and Barker 2006) to incorporate model selection uncertainty into the determination of density regulation's relative contribution to population processes (Bradshaw et al. 2006; Brook and Bradshaw 2006; Chamaillé-Jammes et al. 2008). Brook and Bradshaw (2006) recently evaluated the relative strength of evidence of different dynamical models (density-dependent and density-independent) in long-term abundance time series of 1,198 species—with the conclusion that most species demonstrate some form of density regulation.

Several important human diseases are currently or potentially transmitted by the mosquito species present in various areas of Australia, yet little work has been done on mosquito population dynamics in Australia. According to the Australian National Arbovirus and Malaria Advisory Committee's annual report for 2004–2005, Ross River virus disease (RRV) (45%) and Barmah Forest virus disease (BFV) (30%) are the most commonly reported mosquito-borne diseases in Australia. In addition, dengue virus infection (DENV), Kunjin virus infection (KUNV) and Murray Valley encephalitis virus infection (MVEV) have been detected (Mackenzie et al. 1993; Burrow et al. 1998). The highest national rates of both RRV and BFV occur in the tropical north (Liu et al. 2005), and there are several *Anopheles* species that pose a risk as potential malaria vectors should the disease be introduced through infected human travellers. To tackle the increasing threat of mosquito-borne diseases in this region and to provide general control of human pest species, the Northern Territory Government launched a mosquito monitoring and control programme in the 1980s to reduce the short- and long-term densities of the major mosquito species around

urban areas. Of the 98 mosquito species known to occur in the Northern Territory, six are relatively common human pests: *Aedes vigilax*, *Culex annulirostris*, *Anopheles bancroftii*, *Coquillettidia xanthogaster*, *Culex sitiens* and *Mansonia uniformis*. The two most common species, *Ae. vigilax* and *Cx. annulirostris*, are the most important vectors of RRV and BFV in the Northern Territory (Whelan et al. 1997), with *Cx. sitiens* representing another possible RRV vector. *Aedes vigilax* is a major coastal pest species breeding principally in saline wetlands, whereas *Cx. annulirostris* is a freshwater species found along coastal and inland areas. *Anopheles bancroftii* represents a potential malaria vector.

Using a long-term (15-year) weekly monitoring dataset for these six species, we examined the phenomenological evidence for and strength of density regulation to determine to what extent intrinsic dynamics dictate the rate of change in mosquito abundance. We use a modified version of the methods adopted by Brook and Bradshaw (2006) to (1) examine the multi-model inferential evidence for density regulation in monthly time series data collected from 11 CO₂-trap sites within the Greater Darwin region (Fig. 1), (2) describe the form and strength of the endogenous control mechanism for each species, and (3) evaluate the evidence for spatial variation the feedback mechanism among trap sites. Our objectives are to provide land-use managers with evidence-based advice for optimal mosquito control strategies and to develop insight into the general mechanisms of endogenous control of disease-carrying insects worldwide. While we acknowledge that environmental determinants of mosquito abundance are an essential component in predictive models, our main aim was to quantify the relative strength and form of negative density feedback in tropical Australian mosquitoes in general, rather than predict abundance trends per se.

Materials and methods

Dataset

Mosquito population density data were collected weekly by the Medical Entomology Branch of the Northern Territory Department of Health and Community Services (DHCS) at 11 locations (Fig. 1) in Darwin, Australia for routine surveillance. The study region is situated between 12°22'–25'S latitude and 130°51'–56'E longitude in Greater Darwin near various surrounding swamps (Russell and Whelan 1986). CO₂-baited mosquito traps (Rohe and Fall 1979) were checked weekly at each location. CO₂-baited light traps offer many advantages over other capture techniques (e.g., human bait, aspirators, BG-Sentinel; Williams et al. 2006) because they are

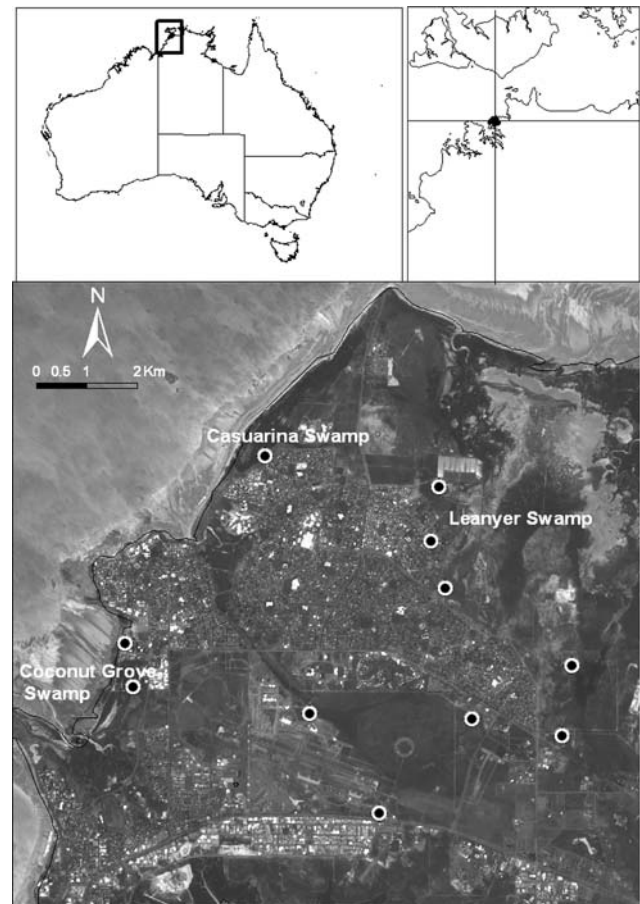


Fig. 1 Map of the Greater Darwin region, Northern Territory, Australia, showing the position of the 11 mosquito trapping sites

generally less labour-intensive, provide all-night collection, offer no bias based on individual attractiveness or skill of the collector, target nulliparous females, and are effective for many generalist-feeding Australian species such as *Ae. vigilax* and *Cx. annulirostris* (Russell and Whelan 1986; Van Essen et al. 1994; Miller et al. 2005; Williams et al. 2006). Indeed, CO₂-baited mosquito traps are effective for registering relative adult abundance and population rates of change (Whelan et al. 2005). For this particular study, we only used the data on female population density due to their blood-feeding behaviour and their importance for disease transmission.

Our initial analysis used simple phenomenological models that avoided considering age structure and overlapping generations (Turchin 2003). Under tropical condition in Darwin, an average female mosquito normally lives for 1–2 weeks (Russell 1987). Larval development of her offspring generally takes 4–10 days with the shorter period evident in *Aedes* species during summer. The final larval stage develops into an active comma-shaped pupa from which the adult mosquito emerges about 2 days later.

It takes around 2 weeks to complete a single generation in the mosquito life cycle. To avoid potential problems associated with overlapping generations in our dataset (e.g. Lande et al. 2002), fortnightly and monthly data of *Ae. vigilax* and *Cx. annulirostris* were tested to evaluate the sensitivity of the models assessed to variation in the duration of the transition interval chosen (2 or 4 weeks). We found no evidence that model ranking or strength of effect differed substantially when using either of the two intervals (results not shown), so we present all model results based on monthly density data for all species. The completed dataset spans 180 months (15 years), ranging from January 1991 to December 2005 (Fig. 2) at 11 locations.

Time series analysis

All analyses were done in the R Package V2.4.0 (R Development Core Team 2004). We used an autocorrelation function (ACF) to determine if there were lagged density responses, and the partial autocorrelation function (PACF) to determine the strength of relationships, i.e., to detect dependencies between sequential densities after removing the autocorrelation effect (Turchin 2003).

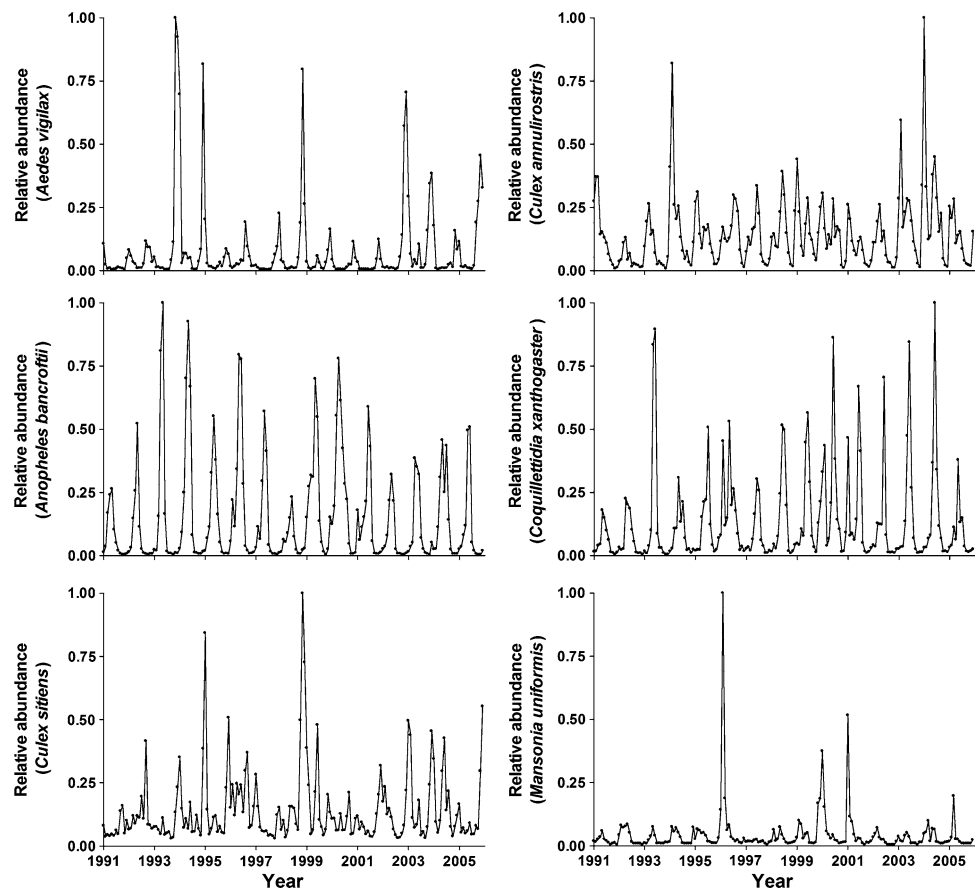
Population dynamics models

Although there are many potential mathematical simplifications of complex population dynamics in time series (e.g., Hall and Cummins 2005; Yamamura et al. 2006), we used an a priori model-building strategy to arrive at a set of five population dynamics models commonly used to describe phenomenological time series data (Turchin 2003; Brook and Bradshaw 2006) and applied these to our mosquito density datasets. All five models can be derived from the generalised θ -Ricker population growth model according to the transformation of r_m and θ :

$$\log_e \left(\frac{N_{t+1}}{N_t} \right) = r = r_m \left[1 - \left(\frac{N_t}{K} \right)^\theta \right] + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \quad (1)$$

where N_t denotes mosquito population size at time t , r = realised population growth rate, r_m = maximal intrinsic r , K = carrying capacity, θ controls the shape of the relationship between r and N_t , and ε_t represents the environmental variability and other unexplained factors. Due to insufficient information, we could not determine the relative contribution of measurement versus process error

Fig. 2 Relative abundance monthly time series for the six most common mosquito species caught in Darwin over all years examined (1991–2005). Maximum values are set to 1.0



(Freckleton et al. 2006; see also “Discussion”), so only total error (ε_t) was considered.

Density-independent models assume constant growth without the influence of density. Two density-independent models were applied: random walk with $r_m = 0$ (RW, Eq. 2); and exponential growth with $K \rightarrow \infty$ (EX, Eq. 3). In contrast, density-dependent models consider r as related linearly or non-linearly to N_t : a stochastic form of the Ricker-logistic model with $\theta = 1$ (RL, Eq. 4); a stochastic Gompertz-logistic (Cushing) model with logarithm-transformed N_t and K , with $\theta = 1$ (GL, Eq. 5); and a generalised θ -Ricker growth model (TR, Eq. 1).

$$r = 0 + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \quad (2)$$

$$r = r_m + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \quad (3)$$

$$r = r_m \left[1 - \left(\frac{N_t}{K} \right) \right] + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \quad (4)$$

$$r = r_m \left[1 - \left(\frac{\log_e(N_t)}{\log_e(K)} \right) \right] + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \quad (5)$$

All models except TR were fitted on the basis of maximum-likelihood using linear regression. For TR, we applied non-linear regression based on both Nelder–Mead and quasi-Newton optimisation (Dennis and Taper 1994) initiated with parameter estimates of r_m , K and θ derived from a simulation routine analogous to the approach employed by Sibly et al. (2005). We first set a vector ranging from near 0 to twice the maximum observed r or N (for the r_m and K vectors, respectively) and near 0–10 for the θ vector. Each vector had 50 intervals between minimum and maximum values. For each of the $50 \times 50 \times 50$ (125,000) combinations of r_m , K and θ , we calculated predicted r using Eq. 1 and the maximum log-likelihood, and stored the successively larger values of the latter. The combination of r_m , K and θ producing the maximum log-likelihood were subsequently used as the starting parameters for the Nelder–Mead and quasi-Newton optimization (implemented using the `optim` function in the R Package; R Development Core Team 2004). Both optimisation algorithms produced the same results.

Model comparison

To rank and weight the five models in the a priori set ($i = 1$ –5), three separate methods were used because each can provide slightly different rankings based on the size of the dataset and presence/absence of tapering effects (Burnham and Anderson 2004; Link and Barker 2006): (1) Akaike’s Information Criterion (AIC_c) corrected for small sample sizes (Akaike 1973; Burnham and Anderson 2002), and (2) the Bayesian Information Criteria (BIC) (Link and Barker 2006), and jack-knifed cross-validation (C-V)

(Turchin 2003). 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. AIC_c weighting can favour 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). C-V is a computationally expensive analogue of AIC and gives a direct indication of whether mostly “noise” or “signal” is being captured by the goodness-of-fit metric ($R_{\text{predicted}}^2$). AIC_c and C-V therefore provide information on the existence of tapering effects necessary to maximise predictive capacity (Link and Barker 2006). Given the large sample size in this study ($n = 180$) and our focus on identifying the source of variation in r , we considered BIC weighting primarily to determine mosquito population dynamical model ranking.

Spatial heterogeneity and temporal trends

To test for spatial heterogeneity in the type of density-dependent response among trap sites, we fitted a series of linear mixed-effects models. This was based on the top-ranked model from the previous procedure (GL), elaborated to include variation in the intercept and slope terms to represent potentially different patterns among locations. The model variants were: (1) intercept only as a random effect; (2) slope only set as a random effect; (3) intercept and slope as independent random effects; and (4) a GL model without spatial random effects. We employed the same MMI-ranking procedures described above to determine model support.

We tested for temporal trends (i.e., declining or increasing populations *on average*, despite any oscillatory behaviour). This model set incorporated a time sequence (t) into the GL model, as well as a t^2 term to account for possible non-linear (quadratic) trends. Seasonality was investigated by coding months as “wet” (November–April) or “dry” (May–October) to mimic the summer monsoonal pattern of rainfall typical of the Australian wet–dry tropics (Meehl et al. 2006). As before, the full MMI procedure was applied.

Results

The six mosquito species showed different seasonal changes in abundance over the 15-year monitoring period

(Figs. 2, 3, 4). Saline-breeding species (*Ae. vigilax* and *Cx. sitiens*) have relatively lower densities in the dry season, but most freshwater species have one or two peaks throughout the year. Since the dominant species are *Ae. vigilax* and *Cx. annulirostris* (Fig. 3), we have taken them as examples to summarise the major differences between saline- and freshwater-breeding species. Densities of *Ae. vigilax* decrease from a wet season peak between November and January, and then rapidly decline to a dry season low in July (Fig. 4a), whereas *Cx. annulirostris* density increases rapidly with the onset of rains in the early part of the wet season and maintains this high density throughout much of the dry season, before collapsing again from August to November (Fig. 4d). For *Ae. vigilax*, the wet and dry season \bar{r} were -0.439 and 0.466 , respectively (if season is ignored, $\bar{r} = 0.010$), while those of *Cx. annulirostris* were 0.369 and -0.345 , respectively (mean overall $\bar{r} = 0.011$). Thus, *Cx. annulirostris* appears to depend strongly on the rain received during the wet season, with a greater capacity for population increase in the wet season and rapid population crashes during the dry season.

The ACF also depicts marked cycles in each of these dominant species' abundance time series. The annual (12-month) cycle is clearly dominant from the ACF, and there is a strong positive correlation of mosquito population density between successive months (lag = 1) (Fig. 5a, c). We also detected a strong negative correlation between density 6 months apart (lag = 6) for *Ae. vigilax* (Fig. 5a), and a 4-month lag for *Cx. annulirostris* (Fig. 5c). The partial autocorrelation function showed a strong negative feedback at lags of 2 months for both species (Fig. 5b, d).

When pooled over all trapping sites, the combined MMI evidence for density dependence was $>99\%$ for all mosquito species, based on the sum of the $wAIC_c$, $wBIC$ or wC .

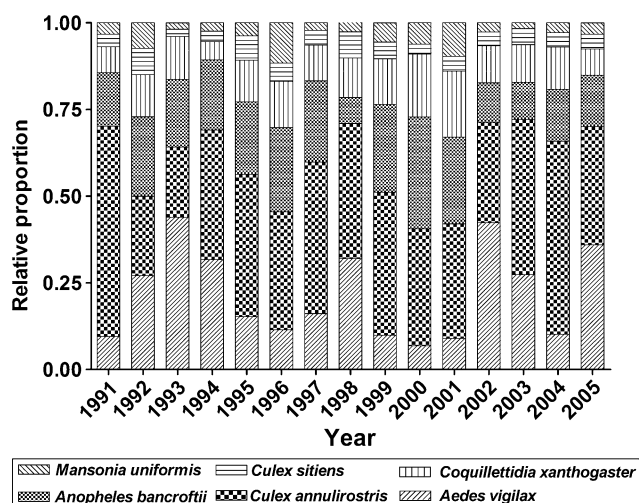


Fig. 3 Relative proportional abundance of the six most common mosquito species from 1991–2005

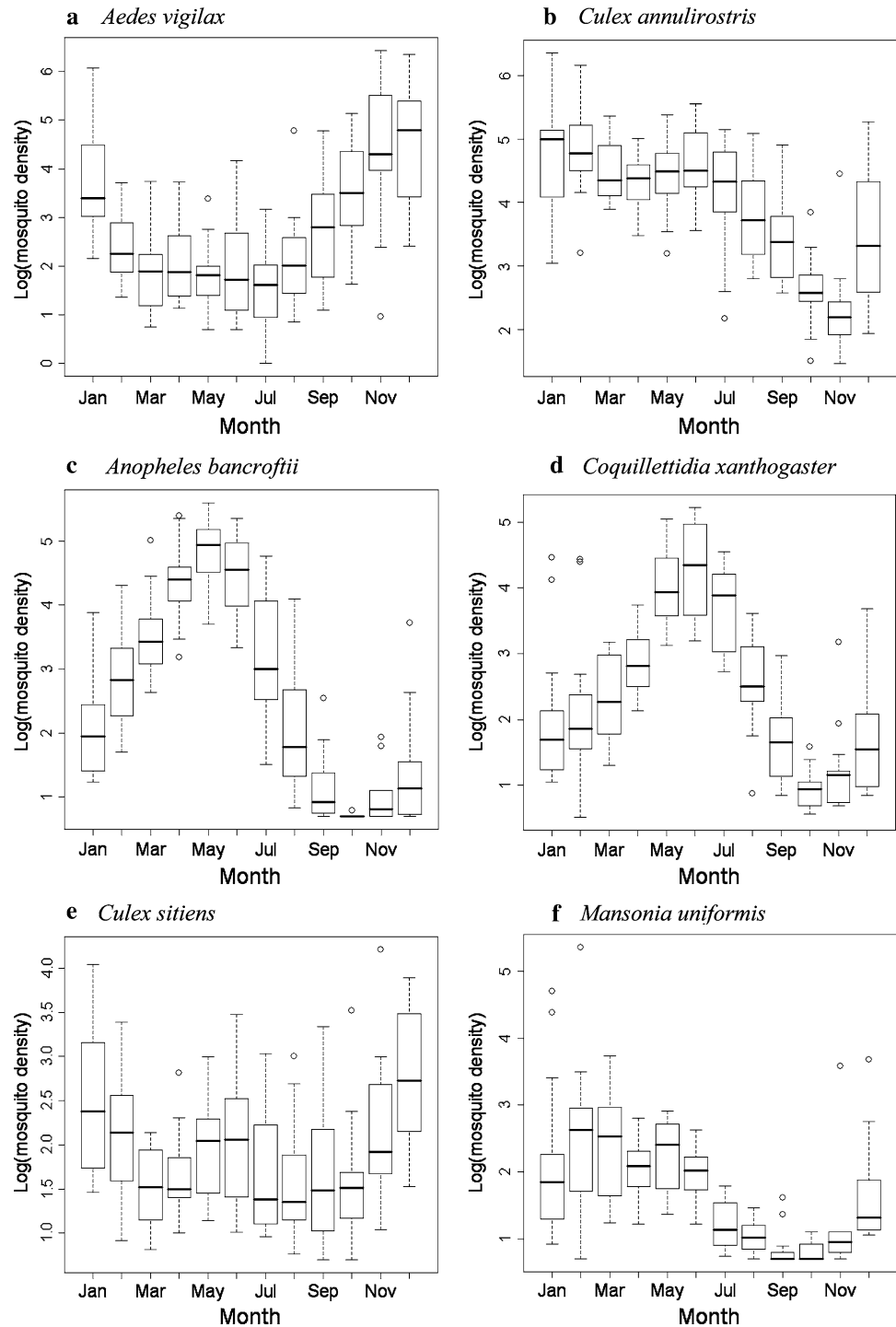
V for the RL, GL and TR models (Table 1; full model rankings shown for *Ae. vigilax* and *Cx. annulirostris*; for sub-dominant species only the best-fitting model results are shown). All metrics indicated the greatest and overwhelming support for the Gompertz-logistic (GL, or Cushing) model. Indeed, $wBIC$ for the GL model was $>86\%$ of the total weight. BIC is generally considered more appropriate for detecting main effects with large sample sizes, because under such circumstances AIC_c tends to favour more complex models (Link and Barker 2006). The percentage deviance explained (% DE) in r by density was 26.90% for *Cx. annulirostris*, and 12.76% for *Ae. vigilax*, suggesting a stronger density-feedback mechanism in the former species. We tested this hypothesis directly by comparing the slopes of the r versus $\log_e(N)$ (GL) relationship derived from the standardised time series, where maximum density for each species was set to 1 and all other values rescaled. The slope of the relationship for *Ae. vigilax* was -1.608 ($\hat{\sigma} = 0.904$), and -2.564 for *Cx. annulirostris* ($\hat{\sigma} = 0.618$), reinforcing the idea of a stronger negative feedback mechanism in *Cx. annulirostris* (Fig. 6).

The degree of spatial heterogeneity in the strength of density feedback was different for each species (Table 2; full model rankings shown for *Ae. vigilax* and *Cx. annulirostris*; for sub-dominant species only the best-fitting model results are shown). There was no clear evidence for spatial variation in *Ae. vigilax* ($wAIC_c = 0.596$ and $wBIC = 0.684$ for the no random-effect model; Table 2). In contrast, there was little evidence to support the aspatial model in the remaining five species. For instance, *Cx. annulirostris* had the strongest evidence for an intercept-only spatial effect ($wAIC_c = 0.622$ and $wBIC = 0.998$; Table 2). Although there was some suggestion of a small long-term increase in both populations ($\bar{r} > 0$, see above), this was not sufficiently strong to support a time effect in the models considered (Table 3). Except for *Cx. sitiens*, the remaining species demonstrated strong support for the GL model including season (wet/dry), and weak evidence for an effect of time (Table 3). The best-fitting models and their estimated coefficients (with SE in brackets) for *Ae. vigilax* and *Cx. annulirostris* were: $\hat{r}_{\text{vigilax}} = 0.918(0.174) - 0.189(0.057) \log_e N_t - 0.776(0.157) \times \text{season}$ and $\hat{r}_{\text{annulirostris}} = 1.263(0.268) - 0.394(0.062) \log_e N_t - 0.691(0.123) \times \text{season}$.

Discussion

Multi-model inference demonstrates clearly that mosquito populations in tropical north Australia exhibit strong endogenous control, explaining between approximately 10–20% of the variation in population rate of change among the species examined. This is an important result for management of these pests because it indicates that control measures

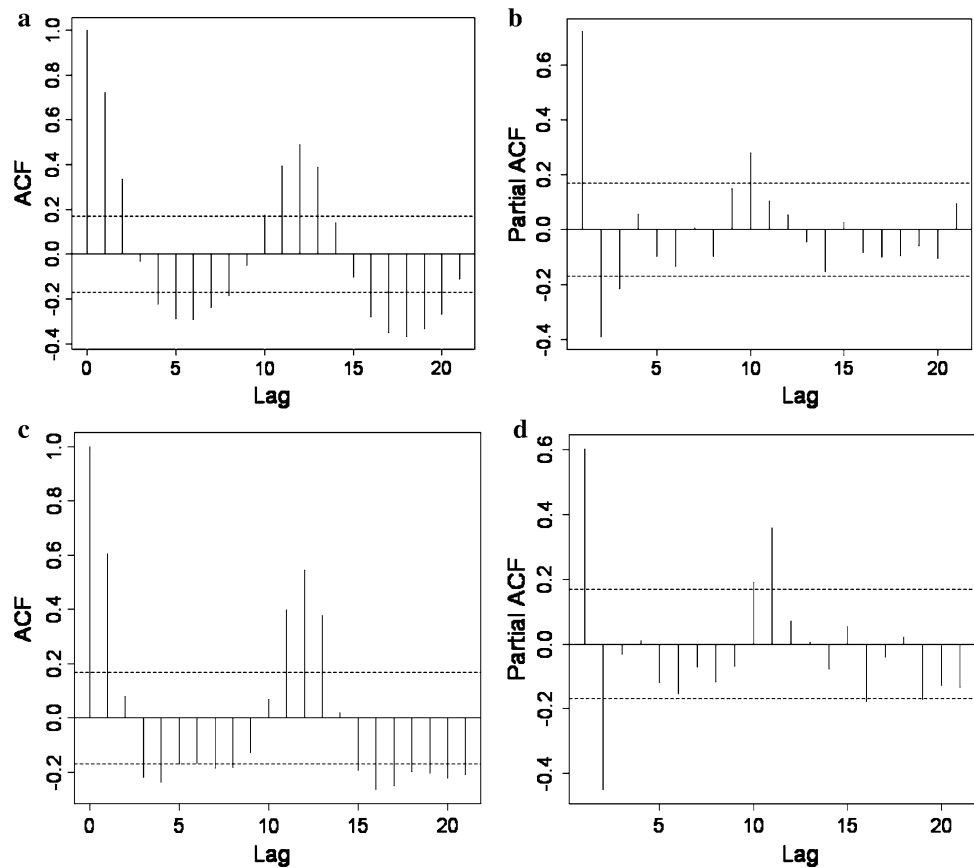
Fig. 4 Box and whisker plots showing the monthly variation in population density of six mosquito species over all years examined (1991–2005). Monthly values show the smallest and largest observation, lower and upper quartiles and median per month



failing to account for intrinsic dynamics will likely overestimate the medium- to long-term effectiveness of density suppression programmes. Our results, derived from a unique long-term database covering more than 180 generations of all mosquito species examined, support the view that the population dynamics of most species are influenced measurably by density-dependent processes (Zeng et al. 1998; Brook and Bradshaw 2006; Yamamura et al. 2006).

Consistent with previous findings that organisms with high turn-over rates such as insects generally demonstrate strong evidence for a Gompertz-logistic-like negative feedback (Sibly et al. 2005; Brook and Bradshaw 2006; Yamamura et al. 2006), the GL (Cushing) model was strongly supported in all six mosquito species we examined. The GL model expresses rates of population growth as a negative log-linear relationship with density, with high

Fig. 5 Autocorrelation functions (ACF) for (a) *Ae. vigilax* and (c) *Cx. annulirostris*, and partial autocorrelation functions (PACF) for (b) *Ae. vigilax* and (d) *Cx. annulirostris*. Time step lags are given in “month” units



r at low densities which declines rapidly as population size increases and then tapers to an asymptote (Turchin 2003). This functional form evokes a density-feedback mechanism that promotes over-compensatory population responses, such as rapid peaks and crashes after successive generations (Fig. 3). Moreover, in all cases, the more highly parameterised θ -Ricker model with θ of 0.121 and 0.005 for *Ae. vigilax* and *Cx. annulirostris*, respectively, had support (Table 1). A value of $\theta < 1$ also results in a concave function form of the GL-type (Sibly et al. 2005; Brook and Bradshaw 2006).

We note that some caution should be exercised in interpreting the magnitude of the concave function estimated by the GL model. We were unable to account explicitly for measurement error and assumed that the relative-abundance estimates of N did not overly bias r among sample sessions. Substantial measurement error can not only lead to an over-estimate of the magnitude of the negative feedback mechanism estimated from phenomenological time series, but can also result in an under-estimation of θ such that concavity in the r versus N relationship is exaggerated (Freckleton et al. 2006). Future work should be directed towards deriving estimates of measurement error in the sampling technique. This will permit the use of Bayesian hierarchical approaches, which

can easily and logically incorporate the uncertainties embedded in the models. Gibbs sampling, a Bayesian method which uses Markov chain Monte Carlo simulation, can simulate measurement error and model its effects on the interpretation of dynamical model estimates (Spiegelhalter et al. 2002).

Competitive interactions between aquatic larvae are considered to be some of the most important mechanisms responsible for endogenous control in mosquitoes. Adult female body size (and hence future fitness) is highly sensitive to larval density, and female larvae suffer greater mortality rates in higher density populations (Juliano 1998; Agnew et al. 2000; Gimnig et al. 2002; Shone et al. 2006). The 2-month density lag indicated by the PACF plots (Fig. 5c, d) may partially result from reduced survival or fertility in generations arising from high larval densities. Density regulation may also be driven by predator effects (i.e., predatory fish, amphibians or insects feeding on larvae) and physical parameters (speed of drying of pools; habitat quality). However, predator densities or transient pooling are unmeasured in this system so we cannot judge the potential mechanism of predators in eliciting density feedback. Nonetheless, there is good evidence that female *Culiseta longiareolata* mosquitoes avoid ovipositing in pools containing high numbers of *Notonecta maculata*

Table 1 Strength of evidence for five alternative models of mosquito population dynamics, as judged by Akaike's Information Criterion corrected for small sample sizes (AIC_c), Bayesian Information Criterion (BIC) and cross-validation (C-V)

	% DE	ΔAIC _c	wAIC _c	ΔBIC	wBIC	R ² _{pred}	wC-V
<i>Ae. vigilax</i>							
GL	12.76	0.00	0.702	0.00	0.861	0.526	0.589
TR	12.89	1.94	0.266	4.70	0.082	0.523	0.374
RL	8.26	6.22	0.032	6.22	0.038	0.506	0.037
RW	-0.01	13.49	0.001	7.87	0.017	0.474	0.001
EX	0.00	15.54	<0.001	12.75	0.001	0.466	<0.001
<i>Cx. annulirostris</i>							
GL	26.90	0.00	0.746	0.00	0.920	0.344	0.513
TR	26.86	2.17	0.252	4.94	0.078	0.344	0.486
RL	16.00	12.09	0.002	12.09	0.002	0.284	0.002
RW	-0.02	25.70	<0.001	20.05	<0.001	0.211	<0.001
EX	0.00	27.73	<0.001	24.93	<0.001	0.199	<0.001
<i>An. bancroftii</i>							
GL	9.71	0.00	0.892	0.00	0.993	0.684	0.700
<i>Cq. xanthogaster</i>							
GL	11.48	0.00	0.749	0.00	0.980	0.519	0.647
<i>Cx. sitiens</i>							
GL	22.45	0.00	0.779	0.00	0.983	0.328	0.903
<i>Ma. uniformis</i>							
GL	21.44	0.00	0.818	0.00	0.987	0.470	0.981

The models are a random walk (RW), exponential growth (EX), Ricker-logistic (RL), Gompertz-logistic (GL) and θ -Ricker (TR). Highest-ranked models are shown in boldface. Also shown is the percent deviance explained (% DE), change in information criterion relative to the top-ranked model (ΔAIC_c, ΔBIC), predicted R² for the C-V and model weights (wAIC_c, wBIC, wC-V). All five dynamical model results are shown for the two dominant species (*Ae. vigilax* and *Cx. annulirostris*); only the top-ranked model is shown for the remaining sub-dominant species)

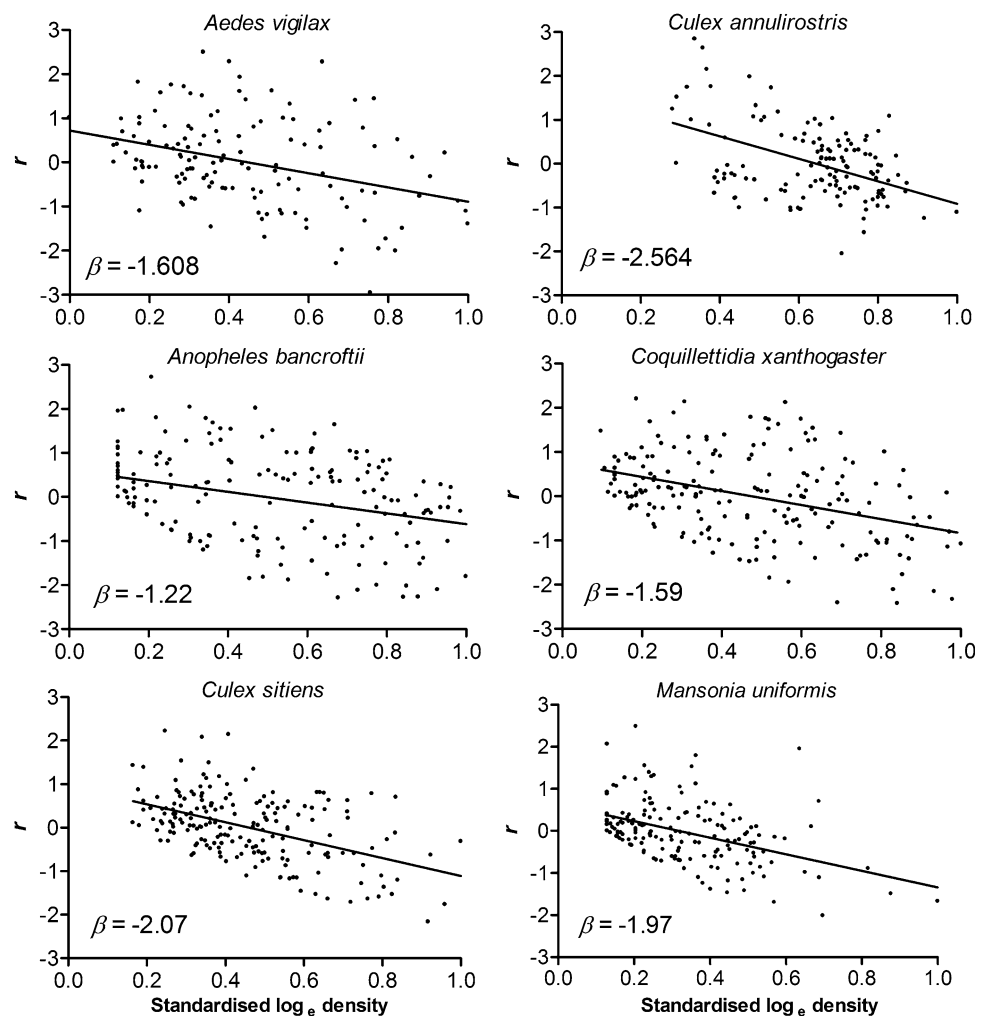
larval predators, and they are more likely to choose pools with fewer conspecifics larvae present (Kiflawi et al. 2003; see also Reiskind and Wilson 2004). Female *Aedes australis* mosquitoes also oviposit less in pools inhabited by predatory *Limnodynastes peronii* tadpoles (Mokany and Shine 2003). However, the influence of larval density on mosquito oviposition behaviour can be considerably more complex. Edgerly et al. (1998) found a positive relationship between *Aedes triseriatus* larval density and female oviposition preference, and Mokany and Shine (2003) found a similar relationship for *Culex quinquefasciatus* and *Ae. australis*, suggesting that high larval density may instead act as a cue for habitat stability and quality. Likewise, Grech et al. (2007) found that the *Anopheles stephensi* daughters of parents reared as larvae in low food conditions produced larger egg clutches than those reared in high-food conditions.

The strength of the feedback itself differed markedly between species, with *Cx. annulirostris* being more sensitive to variation in density than other species at low population size (Fig. 6). This suggests that a common limiting mechanism like fish, amphibian or insect predation is unlikely unless there is strong prey species selection by certain predators. Other possible density feedback mechanisms including adult competition for blood meals (cf. Saul 2003), although data describing intra- or inter-specific competition in this mosquito species assemblage are currently unavailable. Furthermore, control of *Cx. annulirostris* may be more difficult than that of other species because *Cx. annulirostris* has a greater rebound potential following reductions due to insecticide spraying operations. Our findings suggest that *Cx. annulirostris* control must therefore be a continuous and sustained activity to reduce population growth that tends constantly toward exponential growth at low densities.

Of course, mosquito population size is not solely a product of density regulation. Exogenous factors such as water availability, wind speed, temperature and other environmental attributes like vegetation type also influence relative abundance (Shone et al. 2006), even though the exogenous component of population change is often treated as an unspecified stochastic process (Sæther et al. 2000; Turchin 2003). Non-random exogenous effects include trends and periodic changes in the environment such as seasonality, and if ignored, may lead to the overestimation of risk factors (Sun et al. 2000). Our analysis of spatial heterogeneity among trapping sites using a random-effects model revealed an important aspect of mosquito population dynamics that can be used to streamline monitoring and control operations. *Ae. vigilax*, a saltwater species, showed the same density-dependent patterns regardless of trap site, whereas other species were highly spatially structured (Table 2). The higher dispersal capacity of *Ae. vigilax* (Gilles et al. 2004) means that ultimately, some combination of mechanistic models that incorporate dispersal probability among sub-populations will be required to examine the potential attenuation of density-dependent signals arising from mobility (Wang et al. 2006; Bradshaw 2008).

The majority of current and historical monitoring sites around Darwin are located along coastal swamp regions and seawater drainage wetlands (reticulation), such that during the wet season (November–April), large amounts of rain and surface runoff dilute salt concentrations in some drainages and so produce natural freshwater wetlands (swamps and marshes). These more temporally and spatially ephemeral freshwater breeding sites add a degree of spatial variability into the dynamics of the freshwater-obligate species, so monitoring must be designed to take this variation into account. The spatial consistency of *Ae.*

Fig. 6 Relationship between population growth rate (r) and standardised log-transformed population density for all six-mosquito species examined



vigilax's dynamics is probably due, in part, to its long flight ability (Gilles et al. 2004). Relatively high populations have been recorded at Katherine (250 km southeast of Darwin) in the early wet season, which is up to at least 100 km from the nearest tidally influenced breeding site (Medical Entomology Branch Annual Report; DHCS, unpublished data). *Culex sitiens*, a localised coastal pest, breeds in brackish coastal pools or swamps and has a more spatially clustered distribution. We found that this species' population does not demonstrate precipitous declines to the same extent as the freshwater species in September–November because the former can use the increasingly salty water to breed during this period.

The simple addition of the *season* term to the GL model increased the amount of variation explained for all species. For instance, the variance described for *Cx. annulirostris* increased from 26.97 to 53.90% after introducing seasonality. Therefore, over half of the variation in population growth rate of *Cx. annulirostris* can be explained by a simple model incorporating direct density dependence and seasonality (the latter incorporating environmental

determinants of population growth such as changing temperature, humidity and water availability/salinity). The different seasonal responses of different species are clearly an important consideration for control operations. For example, with the onset of high rainfall in January, populations of saltwater-breeding species such as *Ae. vigilax* begin to decline, whereas those of freshwater species are expected to have one or two peaks in mid-dry season (May–June) and early wet season (January). This reinforces the notion that the latter species require a greater degree of sustained control throughout the year.

In considering model parsimony, we only used a two-level seasonal factor in our models. We argue that this factor appropriately reflects the monsoonal variation that characterises northern Australia's tropical regions without attempting to capture subtle month-to-month variation that would require estimating many more parameters. Further, our emphasis was to quantify the relative strength and form of negative density feedback in tropical Australian mosquitoes in general rather than predict abundance trends; therefore, we specifically avoided accounting for the

Table 2 Spatial heterogeneity analysis using multi-model inference

	ΔAIC_c	wAIC _c	ΔBIC	wBIC
<i>Ae. vigilax</i>				
Spatial random effects				
Intercept only	1.59	0.269	1.8	0.278
Slope only	5.59	0.036	5.8	0.038
Intercept and slope	3.59	0.099	15.8	0.000
No random effects				
No spatial heterogeneity	0.00	0.596	0.0	0.684
<i>Cx. annulirostris</i>				
Spatial random effects				
Intercept only	0	0.622	0	0.998
Slope only	13	0.001	13	0.001
Intercept and slope	1	0.377	14	0.001
No random effects				
No spatial heterogeneity	94.47	0.000	94.32	0.000
<i>An. bancroftii</i>				
Spatial random effects				
Intercept and slope	0	0.960	0	0.629
<i>Cq. xanthogaster</i>				
Spatial random effects				
Intercept only	4	0.107	0	0.422
<i>Cx. sitiens</i>				
Spatial random effects				
Intercept only	0	0.622	0	0.953
<i>Ma. uniformis</i>				
Spatial random effects				
Intercept and slope	0	0.971	0	0.736

Three spatial models and one aspatial model are contrasted for each species (see “Methods”)

Highest-ranked models for each species according to Akaike’s Information Criterion corrected for small sample sizes (AIC_c) and Bayesian information Criterion (BIC) are shown. All five dynamical model results are shown for the two dominant species (*Ae. vigilax* and *Cx. annulirostris*; only the top-ranked model is shown for the remaining sub-dominant species)

complex harmonic periodicity in our analyses. The AR-IMA method developed by Box et al. (1994) may provide better predictive power in this regard, but we specifically avoided adopting this approach to maximise model parsimony (Burnham and Anderson 2002). Other methods include the unit root test (Hall and Cummins 2005), although the approach is not yet widely used by ecologists.

A modelling approach linking correlative environmental data to endogenous dynamics would be required to tease apart the drivers of exogenous variation in these mosquito species. That said, our endogenous-focused approach has revealed that some of the most basic considerations of density regulation can provide useful guidance regarding the timing and spatial configuration of effective control.

Table 3 Gompertz-logistic models incorporating time (*t*), the square of time (*t*²) and season (wet/dry), to test the hypotheses for linear and non-linear temporal trends and different regulation patterns between seasons

	% DE	ΔAIC_c	wAIC _c	ΔBIC	wBIC	R^2_{pred}	wC-V
<i>Cx. annulirostris</i>							
GL.S	53.90	0.00	0.539	0.00	0.893	0.468	0.525
GL.T.S.TS	56.16	1.84	0.215	7.28	0.023	0.461	0.216
GL.T.S	53.90	2.16	0.184	4.89	0.077	0.460	0.186
GL.T.T2.S	53.93	4.31	0.062	9.76	0.007	0.452	0.073
GL	26.90	27.80	<0.001	25.03	<0.001	0.344	<0.001
GL.T	26.94	29.88	0.001	29.88	<0.001	0.334	<0.001
GL.T.T2	26.97	32.02	<0.001	34.76	<0.001	0.323	<0.001
<i>Ae. vigilax</i>							
GL.S	29.28	0.00	0.552	0.00	0.888	0.595	0.577
GL.T.S	29.45	1.93	0.211	4.66	0.087	0.589	0.210
GL.T.T2.S	30.31	2.94	0.127	8.36	0.014	0.585	0.112
GL.T.S.TS	30.10	3.23	0.110	8.65	0.012	0.584	0.101
GL	12.76	20.72	<0.001	17.95	<0.001	0.526	<0.001
GL.T	13.22	22.20	<0.001	22.20	<0.001	0.521	<0.001
GL.T.T2	14.20	23.01	<0.001	25.74	<0.001	0.517	<0.001
<i>An. bancroftii</i>							
GL.S	73.24	0.00	0.482	0.00	0.900	0.787	0.444
<i>Cq. xanthogaster</i>							
GL.S	38.43	0.00	0.611	0.00	0.920	0.567	0.517
<i>Cx. sitiens</i>							
GL	39.53	0.00	0.315	0.00	0.769	0.235	0.319
<i>Ma. uniformis</i>							
GL.S	75.80	0.00	0.561	0.00	0.912	0.529	0.475

Model types include: basic Gompertz-logistic (GL), seasonal GL (GL.S), time-series sequence GL (GL.T), quadratic time-series sequence GL (GL.T.T2), season-time series GL (GL.T.S), season-quadratic time-series GL (GL.T.T2.S) and season-time series interaction GL (GL.T.S.TS). Highest-ranked models are shown in boldface. Also shown is the per cent deviance explained (% DE), change in information criterion relative to the top-ranked model (ΔAIC_c , ΔBIC), predicted *R*² for the C-V and model weights (wAIC_c, wBIC, wC-V). All five dynamical model results are shown for the two dominant species (*Ae. vigilax* and *Cx. annulirostris*; only the top-ranked model is shown for the remaining sub-dominant species)

Future modelling must also consider the periodicity and potential influence of environmental change (e.g., global warming) on long-term predictions of control effectiveness via more precise predictions of mosquito abundance. Control models that attempt to account for the potential impacts of environmental change will assist governments in taking prompt or pre-emptive action by establishing early-warning systems for disease outbreaks in human populations.

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