

REPORT

Drought-induced mosquito outbreaks in wetlands

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Abstract

Mosquitoes are not only a nuisance, but also vector many important human and animal diseases. Here, in opposition with the dogma that increased precipitation predicts mosquito abundance, we hypothesize that mosquitoes should show population outbreaks after drought years. Specifically, we suggest that in wetlands that never dry (permanent), predators limit mosquito abundance, whereas in wetlands that dry yearly (temporary), competitors that are well adapted to predictable drying, limit mosquito abundance. However, in wetlands that dry only during drought years (semi-permanent), mosquito predators and competitors are eliminated and must recolonize following a drought, and the abundance of wetland mosquitoes can skyrocket. We present supportive evidence for this hypothesis from surveys of natural wetlands and from a controlled mesocosm experiment. We conclude that this framework may provide a reliable way to predict and prepare for year-to-year variation in mosquito abundances at large spatial scales.

Keywords

Competition, drought, food web, mosquito, outbreak, precipitation, predation.

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INTRODUCTION

Mosquitoes. ‘No animal on earth has touched so directly and profoundly the lives of so many human beings’ (Spielman & D’Antonio 2001). In addition to being a general nuisance to humans, mosquitoes are vectors for several important human diseases, such as malaria, dengue fever, yellow fever and West Nile virus, as well as diseases of domesticated animals, such as equine encephalitis and canine heartworm (e.g. Mulla 1994; Maguire *et al.* 1999; Rose 2001; Hay *et al.* 2002). Although a great deal of research is focused on understanding the molecular biology of mosquitoes and their role as disease vectors, basic mosquito ecology is often poorly integrated into these studies (Curtis 2002; Enserink 2002).

The vast majority of species show highly variable population densities through time (Fagan *et al.* 2001), and mosquitoes are no exception (Spielman & D’Antonio 2001). It is widely thought that abiotic factors, particularly precipitation, limit mosquito abundance and thus mosquito populations should positively covary with precipitation. The reasoning for this supposition is that precipitation creates habitats for mosquitoes to lay their eggs and for their aquatic larvae to grow. Surprisingly, however, precipitation almost never correlates with mosquito abundance in the long-term; instead, our ability to predict mosquito abundance has been

limited to very short time scales (e.g. Aniedu 1992; Vandyk & Rowley 1995; Dhileepan 1996; Lindblade *et al.* 1999; Webb & Russell 1999; Gleiser *et al.* 2000; Wegbreit & Reisen 2000). Currently, no reliable information exists to predict year-to-year variation in mosquito abundance, although it would allow for more informed management strategies, including judicious use of pesticides, which can often have adverse effects on ecosystems, and preparations for the protection against and treatment of mosquito-vectored diseases.

In this article, we use an emerging conceptual framework from the community ecology of aquatic food webs to produce and test a novel hypothesis regarding year-to-year variation in mosquito abundance. Specifically, we argue that because larval mosquitoes are components of a much larger metacommunity of interacting species, the interaction between biotic interactions (competitors and predators) and abiotic constraints (habitat drying) is essential for understanding the controls on mosquito abundance. We further suggest that by placing mosquitoes into a broader community context, a much more predictive framework can be developed for understanding and predicting year-to-year variation in mosquito abundances.

Many species of mosquitoes are habitat generalists which breed, grow as larvae and emerge from a wide variety of

aquatic habitats (Carpenter & LaCasse 1955). These species, including many members of the genera *Anopheles*, *Culex* and *Culiseta*, are also some of the most important human pests and disease vectors. In eastern North America, some of the most common mosquito species are members of the *Anopheles quadrimaculatus* species complex and *Culex pipiens*. Although these species have somewhat distinct habitat preferences, they readily lay eggs in, and emerge from wetlands of all types (Carpenter & LaCasse 1955). Further, although *C. pipiens* and to a lesser degree *A. quadrimaculatus*, will also breed in smaller water-filled habitats (e.g. containers, ditches), which are often associated with humans, wetlands provide a much greater area for potential larval habitats, and often produce many more adult mosquitoes, than the smaller habitats traditionally associated with mosquito control. As such, we suggest that understanding the dynamics of mosquitoes in these wetland habitats will provide a much better understanding of yearly variation in the abundances of mosquitoes in the landscape.

In wetlands, the abundances of mosquito larvae are often limited by biotic factors, such as predators and competitors (Blaustein & Karban 1990; Blaustein & Margalit 1996; Blaustein 1998; Stav *et al.* 2000; Mokany & Shine 2003). In addition, the importance of these biotic interactions varies depending on the type of wetland. Wetlands can be divided into three classes – temporary, permanent and semi-permanent – based on their probability of retaining standing water throughout the year; this in turn determines the types of species that can live in those habitats and their interspecific interactions (Schneider & Frost 1996; Wellborn *et al.* 1996; Williams 1996). Permanent wetlands always retain standing water. In these habitats, predators, including fish and many insects, can complete their life cycles and reach very high densities. Thus, we predict that mosquito densities will be low in permanent wetlands as a result of predation. Temporary wetlands are those that fill and dry every year. Although some predators subsist in these temporary habitats (Spencer *et al.* 1999), most of the more efficient mosquito predators (e.g. fish, large insects) cannot live in these habitats because of their drying. Alternatively, mosquito competitors, which can adapt to the predictable yearly drying of these wetlands (e.g. zooplankton with resting eggs), are often quite dense in the absence of predators. Thus, we predict that the number of mosquitoes emerging from temporary wetlands will be low in temporary habitats as a result of strong competitive interactions. This effect could either be because of lower rates of emergence if high competitor density slows the rate of larval development, or because of higher larval mortality and/or avoidance of oviposition by females in wetlands with high competitor density. Semi-permanent wetlands are those that retain standing water in most years, but periodically dry when precipitation and the water table are particularly low.

In years prior to a drying event, we predict that predators will be common, as in permanent wetlands, because the habitat has retained standing water for several seasons, allowing sufficient time for predator colonization. As a result, in most years, mosquito densities will be low in semi-permanent wetlands. In years following a drying event, however, we predict that both efficient mosquito predators and mosquito competitors will be rare, as neither group of species are well adapted to drying events. Furthermore, because mosquitoes have extremely rapid generation times (weeks) relative to their predators and can readily disperse among habitats, we predict that mosquitoes should show rapid population increases in semi-permanent wetlands in years following a drought event.

In this study, we evaluate this hypothesis by using two complimentary approaches. First, we censused larval mosquitoes, and their potential predators and competitors in natural wetlands that varied in their probability of retaining permanent standing water during normal and drought years. Second, we established a long-term experiment in artificial wetland mesocosms where we manipulated the permanence of wetlands experimentally so that they dried every year, one of every 3 years, or never, and then measured the response of mosquitoes, their competitors and their predators.

METHODS

Natural history and species involved

Larvae of the two most common mosquito species encountered in the natural and artificial wetlands, *A. quadrimaculatus* and *C. pipiens* (>95% of the larval mosquito community), and other types of mosquito larvae, utilize different feeding behaviours and have slightly different diets (e.g. Merritt *et al.* 1992). They are both generalists, however, and readily consume detritus, microbes and algae, both from the benthos and the water column. As such, they are likely to compete for resources with several other co-occurring species. Potential mosquito competitors in these wetlands included several insects (Chironomidae, some Corixidae), molluscs (Pulmonate snails), anuran larvae (Ranidae, Hylidae), amphipods, and cladoceran and copepod zooplankton. Common mosquito predators included small fishes (mainly Cyprinidae and Gasterosteiridae), larval salamanders (Ambystomatidae, Salamandridae), and several types of insects, including Hemiptera (e.g. Notonectidae, Naucoridae, other Corixidae), Coleoptera (Dyticidae) and Odonata (Libellulidae, Aeshnidae, Coenagrionidae, Lestidae).

There are certain complexities associated with grouping species only as competitors and predators, which we do not explicitly consider here because of space limitations and the coarse level of predictions that we are trying to test here. For example, *C. pipiens* and *A. quadrimaculatus* vary in their

relative preferences for grazing on surfaces vs. in the water column, and thus are more likely to compete differentially with grazers (e.g. snails and tadpoles) or filter feeders (e.g. zooplankton). As a result, surface grazers may actually facilitate filter-feeding mosquitoes and filter feeders may facilitate grazing mosquitoes indirectly. However, when both groups of competitors are present, their overall effect on mosquitoes should be negative, and so we only consider their negative effects here. In addition, some species which we call competitors may also eat mosquitoes to a limited degree. Nevertheless, our groupings provide a first approximation of how biotic interactions limit mosquito densities.

Wetland surveys

Wetlands were identified in north-west Pennsylvania (Crawford County, USA), and were followed from 1998 to 2001. The year 1999 was a particularly dry year, in which several wetlands only dried in that year, but not in 1998, 2000 or 2001. Wetlands that dried only in 1999 were classified as semi-permanent, those that dried every year were classified as temporary, and those that never dried were classified as permanent. We chose three wetlands from each permanence category that were similar in total surface area and water chemistry for sampling and analyses. Mosquito larvae, predators and competitors were sampled during May of each year. Macroinvertebrates were sampled in 5–10, 1 m sweeps (depending on the size of the wetland) using a 0.1 m width D-net with 0.5 mm mesh. Zooplankton were sampled using 5–10 vertical pulls of a 10 cm diameter 48 µm mesh net. All animals were counted and classified according to three categories – mosquitoes, potential competitors or potential predators – and converted to biomass using species and size-specific dry-weight conversions.

Our methods were chosen so as to standardize sampling as much as possible across these highly divergent wetland types. However, because the wetland types differ markedly in several factors, notably their geomorphic structure and vegetation, this could have created sampling biases when trying to compare among the wetland types. We have used a variety of sampling methods in these types of wetlands, and find our estimates relatively robust, at least qualitatively, to each other (J. M. Chase, unpublished data). Nevertheless, we cannot say for certain whether such a bias was introduced; if it was, it could have either increased or decreased any observed differences among trophic groups within the natural wetlands.

Experimental mesocosms

In 1999, as part of a larger experiment, we established thirty six 1140 litre mesocosms (1.5-m diameter Rubbermaid cattle tanks) in full sunlight in a large old field near the

Pymatuning Laboratory of Ecology, University of Pittsburgh (Crawford County, PA, USA). Each tank was filled with 4–6 cm of topsoil and nutrient poor well water so that they were two-thirds full. Further, each tank was inoculated with a wide variety of species (e.g. macrophytes, plankton, macroinvertebrates and larval amphibians) that occurred in the regional species pool, and left open so that natural colonization of mosquitoes and other species could occur.

Permanence (three levels) and nutrients (three levels) were manipulated in a factorial design with four replicates for each treatment. There were no main or interactive effects of the nutrient treatments (ANOVA; $P > 0.2$) on any of the response variables of interest here, and thus we do not discuss them further here. To manipulate permanence we connected a 5 cm diameter PVC pipe to the bottom drain of each mesocosm, so that we could slowly dry them over the course of the summer (from June to September); wetlands naturally refilled over the winter with precipitation and were topped-off with well water in early spring when necessary.

Each mesocosm was assigned to one of three permanence treatments: (1) permanent (never dry), (2) temporary (dry every year), (3) semi-permanent (dry in the second year of the 3 years). In April–June 2001, we censused mosquitoes, potential mosquito competitors and potential mosquito predators, in each mesocosm biweekly. As we were primarily interested in how many mosquitoes emerged from each different larval environment to become reproductive adults, we censused pupal exuviae that were left behind upon successful metamorphosis of a pupae into an adult mosquito. Exuviae were counted and removed from the mesocosm on each sampling date. Macroscopic mosquito predators and large competitors were censused in two ways: (1) visually by counting organisms on the sides of the mesocosm and the surface of the vegetation and ground, and (2) with a 10 cm × 10 cm net with 0.33 mm mesh net 10 cm; we swept the net through the vegetation 10 times and counted all organisms captured. The numbers were converted to dry-weight estimates as above. Zooplankton were censused by collecting 5 L of water in an integrated tube sampler, and were preserved and counted as above.

RESULTS

Wetland surveys

Repeated measures ANOVA showed a significant effect of wetland permanence type ($F_{2,6} = 20.7$, $P < 0.002$), year ($F_{2,4} = 17.93$, $P < 0.001$) and their interaction ($F_{2,4} = 17.0$, $P < 0.001$) on larval mosquito biomass. We found a significant effect of wetland permanence type ($F_{2,6} = 25.56$, $P < 0.001$), a marginally significant effect of year ($F_{2,4} = 3.39$, $P = 0.07$) and a marginally significant wetland permanence type by year interaction ($F_{2,4} = 3.05$,

$P = 0.06$) on competitor biomass. Finally, we found a significant effect of wetland permanence type ($F_{2,6} = 22.43$, $P < 0.002$), year ($F_{2,4} = 15.62$, $P < 0.001$) and their interaction ($F_{2,4} = 21.63$, $P < 0.001$) on predator biomass. Following the significant main effects of wetland permanence type, we used Tukey's HSD for pairwise comparisons.

In 1999 and 2001, mosquito abundance was not different among any wetland type (Tukey's HSD; $P > 0.3$). However, in 2000, following the drought event, mosquito abundance was highest in semi-permanent wetlands (Tukey's HSD; $P < 0.001$), showing a 15-fold increase, but equally low in temporary and permanent wetlands (Tukey's HSD; $P > 0.4$) (Fig. 1a). Competitor biomass was highest in temporary wetlands in all 3 years compared with both the permanent and semi-permanent wetlands (Tukey's HSD; $P < 0.05$). However, competitor biomass was not different between permanent and semi-permanent habitats in 1999 and 2001 (Tukey's HSD; $P < 0.4$), but was much lower in semi-permanent habitats in 2000, following the drought year (Tukey's HSD; $P < 0.01$) (Fig. 1b). Predator biomass was much higher in permanent and semi-permanent wetlands than in temporary wetlands in 1999 and 2001 (Tukey's HSD; $P < 0.05$), and there was no difference between the permanent and semi-permanent wetlands (Tukey's HSD; $P > 0.4$). However, in 2000 (following the drought), predator biomass was highest only in the permanent wetlands (Tukey's HSD; $P < 0.01$), and equally low in both the semi-permanent and temporary habitats (Tukey's HSD; $P > 0.5$) (Fig. 1c).

Experimental mesocosms

Only two species of mosquito, *A. quadrimaculatus* and *C. pipiens*, were encountered in the majority of these mesocosms throughout the growing season. Some other species, notably *Aedes* spp. and *Culiseta* spp., were observed in $<5\%$ of the mesocosms, and were generally observed only once in any given mesocosm. In all, mosquito species other than *A. quadrimaculatus* and *C. pipiens* represented $\ll 1\%$ of the larvae encountered in these mesocosms, and thus we do not include them in the following analyses.

As a result of the large responses of all three groups of species (mosquitoes, their competitors and their predators) to the treatments, variances were not equal among treatments for each response variable (Bartlett's-Box F -test; $P > 0.05$). Thus, rather than parametric ANOVA, we used nonparametric Kruskal-Wallis tests (ANOVA gives qualitatively identical results in all cases). In the third year of the experiment (2001), following the experimentally induced drought, the wetland permanence treatment (temporary, permanent and semi-permanent) significantly affected the number of emerging adults of both common mosquitoes

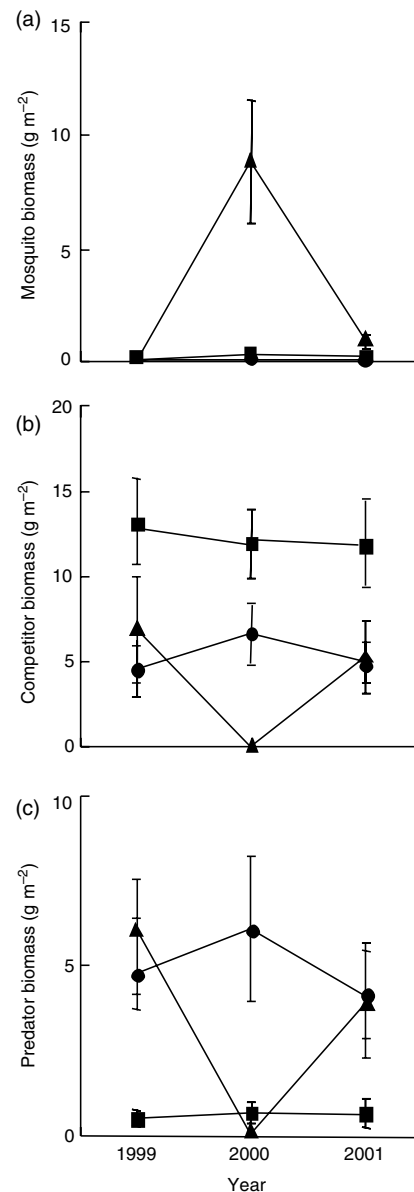


Figure 1 Biomass (± 1 SE) of mosquitoes (a), their competitors (b) and their predators (c) over the 3-year period (1999–2001) within natural wetlands that varied in permanence. Squares represent temporary wetlands (dried every year), circles represent permanent wetlands (never dried) and triangles represent semi-permanent wetlands (dried during the 1999 drought year).

species (Kruskal-Wallis; *A. quadrimaculatus* d.f. = 2, $H = 24.54$; *C. pipiens* d.f. = 2, $H = 15.95$, $P < 0.0001$), competitor biomass (Kruskal-Wallis; d.f. = 2, $H = 29.38$, $P < 0.0001$), and predator biomass (Kruskal-Wallis; d.f. = 2, $H = 27.37$, $P < 0.0001$).

The number of adult mosquitoes that emerged from these wetlands was over 20-fold higher in the semi-

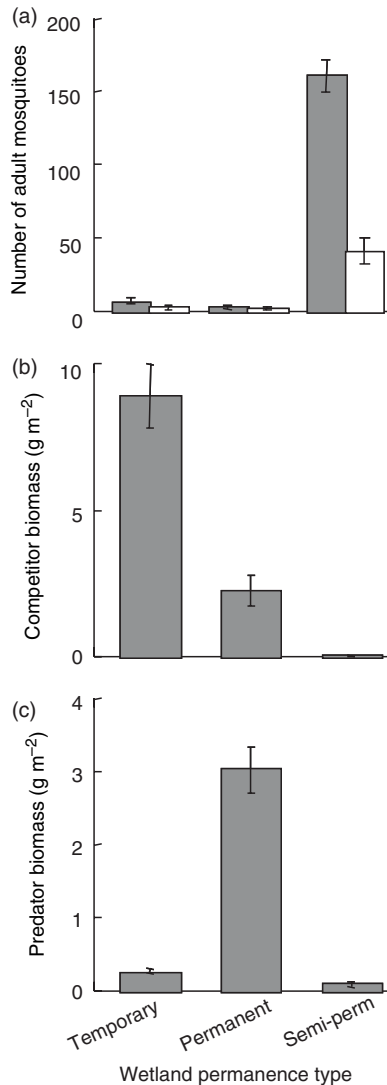


Figure 2 Number (± 1 SE) of emerged adult mosquitoes (a) and biomass (± 1 SE) of their competitors (b) and predators (c) within mesocosms where permanence was experimentally manipulated. Data are only presented for 2001, which was the year immediately following the experimental drought event in the semi-permanent mesocosms. The number of emerging adult mosquitoes is shown for the two most common species, *Anopheles quadrimaculatus* (dark bars) and *Culex pipiens* (white bars); other mosquito species represented $\ll 1\%$ of the mosquitoes encountered in these wetlands.

permanent treatments than in either the temporary or permanent treatments (Tukey's HSD; $P < 0.01$), whereas the number of mosquitoes that emerged from the permanent and temporary treatments were uniformly low, and not different from one another (Tukey's HSD; $P > 0.3$) (Fig. 2a). Competitor biomass was highest in the temporary treatments, intermediate in the semi-permanent treatments and lowest in the permanent treatments (all Tukey's HSD;

$P < 0.05$) (Fig. 2b). Predator biomass was highest in the permanent treatments (Tukey's HSD; $P < 0.01$), but equally low in both the temporary and semi-permanent treatments (Tukey's HSD; $P > 0.2$) (Fig. 2c). Thus, this experiment provides evidence that these wetland mosquitoes show population outbreaks following a drought event in semi-permanent habitats, and that this is associated with lower predator and competitor biomass.

DISCUSSION

We found that mosquito density increased dramatically following a natural drought event in a survey of wetlands, and after an experimental drought event in outdoor mesocosms intended to mimic many features of natural wetlands. These patterns are consistent with our hypothesis that predators and competitors limit mosquito populations in permanent and temporary wetlands, respectively, whereas in semi-permanent wetlands, mosquito densities can outbreak following drought years because of the loss of both these groups of interactors. The reason this occurs is most likely because these mosquitoes are habitat generalists and opportunists, and following a drought event, they can quickly re-colonize these wetlands. Although predators can also recolonize these semi-permanent habitats following drought, particularly when many individuals are in their terrestrial adult stage (e.g. dragonflies), mosquitoes typically have much more rapid population dynamics (on the order of weeks) than predators (on the order of months to years), allowing them to escape control by predators and achieve population outbreaks in a very short period of time.

As an alternative to the predator and competitor limitation hypothesis that we propose, it is possible that the patterns we observed may have resulted from different mechanisms. For example, if the act of wetland drying itself induced some sort of difference in larval food supply or related factor, then we would expect the same pattern of mosquito density increases following wetland drying. However, we feel that this scenario is unlikely as mosquitoes were rare in both natural and experimental temporary wetlands, which dried in the same manner as the semi-permanent wetlands, but did not show similar increases in mosquito abundance.

From our results, we cannot discern whether the differences in mosquito abundance are the result of differential oviposition by adult mosquitoes or differential mortality of larval mosquitoes. Several species of mosquito have been observed to preferentially oviposit eggs in habitats without predators (Chesson 1984; Petranka & Fakhoury 1991; Angelon & Petranka 2002; Spencer *et al.* 2002; Kilfawi *et al.* 2003a); furthermore, some evidence also suggests that mosquitoes can similarly detect and respond to habitats with different densities of competitors (Blaustein &

Kotler 1993; Edgerly *et al.* 1998; Kiflawi *et al.* 2003b; Mokany & Shine 2003). A recent study has suggested that whether mosquitoes can behaviourally avoid oviposition in habitats with predators, or whether predators simply reduce larval mosquito abundance through direct mortality, can have quantitative effects on the overall response of mosquito populations to the presence of predators (Spencer *et al.* 2002). However, whether the effect of predators and competitors observed in our study was primarily because of direct mortality or indirect behavioural decisions (oviposition habitat selection) is not likely to alter the qualitative predictions of spatial and temporal variation in mosquito abundances in food webs that we have discussed here. In addition, although oviposition behaviour may have played a role in the patterns we observed, in a separate study, we found that differential mortality because of the presence of competitors and predators, while all else was equal, had a strong negative effect on the number of emerging adult mosquitoes similar to that observed here (T. Knight, J. Chase, C. Goss & J. Knight, unpublished data).

Our main prediction and results are in opposition to the widely recognized hypothesis that mosquito densities should be highest when precipitation is highest. Although precipitation sometimes correlates with mosquito densities in the short-term, it does not predict year-to-year variation in mosquito abundance (e.g. Aniedu 1992; Vandyk & Rowley 1995; Dhileepan 1996; Lindblade *et al.* 1999; Webb & Russell 1999; Gleiser *et al.* 2000; Wegbreit & Reisen 2000). Other hypotheses to explain yearly variation in mosquito abundance similarly have little quantitative support. Some mosquito ecologists suggest that all mosquito species respond to the environment differently, and that no single factor could reliably predict the variation in mosquito densities (Spielman & D'Antonio 2001). We agree that mosquito species have very different natural histories, and likely respond to environmental variation in different ways. However, we suggest that some of the most extensive potential larval habitats are wetlands, and that many species of mosquitoes are habitat generalists able to take advantage of year-to-year variation in the suitability of these habitats, and thus are likely to fit into our predictions.

Despite our supportive data at relatively small spatial and short temporal scales, other information will be necessary in order to determine how well our hypothesis, which is based on local biotic interactions among mosquito larvae imbedded within food webs, scales up to longer time series across large spatial scales. We are currently amassing such data. For now, however, we suggest that mosquito outbreaks are likely to occur following drought years so long as: (1) suitable larval habitats, and the larval stage in general, are limiting to overall mosquito population dynamics, (2) some mosquito species can potentially

utilize wetlands for larval habitats, (3) predators and competitors are negatively affected by drought and have slower generation times than mosquitoes, and (4) semi-permanent wetland habitats represent a significant proportion of potential larval mosquito habitats.

In conclusion, we predict that mosquito densities are controlled by an interaction between abiotic (habitat availability and precipitation) and biotic (competition and predation) factors, and that outbreaks are likely to occur on a landscape level following drought years. Our hypotheses and observations are based on species that are able to utilize wetlands as larval habitats, but similar patterns have been suggested for species that specialize on a limited set of container habitats (Lounibos 1983, 1985; Bradshaw & Holzapfel 1988). Further, our observations may lend insight into understanding patterns of mosquito-borne diseases, and the potential for global climate change to influence mosquito population dynamics and disease incidence. Although some statistical correlations between disease incidence and precipitation have been found, there is little predictability or mechanistic understanding of these patterns as of yet (Hay *et al.* 2000). If our model for mosquito outbreaks translates to mosquito abundances at the landscape level, then we would predict that the likelihood of disease outbreaks might increase in years following drought years; a pattern that seems to occur at least in Saint Louis encephalitis outbreaks in North America (e.g. Shaman *et al.* 2002; although these authors present a more complex hypothesis for the underlying mechanism of this pattern), and perhaps several other diseases. However, a variety of other factors associated with the epidemiology of disease transmission will also vary from year to year, such as changes in the stress experienced by the host populations (Lafferty & Holt 2003), or changes in host behaviour and immunity (Shaman *et al.* 2002). Finally, although global climate change is controversial, there is evidence that climatic variability and periodic drought conditions, such as that associated with the El Niño-Southern Oscillation, has increased as a result of anthropogenic influences (Tudhope *et al.* 2001). We suggest that such variability will increase the frequency and possibly the magnitude, by which mosquito population outbreaks, and possibly their associated health problems, occur.

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