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Desiccation and thermal tolerance of eggs and the coexistence of competing mosquitoes

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Abstract We tested the hypothesis that differences in temperature and desiccation tolerances of eggs of the container-dwelling mosquitoes *Aedes albopictus* and *Aedes aegypti* influence whether invading *A. albopictus* coexist with or exclude *A. aegypti* in Florida. In the laboratory, egg mortality through 30 days for *A. albopictus* was strongly temperature and humidity dependent, with low humidity and high temperature producing greatest mortality. In contrast, mortality through 30 days and through 60 days for *A. aegypti* was very low and independent of temperature and humidity. Mortality through 90 days for *A. aegypti* showed significant effects of both temperature and humidity. In the field, the proportion of vases occupied by *A. albopictus* was significantly lower at four of six sites at the start of the wet season (after a dry period) versus well into the wet season (after containers had held water for weeks). The proportion of vases occupied by *A. aegypti* was independent of when during the wet season vases were sampled. These results imply that dry periods cause disproportionately greater mortality of *A. albopictus* eggs compared to *A. aegypti* eggs. Container occupancy at tire and cemetery sites was significantly related to two principal components derived from long-term average climate data. Occupancy of containers by *A. albopictus* was greatest at cool sites with little or no

dry season, and decreased significantly with increasing mean temperature and increasing number of dry months. In contrast, occupancy of containers by *A. aegypti* was lowest at cool sites with little or no dry season, and increased significantly with increasing mean temperature and increasing dry season length, and decreased significantly with total precipitation and number of wet months. We suggest that local coexistence of these species is possible because warm, dry climates favor *A. aegypti* and alleviate effects of competition from *A. albopictus* via differential mortality of *A. albopictus* eggs.

Keywords *Aedes aegypti* · *Aedes albopictus* · Climate · Interspecific competition · Mechanisms of coexistence

Introduction

The means by which species may persist in the presence of more effective competitors have been investigated in detail both theoretically (e.g., Atkinson and Shorrocks 1981; Grover 1997; Chesson 2000) and empirically (e.g., Connell 1961; Spiller 1984; Hemphill 1991; Ives 1991). Because of the increasing commonness of invasive species (reviewed by Williamson 1996; Simberloff et al. 1997), and associated increasing interest in their competitive impacts on resident species (e.g., Livdahl and Willey 1991; Edgerly et al. 1993; Human and Gordon 1996; Petren and Case 1996; Juliano 1998), ecologists are continually presented with new questions about whether any environmental conditions may allow coexistence of competitors. Such investigations are necessary for application of ecological theory to the amelioration of impacts of invasive species, and are also of basic interest as tests of our understanding of general coexistence mechanisms.

The recent invasion of the Americas by the Asian Tiger mosquito, *Aedes albopictus*, provides an ideal opportunity to investigate mechanisms of coexistence of competitors, and how a resident species may persist despite invasion of a superior competitor. *A. albopictus*

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was first recorded in North America in the mid-1980s (Hawley 1988). Since then it has spread throughout much of the southeastern United States, where it is now one of the most common mosquitoes in many areas (Moore 1999). Its spread through Florida has been particularly well documented (O'Meara et al. 1995). *A. albopictus* larvae develop in discarded tires, cemetery vases, water-filled tree holes, and other containers, with discarded tires the characteristic habitat in North America (Hawley 1988). Adults are generalist blood feeders that lay desiccation-resistant eggs above the water line. These eggs hatch when flooded, and the larvae feed on microorganisms and detritus. There has been considerable interest in the potential and observed impacts of *A. albopictus* on North American container-dwelling *Aedes* (e.g., Livdahl and Willey 1991; Edgerly et al. 1993; Juliano 1998; Daugherty et al. 2000; Teng and Apperson 2000). In Florida (Hornby et al. 1994; O'Meara et al. 1995), and the southeastern United States in general (Hobbs et al. 1991; McHugh 1993; Mekuria and Hyatt 1995), there has been a well-documented decline in the abundance of *A. aegypti*, sometimes to local extinction, following invasion of *A. albopictus*. This decline is consistent with the hypothesis that interspecific competition, probably among larvae, is the mechanism by which *A. albopictus* displaces *A. aegypti*, which is a specialist on man-made containers, particularly discarded tires (Christophers 1960; Frank 1981). Field (Juliano 1998) and laboratory (Barrera 1996; Daugherty et al. 2000) competition experiments using decaying plant material as a substrate for the bacterial food of larvae indicate that *A. albopictus* is superior to *A. aegypti* in resource competition, maintaining greater population growth at higher combined densities (Juliano 1998; Daugherty et al. 2000), and producing greater survivorship during periods of low food availability (Barrera 1996). Thus, it seems likely that resource competition among larvae is a major process contributing to the displacement of *A. aegypti* by *A. albopictus* in much of the southeastern United States.

The demonstration of this competitive outcome raises another question: How can *A. aegypti* manage to persist at some locations despite invasion by *A. albopictus*? Alteration of the outcome of competition due to variation in abiotic environmental effects on the competitors (Dunson and Travis 1991; Hemphill 1991; Warner et al. 1993; Chesson 2000) is one possibility. On the Florida peninsula, *A. aegypti* persists in southern, urban areas, despite invasion by *A. albopictus* (Hornby et al. 1994; O'Meara et al. 1995). This geographic pattern of persistence of *A. aegypti* suggests that abiotic environmental factors, such as temperature, humidity, and drought may affect the outcome of this competitive interaction. The southern part of the Florida peninsula is characterized by a subtropical climate, with warm temperatures and low rainfall in the winter months. Farther north on the peninsula, there is greater winter rain, and in the Florida panhandle, there is a pronounced secondary peak in rainfall in the winter (Fernald and Patton 1985). There are sever-

al prominent examples of local persistence of poorer competitors when they can tolerate more extreme physical conditions than can superior competitors (e.g., Connell 1961; Hemphill 1991) or cases where different physical environments yield different competitive outcomes (e.g., Dunson and Travis 1991; Warner et al. 1993). Studies of *A. albopictus* and *A. aegypti* in Asia have demonstrated that these species differ in desiccation tolerances of adults and eggs, but also that there is pronounced geographic variation for both traits within both species (Sota and Mogi 1992a, b; Mogi et al. 1996). Thus, there is a need to compare desiccation and temperature tolerances of *A. albopictus* and *A. aegypti* from Florida, and to determine if the pattern of local coexistence versus exclusion observed in the field in Florida can be accounted for by differences in desiccation or temperature tolerance. The focus of this paper is on eggs, because it is the egg stage of these species that is the most likely to survive though unfavorable periods (Sota and Mogi 1992b). Our hypothesis is that persistence of *A. aegypti* in Florida results from greater survivorship of *A. aegypti* eggs, and correspondingly low survivorship of *A. albopictus* eggs, through dry or hot periods, and that local elimination of *A. aegypti* following invasion by *A. albopictus* has occurred at sites where wetter, cooler conditions prevail. We test three predictions derived from this hypothesis:

1. *A. aegypti* eggs will survive longer at low relative humidity or at high temperature than will *A. albopictus* eggs.
2. Over the dry season, there is greater mortality of *A. albopictus* eggs, so that as the wet season begins, and previously dry containers fill with water, the proportion of containers occupied by *A. albopictus* will be lower than that observed during the middle of the wet season, after vases have been filled for an extended period. Further, we predict that this seasonal difference will not be present in vase occupancy by *A. aegypti*.
3. The likelihood of finding *A. aegypti* in containers at various locations in Florida increases with the mean temperature and with duration of seasonal dry periods, and decreases with the wetness of a site, whereas the likelihood of finding *A. albopictus* in containers decreases with temperature and duration of seasonal dry periods, and increases with wetness of the site.

Materials and methods

Egg mortality at controlled humidity and temperature

We established laboratory colonies of *A. albopictus* and *A. aegypti* from field-collected larvae and pupae from sites in southeastern Florida. Field-collected individuals were allowed to eclose in the laboratory, and the adults housed in 0.6 m³ cages, at 22–25°C, and 16:8 L:D photoperiod, including 1.5 h dawn and dusk phases. We provided adults with continuous access to ~10% sucrose and weekly blood meals from anesthetized mice. For this experiment we used eggs that were offspring of field-collected individuals. Eggs were laid on paper towels in water-filled cups, and stored at ~22°C and high humidity for 1 week to achieve full embryonation.

We placed replicate batches of *A. aegypti* eggs (mean±SE batch size=35±2, range=2–335 eggs, from a sample of 264 batches counted) and *A. albopictus* eggs (mean±SE batch size=12±1, range=2–56 eggs, from a sample of 96 batches counted) into open shell vials and housed these vials in 250 mm plastic desiccators within environmental chambers (Percival VL, photoperiod 14:10 L:D) at 22, 24, and 26°C. We established different relative humidities in different desiccators using saturated salt solutions (Winston and Bates 1960). Our goal was relative humidities of approximately 25%, 55%, 75%, and 95%, and we chose saturated solutions of KCOOH, NaCl, and NaBr·2H₂O, and deionized water, respectively, to establish these humidities. Solutions were monitored for saturation weekly and salts added as needed. We monitored ambient relative humidity in each desiccator using Fisher Brand Humidity Pens. Mean relative humidities for all temperature–humidity combinations ($n=12\text{--}20$ observations) were within 5% of the desired humidities, and differed among temperatures by 0.8–5.9%. Means ± 95% confidence intervals for KCOOH, NaCl, and NaBr·2H₂O, and deionized water were: 27.1%±1.0%; 55.5%±0.6%; 76.0%±0.9%; and 95.4%±1.0%, respectively.

We assayed batches of eggs for mortality after approximately 1 month for both species, and because we had abundant *A. aegypti* eggs and mortality of *A. aegypti* was very low after 1 month, we also assayed mortality of *A. aegypti* eggs after approximately 2 and 3 months. We removed batches of eggs from the desiccators and immersed the eggs in approximately 1% nutrient broth solution in hatching tubes (Novak and Shroyer 1978). We counted the number of hatchling larvae after approximately 24 h of immersion. We then bleached unhatched eggs (Mortenson 1950) and counted unhatched, fully embryonated eggs as deaths. We estimate mortality for each replicate batch as deaths/(deaths+hatchlings). As is inevitable with this type of investigation, some eggs were lost in the process of handling and bleaching, and we ignored these, under the assumption that such losses should be independent of whether the egg was alive. Other authors have used a similar approach (e.g., Sota and Mogi 1992b).

We compared proportion mortality of *A. aegypti* and *A. albopictus* eggs after 1 month using multiple logistic regression (Juliano 1993), with temperature (22, 24, 26°C) and relative humidity (25%, 55%, 75%, 95%) as continuous variables, and species as a categorical variable. We implemented this logistic regression using the CATMOD procedure of SAS (SAS Institute 1989), and defining populations as the replicate batches of eggs, so that degrees of freedom were determined by the number of replicate batches, rather than the number of individual eggs. We included in our initial model all main effects and interactions, and then deleted the highest order interaction (three-way) when it was not significant, and retested the reduced model. Because we found strong species-by-environment interactions, indicating the relationships of mortality to temperature and humidity differed between the species (see Results) we analyzed these data further by estimating regressions of mortality versus temperature, relative humidity, and interaction for each species separately.

For *A. aegypti* only, we ran another logistic regression of mortality versus temperature, relative humidity, and time of exposure (days), and all interactions. Data used for this regression included the same egg batches used for comparison to *A. albopictus* at 1 month. As with regressions at 1 month, we omitted the highest order interaction when it was not significant and reran the reduced logistic regression with all main effects and two-way interactions.

Seasonal changes in container occupancy

In 2000, we sampled six cemetery sites known to have persistent populations of *A. aegypti* several years after invasion by *A. albopictus*. We sampled five sites in Tampa, Fla. (26th St. Cemetery, Myrtle Hill Cemetery, Orange Hill Cemetery, Rose Hill Cemetery, and Woodlawn Cemetery) and one in Palmetto, Fla. (Palmetto Cemetery). One sample was obtained from each site at the end of the dry season (June), after rains had filled vases at each cemetery following a prolonged period with little or no rainfall and little or no water in the vases. Another sample was obtained from each

cemetery well into the rainy season (September), after the vases at each site had been well filled by regular rainfall. For Rose Hill (both months) and Myrtle Hill (June only) we sampled the vases on two dates 7–14 days apart. For all other sites, we took each sample on a single day. We probably sampled some of the same vases in June and September, but we did not keep track of the identities of vases between months. At Palmetto Cemetery, many of the vases we sampled in June were standard plastic cemetery vases (Diamond Line Container Co., Akron, Ohio) that we had placed at the site in June 1999 and had left undisturbed for the following year.

To sample a vase, we removed the entire contents, by dumping when possible, or using a kitchen baster for liquid and manually removing remaining detritus, and brought the contents to the laboratory for counting and identification of mosquitoes. For each vase we counted larvae and pupae of *A. albopictus* and *A. aegypti* (and other mosquitoes), rearing young larvae to the fourth instar to facilitate identification. We defined occupancy by each species as the proportion of vases yielding mosquitoes that yielded *A. albopictus* or *A. aegypti*. We tested for dependence on season (June vs September) of the proportion of vases occupied by *A. albopictus* for each cemetery using Fisher's exact test (two-tailed), and correcting for multiple tests using the Bonferroni method (Sokal and Rohlf 1995). For comparison, we also tested for dependence on season of proportion of vases occupied by *A. aegypti* using the same procedures.

Container occupancy and climate

We obtained data on mosquito occurrence from regular monitoring surveys of cemetery and tire sites. We gathered these data by collecting the entire contents of cemetery vases or substantial samples of contents of tires at a site and recording the number of containers with water that yielded *Aedes* mosquitoes, and the number that yielded *A. aegypti* or *A. albopictus*. Some containers yielded other *Aedes* (*A. triseriatus* or *A. bahamensis*) and these were counted in the total of containers yielding *Aedes*. Prior to invasion by *A. albopictus*, many of the sample sites were occupied by *A. aegypti*. For most of the 214 sites, we used the last 4 years of data (1997–2000) and summed the number of containers within each sample site across years for this period. At three sites, the most recent samples were from 1990–1994 (see Appendix), and in these cases we summed the numbers of containers within a sample site for the most recent year. We use proportion of containers occupied as a measure of abundance of *A. aegypti* and *A. albopictus* at each sample site, and attempt to predict this measure of abundance based on climate data. For sample site names, sample dates, and numbers of containers, see Appendix.

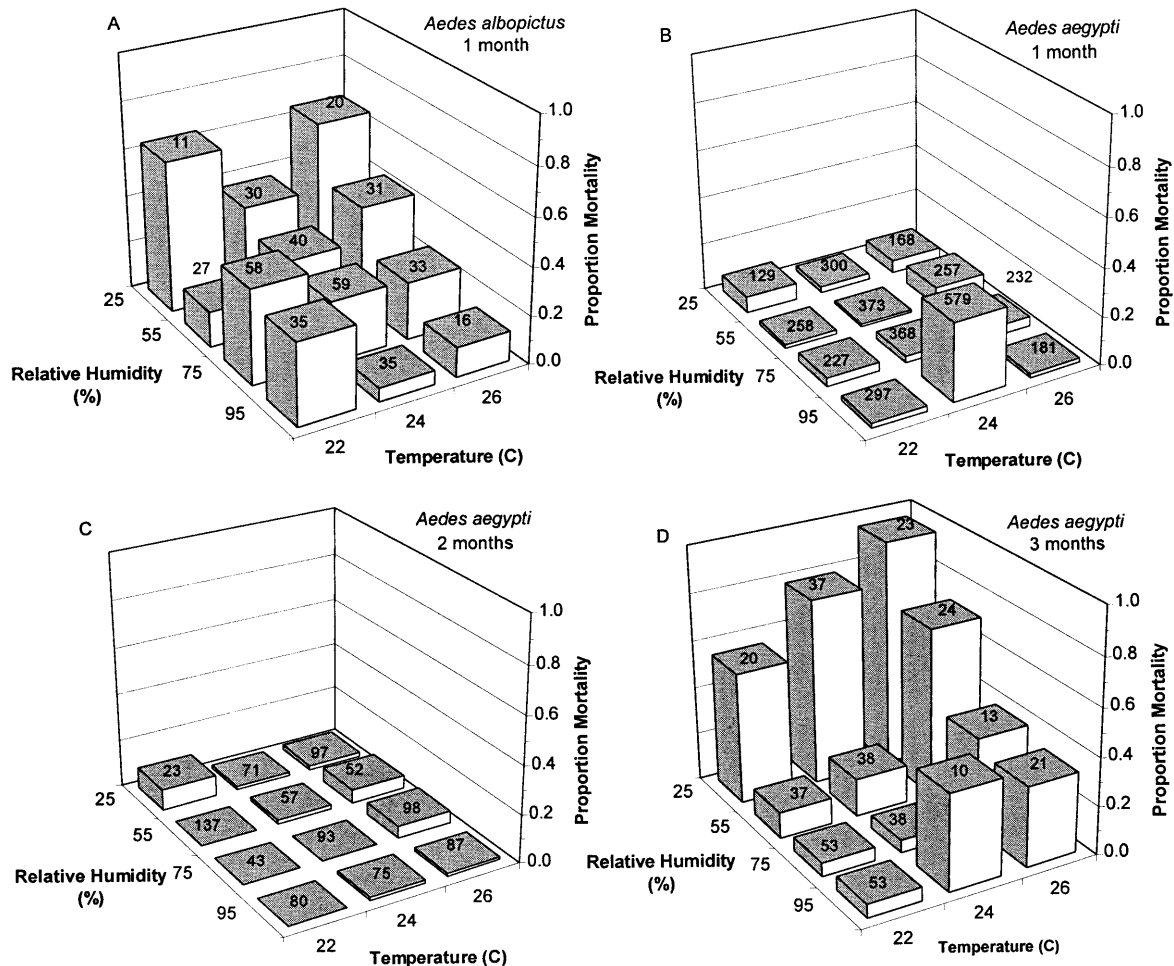
We obtained means for monthly precipitation, annual precipitation, and annual mean temperature for 49 Florida meteorological stations from the Southeast Regional Climate Center, National Oceanic and Atmospheric Administration (URL: http://water.dnr.state.sc.us/water/climate/sercc/norm_station.html#FL). These values represent the period from 1961 to 1990, and we use them to indicate the long-term averages at each of these sites. From these data, we determined for each station: (1) mean annual precipitation; (2) number of wet months (>100 mm mean precipitation); (3) number of dry months (<50 mm mean precipitation); and (4) mean annual temperature. Our criterion for wet months is the same as that used by Sota and Mogi (1992b). We then paired mosquito sampling sites with the nearest meteorological site to determine the relationship between climate variables and prevalence of *A. aegypti* and *A. albopictus*. When sample sites fell between two meteorological sites, we used the mean temperature and precipitation data for the two meteorological sites as our measure of local climate (see Appendix). The resulting data set included 30 of the original meteorological sites and 8 averaged meteorological sites. Most meteorological sites had multiple mosquito sampling sites nearby, and we treated these sampling sites as independent observations.

Because of strong correlations among these climate variables (see Results) we used principal components analysis (PCA)

(Hatcher and Stepanski 1994) to extract independent principal components that summarized climatic variation among the 38 meteorological sites. We estimated principal components using PROC FACTOR (SAS Institute 1989), and retained principal components only if their eigenvalues exceeded 1.00 (Hatcher and Stepanski 1994). The result was retention of two principal components summarizing >79% of the variation in climate variables (see Results). We interpreted these PC scores based on factor loadings after VARIMAX rotation (Hatcher and Stepanski 1994). We then used these two principal component scores (PC1, PC2) as independent variables for regressions of container occupancy.

We analyzed these data by first testing a logistic regression (Juliano 1993) model relating presence in a container to PC1, PC2, and the type of container sampled (TYPE = tire or cemetery vase) (SAS Institute 1989, PROC CATMOD). Because we found significant effects and interactions involving site type (see Results), we ran separate stepwise logistic regressions for the two site types, regressing frequency of container occupancy by *A. aegypti* or *A. albopictus* vs PC1, PC2, PC1², PC2², and the interaction of PC1 and PC2 (SAS Institute 1995, PROC LOGISTIC). We report the resulting logistic regressions, along with significance levels and parameter estimates for each variable retained in the stepwise model, and illustrate the results with graphical representations of the regression surfaces.

Fig. 1a–d Mortality of eggs at different relative humidities and temperatures. Numbers of eggs tested are above each bar. **a** *Aedes albopictus* at 1 month. **b** *A. aegypti* at 1 month. **c** *A. aegypti* at 2 months. **d** *A. aegypti* at 3 months



Results

Egg mortality at controlled humidity and temperature

Logistic regression of mortality of eggs at one month yielded no significant three-way interaction ($\chi^2=3.11$, $df=1$, $P=0.0779$), and this interaction was dropped from the logistic model. In the reduced model, main effects of temperature ($\chi^2=6.13$, $df=1$, $P=0.0133$) and relative humidity ($\chi^2=5.92$, $df=1$, $P=0.0150$) were significant, but more importantly, highly significant interactions of temperature and species ($\chi^2=7.71$, $df=1$, $P=0.0055$) and relative humidity and species ($\chi^2=85.92$, $df=1$, $P<0.0001$) indicate that the effects of temperature and relative humidity on mortality of eggs differed significantly between the species (Fig. 1 a, b). There was a very clear difference between the two species in the overall mortality of eggs (Fig. 1a, b) which is also evident in the strong effect of species in the logistic regression ($\chi^2=24.79$, $df=1$, $P<0.0001$). Egg mortality for *A. albopictus* was high after 30 days except for eggs held at the highest humidity (Fig. 1a). In contrast to *A. albopictus*, mortality of *A. aegypti* eggs was uniformly low at all humidity–temperature combinations except for 95% relative humidity, 24°C (Fig. 1b). Inspection of the raw data indicated that high mortality at this combination resulted primarily

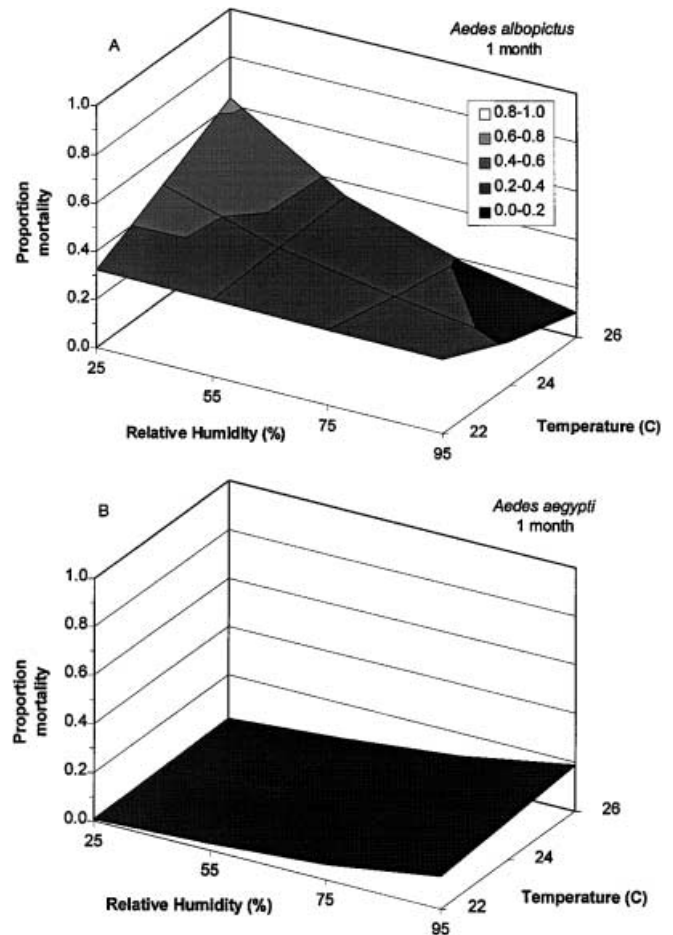
Table 1 Logistic regressions testing the relationships of egg mortality at 1 month to relative humidity and temperature for *Aedes aegypti* and *A. albopictus*

Source	<i>A. aegypti</i> (n=150 batches)				<i>A. albopictus</i> (n=64 batches)			
	df	Parameter (SE)	χ^2	P	df	Parameter (SE)	χ^2	P
Intercept	1	-12.219 (5.115)	5.71	0.0169	1	-12.988 (5.708)	5.18	0.0229
Relative humidity	1	+0.086 (0.062)	1.92	0.1657	1	+0.210 (0.083)	6.36	0.0117
Temperature	1	+0.289 (0.210)	1.91	0.1673	1	+0.558 (0.237)	5.55	0.0184
Relative humidity* Temperature	1	-0.002 (0.003)	0.61	0.4343	1	-0.010 (0.003)	7.55	0.0060
Likelihood ratio	146		940.94	<0.0001	60		178.71	<0.0001

from one batch of eggs that had complete hatching failure. Other batches of eggs at this humidity–temperature combination produced mortality estimates more similar to those for other humidity–temperature combinations. (Fig. 1b).

Separate logistic regressions for each species provided further insight into the different effects of temperature and humidity on mortality of eggs (Table 1). For *A. aegypti*, neither temperature nor humidity, nor their interaction significantly affected mortality of eggs. In contrast, for *A. albopictus*, effects of temperature, humidity, and interaction were all significant (Table 1). For *A. albopictus*, the egg mortality surface (Fig. 2a) indicates a strong and significant decline in mortality with increasing relative humidity at both 26 and 24°C, but at 22°C, mortality of eggs appears to be unaffected by relative humidity (Fig. 2). Thus, the interaction of humidity and temperature for mortality of *A. albopictus* eggs appears to arise because relative humidity does not affect mortality at the lowest temperature. For *A. aegypti*, the egg mortality surface is largely flat, indicating low mortality under all conditions, with only a slight and nonsignificant increase at higher relative humidities (Fig. 2b). Mortality of the two species is similar only at 95% relative humidity and temperatures of 24°C or 26°C (Fig. 2a, b). At 22°C, where egg mortality for both species is largely independent of relative humidity (Fig. 2a, b), mortality of *A. albopictus* eggs is considerably greater than that observed for *A. aegypti* eggs (Figs. 1, 2).

Logistic regression of egg mortality of *A. aegypti* over 3 months, yielded no significant three-way interaction ($\chi^2=0.38$, $df=1$, $P=0.5390$) and this interaction was dropped from the model. In the reduced model, there were strong significant interactions of both temperature and humidity with time (Table 2) indicating that the rate of increase in cumulative egg mortality over time was dependent on both temperature and humidity. The interaction of temperature and humidity was not significant (Table 2). As was true at 30 days, observed mortalities of *A. aegypti* eggs were very low at 60 days (Fig. 1c). Fitted surfaces to predict egg mortality at 30 and 60 days were both largely flat (Fig. 3a, b), indicating that envi-

**Fig. 2a, b** Logistic regression surfaces for mortality of eggs at different relative humidities and temperatures at 1 month. Regression statistics in Table 1. **a** *A. albopictus*. **b** *A. aegypti*

ronmental conditions had little effect on egg mortality of *A. aegypti* through 60 days. At 90 days, however, egg mortality was considerably greater (Fig. 1d) and more strongly related to environmental conditions (Figs. 1, 3). The fitted surface predicting egg mortality at 90 days indicates that mortality declines sharply as temperature de-

Table 2 Logistic regression for the relationships of egg mortality to relative humidity, temperature, and time for *A. aegypti*. Total $n=255$ batches of eggs, including the 150 batches of eggs used for comparison to *A. albopictus* at 1 month (see Table 3)

Source	df	Parameter (SE)	χ^2	P
Intercept	1	-6.402 (5.038)	1.61	0.2038
Relative humidity	1	+0.088 (0.047)	3.54	0.0597
Temperature	1	-0.141 (0.206)	0.47	0.4937
Time	1	-0.049 (0.048)	1.04	0.3086
Relative humidity×Time	1	-0.0016 (0.0001)	189.33	<0.0001
Temperature×Time	1	+0.0073 (0.0020)	13.70	0.0002
Relative humidity×Temperature	1	+0.0001 (0.0019)	<0.01	0.9450
Likelihood ratio	248		1269.07	<0.0001

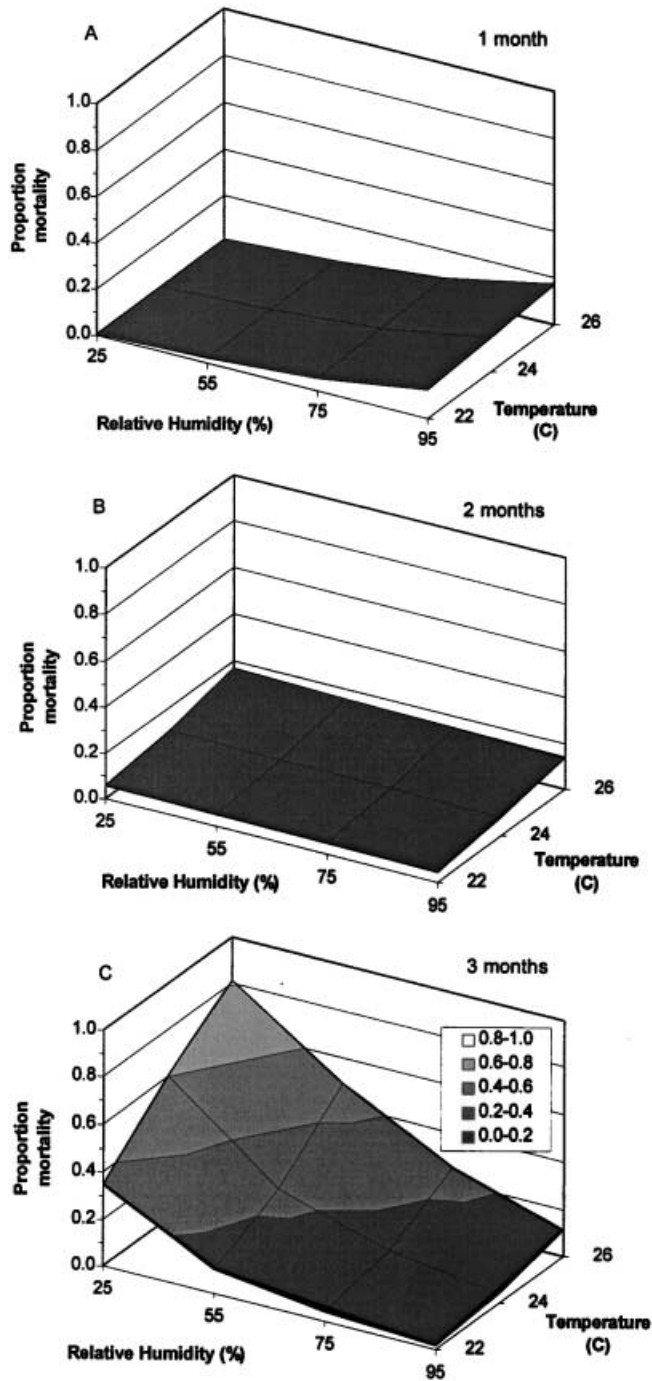


Fig. 3a–c Logistic regression surfaces for mortality of *A. aegypti* eggs exposed to different relative humidities and temperatures for different periods. Regression statistics in Table 2. **a** At 1 month **b** At 2 months. **c** At 3 months

creases and as relative humidity increases so that even at 90 days, *A. aegypti* eggs have very low cumulative mortality at 22°C and 95% relative humidity (Fig. 3c). The observed mortality data (Fig. 1d) suggest generally low mortality of *A. aegypti* eggs at relative humidities of 55% or greater at temperatures of 24°C or less, and fairly low mortality at relative humidities of 75% or greater even at a high temperature of 26°C.

Seasonal changes in container occupancy

The proportion of vases occupied by *A. albopictus* was significantly lower at the start of the wet season (June) than later in the wet season (September) at four of the six cemetery sites (experimentwise $\alpha>0.05$, Fisher exact tests, Fig. 4a). At Orange Hill Cemetery and Woodlawn Cemetery, *A. albopictus* was completely absent in the sample taken at the start of the wet season (Fig. 4a). In contrast, the proportion of vases occupied by *A. aegypti* did not differ significantly between the two seasonal samples for any of the six cemeteries (Fig. 4b), indicating that the lower proportion of vases occupied by *A. albopictus* early in the wet season is not a general seasonal effect on all *Aedes*.

Container occupancy and climate

There were strong positive correlations between mean temperature and number of dry months, and between mean annual precipitation and number of wet months, but number of dry months was negatively correlated with mean annual precipitation (Table 3). The first two principal components were retained for analysis and accounted for almost 80% of the variance in the data (Table 4). Factor loadings after rotation (Table 4) indicated that the first principal component (PC1) was strongly and positively correlated with mean temperature and number of dry months (mean precipitation <50 mm). Thus, high values of PC1 correspond to warm sites with pronounced seasonal rain, whereas low values of PC1 correspond to cool sites without a dry season. The second principal component (PC2) was strongly and positively correlated with mean annual precipitation and with number of wet months (months with >100 mm precipitation) (Table 4). Thus, high values of PC2 correspond to sites receiving abundant precipitation and with numerous wet months, whereas low values of PC2 indicate little precipitation

Fig. 4a, b Proportions (+SE) of cemetery vases occupied by each species at six cemeteries in June and September. Numbers of vases yielding mosquitoes in June and September are beneath cemetery names. Asterisks indicate significant differences between June and September (experimentwise $\alpha=0.05$, Bonferroni method). **a** *A. albopictus*. **b** *A. aegypti*

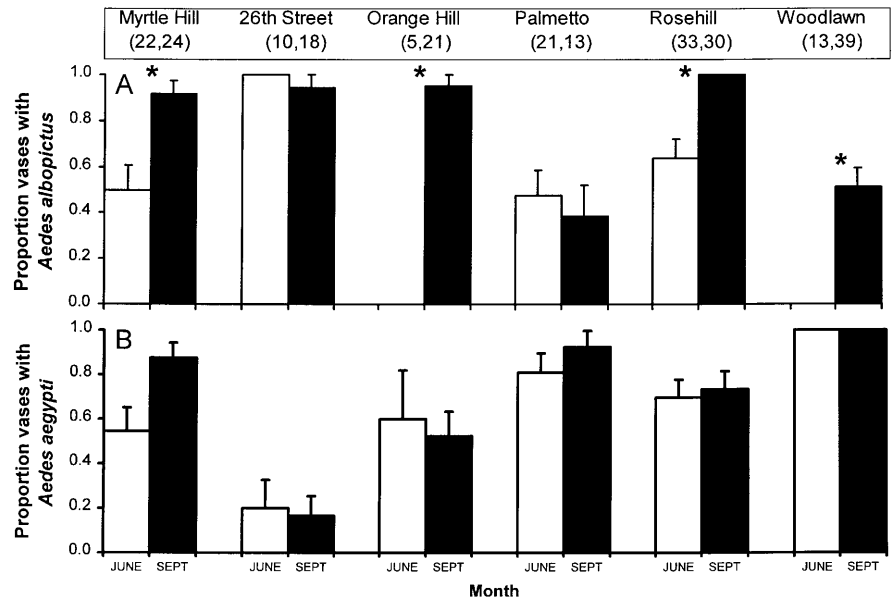


Table 3 Climate variables: summary statistics and correlation matrix. Boldfaced correlation coefficients are significant at overall $\alpha=0.05$ (Bonferroni adjustment, Sokal and Rohlf 1995)

$n=38$ meteorological sites	Mean temperature (°C)	Mean annual precipitation (mm)	Wet months (mean >100 mm)	Dry months (mean <50 mm)
Mean (SD)	22.6 (1.3)	1275.4 (112.8)	5.1 (0.8)	1.5 (1.5)
Minimum, maximum	20.0, 25.4	992.1, 1543.3	4, 8	0, 6
Correlation matrix				
Mean temperature		-0.103	+0.052	+0.596
Mean annual Precipitation			+0.501	-0.382
Wet months (>100 mm)				-0.171

Table 4 Climate variables: principal component analysis, eigenvalues, and factor loadings for PCs with eigen values >1.0. Bold typeface factor loadings indicate original variables that are strongly correlated with rotated PCs

Principal components analysis	PC1	PC2	PC3	PC4
Eigenvalue	1.89	1.30	0.48	0.34
Proportion variance	0.472	0.374	0.120	0.084
Cumulative	0.472	0.797	0.916	1.000
Original variable	Factor loadings (VARIMAX rotated)			
Mean temperature	+0.91	+0.10		
Mean annual precipitation	-0.23	+0.84		
Wet months (>100 mm)	+0.07	+0.88		
Dry months (<50 mm)	+0.86	-0.29		

and few wet months. These PCs thus establish two orthogonal climatic variables that can be used in regressions of container occupancy.

Container occupancy by *A. albopictus* was significantly affected by interactions of climate PC1 and PC2 with container TYPE ($\chi^2 > 166$, $P < 0.0001$, $df=1$, for each PC); hence separate stepwise logistic regressions were run for tires and for cemetery vases. Occupancy of cemetery vases was significantly and negatively related to PC2 and PC2², and positively related to the interaction of PC1 and PC2 (Table 5). The final stepwise regression explained over 51% of the variance in vase occupancy (adjusted R^2 , SAS Institute, 1995) (Table 5, compare Fig. 5a, b). Observed occupancy (Fig. 5a) was high for a broad range of PC1 scores and low to moderate PC2 scores. The resulting response surface predicted high oc-

cupancy for much of this range, and predicted low vase occupancy at high values of PC1 and low values of PC2 (i.e., warm sites with a long dry season and low precipitation – Fig. 5b). Predicted vase occupancy was also low at high values of PC2 (i.e., sites with high precipitation), regardless of PC1 (Fig. 5b). Tire occupancy was significantly and negatively related to PC1, PC1², and PC2² (Table 5). Observed occupancy was highest at sites with low PC1 and moderate PC2 (Fig. 5c). The final stepwise regression explained over 40% of the variance in tire occupancy (Table 5, compare Fig. 5c, d), and the response surface predicted high occupancy of tires at low values of PC1 (i.e., cool sites with a little dry season) and declining occupancy as PC1 increased (i.e., as temperature and length of the dry season increased – Fig. 5d). There was also a minor decline in tire occupancy predicted as

Table 5 Stepwise logistic regressions (SAS Institute 1995, PROC LOGISTIC) of container occupancy by *A. aegypti* and *A. albopictus* versus climate principal components (PC1 and PC2) in cemeteries and tire sites in peninsular Florida, 1994–2000

Source	df	Cemetery sites (n=58)			Tire sites (n=156)		
		Parameter (SE)	χ^2	P	Parameter (SE)	χ^2	P
<i>A. albopictus</i>							
Intercept	1	+3.22 (0.19)	290.68	0.0001	+1.58 (0.15)	107.79	0.0001
PC1	1				-1.20 (0.10)	140.02	0.0001
PC1 ²	1				-0.34 (0.09)	16.12	0.0001
PC2	1	-1.09 (0.08)	175.42	0.0001			
PC2 ²	1	-1.52 (0.10)	253.13	0.0001	-0.29 (0.05)	30.25	0.0001
PC1×PC2	1	+0.73 (0.19)	15.49	0.0001			
		Adjusted R ² =0.502			Adjusted R ² =0.404		
<i>A. aegypti</i>							
Intercept	1	-6.58 (0.70)	88.71	0.0001	-0.24 (0.09)	6.34	0.0118
PC1	1	+3.38 (0.57)	35.37	0.0001	+1.25 (0.09)	181.10	0.0001
PC1 ²	1	+1.05 (0.22)	21.94	0.0001			
PC2	1	-1.24 (0.34)	13.45	0.0002	-0.31 (0.09)	12.22	0.0005
PC2 ²	1	+2.02 (0.13)	231.61	0.0001			
PC1×PC2	1	+2.82 (0.52)	28.87	0.0001	-0.40 (0.10)	17.01	0.0001
		Adjusted R ² =0.662			Adjusted R ² =0.386		

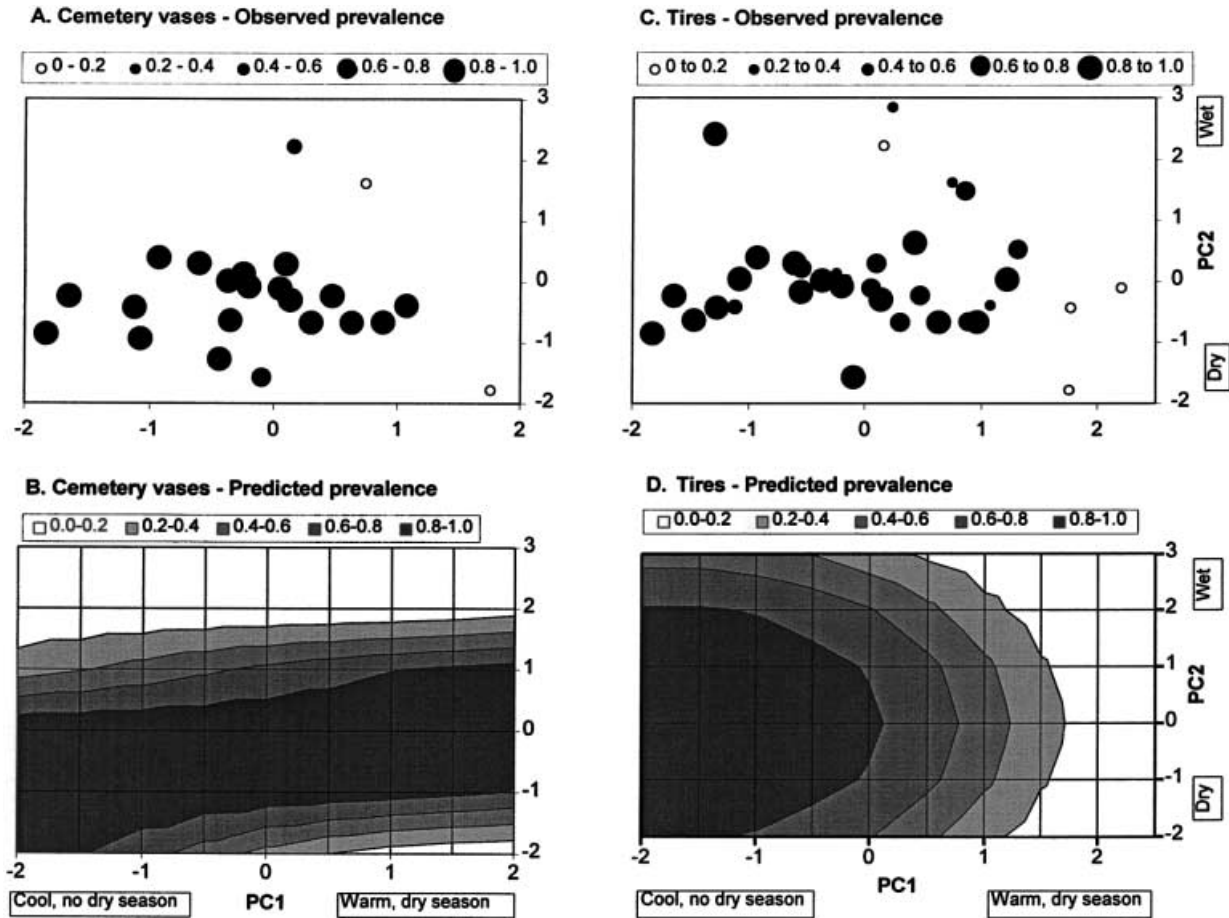


Fig. 5a–d Proportion of containers occupied by *A. albopictus* (=prevalence) versus climate principal components (Tables 3, 4). Observed values represent pooled samples from all mosquito sampling sites associated with each meteorological site. For individual mosquito sampling site data, see Appendix. Predicted values are from stepwise logistic regressions (Table 5). Cemetery vases: **a** observed; **b** predicted. Tires: **c** observed; **d** predicted

PC2 increased or decreased (i.e., as precipitation increased or decreased – Fig. 5d), an effect related to the significance of the PC2² effect.

Container occupancy of *A. aegypti* was significantly affected by interactions of climate PC1 and PC2 with container TYPE ($\chi^2 > 11$, $P < 0.0001$, $df = 1$, for all for in-

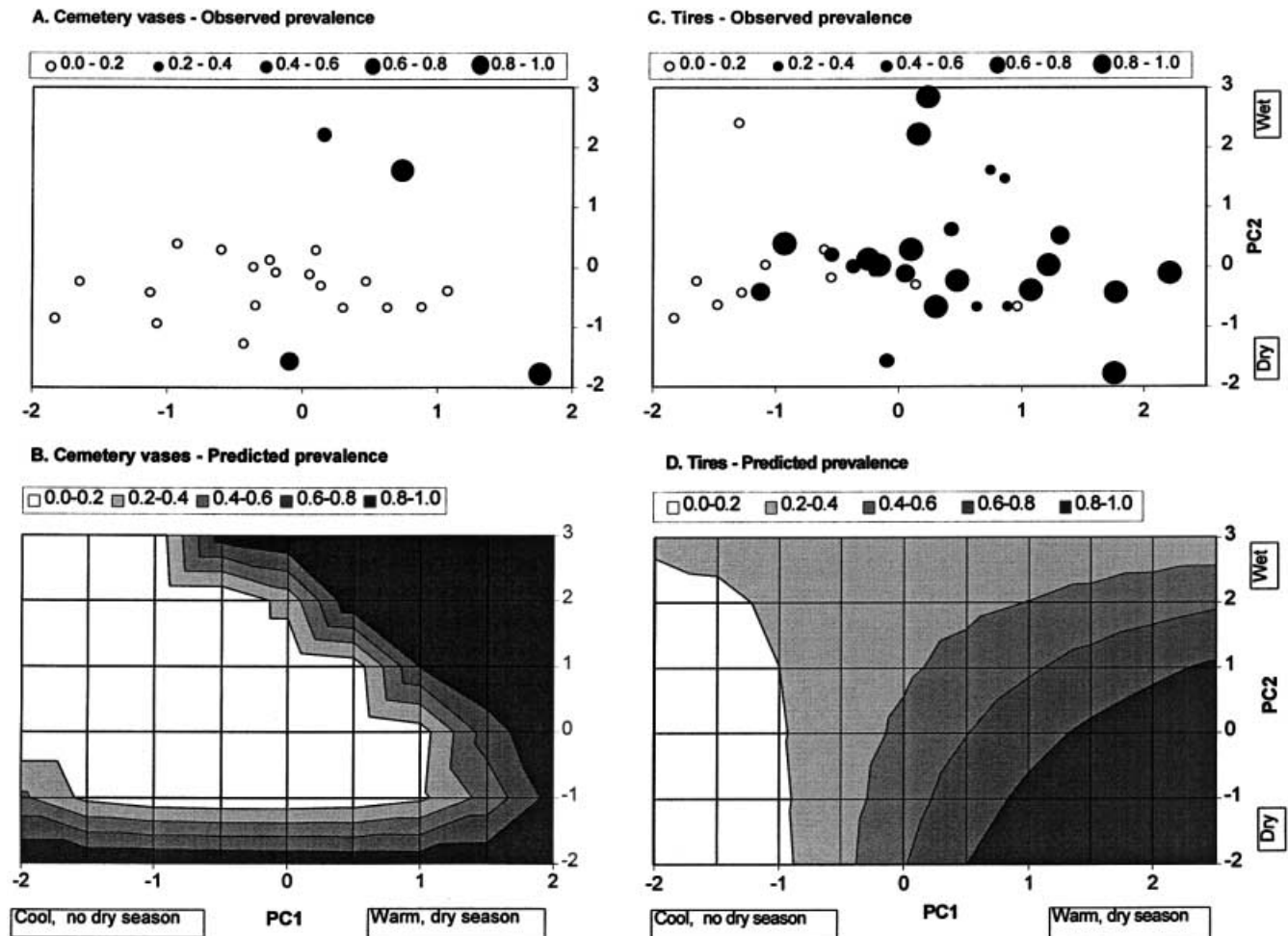


Fig. 6a–d Proportion of containers occupied by *A. aegypti* (=prevalence) versus climate principal components (Tables 3, 4). Observed values represent pooled samples from all mosquito sampling sites associated with each meteorological site. For individual mosquito sampling site data, see Appendix. Predicted values are from stepwise logistic regressions (Table 5). Cemetery vases: **a** observed; **b** predicted. Tires: **c** observed; **d** predicted

teractions); hence separate stepwise regressions were run for tires and cemetery vases. Observed vase occupancy was low for nearly all sites (Fig. 6 a) and was significantly and positively related to PC1, PC1², PC2², and interaction of PC1 and PC2, and negatively related to PC2 (Table 5). The final stepwise regression explained over 66% of the variance in vase occupancy (Table 5, compare Fig. 6a, b), and the resulting response surface (Fig. 6b) was the most complex of all those fitted (compare to Figs. 5b, d, 6b, d). The regression predicted high occupancy for high values of PC1 (i.e., warm sites with long dry seasons), low values of PC2 (i.e., sites with low precipitation), and high values of PC2 combined with high-to-moderate values of PC1 (i.e., high precipitation, moderately warm sites, with some dry season – Fig. 6b). Predicted vase occupancy fell to low values at low values of PC1 and high values of PC2 (i.e., at cool sites without a dry season, and with high precipitation –

Fig. 6b). Observed tire occupancy was lowest at low values of PC1 (Fig. 6c), and was significantly and positively related to PC1, and negatively related to PC2 and interaction of PC1 and PC2 (Table 5). The final stepwise regression explained over 38% of the variance in tire occupancy (Table 5, compare Fig. 6c, d), and the response surface predicted high occupancy of tires at high values of PC1 and low values of PC2 (i.e., warm sites with a long dry season and overall low precipitation – Fig. 6d). The regression predicted declining occupancy as PC1 decreased and as PC2 increased (i.e., as temperature and length of the dry season decreased, and as precipitation increased – Fig. 6d).

Discussion

Our data show very clearly that eggs of *A. albopictus* and *A. aegypti* differ dramatically in their vulnerability to mortality due to low humidity and temperature. As demonstrated for Asian strains (Sota and Mogi 1992b), we find that *A. albopictus* eggs are much more sensitive to desiccation than are *A. aegypti* eggs, which are largely unaffected by the test humidities and temperatures at 30 or even 60 days. The worst conditions for eggs of *A. albopictus* are relatively high temperature and low relative

humidity (Fig. 1a). Effects of relative humidity and temperature on *A. albopictus* egg mortality interact, with humidity having relatively little effect at lower temperatures (Fig. 2a). However, mortality of *A. albopictus* eggs was almost always substantially greater than that of *A. aegypti* eggs, which had extremely low mortality at 30 days under nearly all circumstances tested. From this laboratory experiment, we conclude that when eggs of these two species remain unflooded for a period of 30 days, there will be strong differential mortality, with *A. albopictus* suffering much greater mortality. When eggs hatch after a period without rainfall, there should be a reduction in the abundance of hatching larvae of *A. albopictus* relative to *A. aegypti*. The only conditions under which we would not expect this effect are very high humidity (95%) and high temperature (26°C), where both species should have very low mortality of eggs. In the environments that these species are likely to encounter in Florida, eggs on the sides of water-filled containers during the warm parts of the year should have relatively high survivorship. However, eggs exposed to dry containers, either in the dry periods characteristic of the winter in southern Florida, or during rare summer droughts (Fernald and Patton 1985), should yield greater death of *A. albopictus* relative to *A. aegypti*. Our data suggest that these effects should be accentuated in south Florida, with warmer temperatures, due to the interaction of temperature and low humidity on survival of *A. albopictus*.

Our survey of cemetery vases at the beginning and middle of the wet season strongly supports the predictions we derive from our laboratory studies. Significantly lower vase occupancy by *A. albopictus* following a seasonal dry period suggests that the dry period is causing mortality of *A. albopictus* eggs. The absence of this effect for *A. aegypti* suggests that this species has the ability to survive extended dry periods in its environmentally resistant egg. These data are consistent with the hypothesis that dry periods reduce the effects of interspecific competition on *A. aegypti* by reducing populations of *A. albopictus* via egg mortality, creating more containers without *A. albopictus*. Such an environmental effect on competitive interactions could facilitate coexistence of *A. aegypti* with *A. albopictus* because competition is disrupted by dry periods, resulting in a period of population increase for *A. aegypti*.

We find a pronounced effect of average climate (quantified by PC1 and PC2) on distribution of these species in peninsular Florida, as measured by frequency of container occupancy. Relationships of distribution to climate are broadly consistent with the results from both the laboratory experiments on egg desiccation and the short term study of effects of a dry period. In particular, the relationships of container occupancy to PC1 (a quantitative description of warmth and seasonal drought) for the two species tend to be opposite (Table 5, compare Figs. 5 and 6). As PC1 increases toward warmer sites with longer dry seasons, occupancy by *A. albopictus* tends to decrease, whereas occupancy by *A. aegypti*

tends to increase (compare in particular Figs. 5d and 6b, d). Only *A. albopictus* occupancy of cemetery vases does not show this pattern, but even in that case, predicted occupancy is low for warm sites, with a long dry season and little overall precipitation (Fig. 5b).

One striking result we did not anticipate is the difference in relationships of container occupancy to climate for tires versus cemetery vases (see regression results, Table 5). Mean temperature and seasonal drought (PC1) was a better predictor for tires than for cemetery vases (see Figs. 5, 6). There are several potential explanations for the differences between cemetery and tire sites. First, cemetery and tire sites are neither equally distributed, nor equally sampled across the Florida peninsula. We located more tire sites overall, and more tire sites in extreme northern Florida and in the Florida Keys (see Appendix). The result was that climates associated with tire sites spanned a greater range of values of PC1 and PC2 than was the case for cemetery sites (compare Fig. 5a, c), and this may contribute to the more clearly distinct relationships of climate to tire occupancy. A more interesting explanation for the difference is that the different types of containers may have different water holding properties, which may influence distribution of these two species. Tires are larger containers than most cemetery vases, which suggests that drying of tires should be less common. However, cemetery vases may receive supplemental water from sprinkling for landscape maintenance, and may be less prone to human disturbance (e.g., movement, which often occurs when there is a clean up of tire piles). At present there are no empirical data on the relative water holding ability or frequency of drying of these two container types in the field.

Distribution of these species relative to climate in peninsular Florida is consistent with qualitative patterns of distribution of these species relative to climate elsewhere in their ranges (e.g., Mattingly 1958; Fontenille and Rodhain 1989). Our data relating long-term average climate to distribution and abundance of *A. aegypti* are strikingly incongruent with Moore's (1985) analysis of local abundance of *A. aegypti* relative to recent weather. Moore (1985) found that amount of recent rainfall was positively related to *A. aegypti* abundance, whereas recent temperature data were not useful for predicting *A. aegypti* abundance. This discrepancy may derive in part from the difference in effects of recent weather versus effects of climate (i.e., long term averages) on mosquito distribution and abundance, and in part from the interaction of a competitor like *A. albopictus* (absent in the time and place studied by Moore 1985) with effects of the abiotic environment on distribution of *A. aegypti*. In the short term, rainy weather certainly provides larval habitat for *A. aegypti*, and so may increase local abundance. However, a climate that is cool and wet facilitates invasion by *A. albopictus*, and resulting reductions of *A. aegypti* via interspecific competition.

We have evaluated only the effects of humidity and temperature on survival of nondiapaused eggs of these species. Temperate-zone strains of *A. albopictus* have

egg diapause, and diapause eggs of Asian strains are more resistant to death from desiccation at 44% relative humidity up to 60 days (Sota and Mogi 1992a). The photoperiod and temperature necessary to induce diapause in *A. albopictus* is variable, and the prevalence of diapause induction under natural conditions in peninsular Florida is poorly known (L.P. Lounibos, personal communication).

These data are consistent with our hypothesis that persistence of *A. aegypti* and coexistence with *A. albopictus* is dependent on disruption of competition due to mortality of eggs of *A. albopictus* during dry periods. Warm temperatures and desiccation appear to limit distribution and abundance of *A. albopictus* within peninsular Florida. Because survival of *A. aegypti* eggs is not affected by temperature-humidity conditions for up to 60 days, it is unlikely that its greater abundance in warmer, drier areas of Florida is a direct effect of climate on this species. Rather, the observed distribution pattern of *A. aegypti* is likely an indirect effect of climate limiting its major competitor *A. albopictus*. The previous range limit of *Aedes aegypti* in North America was situated far to the north of the northern part of Florida (Darsie and Ward 1981; Mekuria and Hyatt 1995), indicating that this species can survive in relatively cool climates. Reports of reduction or elimination of *A. aegypti* from more northern parts of its former range following invasion by *A. albopictus* have come from South Carolina (Mekuria and Hyatt 1995), Alabama (Hobbs et al. 1991), and north Florida (McHugh 1993), all areas that are cooler and wetter than the Florida peninsula (Southeast Regional Climate Center, http://water.dnr.state.sc.us/water/climate/sercc/norm_station.html). Thus we suggest that warmer, drier locations provide a refuge for *A. aegypti* from competition with *A. albopictus*, in much the same way that harsher physical conditions provide refuges from competition for other species (e.g., Connell 1961; Hemphill 1991). The two species show distinct survival responses to seasonal or stochastic fluctuations in temperature and moisture, and also buffered population growth due to their environmentally resistant eggs (particularly for *A. aegypti*). These data suggest that coexistence results from the mechanisms described in the theoretical framework of the storage effect (Chesson 2000).

Climate effects on egg survival may explain much of the variation in the current distribution of these two species in Florida, but they do not explain all aspects of their distribution (note substantial unexplained variance in the logistic regressions for distribution, Table 5). *A. aegypti* remains fairly common in some wetter, cooler areas, and has been eliminated in some warmer, drier areas. O'Meara et al. (1995) suggested that persistence of *A. aegypti* was associated with urban areas, whereas this species had been reduced or eliminated in more suburban and rural areas. This relationship to human activity and land use is not taken into account directly in our evaluation of effects of climate. However, urban environments are often warmer than surrounding non-urban areas (McIntyre 2000). Some of the differences we ob-

served in distribution of these species across cemetery vases versus tires may also be related to differences in the positions of cemeteries versus tire yards along a rural-urban gradient. Many other factors are likely to vary along a rural-urban gradient (e.g., container type and density, hosts for blood meals, vegetation cover) and a full understanding of the factors shaping the distribution of these species in Florida must include analysis of land use and human activity.

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References

- Atkinson WD, Shorrocks B (1981) Competition on a divided and ephemeral resource. I. a simulation model. *J Anim Ecol* 50:461–471
- Barrera R (1996) Competition and resistance to starvation in container-inhabiting *Aedes* mosquitoes. *Ecol Entomol* 21:117–127
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Christophers SR (1960) *Aedes aegypti* (L.) the yellow fever mosquito: its life history, bionomics and structure. Cambridge University Press, Cambridge
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Darsie RF Jr, Ward RA (1981) Identification and geographical distribution of the mosquitoes of North America, north of Mexico. *Mosq Syst Suppl* 1:1–313
- Daugherty MP, Alto BW, Juliano SA (2000) Invertebrate carcasses as a resource for competing *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). *J Med Entomol* 37:364–372
- Dunson WA, Travis J (1991) The role of abiotic factors in community organization. *Am Nat* 138:1067–1091
- Edgerly JS, Willey MS, Livdahl TP (1993) The community ecology of *Aedes* egg hatching: implications for a mosquito invasion. *Ecol Entomol* 18:123–128
- Fernald EA, Patton DJ (eds) (1985) Water resources atlas of Florida. Florida State University, Tallahassee
- Fontenille D, Rodhain F (1989) Biology and distribution of *Aedes albopictus* and *Aedes aegypti* in Madagascar. *J Am Mosq Cont Assoc* 5:219–225
- Frank JH (1981) Recycling of discarded tires for control of *Aedes aegypti*. *J Fla Anti-Mosq Assoc* 52:44–48
- Grover JP (1997) Resource competition. Chapman and Hall, London
- Hatcher L, Stepanski EJ (1994) A step-by-step approach to using the SAS system for univariate and multivariate statistics. SAS Institute, Cary, N.C.
- Hawley WA (1988) The biology of *Aedes albopictus*. *J Am Mosq Cont Assoc* ([Suppl] 4):1–39
- Hemphill N (1991) Disturbance and variation in competition between two stream insects. *Ecology* 72:864–872
- Hobbs JH, Hughes EA, Eichold BH II (1991) Replacement of *Aedes aegypti* by *Aedes albopictus* in Mobile, Alabama. *J Am Mosq Cont Assoc* 7:488–489
- Hornby JA, Moore DE, Miller TW Jr (1994) *Aedes albopictus* distribution, abundance, and colonization in Lee County, Florida, and its effect on *Aedes aegypti*. *J Am Mosq Cont Assoc* 10:397–402

- Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105:405–412
- Ives AR (1991) Aggregation and coexistence in a carrion fly community. *Ecol Monog* 61:75–94
- Juliano SA (1993) Nonlinear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Chapman and Hall, New York, pp 159–182
- Juliano SA (1998) Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79:255–268
- Livdahl TP, Willey MS (1991) Prospects for an invasion: competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science* 253:189–191
- Mattingly PF (1958) The subgenus *Stegomyia* (Diptera: Culicidae) in the Ethiopian region. II Distribution of species confined to the East and South African sub-region. *Bull Brit Mus (Nat Hist) Entomol* 3:1–65
- McHugh CP (1993) Distributional records for *Aedes* mosquitoes from the U.S. Air Force oviptrapping program – 1992. *J Am Mosq Cont Assoc* 9:352–355
- McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. *Ann Entomol Soc Am* 93:825–835
- Mekuria Y, Hyatt MG (1995) *Aedes albopictus* in South Carolina. *J Am Mosq Cont Assoc* 11:468–470
- Mogi M, Miyagi I, Abadi K, Syafruddin (1996) Inter- and intra-specific variation in resistance to desiccation by adult *Aedes (Stegomyia)* spp. (Diptera: Culicidae) from Indonesia. *J Med Entomol* 33:53–57
- Moore CG (1985) Predicting *Aedes aegypti* abundance from climatological data. In: Lounibos LP, Rey JR, Frank JH (eds) *Ecology of mosquitoes: proceedings of a workshop*. Florida Medical Entomology Laboratory, Vero Beach, pp 223–235
- Moore CG (1999) *Aedes albopictus* in the United States: current status and prospects for further spread. *J Am Mosq Contr Assoc* 15:221–227
- Mortenson EW (1950) The use of sodium hypochlorite to study *Aedes nigromaculis* (Ludlow) embryos (Diptera: Culicidae). *Mosq News* 10:211–212
- Novak RJ, Shroyer DA (1978) Eggs of *Aedes triseriatus* and *Aedes hendersoni*: a method to stimulate optimal hatch. *Mosq News* 38:515–521
- O'Meara GF, Evans LF Jr, Gettman AD, Cuda JP (1995) Spread of *Aedes albopictus* and decline of *Ae. aegypti* (Diptera: Culicidae) in Florida. *J Med Entomol* 32:554–562
- Petren K, Case TJ (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77:18–132
- SAS Institute (1989) *SAS/STAT users guide*, version 6. SAS Institute, Cary, N.C.
- SAS Institute (1995) *Logistic regression examples using the SAS System*. SAS Institute, Cary N.C.
- Simberloff D, Smith DC, Brown TC (eds) (1997) *Strangers in paradise. Impact and management of nonindigenous species in Florida*. Island Press, Covelo, Calif
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. Freeman, New York
- Sota T, Mogi M (1992a) Survival time and resistance to desiccation of diapause and non-diapause eggs of temperate *Aedes (Stegomyia)* mosquitoes. *Entomol Exp Appl* 63:155–161
- Sota T, Mogi M (1992b) Interspecific variation in desiccation survival time of *Aedes (Stegomyia)* mosquito eggs is correlated with habitat and egg size. *Oecologia* 90:353–358
- Spiller DA (1984) Seasonal reversal of competitive advantage between two spider species. *Oecologia* 64:322–331
- Teng H-J, Apperson CS (2000) Development and survival of immatures *Aedes albopictus* and *Aedes triseriatus* (Diptera: Culicidae) in the laboratory: effects of density, food, and competition on response to temperature. *J Med Entomol* 37:40–52
- Warner SC, Travis J, Dunson WA (1993) Effect of pH variation on interspecific competition between two species of hyliid tadpoles. *Ecology* 74:183–194
- Williamson M (1996) *Biological invasions*. Chapman and Hall, New York
- Winston PW, Bates DH (1960) Saturated solutions for the control of humidity in biological research. *Ecology* 41:232–237