Consider first case without rarefaction
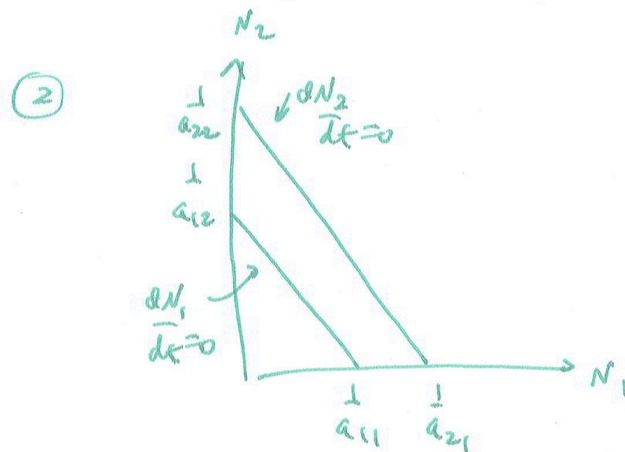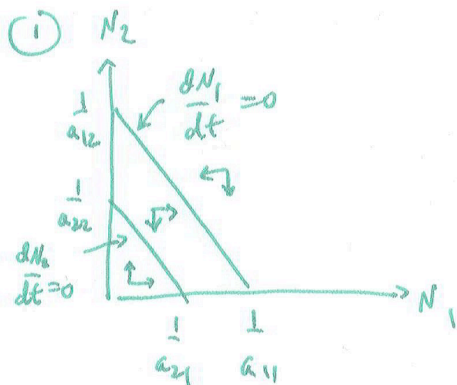
$$\frac{dN_1}{dt} = r_1 N_1 (1 - a_{11} N_1 - a_{12} N_2)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - a_{21} N_1 - a_{22} N_2)$$

Two scenarios where coexistence is impossible

①
N_2

$\frac{1}{a_{12}}$ $\frac{dN_1}{dt} = 0$

$\frac{1}{a_{22}}$

$\frac{dN_2}{dt} = 0$

N_1

$\frac{1}{a_{21}}$ $\frac{1}{a_{11}}$

②
N_2

$\frac{1}{a_{22}}$

$\frac{dN_2}{dt} = 0$

$\frac{1}{a_{12}}$

$\frac{dN_1}{dt} = 0$

N_1

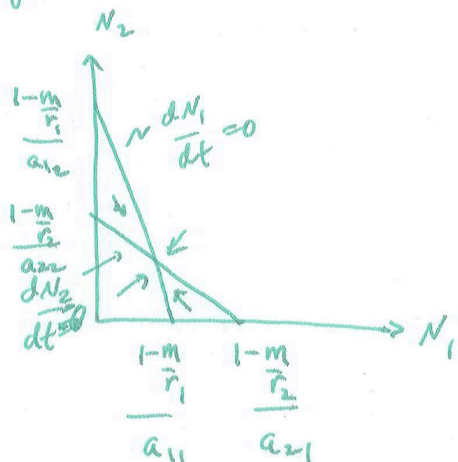$\frac{1}{a_{11}}$ $\frac{1}{a_{21}}$

How can rarefaction make co-existence possible?

rarefaction equations

$$\frac{dN_1}{dt} = r_1 N_1 (1 - a_{11} N_1 - a_{12} N_2) - m N_1$$
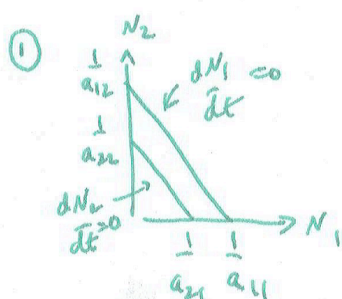$$= r_1 N_1 \left(\left(1 - \frac{m}{r_1} \right) - a_{11} N_1 - a_{12} N_2 \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 (1 - a_{21} N_1 - a_{22} N_2) - m N_2$$
$$= r_2 N_2 \left(\left(1 - \frac{m}{r_2} \right) - a_{21} N_1 - a_{22} N_2 \right)$$

Stable

Equilibrium occurs in this case:

N_2

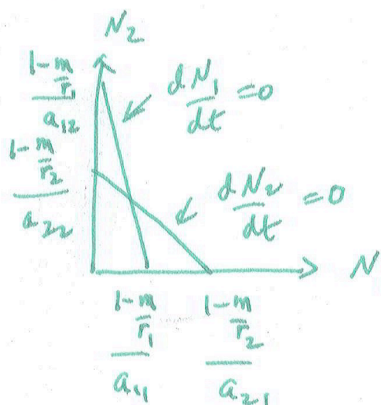$\dfrac{1-\frac{m}{r_1}}{a_{12}}$

$\dfrac{1-\frac{m}{r_2}}{a_{22}}$

$\dfrac{dN_2}{dt}=0$

$\dfrac{dN_1}{dt}=0$

$\dfrac{1-\frac{m}{r_1}}{a_{11}}$ $\dfrac{1-\frac{m}{r_2}}{a_{21}}$

N_1

First consider going from

①

N_2

$\dfrac{1}{a_{12}}$

$\dfrac{1}{a_{22}}$

$\dfrac{dN_1}{dt}=0$

$\dfrac{dN_2}{dt}=0$

$\dfrac{1}{a_{21}}$ $\dfrac{1}{a_{11}}$ N_1

$\Longrightarrow$

N_2

$\dfrac{1-\frac{m}{r_1}}{a_{12}}$

$\dfrac{1-\frac{m}{r_2}}{a_{22}}$

$\dfrac{dN_1}{dt}=0$

$\dfrac{dN_2}{dt}=0$

$\dfrac{1-\frac{m}{r_1}}{a_{11}}$ $\dfrac{1-\frac{m}{r_2}}{a_{21}}$ N_1

For this particular shift to occur with rarefaction requires shift in where isoclines cross N_1 axis

In unstable case

$\dfrac{1}{a_{21}} < \dfrac{1}{a_{11}}$

$\dfrac{a_{11}}{a_{21}} < 1$

Stable case

$\dfrac{1-\frac{m}{r_1}}{a_{11}} < \dfrac{1-\frac{m}{r_2}}{a_{21}}$

$\dfrac{1-\frac{m}{r_1}}{1-\frac{m}{r_2}} < \dfrac{a_{11}}{a_{21}}$

For both conditions to hold

$$\boxed{\dfrac{1-\frac{m}{r_1}}{1-\frac{m}{r_2}} < \dfrac{a_{11}}{a_{21}} < 1}$$

This is one way (or set of conditions) for which system could move from being unstable to stable coexistence.

7.2

(a) $\dfrac{dP_1}{dt} = m_1 P_1 (1-P_1) - e P_1 = 0$

$$m_1 P_1 - m_1 P_1^2 - e P_1 = 0$$

$$m_1 - e = m_1 P_1$$

$$\hat{P}_1 = \frac{m_1 - e}{m_1}$$

$\hat{P}_1 > 0$ when $m_1 > e$, or when the colonization rate of species 1 exceeds the extinction rate.

(b) $\dfrac{dP_2}{dt} = m_2 P_2 (1-P_1-P_2) - m_1 P_1 P_2 - e P_2 = 0$

$$m_2 P_2 - m_2 P_2 P_1 - m_2 P_2^2 - m_1 P_1 P_2 - e P_2 = 0$$

Substitute $\hat{P}_1 = \dfrac{m_1 - e}{m_1}$, solve for $\hat{P}_2$

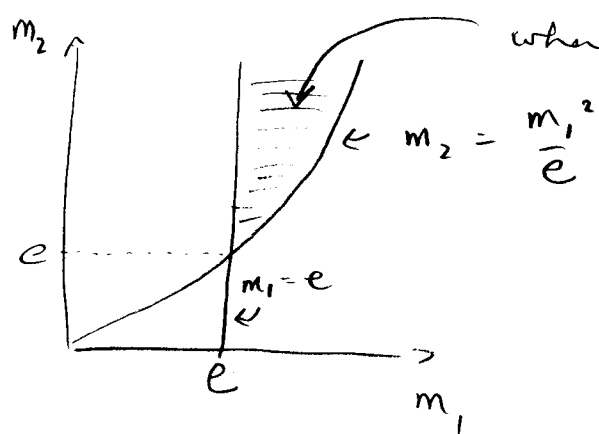$$m_2 - m_2 \left(\frac{m_1 - e}{m_1}\right) - m_2 \hat{P}_2 - m_1 \left(\frac{m_1 - e}{m_1}\right) - e = 0$$

$$m_2 - m_2 \left(\frac{m_1 - e}{m_1}\right) - m_1 + e - e = m_2 \hat{P}_2$$

$$\hat{P}_2 = \frac{m_2 - m_1 - m_2 \left(\frac{m_1 - e}{m_1}\right)}{m_2}$$

$$= 1 - \frac{m_1}{m_2} - 1 + \frac{e}{m_1}$$

$$\boxed{\hat{P}_2 = \frac{e}{m_1} - \frac{m_1}{m_2}}$$

For both species to survive

$$\frac{e}{m_1} > \frac{m_1}{m_2} \quad \text{and} \quad m_1 > e$$

$m_2 = \frac{m_1^2}{e}$

$m_1 = e$

where both species survive, the colonization rate of both species exceeds the extinction rate, Species 2 must also compensate for the fact it is always outcompeted by Species 2 by having a greater colonization rate. $m_2 > \frac{m_1^2}{e}$

7.2 (c)

For both species to survive

$$m_2 > e \;\; ; \;\; m_1 > e \;\; ; \;\; m_2 > m_1$$

Thus $m_2 > m_1 > e$

$$\hat{p}_1 = \frac{m_1 - e}{m_1} \;\;\;\; , \; \hat{p}_2 = \frac{e}{m_1} - \frac{m_1}{m_2}$$

$$\hat{p}_1 = 1 - \frac{e}{m_1}$$

As e increases, $m_1 > e$ is violated first, leading to $\hat{p}_1 < 0$.

| Species 1 would be eliminated first. |

7.2 (d)

If both species have positive equilibrium levels, as e increases, $\hat{p}_2$ increases.

The equilibrium level of species 2 is positively correlated with the extinction rate. This makes sense because as species 1 declines, species 2 has more patches available to colonize.

7.2)

(a) $\frac{dP_1}{dt} = 0 = m_1 \hat{P}_1(1-\hat{P}_1) - e\hat{P}_1$

$\Rightarrow \quad e\hat{P}_1 = m_1\hat{P}_1(1-\hat{P}_1) \qquad$ OR $\qquad \Rightarrow \boxed{\hat{P}_1 = 0}$

$\Rightarrow \quad e = m_1(1-\hat{P}_1)$

$\Rightarrow \quad \frac{e}{m_1} = 1 - \hat{P}_1$

$\Rightarrow \quad \boxed{\hat{P}_1 = 1 - \frac{e}{m_1}}$

For $\hat{P}_1 > 0$, $\quad \frac{e}{m_1} < 1 \Rightarrow e < m_1$

An ecological interpretation of this would be that the equilibrium is positive when at equilibrium, the rate of extinctions is less than the rate at which empty sites are colonized.

(b) Let $P_1 = \hat{P}_1 = 1 - \frac{e}{m_1}$

Then $\frac{dP_2}{dt} = m_2 P_2(1-P_1-P_2) - m_1 P_1 P_2 - eP_2 = m_2 P_2\left(1-1+\frac{e}{m_1}-P_2\right) - m_1\left(1-\frac{e}{m_1}\right)P_2 - eP_2$

Set $\frac{dP_2}{dt} = 0 = m_2 \hat{P}_2\left(1-1+\frac{e}{m_1}-\hat{P}_2\right) - m_1\left(1-\frac{e}{m_1}\right)\hat{P}_2 - e\hat{P}_2$

$0 = m_2\hat{P}_2\left(\frac{e}{m_1}-\hat{P}_2\right) - m_1\hat{P}_2 + e\hat{P}_2 - e\hat{P}_2$

$0 = \frac{-m_2\hat{P}_2 e}{m_1} + \hat{P}_2^{\,2} m_2 + m_1\hat{P}_2$

$0 = \hat{P}_2^{\,2} m_2 + \hat{P}_2\left(m_1 - \frac{m_2 e}{m_1}\right)$

$0 = \hat{P}_2 m_2 + m_1 - \frac{m_2 e}{m_1}$

$\frac{m_2 e}{m_1} - m_1 = \hat{P}_2 m_2$

$\boxed{\frac{e}{m_1} - \frac{m_1}{m_2} = \hat{P}_2}$

For $\hat{P}_2 > 0$, $\quad \frac{e}{m_1} - \frac{m_1}{m_2} > 0$

$\Rightarrow \quad \frac{e}{m_1} > \frac{m_1}{m_2}$

$\Rightarrow \quad em_2 > m_1^{\,2}$

For $\hat{P}_1 > 0$, $\quad e < m_1 \quad$ (see above)

$\therefore \quad m_1 m_2 > em_2 > m_1^{\,2}$

$\Rightarrow \quad m_1 m_2 > m_1^{\,2} \quad \Rightarrow \quad \underline{m_2 > m_1} \qquad$

So for $\hat{P}_1, \hat{P}_2 > 0$, which would mean that both species are surviving at equilibriums, $\boxed{m_2 > m_1}$

~~the~~ Meaning the colonization rate of the Non-dominant species must be greater than the colonization rate of the dominant species.

This makes perfect sense from an ecological species. If the rate of colonization of the dominant species were greater, or even equal to, the colonization rate of the non-dominant species, then the non-dominant species couldn't compete and would be driven to extinction. Thus, in order to make up for its lack of competitive dominance, the non-dominant species must have a much greater colonization rate.

As an aside, this provides an example of a mechanism that explains how metacommuni~~tessy~~ty structure can increase species richness / diversity in an ecosystem.

(C.) At ~~equilibrium~~ positive equilibrium, $m_2 > m_1 > e$, (see above part a and b).

Thus as e, the rate of extinctions increases, e will be greater than m_1 before it is greater than m_2.

i.e. $m_2 > m_1 > e \rightsquigarrow m_2 > e > m_1 \rightsquigarrow e > m_2 > m_1$

Since $e > m_1$ before $e > m_2$, the ~~𝓍~~ population of the dominant species will ~~be~~ be knocked out of equilibrium and will tend to ~~the a negative zero~~ equilibrium before the population of the non-dominant species will.

Thus, at equilibrium and as the extinction rate is increased, the Dominant species ~~s~~, ~~p~~ Sp. 1, will be eliminated first.

(d) Assuming both species have positive equilibrium levels,

$$\hat{P}_2 = \frac{e}{m_1} - \frac{m_1}{m_2} \qquad \text{(see above)}$$

Thus as e increases, $\frac{e}{m_1}$ increases and then $\frac{e}{m_1} - \frac{m_1}{m_2} = \hat{P}_2$ increases.

So increasing the extinction rate increases the equilibrium level of species 2.

This may seem counter-intuitive at first glance, but upon closer inspection, it makes a great deal of sense. Since sp. 2 is a good colonizer but a poor competitor, it's growth rate is

limited more by the competition with species 1 than by extinctions. Thus, as the extinction rate increases, ~~sp.2~~ ~~extinct~~ sp.1 is impacted more than sp.2, and the decline of sp.1 allows sp.2 to ~~the~~ escape the competition pressures and increase its equilibrium level.

7.4

a) What has been found is both in nature and in the lab, all possible outcomes of coexistence or elimination of one species or the other, plus parameters are difficult to measure. One possible way to test the Lotka-Volterra model is to make a fixed environment of organisms grown together and in isolation. In this set-up it is easy to determine the carrying capacities of each species. In the field, measuring carrying capacities is not easy. In isolation each species will be at their respected carrying capacities. According to the model, the point of coexistence lays above the isocline that joins the two separate carrying capacities. However, experimentally it has been shown that this equilibrium point lays below the line, therefore rendering the Lotka-Volterra model inadequate even for simple controlled systems. This means the isocline lines must in fact be curved. This can be achieved by taking into account frequency dependent competition, energetic considerations, and age dependence, all of which the mathematical model does not take into account (Hastings). The Lotka-Volterra takes into account species 1's effect on itself and on species 2, species 2's effect on itself and on species 1. These parameters are among those that are difficult to measure both in the field and in the laboratory.

b) In the field we would like to be able to isolate the association of two species specifically on the level of competition. Tracking the population sizes of these two populations can be difficult in nature due uncontrolled extrinsic factors such as predation, changes in weather, migration, etc. You can constantly keep counting individuals present in species 1, but it may be very difficult to ascertain whether those changes in numbers are only due to its competition with the other species and not some other random factor. In the laboratory you can isolate and fix your conditions making the direct influence on population size strictly due to some form of competition. It is also a lot easier to count individuals in the lab. Even though the lab situation might seem more appealing, the research itself loses the spontaneity and the variability present in nature that may challenge our models, allowing us to strengthen our understand of actual biological interactions.

c) The main assumption of competition theory is that the greater the resource overlap between species, the greater the interspecific competition relative to intraspecific completion. Competition theory does not predict that all possible combinations of species should show substantial competition. Only species on the same trophic level as the manipulated species are considered as candidates for competition unless they clearly have the potential to compete for space. In particular, species affected indirectly are excluded. Specifically the form of competition looking at resources is called exploitative competition, which includes consumptive competition (consummation of a quantity of resource by one individual depriving the other). Overgrowth competition can also play into competition for resources as some individuals can grow large and block sunlight to other individuals, for example. Consumptive competition is the most common form of exploitative competition in all but marine organisms (Schoener, 1983).

d) In the field, there are several ways the population can be manipulated to show effects of interspecific competition. The abundances (densities) of one or more hypothetically competing can be changed by, removal, introductions, or a mixture of both. For animals, removal generally means to physically transport the entire organism from the study plot. For plants, this is done by cutting the roots of potentially competing plants around the plots boundaries. Plants can also be entirely removed and replaced. Introductions include physically transporting organisms to an area where one or more species already exists or clearing an entire area of all species and introducing new organisms one at a time (Schoener, 1983).

Sonja Kolstoe
Population Ecology (BI 571)
Spring 2013
Homework 5
Excerpt Problem 7.4

- 7.4

Article:Juliano, S. A. (1998). Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition?. Ecology, 79(1), 255-268.

a. Describe competition in the laboratory and the field using Lotka Volterra equations.

$$\frac{dN_1}{dt} = \frac{r_1 N_1}{K_1}(K_1 - N_1 - \alpha_{12}N_2) - p_1 N_1 - p_{12}N_1 N_2$$

where p_1 is the coefficient of the parasite's effect on species 1 and p_{12} is the parasites effect as a result of both species being present. The same can be then said for species 2:

$$\frac{dN_2}{dt} = \frac{r_2 N_2}{K_2}(K_2 - N_2 - \alpha_{21}N_1) - p_2 N_2 - p_{21}N_1 N_2$$

Dominance or co-existence can result as the research has shown.

b.

The paper looks at the competition between container-dwelling mosquitoes of *Aedes albopictus* and *Aedes aegypti*. It was noted that in South Florida there were sites were invasions of *A.albopictus* resulted in the decline of *A.aegypti*. The main focus of the research was on interspecies competition at the larvae stage of mosquitos when they are in competition as container-dwelling mosquito.*A. albopictus* is a generalist both in terms of food and habitat requirements as well as is adaptable to different climates. Studies cited in the study looked at the interaction of these two mosquitoes in artificial containers but in the laboratory setting *A.aegypti* is often the dominant species when yeast or liver powder is given as the resource. Also, the studies have noted that the *A. aegypti* are quicker to mature. Another factor that Juliano (1998) points out that one species may be more affected by parasites a site which then plays into which becomes dominant. In terms of the Lotka Volterra equations I would say the interspecies coefficients α_{12} and α_{21} are close to 1 given

the common use of resources and subsequent habitat. The predator factor may have an effect that is similar to removal of a part of a researcher.

c. Discuss the approach of looking at overlap in resources used by putative competitors.

The approach of looking at overlap in resources shows that the mosquito *A. albopictus* as a generalist is able to better or more efficiently exploit resources in an environment than *A. aegypti*. As a result in places they overlap the species that is better adapted, less affected by parasites dominates at a site. To look at how overlap in resource usage affects competition, Juliano consider the following field experiments: experimental cages as well as different treatments effects meant to mimic different starting conditions and resource availability (in this case leaf litter).

d. Discuss experimental field manipulations of populations.

Treatments: five tires held 12 cages

1. Varied combinations of two species in the starting level
2. Different resource levels (leaf little)
3. Different density levels

By manipulating the above factors Juliano was able to find that the primary factor determining survivorship to adulthood to include accounting for whether parasites influenced the outcome of which species prevailed or became dominant. He finds that density and availability of resources played a large role in determining the survival of *A. aegypti* or was replaced by *A.albopictus*.

SPECIES INTRODUCTION AND REPLACEMENT AMONG MOSQUITOES: INTERSPECIFIC RESOURCE COMPETITION OR APPARENT COMPETITION?

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Abstract. Mechanisms by which an introduced container-dwelling mosquito, *Aedes albopictus,* may cause declines in a resident container-dwelling mosquito, *Aedes aegypti,* in South Florida were tested using a combination of field experiments and field observations. Field experiment 1 tested which species has a competitive advantage as larvae developing in water-filled tires. Densities and availability of resources (leaf litter, which is a substrate for microorganisms fed upon by larvae) were manipulated in a factorial design. Contrary to previous laboratory experiments, *A. albopictus* was clearly the superior competitor in this tire environment, maintaining positive population growth at higher combined density and lower per capita resource availability than did *A. aegypti.* The primary determinant of success in this experiment was survivorship to adulthood, and *A. aegypti* only survived well in this environment when raised alone at low density, with high resource availability. Field experiment 2 tested whether this advantage for *A. albopictus* resulted from apparent competition mediated by shared protozoan parasites in the genus *Ascogregarina.* In field experiment 2, *A. albopictus* larvae had moderate to high levels of parasitism, but *A. aegypti* larvae were virtually free from *Ascogregarina* in all experimental tires, implying that *Ascogregarina* played little or no role in producing the advantage for *A. albopictus* in field experiment 1. Thus, apparent competition does not appear to be necessary to account for the replacement of *A. aegypti* by *A. albopictus.* As a first step toward understanding variation in the outcome of this invasion, numbers of *Aedes* immatures and masses of adults from field collected pupae (indicators of the intensity of competition) were compared for three sites with known histories of invasion by *A. albopictus* and decline of *A. aegypti.* Differences among sites in both number of *Aedes* per container and masses of adults of both species were consistent with the hypothesis that intensity of competition varies among sites, and suggest that *A. aegypti* persists only at sites where interspecific competition is less intense. Resource competition among larvae appears to be sufficient to account for replacement of *A. aegypti* by *A. albopictus* in suburban and rural areas of South Florida, which may have been marginal habitats for *A. aegypti.*

Key words: Aedes aegypti; Aedes albopictus; *aquatic insects;* Ascogregarina; *biological invasion; competitive superiority; container mosquitoes; field experiment; introduced species; protozoan pathogens; resource competition.*

INTRODUCTION

Introduced species interest ecologists for at least two distinct reasons. From a practical perspective, understanding the ecology of introduced species and their effects on other members of their communities may be vital for alleviating undesirable effects (e.g., reductions or extinctions of native species), or, more rarely, accentuating desirable effects (e.g., biological control) of those introduced species. From a basic perspective, introduced species provide ecologists with the opportunity to study nonequilibrium systems, and therefore to test our understanding of how biotic interactions such as predation, competition, and mutualism affect populations and communities (Hill and Lodge 1994, Petren and Case 1996). The effects of these interactions may

be transient in many undisturbed systems, and therefore difficult to study at a meaningful temporal and spatial scale. Invasions by introduced species provide one kind of large-scale perturbation that can yield information about the effects of those interactions (Diamond 1986, Lodge 1993, Hill and Lodge 1994, Petren and Case 1996). Simply following trajectories of populations and communities during invasions cannot resolve which mechanisms are producing the observed effects of the invader on the native species. Different interactions, alone or in combination, can yield the same trajectories. The ideal situation is to link observational data on trajectories of systems subject to invasion with manipulative field experiments that can test hypothesized mechanisms for the observed changes. Such approaches, although uncommon, have been very productive as ways of understanding the interactions that lead to effects of introduced species on native communities (e.g.,

crayfish: Garvey et al. 1994, Hill and Lodge 1994; geckos: Petren et al. 1993, Petren and Case 1996, Case et al. 1994, Hanley et al. 1995).

When invasion by an introduced species is correlated with declines in abundance of native species, a number of alternative processes may explain that correlation. Invaders may negatively affect natives via interspecific competition (e.g., Hill and Lodge 1994, Human and Gordon 1996, Petren and Case 1996), predation (e.g., Porter and Saviagno 1990), habitat alteration (e.g., Bertness 1984), apparent competition mediated by shared enemies (e.g., van Riper et al. 1986, Settle and Wilson 1990), or the introduced species may only increase when some external disturbance (e.g., weather, man-made environmental change) causes a decline in populations of resident species (e.g., Herbold and Moyle 1986). More than one of these processes may act in any single system (e.g., Garvey et al. 1994). The challenge to the basic ecologist is to resolve which of these processes are responsible for the observed changes in populations and community composition. Experimental manipulations are necessary to determine what processes are leading to replacement of a native by an introduced species.

Aedes albopictus is a mosquito, native to Asia, that was introduced to North America during the 1980s (Hawley 1988, O'Meara et al. 1995). Since introduction, *A. albopictus* has spread rapidly in the southern United States and in some urban areas in the north (Hawley 1988, O'Meara et al. 1992, 1993, 1995). Because this species is a vector of human arboviruses (Hawley 1988, Mitchell 1995), successful invasion may have important practical consequences. Females deposit desiccation resistant eggs above the water line in containers (e.g., bird baths, cemetery vases, discarded tires, natural tree holes); eggs hatch when flooded, except during winter diapause, and larvae develop in water-filled containers, feeding on microorganisms and detritus (Hawley 1988). *Aedes albopictus* has been a successful introduced species in North America, Pacific Islands (Hawley 1988), South America (Barrera 1996), Africa, and Europe (Mitchell 1995). Success of *A. albopictus* as an invader seems to result from its generalized habitat and food requirements, desiccation resistant eggs, adaptability to different climatic conditions, and an ability to live in human-dominated habitats (Hawley 1988, Focks et al. 1994).

Aedes albopictus potentially interacts with a number of other container-dwelling mosquitoes. In North America, most investigations have focused on interactions between *A. albopictus* and other container-dwelling *Aedes* such as *A. triseriatus* and *A. aegypti* (Livdahl and Willey 1991, Black et al. 1989, Ho et al. 1989, Novak et al. 1993, Barrera 1996). The interaction of *A. albopictus* with *A. aegypti* is the most interesting, and the best studied, for a number of reasons. These two species develop in artificial containers and can be very common in human-dominated areas. Increase and spread of *A. albopictus* appears to be strongly correlated with declines in the prevalence of *A. aegypti* at some, but not all sites in Florida (O'Meara et al. 1993, 1995, Hornby et al. 1994) and other parts of North America (Hobbs et al. 1991, Mekuria and Hyatt 1995). Often, *A. albopictus* appears to displace *A. aegypti* in suburban and rural areas, whereas in urban environments of South Florida, though *A. albopictus* invades, *A. aegypti* does not decline and may remain the dominant species (Hornby et al. 1994, O'Meara et al. 1995). Ultimately, any explanation for the decline of *A. aegypti* after invasion by *A. albopictus* must include a mechanistic account of the variable effects of invasion on *A. aegypti*.

Interspecific competition among larvae is, perhaps, the most obvious hypothesis for this observed pattern of invasion and decline. Laboratory studies of competition between these species clearly show that competition may occur. Paradoxically, *A. aegypti* often appears to be the superior competitor under laboratory conditions (Moore and Fisher 1969, Black et al. 1989, Ho et al. 1989). However, these laboratory competition experiments are of questionable value as tests of what occurs in nature because investigators have usually used resources (e.g., yeast, liver powder) that are not the typical resources exploited in nature, and have used laboratory-adapted strains that may be very different from field populations. Also, these investigations typically inferred competitive advantage based on only one of several population growth correlates (usually time to maturity, which is typically less for *A. aegypti*), and these investigations have often employed poor statistical analyses (e.g., pseudoreplication), rendering conclusions from the experiments questionable.

One popular alternative hypothesis for the pattern of invasion and decline is apparent competition via the gregarine protozoan parasite *Ascogregarina taiwanensis* (Blackmore et al. 1995). Though these species have a number of parasites (Christophers 1960, Hawley 1988), those suggesting this hypothesis have focused on *A. taiwanensis* because they are common in nature and may have asymmetrical effects on these *Aedes* species (Munstermann and Wesson 1990, Garcia et al. 1994, Blackmore et al. 1995). *Ascogregarina taiwanensis* primarily parasitizes *A. albopictus,* and in the laboratory can also infect *A. aegypti* (Munstermann and Wesson 1990, Garcia et al. 1994). High parasite loads of *A. taiwanensis* may sometimes have greater detrimental effects on *A. aegypti* than on *A. albopictus* in the laboratory (Munstermann and Wesson 1990; S. Paulson, *personal communication*). Another species, *Ascogregarina culicis*, parasitizes *A. aegypti*, but in the laboratory cannot infect *A. albopictus* (Beier and Craig 1985, Munstermann and Wesson 1990). In principle, this asymmetry in effects of *A. taiwanensis* could result in apparent competition (Holt and Lawton 1994), and thus lead to the observed pattern of invasion by *A. albopictus* followed by the decline of *A. aegypti*. The

hypotheses of interspecific competition or of apparent competition are not necessarily mutually exclusive.

To determine the role of competition in the replacement of *A. aegypti* by *A. albopictus,* the intensity of competition in nature must be estimated, particularly because at some sites, invasion by *A. albopictus* is closely associated with decline of *A. aegypti,* whereas at other sites, *A. aegypti* persists after invasion (O'Meara et al. 1995). One hypothesis for this pattern is that the intensity of competition varies from site to site, and that where competition is most intense, *A. aegypti* is eliminated, whereas where competition is weak (e.g., because of high nutrient availability or because mosquito densities are limited by other factors in the terrestrial environment), *A. aegypti* persists. This hypothesis leads to one prediction that can be tested with observational data from field sites with known histories of invasion and decline: Elimination of *A. aegypti* should be associated with measures of intensity of competition. One such measure is the body size of field collected mosquitoes (Fish 1985). Competition among larvae results in reduced adult body size in nearly all mosquitoes, including these two mosquitoes (e.g., Black et al. 1989). Body size is an imperfect index of competition among larvae because it is also affected by temperature (Fish 1985), however it can be readily obtained from field collected samples. Other indices of competition, such as densities of mosquitoes (number/mL), provide some useful information, but the utility of density is limited by the difficulty of quantifying per capita resource availability for container mosquitoes.

In this paper I report the results of a field experiment testing the hypothesis that *A. albopictus* has a strong competitive advantage over *A. aegypti,* along with a supporting field experiment and field observations that enable me to answer the following questions: (1) When competition occurs, which species, if any, has a competitive advantage? (2) Is apparent competition mediated by *Ascogregarina* a necessary and sufficient mechanism for any interspecific effect of *A. albopictus* on *A. aegypti* in the field? (3) For a small set of sites with known histories of invasion by *A. albopictus,* is the intensity of competition related to *A. aegypti* population persistence?

METHODS

Study site and source of mosquitoes

The experiments were conducted at the Florida Medical Entomology Laboratory (FMEL), Vero Beach, Florida (27.4° N, 80.3° W). The study site was an oak–palmetto hammock located immediately adjacent to the main laboratory. This site contains both natural tree holes and discarded tires that have been in the hammock from 2 to >10 yr. Prior to invasion by *A. albopictus,* tires at this site contained both *A. triseriatus* and *A. aegypti* (S. A. Juliano, *personal observation*; L.

P. Lounibos, *personal communication*). *Aedes albopictus* arrived in Indian River County in 1990 (O'Meara et al. 1995) and became abundant in these tires in 1991 (L. P. Lounibos, *personal communication*). Other container-dwelling mosquitoes, such as *Corethrella appendiculata* and *Toxorhynchites rutilus,* which are predators of other aquatic insects, were also present at this site (Lounibos 1985).

Aedes used in these experiments were first generation progeny of individuals collected as immatures in nature. Larvae and pupae of *A. albopictus* were collected from discarded tires in and around Vero Beach, Florida. Larvae and pupae of *A. aegypti* were collected from the same sites near Vero Beach, and also from discarded tires at sites near Port Salerno, in Martin County, ~60 km south of Vero Beach, where *A. aegypti* were more abundant. Immatures were sorted by species and reared to adulthood in the laboratory. Adults were provided with blood meals from restrained domestic chickens (housed and maintained in accordance with National Institutes of Health [NIH] guidelines for animal care), and eggs were deposited on paper towels.

Field experiment 1: Which species has a competitive advantage?

Determining competitive advantage.—There are several alternative models of interspecific competition and competitive exclusion (e.g., Lotka-Volterra models, resource competition models) each incorporating different parameters that quantify competitive advantage (e.g., Lotka-Volterra competition coefficients, resource consumption vectors; Livdahl and Willey 1991, Tilman 1982). One criterion for competitive advantage that can be applied whatever model is chosen is that the superior competitor is the one that can maintain positive population growth at a greater combined density or a lower per capita resource availability than its competitor. The inference of competitive advantage is particularly clear cut if one species can maintain positive population growth under conditions that yield negative population growth for the other species. I used this approach.

Experimental cages.—The experiments were done in field cages, similar to those described by Léonard and Juliano (1995), suspended in the water column of tires. Each cage consisted of a 150-µm nylon mesh cylinder, sealed with silicone sealant, and attached at the bottom to the lid of a 30-mL plastic jar. The jar lid (diameter = 40 mm) had a circular opening of 30 mm cut into the top, and was affixed to the nylon mesh cylinder using silicone sealant. Near the top of the cage there was a PVC pipe ring attached to the net using silicone sealant. The top of the cage was folded over and closed with a binder clip. The plastic jar (diameter = 43 mm, height = 21 mm) screwed into the jar lid; it provided a receptacle for leaf litter (see *Treatments* below) and retained water when the cages were removed from the tires. Cages measured 221 mm in height, with an inside diameter of 35 mm. When suspended in the tires, water

filled the cages to a depth 80 to 130 mm, and each cage held 77 to 125 mL of water.

Treatments.—Each of five tires held 12 cages each. Every cage within a tire contained a different treatment that consisted of combinations of the two mosquito species in a small response surface design for testing competition (Goldberg and Scheiner 1993) replicated at two different resource (leaf litter) levels. Mosquito combinations appeared at low density (20 hatchling larvae/cage) or high density (60 hatchling larvae/cage). At low density, each species appeared alone (20 *A. albopictus*, abbreviated 20ALB; 20 *A. aegypti*, abbreviated 20AEG). At high density, each species appeared alone (60 *A. albopictus*, abbreviated 60ALB; 60 *A. aegypti*, abbreviated 60AEG), or in combination with the other species (20 *A. albopictus* + 40 *A. aegypti*, abbreviated 20ALB + 40AEG; 40 *A. albopictus* + 20 *A. aegypti*, abbreviated 40ALB + 20AEG). Resource levels were 0 or 1 g of *Quercus virginiana* (live oak) leaf litter.

Upright tires were covered with 1-cm wire screen, which excluded vertebrates and provided attachment points for the cages. Water volumes were brought up to maximum using water collected from other nonexperimental tires at this site and filtered through a 250-μm nylon mesh to remove invertebrates. Water levels in the experimental tires were maintained by weekly additions of deionized water, which simulated regular rainfall. Daytime water temperature, pH, and conductivity were measured weekly in each tire.

Fallen live oak leaves were dried at 60°C, broken into quarters, and partitioned into 1.00-g allotments. These were placed into appropriate cages and then all cages were suspended in tires on 13 August 1993. Leaves were left to soak and to be colonized by microorganisms in tires for 4 d. On 17 August, eggs for the experiment were synchronously hatched (Novak and Shroyer 1978), and 24 h later, larvae were counted into appropriate groups, and added to all cages.

Data collection.—Initially, cages were checked every 2 d to determine developmental stages of larvae. When pupae appeared (day 7), cages were checked daily for emerging adults. For each adult, species and sex were determined, and labeled adults were dried at 60°C and weighed to the nearest 0.0001 mg using a Cahn C31 ultramicrobalance. Masses of adults, days from hatch to adulthood, and number of adults were the basic data collected from this experiment. The last adult mosquito emerged from an experimental cage on 30 October, 74 d after hatch. The experiment was ended on 3 November (day 78). Only one larva (*A. albopictus*) remained.

Data analyses.—I calculated a composite index of population performance based on r' (Livdahl 1982, 1984, Livdahl and Sugihara 1984), which estimates the realized per capita rate of population change ($dN/N\,dt = r$, the exponential growth rate) within each replicate cage. The estimate used was $\lambda' = \exp(r')$, which is

analogous to the finite rate of increase $\lambda = \exp(r)$ (Pianka 1988). In demographic analyses, λ is preferable to r because λ is estimable even if no individuals survive to reproductive age ($\lambda = 0$), whereas r is not estimable ($r = -\infty$) in that circumstance (Lenski and Service 1982). The same relationship holds for λ' and r' (Léonard and Juliano 1995, Grill and Juliano 1996).

The composite index was calculated for each species within each replicate as

$$\lambda' = \exp(r')$$

$$= \exp\left[\frac{\ln\left[(1/N_0)\sum_x A_x f(w_x)\right]}{D + \left[\sum_x x A_x f(w_x)\Big/\sum_x A_x f(w_x)\right]}\right] \quad (1)$$

where r' is the composite index of performance developed by Livdahl and Sugihara (1984; see also Livdahl 1982, 1984). In the expression for r' (in brackets in Eq. 1), N_0 is the initial number of females in the cohort (assumed to be 50% of the cohort), A_x is the number of females eclosing on day x, w_x is a measure of the mean size of females eclosing on day x, $f(w_x)$ is a function relating production of female eggs to female size, and D is the time between adult eclosion and reproduction. The summations are taken across days (x). A_x and w_x were determined for each species within each replicate cage; D was assumed to be 12 d for *A. aegypti* (Grill and Juliano 1996) and 14 d for *A. albopictus* (Livdahl and Willey 1991). Regressions relating production of female eggs to size at eclosion (taken from the literature) were

A. aegypti:

$$f(w_x) = 17.11 + 16.59(w_x^{0.765}) \quad (2)$$

$$r^2 = 0.10, \qquad N = 57, \qquad P < 0.05$$

(w_x = dry mass in milligrams; Colless and Chellapah 1960, Grill and Juliano 1996) and

A. albopictus:

$$f(w_x) = 17.2w_x - 14.0 \quad (3)$$

$$r^2 = 0.03, \qquad N \text{ and } P \text{ not reported}$$

(w_x = wing length in millimeters; Livdahl and Willey 1991). Because these regressions explained relatively little of the observed variation in fecundity, I also calculated λ' using alternative values for $f(w_x)$ in Eq. 1, to see if different functions substantially altered λ' and the conclusions of the analysis. First, I assumed no relationship of fecundity and size, and used reported mean fecundities of *A. aegypti* (51.8 eggs/female or 25.9 female offspring/female [Colless and Chellapah 1960]) and *A. albopictus* (65 eggs/female, or 32.5 female offspring/female; Hawley 1988) in calculating λ'.

Second, I assumed that slopes of the fecundity–size relationships were twice the values reported in Eqs. 2 and 3 (i.e., new values of 33.18 in Eq. 2 for *A. aegypti* and 34.4 in Eq. 3 for *A. albopictus*) and used the new values of $f(w_x)$ to calculate λ'. In both cases, resulting values of λ' increased by <0.5% of the original value for *A. aegypti*, and by 0.5 to 2.0% of the original value for *A. albopictus*. Conclusions of statistical analyses were identical, hence I am confident that the conclusions are not sensitive to the fecundity–size relationships (see also *Discussion*: *Which species has a competitive advantage?*). I will report only the results of the original analysis.

For analysis of λ', no transformation yielded data that met assumptions of normality and homogeneous variance. I therefore used randomization ANOVA (Manly 1991*a*, *b*) to analyze λ' as a randomized complete block design, with four different density–species composition combinations as treatments, two litter levels, interaction, and individual tires as blocks. Following ANOVA, I tested pairwise comparisons of all treatment means using randomization methods (Manly 1991*a*, *b*) at an experimentwise $\alpha = 0.05$ (sequential Bonferroni method; Rice 1989). In addition, I determined 95% confidence intervals for each mean using the percentile bootstrap method (Dixon 1993). I examined these intervals for inclusion of $\lambda' = 0$ (cohort dies out in one generation) and $\lambda' = 1.0$ (cohort stable, with no net growth or decline).

In order to determine which correlates of population growth were most affected by competition, I analyzed data on survivorship (sexes pooled) and mass at adulthood (each sex) by two-factor, randomized complete block ANOVA, with treatment, litter, and interaction as effects, and tire as a block. Survivorship was arcsine square-root transformed to meet assumptions of homogeneous variance and normality. For mass at adulthood, untransformed data came closest to meeting assumptions of homogeneous variance and normality. Because treatment–litter interactions were often significant (see *Results*: *Field experiment 1*) significant treatment effects were further analyzed using pairwise comparisons among treatment least squares means (SAS Institute 1989, PROC GLM) within a litter level, with a sequential Bonferroni adjustment for the number of tests done (experimentwise $\alpha = 0.05$). I did similar analyses on median time to adulthood (each sex), however, this analysis contributed little additional information and is therefore omitted in the interest of brevity.

Pearson correlations of mean λ' for each species in each block (tire) with block mean daytime temperature, conductivity, and pH were determined. Because of the low sample size (five tires), significance tests on these correlations had very low power, and these correlations are used only as a preliminary indication of the physical variables that may be related to population performance.

Field experiment 2: What is the prevalence and role of Ascogregarina?

Detecting gregarines.—Gregarine parasites can be reliably detected by dissecting living late-instar mosquito larvae, and searching the mid- and hindguts for parasites (Munstermann and Wesson 1990, Blackmore et al. 1995). Field experiment 1 was not conducive to such dissections, as the mosquitoes were allowed to reach adulthood, when *Ascogregarina* are harder to detect. To determine the likelihood of larvae of both species acquiring *Ascogregarina* in experimental cages in these tires, I placed separate batches of 25 newly hatched *A. aegypti* and *A. albopictus* into cages (without litter) like those used in field experiment 1, and placed those cages into tires at this site after field experiment 1 was done (beginning 5 November 1993). One cage for each mosquito species was placed into each of the five tires used in field experiment 1. Additional tires (previously used in different experiments) received one cage each for *A. albopictus* (five tires) and one cage each for *A. aegypti* (five tires). *Ascogregarina* are not transmitted from larva to larva, but instead infect via oocysts defecated by infected adults and ingested by larvae (Beier and Craig 1985). Thus, placing species in separate cages provided an appropriate assay for infections acquired from ambient oocysts in experimental cages, and simplified species identification at the time of dissection. For each species, two control groups of 25 newly hatched larvae were reared in the laboratory in covered beakers that did not harbor *Ascogregarina*.

Data collection.—Larvae in the third and fourth instar were collected from cages and dissected under a compound microscope (method based on that of Munstermann and Wesson 1990). The head and gut of the larva were removed and the gut gently teased open in tap water. The gut contents were dispersed and a cover slip applied. The mount was scanned at $100\times$ for the large (5–60 μm) trophonts of these protozoans, which remained alive, mobile, and easily seen for many minutes in such mounts. Numbers and proportions of larvae of each species that were parasitized were determined, along with counts of the number of parasites within each larva. Control larvae reared in the laboratory were also dissected. Though *Ascogregarina* are easily seen in such dissections, species determinations (*A. culicis* or *A. taiwanensis*) are much more difficult (Blackmore et al. 1995), and I was unable to identify these parasites to species. The important question for this study is: Are both *A. albopictus* and *A. aegypti* parasitized in these tires, and is such parasitism likely to affect the outcome of the competition experiment?

Field samples: Is competition related to A. aegypti persistence?

Assessing intensity of competition.—Field experiment 1 was designed to determine which species has

TABLE 1. Randomization ANOVA for λ', the estimated finite rate of increase for the cohort, and least squares ANOVA for survivorship to adulthood of *Aedes albopictus* and *Aedes aegypti* in field experiment 1.

| | | λ', the estimated finite rate of increase | | | | Survivorship | | | |
| | | *Aedes albopictus* | | *Aedes aegypti* | | *Aedes albopictus* | | *Aedes aegypti* | |
Source	df	ss (%)	P	ss (%)	P	F	P	F	P
Tire	4	8.46	0.8473	6.82	0.6244	4.13	0.0094	3.03	0.0342
Litter	1	6.38	0.0004	23.41	0.0004	69.79	0.0001	70.99	0.0001
Treatment	3	10.58	0.0285	23.01	0.0265	23.18	0.0001	43.67	0.0001
Litter × Treatment	3	7.04	0.6421	7.12	0.4378	3.33	0.0336	4.49	0.0108
Error	28								

an advantage when competition occurs. To estimate the intensity of competition in nature, I did a field study wherein I sampled newly emerged adults at three sites. Two of these sites had known histories of invasion and decline. I determined numbers and sizes of males and females of both species to test whether elimination or persistence of *A. aegypti* coincided with the most (indicated by low average adult size) or the least (indicated by high average adult size) intense competition, respectively.

Study sites.—I sampled three cemeteries in southern Florida where *Aedes* inhabit water-filled stone cemetery vases. Oaklawn Cemetery, located in central Tampa, is a small cemetery where both species persist, but the precise time of colonization is not known. I chose Oaklawn because of its location in an urban area such as those in which *A. aegypti* persists after invasion by *A. albopictus* (Hornby et al. 1994, O'Meara et al. 1995). Rose Hill Cemetery, located on the outskirts of Tampa, has been extensively sampled by O'Meara et al. (1995) since 1990. Until summer 1990, only *A. aegypti* inhabited vases at Rose Hill. *Aedes albopictus* was first collected in summer 1990, and became the most prevalent species (greatest percent of vases occupied) in 1994. However, *A. aegypti* has remained common at Rose Hill (O'Meara et al. 1995). Oak Hill Cemetery, located in Lakeland, has also been extensively sampled by O'Meara et al. (1995) since 1991. Up to August 1991, only *A. aegypti* inhabited vases at Oak Hill. *Aedes albopictus* arrived in 1991, increased rapidly in prevalence, and became the most prevalent species in November 1991. *Aedes aegypti* apparently went extinct at Oak Hill in May 1992, and remains absent at this site (O'Meara et al. 1995).

Data collection and analysis.—All three cemeteries were sampled on 5 July 1994. At each site, contents of water-filled vases were collected with a turkey baster, and the container flushed with ~100 mL of tap water. Sizes of cemetery vases were similar, but the amount of fluid varied, and no attempt was made to determine volumes. All mosquito larvae and pupae were collected and brought back to the laboratory. Numbers of individuals of both species were determined, and pupae were allowed to eclose. Because the pupa is a non-feeding stage, all resources that go into determining adult size have already been acquired. Therefore, the

sizes of adults emerging in the laboratory from field collected pupae are indicators of the per capita resource availability in the field site. Adults of the two species were identified, sexed, dried at 60°C, and weighed to the nearest 0.0001 mg using a Cahn C31 ultramicro-balance.

Numbers of immatures of each species collected from containers at each cemetery were analyzed using a Kruskal-Wallis test. Mean masses of adult mosquitoes within each species–sex combination were determined for each container, and were compared among cemeteries using ANOVA, with cemetery, container within cemetery (a random effect), sex, and sex–cemetery interaction as model effects. Because the data were unbalanced, the container-within-cemetery mean square was not appropriate for testing for the cemetery effect, and Satterthwaite's approximate F test was used (see Montgomery 1976, SAS Institute 1989 for details). When sex–cemetery interactions were not significant, adjusted means for each cemetery, pooling the sexes, and adjusting so that the two sexes contribute equally to the mean in each cemetery, were compared using Bonferroni t tests and an experimentwise $\alpha = 0.05$.

RESULTS

Field experiment 1

Estimated finite rate of increase (λ').—For both *A. albopictus* and *A. aegypti,* the pattern of results from randomization ANOVA was the same: both litter and treatment significantly affected λ', but litter–treatment interaction did not (Table 1). For both species, λ' was consistently and significantly greater with litter than without litter (Fig. 1). For *A. albopictus,* pairwise comparisons among treatments (pooling across litter levels) indicated that λ' was significantly greater for 20ALB than for each of the three high-density treatments, which, in turn, were indistinguishable (Fig. 1). For *A. aegypti,* only the pairwise comparison between 20AEG and 40ALB + 20AEG was significant (with 20AEG yielding greater λ', see Fig. 1). All other pairwise differences were nonsignificant (Fig. 1).

In addition to comparing treatment means for λ', it is useful to compare each treatment mean to the value indicating zero net growth, $\lambda' = 1$, and in particular to identify what (if any) competitive conditions result
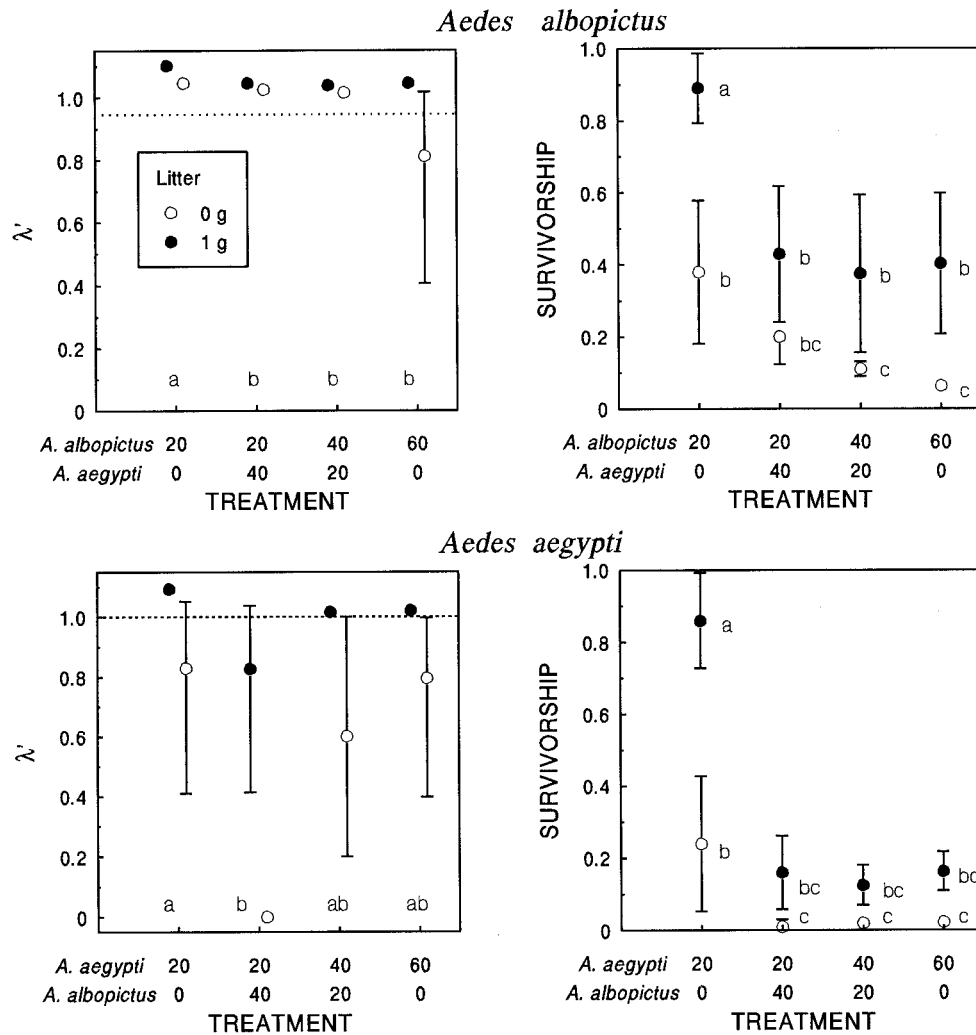
Aedes albopictus

Aedes aegypti

Fig. 1. Mean estimated rate of increase (λ') and mean survivorship, each $\pm 95\%$ confidence intervals for each treatment–litter combination in field experiment 1. For all treatment–litter combinations for both *A. albopictus* and *A. aegypti*, $N = 5$. Confidence intervals for λ' were generated using the percentile bootstrap method (Dixon 1993), whereas confidence intervals for survivorship are based on normal theory; where points lack error bars, the confidence interval was too small to show on the graph. For survivorship, though raw data are plotted, statistical analyses were done on arcsine square-root transformed proportions. Treatment means pooled across litter (λ') or treatment–litter means (survivorship) sharing the same letter are not significantly different at Bonferroni experimentwise $\alpha = 0.05$. The dotted lines at $\lambda' = 1.0$ on graphs of λ' correspond to zero net growth of the experimental cohorts.

in populations that, on average, decline. For *A. albopictus*, bootstrap 95% confidence intervals for mean λ' are greater than 1 under all conditions used in this experiment, except for the 60ALB treatment without litter (Fig. 1). Though mean λ' for the 60ALB treatment without litter was less than 1, the associated 95% confidence interval included 1 (Fig. 1). These estimates imply that *A. albopictus* cohorts would be increasing under most of these experimental conditions. In contrast, for *A. aegypti,* in the absence of litter all treatments yielded mean $\lambda' < 1$, and for the 40ALB + 20AEG and the 60AEG treatments 95% confidence intervals did not include 1 (Fig. 1). Even in the presence of litter, the 40ALB + 20AEG treatment yielded a mean

λ' less than 1, though the associated 95% confidence interval included 1 (Fig. 1). These estimates imply that *A. aegypti* cohorts would often be decreasing under these experimental conditions, particularly when litter availability is low.

Survivorship.—For both *A. albopictus* and *A. aegypti,* survivorship was significantly affected by litter, treatment, and interaction (Table 1). For both species, survivorship tended to be much lower without litter in the cages (Fig. 1). For *A. aegypti* in particular, survivorship without litter at high densities approached 0 (Fig. 1). Comparisons of treatment means within litter levels for both species indicated the similar general patterns of treatment effects on survivorship (Fig. 1).

TABLE 2. Least squares ANOVA for mass at adulthood for *Aedes albopictus* and *Aedes aegypti* in field experiment 1.

	Aedes albopictus						*Aedes aegypti*					
	Females			Males			Females			Males		
Source	df	F	P	df	F	P	df	F	P	df	F	P
Tire	4	6.21	0.0011	4	2.01	0.1239	4	4.02	0.0159	4	0.91	0.4833
Litter	1	8.11	0.0083	1	1.10	0.3045	1	0.34	0.5656	1	0.49	0.4953
Treatment	3	10.83	0.0001	3	3.13	0.0434	3	0.64	0.5985	3	0.57	0.6414
Litter × Treatment	3	8.32	0.0004	3	10.25	0.0001	2	4.83	0.0210	3	0.87	0.4815
Error	27			25			19			14		

For *A. albopictus* with litter, survivorship was significantly greater at low density (20ALB) than in any of the high-density treatments (60ALB, 40ALB + 20AEG, 20ALB + 40AEG), and all three high-density treatments were indistinguishable (Fig. 1). For *A. albopictus* in the absence of litter, survivorship was significantly greater in treatment 20ALB than in treatments 40ALB + 20AEG and 60ALB (Fig 1). However, treatments 20ALB and 20ALB + 40AEG were indistinguishable, as were all three high-density treatments (20ALB + 40AEG, 40ALB + 20AEG, and 60ALB) (Fig. 1). For *A. aegypti* at both litter levels, the low-density treatments (20AEG) yielded significantly greater survivorship than did the three high-density treatments (60AEG, 40ALB + 20AEG, 20ALB + 40AEG), which were indistinguishable (Fig. 1)

Mass at adulthood.—For *A. albopictus,* mass at adulthood for both sexes was significantly affected by treatment and litter–treatment interaction (Table 2). In addition, litter significantly affected mass at adulthood for females only (Table 2). The pattern of differences among treatment means within litter levels was the same for both sexes (Fig. 2). In the absence of litter, mean masses for both sexes were indistinguishable among the four treatments (Fig. 2), whereas in the presence of litter, mean masses of both sexes from the low-density treatment (20ALB) were significantly greater than were masses from the three high-density treatments (60ALB, 40ALB + 20AEG, 20ALB + 40AEG), which in turn were indistinguishable (Fig. 2).

For *A. aegypti*, masses at adulthood for females were significantly affected by litter–treatment interaction (Table 2). Individual means for treatments within litter levels varied somewhat (Fig. 2), but pairwise comparisons yielded no significant differences (Fig. 2). For males, mean masses were not significantly affected by litter, treatment, or litter–treatment interaction (Table 2). Individual means for masses of males within a litter level were all very similar (Fig. 2).

Correlations of λ′ with physical variables.—None of the correlations of mean λ′ for a tire with mean conductivity, pH, and temperature were significant. For *A. aegypti,* mean λ′ was negatively and rather strongly correlated with tire mean conductivity, mean pH, and temperature ($r = -0.83, -0.80,$ and -0.60, respectively), suggesting better performance in tires with low-

er solute concentration, pH, and temperature. In contrast, the corresponding correlations for λ′ for *A. albopictus* were positive ($r = 0.39, 0.20,$ and 0.57, respectively), suggesting better performance in containers with greater solute concentration, pH, and temperature.

Field experiment 2: What is the prevalence of Ascogregarina?

Of 142 late-instar *A. albopictus* that were dissected, 31 (21.8%) yielded *Ascogregarina.* Within tires that yielded parasitized larvae, percentage of larvae parasitized ranged from 9.1% to 76.9%. In contrast, of 117 late-instar *A. aegypti* that were dissected, only 1 (0.8%) yielded *Ascogregarina.* The frequency of parasitized larvae was significantly greater for *A. albopictus* than for *A. aegypti* (likelihood ratio $G = 33.15$, df = 1, $P < 0.001$). The frequency of tires yielding *Ascogregarina*-parasitized *A. albopictus* (5 of 10) was also significantly greater than the frequency of tires yielding *Ascogregarina*-parasitized *A. aegypti* (1 of 10) (likelihood ratio $G = 4.07$, df = 1, $P = 0.044$). Of the 5 tires used in the competition experiment, 3 yielded no parasitized larvae of either species, and all 5 yielded no parasitized *A. aegypti.* None of the laboratory controls of either species yielded *Ascogregarina.*

Field samples: Is competition related to A. aegypti persistence?

At Oaklawn Cemetery in Tampa, 6 of 8 containers yielded *Aedes,* and all 6 containers yielded *A. aegypti,* but only 4 of these 6 containers yielded *A. albopictus* (Table 3). More individuals of *A. albopictus* were collected than were individuals of *A. aegypti,* but this was largely due to one container that yielded >68% of these *A. albopictus.* At Rose Hill Cemetery, 41 of 47 containers yielded *Aedes,* with 29 yielding *A. aegypti* and 35 yielding *A. albopictus* (Table 3). More individuals of *A. albopictus* were collected than were individuals of *A. aegypti.* At Oak Hill cemetery, 30 of 31 containers yielded *A. albopictus* and no containers yielded *A. aegypti* (Table 3) as expected based on work by O'Meara et al. (1995). Numbers of *Aedes* immatures per container differed significantly among cemeteries (Kruskal-Wallis $\chi^2 = 12.868$, df = 2, $P = 0.0016$). Pairwise multiple comparisons indicated that number of *Aedes*
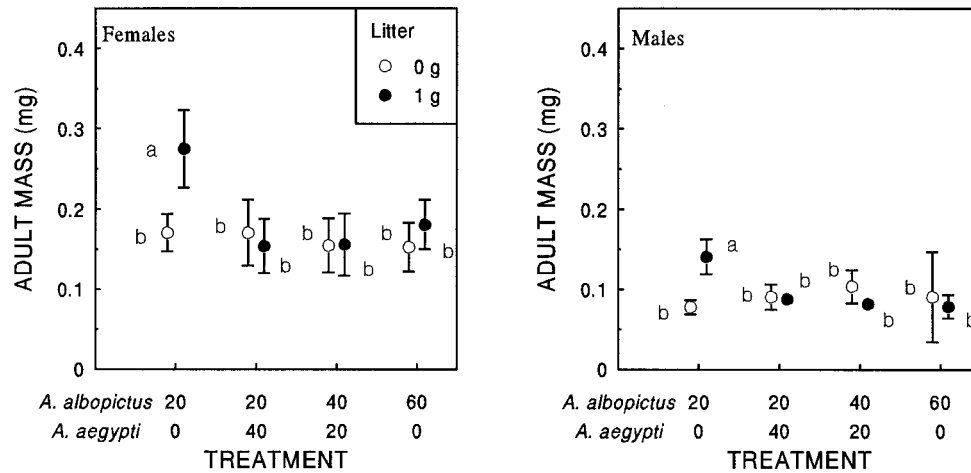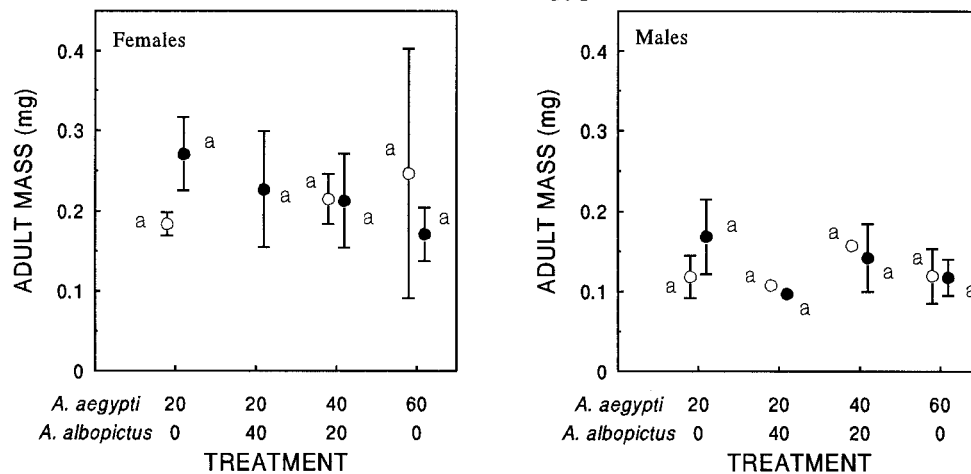
Aedes albopictus

Aedes aegypti

FIG. 2. Mean of mean adult masses ± 95% confidence intervals for each treatment–litter combination in field experiment 1. For female *A. aegypti*, the mean for 40ALB + 20AEG is absent because this treatment yielded no surviving females in any of the 5 tires. Treatment–litter means sharing the same letter are not significantly different at Bonferroni experimentwise $\alpha = 0.05$.

TABLE 3. Numbers of containers and median abundances per container for *A. albopictus* and *A. aegypti* in field samples from three cemeteries. Median abundances followed by the same superscript letter are not significantly different at experimentwise $\alpha = 0.05$ (nonparametric pairwise comparisons following Kruskal-Wallis test; Zar 1996).

	Number of water-filled containers				*Aedes*/container: Median (1st quartile, 3rd quartile)
Cemetery	Sampled	Yielding *A. albopictus* only	Yielding *A. aegypti* only	Yielding both species	
Oak Hill	31	30	0	0	45[a] (20, 83)
Oaklawn	8	0	2	4	12[b] (5, 102)
Rose Hill	47	12	5	24	11[b] (4, 43)

TABLE 4. ANOVAs for differences among three cemeteries in masses of *Aedes albopictus* and *Aedes aegypti* adults emerging from field collected pupae. Because of the unbalanced nature of the data, Satterthwaite's approximate F tests (SAS Institute 1989) were used for tests of the Cemetery effect. In this case, these tests make use of denominator mean squares that are combinations of mean squares for Container(Cemetery) and Error, resulting in noninteger degrees of freedom for the denominator (given in the Table).

Source	*Aedes albopictus*			*Aedes aegypti*		
	df	F	P	df	F	P
Cemetery	2, 46.3	4.75	0.0134	1, 15.4	12.05	0.0033
Container(Cemetery)	43, 19	4.05	0.0009	17, 6	4.40	0.0379
Sex	1, 19	29.30	0.0001	1, 6	46.01	0.0005
Sex × Cemetery	2, 19	0.78	0.4745	1, 6	5.57	0.0563
Error	19			6		

per container was significantly greater at the Oak Hill Cemetery (*A. aegypti* gone) than at Rose Hill and Oaklawn Cemeteries (*A. aegypti* present), which, in turn, did not differ significantly (Table 3).

For both species, sizes of newly emerged adults differed significantly among the three cemeteries (Table 4). Although sizes of the sexes were significantly different (Table 4), there was no significant sex–cemetery interaction (Table 4), indicating that inter-cemetery differences in size were consistent between the two sexes within each species. For *A. albopictus,* mean masses were significantly greater at Oaklawn Cemetery (*A. aegypti* present) than at Oak Hill Cemetery (*A. aegypti*

gone) (Fig. 3). For *A. aegypti,* mean masses were significantly greater at Oaklawn Cemetery than at Rose Hill Cemetery (Fig. 3).

DISCUSSION

Which species has a competitive advantage?

Field experiment 1 was designed to resolve which species could maintain positive population growth under conditions of severe competition, and thus be competitively superior. Based on analysis of estimated finite rate of increase (λ'), it seems clear that *A. albopictus* is competitively superior to *A. aegypti* under these field conditions. Estimated finite rate of increase for *A. aegypti* was more severely reduced by resource scarcity in the no-litter treatments, and by increasing density. This reduction in λ' was most pronounced when *A. aegypti* was combined with *A. albopictus,* particularly when *A. aegypti* was in the minority. Because both resource abundance and densities were manipulated in this experiment, and because low resources produced negative effects on population performance similar to those of increased density, it seems likely that resource competition among these container *Aedes* is the primary mode of interaction, an inference that is consistent with previous work on competition in container mosquitoes (e.g., Barrera 1996).

The observed competitive advantage of *A. albopictus* in my field experiment contrasts sharply with previous laboratory studies of these species that have tended to show that *A. aegypti* was the superior competitor (e.g., Moore and Fisher 1969, Ho et al. 1989, Black et al. 1989). These past studies used various artificial diets in competition experiments, rather than the natural food of these species (plant detritus and associated micro-organisms), and one likely explanation is that the different outcomes of these competition experiments reflect this difference in resources. In a comparison of starvation resistance of these two species, *A. aegypti* endured starvation much better than did *A. albopictus* when previously fed on a laboratory diet of liver powder and yeast, whereas *A. albopictus* endured starvation much better than did *A. aegypti* when previously fed on a natural diet of leaf litter (Barrera 1996). This greater resistance to starvation after rearing on leaf
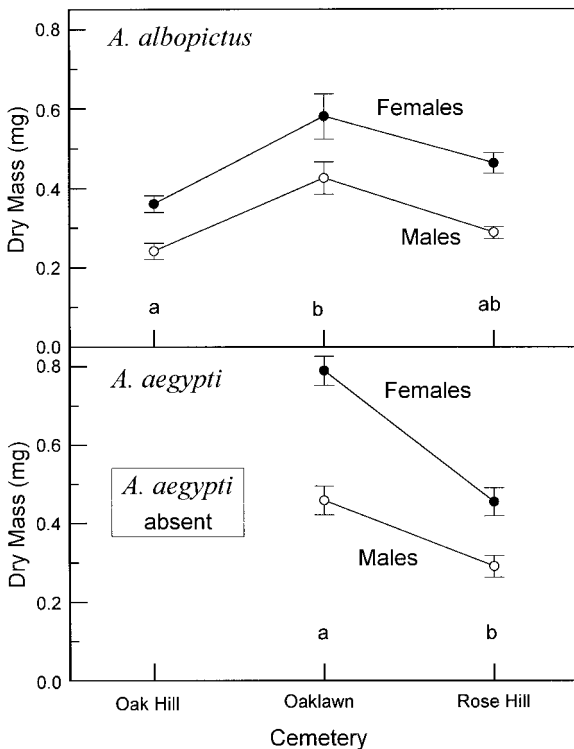

FIG. 3. Least squares means (±95% confidence intervals) for adult masses from pupae collected from cemetery vases at three cemeteries. Cemetery sites sharing the same letter are not significantly different at Bonferroni experimentwise α = 0.05.

detritus was inferred to render *A. albopictus* superior to *A. aegypti* in competition in typical natural environments where litter is the main resource (Barrera 1996), and this conclusion is strongly supported by the results of field experiment 1.

That the outcome of interspecific competition might depend on resource type has been demonstrated in several study systems (e.g., Tilman 1982, Gilpin et al. 1986). Dependence of outcomes of interspecific competition on resource type suggests differences in resource use; however, there are no data available to determine how or why any such differences in resource use arise (Barrera 1996). In addition, such dependence of outcomes on conditions illustrates the importance of doing competition experiments under conditions that closely approximate the relevant natural environment, and has important implications for how we study species interactions involving introduced species that occur over a wide geographic and environmental range. *Aedes albopictus* interacts with resident species in urban, suburban, and rural areas, in a variety of natural and artificial containers, and across a wide latitudinal range (Hawley 1988, Livdahl and Willey 1991, Hornby et al. 1994, O'Meara et al. 1995, Mekuria and Hyatt 1995). The nature and mechanisms of species interactions may differ in different ecological conditions. Thus, my experiment does not yield the only ''correct'' conclusions about the impact of this introduced species. The results of this experiment do indicate that in suburban tires in wooded areas of Florida, *A. albopictus* appears capable of excluding *A. aegypti* via resource competition among larvae. To understand fully the process of range expansion by *A. albopictus,* we need similar experiments under other circumstances (e.g., more urban habitats, less wooded areas, other container types).

The inference that *A. albopictus* is competitively superior in these tire habitats depends primarily on the index λ', which is subject to error, and therefore an imperfect estimate of population rate of increase. In this estimate, the most obvious source of error is the low precision in estimating fecundity from body size (note low r^2's for regressions: Eqs. 2 and 3). Better estimates would, of course be desirable, but conclusions of this analysis are the same even under radically different assumptions about fecundity–size relationships for both species (see *Methods*: *Data analysis*). In addition, treatment differences in female mass are largely nonsignificant, particularly for *A. aegypti* (Fig. 2). The major factor determining λ' appears to be the number of surviving adult females. Survivorship of *A. aegypti* was <5% in high combined-density treatments without litter (Fig. 1), suggesting that *A. aegypti* is very sensitive to low per capita food availability. In contrast, *A. albopictus* manages to produce substantially more surviving adults—up to 20%—at high combined density in the absence of litter (Fig. 1). Even with litter present, *A. aegypti* survivorship at high combined den-

sity is very low, typically <20% (Fig. 1). In contrast, *A. albopictus* survivorship at high combined density, with litter, averages ~40% (Fig. 1). Poor survivorship of *A. aegypti* was clearly a product of high density and low per capita food, as survivorship of *A. aegypti* at low density with litter was very high (Fig. 1). This high survivorship when well fed and uncrowded demonstrates that these tires were a suitable habitat for *A. aegypti* as long as intra- or interspecific competition were negligible. These results suggest that *A. albopictus* is less sensitive to negative effects of high combined *Aedes* density or low per capita food availability than is *A. aegypti,* and that this difference results in a competitive advantage for *A. albopictus*. These results are, again, entirely consistent with laboratory comparisons of starvation resistance in these two species, which showed that under high-density conditions with interspecific competition, survivorship to adulthood of *A. aegypti* was only 8.7%, whereas that for *A. albopictus* was 41.7% (Barrera 1996).

What is the prevalence and role of Ascogregarina*?*

By itself, the outcome of field experiment 1 is potentially consistent with the hypothesis that apparent competition leads to the replacement of *A. aegypti* by *A. albopictus*. Under this hypothesis, competition in the laboratory in the absence of *Ascogregarina taiwanensis* (e.g., Moore and Fisher 1969, Ho et al. 1989, Black et al. 1989) favors *A. aegypti,* but competition in nature and in field experiments (like the one described in this paper), where *A. taiwanensis* may be present, favors *A. albopictus*. This hypothesis predicts that *Ascogregarina* parasitism, particularly of *A. aegypti,* should be high in field experiment 2, and this prediction is clearly refuted by the data. Identification of *Ascogregarina* species is problematic; however, it is likely that *Ascogregarina* in experimental larvae were *A. taiwanensis* because virtually all were found in *A. albopictus*. Parasitism of individual larvae (<1% of *A. aegypti* parasitized by *Ascogregarina*), and prevalence of the *Ascogregarina* across experimental tires (3 of 5 tires yielded no *Aedes* parasitized by *Ascogregarina*), indicate that *Ascogregarina* played very little role in determining the competitive disadvantage of *A. aegypti* in field experiment 1. Thus, apparent competition via this shared enemy does not seem necessary to explain the displacement of *A. aegypti*. If parasitism by *A. taiwanensis* contributes in any way to declines of *A. aegypti* in nature, it must do so by accentuating the basic competitive advantage of *A. albopictus* over *A. aegypti*. Other studies have in fact provided little or no evidence of detrimental effects of *A. taiwanensis* on *A. aegypti* in the laboratory (Garcia et al. 1994) or in nature (Blackmore et al. 1995).

Is competition related to A. aegypti *persistence?*

Field experiment 1 shows that when these two species compete for their typical food resource in tires in

the field, *A. albopictus* has a competitive advantage. Field experiment 2 shows that this competitive advantage does not depend on the effects of ascogregarine parasites on *A. aegypti*. Together, these experiments suggest that interspecific competition for food resources could cause a decline in *A. aegypti* after invasion by *A. albopictus*. Additional information is needed in order to infer that interspecific competition is in fact the cause of such a decline in nature. The data on densities and adult sizes at three cemeteries are a preliminary step in testing the hypothesis of interspecific competition. Adult size in mosquitoes is a good indicator of density dependence among larvae (Fish 1985, Ho et al. 1989, Black et al. 1989, Livdahl and Willey 1991, Novak et al. 1993, Grill and Juliano 1996), and provides a preliminary comparison of the intensity of competition at 3 different sites. One hypothesis for the variable pattern of decline of *A. aegypti* in Florida after invasion by *A. albopictus* is that the intensity of competition varies from site to site, and that where competition is most intense (e.g., due to low resource levels), *A. aegypti* is eliminated, whereas where competition is weak, *A. aegypti* persists. The data from these cemeteries are consistent with this hypothesis, with the greatest density and the lowest individual masses observed at Oak Hill cemetery, where *A. aegypti* has gone extinct following invasion by *A. albopictus*. The hypothesis of variation in intensity of competition therefore seems to need further testing over a wider geographic and habitat scale. Masses of adult *Aedes* from the cemetery sites are typically greater than those from field experiment 1 (compare Figs. 2 and 3), suggesting that competition in nature may not be as intense as that created in field experiment 1.

There are at least two other hypotheses for the variable decline of *A. aegypti* following invasion by *A. albopictus*. Previous studies (e.g., Moore and Fisher 1969, Ho et al 1989, Black et al. 1989) suggesting a competitive advantage for *A. aegypti* in the aquatic environment lead to one alternative hypothesis: Competitive advantage in this system depends on the nature of the container and the substrate, and under some conditions *A. albopictus* is competitively superior, whereas under other conditions *A. aegypti* is competitively superior. Displacement of *A. aegypti* by *A. albopictus* in nonurban habitats of South Florida and all habitats of North Florida, but not in urban areas of South Florida (O'Meara et al. 1993, 1995) suggests the second alternative hypothesis: Because *A. aegypti* is tropical and favors humans as a blood source (Christophers 1960), more temperate habitats (North Florida) and habitats with fewer human hosts (nonurban areas) are marginal habitats for this species where it can persist only in the absence of interspecific competition in the larval stages. In contrast, North American *A. albopictus* appear to have a temperate zone origin, and are generalists in host choice (Hawley 1988). Blood meals determine fecundity in mosquitoes, and an abundance of *A. ae-gypti*'s preferred hosts, in combination with a favorable climate, would increase maximum population growth rate, and thus decrease the equilibrium resource requirement for population persistence in resource competition (see Tilman 1982 for details). Simulations of resource competition models show that such effects on maximal population growth rate could allow stable coexistence of a weaker competitor (i.e., *A. aegypti*) with a superior competitor (i.e., *A. albopictus*) if these same factors had less effect on the superior competitor (S. A. Juliano, *unpublished data*). This hypothesis differs from the previous hypothesis in postulating that *A. albopictus* is superior to *A. aegypti* in competition among larvae in all areas. Data from the present study do not test these alternative hypotheses, and competition experiments in habitats where *A. aegypti* has survived invasion by *A. albopictus,* and perhaps more importantly, where *A. albopictus* has been introduced but has not become established, are necessary.

General implications of this mosquito invasion

These results on interactions among *A. albopictus* and *A. aegypti* parallel some recently published accounts of interactions among invaders and residents in other systems. For example, on some Pacific islands a recently introduced house gecko is displacing native house geckos (Case et al. 1994). Interspecific resource competition seems to be the main cause of this displacement (Petren and Case 1996), and shared parasites appear to play a minor role in the displacement of the native (Hanley et al. 1995). In the gecko systems, as in these competing mosquitoes, the resident appears to be displaced in some habitats but not others (Case et al. 1994). A similar pattern is observed in fishes of western North America, where introduced species frequently displace natives in man-made reservoirs, but natives dominate in their original stream habitats (Herbold and Moyle 1986). This pattern of resident species being displaced by invaders in only some habitats suggests that detrimental effects of invaders on residents may occur most frequently in areas that are, for some reason, only marginally suitable for the residents. *Aedes aegypti* is itself an introduced species in North America, having arrived perhaps as early as the 15th century, and subsequently being reintroduced from multiple sources (Tabachnick 1991). As an anthrophilic, artificial-container mosquito, *A. aegypti* may have occupied many less suitable man-made habitats in the absence of strongly competing species. With the recent introduction of *A. albopictus,* the habitat distribution of *A. aegypti* appears to be contracting to urban areas in the extreme south. If these patterns from lizards, fish, and mosquitoes have some generality, we may expect successfully introduced species to restrict the geographic and ecological distributions of resident species, but that residents will persist in their optimal habitats, if those ideal habitats have not been degraded or destroyed by human activities.

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