

**COEXISTENCE, EXCLUSION, OR NEUTRALITY? A META-ANALYSIS
OF COMPETITION BETWEEN *Aedes albopictus* AND RESIDENT
MOSQUITOES**

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ABSTRACT

Competition experiments estimating the relative effects of inter- and intraspecific competition can help to resolve whether interspecific competition results in coexistence or exclusion. For mosquitoes, most such experiments have focused on invasive *Aedes albopictus* and its interactions with resident *Aedes*. A meta-analysis of such experiments tested whether the effect of interspecific competition is greater than, less than, or equal to that of intraspecific competition, and whether competitive outcomes are dependent on food quality. For *A. albopictus* and *A. aegypti*, there was significant context dependence, with interspecific competitive advantage for *A. albopictus* with low food quality, and competitive equivalence with high food quality. Meta-analysis of survivorship yielded more significant effects than did estimated rate of increase. Competitive effects and competitive responses of each species yielded similar results. This meta-analysis suggests competitive exclusion of *A. aegypti* by *A. albopictus*, and is thus consistent with field sampling, qualitative reviews, and interpretations from individual publications. For *A. albopictus* and *A. triseriatus*, most results indicated competitive equivalence and no context dependence, and are thus contrary to previous qualitative reviews and to interpretations from individual publications. For both pairs of species, published results suitable for meta-analysis remain scarce, and better experimental designs and improved analysis and reporting of statistical results are needed. Greater emphasis needs to be placed on estimating species' inter- and intraspecific competitive effects, rather than the more common, but theoretically less interesting, competitive responses. Experiments without low-density controls (i.e., replacement series) are inadequate for comparing competitive effects and responses.

Keywords: interspecific competition, *Aedes albopictus*, *Aedes aegypti*, *Aedes triseriatus*, container-dwelling mosquitoes, competitive effect, competitive response

INTRODUCTION

The archetypical question of community ecology is: Is local stable coexistence of competitors possible, or is competitive exclusion likely (Hutchinson, 1959; Chesson, 2000; Chase and Leibold, 2003)? Fundamental to answering this question is evaluation of the relative strengths of inter- and intraspecific competition (Chesson, 2000). If interspecific competition has a lower impact than intraspecific competition for both competitors, stable local coexistence is possible (Chesson, 2000). If interspecific competition has a greater impact than intraspecific competition for one or both competitors, local competitive exclusion is expected (Chesson, 2000). In contrast, when inter- and intraspecific competition have the same effects, competitors are equivalent, and neutral competitive dynamics may be the result, with community diversity determined by ecological drift (Hubbell, 2001; Adler et al., 2007). These outcomes are interesting to community ecologists posing questions about processes maintaining diversity in specific communities, and to the maintenance of diversity in general (Chesson, 2000; Shea and Chesson, 2002; Adler et al., 2007). When the competitors are vectors of human disease, and when vector species invade new areas, these questions about coexistence can take on practical importance (reviewed by Juliano and Lounibos, 2005; Juliano, 2009). If invaders exclude residents, local disease transmission may be altered by replacement of one vector by another. If invaders and residents coexist, local disease transmission may also change, if the two vectors have different characteristics (e.g., activity periods, vectorial capacity, host choice).

Introductions of nonnative mosquitoes have presented ecologists and medical entomologists with a challenge of understanding how communities of mosquitoes may be altered by those invasions and the possible health implications of those changes. One species, *Aedes albopictus*, has attracted the most recent attention as an introduced vector and potential competitor of resident mosquitoes (Hawley, 1988; Lounibos, 2002; Juliano and Lounibos, 2005; Juliano, 2009). *Aedes albopictus* is a widely introduced vector of arboviruses that competes with resident container-dwelling vectors, principally *Aedes aegypti* and *Aedes triseriatus*. There have been multiple investigations of competition between *A. albopictus* and resident species (reviewed by Juliano, 2009). These experiments often contain environmental manipulations in various ways, in an attempt to determine not only what the outcome of competition may be (exclusion, coexistence, neutral dynamics), but also, how those outcomes may vary with ecological context. Attempts to synthesize these results have led to several reviews of this literature (Juliano and Lounibos, 2005; Juliano, 2009) using simple enumeration (“vote counting”—Gurevitch and Hedges, 2001) to evaluate these experiments in aggregate. Formal meta-analysis is widely regarded as a preferable approach to synthesizing results from multiple investigations (Gurevitch et al., 1992, 2000; Gurevitch and Hedges, 1999, 2001), despite some potential limitations of how those meta analyses are implemented (Osenberg et al., 1997, 1999; Osenberg and St. Mary, 1998), and a meta-analysis of these investigations seems likely to provide new and better insight into the nature of competition among these *Aedes* species.

In this paper, I conduct a meta-analysis of published investigations of competition between larvae of *A. albopictus* and *A. aegypti*, testing specifically whether impact of interspecific competition on two population growth correlates, estimated rates of increase and survivorship, is greater or less than the impact of intraspecific competition. Thus, I evaluate whether coexistence or competitive exclusion is likely. A similar analysis is also done for a smaller set of published investigations of competition between larvae of *A. albopictus* and *A. triseriatus*. In both cases, I evaluate context dependence in the outcomes of competition for one variable, food quality, which has been postulated to alter the outcome of competition for these species (Murrell and Juliano, 2008; Juliano, 2009). In addition to evaluating expected outcomes for these species, I draw upon existing ecological theory (Chesson, 2000) to derive statistical approaches relevant to the methods used in most competition experiments. The statistical approach described can be useful not only for meta-analysis of competition experiments but also for evaluating the results of single experiments.

COMPETITION MODELS VS. EXPERIMENTS

Though the criterion for stable coexistence of competitors (interspecific competition has less impact than intraspecific competition) is well known, there is a mismatch between the way competition experiments are typically done and analyzed and the effects that must be compared in order to determine whether stable coexistence, exclusion, or neutrality are expected (Goldberg and Barton, 1992; Chesson, 2000). Chesson (2000) presents an alternative version of the Lotka–Volterra model that makes this mismatch clear. For two species, per capita rates of increase are given by:

$$dN_1/N_1 dt = r_1 [1 - \alpha_{11}N_1 - \alpha_{12}N_2]$$

$$dN_2/N_2 dt = r_2 [1 - \alpha_{22}N_2 - \alpha_{21}N_1]$$

where N_s indicate abundance of the two competitors, r_s are the maximal rate of increase, and α_s are the absolute competition coefficient, quantifying the impact of density of each species (N_1, N_2) on rates of increase. These are related to the standard relative competition coefficients present in the standard version of the Lotka–Volterra competition model (Chesson, 2000) but differ primarily in that both inter- and intraspecific competition are quantified with coefficients that relate density (N) to decline in rate of increase (dN/Ndt) (Table 1). Graphically, the intraspecific absolute competition coefficients (α_{11}, α_{22}) and the interspecific absolute competition coefficients (α_{12}, α_{21}) define axis intercepts for zero growth isoclines (Fig. 1). Thus, we see from Fig. 1 that for, stable coexistence, $1/\alpha_{11} < 1/\alpha_{21}$ and $1/\alpha_{22} < 1/\alpha_{12}$. In words: the impact of interspecific competition from a species must be less than the impact of intraspecific competition from that species. This observation points out two meanings of the terms “impact of interspecific or intraspecific competition”. Coefficients may be described as competitive effects of a species (i.e., a species’ ability to suppress population growth; effects of species 1 are α_{11} and α_{21}), or as the competitive responses of a species (i.e., a species’ ability to resist

Table 1
Competitive effects from the standard (relative) two-species Lotka–Volterra model and in Chesson’s (2000) absolute two-species Lotka–Volterra model

Effect of species	on species	Relative Lotka–Volterra	Absolute Lotka–Volterra
1	2	α_1	$\alpha_{21} = \alpha_1/K_1$
1	1	1	$\alpha_{11} = 1/K_1$
2	2	1	$\alpha_{22} = 1/K_2$
2	1	α_2	$\alpha_{12} = \alpha_2/K_2$

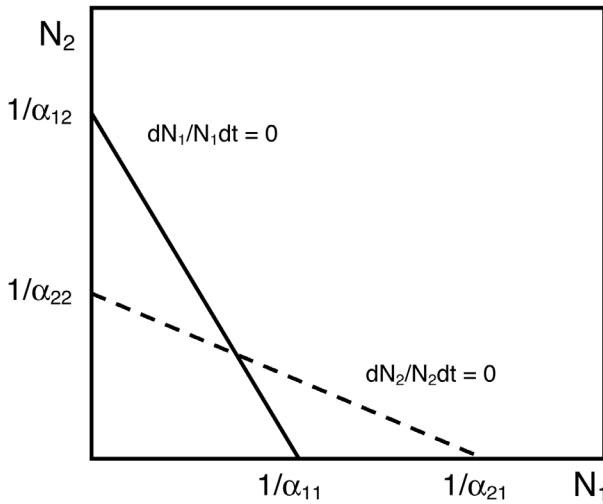


Fig. 1. Isoclines for Chesson’s (2000) absolute Lotka–Volterra competition model, showing isoclines for stable coexistence. Parameter definitions in Table 1.

suppression of population growth; responses of species 1 are α_{11} and α_{12}) (Goldberg and Fleetwood, 1987). Most competition experiments are well designed to compare inter- and intraspecific competitive responses of a species, but what we need in order to understand the potential for coexistence or exclusion is a comparison of inter- and intraspecific competitive effects of a species (Chesson, 2000).

A minimal competition experiment involving two species includes at least 5 treatments. Each species may be raised alone at some density N (treatments N_1 and N_2 in Table 2). Each species is also raised alone at some greater density (say $2N$; treatments $2N_1$ and $2N_2$ in Table 2). Finally the two species are raised together at an overall density of $2N$ (treatment N_1N_2 in Table 2). More densities may be used, but this experiment represents the smallest response surface design (Goldberg and Scheiner, 2001), and combines the typical addition series and replacement series (Goldberg and Scheiner, 2001). For each replicate of each treatment, some response variable (Y), indicating the success or performance of each species, is quantified. Treatments with both species yield two responses (Y_1 and Y_2). Data analysis proceeds by analyzing competitive effects of

Table 2

Effects used in this meta-analysis. N_i refers to the density of individuals of species i in a treatment. \bar{Y}_{N_i} is the mean response variable (e.g., survivorship, rate of increase) from a treatment for species i . When two subscripts are present (e.g., $\bar{Y}_{N_1N_2}$) the first subscript indicates the species for whom the response is measured. The subscript 2_{N_i} indicates that species i is present at a density twice that indicated by the subscript N_i

1. Treatment means from experiment					
Treatment	N_1	$2N_1$	N_1N_2	$2N_2$	N_2
Mean for species 1	\bar{Y}_{N_1}	\bar{Y}_{2N_1}	$\bar{Y}_{N_1N_2}$		
Mean for species 2			$\bar{Y}_{N_2N_1}$	\bar{Y}_{2N_2}	\bar{Y}_{N_2}
2. Effects calculated from treatment means					
Description of effect	Calculation (α parameters as in Table 1)				
Interspecific vs. Intraspecific competitive effects of species 2	[$\bar{Y}_{N_1N_2} - \bar{Y}_{N_1}$] - [$\bar{Y}_{2N_2} - \bar{Y}_{N_2}$] = $\alpha_{12} - \alpha_{22} =$ Competitive Effect ₂				
Interspecific vs. Intraspecific competitive effects of species 1	[$\bar{Y}_{N_1N_2} - \bar{Y}_{N_2}$] - [$\bar{Y}_{2N_1} - \bar{Y}_{N_1}$] = $\alpha_{21} - \alpha_{11} =$ Competitive Effect ₁				
Interspecific vs. Intraspecific competitive response of species 1	[$\bar{Y}_{N_1N_2} - \bar{Y}_{N_1}$] - [$\bar{Y}_{2N_1} - \bar{Y}_{N_1}$] = $\alpha_{12} - \alpha_{11} = \bar{Y}_{N_1N_2} - \bar{Y}_{2N_1} =$ Competitive Response ₁				
Interspecific vs. Intraspecific competitive response of species 2	[$\bar{Y}_{N_1N_2} - \bar{Y}_{N_2}$] - [$\bar{Y}_{2N_2} - \bar{Y}_{N_2}$] = $\alpha_{21} - \alpha_{22} = \bar{Y}_{N_2N_1} - \bar{Y}_{2N_2} =$ Competitive Response ₂				

N_1 and N_2 on means, either \bar{Y}_1 or \bar{Y}_2 . For example, analysis of \bar{Y}_1 yields a comparison of means for treatments N_1 and $2N_1$ ($\bar{Y}_{2N_1} - \bar{Y}_{N_1}$), quantifying α_{11} , which is both the intraspecific competitive effect and response of species 1, and also comparison of means for treatments N_1N_2 and N_1 ($\bar{Y}_{N_1N_2} - \bar{Y}_{N_1}$), quantifying α_{12} , which is both the interspecific competitive effect of species 2 and response of species 1. Thus, data analysis is best designed for estimating and comparing inter- and intraspecific competitive responses of each species (Goldberg and Barton, 1992; Chesson, 2000; Goldberg and Scheiner, 2001). Formal statistical comparison of inter- and intraspecific competitive effects of each species would have to include both Y_1 and Y_2 which is typically not done, because analyses typically focus on each species' responses individually as a target species (Goldberg and Scheiner, 2001).

Although analyses of most experiments on competition do not include a direct comparison of inter- and intraspecific competitive effects or responses of a species, most experiments, like the minimal response surface described above, include the information necessary to estimate the relevant effect sizes. Thus, most competition experiments can allow a meta-analytic comparison of the inter- and intraspecific competitive effects and responses of a species, and my approach in this meta-analysis is to obtain and to analyze those effects wherever possible. The structure of the necessary comparisons is described in Table 2. For this meta-analysis of competition experiments, I test whether an effect estimating the difference in the interspecific competitive effects and responses and intra-

specific competitive effects and responses of a species are significantly different from 0. For a simple competition experiment there would be four treatments involved (Table 2). As constructed in Table 2, if the mean of this effect size across a set of experiments is significantly greater than 0, the effect of interspecific competition is **less** than that of intraspecific competition. If, instead, the effect is significantly less than 0, the effect of interspecific competition is **greater** than that of intraspecific competition. I also do a meta-analysis testing whether responses to interspecific competition and intraspecific competition of a species (Table 2) are different, as this test may serve as a readily-available surrogate for the more theoretically relevant comparison of competitive effects of a species. From Table 2, it is evident that estimating the relative effects of inter- vs. intra-specific competition of a species requires treatments at both a low and a high density, and some competition experiments (replacement or substitution series) lack such treatments (Goldberg and Scheiner, 2001). Because replacement series designs are reasonably common in the literature on competition among *Aedes* (e.g., Novak et al., 1993; Daugherty et al., 2000), the approximate test based on inter- vs. intraspecific competitive responses of a species may be valuable since it can be estimated even when low-density, single-species treatments are absent (Table 2).

METHODS

META-ANALYSIS

The statistical tools of meta-analysis have been widely described in the ecological literature (e.g., Gurevitch et al., 1992, 2000; Hechtel and Juliano, 1997; Goldberg et al., 1999; Hedges et al., 1999; Gurevitch and Hedges, 1999, 2001; Borowicz, 2001; Morris et al., 2007; Vonesh and Blaustein, 2010), and will not be repeated here. All analyses were conducted using MetaWin 2.0 statistical software (Rosenberg et al., 2000). The most widely used meta-analytic measure of effect size is Hedges' d (Hedges and Olkin, 1985), and this is the principal measure I use. I use Q_{total} as my test for heterogeneity among effect sizes, and the random effects model for categorical effects (Gurevitch and Hedges, 1999, 2001; Rosenberg et al., 2000). Use of Hedges' d has been criticized on several grounds (Osenberg et al., 1997, 1999, Osenberg and St. Mary, 1998) but several of these are circumvented by the approach taken in this analysis. Osenberg and St. Mary (1998) noted that Hedges' d does not estimate per capita effects, which are often of primary importance for ecological questions such as those posed here. In the present meta-analysis, I compare results from density manipulations and pose a question explicitly about per capita effects: I compare results for manipulating densities of mosquitoes and choose treatments that used the same control and manipulated densities for both intra- and interspecific competition. Thus, although some of these experiments used different densities (see below), I always compare the effects of the same change in intra- and inter-specific densities within an experiment, and so contrast per capita inter- vs. intraspecific competitive impacts. Further, the preferred variable for this analysis was an estimate of per capita increase in cohort experiments with mosquitoes (see below). Osenberg et al. (1999) note that Hedges' d , and meta-analysis in general, often overem-

phasize statistical tests of hypotheses even when the null hypothesis of an effect size of 0 is not biologically meaningful. The nature of my biological question renders this null hypothesis meaningful: theory outlined above indicates that testing whether the difference in impacts of inter- and intra-specific competition is 0 is precisely what is needed to assess the outcome of competitive interactions.

A further potential difficulty with Hedges' d is its assumption that effects are additive (Osenberg and St. Mary, 1998; Osenberg et al., 1999; Morris et al., 2007) even though many biological effects may be multiplicative. Additive competitive effects may best be estimated as a difference between treatment means, but multiplicative competitive effects require an alternative metric involving a ratio of treatment means, like the log response ratio (Osenberg et al., 1999; Morris et al., 2007). In the Lotka–Volterra models that serve as the basis for my evaluation of competition, effects of density on per capita growth rates are assumed to be additive (Gotelli, 1995), suggesting that at least for effect sizes or per capita growth rates, Hedges' d may indeed be appropriate. A further difficulty with ratios arises when some of the observed values for the meta-analysis take on a value of 0, or when numerator and denominator of the ratio have opposite signs, rendering use of ratios or logarithms impossible. Using log response ratio for meta-analysis of the data sets reported in this paper often yielded non-estimable log response ratios because of one or more of these problems, rendering analysis of log response ratios difficult to interpret. Thus, for this paper, I report only Hedges' d .

In addition to testing overall effect sizes, I tested for differences between two a priori categories of experimental conditions: high food quality and low food quality (the nature of food quality in each experiment is explained below and in the Appendix). I used Q_b (Rosenberg et al., 2000) as my test for differences between these groups. Because sample sizes were relatively small, I used bootstrapping and randomization tests (Manly, 1991) as provided by MetaWin 2.0 (Rosenberg et al., 2000) for statistical inference whenever possible.

DATA

The focus of my analysis is on competitive interactions of *Aedes albopictus* and its two most commonly investigated competitors, *Aedes aegypti* and *Aedes triseriatus*. Papers used in this analysis (see Appendix) were those cited in a recent review of experiments on competition among mosquito larvae (Juliano, 2009) plus publications that appeared shortly after that review was submitted (Leishnam et al., 2009). The minimum experimental design required for analysis comparing effects of inter- and intraspecific competitive effects of a species included treatments described in Table 2. Some experiments contained more treatment combinations (e.g., Braks et al., 2004) and these treatments were ignored for the purposes of meta-analysis. Some experiments lacked a treatment with two competing species at equal abundance (N_1N_2 ; Table 2) and instead had two species at an overall high density but in unequal abundances (e.g., Juliano, 1998). For these experiments, I used whichever treatments had species' abundances that were the closest to equality, as long as there was an appropriate low-density control treatment for comparison. Further, for the data to be used in these analyses, authors had

to provide (as summary values, graphs, or raw data) treatment means, some measure of variation (SE, SD, MSE), and sample size. Several potentially useful experimental studies had to be omitted because authors did not provide measures of variation or sample size (e.g., Black et al., 1989; Ho et al., 1989; Livdahl and Willey, 1991; Barrera, 1996). Other experiments on competition between these pairs of species had to be omitted because they did not include the relevant treatments (Juliano et al., 2004; Griswold and Lounibos, 2005; Costanzo et al., 2005a). In addition, several published studies made use of replacement series designs (Novak et al., 1993; Daugherty et al., 2000; Bevins, 2007) or other designs that lack a low-density control (Teng and Apperson, 2000). These investigations could not be used to compare inter- and intraspecific competitive effects of a species, but could contribute to comparisons of inter- and intraspecific competitive responses of a species (Table 2).

Many experiments on these competitors report results of competition under multiple environmental conditions, including different temperatures (e.g., Teng and Apperson, 2000; Lounibos et al., 2002), different food quality (e.g., Daugherty et al., 2000; Yee et al., 2007; Murrell and Juliano, 2008), quantity (e.g., Novak et al., 1993; Braks et al., 2004; Juliano, 2009), or renewal schedule (Bevins, 2007), different presence of pathogens (Aliabadi and Juliano, 2002), or different population origin (Leisham et al., 2009). Because one of my questions concerns environmental effects on heterogeneity of the outcome of competition, I chose to count as a single experiment each set of replicated cohorts run under one set of conditions. This inevitably results in some dependence of results among linked experiments from the same study (Gurevitch and Hedges, 2001; Gurevitch et al., 1992, 2000). Such nonindependence seems to be present in most ecological meta-analyses (Gurevitch et al., 2000; Morris et al., 2007), and is an inevitable result of attempting to assess the context dependence of ecological effects across multiple studies.

Many experiments on these competitors measure multiple response variables (e.g., estimated rates of increase, survivorship, mean adult sizes, median development times). For the question of coexistence, the most relevant response variable is per capita rate of increase, hence the preferred variable is some estimate of rate of per capita increase. The estimate r' (Livdahl and Sugihara, 1984) is a demographic estimate of instantaneous per capita rate of increase for a cohort based on survivorship, estimated female fecundity based on adult size, and time to maturity (described in detail by Livdahl and Sugihara, 1984; Livdahl and Willey, 1991). A transformed version of this index, $\lambda' = \exp(r')$ is also used commonly and provides an estimate of the finite rate of increase for a cohort (Juliano, 1998). One of these indices was reported by 7 published investigations of competition between *A. albopictus* and *A. aegypti* (yielding 23 experiments under distinct conditions), and studies using either index were used for a meta-analysis of effects of competition on rate of increase. All of these investigations also reported usable data on survivorship to adulthood, and meta-analysis of this variable was also done for comparison. One additional investigation (Daugherty et al., 2000) reporting results of a replacement series under 3 experimental conditions was added to the data set for analyses of competitive responses to inter- and intraspecific competition.

For experiments on *A. albopictus* and *A. triseriatus*, experimental designs and data reported were much more heterogeneous compared to those used for *A. albopictus* and *A. aegypti*. Relatively few investigations (2/5 published studies, yielding 8 experiments) reported estimates of rates of increase and had low density controls. An additional 3 investigations (Novak et al., 1993; Teng and Apperson, 2000; Bevins, 2007), reporting 7 separate experimental conditions, included sufficient data for analysis of survivorship, though all these experiments lacked low-density control treatments.

HYPOTHESES

I tested two hypotheses derived a priori from individual investigations (e.g., Murrell and Juliano, 2008) or from vote counting reviews (e.g., Juliano, 2009) of competition between these species. First, because *A. albopictus* has been deemed the superior competitor to both *A. aegypti* and *A. triseriatus* (e.g., Livdahl and Willey, 1991; Juliano, 1998; reviewed by Lounibos, 2002; Juliano and Lounibos, 2005; Juliano, 2009), I tested the hypothesis that stable coexistence of this invader with these competitors would not be possible. This hypothesis predicts that the interspecific competitive effect of *A. albopictus* will be significantly greater than its intraspecific competitive effect, and also that the interspecific competitive effect of the other species (*A. aegypti* or *A. triseriatus*) will be significantly less than its intraspecific competitive effect. This is a prediction of competitive asymmetry, consistent with *A. albopictus* competitively excluding either of the other species. Finding that either competitive effects of inter- and intraspecific competition are indistinguishable (i.e., neutrality) or that interspecific competitive effects are less than those of intraspecific competition for both species (i.e., stable coexistence expected) would fail to support this hypothesis.

Second, Juliano (2009) postulated that the outcome of interspecific competition between *A. albopictus* and *A. aegypti* or *A. triseriatus* was dependent on food quality, specifically on the rate of detritus decay or its nitrogen content (see also Livdahl and Willey, 1991; Daugherty et al., 2000; Murrell and Juliano, 2008; Yee et al., 2007). For the purposes of this meta-analysis, I deemed any detritus largely originating from deciduous or coniferous tree leaves to be low quality, and any detritus that included substantial animal material (dead insects, liver powder), yeast, or grass to be high quality (Appendix; see also discussion of the issue of detritus quality by Yee et al., 2007; Murrell and Juliano, 2008; Juliano, 2009). This hypothesis predicts that competitive asymmetry (see above) should be reduced or reversed as food quality increases. Because the same investigations also contributed to vote-counting reviews (e.g., Juliano, 2009) that generated these hypotheses, this meta-analysis cannot be viewed as an independent test of that hypothesis, but instead, serves as a test of whether a hypothesis generated by a qualitative analysis is supported by more rigorous statistical analysis.

RESULTS

As constructed in this paper, a mean effect size significantly >0 indicates that interspecific competition has a **lesser** effect than does intraspecific competition. A mean effect

size significantly <0 indicates that interspecific competition has a **greater** effect than does intraspecific competition. A mean effect size not significantly different from 0 indicates statistical equivalence of inter- and intraspecific competition.

COMPETITION BETWEEN *A. ALBOPICTUS* AND *A. AEGYPTI*

COMPETITIVE EFFECT

For competitive effects of *A. albopictus* on estimated per capita rate of increase, there were no significant differences in results for high vs. low food quality, and none of the effect sizes were significantly different from 0, indicating that for per capita rate of increase, effects of inter- and intraspecific competition were indistinguishable for *A. albopictus*. Thus, for per capita rate of increase, meta-analysis is consistent with competitive equivalence of these species. In contrast, for competitive effects of *A. albopictus* on survivorship, there was a significant difference in the results for high- vs. low-food quality (Fig. 2). Low quality food yielded an effect size significantly <0 , indicating that the interspecific effect of *A. albopictus* was significantly greater than its intraspecific effect. For high food quality, the effect size was positive, but not significantly >0 , indicating equivalence of competitive effects with high-quality food.

For competitive effects of *A. aegypti* on estimated per capita rate of increase, there was also no significant difference between low and high food quality (Fig. 2), and all effect sizes were not significantly different from 0, consistent with equivalence of inter- and intraspecific effects (Fig. 2). For effects on survivorship, although there was no significant difference between low and high food quality, effect sizes for low quality food and for the combined data were significantly >0 , indicating that the interspecific effect of *A. aegypti* on survivorship was significantly less than its intraspecific effect.

In aggregate, the results for competitive effects of these two species are partially consistent with competitive asymmetry, with *A. albopictus* having a competitive advantage over *A. aegypti*, particularly at low food quality. The results are consistent with high quality food producing equality of competitors (Fig. 2). The results for competitive effects of these species are not equivalent for estimated rate of increase and survivorship, with analysis of effects on survivorship showing more differences due to food quality, and more differences of inter- and intraspecific effects (Fig. 2).

COMPETITIVE RESPONSE

For competitive responses of *A. albopictus* estimated per capita rate of increase, patterns of effects were similar for estimated per capita rate of increase and for survivorship (Fig. 3). In both cases, there was a significant difference in effects with high vs. low food quality, with high food quality producing negative effects (significantly <0 for per capita rate of increase, but not for survivorship), and low food quality producing positive effects (significantly >0 for rate of increase, but not for survivorship). Thus, with low food quality, the trend was for *A. albopictus* to have a better competitive response to (i.e., be less affected by) interspecific competition than to intraspecific competition, whereas

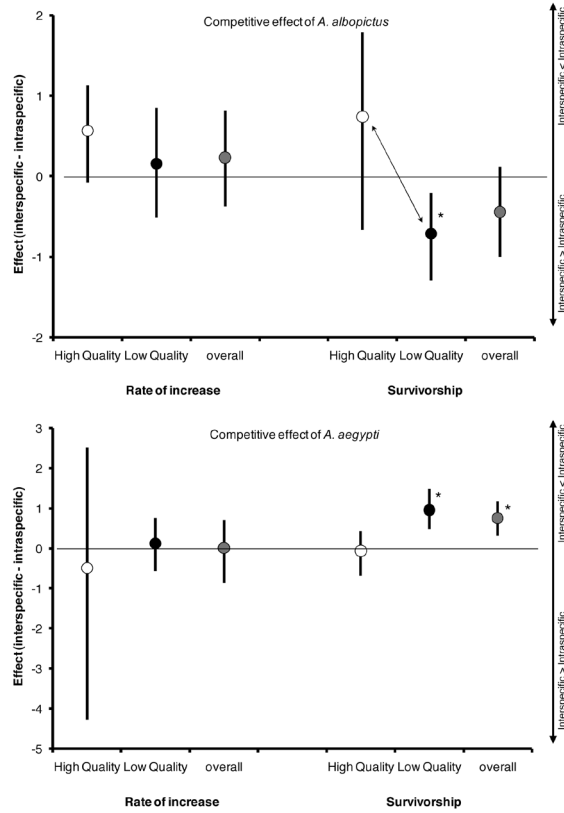


Fig. 2. Effect sizes (\pm bootstrap 95% confidence intervals) for the difference in the inter- and intraspecific competitive effects of *A. albopictus* (top) and *A. aegypti* (bottom). Negative values indicate interspecific > intraspecific. Arrows indicate a significant ($p < 0.05$) difference between low quality food and high quality food. Effect sizes significantly different from 0 are highlighted with an *. Sample sizes: high quality food N = 4; low quality food N = 19.

with high food quality, the trend was for *A. albopictus* to have a poorer competitive response to interspecific competition than to intraspecific competition.

For competitive response of *A. aegypti* estimated per capita rate of increase, differences between low and high food quality were never significant (Fig. 3). Effect sizes for both estimated per capita rate of increase and survivorship tended to be negative and were significantly < 0 for the overall test in both cases (Fig. 3), indicating that *A. aegypti* had a poorer competitive response to interspecific competition than to intraspecific competition.

In aggregate, results for competitive responses of these species were similar to those for competitive effects of these species. Both competitive effects and competitive responses indicate competitive asymmetry favoring *A. albopictus*, particularly at low-food

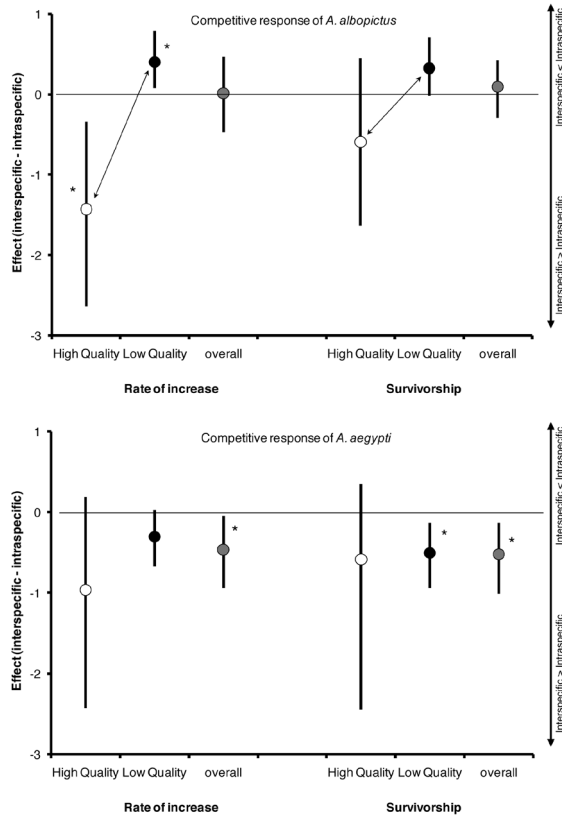


Fig. 3. Effect sizes (\pm bootstrap 95% confidence intervals) for the difference in the inter- and intraspecific competitive responses of *A. albopictus* (top) and *A. aegypti* (bottom). Negative values indicate interspecific > intraspecific. Arrows indicate a significant ($p < 0.05$) difference between low quality food and high quality food. Effect sizes significantly different from 0 are highlighted with an *. Sample sizes: high quality food N = 6; low quality food N = 20.

quality. Only *A. albopictus* yielded differences in competitive effects or responses with food quality.

Another way to examine effect sizes is to test for correlations across experiments in the effect sizes for competitive effects of each species. For both analyses of estimated rates of increase and of survivorship, these correlations were significantly <0 (Fig. 4), indicating that within one experiment, if one calculated effect size was negative (indicating that interspecific competition had a greater impact than intraspecific competition) the other effect size tended to be positive (indicating that interspecific competition had a lesser impact than intraspecific competition). This pattern strongly suggests competitive asymmetry, with competitive advantage changing across experimental conditions. Plots (Fig. 4) indicate that most experiments fell into quadrants of the graph with one effect

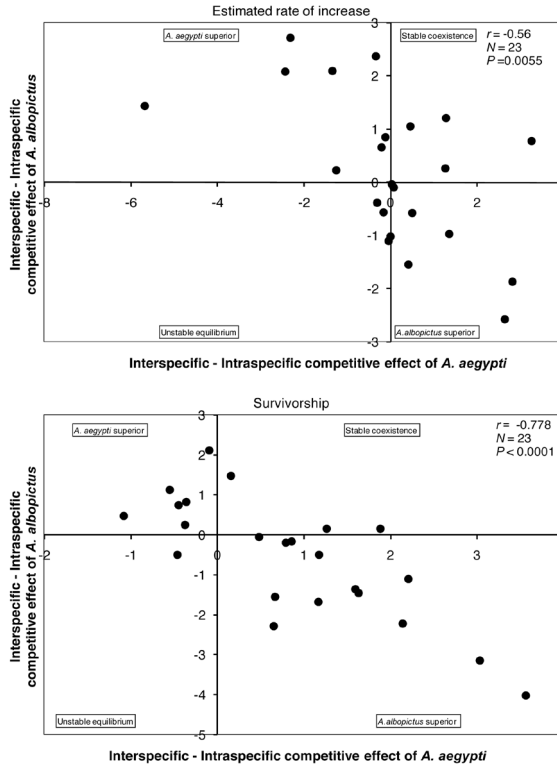


Fig. 4. Bivariate plots and correlation coefficients for the differences in effects of inter- and intraspecific competitive effects of *A. albopictus* and *A. aegypti* estimated from analysis of rate of increase (top) and survivorship (bottom). Expected outcomes of points falling into the four quadrants are indicated in boxes.

>0 and the other <0, and very few effects were both positive (indicating interspecific competition low for both species and suggesting stable coexistence) or both negative (indicating interspecific competition high for both species and suggesting an unstable two-species equilibrium).

Effects sizes for competitive effects vs. competitive responses of the two species differed to some extent, and this may be interpreted in multiple ways. This disparity may simply be a result of random error. Alternatively, it may indicate that the two different ways of calculating effects (i.e., the theoretically important competitive effects of each species on the other and on itself, vs. the more traditional competitive responses to inter- and intraspecific competition) actually estimate fundamentally different aspects of competition. Finally, the disparity may derive from the fact that there were more experiments that could yield estimated competitive responses than competitive effect (see

Introduction). Re-analysis of competitive responses of each species for only those investigations that also yielded estimates of competitive effects of each species (omitting 3 experiments by Daugherty et al., 2000) produced results virtually identical to those for all estimable competitive effects of each species (results not shown); hence, it seems that the last of these explanations is unlikely.

COMPETITION BETWEEN *A. ALBOPICTUS* AND *A. TRISERIATUS*

COMPETITIVE EFFECT

Fewer experiments were available for meta-analysis of competition between *A. albopictus* and *A. triseriatus*, and not surprisingly, meta-analysis yielded fewer significant effects and more equivocal conclusions. For competitive effects of *A. albopictus*, only one effect size, with high food quality and for effects on estimated per capita rate of increase, was significant, and was <0 , indicating that the effect of interspecific competition was greater than that of intraspecific competition. Because there were no significant differences due to food quality (Fig. 5), it is probably best to assess overall effect sizes, which were not significantly different from 0 (Fig. 5), indicating equivalent effects of inter- and intraspecific competition. Similarly, for effects of *A. triseriatus*, there was no difference due to food quality and no significant difference from 0 for the effect sizes (Fig. 5). Thus, the data give no reason to reject the hypothesis of equivalent effects of inter- and intraspecific competition.

COMPETITIVE RESPONSE

Competitive responses of the two species show a somewhat different pattern. There were again no significant differences due to food quality for competitive response of *A. albopictus* or *A. triseriatus* for either estimated per capita rate of increase or for survivorship (Fig. 6). For competitive response of *A. albopictus*, effects with high and low food quality, and overall, were significantly <0 , indicating that the response to interspecific competition was less than that to intraspecific competition (Fig. 6). All other effect sizes were not significantly different from 0 (Fig. 6).

Correlations of effect sizes across experiments again were negative, and the correlation was significant for survivorship, but not for estimated per capita rate of increase (Fig. 7). Thus, for this pair of species, correlations suggest competitive asymmetry, particularly survivorship, in contrast to the results estimating overall effects across all experiments. The much more limited data for competition experiments for *A. albopictus* and *A. triseriatus* render all conclusions for these species more tentative than those for *A. albopictus* and *A. aegypti*.

For *A. albopictus* and *A. triseriatus*, there were 3 investigations (Novak et al., 1993; Teng and Apperson, 2000; Bevins, 2007) that did not estimate rates of increase, and did not have low-density controls that would allow for estimation of effects of responses to inter- and intraspecific competition of the two species. These 3 investigations (a total of 6 experimental conditions) did allow for estimation of the competitive response of each of the species for survivorship, and it is interesting to ask what different conclu-

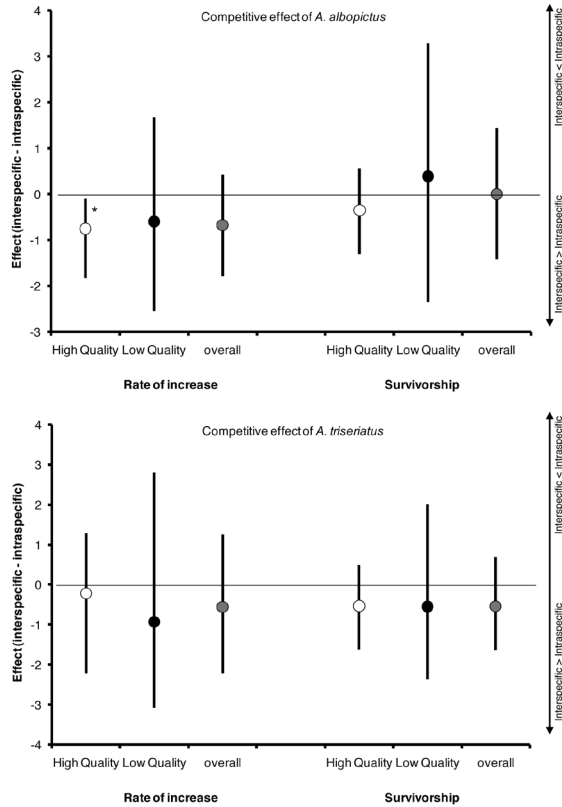


Fig. 5. Effect sizes (\pm bootstrap 95% confidence intervals) for the difference in the inter- and intra-specific competitive effects of *A. albopictus* (top) and *A. triseriatus* (bottom). Negative values indicate interspecific > intraspecific. Effect sizes significantly different from 0 are highlighted with an *. Sample sizes: high quality food N = 4; low quality food N = 4.

sions may arise from this alternative view of effects of competition. Analysis of all of the experiments, totaling 15 separate experimental conditions, would have changed relatively few conclusions (data not shown). The only major change would have been that for competitive response of *A. albopictus* survivorship, this broader analysis would have yielded a significant difference in the responses observed with high vs. low food quality. The added experiments all used high food quality, and with these experiments added, with high food quality there was no significant difference in the effects of inter- and intraspecific competition on *A. albopictus* with high food quality (compare with Fig. 6). For ease of comparison to results for competitive effects of each species, and to results for per capita rate of increase, I report only the meta-analysis of the more limited set of experiments.

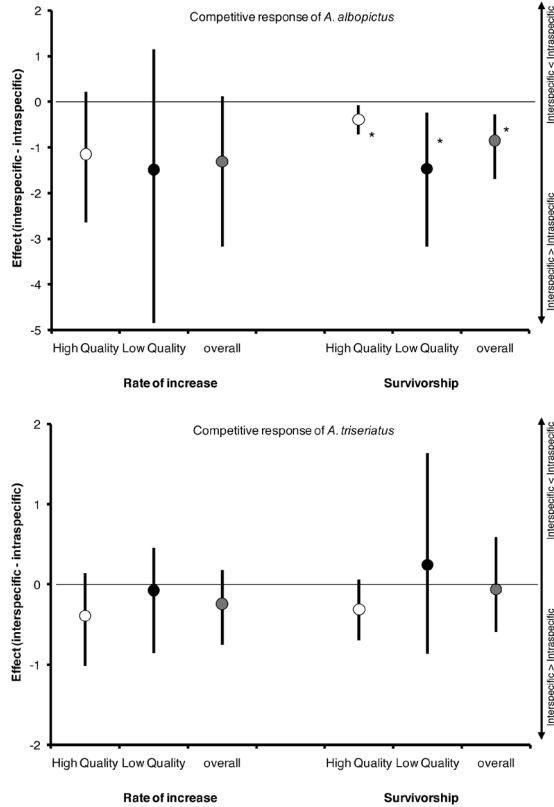


Fig. 6. Effect sizes (\pm bootstrap 95% confidence intervals) for the difference in the inter- and intraspecific competitive responses of *A. albopictus* (top) and *A. triseriatus* (bottom). Negative values indicate interspecific > intraspecific. Effect sizes significantly different from 0 are highlighted with an *. Sample sizes: high quality food N = 4; low quality food N = 4.

DISCUSSION

The central question addressed by this meta-analysis is whether competition between *A. albopictus* and resident species is likely to lead to: 1) a consistent competitive advantage for one species and resulting competitive exclusion; 2) low interspecific competition and resulting stable coexistence; or 3) competitive equivalence consistent with neutrality. For experiments on competition between *A. albopictus* and *A. aegypti*, the results are consistent in indicating that *A. albopictus* has a competitive advantage over *A. aegypti* under the conditions used in these laboratory and field experiments, and the meta-analysis suggests that competitive exclusion of *A. aegypti* by *A. albopictus* is expected. There was, however, some evidence for context dependence of competitive outcomes, with competitive asymmetry with low quality food resources (decaying de-

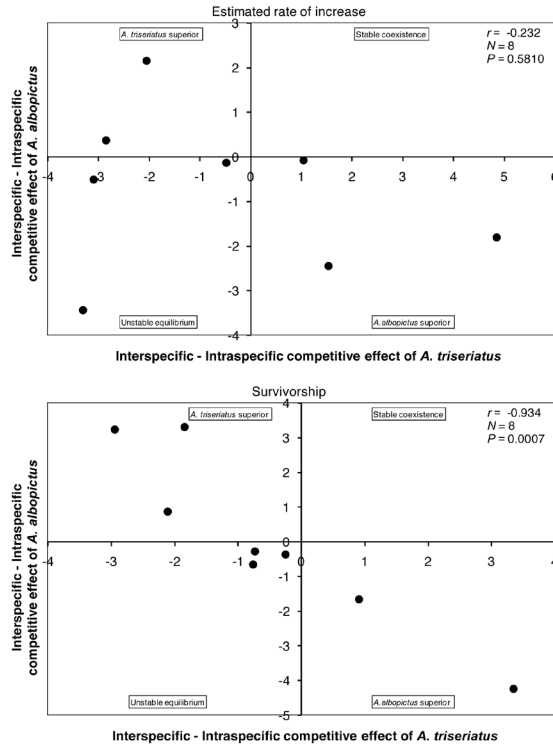


Fig. 7. Bivariate plots and correlation coefficients for the differences in inter- and intraspecific competitive effects of *A. albopictus* and *A. triseriatus* estimated from analysis of rate of increase (top) and survivorship (bottom). Expected outcomes of points falling into the four quadrants are indicated in boxes.

ciduous and coniferous leaves), but competitive equality with high quality food (rapidly decaying detritus such as dead insects or grass clippings, yeast). The meta-analysis results for these two species were similar for evaluations of estimated per capita rate of increase and for survivorship, though patterns were clearer for survivorship. Meta-analysis results were also similar for analysis of competitive effects of each species, which is theoretically the most important result for inferring the outcome of competition, and for competitive responses of each species, which is typically what is analyzed in each individual study.

These results are broadly consistent with both patterns observed in much of southern North America (e.g., Hobbs et al., 1991; McHugh 1993; Hornby et al., 1994; Mekuria and Hyatt, 1995; O'Meara et al., 1995; Harrison et al., 1998; Britch et al., 2008; but see Juliano et al., 2004, for exceptions), and with the interpretation of these experiments by individual authors and vote counting reviews (e.g., Juliano and Lounibos, 2005; Juliano, 2009). The meta-analysis conclusion that there is context dependence, with high quality

detritus leading to reduced competitive asymmetry, is consistent with a vote-counting review (Juliano, 2009), a laboratory experiment (Murrell and Juliano, 2008), and field distributions of *A. aegypti* and *A. albopictus* relative to detritus and nutrient composition (Murrell et al., in press). These combined results suggest an obvious hypothesis for apparent coexistence of these species at some locations in nature: if high-quality detritus is available, and competitive asymmetry is reduced, the time required for competitive exclusion may be long. Long-term persistence (if not stable coexistence) of the two species would then be observed. With competitive equivalence, fitness of two competitors is nearly equal, and even small stabilizing effects (e.g., small differences in resource use or habitat choice) may be sufficient to produce coexistence (Chesson, 2000; Adler et al., 2007). This hypothesis predicts systematic differences in the kinds of detritus (and microbial) resources available to larvae of these species in areas where they coexist vs. areas where *A. albopictus* has replaced *A. aegypti*, and this prediction should be testable in the field (Murrell et al., in press).

For competition between *A. albopictus* and *A. triseriatus*, results are less clear. Evidence for competitive asymmetry, or any deviation from competitive equivalence, is minimal, and evidence for context dependence lacking. The number of investigations of this pair of species is quite small. These meta-analysis results contrast sharply with conclusions of previous individual investigations (e.g., Livdahl and Willey, 1991; Novak et al., 1993; Teng and Apperson, 2000; Aliabadi and Juliano, 2002; Bevins, 2007; Yee et al., 2007) and previous reviews (e.g., Lounibos, 2002; Juliano and Lounibos, 2005; Juliano, 2009) that have suggested strong advantage for *A. albopictus* under most circumstances, but some instances of context-dependent reductions of that advantage (e.g., Livdahl and Willey, 1991; Bevins, 2007; Yee et al., 2007). Some of this disparity may arise because a substantial number of the investigations of competition between this pair of species could not be used in the meta-analysis, either because of absence of low-density control treatment (i.e., they were replacement series designs), or because of lack of reporting of measures of error variance. This problem was more frequent for experiments involving *A. triseriatus* than for experiments involving *A. aegypti*, both in absolute number of investigations and fraction of all published investigations that had to be excluded.

For both these species pairs, the actual number of experimental studies is still quite small, and the number of experiments done under different conditions is also small (compare to numbers of investigations reported by Gurevitch et al., 1992, 2000; Borowicz, 2001; Morris et al., 2007). The low number of investigations of these competitors is striking because *A. albopictus* and *A. aegypti* or *A. triseriatus* are the most commonly investigated competitors among mosquitoes (Juliano, 2009). Thus, even for these relatively well-investigated species, we lack a sufficient number of investigations to draw firm conclusions about competitive asymmetry, coexistence, and context dependence. Expanding the meta-analysis to include more competitors, such as *Aedes japonicus* (Armistead et al., 2008) or *Culex pipiens* (Carrieri et al., 2003; Costanzo et al., 2005b), would increase the number of investigations, but would also broaden the question from one of competitive outcomes between a pair of species to competitive outcomes

among competing mosquitoes, in general. The question addressed by controlled (often laboratory) experiments, like most of those reviewed in this paper, cannot be about the existence of competition because the investigators created conditions likely to produce competitive interactions among the studied species. Rather, the questions addressed in these kinds of experiments are about which, if any, species has an advantage, and under what ecological context that advantage exists (Juliano, 2009). In this context, meta-analysis for particular pairs of competitors is the most relevant approach, akin to meta-analyses of effects of particular medical therapies (e.g., Markou et al., 2004) rather than a meta-analysis of detection of effects in field experiments across many taxa and ecosystems (e.g., Gurevitch et al., 1992, 2000; Morris et al., 2007). Clearly, both kinds of approaches would be valuable for investigations of interspecific competition amongst any group of organisms.

Virtually all of the publications used in this meta-analysis derive from two research groups (S.A. Juliano and L.P. Lounibos) that have been very active in investigating invasion biology of *A. albopictus* in North and South America. Further, many of the experiments included in this analysis are part of the same publications, representing different experimental conditions under which competitive interactions have been investigated. A number of important older studies did not report data in a form suitable for these analyses or did not include low-density control treatments needed for this analysis (e.g., Black et al., 1989; Ho et al., 1989; Livdahl and Willey, 1991; Novak et al., 1993; Barrera, 1996; Teng and Apperson, 2000; Bevins, 2007). As these investigations could be evaluated in vote-counting reviews (e.g., Juliano, 2009) they can contribute to our understanding of competition involving *A. albopictus*, but the greater rigor of meta-analysis compared to vote counting techniques places more stringent limits on which studies can be used. Nevertheless, the limited data set and lack of independence of most of the investigations raises questions about the generality of the conclusions reached in this review. The problem of independence is often present in meta-analysis (e.g., Gurevitch, 1992, 2000). Because some of the conclusions from the present meta-analysis are similar to those derived from earlier vote-counting reviews using more published data, some confidence in the conclusions may be justified, particularly for the inference that *A. albopictus* has a competitive advantage over *A. aegypti* under many conditions, but that high quality resources may reduce or eliminate that advantage. Conclusions about the interactions between *A. albopictus* and *A. triseriatus* are much more tentative because of the limited number of nonindependent data available and the discrepancy of meta-analytic and vote-counting results.

Finally, there is a need for new ways of designing and analyzing competition experiments. Typical analyses of individual competition experiments analyze each competitor separately and necessarily focus on competitive responses (in population growth or its correlates) of a species to inter- and intraspecific competition (Goldberg and Scheiner, 2001). However, it is clear from theory (Chesson, 2000) that what is important for determining coexistence or exclusion are effects of inter- and intraspecific competition from a species, which necessarily requires consideration of two response variables. The results of the meta-analysis, particularly for *A. albopictus* and *A. aegypti*, suggest that those

two kinds of quantifications of competition may be similar (i.e., comparison of competitive responses of a species may be a reasonable approximation of competitive effects of a species). It would nonetheless be advantageous to devise experimental designs that are better for directly addressing competitive effects of a species via formal hypothesis tests. In this context, experiments without low-density controls (i.e., replacement series) are inadequate for evaluating potential for coexistence because they cannot be used to estimate the relative strengths of inter- and intraspecific competitive effects a species. Because there are other criticisms of replacement series designs (Gibson et al., 1999; Joliffe, 2000; Goldberg and Scheiner, 2001), it is advisable that investigators avoid using replacement series designs to investigate interspecific competition. Meta-analysis reduces statistical results to effect sizes, and may suggest a way to use data even from a single two-species experiment to compare effects of inter- and intraspecific effects of a species. By estimating effect sizes for inter- and intraspecific competition, an investigator may be more directly able to compare those effects, perhaps by randomization tests, even within a single experiment.

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APPENDIX

Source	Competitor	Venue	Food quality	Food quantity	Temp. (°C)	Detritus or resource	Other manipulated variables	Density 2N	Density N	Estimated rate of increase	Survivorship
Murrell and Juliano, 2008											
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves		40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	High	High	28	Grass clippings		40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Slash pine needles		40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	High	High	28	Dead insects		40	20	X	X
Juliano, 1998											
	<i>Aedes aegypti</i>	Field	Low	Low		Container water + live oak leaves		60	20	X	X
	<i>Aedes aegypti</i>	Field	Low	High		Container water		60	20	X	X
Braks et al., 2004											
	<i>Aedes aegypti</i>	Field	Low	Low		Container water + low avocado leaves		60	30	X	X
	<i>Aedes aegypti</i>	Field	Low	High		Container water + high avocado leaves		60	30	X	X
Daugherty et al., 2000											
	<i>Aedes aegypti</i>	Laboratory	Low	Low	27	Live oak leaves		40	absent	X	X
	<i>Aedes aegypti</i>	Laboratory	High	High	27	Live oak leaves + low dead insects		40	absent	X	X
	<i>Aedes aegypti</i>	Laboratory	High	High	27	Live oak leaves + high dead insects					

APPENDIX (continued)

Source	Competitor	Venue	Food quality	Food quantity	Temp. (°C)	Detritus or resource	Other manipulated variables	Density 2N	Density N	Estimated rate of increase	Survivorship
Lounibos et al., 2002											
	<i>Aedes aegypti</i>	Laboratory	Low	Low	24	Container water		80	40	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	High	24	Container water + live oak leaves		80	40	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	30	Container water		80	40	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	High	30	Container water + live oak leaves		80	40	X	X
Alto et al., 2008											
	<i>Aedes aegypti</i>	Laboratory	High	High	28	Live oak infusion + yeast:Lactalbumin		320	160	X	X
Alto et al., 2005											
	<i>Aedes aegypti</i>	Laboratory	High	High	28	Live oak infusion + yeast:Lactalbumin		320	160	X	X
Leishnam et al., 2009											
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : E. St. Louis, IL	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Bloomington, IN	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Manassas, VA	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Bartow, FL	40	20	X	X

APPENDIX (continued)

Source	Competitor	Venue	Food quality	Food quantity	Temp. (°C)	Detritus or resource	Other manipulated variables	Density 2N	Density N	Estimated rate of increase	Survivorship
Leishnam et al., 2009											
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Ft. Denaud, FL	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Gainesville, FL	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Ft. Meyers, FL	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Tampa, FL	40	20	X	X
	<i>Aedes aegypti</i>	Laboratory	Low	Low	28	Live oak leaves	Geographic origin of <i>A. albopictus</i> : Daytona, FL	40	20	X	X
Teng and Apperson, 2000											
	<i>Aedes triseriatus</i>	Laboratory	High	Low+ high pooled	15	Rabbit chow + Yeast: Lact-albumin+ oak leaves		20;200;800 pooled	absent		X
	<i>Aedes triseriatus</i>	Laboratory	High	Low+ high pooled	23	Rabbit chow+ Yeast: Lact-albumin + Oak leaves		20;200;800 pooled	absent		X
	<i>Aedes triseriatus</i>	Laboratory	High	Low+ high pooled	31	Rabbit chow+ Yeast: Lact-albumin+ oak leaves		20;200;800 pooled	absent		X
Aliabadi and Juliano, 2002											
	<i>Aedes triseriatus</i>	Laboratory	Low	Low	26	Red oak leaves	Infection of <i>A. albopictus</i> : no <i>Ascogregarina taiwanensis</i>	45	15	X	X
	<i>Aedes triseriatus</i>	Laboratory	Low	Low	26	Red oak leaves	Infection of <i>A. albopictus</i> : with <i>Ascogregarina taiwanensis</i>	45	15	X	X

APPENDIX (continued)

Source	Competitor	Venue	Food quality	Food quantity	Temp. (°C)	Detritus or resource	Other manipulated variables	Density 2N	Density N	Estimated rate of increase	Survivorship
Novak et al., 1993											
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	Liver powder		48	absent	X	X
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	Liver powder		48	absent	X	X
Yee et al., 2007											
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	American elm leaves: dead insect 0:1g		12	6	X	X
	<i>Aedes triseriatus</i>	Laboratory	Low	Low	27	American elm leaves: dead insect 1:0g		12	6	X	X
	<i>Aedes triseriatus</i>	Laboratory	Low	Low	27	American elm leaves: dead insect 1:0.1g		12	6	X	X
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	American elm leaves: dead insect 1:1g		12	6	X	X
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	American elm leaves: dead insect 10:0.1g		12	6	X	X
	<i>Aedes triseriatus</i>	Laboratory	High	High	27	American elm leaves: dead insect 10:1g		12	6	X	X
Bevins, 2007											
	<i>Aedes triseriatus</i>	Laboratory	High	High	24	Liver powder SCHEDULE:	Detritus input schedule: Added in multiple pulses	48	absent	X	X
	<i>Aedes triseriatus</i>	Laboratory	High	High	24	Liver powder	Detritus input schedule: Added once	48	absent	X	X