

Published in final edited form as:

*Ecol Entomol.* 2005 May 1; 30(1): 122–127. doi:10.1111/j.0307-6946.2005.00671.x.

## Does differential predation permit invasive and native mosquito larvae to coexist in Florida?

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### Abstract

1. The hypothesis that selective predation on larvae of the invasive *Aedes albopictus* (Skuse) could account for its stable coexistence with the native mosquito species and inferior competitor *Ochlerotatus triseriatus* (Say) in Florida treeholes and container systems was tested experimentally.

2. Functional responses of the two dipteran predators *Toxorhynchites rutilus* (Coquillett) and *Corethrella appendiculata* (Grabham) were evaluated separately for *A. albopictus* and *O. triseriatus* prey. Both predators exhibited type II functional responses and consistently consumed more of the invasive species. Handling time of *T. rutilus* feeding upon *O. triseriatus* was significantly longer than when preying upon the invasive species.

3. When either predator species was offered varying ratios of the two prey species, *A. albopictus* was consumed preferentially. The absence of a prey ratio effect on preference indicated that switching probably does not occur.

4. The higher maximum feeding rate upon, and preference for, *A. albopictus* suggests that differential predation may foster coexistence of the invasive and native mosquito prey species in Florida.

### Keywords

*Aedes albopictus*; coexistence; *Corethrella appendiculata*; invasive species; native species; *Ochlerotatus triseriatus*; predation; *Toxorhynchites rutilus*; treeholes; vulnerability

### Introduction

Successful invasive species commonly disrupt ecological communities by displacing native species (Sandlund *et al.*, 1999). Such invasive species may be characterised by rapid growth, short lifespan, high fecundity, the ability to utilise a broad range of habitats, association with human activity, and few if any natural enemies in their new habitat (Morton, 1996). Understanding how invaders alter community structure may facilitate prediction of their long-term consequences (Shea & Chesson, 2002).

*Aedes albopictus* (Skuse) is an invasive mosquito species from Asia that has been broadly dispersed via used tyres and has spread rapidly in the past two decades in the U.S.A.

(O'Meara *et al.*, 1995) as well as in southern Europe, West Africa, and South America (Lounibos, 2002). Larvae of this species inhabit treeholes and artificial containers (e.g. tyres) and feed by filtering or browsing upon microbes (Hawley, 1988). The successful spread of *A. albopictus* appears to be linked to its high growth rate and ability to displace other species in this habitat (Barrera, 1996). *A. albopictus* may also gain early access to resources by inhibiting egg hatching of other mosquito species (Edgerly *et al.*, 1993). There is strong evidence that *A. albopictus* has competitively displaced a resident mosquito species, *Aedes aegypti* (L.), from artificial containers throughout much of the southeastern U.S.A. (O'Meara *et al.*, 1995; Juliano, 1998)

In forested areas of the eastern U.S.A., *A. albopictus* has invaded treeholes and containers occupied by the native mosquito *Ochlerotatus triseriatus* (Say), whose larvae also acquire resources by browsing and filtering microbes (Jenkins & Carpenter, 1946). Laboratory studies have shown that *A. albopictus* outcompetes *O. triseriatus* for limiting larval resources (Barrera, 1996). On the basis of microcosm experiments, Livdahl and Willey (1991) predicted that *A. albopictus* would competitively exclude *O. triseriatus* from artificial container habitats. However, despite the strong negative effects of *A. albopictus* on *O. triseriatus* in laboratory experiments, there is no evidence of competitive displacement between these species in nature (Lounibos *et al.*, 2001).

Predation is an important factor structuring aquatic communities and may stabilise communities through density-dependent predation (Holling, 1965; Hassell, 1978) and switching (Murdoch & Oaten, 1975). Switching occurs when the predator chooses the most abundant prey type more often than it would be if chosen at random (Murdoch & Oaten, 1975). Switching can lead to stable coexistence between two prey species by consumption of the more abundant, having a positive effect on the less abundant species; but may only do so in the presence of density-dependent factors. Alternately, when the predator exhibits a strong preference for one species, the prey that can withstand the highest level of predation should persist (Bonsall & Hassell, 1999).

*Toxorhynchites rutilus* (Coquillett) and *Corethrella appendiculata* (Grabham) are the two common dipteran predators of mosquito larvae in peninsular Florida treeholes (Lounibos, 1983; Bradshaw & Holzapfel, 1984). The larger, the culicid *T. rutilus*, is a generalist predator feeding on anything its own size or smaller, including conspecifics (Campos & Lounibos, 2000). The corethrellid *C. appendiculata* is a facultative predator, feeding on microfauna as a small larva and on larger prey, such as first- and second-instar mosquito larvae, in its third and fourth instars (Grabham, 1906; Lounibos, 1985). The predators primarily capture prey by ambushing them (Grabham, 1906; Steffan & Evenhuis, 1981); however, *T. rutilus* may also actively search for prey (Linley & Darling, 1993). Diets of the two predators overlap when *T. rutilus* are in early and *C. appendiculata* in late instars (Lounibos, 1985). Both predator species decrease *O. triseriatus* abundance in treeholes (Bradshaw & Holzapfel, 1983; Lounibos, 1983, 1985), but little research has been done to examine how predation affects the invasion success of *A. albopictus* in this habitat.

The functional response of a predator describes the number of prey eaten per predator across varying densities of prey (Holling, 1965). Calculations of attack constants and handling times from functional response experiments can be used to understand the mechanisms behind single predator–single prey systems, but they may not accurately predict events in systems where multiple prey species are present. Preference for a particular prey species can be predicted from estimates of the attack constant and handling time taken from functional response experiments using a single prey species (Cock, 1978). The first objective of this research was to determine the nature of the functional responses of *T. rutilus* and *C. appendiculata* to individual prey species and to estimate the associated parameters.

Comparisons of parameters allowed determination of whether the predator's response to each prey species differed, and the functional response curves predicted for each prey species the maximum number of prey that could be consumed in a 24-h period. If predators play a role in allowing *A. albopictus* and *O. triseriatus* to coexist, both predators should have a higher maximum feeding rate on the invasive species, and *A. albopictus* should be preferred when *O. triseriatus* and *A. albopictus* are offered to predators in the same microcosm.

## Materials and methods

### Organisms and experiments

Predator larvae and eggs were obtained from laboratory colonies of both species from Florida and maintained in an insectary at  $25 \pm (\text{SD})$  °C, LD 14:10 h and 70% RH. Eggs of *C. appendiculata* and *T. rutilus* were obtained from mated wild caught adults. Larvae of *C. appendiculata* were reared to fourth instars on a diet consisting of cultured nematodes (L. P. Lounibos, unpubl. data). Eggs of Florida *A. albopictus* and *O. triseriatus* were obtained from F1 colonies of these species at the Florida Medical Entomology Laboratory (Lounibos *et al.*, 2001). One day before the start of the experiment, eggs of both prey species were hatched in deoxygenated water.

To determine the functional response and the maximum number of individual prey consumed, each predator was offered 12, 40, 80, 120, 200, or 250 first-instar *A. albopictus* or *O. triseriatus* in 400-ml beakers filled with dechlorinated tap water. *Toxorhynchites rutilus* was added as a first instar (less than 8 h old), and *C. appendiculata* was added as a fourth-instar larva, which had moulted 1–2 days earlier and was deprived of food 1 day prior to the start of the experiment. The treatments were randomly assigned to positions on a single shelf of the insectary, and the predators were allowed to consume prey for 24 h. After 24 h, the predators were removed and the remaining prey were counted. Due to constraints on numbers of prey and predators available, replications were run at different periods under the same controlled conditions. More replicates were run at lower than at higher densities (Juliano, 2001).

In a separate experiment to examine preference, first-instar prey at a fixed density of 100 per 400 ml were offered to each predator at varying ratios of the two prey species. The predators were of the same instar as above. *Corethrella appendiculata* were offered prey at ratios of *A. albopictus* : *O. triseriatus* of 0:100, 20:80, 40:60, 50:50, 60:40, 80:20, and 100:0, which were each replicated four times. *Toxorhynchites rutilus* were offered prey at ratios of *A. albopictus* : *O. triseriatus* of 0:100, 10:90, 30:70, 50:50, 70:30, 90:10, and 100:0, each replicated six times. After 24 h, predators were removed and remaining prey were identified to species and counted under a dissecting microscope.

### Statistical analyses

The shape of the functional response curve was determined by logistic regression of the proportion of prey eaten as a function of the number of prey available (Trexler *et al.*, 1988). Since cubic models are of a high enough order to describe most curves (Juliano, 2001), the following polynomial function was fit:

$$\frac{N_e}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \quad (1)$$

with the procedure CATMOD (SAS Institute Inc, 1989), where  $N_e$  is the number of prey consumed,  $N_0$  is the number of prey available, and  $N_e/N_0$  is the probability that the prey will

be eaten by a predator. The  $P$ -values are parameters to be estimated using maximum likelihood methods. A type II functional response occurs when the linear term (or slope of  $N_e/N_0$  vs.  $N_0$  near  $N_0=0$ ) is negative and a type III functional response occurs when the linear term is positive (Juliano, 2001). The attack constants and handling times for each predator were estimated using iterative nonlinear least squares regression in the procedure NLIN (SAS Institute Inc., 1989) to solve the implicit function given by the random predator equation (Rogers, 1972; Juliano, 2001).

To determine if the functional response parameters were significantly different between prey species for each predator, nonlinear least squares regression was used on the implicit function given by the random predator equation (Rogers, 1972; Juliano, 2001). Each prey species was assigned an indicator variable and compared using the equation:

$$0 = N_0 - N_0 \exp \{ [a + D_a(j)] \{ [T_h + D_{T_h}(j)] (N_e) - T \} \} - N_e \quad (2)$$

where  $j$  is the indicator variable with a value of 0 for *O. triseriatus* and a value of 1 for *A. albopictus*.  $T$  is the amount of time the experiment was run,  $T_h$  is the handling time,  $a$  the attack constant, and  $N_0$  and  $N_e$  are as previously defined.  $D_a$  and  $D_{T_h}$  are the differences in parameter estimates for the two prey species. Parameters were deemed to be significantly different when the 95% confidence interval for the difference in parameters did not include zero. Significance was further tested with a  $t$ -test comparing the differences in parameter estimates to zero (Juliano, 2001).

Prey preference in the two-prey experiment was determined using Manly's  $\alpha$  (Manly, 1974), modified by Chesson (1983) for prey depletion:

$$\alpha = \frac{\ln [(N_A - C_A) / N_A]}{\ln [(N_A - C_A) / N_A] + \ln [(N_T - C_T) / N_T]} \quad (3)$$

where  $N$  is the initial number and  $C$  is the number consumed of *A. albopictus* ( $A$ ) and *O. triseriatus* ( $T$ ). The predicted preference ( $\alpha$ ) for each predator was determined using attack constants from the functional response experiments using a multiplicative model:

$$\hat{\alpha}_a = \frac{a_a}{a_a + a_t - (a_a a_t)} \quad (4)$$

where  $\hat{\alpha}_a$  is the predicted preference for *A. albopictus*, and  $a_a$  and  $a_t$  are attack constants for *A. albopictus* and *O. triseriatus*, respectively, estimated from the functional response. This equation can be used even when prey are not being replaced (Chesson, 1983). Resulting  $\alpha$  values were compared among prey ratios by ANOVA to determine if preference changes with prey ratios. Since  $\alpha$  values did not vary with density, they were pooled and tested against the predicted  $\alpha$  value with a  $t$ -test to determine if there was a significant preference for either prey species.

## Results and discussion

Logistic regressions showed that the linear term was negative for all predator-prey treatments, indicating type II functional responses (Fig. 1). These results were confirmed by plotting observed mean proportions consumed vs. predicted proportions consumed (not shown). However, at the highest density of 250 prey, the number of *A. albopictus* and *O. triseriatus* consumed by both *T. rutilus* and *C. appendiculata* decreased from the 200 prey density (Fig. 1), indicating that predator behaviour at very high prey densities may be influenced by a secondary factor(s).

There were no significant differences among attack constants or handling times between the prey species when exposed to *C. appendiculata*. There were no significant differences in attack constants between prey species exposed to *T. rutilus*, but handling time was significantly greater for *O. triseriatus* than for *A. albopictus* ( $t_{122} = 3.87$ ,  $P < 0.05$ ). The average maximum feeding rate for *C. appendiculata* was  $\approx 24$  prey per 24 h on *A. albopictus* and 18 prey per 24 h on *O. triseriatus* (Fig. 1a,b). The average maximum feeding rate for *T. rutilus* was 21 prey per 24 h on *A. albopictus* and 14 prey per 24 h on *O. triseriatus* (Fig. 1c,d).

$^{ANOVA}$  detected no significant variation in Manly's  $\alpha$  among ratios of prey species with *C. appendiculata* ( $F_{4,21} = 0.98$ ,  $P > 0.4$ ). Predicted preference of *C. appendiculata* for *A. albopictus* was slight, with an  $\alpha$  value of 0.55. When pooled results were compared with an  $\alpha$  level of 0.52 for no preference, *C. appendiculata* consistently consumed fewer *O. triseriatus* than predicted, significantly preferring *A. albopictus* overall ( $t_{21} = 9.24$ ,  $P < 0.001$ ) (Fig. 2a).  $^{ANOVA}$  detected no significant variation in Manly's  $\alpha$  among ratios of prey species with *T. rutilus* ( $F_{4,28} = 0.34$ ,  $P > 0.8$ ). Predicted preference of *T. rutilus* for *A. albopictus* was slight with an  $\alpha$  value of 0.52. When pooled results were compared with an  $\alpha$  level of 0.51 for no preference, *T. rutilus* significantly preferred *A. albopictus* to *O. triseriatus* overall ( $t_{28} = 3.87$ ,  $P < 0.001$ ) (Fig. 2b).

The results of this study suggest that two important predators in Florida container habitats may adversely affect production of the invasive mosquito *A. albopictus* through preferential consumption. The preference for *A. albopictus* by *C. appendiculata* was stronger than that by *T. rutilus*, suggesting that the former, abundant predator in south Florida treeholes (Lounibos, 1983) may be more important for fostering coexistence between these two prey species under the size structure studied. A number of studies have shown that predation as a whole can reduce the effects of competition (Chambers, 1985). When predation is more intense on the superior competitor, the inferior competitor may coexist through a keystone predator effect (Paine, 1966). Here, evidence is provided suggesting that this may be the case in Florida treeholes and containers. This may be especially important in container habitats, where *A. albopictus* is predicted to exclude *O. triseriatus* in the absence of predators. However, in treehole habitats the prey species may be able to coexist (Livdahl & Willey, 1991).

Functional response curves allow for prediction of predation intensity and predator behaviour over a range of conditions and act as a baseline for predicting stability of predator-prey interactions (Cock, 1978). In the current experiment *T. rutilus* and *C. appendiculata* exhibited a type II functional response to changes in prey density, resulting in negative density dependence of predator-induced mortality (Holling, 1965). Type II functional responses are typical of invertebrate predators (Hassell, 1978), have been found in other studies on *Toxorhynchites* and *Corethrella* larvae (Livdahl, 1979; Lounibos, 1983), and are less likely to result in stable predator-prey relationships than are type III responses (Hassell, 1978).

Based on attack constants and handling times, the functional response of the predator to its prey should predict how the predator behaves when multiple prey species are present (Cock, 1978). The lack of any differences between the prey species in handling time, attack constant, or maximum feeding rate when exposed to *C. appendiculata* suggests that this predator reacts similarly when exposed alone to the prey species. This is not surprising from the predator's view since *C. appendiculata* is a generalist and captures its prey primarily by ambush (Grabham, 1906). However, when two prey species were exposed together, *C. appendiculata* consistently consumed more *A. albopictus* (and fewer *O. triseriatus*) than expected based on single species data. This suggests that prey behaviour may affect feeding

preference by this predator and that the presence of *O. triseriatus* may negatively affect *A. albopictus* survival in the presence of *C. appendiculata*. The second predator, *T. rutilus* took significantly longer to handle *O. triseriatus*, resulting in a prediction of slight preference for *A. albopictus*. However, the interspecific difference in attack constants was not significant for either predator species. The results indicate that first-instar *T. rutilus* may consume a larger number of *A. albopictus*, but will reach its maximum feeding rate with fewer *O. triseriatus* larvae. A similar but not significant trend was found for *C. appendiculata*, indicating that both predators may consume the invasive species more easily than the native prey species.

The addition of a second prey species can have a number of direct and indirect effects on both the predator and prey populations. Preference for the invasive species may be important for allowing the two species to coexist. Although both predators preferred *A. albopictus* to *O. triseriatus* under certain conditions, *A. albopictus* has a higher growth and development rate (Barrera, 1996; Lounibos *et al.*, 2001), which may enable it to escape predation by size-selective predators better than *O. triseriatus* (Lounibos *et al.*, 2001). Apparent mutualism occurs between prey species when the presence of one lowers predation rates on the other (Holt & Lawton, 1994). Thus, greater predation intensity on *A. albopictus* may also relax predation on *O. triseriatus*, enabling this species to increase in numbers. Prey that share a common predator should have positive effects on each other's density when the predator switches, shows a strongly saturating functional response, or when the per capita death rate of the predator increases with predator density (Abrams & Matsuda, 1996). However, more available prey resulting from the addition of *A. albopictus* may lead to negative indirect effects among the two prey species by increasing the abundance of predators (Holt, 1977). Thus, multigenerational studies are needed to determine whether *A. albopictus* has an overall positive or negative effect on *O. triseriatus* in the context of shared predators.

## Acknowledgments

Thanks goes to R. Escher, J. Butler, and S. Juliano for providing mosquitoes, insectary space, and statistical assistance, respectively. Previous drafts of the manuscript were improved by comments from S. Juliano, C. Lord, G. O'Meara, and S. Yanoviak. Research was supported in part by NIH grant AI-44793. This is Florida Agricultural Experiment Station Journal Series No. R-10457.

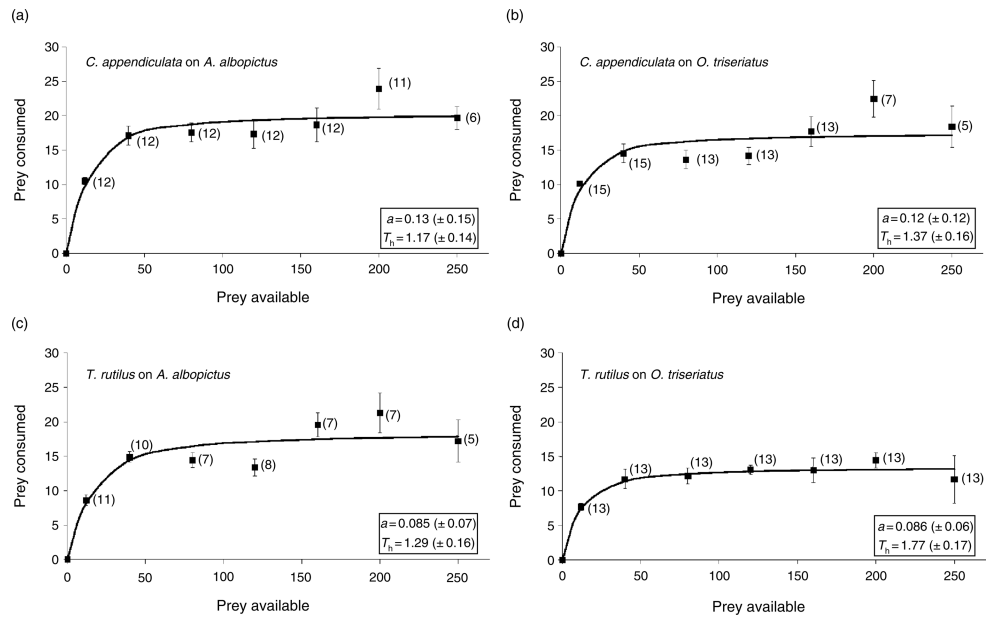
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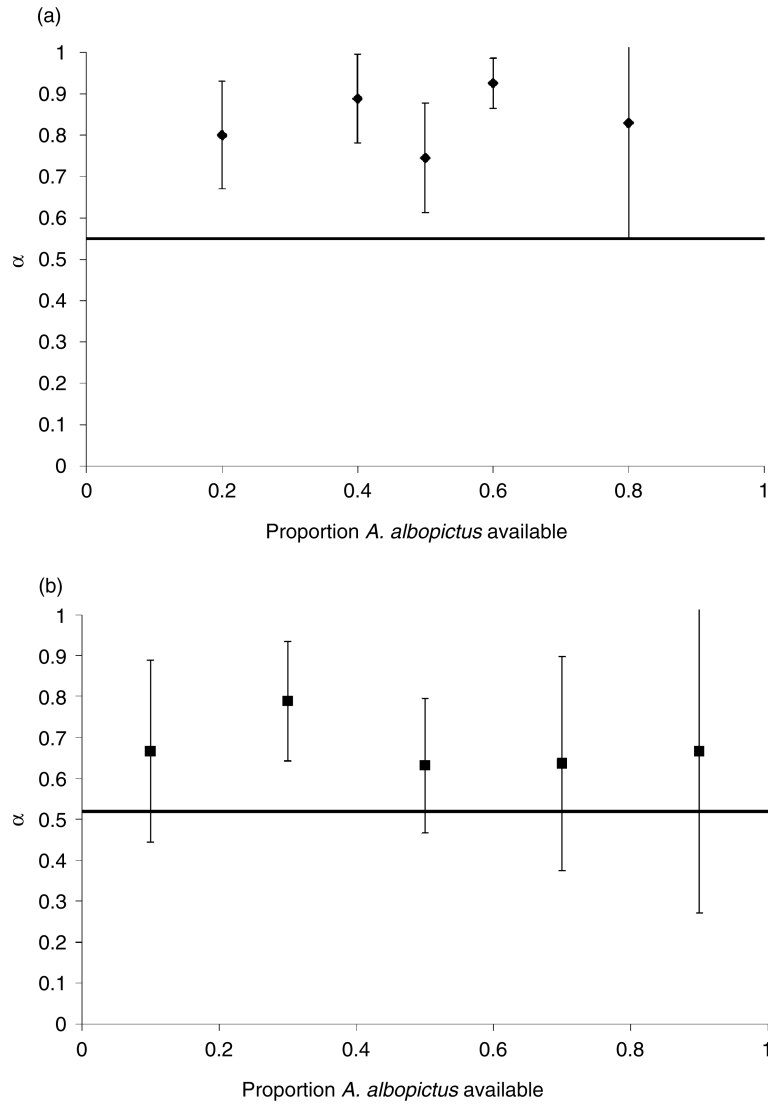
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**Fig. 1.** Functional response of (a) *Corethrella appendiculata* to *Aedes albopictus*, (b) *C. appendiculata* to *Ochlerotatus triseriatus*, (c) *Toxorhynchites rutilus* to *A. albopictus*, and (d) *T. rutilus* to *O. triseriatus*. Each point represents the mean number of prey consumed over a 24-h period, with one SE above and below each point.  $a$  and  $T_h$  are the estimated attack rates and handling times, respectively ( $\pm 95\%$  CI). The solid line is predicted from the random predator model. Number of replicates are indicated in parentheses.



**Fig. 2.** Preference of (a) *Corethrella appendiculata* for *Aedes albopictus* and (b) *Toxorhynchites rutilus* for *A. albopictus* indicated by Manly's alpha ( $\alpha$ ) ( $\pm$ SD) vs. the proportion of *A. albopictus* available. Solid lines indicate no preference for either prey species predicted from the functional response.  $\alpha=0.52$  for *C. appendiculata* and  $\alpha=0.51$  for *T. rutilus*.