

EFFECTS OF A PREDATOR ON PREY METAMORPHOSIS: PLASTIC RESPONSES BY PREY OR SELECTIVE MORTALITY?

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Abstract. Models for organisms with complex life cycles predict decreased size at, and altered time to, metamorphosis for organisms experiencing greater mortality rate during the larval stages. We tested this prediction by exposing larvae of the tree hole mosquito, *Aedes triseriatus*, to predation by the mosquito *Toxorhynchites rutilus* in a series of five experiments. Populations both sympatric and allopatric to the predator were tested, and meta-analysis was used to synthesize the results of all experiments, and to test for heterogeneity of effects of actual vs. perceived predation (predator unable to kill prey). In the presence of this predator, *A. triseriatus* from both sympatric and allopatric populations had lower mass at pupation, as predicted. This effect was present in both sexes, but was more pronounced in females. The presence of the predator also increased time to pupation for females (but not for males). Reduced size at pupation appears to result from decreased growth rate in the presence of the predator, and we tested the hypothesis that this predator induced behavioral changes in *A. triseriatus* that lead to reduced growth (e.g., reduced movement and foraging). Behavioral observations did not support the hypothesis of behavioral change. Meta-analysis revealed significant heterogeneity of the effects of actual predation vs. perceived predation on size at pupation, which decreased significantly only in response to actual predation. There was no significant heterogeneity in the effect of actual predation vs. perceived predation on time to pupation. These results suggest that effects of this predator on metamorphosis of *A. triseriatus* may be products of either facultative responses to the predator or of selective mortality due to predation in experiments with actual predation. Sympatric and allopatric populations of *A. triseriatus* used in these experiments did not differ consistently in size at and time to pupation, nor in their developmental responses to *T. rutilus*. Although these results generally support the predictions of existing models of complex life cycles, they suggest that the mechanisms producing these effects in this system may not be the same as the behavioral mechanisms producing similar effects in amphibian systems.

Key words: *Aedes triseriatus*; behavioral responses; growth rate; life history; meta-analysis; metamorphosis; mortality rate; mosquitoes; predator-prey; *Toxorhynchites rutilus*.

INTRODUCTION

Ontogenetic niche shifts, in which an organism switches habitat or niche during its life history (Gilliam 1982, Werner and Gilliam 1984), are found among fish (e.g., Werner and Hall 1988), amphibians (e.g., Werner 1986, Skelly and Werner 1990) and invertebrates (e.g., Lounibos et al. 1993, Juliano and Stoffregen 1994). Metamorphosis of amphibians and holometabolous aquatic insects is a common example of such a switch, representing a move from an aquatic to a terrestrial habitat. Ecological factors that vary between these habitats may affect this ontogenetic niche shift by favoring differences in size or time at which an organism undergoes metamorphosis. Theoretical studies of ontogenetic niche shifts (e.g., Wilbur and Collins 1973, Gilliam 1982, Werner and Gilliam 1984, Ludwig and

Rowe 1990, Rowe and Ludwig 1991, Abrams et al. 1996) have resulted in clear predictions that have been subjected to experimental tests using amphibians as model systems (e.g., Alford and Harris 1988, Crump 1989, Figiel and Semlitsch 1990, Skelly and Werner 1990, Skelly 1992). If mortality rates are equivalent during pre- and postmetamorphic stages, selection favors a pattern of metamorphosis that maximizes growth rate at all times (Gilliam 1982). However, if mortality rates differ between habitats of pre- and postmetamorphic individuals, the organism faces a trade-off between maximizing growth rate vs. minimizing mortality rate. In this circumstance, fitness is maximized by minimizing the ratio of mortality rate to growth rate across all life history stages, and if all else is equal, greater mortality rate or decreased growth rate during premetamorphic stages should favor decreased size at metamorphosis, and time to metamorphosis may increase, decrease, or remain unchanged, depending on the assumptions built into specific models (Gilliam 1982, Werner and Gilliam 1984, Ludwig and Rowe 1990, Rowe and Ludwig 1991, Abrams et al. 1996).

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Effects of growth rate on size at and time to metamorphosis have been studied extensively via manipulations of food quantity, food quality, or population density for both amphibians and insects. Resulting effects on metamorphosis are generally consistent with models of complex life cycles (e.g., Semlitsch and Gibbons 1985, Banks and Thompson 1987, Alford and Harris 1988, Hard et al. 1989, Juliano 1989, Solbreck et al. 1989, Peckarsky and Cowan 1991, Walker et al. 1991, Lounibos et al. 1993, Ball and Baker 1995, 1996). Effects of mortality rate have also been tested experimentally, primarily using amphibians. Increases in either perceived (Skelly and Werner 1990, Werner 1991, Skelly 1992) or actual (Figiel and Semlitsch 1990) predation on amphibian larvae result in decreased size at metamorphosis, as predicted. These life history responses seem to result primarily from changes in behavior: when predators are present amphibian larvae reduce movement, resulting in a decreased growth rate, and therefore, decreased size at metamorphosis (Figiel and Semlitsch 1990, Skelly and Werner 1990, Werner 1991, Skelly 1992).

Effects of actual or perceived predation on metamorphosis in insects have yielded results similar to those from studies on amphibians (Livdahl 1984, Feltmate and Williams 1991, Lounibos et al. 1993, Peckarsky et al. 1993, Ball and Baker 1995, 1996). Because theory on the effects of predation should apply to insects as well as to amphibians (Ludwig and Rowe 1990, Rowe and Ludwig 1991), insects would seem to be desirable experimental subjects for such tests. The fitness effects of such indirect effects of predation are likely to be even more important for insects, as any effects on size at metamorphosis cannot be compensated for by somatic growth during the adult stage.

In this study, we examined the effects of the predatory mosquito *Toxorhynchites rutilus* (Coq.) on size at and time to metamorphosis of the mosquito *Aedes triseriatus* (Say) in order to test the qualitative predictions of models of how mortality risk affects complex life cycles for insects. In addition to testing effects of the presence of this predator during our experiments, we also compare populations of *A. triseriatus* that differ in co-occurrence with this predator, in order to determine whether local presence or absence of a predator is associated with population differentiation in life history (e.g., Fawcett 1984, Livdahl 1984, Fraser and Gilliam 1987, Solbreck et al. 1989, Crowl and Covich 1990). *A. triseriatus* is found throughout the eastern United States and larvae develop in water-filled tree holes and tires. In the southern part of its range, larvae of *A. triseriatus* are preyed upon by larvae of *T. rutilus*. The abundance of *T. rutilus* declines to the north and this species is completely absent in the northern portions of *A. triseriatus*' range (Bradshaw and Holzapfel 1985). The only insect predator present in the north is *Anopheles barberi* (Coq.), a small facultative predator on young *A. triseriatus* (Livdahl 1982), which occurs

throughout nearly the entire range of *A. triseriatus* (Bradshaw and Holzapfel 1985). Therefore, *T. rutilus* can be a major source of predation on southern populations of *A. triseriatus*, and life history differences among *A. triseriatus* sympatric and allopatric with *T. rutilus* could reflect local adaptation to predation (Livdahl 1984, Juliano 1989, Juliano et al. 1993).

We tested the predictions common to models of effects of mortality risk on metamorphosis in a set of experiments that addressed four specific questions. (1) Does the presence of *T. rutilus* affect size at, or time to, metamorphosis in *A. triseriatus*? Such an effect was observed in a field experiment with free-ranging predators (Lounibos et al. 1993), but the mechanisms producing this effect are unknown. We examined possible mechanisms by answering additional questions. (2) Does perceived predation (*T. rutilus* unable to kill *A. triseriatus*) produce the same effect as actual predation (*T. rutilus* free to kill *A. triseriatus*)? Differences in effects of perceived vs. actual predation on life history may provide information on mechanisms. For example, if size at metamorphosis decreases with both perceived and actual predation, phenotypic plasticity in size can be inferred (i.e., a flexible response, Sih 1987). If, however, only actual predation affects size at metamorphosis, selective predation may be responsible, and a flexible response by *A. triseriatus* is not necessarily inferred. (3) Is the predator effect on metamorphosis caused by slower growth rates, and if so, is this effect mediated by changes in feeding behavior? If so, mechanisms producing predation effects on amphibian metamorphosis can be generalized to this insect system. (4) Do populations sympatric with and allopatric to *T. rutilus* differ in pattern of metamorphosis including the metamorphic response to predators? Fixed differences between populations may indicate that predation by *T. rutilus* is a strong selective force in natural populations.

METHODS

Laboratory rearing of mosquitoes

A. triseriatus allopatric to the predator were collected from tree holes near Normal, Illinois ($\approx 40^{\circ}39' N$, $88^{\circ}50' W$) and Worcester, Massachusetts ($\approx 42^{\circ}11' N$, $71^{\circ}51' W$). Occurrence of *T. rutilus* is rare and sporadic near Normal, Illinois, so we considered this population to be allopatric with *T. rutilus*. Populations from sympatry were collected from tree holes and tires near Vero Beach, Florida ($27^{\circ}31' N$, $82^{\circ}23' W$) and Durham, North Carolina ($35^{\circ}15' N$, $79^{\circ}06' W$). Voucher specimens from all populations were deposited in the insect collection of the Department of Biological Sciences, Illinois State University, Normal, Illinois, USA. Larvae and pupae collected in the field were reared to adulthood and allowed to mate in 0.6-m³ cages. Rearing methods are fully described by Juliano (1989). Progeny of these field-collected individuals were used in all experiments.

TABLE 1. Summary of experimental conditions across five experiments. Abbreviations for predator treatments: 0 = no predators; 1F = one predator feeding; 2F = two predators feeding; 1NF = one predator not feeding; 2NF = two predators not feeding. See *Methods* for further details.

| Conditions | Experiment | | | | |
|---|---------------------|---------------------|----------------------|----------------------|----------------------|
| | 1 | 2 | 3 | 4 | 5 |
| Predators | Caged | Caged | Free | Free | Caged |
| Predator treatments | 0, 1F, 2F, 1NF, 2NF | 0, 1F, 2F, 1NF, 2NF | 0, 1F | 0, 1F | 0, 1F |
| No. <i>Aedes</i> /container | 75 larvae | 75 larvae | 150 larvae | 200 larvae | 75 larvae |
| Total no. of containers | 30 | 40 | 40 | 30 | 40 |
| Density with zero predators | Unmanipulated | Unmanipulated | Unmanipulated | Reduced | Unmanipulated |
| Food (mg·larva ⁻¹ ·d ⁻¹) | 1.0 | 1.0 | 0.5, 1.0 | 0.1 | 0.1 |
| Sympatric populations | Durham | Vero Beach | Durham Vero Beach | Durham Vero Beach | Durham Vero Beach |
| Allopatric populations | Normal | Normal | Normal Worcester | Normal | Normal Worcester |
| Water | Replaced | Replaced | Replaced | Filtered | Filtered |

Toxorhynchites rutilus eggs and larvae were collected near Ashland, Virginia and larvae were reared on *A. triseriatus*. Adults were maintained in 0.6-m³ cages and fed ≈10% sugar water. Because adults do not freely mate in cages, *T. rutilus* were force mated (methods modified from Munstermann and Wasmuth 1985) and allowed to oviposit in black plastic tubs.

Experiments

To test the predicted effects of mortality rate, larvae of *A. triseriatus* from sympatric and allopatric populations were raised in the presence or absence of *T. rutilus* in a set of five experiments (Table 1). The following life history traits were tested for differences among populations and between predator treatments: (1) days to pupation for males and females; (2) size at pupation for males and females; and (3) growth rate (sexes pooled). All experiments were conducted in tap water in 400-mL plastic beakers at a constant temperature (22°C) and photoperiod (16:8 L:D). All cohorts of *A. triseriatus* were added as first-instar larvae (<36 h old). Larvae were fed a fixed per capita ration of liver powder (ICN Biochemicals, Cleveland, Ohio) that was replaced every two other days to compensate for mortality and pupation. By keeping per capita food availability relatively constant over time, we minimized the indirect effect of predation on metamorphosis that may occur via reductions in prey density (Abrams and Rowe 1996). Predators were always added as first-instar larvae. Populations used in each experiment were determined by availability.

All experiments included treatments with and without *T. rutilus*. The experiments differed from one another in a number of ways (Table 1), reflecting our growing understanding of which factors might influence metamorphosis. The most important difference among experiments was that predators were either screened from prey (perceived predation—experiments 1, 2, and 5), so that *A. triseriatus* foraged in the presence of the predator without actual risk of predation,

or were allowed free access to prey (actual predation—experiments 3 and 4), which may provide prey with more cues (e.g., tactile) to the rate of predation. Caged predators (experiments 1, 2, and 5) were placed in nylon screen (240-μm mesh) cylinders ≈3 cm in diameter that were suspended in the water column. The screen allowed for water flow into and out of the cylinders, but larvae were unable to pass. Initial cohorts of *A. triseriatus* were larger in experiments with actual predation (Table 1) so that a sufficient number of survivors would be produced.

Experiments 1 and 2.—Predator treatments included either one or two *T. rutilus* larvae (Table 1). All beakers contained two cages, and zero, one, or two cages contained predators. In half the replicates with predators, the predators were not fed within the cages (Table 1), but were removed every 2 d in order to feed and replaced with another larva at the same stage of development. In half the replicates with predators, the predators were fed in the experimental container during the experiment. *T. rutilus* within the screen cylinders were offered *A. triseriatus* larvae from stock cultures for 24 h out of a 48-h period.

Experiment 3.—Two food levels were used (Table 1), enabling us to test whether effects of predators on metamorphosis were dependent on feeding rate.

Experiments 4 and 5.—Uneaten food rations were removed by filtration using qualitative filter paper, and filtered water was returned to the beaker, whereas in experiments 1, 2, and 3 uneaten food was removed by replacing all the water in the beakers (Table 1).

Behavior.—In experiment 5 we tested for effects of *T. rutilus* and population on behavior. We videotaped *A. triseriatus* larvae on day 9 of the experiment (mostly third- and fourth-instar larvae). Individual beakers, with cages and any *T. rutilus* larvae present, were positioned for recording, and larvae allowed to acclimate for 10 min after this movement. The camera was then turned on and a 10-min continuous view of the entire beaker was recorded. Behavioral observations for each

replicate were obtained from this videotape by recording activity and position of each visible larva at 1-min intervals. Pooling across all larvae and all intervals resulted in 367 ± 7 (mean ± 1 SE) observations per replicate. For each replicate, these pooled observations were used to determine the proportion of observations in four activity categories and three position categories. Activities were: (1) browsing—brushing particles from solid surfaces using the mouth parts, usually with movement via currents generated by the mouth parts; (2) filtering—removing particles from the water via currents generated by the mouth parts, usually with slow movement through the water; (3) thrashing—moving through the water via vigorous lateral flexions of the body; and (4) resting—not feeding or moving (for more detail, see Juliano and Reminger 1992). Positions were defined as: (1) wall—within 1 mm of the beaker wall; (2) cage—within 1 mm of the cage; and (3) middle—away from the wall or cage.

Life history traits.—Pupae were removed daily, and days to pupation recorded for each individual. In experiments 1–3, pupae were isolated until eclosion and mass at pupation determined from the dried adult and its exuvium. In experiments 4 and 5, pupae were sexed and dry mass determined directly. Median days to pupation and mean pupal mass were determined for each sex within a replicate.

In all experiments, three larvae were randomly removed from each replicate on days 0, 4, 8, 12, 16, and 20 and mean dry masses determined. Growth increments for larvae in each replicate were determined as the difference between mean dry masses on consecutive sampling days, averaged over all days, and these were used as estimates of growth rate for each replicate.

Statistical analysis

Analysis of variance with linear contrasts was used to test the effects of population, predation, food level (in experiment 3 only), and interactions on life history traits in each experiment. Effects were considered significant if $P < 0.05$. In all experiments, we predicted that the presence of *T. rutilus* would decrease size at, and alter time to pupation. For experiments 1 and 2, contrasts were also used to test for differences in the effects of feeding vs. nonfeeding *T. rutilus*, and the effects of one vs. two *T. rutilus*. Pairwise comparisons were made using the Bonferroni method for an experimentwise $\alpha = 0.05$. Differences between allopatric and sympatric populations of *A. triseriatus* may suggest that fixed differences among populations of *A. triseriatus* exist, perhaps due to natural selection by predation. Though it would be ideal to test for a region effect (sympatric vs. allopatric) using population as a random effect, we had insufficient numbers of populations to yield such a test with reasonable power. Therefore, we treated populations as fixed effects, and tested the region effect as a contrast. This approach means that our interpretation of the region effect cannot

be generalized beyond the four populations studied. A significant population \times predation interaction could indicate that facultative life history responses to the predator occur in the sympatric populations and not in the allopatric populations (or vice versa). In experiment 3, low food availability should decrease size at pupation, and growth rate, and increase time to pupation. More importantly, a significant food \times predation interaction would suggest that facultative responses to this predator are affected by food availability.

Multivariate analysis of variance (MANOVA) was used to test for effects of population, predation, and their interaction on behavior (activity and position as two separate analyses) of *A. triseriatus* in experiment 5. We were particularly interested in whether *A. triseriatus* reduce feeding and movement in the presence of the predator.

Meta-analysis

Although the outcomes of each of the five experiments are interesting in themselves, it is the results of the set of experiments together that provide the most interesting information on the effects of predation on metamorphosis in *A. triseriatus*. Because all experiments tested the same general prediction, meta-analysis (Gurevitch et al. 1992, Gurevitch and Hedges 1993) was used to integrate the results from all experiments. Because we used factorial designs testing effects of population, predation, and their interaction on life history traits, we used a modified version of meta-analysis appropriate for such a factorial designs (J. Gurevitch and L. V. Hedges, *personal communication*; see Appendix) and based on a mixed model (Gurevitch et al. 1992, Gurevitch and Hedges 1993). Each experiment is represented by a quantitative index called the effect size, which is the difference between the means of two groups divided by their pooled standard deviation. Thus, the effect size indicates the number of standard deviations between the two groups and is independent of sample size and scale of measurement. An effect size of 0.2 is commonly interpreted as “small,” whereas an effect size > 1.0 is commonly interpreted as “very large” (Gurevitch and Hedges 1993). By combining effect sizes from each experiment, and determining the variation in effect size within these combined experiments, a z test can be used to test the null hypothesis that the combined effect size is equal to zero (i.e., there is no difference between groups). A one-tailed test was used to test a priori predictions for size at pupation and growth rate because all models predict decreased size at pupation in response to predation, and because previous results from amphibians and insects indicated decreased growth rates in the presence of the predator. However, time to pupation could increase or decrease in response to decreased growth rates or increased predation (see Skelly and Werner 1990, Abrams and Rowe 1996).

Meta-analysis also enables us to test for differences

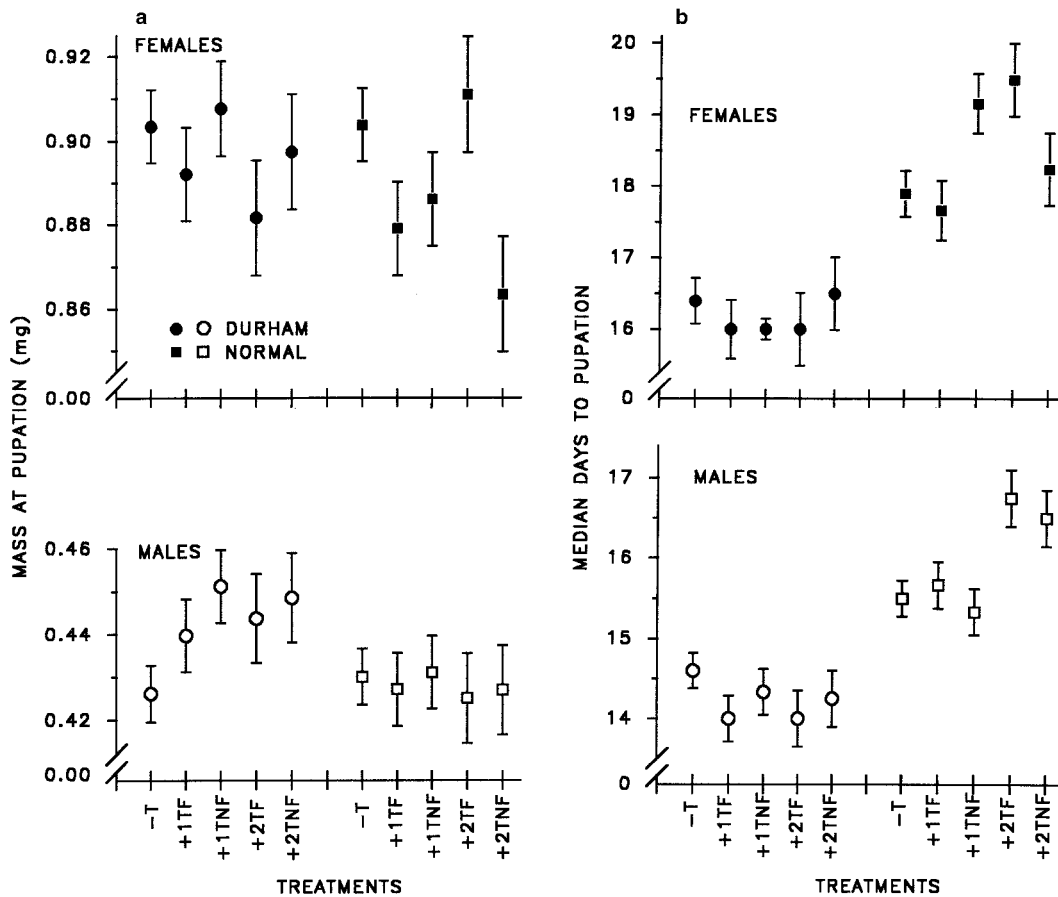


FIG. 1. Responses of female and male *A. triseriatus* from Durham, North Carolina, and Normal, Illinois, in experiment 1. (a) Mass at pupation (adjusted means \pm 1 SE). (b) Median days to pupation (adjusted means \pm 1 SE). Predator treatments include: -T = no *T. rutilus* present, +1TF = 1 *T. rutilus* present and feeding, +1TNF = 1 *T. rutilus* present and not feeding, +2TF = 2 *T. rutilus* present and feeding, +2TNF = 2 *T. rutilus* present and not feeding.

in effect sizes among experiments by combining experiments into sets with common characteristics and testing for significant heterogeneity of effects between these sets (Gurevitch and Hedges 1993). Question 2 listed above calls for an explicit test of whether actual predation (predators free as in experiments 3 and 4) and perceived predation (predators caged as in experiments 1, 2, and 5) produce similar effects. This question is important because if only actual predation produces an effect, this effect may be due to selective predation on a population varying in metamorphic pattern, rather than solely due to facultative changes in pattern of metamorphosis in response to perception of predation.

RESULTS

Experiment 1

Mass at pupation.—There was no significant predator effect (Fig. 1a). Durham males pupated at a significantly larger size than did Normal males (Fig. 1a) ($F_{1,20} = 5.87$, $P = 0.0250$), but females from the two populations did not differ. The predator \times population interaction was not significant for either sex, indicating

that the lack of differences among treatments was consistent between populations.

Median days to pupation.—There was no significant predator effect (Fig. 1b). Populations differed significantly for both males ($F_{1,20} = 79.42$, $P = 0.0001$) and females ($F_{1,20} = 69.39$, $P = 0.0001$), with Durham individuals pupating significantly earlier than Normal individuals (Fig. 1b). There was a significant predator \times population interaction for males ($F_{4,20} = 3.48$, $P = 0.026$). Time to pupation was significantly greater in two predator treatments vs. one predator treatment in the Normal population only (Fig. 1b, $P = 0.0022$). There was no significant predator \times population interaction for females, indicating time to pupation was consistent across predator treatments in both populations.

Growth increment.—There was no significant predator effect. The Normal population showed a significantly lower growth increment (0.153 ± 0.015 mg; adjusted mean \pm 1 SE) than did the Durham population (0.223 ± 0.015) ($F_{1,20} = 10.98$, $P = 0.0035$). There was no significant predator \times population interaction, indicating that the lack of differences among treatments was consistent for both populations.

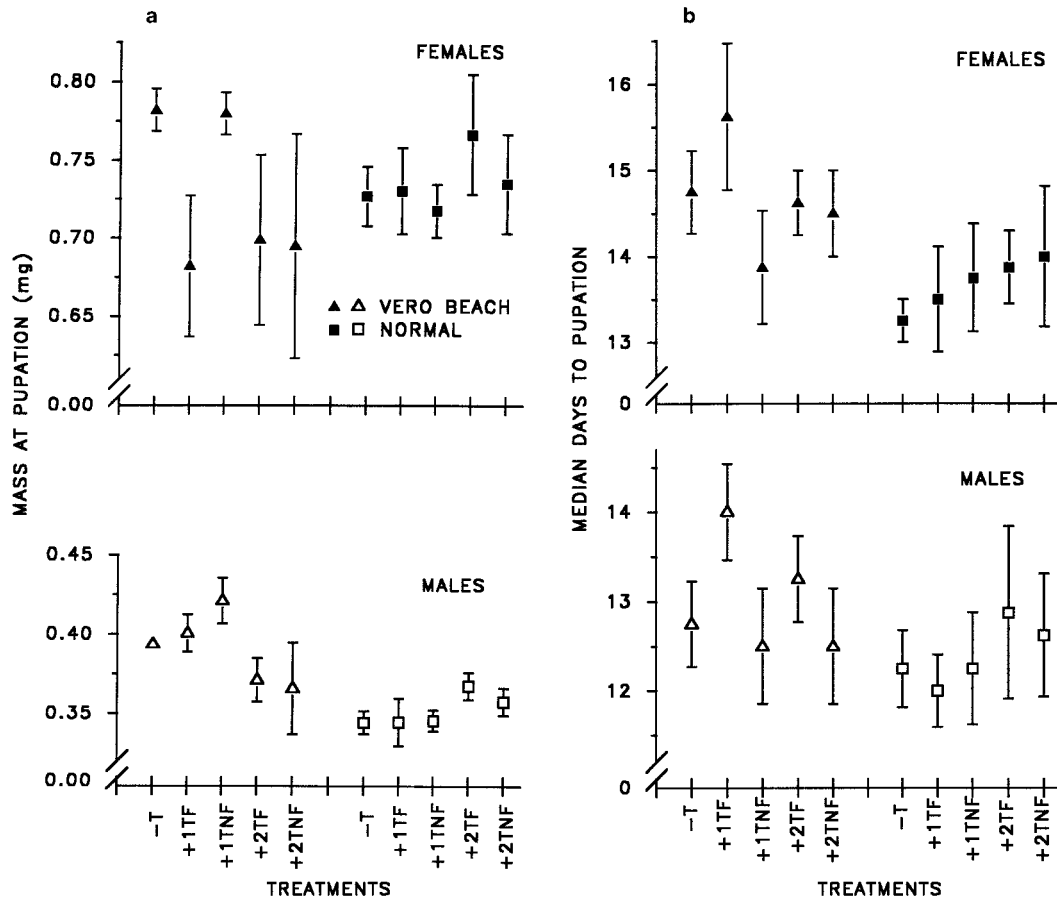


FIG. 2. Responses of female and male *A. triseriatus* from Vero Beach, Florida, and Normal, Illinois, in experiment 2. (a) Mass at pupation (means \pm 1 SE). (b) Median days to pupation (means \pm 1 SE). See Fig. 1 for key to treatments.

Experiment 2

Mass at pupation.—There was no significant predator effect. Vero Beach males pupated at a significantly larger size than did Normal males (Fig. 2a) ($F_{1,30} = 20.23$, $P = 0.00001$), but females from the two populations did not differ. The predator \times population interaction was not significant for either sex, indicating that the lack of differences among treatments was consistent between populations.

Median days to pupation.—There was no significant predator effect (Fig. 2b). Vero Beach females pupated significantly later than did Normal females (Fig. 2b) ($F_{1,30} = 7.23$, $P = 0.0116$), but males did not differ between populations. The predator \times population interaction was not significant for either sex, indicating that the lack of differences among treatments was consistent between populations.

Growth increment.—Experiment 2 yielded no significant effects on growth increment.

Experiment 3

Mass at pupation.—Size at pupation was significantly smaller in the predator treatment vs. the no-

predator treatment for both sexes (Fig. 3a, Table 2). The population effect was not significant for either sex (Table 2). Mass at pupation in the low-food treatment was significantly smaller than in the high-food treatment for both sexes (Fig. 3a, Table 2). There were no significant interactions for either sex (Table 2), indicating that differences between predator or food treatments were consistent among populations.

Median days to pupation.—There was no significant predator effect (Table 2). Normal females pupated significantly later than did Durham, Vero Beach, or Worcester females (Fig. 3b, Table 2). There was no significant population effect for males (Table 2). Time to pupation was significantly greater in the low-food treatment compared to high-food for females only (Fig. 3b, Table 2). Three interactions were significant for females: predator \times population, population \times food, and predator \times population \times food (Table 2). These interactions resulted from much greater time to pupation for females when a predator was present for Normal with low food (Fig. 3b). There were no significant interactions for males (Table 2).

Growth increment.—The predator treatment showed

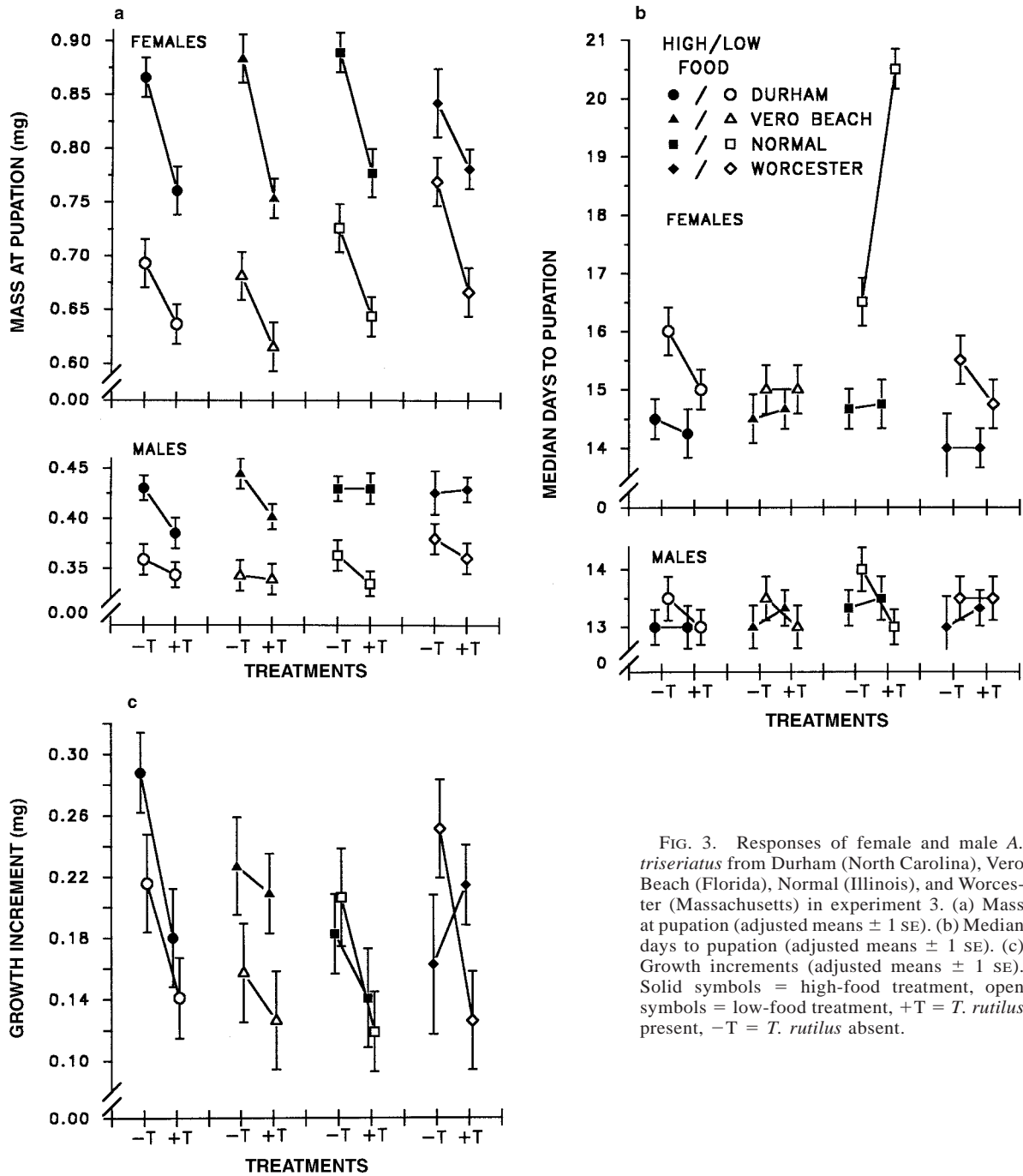


FIG. 3. Responses of female and male *A. triseriatus* from Durham (North Carolina), Vero Beach (Florida), Normal (Illinois), and Worcester (Massachusetts) in experiment 3. (a) Mass at pupation (adjusted means \pm 1 SE). (b) Median days to pupation (adjusted means \pm 1 SE). (c) Growth increments (adjusted means \pm 1 SE). Solid symbols = high-food treatment, open symbols = low-food treatment, +T = *T. rutilus* present, -T = *T. rutilus* absent.

a significantly lower growth increment than did the no-predator treatment (Fig. 3c, Table 2). There was no significant population effect (Table 2). The growth increment was significantly lower in the low-food treatment vs. the high-food treatment (Fig. 3c, Table 2). There were no significant interactions (Table 2), indicating the effect of the predator on growth increment was consistent among populations.

Experiment 4

Mass at pupation.—Size at pupation was significantly smaller in the predator treatment vs. the no-predator treatment (Fig. 4a) for both males ($F_{1,24} = 7.06$, $P = 0.0138$) and females ($F_{1,24} = 7.35$, $P = 0.0122$). There was no significant population effect for either sex. The predator \times population interaction was not significant for either sex, indicating the effect of

TABLE 2. *F* tests from analysis of variance on life history traits of *A. triseriatus* in experiment 3. Error df = 21.

| Source | df | Dependent variables | | | | |
|-------------------------------|----|----------------------|---------|-----------------------|-----------|-----------------------|
| | | Time to pupation (d) | | Mass at pupation (mg) | | Growth increment (mg) |
| | | Females | Males | Females | Males | |
| Predation | 1 | 1.97 NS | 0.64 NS | 67.56**** | 6.50* | 12.28** |
| Population | 3 | 22.89**** | 0.70 NS | 1.88 NS | 1.23 NS | 1.58 NS |
| Food | 1 | 64.81**** | 1.05 NS | 166.16**** | 87.35**** | 4.47* |
| Predation × Population | 3 | 9.91*** | 0.43 NS | 0.19 NS | 0.43 NS | 0.98 NS |
| Predation × Food | 1 | 1.97 NS | 3.75 NS | 1.36 NS | 0.09 NS | 2.67 NS |
| Population × Food | 3 | 15.00**** | 0.11 NS | 1.94 NS | 0.93 NS | 1.62 NS |
| Predation × Population × Food | 3 | 8.53*** | 0.26 NS | 1.00 NS | 1.43 NS | 1.90 NS |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS = $P > 0.05$.

the predator on mass at pupation was consistent among populations.

Median days to pupation.—Time to pupation was greater in the predator treatment vs. the no-predator treatment for males (Fig. 4b) ($F_{1,24} = 26.04$, $P = 0.0001$). Though nonsignificant, the same trend was evident for females (Fig. 4b). The population effect and predator × population interaction were not significant for either sex, indicating that differences between predator treatments were consistent for all populations.

Growth increment.—Experiment 4 yielded no significant effects on growth increment.

Experiment 5

Mass at pupation.—There was no significant predator effect for either sex. There was a significant pop-

ulation effect for both females ($F_{3,27} = 6.90$, $P = 0.0014$) and males ($F_{3,27} = 3.72$, $P = 0.0232$). Vero Beach females were significantly smaller at pupation than were Worcester females (Fig. 5a, $P = 0.0001$). Pairwise comparisons yielded no specific differences between populations for males. The predator × population interaction was not significant for either sex, indicating that the lack of differences between treatments was consistent among populations.

Median days to pupation.—Time to pupation was greater in the predator treatment vs. the no-predator treatment for females (Fig. 5b) ($F_{1,27} = 7.38$, $P = 0.0114$) but not for males. There was a significant population effect for females ($F_{3,27} = 3.92$, $P = 0.0191$), but not for males. Females from Normal pupated significantly later than did females from either Durham

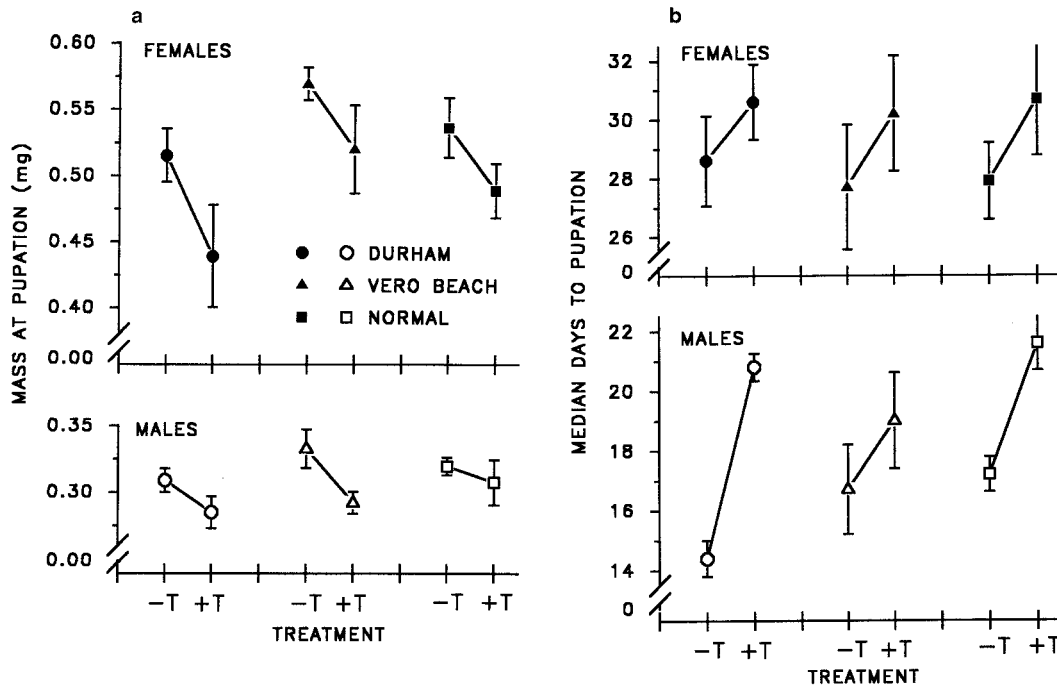


FIG. 4. Responses of female and male *A. triseriatus* from Durham (North Carolina), Vero Beach (Florida), and Normal (Illinois), in experiment 4. (a) Mass at pupation (means ± 1 SE). (b) Median days to pupation (means ± 1 SE). +T = *T. rutilus* present, -T = *T. rutilus* absent.

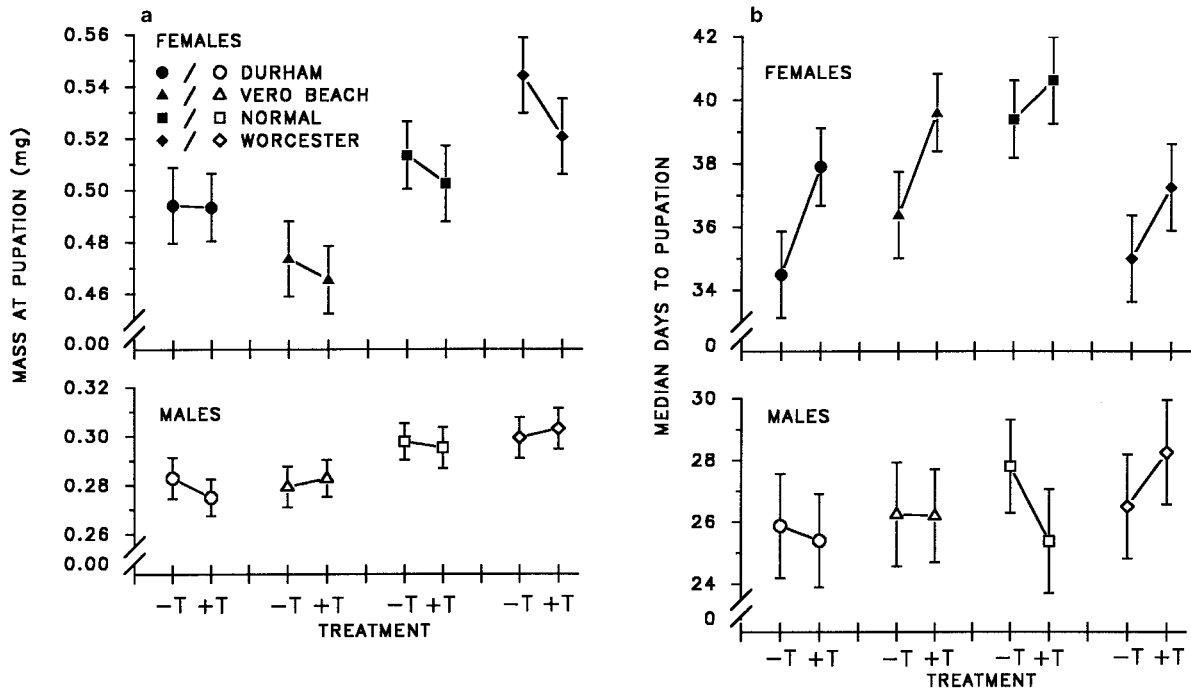


FIG. 5. Responses of female and male *A. triseriatus* from Durham (North Carolina), Vero Beach (Florida), Normal (Illinois), and Worcester (Massachusetts) in experiment 5. (a) Mass at pupation (adjusted means \pm 1 SE). (b) Median days to pupation (adjusted means \pm 1 SE). +T = *T. rutilus* present, -T = *T. rutilus* absent.

($P = 0.0066$) or Worcester ($P = 0.0070$). The predator \times population interaction was not significant for either sex, indicating that differences between predator treatments were consistent for all populations.

Growth increment.—Experiment 5 yielded no significant effects on growth increment.

Behavior.—There was no significant predator effect in MANOVA of activity (Wilks' $\Lambda = 0.87$, $P = 0.30$) or position occupied (Wilks' $\Lambda = 0.89$, $P = 0.40$). There were significant population effects for both activities (Wilks' $\Lambda = 0.49$, $P = 0.03$) and positions occupied (Wilks' $\Lambda = 0.45$, $P = 0.01$). For activity, individuals from Durham thrashed significantly more than did individuals from Vero Beach (Fig. 6, $P = 0.006$), and rested significantly less than did individuals from Normal (Fig. 6, $P = 0.003$). For position, individuals from Vero Beach spent significantly less time in the middle than did individuals from Normal or Worcester (Fig. 6, $P < 0.002$). The predator \times population interaction was not significant for both activity (Wilks' $\Lambda = 0.61$, $P = 0.16$) and position occupied (Wilks' $\Lambda = 0.68$, $P = 0.34$).

Meta-analysis

For all experiments combined, mass at pupation was significantly smaller in the presence of *T. rutilus* for both sexes (Table 3), as predicted. For all experiments, time to pupation was significantly greater in the presence of *T. rutilus* for females, but not for males (Table 3). Although females pupated significantly later and at

a smaller size in the presence of *T. rutilus*, and males pupated at a significantly smaller size in the presence of predators, meta-analysis revealed no significant effect of predators on growth increment (Table 3).

Heterogeneity between experiments with perceived predation vs. those with actual predation was significant for mass at pupation for both sexes (Table 3). Experiments with actual predation yielded significantly lower mass at pupation in the presence of a predator (positive effect sizes, Table 3), whereas experiments with perceived predation yielded no such significant effect on mass at pupation (Table 3). In contrast, heterogeneity between experiments with perceived predation vs. actual predation was not significant for time to pupation for both sexes (Table 3). Heterogeneity between experiments with actual vs. perceived predation was also not significant for growth increment (Table 3).

Meta-analysis revealed only one significant difference between sympatric and allopatric populations of *A. triseriatus*: growth increment for sympatric populations was significantly greater than growth increment for allopatric populations ($P > 0.05$). Meta-analysis yielded no significant predation \times population interaction for any life history trait (all $P \gg 0.05$), indicating that the predator effects were consistent for both sympatric and allopatric populations. In the interests of brevity, details of the meta-analyses for population and interaction effects are omitted.

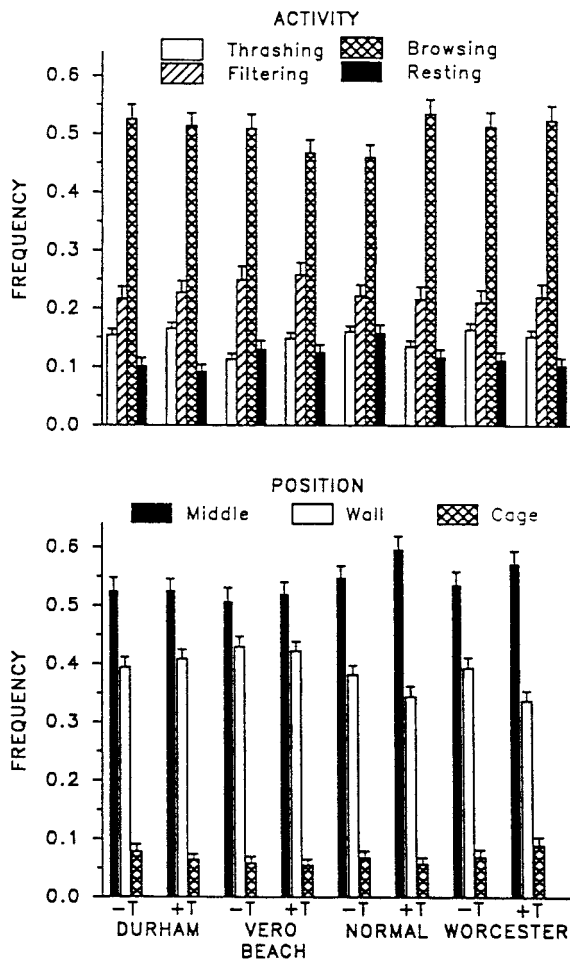


FIG. 6. Frequency of different activities and positions for *A. triseriatus* from Durham (North Carolina), Vero Beach (Florida), Normal (Illinois), and Worcester (Massachusetts) in experiment 5. Activities include: thrashing, filtering, browsing, and resting; positions include: cage, middle, and wall. See *Methods: Experiments: Behavior*. +T = *T. rutilus* present, -T = *T. rutilus* absent.

DISCUSSION

This set of experiments demonstrates that the predator *Toxorhynchites rutilus* has numerous complex, and sometimes subtle, effects on life history and metamorphosis of *Aedes triseriatus* in controlled laboratory conditions. We discuss these effects in light of the four questions posed in the *Introduction*.

Effects on metamorphosis

The presence of *T. rutilus* has clear and significant effects on size at, and time to, metamorphosis of *A. triseriatus*. Mass at pupation was significantly reduced for both females and males, however meta-analysis suggests that *T. rutilus* had a much greater effect on females than on males (overall effect size for females nearly 3 times that of males, see Table 3). The presence of *T. rutilus* also significantly prolonged time to pu-

pation for females, and although this same trend was present in males, it was not significant. These results suggest sexual dimorphism in the effects of this predator on metamorphosis.

Sexual dimorphism of the response to predation was not predicted, but is nonetheless interesting. Past tests of indirect effect of predators on metamorphosis in amphibians have not evaluated intersexual differences in the response (Werner 1986, 1991, Figiel and Semlitsch 1990, Skelly and Werner 1990, Skelly 1992). Among insects, a field experiment testing the effect of actual predation involving the same predator and prey also indicated a sexually dimorphic effect on size at metamorphosis (Lounibos et al. 1993), and the response of *Chironomus* to predators is also sexually dimorphic (Ball and Baker 1996). In contrast, mayflies show no sexual dimorphism in their responses to stonefly predators (Peckarsky et al. 1993). We know of no theoretical studies that have evaluated the conditions necessary for sexually dimorphic responses to predators. Another source of mortality, habitat drying, produced similar sexually dimorphic effects on size at and time to metamorphosis for *A. triseriatus*, suggesting that females are more responsive to mortality sources in general (Juliano and Stoffregen 1994).

If the effects of *T. rutilus* on life history of *A. triseriatus* represent plastic responses, intersexual differences in these effects suggest differences in selective forces acting on the sexes, which may be widely applicable to species that show protandry (Kleckner et al. 1995). For males, it may be advantageous to undergo metamorphosis as early as possible, particularly if males eclosing early have greater access to receptive females. This may favor maximizing development rate at the expense of any increase in size resulting from a prolonged larval period (Kleckner et al. 1995). Males may thus lack flexibility in the timing of metamorphosis in response to a predator, and the decrease in size at metamorphosis of males may result from decreased growth rate. In contrast, for females, size probably plays a relatively greater role in determining fitness, and females may be selected to maximize size, subject to the constraints imposed by mortality risk (Kleckner et al. 1995). This may favor greater plasticity in both size at and time to metamorphosis for females. Thus, females may respond facultatively to predators (and other mortality sources) by altering both growth and development rates, resulting in altered size at and time to metamorphosis.

Actual vs. perceived predation

Although numerous studies of amphibians and insects have examined the effects of either perceived (Skelly and Werner 1990, Werner 1991, Skelly 1992, Peckarsky et al. 1993, Ball and Baker 1995, 1996) or actual (Figiel and Semlitsch 1990, Feltmate and Williams 1991, Lounibos et al. 1993) predation on size at, and time to, metamorphosis, ours is the first set of

TABLE 3. Meta-analysis (Gurevitch and Hedges 1993) of the effect of predation on life history traits for *A. triseriatus*. Effect sizes \pm 95% CI are indicated for each experiment, and for experiments combined.

| Experiment | Dependent variables | | | | |
|------------------------|-----------------------|-----------------------|----------------------|-----------------------|-----------------------|
| | Mass at pupation (mg) | | Time to pupation (d) | | Growth increment (mg) |
| | Females | Males | Females | Males | |
| 1 | 0.690 \pm 1.251 | -0.570 \pm 0.470 | -0.318 \pm 0.680 | -0.106 \pm 1.709 | -0.440 \pm 1.497 |
| 2 | 0.371 \pm 1.256 | -0.097 \pm 0.484 | -0.182 \pm 0.697 | -0.200 \pm 1.716 | 0.605 \pm 1.510 |
| 3 | 2.752 \pm 1.232 | 0.856 \pm 0.337 | -0.470 \pm 0.553 | 0.267 \pm 1.663 | 1.173 \pm 1.464 |
| 4 | 0.921 \pm 1.252 | 0.820 \pm 0.474 | -0.637 \pm 0.684 | -1.817 \pm 1.724 | -0.698 \pm 1.498 |
| 5 | 0.361 \pm 1.211 | 0.044 \pm 0.352 | -0.903 \pm 0.582 | 0.087 \pm 1.670 | 0.499 \pm 1.470 |
| Tests for effect sizes | | | | | |
| All | 1.022 \pm 0.555* | 0.284 \pm 0.182* | -0.572 \pm 0.282* | -0.338 \pm 0.758 NS | 0.238 \pm 0.665 NS |
| Perceived predation | 0.472 \pm 1.401 NS | -0.156 \pm 0.243 NS | -0.520 \pm 0.373* | -0.070 \pm 0.980 NS | 0.223 \pm 0.862 NS |
| Actual predation | 1.852 \pm 0.879* | 0.844 \pm 0.274* | -0.536 \pm 0.430* | -0.737 \pm 1.197 NS | 0.260 \pm 1.047 NS |
| Homogeneity | | | | | |
| χ^2 | 3.99* | 3.81* | 0.003 NS | 0.71 NS | 0.002 NS |

Notes: Effect sizes are differences between means of no predator (-T) and predator (+T) treatments in standard deviation units, i.e., $[(-T) - (+T)] / (\text{pooled standard deviation})$. Perceived Predation = experiments with the predator in a screened cylinder (experiments 1, 2, and 5); actual predation = experiments with the predator free to attack prey (experiments 3 and 4); For tests of H_0 : effect size = 0: NS = $P > 0.05$; * = $P < 0.05$. For tests of H_0 : homogeneous effect sizes for perceived or actual predation: NS = $P > 0.05$; * = $P < 0.05$.

experiments to test for both kinds of effects in the same system. This is also the first attempt to test formally whether perceived and actual predation produce significantly different effects. Meta-analysis shows that effects of actual vs. perceived predation on size at metamorphosis are different, but also, that effects of actual vs. perceived predation on time to metamorphosis are similar. Only in experiments with actual predation did the presence of predators significantly reduce size at metamorphosis for either sex. These differences between the effects on prey size of actual vs. perceived predation suggest at least two hypotheses for mechanisms. First, actual predation may provide more or stronger cues to the presence of the predator (e.g., direct contact, predator feces, partially eaten prey), resulting in a stronger facultative response to the predator. If this hypothesis is correct, then this result would be consistent with the predictions of models of the effects of predation (or mortality in general) on ontogenetic niche shifts (Werner and Gilliam 1984, Rowe and Ludwig 1991, Abrams and Rowe 1996). That an effect of predation on size at metamorphosis may be a product of phenotypic plasticity is not surprising, as *A. triseriatus*, along with many other insects, are widely believed to show great flexibility in metamorphosis in response to a variety of environmental factors (e.g., Fish 1985, Forrest 1987, Hard et al. 1989, Peckarsky and Cowan 1991, Peckarsky et al. 1993, Juliano and Stoffregen 1994). We cannot, however, rule out a second hypothesis: that selective predation contributes to the effects of actual predation on metamorphosis. *T. rutilus* may remove selectively the fastest growing individuals, which are destined to reach rapidly a large size at metamorphosis. The result would be that only

slowly growing larvae of *A. triseriatus* would undergo metamorphosis in the presence of a predator. This hypothesis implies that greater foraging effort and activity lead to both greater growth and greater predation risk. Such a relationship is a common feature of most models (e.g., Werner and Gilliam 1984, Rowe and Ludwig 1991, Abrams and Rowe 1996), and there is independent correlative evidence for a positive relationship between activity and risk of predation in this study system (Juliano and Reminger 1992). These two hypotheses are not mutually exclusive, and both plasticity and selective mortality may influence size at and time to metamorphosis of *A. triseriatus* in the presence of *T. rutilus*. The potential role of selective mortality in nature may be underestimated because recent studies typically manipulate only perceived predation.

Effects on growth and behavior

For female *A. triseriatus*, time to metamorphosis is greater and size at metamorphosis is less in the presence of *T. rutilus*, implying that growth rates of females are lower in the presence of *T. rutilus*. However, any effect of predators on growth was undetectable in meta-analysis of growth increment, and was only significant in one of the five experiments. Detecting an effect of a predator on growth rate independent of observed size at and time to metamorphosis is likely to be difficult in this system. Metamorphosis of male *A. triseriatus* is less affected by this predator and therefore any effects of the predator on growth rates of males would be small. This would create greater variation in the observed growth increment of larvae (sexes pooled), and would thus make any effects of predation on growth rates of females difficult to detect in analyses

pooling the sexes. Because we were unable to determine the sexes of larvae, we may have been unable to detect the reduction of growth rate of females in the presence of the predator that seems necessary to produce the observed reduction in size at metamorphosis and increased time to metamorphosis in females.

Although these life history responses to *T. rutilus* are consistent with the hypothesis of decreased foraging and movement in the presence of the predator, which would lower growth rate in the presence of the predator, our analysis of behavior in experiment 5 revealed no significant caged-predator effect on activity or position. Though experiment 5 yielded a significant increase in time to metamorphosis for females, nonetheless, effects of the caged predators in experiment 5 were less pronounced than the effects of free predators in experiments 3 and 4. This result suggests that there may be stronger behavioral responses to free predators. There is some evidence for such responses to free predators in previous studies of this system. In short-term (30 min) observations of this predator and prey, Juliano and Reminger (1992) showed that fourth-instar *A. triseriatus*, but not other instars, reduced browsing and increased resting in the presence of free *T. rutilus*. Thus, we have some empirical evidence for the sorts of changes that have been well documented in other aquatic organisms (e.g., Sih 1987, Skelly 1992, Peckarsky et al. 1993), but our present result suggests that caged predators may not induce this response, perhaps because cages reduce visual or tactile stimuli that contribute to the behavioral response.

T. rutilus affected metamorphosis in female *A. triseriatus* more strongly than in males, but our behavioral analysis tested for differences for all larvae (sexes pooled). As with determining effects on growth rate, if behavioral effects differ between the sexes, pooling the sexes may make any change in behavior more difficult to detect. Examining the behavior and growth rate of isolated larvae seems to be necessary to resolve whether behavioral changes affecting growth rate are the mechanism yielding effects of this predator on prey metamorphosis.

An alternative explanation for effects of *T. rutilus* on metamorphosis of *A. triseriatus* is that toxic waste products (e.g., NH_3) produced by *T. rutilus* cause reduced growth. However, effects of the predator on life history were significant in experiment 3, wherein water was replaced every 2 d, which would have limited build up of waste products. This observation suggests that excretory products of *T. rutilus* probably do not cause the observed life history effects.

Our experiments clearly show that life history of *A. triseriatus* is affected by the presence of *T. rutilus*, but the mechanisms yielding these changes remain unresolved. Numerous studies have attributed reductions in size at metamorphosis of prey in the presence of a predator to changes in behavior and associated changes in growth rate (Semlitsch 1987, Figiel and Semlitsch

1990, Skelly and Werner 1990, Stamp and Bowers 1991, Werner 1991, Skelly 1992, Peckarsky et al. 1993, Ball and Baker 1995, 1996). Our results suggest the possibility that other sorts of effects may be involved in this mosquito system, though we cannot reject the behavioral change hypothesis as an explanation for the effects of free *T. rutilus* on metamorphosis of *A. triseriatus*.

Sympatric vs. allopatric populations

Fixed differences between these sympatric and allopatric populations were clearly absent in these experiments. This result suggests any differences in life history between populations are unrelated to co-occurrence with *T. rutilus*. This is consistent with other studies using these same populations (Frankino 1993, Juliano et al. 1993, Juliano 1996), which suggest that although there are behavioral and demographic differences among populations of *A. triseriatus*, these differences are not consistently related to allopatry vs. sympatry with *T. rutilus*.

The similar effects of *T. rutilus* on metamorphosis in our sympatric and allopatric populations of *A. triseriatus* may be interpreted in at least three ways. First, this similarity may provide further support for the hypothesis that predator effects on metamorphosis of *A. triseriatus* are direct products of selective mortality, which would affect all experimental populations regardless of history of co-occurrence. Second, facultative behavioral and growth responses to any perception of predation may be nonspecific, evolutionarily conserved traits in mosquitoes, occurring even in response to predators not encountered in nature (e.g., Sih 1986). Third, the northern range limit of *T. rutilus* (determined by freezing of tree holes, Bradshaw and Holzapfel 1985) may fluctuate. After mild winters, *T. rutilus* may expand its range north, and encounter usually allopatric *A. triseriatus* (e.g., Normal, Illinois—Juliano et al. 1993, and even further north—Darsie and Ward 1981). Such occasional co-occurrence with *T. rutilus* may be sufficient to maintain selection for responsiveness to this predator.

Finally, we wish to comment on the utility of meta-analysis for experimental ecology. Meta-analysis has not often been applied in ecological studies, and published applications have involved synthesis of information culled from previously published independent experiments (e.g., Gurevitch et al. 1992, Gurevitch and Hedges 1993). Ours is the first use of the technique for evaluating the results of a set of related experiments designed to address the same question. It is common for ecological experiments to be conducted in several years, or in several places, or on several taxa or populations. Often, investigators obtain different significance levels in these different experiments, and may then take this as evidence for important ecological differences among the experiments. Meta-analysis enables investigators to conduct objective tests for heteroge-

neity among experiments. Statistical significance in any single experiment can depend on such nonecological factors as sample size and random variation among replicates. Thus, the same biological effect may be "significant" in some experiments and "not significant" in others. We feel that meta-analysis has clarified our conclusions in this multi-experiment study. Our study is the first to use meta-analysis for factorial experiments. Often factor interactions may be of greatest interest (i.e., does the effect of a treatment differ among sites? years? species? etc.), which makes the development of methods for meta-analytical tests of interactions important. Other multi-experiment studies may also benefit from meta-analysis. However, when meta-analysis is applied to a related set of experiments from a single study, it is highly likely that the number of experiments will be fairly low, probably between 3 and 10. We need information on the power of the homogeneity test when the number of experiments involved is this low in order to help investigators to interpret significant heterogeneity in these circumstances.

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APPENDIX

For each life history trait, the effect size, d , was calculated as the difference between the mean of two groups of interest divided by the square root of the Mean Square for Error (MSE), from the ANOVA tables and multiplied by a correction factor for small sample size (J. Gurevitch and L. V. Hedges, *personal communication*). The effect size for the population effect (d_p) and predator effect (d_c) are, respectively,

$$d_p = \frac{(Y_{AP} + Y_{AN}) - (Y_{SP} + Y_{SN})}{2\sqrt{MSE}} \times J,$$

$$d_c = \frac{(Y_{SN} + Y_{AN}) - (Y_{SP} + Y_{AP})}{2\sqrt{MSE}} \times J,$$

where Y_{AP} is the mean for the Allopatric populations with Predators present, Y_{AN} is the mean for the Allopatric populations with No predators present, Y_{SP} is the mean for the Sympatric populations with Predators present, and Y_{SN} is the mean for the Sympatric populations with No predators present. J is the correction factor and is calculated as:

$$J = 1 - \frac{3}{[4(N - 2) - 1]},$$

where N = total number of replicates in the experiment. The effect size for the interaction (d_i) is

$$d_i = \frac{(Y_{AP} + Y_{SN}) - (Y_{SP} + Y_{AN})}{2\sqrt{MSE}} \times J_i$$

where J_i is the correction factor for the interaction:

$$J_i = 1 - \frac{3}{[4(N - 4) - 1]}.$$

The variance (v_k) for each factor and the interaction is calculated as:

$$v_k = \frac{1}{4} \left[1/N_{AP} + 1/N_{AN} + 1/N_{SP} + 1/N_{SN} + \frac{d_k^2}{2N} \right],$$

where k is either p, c, or i.

All other calculations were performed as described in Gurevitch and Hedges (1993).