

## PREDATORS REDUCE PREY POPULATION GROWTH BY INDUCING CHANGES IN PREY BEHAVIOR

ERIK H. NELSON,<sup>1</sup> CHRISTOPHER E. MATTHEWS, AND JAY A. ROSENHEIM

Center for Population Biology and Department of Entomology, University of California, Davis, California 95616 USA

**Abstract.** The ability of predators to reduce prey populations is generally ascribed to the consumption of prey individuals. However, predators may also induce behavioral changes in prey individuals, which can reduce prey survival and reproduction. Pea aphid populations are impacted by a variety of predators, many of which induce escape responses in individual aphids. We created disturbance-only predators (surgically manipulated predators that were unable to consume prey, but were still able to forage and interact with prey) and measured their ability to suppress aphid population growth over a six-day period. The greatest reduction in aphid population growth was caused by normal predators that were able to both consume and disturb aphids, but aphid population growth was also strongly reduced by nonconsumptive, disturbance-only predators. These field experiments are the first to show that predators reduce prey population growth partly through predator-induced changes in prey behavior, as well as through consumption of prey individuals.

**Key words:** *Acyrtosiphon pisum*; avoidance; escape behavior; induced defense; nonconsumptive interactions; non-lethal interactions; predation risk; predator disturbance of prey; prey behavior, predator-induced changes; prey population growth; predator effects on prey population; trait-mediated interactions.

### INTRODUCTION

Although the ability of predators to suppress prey populations is well documented, the mechanisms underlying this phenomenon are less clear. It is generally assumed that predators suppress prey populations through consumption: that predators are reducing prey population growth by killing and eating prey individuals. However, in addition to causing mortality, predators can also cause changes in prey characteristics, by inducing defensive responses in prey morphology, physiology, or behavior (Lima 1998b, Tollrian and Dodson 1999). Predator-induced defensive responses can help prey avoid being consumed, but often come at a cost to some other aspect of prey biology. For example, prey individuals that flee to a new habitat may lose feeding or mating opportunities (Sih 1994, Lima 1998b), or risk capture by a different type of predator (Sih et al. 1998), and thereby suffer reduced fecundity or survival. Thus, predators can reduce individual reproduction and survival by their presence alone. The costliness of antipredator behaviors suggests the hypothesis that the negative effect of predators on prey population growth may be mediated not only through consumption of prey individuals, but also through the induction of prey defensive behavior (Sih et al. 1985, Anholt 1997, Lima 1998a, Beckerman et al. 2002). Here we present the results of field experi-

ments that are the first to isolate the behaviorally mediated effects of predators on short-term prey population growth.

We studied the interactions between herbivorous and predatory insects in fields of alfalfa (*Medicago sativa*). Pea aphids (*Acyrtosiphon pisum*) feed by inserting their mouthparts into alfalfa phloem tissue, and they reproduce parthenogenetically at rates of 4–10 offspring/d (Tamaki et al. 1970, Campbell and Mackauer 1977). Pea aphids are attacked by a suite of natural enemies that includes lady beetles, parasitoid wasps, and damsel bugs; they respond to the presence of foraging predators by interrupting their feeding and walking away or dropping off the plant (Losey and Denno [1998a] and references therein). The costs suffered by pea aphids as a consequence of their defensive behavior may include increased mortality (Losey and Denno 1998b) and reduced reproductive output (Tamaki et al. 1970). Damsel bugs (*Nabis* spp.) are generalist predators that feed by piercing aphids with a long proboscis and ingesting body contents. Normal damsel bugs both disturb and consume aphids. We generated nonconsumptive, disturbance-only damsel bugs by using surgical scissors to shorten and blunt their mouthparts. By exposing aphids to these disturbance-only damsel bugs, our experiments tested the ability of damsel bugs to suppress aphid population growth through behavioral mechanisms alone.

### METHODS

#### *Field experiments: aphid population growth*

We enclosed small aphid populations in field cages and added either (a) no predators, (b) disturbance-only

Manuscript received 30 July 2003; revised 22 January 2004; accepted 24 January 2004. Corresponding Editor: R. F. Denno.

<sup>1</sup> Present address: Department of Environmental Science, Policy and Management, Division of Insect Biology, University of California, Berkeley, California 94720 USA. E-mail: ehnelson@nature.berkeley.edu

damsel bugs, or (c) normal damsel bugs, and then measured aphid population growth six days later. We did this twice, in experiments conducted in fields of alfalfa (cultivars: Achiever, Corona, Express, LM455, and Royal) grown on the campus of the University of California in Davis, California, USA (30°32' N, 121°44' W).

The two experiments were conducted in different years and with slightly different methods. In Experiment 1, cylindrical cages with walls of fine nylon mesh (diameter 30 cm, height 47 cm; pore size 150  $\mu$ m [Green-tek, Edgerton, Wisconsin, USA]) were placed over single alfalfa plants that had been thinned to 10 stems. Stems near cage walls were removed to prevent aphids from walking off the plant. Each cage received 10 field-collected pea aphid nymphs and one of three predator treatments: (1) *none*, no predator was added ( $n = 48$  cages); (2) *disturbance only*, a late-instar damsel bug nymph with cut mouthparts was added ( $n = 55$  cages); (3) *normal*, an unmanipulated late-instar damsel bug nymph was added ( $n = 45$  cages). Ideally, the experiment would have included a fourth treatment, *consumption only*, but implementing this treatment, for example by manually removing aphids, would have incidentally disturbed the aphids. Damsel bug nymphs were collected from the field and added to cages within 2 h. The mouthparts of disturbance-only damsel bugs were blunted by amputating the terminal 1.5 segments in the field using a small scissors, leaving 3.5 segments. Similar mouthparts manipulations have been used to isolate the nonconsumptive effects of predators in other systems (e.g., Peckarsky et al. 1993, Wissinger and McGrady 1993, Ball and Baker 1996, Beckerman et al. 1997). Cage densities of damsel bugs were within the range of field densities (the number of damsel bugs per cage-equivalent area of alfalfa ranged from 0.4 to 3.4 individuals). The experiment was blocked by date and field; replicates were distributed among 11 blocks initiated from 25 July to 23 August 2000 in three different fields of alfalfa.

Experiment 2 was conceptually similar to Experiment 1, but the methods were adjusted to better simulate field conditions and reduce between-replicate variability. The same cages were placed over multiple alfalfa plants. Because aphids showed no tendency to walk onto cage walls in Experiment 1, plants were not thinned and were allowed to contact cage walls in Experiment 2. To match the higher densities of plant material, we increased the number of aphids; each cage received 16 aphids: 8 eight-day-old aphids (recently emerged adults) and 8 four-day-old aphids (middle-instar nymphs). The field-collected aphids used in Experiment 1 varied in age, and some were parasitized. To control age and parasitism in Experiment 2, we used aphids that were born of field-collected mothers and reared in the field under cages that excluded parasitic wasps. We used adult damsel bugs rather than nymphs in Experiment 2, and predator cages received two dam-

sel bugs instead of one, to moderate variance arising from predator mortality or escape. Predator hunger levels were standardized by holding the field-collected damsel bugs overnight with an ad libitum supply of aphids for food. Cages were assigned to the same three predator treatments: (1) *none* ( $n = 24$  cages); (2) *disturbance only* ( $n = 24$ ); and (3) *normal* ( $n = 22$ ). Mouthparts amputations of disturbance-only damsel bugs were conducted in the laboratory under CO<sub>2</sub> anaesthesia; normal damsel bugs were anesthetized and touched with the scissors. Cages were distributed among five blocks that were initiated 6–20 June 2001 in four different alfalfa fields.

In both experiments, all cage contents were collected six days after damsel bug addition and returned to the laboratory. Aphids were separated from the plant material and counted. Aphid per capita population growth rate was calculated as (final aphid count)/(initial aphid count) for each cage. In each experiment, a nonparametric rank *F* test was performed to evaluate the effects of predator treatment and experimental block; next, differences among treatments were evaluated as a series of three pairwise one-tailed contrasts, setting  $\alpha = 0.05$  for the entire experiment and adjusting the critical value using the sequential Bonferroni technique (Rice 1989).

#### *Mouthparts amputations: damsel bug survivorship and killing ability*

We gained some insight into the effect of mouthparts amputation on damsel bug survivorship by carefully searching through the cages at the end of each experiment and collecting the surviving damsel bugs. Then, to verify the effectiveness of the mouthparts amputations, we tested the experimental damsel bugs in feeding trials by enclosing each in a petri dish with five pea aphids and monitoring the success of its attacks on the aphids.

#### *Mouthparts amputations: effects on the behavior of damsel bugs and aphids*

Our interpretation of these experiments depends on disturbance-only damsel bugs expressing the foraging behavior and disturbance effects of normal damsel bugs. To address the concern that damsel bugs might forage differently and have different behavioral effects when their mouthparts are cut, we observed the behavior of disturbance-only and normal damsel bugs in laboratory arenas over a six-day period. The behavior of the aphids in the arenas was also monitored.

Arenas were plastic cylinders 10 cm in diameter and 25 cm tall; each contained 10 pea aphids (five adults and five nymphs) and a single stem of alfalfa that was hydrated through a hole in the arena floor. Disturbance-only ( $n = 16$  individuals) and normal ( $n = 11$ ) damsel bugs were generated by the amputation procedure used in Experiment 2, and placed singly in arenas. On days 2, 4, and 6, each damsel bug was continuously observed

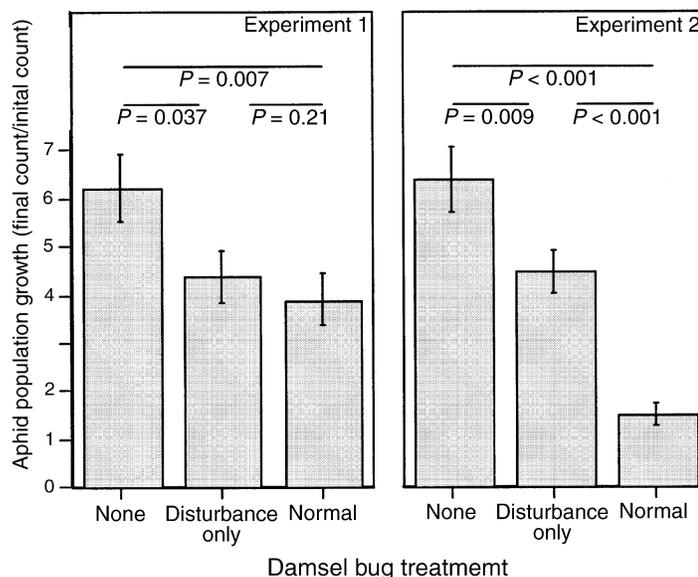


FIG. 1. Per capita population growth rate (mean  $\pm$  1 SE) of pea aphids in field cages containing either no predatory damsel bugs, disturbance-only damsel bugs, or normal damsel bugs. Horizontal lines indicate between-treatment comparisons.  $P$  values were generated by one-tailed contrasts following rank  $F$  tests ( $\alpha = 0.05$  for each experiment; sequential Bonferroni-adjusted critical values).

for three 7-min periods and its behavior recorded using a hand-held computer (Psion Organiser [Psion PLC, London, UK]) running event-recording software (The Observer 3.0, Noldus Information Technology Wageningen, The Netherlands). For each day we calculated the proportion of damsel bug time spent walking, resting, or handling aphids (disturbance-only damsel bugs grappled with aphids, while normal damsel bugs fed on them). We tested for the effect of mouthparts manipulation on damsel bug behavior in a MANOVA with two of the three activities serving as independent response variables (because the three proportions sum to 1.0, only two response variables are linearly independent). We quantified aphid activity by categorizing all pea aphids as feeding on alfalfa or not feeding (walking or resting) at the end of each observation period. The proportion of aphids feeding was calculated for each day in each treatment, and the two treatments were compared with a  $t$  test.

## RESULTS

### *Field experiments: aphid population growth*

In the two field experiments, short-term aphid population growth was greatest in cages with no damsel bugs, lower in cages containing disturbance-only damsel bugs, and lowest in the presence of normal damsel bugs (Fig. 1). Rank  $F$  tests showed overall treatment effects in both experiments (Experiment 1,  $P = 0.04$ ; Experiment 2,  $P < 0.001$ ); block effects were significant in Experiment 1 ( $P < 0.001$ ) but not in Experiment 2 ( $P = 0.25$ ). The suppressive effects of normal damsel bugs, as shown by comparing aphid population growth in the normal and the no-predator treatments, were significant in both experiments (Bonferroni critical value = 0.017;  $P = 0.007$  in Experiment 1 and  $P < 0.001$  in Experiment 2). The suppressive effects of

disturbance-only damsel bugs were marginally nonsignificant in Experiment 1 (Bonferroni critical value = 0.025;  $P = 0.037$ ) and significant in Experiment 2 (Bonferroni critical value = 0.050;  $P = 0.009$ ).

In Experiment 1, normal damsel bugs reduced aphid population growth by 37% relative to no-predator control cages, and disturbance-only damsel bugs reduced aphid population growth by 30%. In Experiment 2, the suppressive effect of normal damsel bugs was 76%, and that of disturbance-only damsel bugs was again 30%. Alternatively, the behaviorally mediated aphid suppression imposed by the disturbance-only damsel bugs may be considered as a percentage of the total aphid suppression imposed by the normal damsel bugs, which were both consuming and disturbing aphids. We found that behavioral effects represented 80% of the total predator effects in Experiment 1, and 39% in Experiment 2.

### *Mouthparts amputations: damsel bug survivorship and killing ability*

The mouthparts amputations reduced damsel bug survivorship. At the end of each field experiment, disturbance-only damsel bugs were missing at rates well above the background mortality rate seen among normal damsel bugs. In Experiment 1, 9% of normal and 49% of disturbance-only damsel bugs were missing; in Experiment 2, 14% of normal and 29% of disturbance-only damsel bugs were missing. This raised the concern that our estimates of behaviorally mediated effects were artificially small, because aphids in the disturbance-only treatment received less exposure to predators than aphids in the normal treatment. However, when we reduced the data sets by excluding cages with missing damsel bugs, our estimates of behavioral effects did not necessarily increase. In Experiment 1, the

estimate of behaviorally mediated population growth suppression was even smaller than when estimated by the complete data set (22% vs. 30%), and in Experiment 2 the suppressive effect was slightly greater (33% vs. 30%). Evidently, the effect of damsel bug survivorship on aphid population growth was minimal or nil.

Feeding trials conducted at the end of each cage experiment showed that a few damsel bugs in the disturbance-only treatments retained some ability to kill aphids, either in part (killed aphids with difficulty, through mauling: 4% of damsel bugs in Experiment 1, 6% in Experiment 2) or in full (killed aphids readily using stylets, despite blunt proboscis: 5% of damsel bugs in Experiment 1, 4% in Experiment 2). Although the petri dish environment of the feeding trials may have limited aphid escape tactics and enhanced damsel bug killing ability, these observations raised the concern that the behaviorally mediated suppression of aphid population growth observed in the disturbance-only treatments might have been artificially exaggerated by consumptive effects. However, when cages containing "killer" disturbance-only damsel bugs were excluded from the data sets, the disturbance-only treatment means changed only very slightly (by +1% in Experiment 1 and +5% in Experiment 2) and the statistical analyses yielded the same qualitative results. Apparently the contamination of our disturbance-only treatment by damsel bugs with residual killing ability was at a level low enough to be indistinguishable from other sources of experimental error.

#### *Mouthparts amputations: effects on the behavior of damsel bugs and aphids*

Mouthparts amputation appeared not to affect damsel bug foraging behavior or the rate at which damsel bugs disturbed aphids from feeding. Activity budgets, monitored in laboratory arenas, were similar for disturbance-only and normal damsel bugs (MANOVA:  $F_{2,17} = 0.06$ ;  $P = 0.94$ ; Fig. 2A). Also, and perhaps more importantly, disturbance-only and normal damsel bugs had similar effects on aphid feeding activity ( $t$  test:  $t_{22} = 0.18$ ;  $P = 0.86$ ; Fig. 2B). Thus, the behavior assay indicates that the disturbance-only damsel bugs closely approximated the behavioral effects of normal damsel bugs.

#### DISCUSSION

This study demonstrates that the non-trophic, behavioral effects of predators on prey individuals can contribute to the suppressive effects of predators on prey populations. Predator-induced suppression of prey population growth has previously been shown in the laboratory, also using pea aphids (Tamaki et al. 1970). Suppression of prey population growth has also been mathematically projected to occur in other organisms, where predator-induced reductions in development and fecundity have been extrapolated to predict reductions in prey population growth rates (Spitze 1992, McPeck

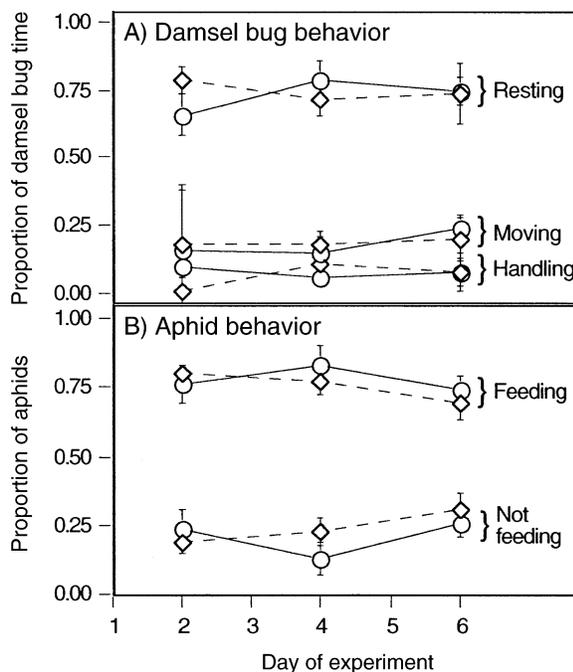


FIG. 2. The effect of mouthparts manipulation on damsel bug and aphid behavior. Data are mean  $\pm$  1 SE. (A) The activity budgets (time spent resting, moving, or handling) of disturbance-only damsel bugs (diamonds) were similar to those of normal, unmanipulated damsel bugs (circles). (B) The behavior (feeding vs. not feeding) of adult pea aphids in arenas with disturbance-only damsel bugs (diamonds) was similar to the behavior of aphids in arenas with normal, unmanipulated damsel bugs (circles).

and Peckarsky 1998, Kuhlmann et al. 1999; projections for the pea aphid appear in a related study [E. H. Nelson, *unpublished manuscript*]). Thus, this study is congruent with previous work that has shown that nonconsumptive predator effects have the potential to impact prey populations, and is the first to demonstrate this concept in field experiments. The attention we draw to nonconsumptive predator effects contrasts with past approaches to predator-prey interactions, which have generally presumed that consumption was the mechanism underlying the effects of predators on prey populations (Sih et al. 1985).

Testing the hypothesis that predators affect prey population through the costs of defensive behavior poses two challenges. First, it is necessary to experimentally separate the consumptive and nonconsumptive effects of the predators; our mouthparts-blocking solution follows an approach used in other systems (e.g., Peckarsky et al. 1993, Wissinger and McGrady 1993, Ball and Baker 1996, Beckerman et al. 1997). Our laboratory-based behavioral assay gave us some assurance that, despite their blocked mouthparts, the disturbance-only damsel bugs adequately represented the disturbance effects of normal damsel bugs. Second, it is necessary to track changes in prey population size (Anholt 1997). The high reproductive rate of the pea aphid al-

lowed us to measure short-term prey population growth: our experiments were of sufficient duration that all inoculum aphids became adults and began reproducing; but aphids born during the experiments did not have time to become adults. Thus, we have measured population growth within the generation time of the pea aphid. Alfalfa fields are an atypical habitat because, during the growing season, they are mowed and the vegetation removed at four- to eight-week intervals. The frequent resetting of this system leads us to believe that nonconsumptive predator effects impact aphid population growth throughout the mowing cycle. Thus, our short-term results suggest that nonconsumptive mechanisms may also play a role in longer-term prey population growth, particularly in our study system. However, demonstrating the longer-term dynamical consequences of nonconsumptive predator effects, or effects on equilibrium prey densities, will await longer-term experiments that span multiple generations of both predator and prey.

The results of our two experiments bear both strong similarities and notable differences. Disturbance-only predators reduced aphid population growth by the same amount in the two experiments, relative to predator-free cages. However, the suppressive effect of normal predators was smaller in Experiment 1 than in Experiment 2; thus, nonconsumptive effects comprised a greater proportion of the total predator effect in Experiment 1 than in Experiment 2. What could explain this difference in the results of the two experiments? One possibility is that a difference in the protocols of the two experiments led to the difference in the results. For example, the reduced alfalfa stem density in Experiment 1 may have increased the costs of disturbance, perhaps by increasing a disturbed aphid's time spent finding an acceptable new feeding site. Or, feeding aphids to the damsel bugs the night before Experiment 2 may have trained them to hunt aphids more efficiently, inducing fewer disturbances. Many other potential explanations linked to protocol differences undoubtedly exist. Another possibility is that the differences arise from year-to-year environmental variation, or other forms of experiment-to-experiment variation. That is, even if we had used the same methods in the two experiments, we would have been surprised to obtain identical results. Indeed, although many readers may consider the results of Experiment 1 to be the more surprising, it may in fact be the results of Experiment 2 that are anomalous. Most likely, the proportion of predator effects that are mediated through disturbance simply varies under a range of conditions, and the results of our two experiments reflect two sets of conditions. Finally, given the errors around our means estimates, the experimental results could be interpreted as being quite similar. Our view is that the two experiments produced the same broad pattern: in both cases, the behavioral effects seen in the disturbance-only damsel bug treatment comprised a substantial portion

of the overall effects of predation seen in the normal damsel bug treatments, 80% in Experiment 1 and 39% in Experiment 2.

The nonconsumptive effects measured in this study have two possible sources: they could result from either fecundity costs (if disturbances cause reduced reproduction) or survival costs (if disturbances cause reduced survival), or both. Aphids used to initiate the cage experiments became adults by the end of the experiments; their offspring did not. Therefore, the final number of adults in the disturbance-only treatment relative to the no-predator treatment provides an indication of survival costs. There was a trend toward fewer adult aphids in the disturbance-only treatments than in the no-predator treatments (17% fewer in Experiment 1 and 19% fewer in Experiment 2 (one-tailed  $t$  tests: Experiment 1,  $P = 0.14$ ; Experiment 2,  $P = 0.05$ ); Appendix), suggesting that predator-induced disturbances may impose some survival costs, which could then contribute to the observed reductions in population growth. Survival costs could be either acute or chronic, depending on whether the risks to aphid survival are large immediately after disturbance or increase gradually with the number of disturbances. In a related study focusing on the behavioral mechanisms underlying the population-level effect seen here, disturbed aphids that were observed under field conditions experienced no acute risks to their survival (E. H. Nelson, *unpublished manuscript*). Chronic survival risks were not assessed; however, the fecundity costs of disturbance were measured, and they were large enough to explain the nonconsumptive effects seen here. Thus, we believe the nonconsumptive effects demonstrated in this study result primarily from fecundity costs, with perhaps some contribution from chronic survival costs.

The strength of nonconsumptive effects, and their prevalence among predator-prey systems, will influence concepts in empirical and theoretical population ecology. For example, the dichotomous characterization of prey as regulated by their predators or their resources collapses when adaptive prey behavior is recognized: induced responses to predators can increase competition for a resource, giving the impression that a species is limited by resources when in fact it is limited by predators as well (Anholt and Werner 1995). Also, because the costs of avoidance behaviors cause a decrease in prey population growth without causing an increase in predator population growth, induced behaviors can add stability to mathematical models of predator-prey dynamics (Ives and Dobson 1987, Ruxton 1995, Fryxell and Lundberg 1998). A rapidly growing body of research on indirect interactions is building appreciation for the role of nonconsumptive effects in multi-species communities. Through induced changes in prey behavior, predators can transmit indirect effects upon their prey's resources, competitors, and other predators (reviewed by Werner and Peacor [2003], Schmitz et al. [2004], and E. L. Preisser, D. I. Bolnick,

and M. F. Benard (*unpublished manuscript*). The work presented here shows that nonconsumptive effects are not limited to transmitting indirect interactions—they can transmit the direct effects of predators on populations of their prey as well.

Predators induce trait shifts in a wide variety of organisms. The defensive responses that prey exhibit in response to predators include changes in morphology, life history, and chemistry as well as behavior—and these responses often carry fitness costs. In any prey organism where defensive trait shifts cause reductions in survival or reproduction, the potential exists for the population-level effects of predators to be mediated partly through their nonconsumptive effects.

#### ACKNOWLEDGMENTS

We thank the UC–Davis Animal Science farm crew for accommodating our research activities; the USDA Regional Research W-185 and the ARCS Foundation for financial support; and T. Bensen, R. Karban, G. Langellotto, S. Lawler, P. Nelson, A. McCall, E. Mondor, J. Rudgers, and three anonymous reviewers for providing comments on the manuscript.

#### LITERATURE CITED

- Anholt, B. R. 1997. How should we test for the role of behaviour in population dynamics? *Evolutionary Ecology* **11**: 633–640.
- Anholt, B. R., and E. E. Werner. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**:2230–2234.
- Ball, S. L., and R. L. Baker. 1996. Predator-induced life history changes: antipredator behavior costs or facultative life history shifts? *Ecology* **77**:1116–1124.
- Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. *Trends in Ecology and Evolution* **17**:263–269.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences (USA)* **94**:10735–10738.
- Campbell, A., and M. Mackauer. 1977. Reproduction and population growth of the pea aphid under laboratory and field conditions. *Canadian Entomologist* **109**:277–284.
- Fryxell, J. M., and P. Lundberg. 1998. Individual behavior and community dynamics. Chapman and Hall, London, UK.
- Ives, A. R., and A. P. Dobson. 1987. Antipredator behavior and the population dynamics of simple predator–prey systems. *American Naturalist* **130**:431–447.
- Kuhlmann, H.-W., J. Kusch, and K. Heckmann. 1999. Predator-induced defenses in ciliated protozoa. Pages 142–159 in R. Tollrian and C. D. Harvell, editors. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Lima, S. L. 1998a. Nonlethal effects in the ecology of predator–prey interactions. *BioScience* **48**:25–34.
- Lima, S. L. 1998b. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* **27**:215–290.
- Losey, J. E., and R. F. Denno. 1998a. The escape response of pea aphids to foliar-foraging predators: factors affecting dropping behaviour. *Ecological Entomology* **23**:53–61.
- Losey, J. E., and R. F. Denno. 1998b. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* **79**: 2143–2152.
- McPeck, M. A., and B. L. Peckarsky. 1998. Life histories and the strengths of species interactions: combining mortality, growth, and fecundity effects. *Ecology* **79**:867–879.
- Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology* **74**:1836–1846.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- Ruxton, G. D. 1995. Short term refuge use and stability of predator–prey models. *Theoretical Population Biology* **47**: 1–17.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters* **7**:153–163.
- Sih, A. 1994. Predation risk and the evolutionary ecology of reproductive behaviour. *Journal of Fish Biology* **45**:111–130.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16**:269–311.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13**:350–355.
- Spitze, K. 1992. Predator-mediated plasticity of prey life history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. *American Naturalist* **139**:229–247.
- Tamaki, G., J. E. Halfhill, and D. O. Hathaway. 1970. Dispersal and reduction of colonies of pea aphids by *Aphidius smithi* (Hymenoptera: Aphidiidae). *Annals of the Entomological Society of America* **63**:973–980.
- Tollrian, R., and S. I. Dodson. 1999. Inducible defenses in cladocera: constraints, costs, and multipredator environments. Pages 177–202 in R. Tollrian and C. D. Harvell, editors. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton, New Jersey, USA.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* **84**:1083–1100.
- Wissinger, S., and J. McGrady. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology* **74**:207–218.

#### APPENDIX

A table representing the final numbers of nymphal and adult pea aphids in the two field cage experiments is available in ESA's Electronic Data Archive: *Ecological Archives* EOBs: E085-052-A1.