DIVERSE TRAIT-MEDIATED INTERACTIONS IN A MULTI-PREDATOR, MULTI-PREY COMMUNITY

Renée P. Prasad and William E. Snyder[1]

Department of Entomology, Washington State University, Pullman Washington 99164 USA

Abstract. Trait-mediated interactions (TMII) can alter the outcome or magnitude of species interactions. We examined how the interaction between a guild of ground and rove beetles and their fly egg prey was altered by a larger predator, the ground beetle *Pterostichus melanarius*, and an additional prey, aphids. In field and laboratory experiments, we manipulated the presence or absence of *P. melanarius* and aphids and recorded the impact of these manipulations on beetle activity and fly egg predation. Individually, aphids, by serving as preferred prey, and *P. melanarius*, by reducing focal beetle activity, weakened egg predation. However, egg predation was restored when both aphids and *P. melanarius* were present together, because aphids triggered greater foraging activity, and thus increased incidental predation of fly eggs, by *P. melanarius*. Thus, TMII among subsets of the community that were disruptive to predation on fly eggs could not be summed to predict the dominant, positive TMII within a more diverse community. Future TMII studies should include more realistic representations of species diversity, and should not ignore the influence of prey on predator behavior.

Key words: alternative prey; indirect effects; multiple predators and prey; predator interference.

INTRODUCTION

Interactions among species can be direct, between species pairs, or indirect, with interactions transmitted through a third, intermediary species (Wootton 1993, Abrams et al. 1996). Early work concentrated on indirect effects mediated by changes in intermediate species' densities. These "density-mediated" indirect interactions (DMII) occur, for example, when predators consume herbivores and initiate trophic cascades (Hairston et al. 1960) or keystone predator effects (Paine 1966). However, more recently, ecologists have become aware that powerful indirect interactions need not involve actual changes in species density, but rather can be mediated by behavioral shifts. These "trait-mediated" indirect interactions (TMII) occur when one species modifies the interaction between a pair of species by changing the behavior, but not density, of an intermediary species (Werner and Peacor 2003, Schmitz et al. 2004).

TMII are now well documented in both terrestrial and aquatic communities (Werner and Peacor 2003, Schmitz et al. 2004). Most examples of TMII come from experiments including three interacting taxa: a predator that alters the behavior of a prey, in turn altering the interaction between the prey and a third species (Huang and Sih 1990, Soluk 1993, Wissinger and McGrady 1993, Schmitz et al. 1997). However, the simplicity of many TMII study communities ignores the complexity

[1] Corresponding author. E-mail: wesnyder@wsu.edu

of more species-diverse, real-world communities. For example, most communities include multiple predator species, providing the opportunity for predator–predator interference (Polis and Strong 1996) or predator–predator facilitation (Losey and Denno 1998), and multiple prey species (Polis 1991, Sih et al. 1998), providing opportunities for prey switching by predators (Siddon and Witman 2004) and apparent competition among prey (Holt and Kotler 1987). Rarely are TMII investigated within communities sufficiently diverse to allow TMII to be propagated simultaneously through multiple channels (Werner and Peacor 2003), despite the fact that multichannel density-mediated indirect effects are known to dramatically impact community structure and function (Polis and Strong 1996, Finke and Denno 2004).

Here, we report interactions within a multiple-predator, multiple-prey community. Our focal predator trophospecies was a guild of small (<1 cm adult length), predaceous ground (Coleoptera: Carabidae) and rove (Coleoptera: Staphylinidae) beetles that are predators of the eggs of root-feeding anthomyiid flies in the genus *Delia* (Fig. 1A). These flies, in turn, are herbivorous pests of Brassicaceae crops (Finch 1996). The small beetles co-occur with a larger (>1.5 cm adult length) ground beetle species, *Pterostichus melanarius* (see Plate 1). *Pterostichus melanarius* does not itself readily feed on fly eggs (Fig. 1B). Rather, in previous work, we found that *P. melanarius* does interfere with fly egg predation because small beetle activity is reduced in the presence of the larger predator (Fig. 1C), which we previously attributed to intraguild predation of small beetles by *P. melanarius* (Prasad and Snyder 2006). Additionally,
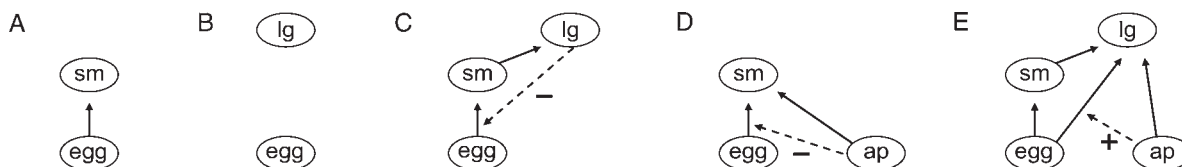
Fig. 1. Interactions among progressively more species-diverse components of our study community. In laboratory feeding trials, (A) smaller beetle species (sm) readily fed on fly eggs, while (B) the larger beetle *P. melanarius* (lg) rarely did (Finch 1996, Prasad and Snyder 2004). Independently, (C) *P. melanarius* and (D) aphid alternative prey (ap) benefited fly eggs indirectly by reducing small beetles' attacks on eggs (Prasad and Snyder, 2006; this study). However, understanding these interactions in isolation did not allow an accurate prediction of dominant interactions in the more complete community, because (E) aphids excited *P. melanarius* foraging, leading to greater egg predation by this larger beetle and negatively impacting fly eggs, an emergent indirect effect of aphids on eggs that could only be realized when all taxa were present. Solid arrows indicate direct interactions and represent energy flow, pointing from resource to consumer. Dashed lines indicate trait-mediated indirect effects and point from the species inducing changed behavior to the species interaction that is altered; labels on the dashed arrows indicate whether the TMII (trait-mediated indirect interaction) strengthens (+) or weakens (−) the interaction.

common alternative prey in the system, aphids, also reduce egg predation by small beetles because beetles switch to attacking aphids when given a choice (Fig. 1D); our previous work did not examine whether *P. melanarius* would interact with aphids in our system, although this species is an aphid predator elsewhere (Snyder and Ives 2001).

However, inferences from earlier work were limited by the segregation of the indirect effects of large predators and alternative prey, and thus the artificial separation of top-down (from *P. melanarius*) and bottom-up (from alternative prey) indirect interactions impacting small beetles and fly egg predation. Here, we report interactions within the more species-diverse community typical of the open field (Prasad and Snyder 2006), where small and large predators, and multiple prey, interact simultaneously.

MATERIALS AND METHODS

Field experiment

Our field experiment examined how the predator *P. melanarius* and aphid alternative prey impacted the behavior of small beetles and predation of fly eggs. We manipulated the presence vs. absence of *P. melanarius* (LG+ and LG−, respectively; Fig. 1), and also the presence vs. absence of aphids (AP+ and AP−, respectively; Fig. 1), within a fully factorial design. Each of the four unique treatment combinations was replicated five times (total $N = 20$). The experiment was conducted in a radish (*Raphnus sativus*) field, planted on 28 May 2004 and located at the Washington State University research farm in Mount Vernon, Washington, USA. The experimental units for the study were $2 \times 2 \times 2$ m field cages, screened on all sides but the bottom (full cage specifications are provided in Prasad and Snyder [2004]). Cages were set up in the field one month after planting (28 June 2004), and enclosed approximately 24 radish plants across three evenly spaced rows.

We manipulated densities of aphid alternative prey by stocking or removing aphids from cages. Three hundred mixed-age aphids were added to all AP+ cages on 2 July. Released aphids were a haphazard mix of the three most common species in local radish fields (green peach aphid [*Myzus persicae*], turnip aphid [*Lipaphis erysimi*], and cabbage aphid [*Brevicoryne brassicae*]; Prasad and Snyder 2006). Aphids were transferred in groups of 30, on pieces of leaf tissue distributed across 10 plants per cage. While aphids spend much of their time on plants, aphids are accessible to ground beetles when aphids fall from the plants (Losey and Denno 1998), when aphid-infested foliage is in contact with the soil surface (Snyder and Ives 2001), and when ground beetles climb into plant foliage to forage (Snyder and Ives 2001). To ensure that aphids were established in or excluded from cages as appropriate by treatment, we made visual counts of aphids on 3 and 12 July; all aphids encountered in AP− cages were removed. We assessed final aphid densities on 18 July by counting all aphids on a haphazardly selected leaf on 10 haphazardly selected plants in each cage.

All cages were stocked with small beetles on 12 July. Small beetles were released as mixed-species assemblages at a density of 28 beetles per cage, generating a typical field density per the 4-m^2 area of crop enclosed within each cage (Prasad and Snyder 2006). The small beetle assemblages were a haphazard mixture of the carabid (*Bembidion lampros*, *Bembidion tetracolom*, *Bradycellus congener*, *Amara littoralis*, *Amara apricaria*) and staphylinid (*Aleochara bilineata*, *Philonthus politus*) beetles that are common in agricultural fields and consume fly eggs (Prasad and Snyder 2004). Our only caveat to the species composition of small beetle assemblages was that at least four of the seven species listed above, and both carabids and staphylinids, were included in each cage. Simultaneous with the small beetle release, groups of 28 *P. melanarius* were added to LG+ cages, also reproducing typical *P. melanarius* density in local agricultural fields (Prasad and Snyder 2006). All beetles were collected from nearby farms within 48 h of the experiment's start.

We monitored beetles using pitfall traps, with each cage containing six of these traps (details as in Prasad and Snyder [2004]). Because beetles must be moving to be captured by pitfall traps, pitfall traps measure a combination of beetle density and activity (Wise 1981).

PLATE 1. In our study system predator guild members include (top row) the large predatory ground beetle *Pterostichus melanarius* and also (bottom row, left to right) the smaller beetle species *Bembidion tetracolom*, *Bembidion lampros*, *Bradycellus congener*, an unidentified Aleocharine morphospecies, and *Aleochara bilineata* (shown with the *Delia* spp. puparium from which it was reared). Photo credit: W. E. Snyder.

We conform to the convention of referring to this metric as "activity-density." Prior to any arthropod manipulations, background levels of predators in the cages were determined by opening pitfall traps for 48 h (from 28 June to 30 June 2004). We determined final *P. melanarius* and small beetle activity-densities by reopening traps from 18 July to 22 July.

We assessed predation on our focal prey, fly eggs, by periodically adding clusters of sentinel fly eggs into all cages, allowing 48 h for predation to occur, and then recollecting eggs and recording how many eggs had been removed. We used *Musca domestica* eggs as a surrogate for the eggs of *Delia* spp. because *M. domestica* was an easier species to propagate (details of *M. domestica* colony maintenance are presented in Prasad and Snyder [2004]); the predators used in this study do not distinguish between eggs of the two fly taxa (Prasad and Snyder 2004). Eggs were added to cages four times, once prior to arthropod manipulation on 30 June, and then three times following manipulation on 12, 14, and 16 July. On each date we added groups of 10 freshly laid *M. domestica* eggs, with each group of eggs attached to a 1-cm^2 piece of peat cut from a transplant pot, to the base of two haphazardly selected plants in each cage (total N = 20 eggs per cage). Sentinel eggs were covered with a thin layer of soil, reproducing placement of eggs by *Delia* spp. (Prasad and Snyder 2004).

Laboratory observations of predator behavior

Small beetle behavior under reproduced field conditions.—In the field experiment reported here, and in all of our earlier work (Prasad and Snyder 2004, 2006), small beetles were monitored using activity-density. Thus, we could not determine whether intraguild predation (i.e., a DMII), vs. reduced activity by small beetles to avoid intraguild predation (i.e., a TMII), triggered lower small beetle activity-density in the presence of *P. melanarius*. Therefore, we recreated the field experiment in laboratory arenas where we could (1) directly observe small beetle foraging activity and (2) destructively sample for small beetles to obtain absolute densities, and thus measure survivorship, at the experiment's conclusion. As in the field experiment, we manipulated the presence vs. absence of aphids (AP+ vs. AP−) and the presence vs. absence of *P. melanarius* (LG+ vs. LG−), with 10 replicates of each of the four unique treatment combinations within a fully factorial design ($N = 40$). However, here our arenas were 36 cm wide × 56 cm long × 10 cm deep plastic tubs, filled with a 5-cm layer of peat moss. All arenas were planted with two small radish plants (one set of true leaves); 40 hours later, 40 mixed-age *M. persicae* were added to one randomly selected plant in AP+ arenas. Three hours after aphid addition, two small beetles, one each of *B. tetracolum* and *B. congener*, were released into all arenas; LG+ replicates also received two *P. melanarius*. Beetles were given 24 hours to acclimate to arenas after which, an hour prior to sunset, 10 freshly laid *M. domestica* eggs were added to all arenas (at the base of the plant housing aphids in AP+, or beneath a randomly selected plant in AP−). Observations began 30 minutes later, 30 minutes before sunset, and beetles were observed every 30 minutes thereafter for 4 hours. A red light was used to allow observations without disturbing the beetles. Small beetle foraging activity (on the soil surface or below the soil surface in a burrow) was recorded at each observation. The morning after these observations, the experiment was terminated and arenas were destructively searched until all small beetles, or their remains, were recovered.
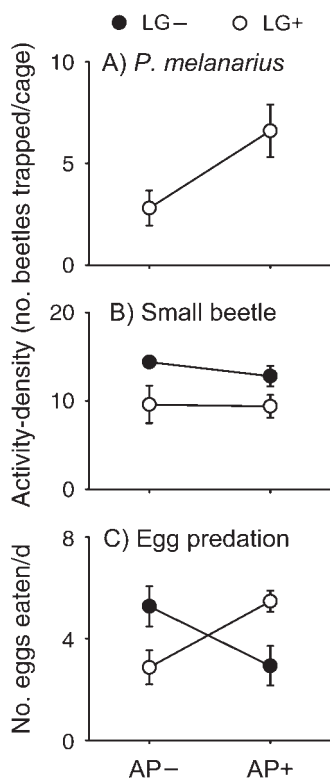
FIG. 2. Activity-densities (mean ± SE) of (A) *P. melanarius* and (B) smaller beetles, recorded at the end of the field experiment. Egg predation (C) was measured three times following arthropod manipulation but is presented as the mean (±SE) number consumed across sample dates because the treatment × time interactions were not significant (Appendix: Table A2). Treatments are: aphids removed (AP−), aphids added (AP+), *P. melanarius* removed (LG−), and *P. melanarius* added (LG+).

Aphid influence on small and large beetle foraging.— We next conducted an additional pair of laboratory experiments, where aphids were manipulated in arenas containing fly eggs and either a single *P. melanarius* or a single *B. tetracolum* (the most common small beetle species). In this experiment, we included only one beetle species within each arena so that we could conclusively attribute egg predation to a single taxon. Arenas were identical to those described previously, with aphids either present or absent (aphid manipulation as in the first laboratory experiment), and 10 replicates of each treatment; beetles and fly eggs were introduced into the arenas as described for the first laboratory experiment. In the first trial, *P. melanarius* was the predator, while, in the second, *B. tetracolum* was the predator. We observed and recorded surface activity every 30 minutes for the first 4 hours, with these observations beginning 30 minutes before sunset, and counted the number of eggs consumed after 10 hours (the following morning). Activity was recorded as either on the surface vs. belowground, and for those beetles on the surface, as either foraging within 5 cm of the plant's base or foraging elsewhere in the arena.

Statistics

All analyses were performed in SYSTAT (Systat Software, Richmond, California, USA). For the field experiment, final aphid and small beetle activity-densities, and premanipulation levels of egg predation, were analyzed using two-way ANOVA, as were data on the proportion of small beetles active on the surface in the first laboratory experiment. Post-manipulation egg predation data in the field experiment were transformed using the variance stabilizing transformation for binomial data (Sokal and Rohlf 1981) and analyzed using repeated measure MANOVA. In the second laboratory experiment, the proportion of replicates where a beetle was observed active on the soil surface and/or foraging near the plant housing fly eggs, and the proportion of replicates in which egg masses were attacked, were compared in the presence vs. absence of aphids using a chi-square test.

RESULTS

Field experiment

Levels of egg predation, and activity-density of small beetles and *P. melanarius*, did not differ among treatments prior to aphid and beetle manipulation (Appendix: Table A1).

Aphid densities at the end of the experiment were significantly higher in treatments where aphids were added (final mean per-plant aphids densities were 164.8 ± 37.1 and 132.8 ± 27.7 for AP+LG− and AP+LG+, respectively, vs. 4.5 ± 2.2 and 8.2 ± 2.9 for AP−LG− and AP−LG+, respectively (mean ± SE); for the aphid main effect, $F_{1,16} = 41.06$, $P < 0.001$); large beetle main or interactive effects were not significant (Appendix: Table A2).

Pterostichus melanarius activity-densities were significantly higher in the presence of aphids (comparison of AP−LG+ to AP+LG+; $t_{1,8} = 2.45$, $P = 0.04$; Fig. 2A). Low background *P. melanarius* activity was observed in cages where *P. melanarius* was not released (activity-densities of 1.00 ± 0.45 and 1.20 ± 0.58 for AP−LG− and AP+LG−, respectively).

Adding *P. melanarius* resulted in significantly lower small beetle activity-density ($F_{1,16} = 8.49$, $P = 0.01$; Fig. 2B); small beetle activity-density was not impacted by the main or interactive effects of aphid addition (Fig. 2B; Appendix: Table A2).

Alternative prey and the larger predator suppressed egg predation when on their own, but not when combined, leading to a statistically significant interaction between aphid and *P. melanarius* manipulation ($F_{1,16} = 11.84$, $P = 0.003$; Fig. 2C; Appendix: Table A2). Treatment effects were consistent through time (Appendix: Table A2).

Laboratory observations of behavior

Small beetle behavior under reproduced field conditions.—Small beetles were observed less frequently on the substrate surface when *P. melanarius* was also in the
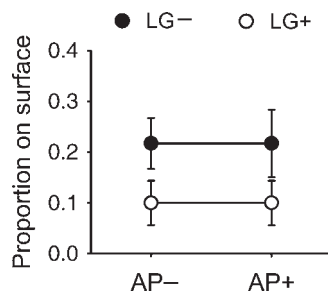
● LG−   ○ LG+

FIG. 3. Proportion (mean ± SE) of small beetles active on the substrate surface in laboratory arenas reproducing treatments from the field experiment. Treatments are as in Fig. 2.

arena ($F_{1,36} = 5.04$, $P = 0.031$, Fig. 3); all other factors had no significant effect on small beetle activity (Appendix: Table A3). At the experiment's conclusion all small beetles, and all *P. melanarius*, were recovered alive.

Aphid influence on small and large beetle foraging.— The proportion of replicates where *P. melanarius* was observed to be active on the soil surface was not affected by the presence of aphids ($\chi^2 = 2.40$, $P = 0.12$; Fig. 4A). However, in the presence of aphids *P. melanarius* were more likely to be seen foraging near plants ($\chi^2 = 10.77$, $P = 0.001$; Fig. 4A) and were more likely to attack fly egg clutches ($\chi^2 = 5.00$, $P = 0.025$; Fig. 4C). In contrast, with aphids present, individual *B. tetracolum* were no more likely to be seen foraging on the soil surface ($\chi^2 = 0.83$, $P = 0.36$; Fig. 4B) or near the plant ($\chi^2 = 0.27$, $P = 0.61$; Fig. 4B). However, *B. tetracolum* were significantly less likely to attack the egg mass when aphids were provided, compared to arenas with no aphids added ($\chi^2 = 5.50$, $P = 0.019$; Fig. 4D).

DISCUSSION

Our field experiment confirmed two indirect interactions that, singly, disrupt fly egg predation by our guild of focal predators (Fig. 1C–D). The presence of the larger carabid beetle *Pterostichus melanarius* reduced activity-densities of small beetles and thus fly egg predation, regardless of the presence of aphids (Fig. 2B). *Pterostichus melanarius* will eat the smaller beetles when housed together in small laboratory arenas without other prey (Prasad and Snyder 2004). However, because our pitfall-trap sampling in the field experiment confounded predator activity and density (Wise 1981), we could not be certain from the field experiment whether small beetles were being eaten by *P. melanarius*, vs. moving less to avoid being eaten (Lang 2003). Therefore, we reproduced the conditions of the field experiment in laboratory arenas where we could recover small beetles at the experiment's end. In this experiment, small beetle surface activity was again reduced and all small beetles were recovered alive, suggesting that reduced small beetle activity-density in the field experiment was a TMII in response to the sometimes intraguild predator.

Aphids, common prey other than fly eggs in this system, also had an indirect disruptive effect on fly egg predation, and again disruption was due to a TMII mediated by changing small beetle behavior (Fig. 1D). Small beetles reduced their feeding on fly eggs when aphids were present, either because small beetles prefer aphids to fly eggs, or because of a simple swamping of the system with prey (Prasad and Snyder 2006). However, the combined impact of aphids and large predators was unexpected. When both aphids and *P. melanarius* were present, fly egg predation returned to levels seen in the treatment lacking both erstwhile disruptive species (compare AP−LG− to AP+LG+; Fig. 2C). Because, in the field, both aphids and *P. melanarius* generally co-occur with our focal predators and prey (Prasad and Snyder 2006), it is likely that these complex, nonadditive, indirect effects impact fly egg predation in the open field. Interestingly, Wallin and Ekbom (1994) found that *P. melanarius* showed lower net displacement from patches containing aphids. This suggests that the heightened foraging behavior in response to aphids that we observed is localized, with beetles foraging more intensely within a limited area while not dispersing from that area.

Other studies have reported a relaxation in intraguild predation with rising densities of nonintraguild prey (e.g., Lucas et al. 1998). We considered, but could reject, the possibility that small beetles recognized that *P. melanarius* was distracted while feeding upon aphid prey, such that small beetles were free to resume normal
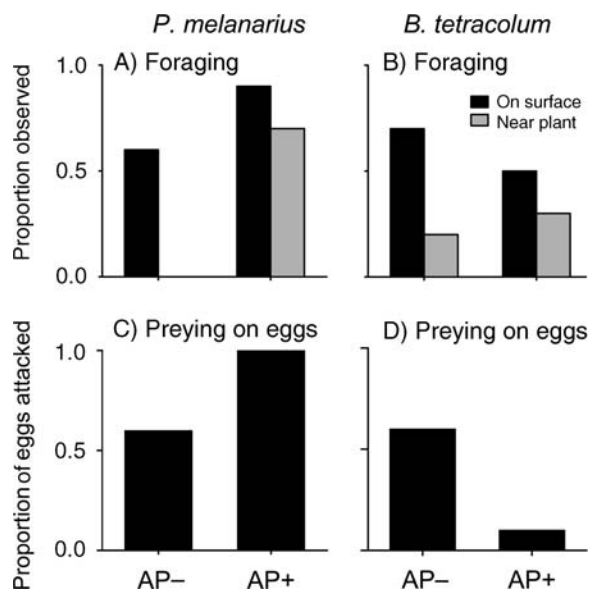

FIG. 4. Proportion of replicates where the beetle was observed foraging on the surface (black bars) and in the vicinity of the plant (gray bars) for (A) *P. melanarius* and (B) the small beetle *B. tetracolum*, and the proportion of egg masses attacked by (C) *P. melanarius* and (D) *B. tetracolum* in these arenas. Treatments are: aphids absent (AP−) and aphids present (AP+).

foraging activity. In both the field (Fig. 2B) and laboratory (Fig. 3), small beetles exhibited reduced activity whenever *P. melanarius* was present, regardless of the presence of aphids. Rather, we suggest that the restoration of fly egg predation, in the presence of both otherwise disruptive forces, occurs because of a change in *P. melanarius* behavior. Previously, based on the results of no-choice feeding assays, we reported that *P. melanarius* rarely feeds on fly eggs (Prasad and Snyder 2004), but in the earlier work we had not examined *P. melanarius* feeding behavior in the presence of multiple prey. In the field experiment, activity-densities of *P. melanarius* were dramatically higher in the presence of aphids (Fig. 2A). Apparently, as foraging activity increased in response to aphids, these beetles also engaged in opportunistic predation of fly eggs. This interpretation was supported by a laboratory microcosm experiment where we observed intensified foraging at the base of aphid-infested plants, and also increased likelihood of egg attack, by *P. melanarius* when aphids were present (Fig. 4A, C). In contrast, for the small beetle *B. tetracolum* foraging activity was unchanged (Fig. 4B), and egg predation reduced (Fig. 4D), in the presence of aphids, consistent with the behavior of small beetles in the field experiment (Fig. 2B). Because of the emergent indirect effect of aphids on egg predation by *P. melanarius*, the two TMII observed in lower diversity subcomponents of the community (e.g., Fig. 1C, D) could not be summed to predict the dominant interactions in the more diverse community (Fig. 1E). It is noteworthy that most other TMII studies include just three species (Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005), with the assumption that interactions among these simplified community components will also occur in more diverse natural communities. Our results suggest that TMII within more simplified community components may be overwhelmed by interactions that occur only in more speciose foodwebs.

It is now well documented that TMII can have dramatic effects on food web structure, with impacts of a magnitude equal to or exceeding those of DMII (Schmitz et al. 2004, Preisser et al. 2005). However, the majority of cases in the TMII literature involve a top-down TMII triggered when prey species change their behavior in the presence of predators (Lima 2002, Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005). In contrast, results from our system revealed two instances of TMII that were bottom up, with prey inducing changed predator behavior: small beetles reduced their foraging on fly eggs in the presence of aphids, while *P. melanarius* increased its foraging on fly eggs in the presence of aphids. The response of small beetles to aphids is similar to other examples in the literature of predators reducing their impact on a focal prey as predators switch to attacking a preferred prey (Eubanks and Denno 2000). However, the response of *P. melanarius* to aphids is more unusual, because their impact on the focal prey increased, rather than

decreased, with the addition of alternative prey. This heightened attack on focal prey with the addition of an alternative prey is consistent with short-term apparent competition (Holt and Kotler 1987) and related shared-predator theory (Harmon and Andow 2004), but has not been previously demonstrated empirically.

Our study included multiple prey and predator species interacting simultaneously, and thus some of the trophic complexity typical in real-world communities (Polis and Strong 1996) but often absent in studies of TMII (Werner and Peacor 2003, Schmitz et al. 2004, Preisser et al. 2005; but see Trussell et al. 2002, Siddon and Witman 2004). Density-mediated interactions occur through multiple channels simultaneously, with community structure resulting from the net effect of often counteracting interactions (Yodzis 1988, Hunter and Price 1992, Wootton 1993), and we should anticipate equally complex conveyance of TMII (DeWitt and Langerhans 2003). For example, in our community, any negative impacts of *P. melanarius* on egg predation due to its suppression of small beetle foraging, or of aphids in also reducing small beetle foraging, were counteracted by increased overall *P. melanarius* foraging activity in the presence of aphids. Thus, we recommend that TMII researchers consider more realistic levels of species diversity in their studies, including both multiple predator and prey species.

LITERATURE CITED

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, New York, New York, USA.

DeWitt, T. J., and R. B. Langerhans. 2003. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. Journal of Sea Research **49**:143–155.

Eubanks, M. D., and R. F. Denno. 2000. Host plants mediate omnivore–herbivore interactions and influence prey suppression. Ecology **81**:936–947.

Finch, S. 1996. Effect of beetle size on predation of cabbage root fly eggs by ground beetles. Entomologia Experimentalis et Applicata **81**:199–206.

Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature **429**:407–410.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control and competition. American Naturalist **94**:421–425.

Harmon, J. P., and D. A. Andow. 2004. Indirect effects between shared prey: predictions for biological control. Biocontrol **49**:605–626.

Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. American Naturalist **130**:412–430.

Huang, C., and A. Sih. 1990. Experimental studies on behaviorally mediated indirect interactions through a shared predator. Ecology **71**:1515–1522.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**:724–732.

Lang, A. 2003. Intraguild interference and biocontrol effects of generalist predators in winter wheat. Oecologia **134**:144–153.

Lima, S. L. 2002. Putting predators back into behavioral predator–prey interactions. Trends in Ecology and Evolution **17**:70–75.

Losey, J. E., and R. F. Denno. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology **79**:2143–2152.

Lucas, E., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. Ecology **79**:1084–1092.

Paine, R. T. 1966. Food-web complexity and species diversity. American Naturalist **100**:65–75.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist **138**:123–155.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Prasad, R. P., and W. E. Snyder. 2004. Predator interference limits fly egg biological control by a guild of ground-active beetles. Biological Control **31**:428–437.

Prasad, R. P., and W. E. Snyder. 2006. Polyphagy complicates conservation biological control that targets generalist predators. Journal of Applied Ecology, *in press*.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology **86**:501–509.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: the effect of predation risk on food web interactions. Ecology **78**:1388–1399.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters **7**:153–163.

Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. Ecology **85**:2938–2945.

Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution **13**:350–355.

Snyder, W. E., and A. R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology **82**:705–716.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman and Sons, San Francisco, California, USA.

Soluk, D. A. 1993. Multiple predators effects: predicting combined functional response of stream fish and invertebrate predators. Ecology **74**:219–225.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence for trait-mediated indirect interactions in a rocky intertidal food web. Ecology Letters **5**:241–245.

Wallin, H., and B. Ekbom. 1994. Influence of hunger level and prey densities on movement patterns in 3 species of *Pterostichus* beetles (Coleoptera, Carabidae). Environmental Entomology **23**:1171–1181.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083–1100.

Wise, D. H. 1981. Seasonal and yearly patterns in the densities of darkling beetles in a montane community. Environmental Entomology **10**:350–358.

Wissinger, S. A., and J. McGrady. 1993. Intraguild predation and competition among larval dragonflies: direct and indirect effects on shared prey. Ecology **74**:207–218.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist **141**:71–89.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508–515.

APPENDIX

Statistical tables (means and results of analysis) from the field experiments (*Ecological Archives* E087-065-A1).