Antipredator Behavior of Spotted Cucumber Beetles (Coleoptera: Chrysomelidae) in Response to Predators That Pose Varying Risks

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ABSTRACT Animals can reduce the risk of being preyed upon by foraging less in the presence of predators. Animals often face a diverse group of predators that vary in their effectiveness at preying upon the animal, and thus pose different potential risks. In laboratory microcosms, we investigated the ability of the spotted cucumber beetle, *Diabrotica undecimpunctata howardi* (Barber), a polyphagous herbivore, to accurately recognize dangerous predators versus taxonomically related predators that posed no true risk, and to adjust the intensity of their antipredator behavior accordingly. Spotted cucumber beetles reduced their feeding, and reduced damage to host plants, in the presence of the large wolf spider *Hogna helluo* (Hentz), which previous experiments identified as the most dangerous predator we examined. Beetles did not significantly alter their feeding rate in the presence of 3 other less-dangerous predators. Laboratory mesocosm studies verified that, indeed, *Hogna* was the most effective at capturing *D. u. howardi* in a structurally complex environment more similar to that in the field. Spotted cucumber beetles responded to *Hogna*, whereas several similar-sized but less-dangerous predators were ignored, suggesting that *D. u. howardi* may have been able to recognize *Hogna* specifically. Our results suggest that reduced feeding by herbivores as a strategy to reduce predation risk can allow predators to improve biological control even when actual predation does not occur.

KEY WORDS southern corn rootworm, generalist predator, predator guild, Carabidae, Lycosidae, trophic cascade

MANY ANIMALS HAVE the ability to recognize the presence of predators and to adjust their behavior to lessen their risk of being preyed upon (Lima and Dill 1990). Early studies often considered the response of would-be prey to single predator species, but behavioral ecologists have begun to recognize that animals often will face a diverse group of natural enemies (Sih et al. 1998). The presence of multiple predators can limit the range of choices open to an animal seeking to reduce its risk of predation–shifting from 1 habitat to avoid a predator may increase risk of predation by a different predator. For example, Losey and Denno (1998) found that pea aphids, *Acyrthosiphon pisum* (Harris), escape ladybug predators by dropping from plants to the ground. However, once on the ground the aphids are subject to predation by carabid beetles.

Despite the recent advances in including increasingly more complex predator communities in empirical studies, most studies have included no more than 2 predator species (Sih et al. 1998). This level of predator diversity still probably greatly underestimates the range of predators an animal will encounter. For example, in an analysis of a desert food web, Polis (1991) found that the average species has been recorded as the prey of ≈10 predator species. The scorpion *Paruroctonus mesaensis* (Stahnke), a common arthropod predator in the same desert community, has been recorded to feed on 125 prey species. It appears that most animals are at risk of falling prey to a diverse group of predators (Strong 1992, Polis and Strong 1996). Further complicating matters, animals encounter both specialist and generalist predators (Polis 1991, Wise 1993), prey at one stage may become predators later in life (Werner and Gilliam 1984, Mittlebach and Osenberg 1993), and the predator community in an animal's environment can change through time (Sih 1997). It is unclear how animals balance the diverse and fluctuating risks of complex predator communities. There is growing evidence that antipredator behaviors can have effects that cascade through multiple trophic levels (Moran and Hurd 1994, Moran et al. 1996, Schmitz et al. 1997, Chase 1998). Increasing our understanding of behavioral responses to diverse predator guilds may be necessary to increase our understanding of complex food webs.

Spotted cucumber beetles, *Diabrotica undecimpunctata howardi* (Barber), are polyphagous herbivores, feeding on a variety of agricultural and old-field plants (Krysan 1986). The larvae feed on roots and develop in the soil, whereas the adults feed on plant foliage and flowers (Godfrey et al. 1998). This life cycle exposes *D. u. howardi* to a variety of predators as they complete their life cycle. Predatory mites, predatory beetles, centipedes, and ants attack the subterranean larvae (Brust and House 1990, Brust 1991).

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Above-ground predators that attack the adults include several vertebrates (Gould and Massey 1984, Whitaker 1995), but arthropods, including spiders (Young 1989, Riechert and Bishop 1990, Johnson 1996, Snyder and Wise 1999) and carabid beetles (Snyder and Wise 1999), appear to pose the major threat.

We have been studying the interactions between generalist predators and *D. u. howardi* and other pests of cucurbits in plantings of cucumber, *Cucumis sativus* L., and squash, *Cucumis pepo* L. Our gardens contain a diverse community of generalist predators. Predatory hemipterans, primarily *Nabis* spp., *Orius* spp., *Geocoris* spp., and a taxonomically diverse group of spiders, dominate the foliage predator community (Snyder 1999, Snyder and Wise 1999). The ground layer is dominated by a diverse guild of active-hunting predators, primarily ground beetles (Coleoptera: Carabidae) and wolf spiders (Araneae: Lycosidae) (Snyder 1999, Snyder and Wise 1999). Through field manipulations of the ground predator guild we have demonstrated that wolf spiders can significantly reduce cucumber beetle densities (Snyder and Wise 1999); these reductions can be sufficient to significantly increase plant productivity (Snyder 1999, Snyder and Wise 1999). Although the predator community at our site is diverse, it appears that only a relatively small proportion of the predators can capture *D. u. howardi* adults. For example, in laboratory feeding studies we have found that the large wolf spider *Hogna helluo* (Hentz) captures *D. u. howardi,* whereas the smaller wolf spider *Pardosa milvina* (Hentz) is unable to capture *D. u. howardi.* Thus, the guild of predators at our site contains species that are dangerous to *D. u. howardi* and other taxonomically related predators that are ineffective at capturing the herbivores.

We conducted a series of experiments in the laboratory designed to address two questions: (1) Can *D. u. howardi* differentiate between dangerous and harmless predators, and adjust the intensity of their antipredator response accordingly; and (2) Do the antipredator responses of the beetles result in reduced plant damage? We exposed *D. u. howardi* to predators that they commonly encounter, but that vary in their ability to capture *D. u. howardi,* while preventing predation from occurring. We recorded beetle feeding behavior, and the cascading effects of any changes in feeding behavior on plant damage. We then conducted an additional experiment to verify that our initial assessment of predator risk, which was based on feeding trials in structurally simple microcosms, was consistent with predator attack rates in more realistic laboratory arenas.

Materials and Methods

All arthropods used in these experiments were collected from the Spindletop Research Farm, University of Kentucky, Lexington, KY. Spotted cucumber beetles were hand collected from plantings of summer squash, *Cucumis pepo* (L.) 'Yellow Crookneck'; details of these plantings have been reported elsewhere (Snyder 1999, Snyder and Wise 1999). Beetles were returned to the laboratory and individually housed in petri dishes (10 by 2 cm) that also contained a moistened dental wick to provide water and a 1-cm^3 section of squash fruit as food. Beetles were used in experiments within 24 h of being collected.

Predators were collected from old-field vegetation surrounding the squash gardens using pitfall traps (Snyder and Wise 1999, Snyder 1999). Pitfall traps were emptied every 24 h to minimize stress to the predators. Predators were maintained in the laboratory in 30 by 15 by 10-cm plastic boxes containing potting soil to a depth of 1 cm. The sides of each container were misted with water once every 48 h to provide drinking water and maintain humidity. Carabid beetles were fed dog food; lycosid spiders were fed live domestic house crickets, *Acheta domestica* (L.). Predators were used in the behavioral studies within 1 mo of their collection from the field.

Squash plants used in the laboratory experiments were 14-d-old seedlings of summer squash plants, of the same variety planted in the field. At this stage, plants had 2 cotyledons and 2 true leaves. Plants were grown in a greenhouse with a photoperiod of 12:12 (L:D) h, and temperatures that fluctuated between 22 and 27°C. For each experiment we grew 100, individually planted, squash plants. From these we selected plants most similar in size to be used in the experiments; plants were then randomly assigned to treatment.

Assignment of Predator Risk. Initial determination of predator risk was made based on a series of feeding trials reported in Snyder and Wise (1999). Briefly, the feeding trials were conducted in small plastic box microcosms (30 by 15 by 10 cm) in the laboratory. The microcosms contained a 1-cm layer of moist potting soil. A single individual of each of the 4 most common species of ground dwelling predators in local agricultural fields was paired with a *D. u. howardi* adult for 3 d; at the end of this exposure period, *D. u. howardi* mortality was recorded. The wolf spider *Hogna helluo,* which has an adult body length >1 cm and is the largest wolf spider at our site, was a highly effective predator of *D. u. howardi. H. helluo* consumed *D. u. howardi* 100% of the time. The smaller wolf spider *Pardosa milvina* (adult length of ≈0.5 cm) was never recorded feeding on *D. u. howardi.* The carabid *Cyclotrachelus sodalis* (Chaudoir) was as effective a predator as *Hogna,* consuming *D. u. howardi* in 100% of the trials. However, the carabid *H. pennsylvanicus* (De Geer) was rarely recorded to feed on *D. u. howardi,* although both carabid species are very similar in size (both have an adult length of ≈1.5 cm). Based on the results from these feeding trials in structurally simple microcosms, the risk posed by the predators, from most to least dangerous, was *H. helluo* = *C. sodalis* > *H. pennsylvanicus* ≥ *P. milvina.*

Microcosms. Our microcosms were modified "mosquito breeders" (Bioquip, Gardena, CA). The mosquito breeders consist of 2 cylinders (10 cm diameter, 10 cm high), each open at one end. The 2 cylinders screw together with a plastic ring, forming a single

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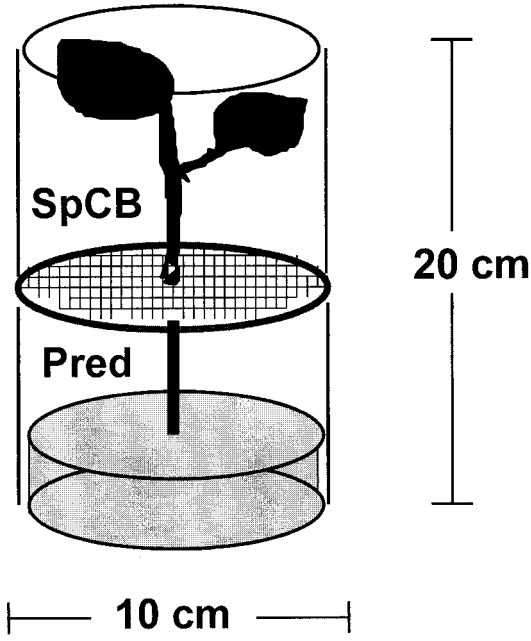

Fig. 1. Design of microcosms used in experiments 1 and 2. Predators were housed in the lower, and herbivores in the upper chambers, separated by a screen barrier. Pred, chamber housing predator; SpCB, chamber housing spotted cucumber beetle.

continuous tube. By placing a circular piece of aluminum screen around the aperture of the plastic ring that joined the 2 halves of the microcosm, we divided the tubes into 2 chambers (Fig. 1). Squash plants were planted in the bottom chamber, in 3 cm of potting soil. The circle of screen was wrapped around the stem of the plant, so that several centimeters of the stem were in the lower chamber but several centimeters of the stem and the foliage were contained in the upper chamber. Predators were housed in the lower chamber, when predators were included in the treatment, and spotted cucumber beetles were housed in the upper chamber (Fig. 1). Within these microcosms, *D. u. howardi* were exposed to olfactory, visual, and vibrational cues indicating the predators' presence, but predators could not attack the herbivores. Plants in no-herbivory control treatments were housed in microcosms of identical construction, but arthropods were not added.

Experiment 1: Can *D. u. howardi* Accurately Assess Risk? In tube microcosms, we subjected single *D. u. howardi* adults to one of the following predator treatments, arranged from most to least actual predation risk: *H. helluo*, *C. sodalis*, *H. pennsylvanicus*, *P. milvina*, adult domestic cricket, and no predator present. Thus, our predator treatments included a range of actual predation risk, from *H. helluo*, which were effective predators of *D. u. howardi* in the simple microcosms, to *P. milvina*, which we found to be entirely ineffective at capturing *D. u. howardi.* A set of replicates containing domestic crickets was included to control for the effect of an active, but nonpredatory, arthropod on *D. u. howardi* feeding behavior.

We established 5–6 replicates of each treatment. First, predators were added to the bottom chambers of the microcosms; herbivores were added 24 h later. Microcosms were housed in an environmental chamber. We made observations of arthropods in each microcosm 4 times a day (at 0800, 1200, 1600, and 2400 hours), for 2.5 d. At each observation, we recorded whether each beetle was feeding. A beetle was scored as feeding if its mouthparts were on the plant, and the animal was chewing.

At the end of the 2.5-d observation period, we harvested the above-ground foliage of each plant. First, for each plant we recorded whether the following structures showed feeding damage: stem below cotyledons, stem above cotyledons, each of 2 cotyledons, and each of 2 true leaves. Thus, each plant was assigned a damage score from 0 (no areas damaged) to 6 (all areas damaged). A region was scored as damaged if any feeding damage on the structure was observed. Plant damage served both as a record of feeding over the entire exposure period and indicated whether changes in feeding behavior might have a cascading impact on plant health.

Experiment 2: Cascading Effects of Antipredator Behavior. We followed the same general methodology as experiment 1, with several modifications to allow us to look for cascading effects of *D. u. howardi* antipredator behavior on plant biomass. In this 2nd experiment, we placed 3 *D. u. howardi* in each microcosm, made observations for 6 d, and placed microcosms in a greenhouse to encourage more rapid plant growth. Spotted cucumber beetle densities in this experiment, although higher than in experiment 1, were still within the range of densities observed in the field (Snyder 1999). Temperatures in the greenhouse ranged from 22 to 27°C, with a photoperiod of 12:12 (L:D) h. Squash plants were heavily watered at the start of the experiment, then were not watered again. Humidity on microcosm sides provided ample drinking water for the *D. u. howardi* and predators.

To allow greater replication within predator treatments, we limited the 2nd experiment to 1 true risk per apparent risk pair: *H. helluo* represented a true risk of predation, whereas the smaller wolf spider *P. milvina* is unable to capture *D. u. howardi* adults. Another group of microcosms did not contain a predator. A 4th group of microcosms, handled identically to the other treatments but containing neither *D. u. howardi* nor predators, was included as a control to allow us to measure plant growth in the absence of herbivores. Herbivore feeding behavior was observed and recorded twice each day, at 0800 and 1600 hours, for 6 d, after which we harvested the above-ground foliage of each plant. We found that most structures of most plants had at least some feeding damage; thus, we did not grade damage as in experiment 1. Instead, we weighed above-ground foliage as a measure of plant productivity.

Experiment 3: Actual Predation Risk. The feeding experiments in Snyder (1999) and Snyder and Wise

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(1999) were conducted in relatively simple microcosms. Snyder (1999) found that feeding trials in those simple microcosms overestimated the rate at which carabid beetles and wolf spiders were able to capture 2 other cucurbit herbivores, the striped cucumber beetle *Acalymma vittatum* (F.) and the squash bug *Anasa tristis* (DeGeer). However, feeding trials in larger, more complex mesocosms yielded predation rates that correspond closely with the results of manipulative field experiments (Snyder 1999). To ensure that we were accurately assigning predation risk, we investigated predation on *D. u. howardi* by the 2 predators that were most dangerous to *D. u. howardi* in the simple microcosms, *H. helluo* and *C. sodalis*, in the more complex microcosms used by Snyder (1999).

Mesocosms consisted of 37.8-liter (10-gallon) aquaria, covered with a screen lid, and housed in a greenhouse with a photoperiod of 12:12 (L:D) h, with temperatures fluctuating between 22 and 27°C. The bottom of each mesocosm was covered with ≈5 cm of moist potting soil. We planted a single, 3-wk-old squash plant in the center of each mesocosm, and then covered the base of the plant with a layer of straw mulch. The squash plants used were 15–20 cm tall, with 3 true leaves, and cotyledons still attached.

We added 5 *D. u. howardi* to each of 24 mesocosms. Herbivores were added before predators to give the *D. u. howardi* time to acclimate to their surroundings before being subjected to predation. After the 24-h acclimation period, we added predators to the microcosms according to the following treatments: neither predator, adult female *H. helluo* added, 1 adult female *C. sodalis* added, both predators added. *H. helluo* and *C. sodalis* do not prey upon one another (Snyder and Wise 1999), although they may exhibit nonfatal antagonistic interactions (Snyder 1999). For these experiments, the predators were starved for 2 d before being added to the microcosms (for a total of 3 d) before spotted cucumber beetle prey were added. The short starvation period was used to ensure that predators had similar hunger levels, although this procedure could have increased their attack rate compared with average field values.

Seven days after the *D. u. howardi* were added, we carefully hand-searched each mesocosm and collected all *D. u. howardi* that remained, and also verified that the predators were alive (no predators died during the course of the experiment). Then, above-ground foliage of each squash plant was harvested, returned to the laboratory, and weighed. After the plant harvest, each mesocosm was searched again to verify that we did not miss any arthropods.

Statistics. For the experiments on antipredator behavior (experiments 1 and 2), we analyzed the summed number of times each individual was observed feeding during the entire trial period. In experiment 1 we assessed plant damage by analyzing the number of regions damaged for each plant. In experiment 2 we analyzed plant weights. Data were analyzed using one-way analysis of variance (ANOVA), followed by a posthoc test (the Tukey honest significant difference) when significant treatment effects were detected, to identify like groups. A one-tailed criterion was used to determine statistical significance of the predator treatment on feeding frequency and plant damage because we predicted that the presence of predators would lead to reduced, not increased, feeding by *D. u. howardi* (Rice and Gaines 1994). Data were log-transformed to meet the assumptions of ANOVA when necessary.

For the actual risk experiment (experiment 3), we analyzed *D. u. howardi* survivorship and plant weights by two-way ANOVA. Because the system was closed (i.e., immigration was not allowed, and no in situ reproduction occurred), the multiplicative model was most appropriate to test for interaction between the 2 predators (Sih et al. 1998). Thus, we log-transformed all data before performing statistical analyses. Plant weights from the single predator treatments were compared with those in the no-herbivore controls using *t*-tests.

Results

Experiment 1. *D. u. howardi* changed their rate of feeding with predator manipulation ($F = 2.55$; df = 1, 5; $P = 0.022$; Fig. 2A). The significant difference was a result of reduced feeding when the beetles were exposed to the presence of *H. helluo*—feeding in that treatment was significantly less frequent than in the no-predator treatment ($P = 0.022$). Feeding in the *H. helluo* treatment was observed marginally less frequently than in the *P. milvina* and *H. pennsylvanicus* treatments ($P = 0.064$ and $P = 0.055$, respectively). Observations of feeding in the *H. helluo* treatment did not differ from that in the cricket and *C. sodalis* treatments; no other treatments were significantly different from one another ($P > 0.10$ for all comparisons).

The reduction in *D. u. howardi* feeding in response to *H. helluo* was sufficient to significantly reduce plant injury ($F = 3.64$, df = 1, 5; $P = 0.009$; Fig. 2B). Damage in the *H. helluo* treatment was significantly less than that in all other treatments except the cricket treatment ($P < 0.05$).

Experiment 2. *D. u. howardi* feeding rate was significantly affected by predator treatment ($F = 3.52$; df = 1, 2; $P = 0.041$; Fig. 2C). *D. u. howardi* exposed to *H. helluo* fed significantly less than those in the no predator ($P = 0.021$) and *P. milvina* treatments ($P = 0.040$). Feeding in the *P. milvina* treatment was similar to when no predator was present ($P = 0.777$).

Reduced *D. u. howardi* feeding in response to *H. helluo* had a nearly statistically significant ($F = 2.12$; df = 1, 3; $P = 0.055$; Fig. 2D) effect on plant growth. Plants were largest in the *H. helluo* and no herbivore treatments, and smallest in the no predator and *P. milvina* treatments.

Experiment 3. *H. helluo* significantly reduced *D. u. howardi* densities (*H. helluo* main effect: $F = 130.92$, df = 1, 20; $P < 0.001$; Fig. 3A), but *C. sodalis* was ineffective at preying upon *D. u. howardi* (*C. sodalis* main effect: $F = 0.74$, df = 1, 20; $P = 0.40$). The nearly

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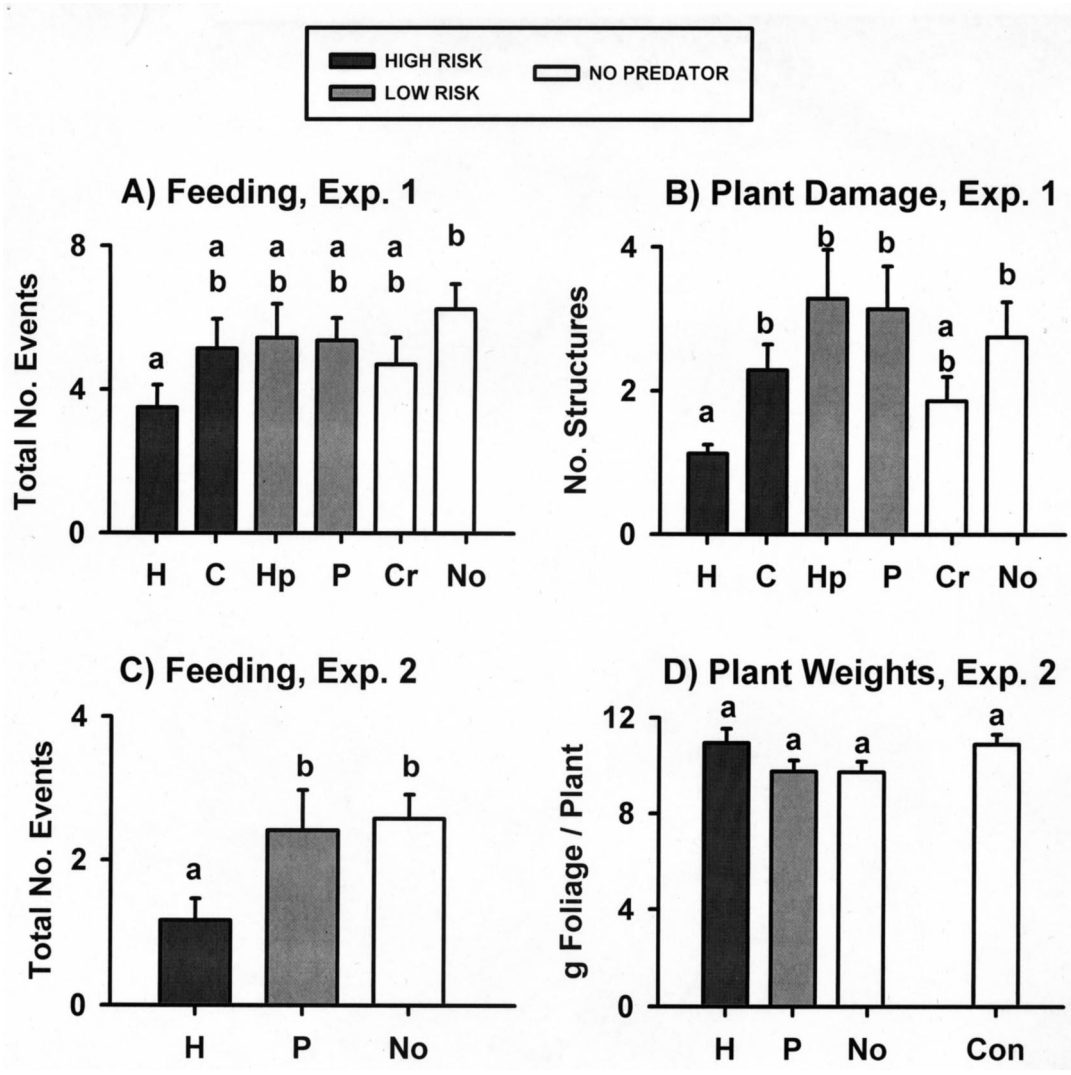

Fig. 2. Effects of predator treatment on (A) total number of feeding observations per beetle and (B) resulting plant damage in the 1st experiment; and in experiment 2, effects on (C) total number of feeding observations per beetle and (D) plant weights (means ± 1 SE). In both experiments the herbivores were exposed to tactile, olfactory, and visual cues indicating predator presence or absence, but predation was prevented. Predator treatments: H, *H. helluo;* C, *C. sodalis;* Hp, *H. pennsylvanicus;* P, *P. milvina;* Cr, domestic house cricket; No, no predator present; Con, no herbivore or predator present. Columns with the same lower-case letter do not significantly differ ($P > 0.05$). Spotted cucumber beetles reduced their feeding rate, and thus did less damage to plants, when they were housed with the most dangerous predator, the wolf spider *H. helluo.*

significant interaction term ($F = 3.43$; df = 1, 20; $P = 0.078$) is difficult to interpret—mortality in the treatment where 1 adult *H. helluo* was added was so great that carabid predation probably could not have increased mortality when both predators were added.

The reduction of *D. u. howardi* by *H. helluo* caused a cascading increase in squash growth ($F = 10.72$; df = 1, 20; $P = 0.003$; Fig. 3B); *C. sodalis* did not alter *D. u. howardi* densities and had no impact on squash plant weights ($F = 0.08$; df = 1, 20; $P = 0.777$), and the interaction term was nonsignificant ($F < 0.01$; df = 1, 20; $P = 0.986$).

Discussion

Diabrotica undecimpunctata howardi consistently reduced their feeding in the presence of *H. helluo,* but reacted only weakly or not at all to the other predators we examined. The *D. u. howardi* response to *H. helluo* followed our predictions—in earlier studies, these wolf spiders were always able to capture *D. u. howardi.* However, we also expected *D. u. howardi* to react to the carabid *C. sodalis,* which was as effective as *H. helluo* in capturing *D. u. howardi* in simple laboratory arenas. Our mesocosm experiments offer an explana-

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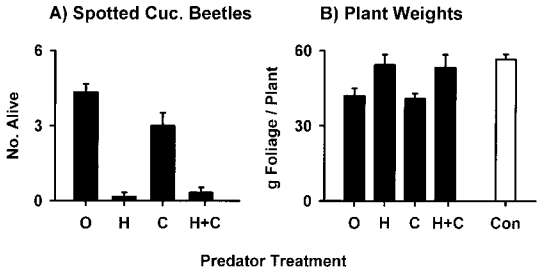

Fig. 3. Number of *D. u. howardi* alive, and plant weights, from microcosms containing the most dangerous predators (mean ± 1 SE). In this experiment, the herbivore and predator were not separated from one another, and thus predation could occur. Predator treatments: O, neither predator; H, *Hogna helluo;* C, *C. sodalis;* H+C, *H. helluo* and *C. sodalis;* Con, no herbivore or predator present.

tion for this apparent discrepancy. In more realistic arenas, *H. helluo* remained an effective predator of *D. u. howardi*, but *C. sodalis* was largely ineffective. Thus, it appears that *D. u. howardi* effectively judged the predation risk that they would face under field conditions. Furthermore, because recognition of dangerous predators by *D. u. howardi* resulted in reduced plant damage, the shift in their behavior had a cascading impact on plants.

Differentiating Between High and Low Risk Predators. Antipredator behaviors, such as remaining still and thus cryptic, or remaining in a refuge, carry the cost of reduced foraging opportunities (Lima and Dill 1990). Animals can reduce the cost of avoiding predators by using these behaviors only when predation risks exceed potential gains from foraging (Bouskila and Blumstein 1992, McNamara and Houston 1994, Rothley et al. 1997). Modeling efforts have produced the prediction that animals can increase their fitness by accurately assessing predation risk, and thus these abilities should be selected for (Bouskila and Blumstein 1992). Consistent with these predictions, we found that *D. u. howardi* were able to differentiate between truly dangerous predators, and those that were taxonomically related but were not truly dangerous. *D. u. howardi* face a wide variety of arthropod and vertebrate predators in both agricultural fields and less-disturbed habitats (Gould and Massey 1984, Young 1989, Riechert and Bishop 1990, Brust and House 1990, Brust 1991, Whitaker 1995, Johnson 1996, Snyder and Wise 1999). The ability to recognize and respond to only the most dangerous predators may allow *D. u. howardi* to minimize the costs associated with predator avoidance.

Insects have been reported to detect predators using chemical (Chivers et al. 1996b, Schaffer and Robinson 1996, Wisenden et al. 1997) and vibrational (Brodsky and Barlow 1986) cues. In our arenas, all of these cues were available to *D. u. howardi,* so we can only speculate on the mechanism the herbivores used to detect and differentiate between predators. It seems unlikely that the *D. u. howardi* used size as the sole cue. The predators *H. helluo, C. sodalis,* and *H. pennsylvanicus* all have similar adult body sizes (length of ≈1.5 cm), but *D. u. howardi* only reacted to *H. helluo.* Shape and body markings by themselves also appeared to be unimportant, because *D. u. howardi* reacted to *H. helluo* but ignored *P. milvina,* although both predators are very similar in appearance. However, the beetles may use size and shape together to recognize a given predator.

Diabrotica undecimpunctata howardi adults are not unique in their ability to accurately differentiate between dangerous and nonthreatening predators. Gerlai (1993) found that paradise fish, *Macropodus opercularis* (L.), reduced their activity in response to predatory fish, but not when paired with similar-looking fish that were not dangerous. Similarly, Chivers et al. (1996a) found that larvae of the salamander *Ambystoma macrodactylum columbianum* (Baird), which have both cannibalistic and noncannibalistic morphs, only exhibit antipredator behaviors when housed with cannibalistic conspecifics. Pairing larvae of the damselfly *Ischnura posita* (Hagen) with both threatening and nonthreatening species, Schaffer and Robinson (1996) reported that the larvae responded to each dangerous predator with the specific escape behavior that was most effective against that predator. However, animals do not always respond adaptively—Bazin and Sealy (1993) found that kingbirds, *Tyrannus tyrannus* (L.), responded equally strongly to the approach of birds that were nest parasites or predators as to nonthreatening bird species. In the studies cited above, the authors suggested that visual and chemical cues, usually in combination, were important for allowing the focal species to recognize and differentiate between predators.

Implications for Biological Control. Ecologists have begun to appreciate that reduced feeding by herbivores can lead to cascading effects on plant productivity. Several studies found that reduced feeding by grasshoppers in response to the presence of predators can generate strong trophic cascades, even when predation is experimentally prevented (Schmitz et al. 1997). In our study, *D. u. howardi* recognized *H. helluo* as a dangerous predator, reduced their rate of feeding, and thus reduced the amount of damage to plants. The intensity of the behavior-mediated trophic cascade in experiment 2 (Fig. 2D) was similar in intensity to that recorded in Exp. 3 (Fig. 3B), in which spiders were allowed to feed upon the cucumber beetles. *D. u. howardi* are pests on many agricultural crops, including corn, *Zea mays* L.; cucurbits, *Cucurbita* spp.; soybeans, *Glycine max* L.; and cotton, *Gossypium hirsutum* L. Reductions in *D. u. howardi* feeding in the presence of predators, if they are as strong in the field as in the laboratory, may thus represent an under-appreciated benefit of generalist predators to the biological control of insect pests. Examinations of predator impacts in agricultural systems often measure changes in pest densities (Luck et al. 1988). Although behavioral responses to predators may be nonlethal to the pest, the effects of antipredator behaviors in reducing pest damage and increasing yields can be easily overlooked and may deserve more attention.

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