



Biotransfer of Selenium: Effects on an Insect Predator, *Podisus maculiventris*

DANEL B. VICKERMAN* AND JOHN T. TRUMBLE

Department of Entomology, University of California, Riverside CA 92521, USA

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Abstract. The effects of selenium (Se) accumulation in phytophagous insects on predators in the next trophic level were investigated. The generalist predator *Podisus maculiventris* Say (Hemiptera: Pentatomidae) was fed an herbivore *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae) larvae from control diet and diets at two Se levels (0, 109, and 135 $\mu\text{g/g}$ sodium selenate dry weight added). Predators reared on larvae grown on diets with sodium selenate took longer to complete each developmental stage and had significantly higher mortality rates. Predators achieving the adult stage on Se-containing hosts weighed 20% less than those feeding on control larvae. Reduced adult weight of insects has been associated with reduced fitness (longevity, egg production, etc.), which would have long-term negative impacts on population dynamics. These developmental and mortality effects resulted from biotransfer of Se, not biomagnification since the trophic transfer factor was less than 1.0 (~ 0.85). Host larvae in Se-treatments contained significantly more total Se (9.76 and 13.0 $\mu\text{g/g}$ Se dry weight host larvae) than their predators (8.34 and 11 $\mu\text{g/g}$ Se dry weight predatory bugs, respectively). Host larvae and predators in the control groups did not differ in their Se content. These data demonstrate that Se in the food chain may have detrimental population level effects on insects even in the absence of biomagnification, given the host contains significantly elevated concentrations of selenium.

Keywords: biomagnification; biotransfer; insects; phytoremediation; selenium

Introduction

Selenium (Se) contamination of the environment has become a major concern in the US in the last two decades. Fish have been poisoned by Se-contaminated coal fly ash, which occurs as effluent from the combustion of coal in the generation of electricity (Besser et al., 1996; Lemly, 1996). Drainage water resulting from agricultural irrigation of seleniferous soils has also caused accumulation of Se in reservoirs in the western US, killing fish and waterfowl (Presser and

Ohlendorf, 1987; Presser et al., 1994; Lemly, 1997). Herbivorous insects feeding on algae are known to bioaccumulate Se (Malchow et al., 1995; Thomas et al., 1999) and are important primary consumers in the aquatic food chain of reservoirs and ponds where bioaccumulation has occurred (Schuler et al., 1990).

Considerably less information is available for terrestrial systems even though soil contamination by Se has become a significant problem in eight western states, including 1.5 million acres of farmland (Brown et al., 1999). The potential hazards of elevated Se levels to terrestrial arthropods are not well understood. Terrestrial arthropods may be important

*To whom correspondence should be addressed. Tel.: (909) 787-2627; Fax: (909) 787-3086; E-mail: danel.vickerman@ucr.edu

in Se biomagnification or biotransfer because of their roles as herbivores that are fed upon by higher trophic level organisms. For example, at certain times of the year terrestrial invertebrates make up more than half of the diet of some predatory birds at Se-affected sites such as Kesterson Reservoir in Merced County, CA, USA (Santolo and Yamamoto, 1997), where several terrestrial bird species were found to have elevated blood-Se levels (Santolo and Yamamoto, 1999). However, unlike the insectivorous birds and fish, very little information is available on the importance of Se to predatory terrestrial insects. Such insects play a critical role in suppressing and managing populations of herbivorous insects (DeBach, 1973), and also serve as food for higher trophic levels. Thus, any effects of Se-contaminated prey on the population dynamics of predatory insects, and the potential accumulation of Se in these predators, would be likely to impact both the ecology of affected ecosystems and biologically-mediated movement of Se in contaminated areas.

Several studies have demonstrated the toxicity of Se to terrestrial insect herbivores fed Se-amended diets (Hogan and Cole, 1988; Hogan and Razniak, 1991; Trumble et al., 1998; Martin-Romero et al., 2001), and Se-irrigated plants (Bañuelos et al., 1999; Vickerman et al., 2002a,b). Selenium has been shown to accumulate preferentially in the malpighian tubules and the midgut of insects, but has been shown to increase in the rest of the body after a saturation point is reached (Simmons et al., 1988; Hogan and Razniak, 1991; Lalitha et al., 1994). Most of the previous studies on terrestrial insects have used Se as an aid to study specific insect physiological systems (Simmons et al., 1988; 1989a,b; Hogan and Razniak, 1991; Lalitha et al., 1994). Relatively few reports are available on the potential ecological consequences of Se accumulation in host plants and herbivorous insects (Bañuelos et al., 1999; Vickerman et al., 2002a,b). There is even less information on the effects of Se on the third trophic level (insect predators and parasitoids) which prey on other insects (Wu et al., 1996).

This study therefore was conducted to determine potential effects on the life cycle of a predatory insect following consumption of Se-containing prey. Our objectives were to use a model system to describe development and survival of a predatory insect fed prey larvae exposed to different concentrations of Se, and to document possible biotransfer of Se from the phytophagous prey to the insect predator.

Methods

Survival and development

Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae), the beet armyworm, was chosen as a host because baseline studies on Se toxicity for this insect have been established both on artificial diets and on plants (Trumble et al., 1998; Vickerman et al., 2002b). Additionally, *S. exigua* is a cosmopolitan generalist herbivore and a crop pest of economic importance in areas of the USA where selenium is a problem. The host range of *S. exigua* includes native and introduced plants in the families Lilaceae, Fabaceae, Solanaceae, Malvaceae, Chenopodiaceae, Apiaceae, Asteraceae, and Amaranthaceae that can be found in both cultivated and uncultivated areas (Metcalf and Flint, 1962; Peterson, 1962; Pearson et al., 1989).

Beet armyworm eggs were obtained from our laboratory colony that was field collected in Ventura Co., CA, USA and maintained on artificial diet from the Bioserv Company (Frenchtown, NJ, USA). Larvae were fed three treatment levels of Se incorporated into diet: (1) a control, with no Se added; (2) level one treatment with 25 µg/g wet weight sodium selenate and; (3) level two treatment with 31 µg/g wet weight sodium selenate (based on lethal concentration LG₇₀ LC₉₀ values from Trumble et al. (1998); wet to dry conversion, 4.350). The sodium selenate was dissolved in deionized water and mixed into the artificial diet before the agar had set up. These larvae were fed to the predatory bugs. The selected concentrations are within the wide range of Se known to occur in plants (<1–4,000 µg/g dry weight; Lauchli, 1993), and in a form known to occur within the plants (Ge et al., 1996). Plant Se concentrations vary depending on many factors including plant physiology, soil chemistry, and Se levels (Lauchli, 1993). The majority of living plants, however, are thought to accumulate Se at levels less than 100 µg/g (Bañuelos et al., 1997).

Podisus maculiventris Say (Hemiptera: Pentatomidae), the spined soldier bug, is a generalist predator native to North America that feeds mostly on hairless lepidopteran larvae including *Spodoptera* species (Clausen, 1972). This predatory bug has piercing, sucking mouthparts. In the first stadium these bugs often remain aggregated, feeding on plant tissue near their egg mass. From the second stadium on, these bugs are predators. Eggs were obtained from a commercial producer (Koppert Biological, Romulus,

MI) and held in an environmental chamber until hatch at $27 \pm 1^\circ\text{C}$ and 16:8 (L:D) photoperiod. First-instar nymphs were sustained on organically grown green beans until molting into the second stadium.

Bug nymphs, synchronized in age at the second stadium, were contained individually in 30 ml plastic cups and randomly assigned to treatment groups. Six sets of thirty bugs were grown on *S. exigua* larvae from each of the three diet treatments (180 individual predators in each treatment). Nymphs were reared at $27 \pm 1^\circ\text{C}$ and 16:8 (L:D) photoperiod with fluorescent lighting. One host larva was fed to each bug every day. Host larvae were standardized by size across groups for each day, such that even a slower growing predator would still receive the same size host as the control predators for a given day. Second-instar predatory bugs from the control group were fed second-instar larvae, third and fourth-instar control group predators were fed increasing sizes of third-instar larvae, and fifth-instar control group predators were fed fourth-instar larvae. Predator mortality and developmental stage of newly dead and surviving insects were recorded daily. Mean days to each developmental stage, and percent survival to adult were calculated for all treatments. Bugs were not fed the day of molting into the adult stage in order to clear the gut of undigested food potentially containing Se; wet weight was recorded the day after, and they were held in ultracold freezer (-60°C) until processing for Se analysis.

Biotransfer

Adult *Podisus maculiventris* from the survival and development bioassays were freeze-dried and then ground for Se analysis using a mortar and pestle with the addition of liquid nitrogen. Bugs in each group were pooled to achieve the required sample weight for Se analysis; three samples were available from each treatment.

Bugs not used in survival and development studies were randomly assigned to replicates at the second stadium, and fed one larva each day from their respective treatments. Two days after *P. maculiventris* nymphs reached the fifth stadium bugs were not fed for 24 h in order to clear the gut of undigested food potentially containing Se. These insects were then placed in an ultracold freezer on day 3 and held for processing. Whole bugs were ground for Se analysis using a mortar and pestle with the addition of liquid

nitrogen. Nymphs in each group were pooled to achieve the required sample weight for Se analysis; three samples were taken from each treatment.

Additionally, groups of second, third, and fourth-instar *S. exigua* larvae from all treatments were removed from diet for 24 h to clear the gut, then freeze-dried, and ground with a mortar and pestle in preparation for Se analysis. Larvae in each group were pooled to achieve the required sample weight; three samples were taken for each larval stage in each treatment. All insects were reared at $27 \pm 1^\circ\text{C}$ and 16:8 (L:D) photoperiod with fluorescent lighting.

Selenium analysis (total Se) of all insect samples was performed by the University of California, Division of Agriculture and Natural Resources Laboratories at Davis CA using nitric/perchloric acid digestion/dissolution of samples, and determination by vapor generation using inductively coupled argon plasma spectrometric analysis (Tracy and Möller, 1990). Reagent blanks were used throughout the entire analytical process to verify lack of contamination; use of duplicate samples (10% of those submitted) as well as blind duplicates (5%) were used to verify that the results are reproducible with a relative percent difference within 8%. Sample spikes were used to check accuracy. Additionally, two standard reference materials were analyzed with each set of samples to verify accuracy; samples were reanalyzed for results with a difference greater than ± 2 SD (<http://groups.ucanr.org/danranlab/QA-QC/>).

Statistical analysis

For the survival and development bioassays with *P. maculiventris*, comparisons were made among effects of feeding on control, level one, or level two Se-fed host larvae in each statistical analysis. Differences ($P < 0.05$) were determined for percent survival to adult, using the nonparametric Kruskal–Wallis Test with *post hoc* separations determined using the Mann–Whitney *U* test (StatView, 2000–2001). A one-factor analysis of variance (AOV) was used to determine differences ($P < 0.05$) for each comparison including adult weight, developmental stage at death, day of death, and number of days to each developmental stage (StatView, 2000–2001). To determine mean separations between treatments, the AOV was followed, where appropriate, by Fisher's Protected Least Significant Difference *post hoc* test (PLSD; StatView, 2000–2001).

One of our main objectives was to determine if total Se in the insect predator was greater than that of their host larvae in order to assess whether biomagnification or biotransfer of Se was occurring. Although a two-way analysis comparing the total Se of treatment groups of both insect species against all development stages was desirable, this was not possible due to a correlation of the dependent variables (StatView, 2000–2001). Therefore, the total Se for each developmental stage was averaged, allowing us to compare mean Se among all diet treatments using a one-factor AOV (StatView, 2000–2001). The AOV was followed by Fisher's PLSD, to determine mean separations between treatments (StatView, 2000–2001).

A two-factor AOV comparing total Se for all treatments and development stages of *S. exigua* host larvae, yielded a significant interaction between these main effects ($F_{4,18} = 7.328$; $P = 0.001$; StatView, 2000–2001). Therefore, orthogonal contrasts were used to describe this interaction; we then calculated Fisher's PLSD *post hoc* comparisons to determine differences ($P < 0.05$) among development stages within Se-treatments (Sokal and Rohlf, 1995). For *P. maculiventris*, the predatory bugs, a two-factor AOV was used to compare total Se for bugs in each treatment and development stage followed by Fisher's PLSD (StatView, 2000–2001).

Results

Survival and development

Predatory bug survival to the adult stage was reduced by feeding on herbivores that were given a diet with either level-one concentrations or level-two concentrations of Se (59% and 58% survival, respectively) compared to the control (89% survival; Fig. 1; $H = 11.371$; $P = 0.003$). In addition, predators that were fed hosts from either of the Se treatments weighed 20% less at the adult stage than bugs fed control larvae (Fig. 2; $F_{2,351} = 59.97$; $P < 0.001$). There was no difference between the two Se treatments for either survival to adult or adult weight ($P > 0.05$).

Predators fed diet of Se-containing host larvae had decreased developmental rates. Predatory bugs fed control larvae achieved stadia three, four, five, and adult faster than those fed Se treatments (Fig. 3; $F_{2,451} = 32.45$; $P < 0.001$; $F_{2,451} = 67.77$; $P < 0.001$; $F_{2,389} = 52.84$; $P < 0.001$; $F_{2,360} = 96.58$; $P < 0.001$, respectively). There was no difference between the

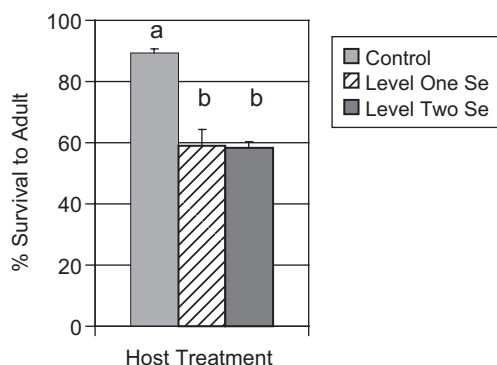


Figure 1. Mean (\pm SE) percent survival to the adult stage for *P. maculiventris* on control and Se-fed *S. exigua* larvae. Differences among treatments are indicated with letters (Mann-Whitney *U* Test; StatView, 2000–2001).

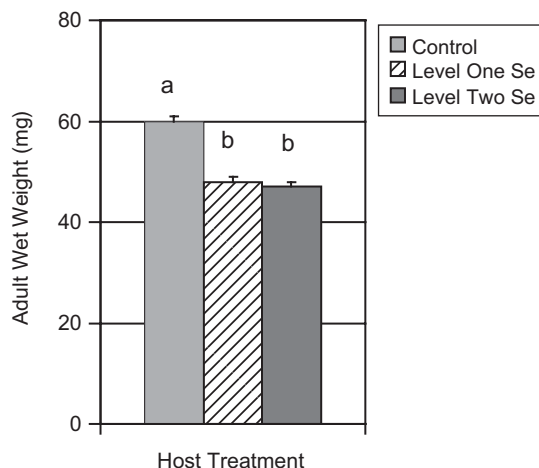


Figure 2. Mean (\pm SE) adult wet weight of *P. maculiventris* on control and Se-fed *S. exigua* larvae. Differences among treatments are indicated with letters (Fisher's PLSD; StatView, 2000–2001).

level two and level one Se treatments for developmental times to the third stadium ($P > 0.05$), but for development to stadia four, five, and adult the level two-Se treatment slowed growth significantly ($P < 0.001$; $P < 0.001$; $P < 0.002$, respectively). Other developmental parameters such as development stage at death and day at death were not significantly affected by host larval treatment (Table 1; $F_{2,159} = 0.275$; $P = 0.760$; $F_{2,159} = 0.513$; $P = 0.600$, respectively).

Biotransfer

Host larvae from control and Se-treatments, and predators fed these larvae, differed significantly in their

total Se content (Fig. 4; $F_{5,39} = 216.23$; $P < 0.001$). All *post hoc* comparisons were different at the $P < 0.01$ level or higher, with the exception of control hosts versus control-fed predators ($P = 0.684$). Specifically, these data showed that both the level-one Se and level two-Se-fed host larvae had more total Se than their predators ($P = 0.009$ and $P = 0.001$, respectively) indicating that the trophic transfer factor was less than 1.0 (~0.83–0.87) and that biomagnification did not occur. It was also demonstrated that Se accumulation increased with treatment for both herbivore host larvae and the predatory bugs in this system (Fig. 4).

Orthogonal contrasts were used to explain the significant interaction between total Se for treatment, and developmental stage of host larvae fed control diet and Se-treated diets. The significant interaction

for these main effects was explained by the differences in control Se content versus the average Se content in the two Se-treatments. This has been described by the significant interaction found when total Se for stadia two vs. three and four are contrasted with control vs. level one and level two-Se treated larvae ($F_{1,18} = 23.01$; $P < 0.001$) and stage three vs. four contrasted with control vs. level one and level two-Se treated larvae ($F_{1,18} = 4.69$; $P = 0.044$). However, for stages two vs. three and four, and stage three vs. four contrasted for level one vs. level two-Se treated larvae, no interactions were observed ($F_{1,18} = 0.12$; $P = 0.731$; $F_{1,18} = 1.47$; $P = 0.240$, respectively); therefore *post hoc* tests were calculated for total Se of larval stadia within each Se-treatment group and among Se-treatments, but not for the control group.

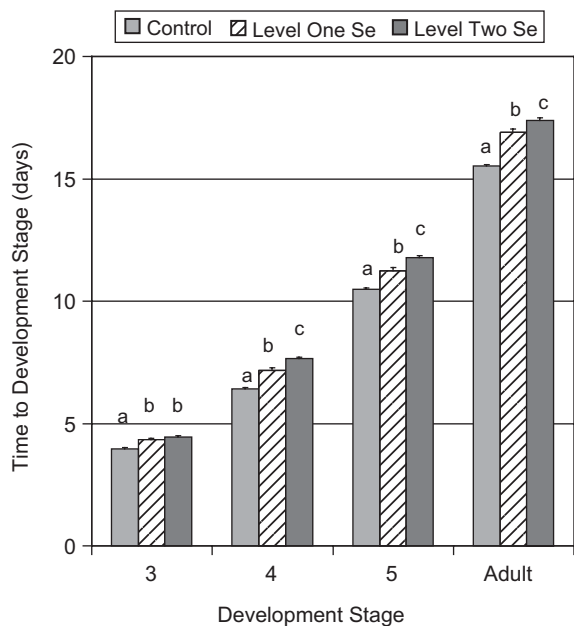


Figure 3. Mean (±SE) days to each developmental stage for *P. maculiventris* nymphs on control and Se-fed *S. exigua* larvae. Differences among treatments are indicated with letters (Fisher's PLSD; StatView, 2000–2001).

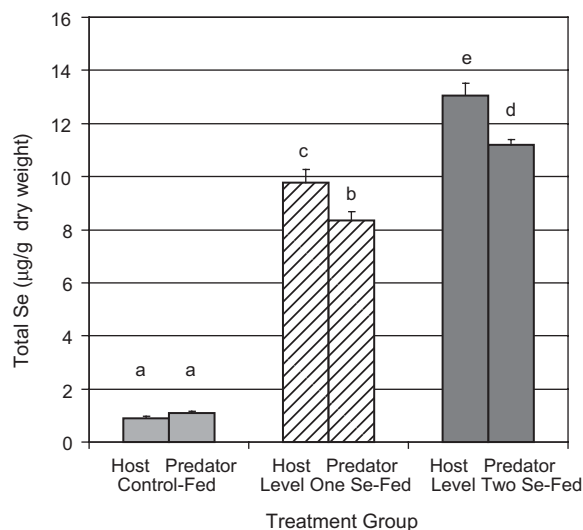


Figure 4. Mean (±SE) total Se in *S. exigua* host larvae and *P. maculiventris* predatory bugs fed control and Se-fed *S. exigua* larvae (0, 109, 135 µg/g sodium selenate dry weight added to artificial diet). Total Se values for stadia were averaged for each treatment group. Differences among treatment groups are indicated with letters (Fisher's PLSD; StatView, 2000–2001).

Table 1. Mean (±SE) developmental stage at death and day of death for *P. maculiventris* nymphs fed level one Se-treated, level two Se-treated, or control *S. exigua* host larvae (day 1 = day of molting into the second stadium)

Predatory bugs survival and development	Host treatment			P*
	Control	Level one-Se	Level two-Se	
Development stage at death	3.21 ± 0.25	3.39 ± 0.16	3.46 ± 0.16	0.758
Day of death	7.58 ± 0.99	8.96 ± 0.71	9.03 ± 0.68	0.600

*Significant differences among treatments determined by one-factor AOV (StatView, 2000–2001).

Total Se levels in host larvae increased with larval stadium within the level-two and level-one-Se treatment groups (Fig. 5; $P < 0.05$), differences among larval stadia for control-fed larvae were not compared because of the significant interactions described previously. Predator total Se increased with host Se-treatment (Table 2; $F_{2,12} = 419.39$; $P < 0.001$; $P < 0.001$, all *post hoc* comparisons), but did not differ between fifth stadium and newly molted adult in our bioassays ($F_{2,12} = 0.07$; $P = 0.801$). There was no significant interaction between the main effects in this AOV ($F_{2,12} = 0.04$; $P = 0.964$).

Discussion

Biotransfer, but not biomagnification, of Se was observed in our model system for both herbivores

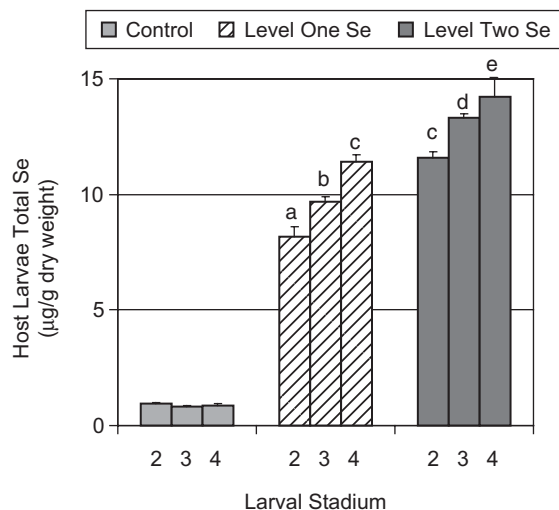


Figure 5. Mean (\pm SE) total Se in *S. exigua* host larvae fed control and Se-fed *S. exigua* larvae (0, 109, 135 $\mu\text{g/g}$ sodium selenate dry weight added to artificial diet). Differences among development stages and treatments are indicated with letters (Fisher's PLSD; Sokal and Rohlf, 1995).

and predators. The levels of Se found in our predators and herbivores is similar to that reported at Kesterson Reservoir in 1995 (overall invertebrate mean, 11.7 $\mu\text{g/g}$ Se dry weight; CH2M HILL, 1995). Total Se contents in the Se-treatment *S. exigua* larvae (9.76 and 13.0 $\mu\text{g/g}$ Se dry weight of larvae) decreased by an order of magnitude from the concentrations included in the artificial diets (109, 135 $\mu\text{g/g}$ dry weight sodium selenate). Similarly, the prey larvae in both Se-treatment groups had significantly more total Se than the predators (8.34 and 11.2 $\mu\text{g/g}$ Se dry weight predatory bugs). This observation was consistent despite the increase seen for total Se content of both host larvae and predatory bugs with increased Se in their food source.

The lack of biomagnification in secondary consumers also has been reported for arthropod predators feeding on herbivorous insects in an area heavily contaminated with metals (Mackey et al., 1997). Our results, and those of Mackay et al. (1997), are in contrast with those of Wu et al. (1995), where mantids (a generalist insect predator) had significantly higher total Se levels than grasshoppers (the predominant primary consumers) collected from the same grassland sites. Additionally, mantids collected from Kesterson in 2001 contained higher levels of Se than grasshoppers (CH2M HILL, unpublished data). Over multiple years of collections from Kesterson, predatory invertebrates (i.e., predatory beetles, bugs, and spiders) have had higher total Se concentrations than the herbivores sampled from the same locations (CH2M HILL, 1995; G. Santolo, personal communication).

In interpreting our results, it should be considered that the form of selenium fed to these insects could also be important in determining the amount of Se transfer. The dramatic difference between trophic transfer from diet to beet armyworm as compared to that from beet armyworm to spined soldier bug, may

Table 2. Mean (\pm SE) total Se (in $\mu\text{g/g}$) dry weight for *P. maculiventris* fifth-instar nymphs and adults fed level one Se-treated, level two Se-treated, or control *S. exigua* host larvae

Predatory bugs developmental stage	Control	Host treatment		
		Level one-Se	Level two-Se	
Fifth Stadium adult	1.17 \pm 0.026	8.32 \pm 0.685	11.3 \pm 0.229	a*
	1.03 \pm 0.074	8.36 \pm 0.330	11.1 \pm 0.372	a
	a*	b	c	

*Significant differences ($P < 0.05$) among treatments or between development stage are indicated by letters a,b,c; values with the same letters are not different (Fisher's PLSD; StatView, 2000–2001).

reflect, in part, the form of Se used. Although only selenate was fed to the larval hosts, it is likely that the larvae transformed some of the Se to organic forms contributing to the total Se consumed by the predator. Further research is needed to follow different seleno-species through insect food chains.

We have shown that Se biotransfer reflects the Se concentration in food, but additional factors such as the behavior, feeding mode (tissues consumed), and physiology of the predator may also determine how much Se is accumulated in insect tissues. One could reasonably expect predatory arthropods will vary in susceptibility to Se. Herbivorous insects have been shown to differ in their susceptibility to concentration and form of Se in their food (Maier and Knight, 1993; Trumble et al. 1998). Such variability in susceptibility has also been described for arthropod predators fed nickel-containing hosts (Boyd and Wall, 2001). In studies with metal contaminants, concentration within a trophic level varied more than between trophic levels suggesting that physiology of the organism may play a large role (Laskowski, 1991). Herbivores have shown a behavioral response to Se in their diet, and can, in choice-tests, modify the amount of Se consumed (Vickerman and Trumble, 1999; Vickerman et al., 2002b). If predators are similarly sensitive to Se in their diet, they could dilute their Se intake by preferentially consuming only prey tissues with lower Se contents, or prey with lower total Se levels, thus lowering the amount of Se in their food. However, in the field, factors such as availability of the host and availability of other prey species may also have a large effect on the prey items consumed and therefore affect the amount of Se biotransfer.

Although biomagnification did not occur in this experimental insect–insect system, biotransfer (trophic transfer factor of ~ 0.85) of Se in the food chain had detrimental effects on development and survival that would have substantial population level effects on *P. maculiventris*. In addition to reduced survival and decreased weight, delayed development would decrease the intrinsic rate of population increase and expose the predators to additional mortality from other predators or adverse environmental factors. Furthermore, the transfer of Se from primary to secondary consumers may result in increased bioavailability of Se to terrestrial organisms at higher levels of the food chain.

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