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Developmental Responses of a Terrestrial Insect Detritivore, *Megaselia scalaris* (Loew) to Four Selenium Species

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Abstract. *Megaselia scalaris* (Loew) (Diptera: Phoridae) is an important and ubiquitous terrestrial detritivore that consumes both animal and plant material. Because both plants and animals convert selenium pollutants into various forms, the relative toxicities of ecologically relevant concentrations of sodium selenate, sodium selenite, seleno-L-methionine, and Se-(methyl) selenocysteine hydrochloride to larvae were assessed in diet bioassays. In addition, ovipositional preferences of adults and developmental effects on the eggs and larvae were measured. With chronic exposure selenocysteine was the most toxic of the selenium species to the larvae (LC_{50}: 83 μg/g wet weight), followed by seleno-L-methionine (LC_{50}: 130 μg/g), selenate (LC_{50}: 258 μg/g), and selenite (LC_{50}: 392 μg/g). Ovipositing females did not discriminate between the highest treatment concentrations of any of the pollutants as compared to the controls, indicating a lack of avoidance behavior. Larval development time was significantly increased with exposure to selenate at 100 μg/g wet weight and above, selenite at 300 μg/g and above, and at 50 μg/g and 25 μg/g and above for seleno-L-methionine and selenocysteine respectively. Pupal development was not affected by any of the selenium treatments. Significant differences between male and female adult eclosion times were observed, with females eclosing later than males as selenium concentrations increased. Significant decreases in larval survival relative to controls occurred at the lowest treatment tested (100 μg/g) for both selenate and selenite and at 100 μg/g for seleno-L-methionine, and 50 μg/g for selenocysteine. The population level implications of lack of avoidance of contaminated food, and the effects of increased development times, reduced survivorship, and non-synchronized male and female emergence are discussed.

Keywords: sodium selenate; sodium selenite; seleno-L-methionine; and selenocysteine; *Megaselia scalaris*

Introduction

Selenium (Se) has come to the forefront as an environmental pollutant in the last 20 years due to negative effects on wildlife populations. Fish and waterfowl were visibly affected at Belews Lake, NC where a coal fly ash receiving pond was contaminated (Besser et al., 1996; Lemly, 1996). Agricultural runoff containing selenium leached from the soil was the source of contamination in Kesterson Reservoir, CA with similar effects on wildlife (Ohlendorf et al., 1990; Lemly, 1993; Presser et al., 1994; Lemly, 1997). Selenium contamination has also been implicated in the large-scale decline of endangered fish in the Colorado River basin (Hamilton, 1999). In all of these cases, Se foodchain transfer and subsequent biotransformation have been primarily responsible (Lemly, 1993; Fan et al., 2002).

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In terrestrial systems, vegetation can accumulate soluble forms of Se either from underground contamination plumes, by irrigation with contaminated water, or by growing near surface water that is contaminated (Frankenberger and Engberg, 1998). Soils can be categorized as non-seleniferous, containing <0.1–4.3 μg/g of selenium, or seleniferous, containing 1–80 μg/g, but up to 1200 μg/g (McNeal and Balistrieri, 1989). Selenium levels in topsoils and efflorescences in California's central valley are as high as 50 μg/g (Brown et al., 1999), of which the soluble fraction is available to the plants. Plants accumulating Se have been categorized as non-accumulators (with tissue concentrations ranging from < 50 μg/g dry weight of plant tissue) to high accumulators (which may have > 4000 μg/g Se, Rosenfeld and Beath, 1964). Ge et al. (1996) showed that plants grown under standard nutritional conditions with addition of sodium selenate were found to contain methyl-selenocysteine, selenocystine, selenite, selenomethionine, and selenate, in that order of abundance. While plants are known to volatilize selenium, the volatile forms are created by the active reduction of organic and inorganic forms of selenium by the plant (Zayed et al. 1998). The reduction of organic and inorganic selenium would not be expected to continue when the plant dies, until microorganisms begin the degradation of the plant tissue. Thus, concentrations available to both herbivores and detritivores can be substantial.

Very little information on Se transfer and speciation is available for arthropods. In aquatic systems, insects feeding on algae are known to bioaccumulate Se (Malchow et al., 1995; Thomas et al., 1999) and are important primary consumers and prey in systems where bioaccumulation has been demonstrated (Lemly, 1993). In terrestrial systems, transfer of Se from plants to herbivores has been documented (Trumble et al., 1998; Bañuelos et al., 1999; Vickerman et al., 2002a, and references therein), as has the transfer from an herbivore to an insect predator (Vickerman and Trumble, 2003).

While the plant–herbivore route for biotransfer of Se is undoubtedly important, the role of detritivores in terrestrial systems also warrants examination. These insects are responsible for the decomposition of many of the plants and animals that have been exposed to Se contamination. Detritivores can be exposed to Se at the concentrations found in the environment, but also in the forms and concentrations that have resulted from biotransformation and/or accumulation by plants, animals, or bacteria. Any negative effect on detritivores could be ecologically significant not only because of their critical role in recycling nutrients, but also because they occupy a critical link in trophic webs, and are routinely eaten by predatory insects, fish, mammals, and birds.

Se has several valent states (−2, 0, 4, 6), and is found in many forms in the environment. We are investigating four of these forms; selenate (+6), selenite (+4), and two organically complexed species, seleno-L-methionine and selenocysteine. Selenate and selenite are the dominant forms of dissolved Se in natural and contaminated waters, while the organic species are most likely the product of biotransformation by microphytes and bacteria (Fan et al., 2002). Many studies have used seleno-DL-methionine (Trumble et al., 1998; Vickerman and Trumble, 2003; Zayed et al., 1998), which contains a 50:50 ratio of the two stereoisomers of the compound. However, Heinz et al. (1996) and Hoffman et al. (1996) found stereospecific effects with significantly higher mortality in Mallard ducklings exposed to the L-form of the selenium compound. We elected to use seleno-L-methionine as opposed to seleno-DL-methionine to ensure that the concentrations that we would be comparing with the other forms of selenium would be equal, and not diluted by potential stereo-specific sensitivity. Overall the primary objective of this study was to determine toxicities to *Megaselia scalaris* of four Se species that detritivores would likely encounter. *M. scalaris* was selected as a test organism. It is a small yellowish-brown phorid of nearly cosmopolitan distribution. Morphological studies have shown well-developed pharyngeal ridges in *M. scalaris* larvae, which Dowding (1967) found were present only in cyclarrhophous diptera capable of feeding on a wide variety of decaying material. Larvae of this species have been reported developing on a wide variety of host materials including decaying meat, insects, and a broad selection of decomposing plant material (Robinson, 1971). Thus, this species is a detritivore, and likely to feed on decaying plants or animals

contaminated with many different pollutants, including selenium.

Acute toxicity from Se is rarely a problem in aquatic and especially terrestrial systems, rather it is the chronic toxicity that results from oral uptake and foodchain transfer which lead to elevated Se concentrations and ensuing toxicity (Saiki et al., 1993; Maier and Knight, 1994). In addition, Stark and Banks (2003) reported that 95% of the literature they reviewed used mortality and median lethal dose/concentration as a toxicological endpoint. They suggested measures of the rate of population growth result in more accurate assessments of the impact of toxicants because both lethal and sub-lethal effects of the toxicant are included. Similarly, Forbes and Calow (1999) found that demographic toxicological studies of life table responses provided more accurate assessments of toxicity than lethal concentration estimates. Accordingly, we used lifetime exposure toxicity testing in our experiments instead of traditional 24-h acute toxicity testing to determine relative toxicity values. In addition, we were interested in ecological endpoints (delayed development, egg mortality, ovipositional choice, larval mortality, and sex-linked effects) other than adult mortality that could have chronic population level effects that would not be apparent from a standard toxicological analysis.

Methods

A laboratory colony of *M. scalaris* was established in 2001 from adult flies found feeding in an alfalfa-based diet (Mandeville et al., 1988) used for another insect species. The flies were reared at a constant 26 °C a photoperiod of 16:8 L:D. For all tests, age of the eggs was synchronized by allowing groups of approximately 25 adult females from the colony to oviposit on Fisher's *Drosophila* Diet (Fisher Scientific, Pittsburg, PA, U.S.A.) in Petri dishes for 2 h.

Sodium selenate and sodium selenite were each dissolved in HPLC grade water and used to make *Drosophila* diet containing 0 (control), 100, 200, 300, 400, and 500 μg/g of selenate or selenite treatments. Similarly, seleno-L-methionine and selenocysteine were each dissolved in HPLC grade water and used to make *Drosophila* diet containing 0 (control), 0.5, 5, 25, 50, and 100 μg/g selenium treatments. Unless specifically noted, all concentrations in diets reported in the text and tables are in wet weight, but can be converted to dry weight by multiplying by 3.59 for comparison. The concentrations in the diets are within the ranges found occurring in plants at contaminated sites (Lauchli, 1993; Vajpayee et al., 1999) and in forms known to occur within plants (Ge et al., 1996). These diets, blue in color, provided excellent contrast with the white eggs, white larvae, and yellow–brown puparia of the insects, greatly facilitating counts. To achieve the desired concentrations of Se, A.C.S. certified sodium selenate, sodium selenite, seleno-L-methionine, or Se-(methyl) selenocysteine hydrochloride (Sigma-Aldrich, USA) were serially diluted, and then used to hydrate the dry diet. All bioassays were maintained at 28 ± 2 °C, ca. 75% RH, and 14:10 (L:D) photoperiod with fluorescent lighting. Tests were conducted for ovipositional preference, effects on egg hatch, development rate and survival as described below.

Oviposition studies

To measure the potential for ovipositional preference or avoidance of contaminated food, diets were prepared using 0 (control), 100, 200, 300, 400, and 500 μg/g for sodium selenate and sodium selenite. Diets were also prepared using 0 (control), 0.5, 5, 25, 50, and 100 μg/g for seleno-L-methionine and selenocysteine. Diets initially were dispensed into the bases of Petri dishes to a depth of 1.2 cm. A #9 cork borer was then used to cut cylinders of diet (1.2 cm depth × 1.2 cm diameter) from diets with each selenium concentration. These cylinders provided uniform shapes and quantities of diet for oviposition. The diet cylinders were arranged in groups of four in larger Petri dishes (2.2 cm depth × 7.5 cm diameter), with pairs of controls alternating with pairs of treatment cylinders containing a single concentration. Approximately 10 pairs of flies (males and females) were introduced into each dish, and allowed to oviposit for 2 days. Each concentration was replicated 10 times, requiring ca. 1200 adult flies for the test. At the end of the oviposition period, the numbers of eggs on treatment and control cylinders were recorded for each dish. Oviposition preference was analyzed using the Wilcoxon Signed Rank nonparametric procedure

for paired comparisons (Tallamy et al., 1997; StatView, 1998; Vickerman et al., 2002a).

Because of a known potential for insect eggs to absorb liquid from the surface of the diet (Chapman, 1975) and possibly acquire selenium, an additional analysis was conducted to determine if numbers of non-eclosing eggs differed with selenium concentration. Eggs less than 2 h old were transferred to the surface of *Drosophila* diets containing concentrations of 0, 100, 200, 300, 400, and 500 μg/g of sodium selenate or sodium selenite, and 0, 0.5, 5, 25, 50, and 100 μg/g of seleno-L-methionine or selenocysteine. The number of eggs eclosed after 12 h were assessed for each of eight replicates per concentration for each compound. These rates were compared against the controls for each compound using ANOVA (StatView, 1998).

Development and survival studies

Selenium-contaminated *Drosophila* diet was prepared as described earlier in concentrations of 0–500 μg/g for sodium selenate or sodium selenite, and 0–100 μg/g of seleno-L-methionine or selenocysteine. These diets were dispensed into one side of 75 ml clear plastic, divided Petri dishes. To pupariate, larvae either move to the surface or leave the food (Trumble and Pienkowski, 1979). With this experimental set-up, the diet-free side of the dish provided a preferred site for pupariation. Each Petri dish received 20 eggs. Additionally, the potential confounding effects of slowed eclosion or egg mortality were eliminated by removing any eggs that had not hatched within 12 h (mean <10%). Eight replicate Petri dishes containing 20 eggs each were tested for each concentration, for a total of 960 eggs. The dishes were examined daily, and numbers of puparia were recorded. The date of adult emergence and sex of emerging adults were also recorded daily for each dish for 35 days, or until all individuals had completed development to the adult stage. This procedure allowed documentation of the larval development period, the duration of puparial development, the total (larval and puparial) developmental time, and the number of individuals surviving to the adult stage. All development and survival data were analyzed using analysis of variance (ANOVA) (StatView, 1998). Percentage data were transformed with an arcsine transformation prior to analysis to confer normality, and back-transformed for presentation. As appropriate, ANOVA was followed by a *post hoc* analysis with Tukey's HSD to determine developmental or survival differences between individual concentrations within a selenium compound.

Relative toxicity of selenium compounds

To measure the mean lethal concentration that kills 50% of the population or LC_{50} for each of the selenium species, diets were prepared using 0 (control), 100, 200, 300, 400, and 500 μg/g for sodium selenate and sodium selenite. Diets were also prepared using 0 (control), 0.5, 5, 25, 50, and 100 μg/g for selenocysteine and 0 (control), 0.5, 5, 25, 50, 100, 200, 400, and 800 μg/g for seleno-L-methionine. These diets were also dispensed into one side of 75 ml clear plastic, divided Petri dishes. Each Petri dish received 20 eggs. Any potential confounding effect of egg mortality due to handling was eliminated by removing any eggs that had not hatched within 12 h (mean <10%). Eight replicate Petri dishes containing 20 eggs each were tested for each concentration, for a total of 960 eggs for sodium selenate, sodium selenite, and selenocysteine, and 1440 eggs for seleno-L-methionine. The dishes were examined daily, and any mortality was recorded in the puparial or adult stage of development. The mean lethal concentration values were calculated using probit analysis (Minitab Statistical Software, 2000), and we fitted the data for each selenium species to a logistic model to test for equal slope parameters (SAS System for Windows 2001).

Results

Ovipositional preference study

There was no significant difference in oviposition preference by female *M. scalaris* between the controls and the highest levels that we tested for each of the selenium compounds. Selenate and selenite were tested at a maximum rate of 500 μg/g, (ANOVA, p values ≥0.441); seleno-L-methionine and selenocysteine were tested at a maximum rate of 100 μg/g (ANOVA, p values ≥0.069). The eggs of *M. scalaris* were, for the most part, not affected by

the presence of selenium in the diet. Over a range of selenate and selenite concentrations from 100 μg/g to 500 μg/g, there were no significant differences in the number of eggs hatching compared to the control (ANOVA $p = 0.41$ and 0.065, respectively). We found a similar result for the organic form, seleno-L-methionine, over a range of 0.5–100 μg/g with no significant difference between treatments and control (ANOVA, p value = 0.226). However, at the highest concentration of selenocysteine (100 μg/g), significantly fewer eggs hatched than in the control ($F_{5,42} = 3.91$; $p = 0.005$). Thus, excluding the highest concentration of selenocysteine, either the eggs did not absorb appreciable amounts of selenium, or the selenium did not have measurable effects on this life stage. Therefore, eggs oviposited on food contaminated with selenate or selenite could be expected to eclose in normal numbers up to concentrations of 500 μg/g. Similarly, eggs laid on food contaminated with seleno-L-methionine or selenocysteine could be expected to eclose in normal numbers up to concentrations of 100 μg/g and 50 μg/g, respectively.

Development and survival studies

Significant delays in larval developmental time occurred at concentrations as low as 100 μg/g for selenate and 300 μg/g for selenite ($F_{\text{selenate–5,41}} = 37.60$, $F_{\text{selenite–5,41}} = 20.03$; $p = 0.001$, Fig. 1). Seleno-L-methionine and selenocysteine also significantly lengthened the time required for larval development ($F_{\text{selenomethionine–5,34}} = 3.52$, $p = 0.007$, $F_{\text{selenocysteine–5,42}} = 3.87$; $p = 0.006$) at a concentration of 50 μg/g for seleno-L-methionine and at 25 μg/g or higher for selenocysteine (Fig. 2). None of the selenium species caused any significant differences in the number of days required to complete pupariation (selenate, $p = 0.259$, $F_{5,41} = 1.36$; selenite, $p = 0.085$, $F_{5,41} = 2.10$; seleno-L-methionine, $p = 0.084$, $F_{5,34} = 2.14$; selenocysteine, $p = 0.250$, $F_{5,42} = 1.38$). Thus, once pupariation occurs, development to the adult stage proceeds in a consistent time period regardless of exposure to the selenium compounds or concentrations tested.

Sex-linked differences in overall developmental rates were observed for the organic forms of selenium. Because there were no differences in time to development in the puparial stage, the effects occurred during the larval stage. Selenate and selenite did not cause a difference, but both seleno-L-methionine and selenocysteine did cause a significant increase in the number of days that females took to emerge as compared to males at 25 μg/g ($F_{\text{selenomethionine–5,33}} = 6.402$, $p = 0.001$; $F_{\text{selenocysteine-5,42}} = 4.109$, $p = 0.004$, Fig. 3). At the highest level tested (500 μg/g), no females emerged in the selenate treatment, suggesting relatively high concentrations could eliminate reproductives. Mortality was also a factor at the higher concentrations in the organic forms, as animals exposed to the higher treatment levels died as development time was extended. Subsequently, the longest average delay in female emergence was recorded at the third highest treatment for seleno-L-methionine, (25 μg/g, 4.6 days), and at the second highest treatment (50 μg/g, 3.1 days) for selenocysteine.

Larval survival was significantly reduced by each of the selenium species, but puparial survival was not (< 5% for any treatment). Selenate decreased larval survival by 28% at the lowest concentration tested (100 μg/g) and decreased larval survival by 79% at the highest treatment (500 μg/g). Selenite had a similar effect, decreasing larval survival by 19% at the lowest treatment (100 μg/g) and by 58% at the highest treatment (500 μg/g). Seleno-L-methionine was more potent than the non-organic forms, with a 22% decrease at 100 μg/g, and a 97% decrease in larval survival at 400 μg/g. Selenocysteine was the most potent form of Se tested, reducing larval survival by 28% at 50 μg/g, and 58% at 100 μg/g. Thus, nearly all of the observed mortality occurred during the larval stage and each selenium species affected the larval development differently.

Relative toxicity of selenium compounds

As reflected by the effects on larval survival, *M. scalaris* appear to be most sensitive to selenocysteine, followed by seleno-L-methionine, selenate, and then selenite. The log-dose probit analyses further demonstrated this pattern. Table 1 shows the concentrations that killed 50% of the population over chronic lifetime exposures (LC_{50}). Since none of the LC_{50} 95% confidence limits for any of the compounds overlap, and we rejected the null hypothesis of equal slope parameters ($\chi^2_3 = 15.53$,

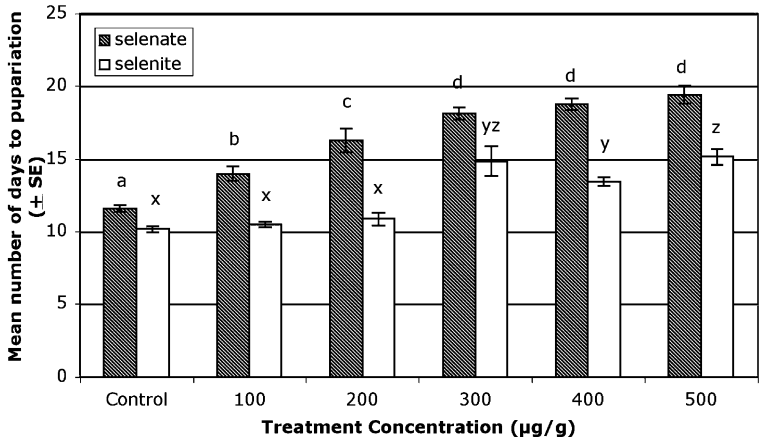

Figure 1. Effects of selenate and selenite on the mean number of days to reach pupariation for *M. scalaris*. Bars (mean ± SE) with the same letters are not significantly different within Se species (selenate, a–c; selenite, x–z) at the $p < 0.05$ level (ANOVA, Fisher's PLSD Test, StatView, 1998).

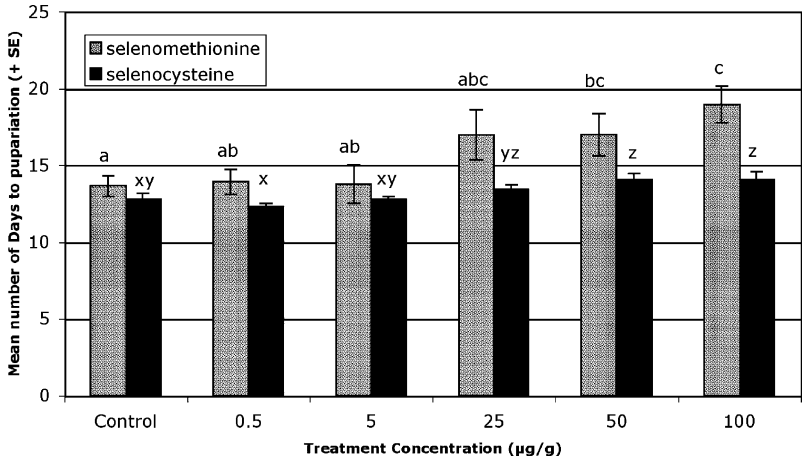

Figure 2. Effects of seleno-L-methionine and selenocysteine on the mean number of days to reach pupariation for *M. scalaris*. Bars (mean ± SE) with the same letters are not significantly different within Se species (seleno-L-methionine, a–c; selenocysteine, x–z) at the $p < 0.05$ level (ANOVA, Tukey's HSD Test, StatView, 1998).

$p = 0.0014$) using a logistic model incorporating data from the four selenium species, we conclude that the response curves are distinct. Thus *M. scalaris* is approximately four times more sensitive to selenocysteine than to selenite, and overall the organics are approximately twice as toxic to *M. scalaris* than the non-organics.

Discussion

M. scalaris females did not distinguish between controls and the highest treatment concentrations of the four selenium species that we tested when choosing an oviposition site. Therefore, we would expect eggs to be oviposited readily on Se-contaminated food sources. Because the eggs are immobile, and the larvae are not capable of substantial movement, offspring are restricted to the food source chosen by the females at the time of oviposition. This contrasts with herbivores that have shown sensitivity to Se in their diet, and can behaviorally modify the amount of Se consumed in choice-tests (Vickerman and Trumble, 1999; Vickerman et al., 2002a).

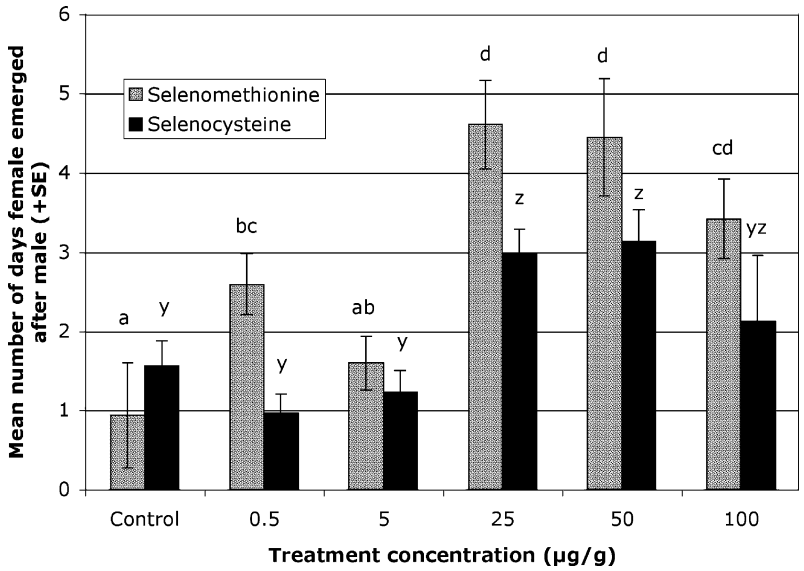

Figure 3. Concentration dependent delays on female emergence compared with that of males due to seleno-L-methionine and selenocysteine. Bars (mean ± SE) with the same letters are not significantly different within Se species (seleno-L-methionine, a–d; selenocysteine, y–z) at the $p < 0.05$ level (ANOVA, Fisher's PLSD Test, StatView, 1998).

While we found that the eggs are not usually directly affected by form of Se (only the highest concentration of selenocysteine interfered with viability), larvae would experience delayed development or mortality dependent upon the concentration of selenium in the food source. These results were not unexpected. Studies using insect herbivores (Hogan and Cole, 1988; Trumble et al., 1998; Bañuelos et al., 1999; Vickerman and Trumble, 1999), or insect predators (Vickerman and Trumble, 2003) also found reduced survivorship and/or delayed development. Our results show that Se contamination similarly affects insect detritivores. Delays in larval development (up to 8 days for selenate) could have serious implications for the survival of a population exposed to these levels of selenium contamination. Additional development time increases exposure to predators and parasites, and would likely impact population fitness in many natural systems because the availability of food sources for the larvae may be temporary, and extending larval development times could exceed duration of the suitability of the food supply.

The concentrations of selenium that we found to affect larval development were different for the non-organic and organic forms of selenium. Rosetta and Knight (1995) and Besser et al. (1993) found that organic selenium species are much more bioavailable than the inorganic species and play a key role in Se ecotoxic effects. This agrees with our results as we found selenate and selenite treatments had a significant effect on larval development time at 100 µg/g and 300 µg/g, respectively, while seleno-L-methionine and selenocysteine treatments

Table 1. Mean lethal concentrations (LC_{50}) in a larval chronic exposure test calculated for *Megasilia scalaris* for selenate, selenite, seleno-L-methionine and selenocysteine in artificial diet

Selenium species	Number of insects tested	LC_{50} concentration (µg/g)	95% Confidence limits
Selenate	862	258	231–287
Selenite	884	392	326–510
Seleno-L-methionine	1207	130	117–143
Selenocysteine	877	83	73–98

Log-dose Probit analysis performed using Minitab Version 13 (2000).

significantly delayed larval development at levels as low as 50 μg/g for both compounds. Conversely, Trumble et al. (1998) found that larval development of the herbivore *Spodoptera exigua* was delayed with exposure to sodium selenate at 4 μg/g wet weight, and sodium selenite at 12 μg/g wet weight, but development time was not delayed with exposure to seleno-DL-cysteine or seleno-DL-methionine at concentrations as high as 30 μg/g wet weight. Thus, there appears to be variability in response between insect species and potentially between insect guilds (herbivores versus detritivores). This variability in response could also be partly attributed to the compounds tested. While we used one form of selenomethionine and selenocysteine, Trumble et al. (1998) used DL forms of these two compounds, effectively reducing the treatment concentration by half if *S. exigua* exhibits stereo-specific sensitivity to these compounds as Heinz et al. (1996) and Hoffman et al. (1996) found for mallard ducklings.

We also found a novel difference in toxicant potency between the non-organic and organic forms. While *M. scalaris* larval development was delayed at relatively lower concentrations by the organic forms, the chronic LC_{50} results indicate that selenocysteine was the most toxic with an LC_{50} of 83 μg/g, followed by seleno-L-methionine (130 μg/g), selenate (258 μg/g), and finally selenite (392 μg/g). Again this contrasts with Trumble et al. (1998) who found that selenite was the most toxic form tested against *S. exigua*, with an LC_{50} of 9.14 μg/g wet weight. Selenocysteine was intermediate with an LC_{50} of 15.21 μg/g wet weight. The least toxic forms, sodium selenate and seleno-L-methionine, had LC_{50}s below 50 μg/g wet weight. A comparison of the LC_{50} values shows that *M. scalaris* is not as sensitive to selenium as *S. exigua* in any of the various forms. We hypothesize that this may be due to life history traits associated with a detritivorous diet. Detritivores are exposed not only to plant defensive compounds, but possibly to many additional compounds as vegetation decays.

Finally, we found that the organic selenium species desynchronized male and female adult emergence times. This has the potential to be among the most serious of the consequences of Se contamination. In control diets females eclose 1 day after the males; however, we found additional delays for diets containing any of the four selenium species, with the longest average additional delay recorded at 4.5 days (50 μg/g diet of seleno-L-methionine). We speculate that the additional developmental time normally required by females over males is due to their larger size. The ingestion of additional food to attain a larger biomass might expose the females to enough additional selenium to further increase developmental time. In the laboratory, males that eclosed in dishes without free water generally died within 24 h (personal observation). Thus, males may not live long enough, or they may not stay in the vicinity of the remaining members of their cohort if females are not available. Because decaying food sources tend to be temporary, this asynchrony is may result in few males left to fertilize the late emerging females from a Se contaminated food source. If food sources were limited, this would have destabilizing effects on a natural population of *M. scalaris*.

Although the present study examined the effects of Se on a detritivore in an artificial diet in order to eliminate confounding effects of variable nutrition, future investigations will need to incorporate the effects of defensive compounds or pollutant mixtures before accurate predictions can be made regarding the effects of Se on detritivore and ecosystem function.

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