

## MINI REVIEW

# The impacts of metals and metalloids on insect behavior

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**Abstract**

In toxicology studies, the use of death as an endpoint often fails to capture the effects a pollutant has on disruptions of ecosystem services by changing an animal's behavior. Many toxicants can cause population extinctions of insect species at concentrations well below the EC<sub>25</sub>, EC<sub>50</sub>, or EC<sub>90</sub> concentrations traditionally reported from short-term bioassays. A surprising number of species cannot detect metal and metalloid contamination, and do not always avoid food with significant metal concentrations. This frequently leads to modified ingestion, locomotor, and reproductive behaviors. For example, some species show a tendency to increase locomotor behaviors to escape from locations with elevated metal pollution, whereas other insects greatly decrease all movements unrelated to feeding. Still others exhibit behaviors resulting in increased susceptibility to predation, including a positive phototaxis causing immatures to move to exposed positions. For purposes of reproduction, the inability to avoid even moderately polluted sites when ovipositing can lead to egg loss and reduced fitness of offspring. Ultimately, impaired behaviors result in a general reduction in population sizes and species diversity at contaminated sites, the exceptions being those species tolerating contamination that become dominant. Regardless, ecosystem services, such as herbivory, detritus reduction, or food production for higher trophic levels, are disrupted. This review evaluates the effects of metal and metalloid pollution on insect behaviors in both terrestrial and aquatic systems reported in a diverse literature scattered across many scientific disciplines. Behaviors are grouped by ingestion, taxis, and oviposition. We conclude that understanding how insect behavior is modified is necessary to assess the full scope and importance of metal and metalloid contamination.

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**Introduction**

Despite the importance of insects in most ecosystems, and the worldwide pollution of systems by heavy metals, surprisingly little information is available on the effects of metal and metalloid pollution on the behaviors of insects. Stark & Banks (2003) reviewed the available literature on toxicant effects on insects and determined that 95% of the reports used the lethal concentration, LC<sub>50</sub> (50% of insects die), or simple mortality as a toxicological endpoint. Although short-term assays are efficient and allow for comparisons between compounds and insect species, they may not always provide a clear ecological picture on the

potential effects of contaminants. For example, toxicants can affect populations enough to cause extinction at levels well below the LC values reported in the literature (Bechmann, 1994). Because insect behaviors are key contributors to the ecology of insect interactions with other plant and animal species, as well as with their abiotic environments, these behaviors are critical to the stability and diversity of ecosystems (Fisher, 1998). Thus, our review focuses on ecologically important behaviors related to ingestion, taxis, and reproduction as affected by natural and anthropogenic sources of a widespread class of pollutants: the heavy metals and metalloids.

Although there are many natural sources of elevated concentrations of metals (Boyd, 2004), anthropogenic activities such as mining, smelting, and industrial use have created both localized and regional pollution problems in

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nearly every country in the world (Nriagu, 1996). In some cases the pollution has been extensive enough to lead to environmental disasters and ecosystem shutdown (Hopkin, 1989; Sainz et al., 2004). Insects may be exposed by direct contact with dissolved elements in aquatic systems, via contact with contaminated soils, through airborne pollution or atmospheric deposition, and through herbivory on plants that have sequestered these materials. Predators and parasites are also exposed when feeding on insects that contain elevated concentrations of these elements (Vickerman & Trumble, 2003). A few of the more common metal and metalloid pollutants that are discussed in this paper are briefly characterized below. A detailed description of every metal is beyond the scope of this paper, instead a few key references have been included.

Zinc (Zn) is a common metal in the earth's crust, averaging about  $75 \text{ mg kg}^{-1}$  soil (Emsley, 2001). For animals, Zn is an essential element; however, levels of  $100\text{--}250 \text{ mg day}^{-1}$  can cause significant health effects (OhioEPA, 2002). Zinc is commonly used in manufacturing of paints, dyes, wood preservatives, and rubber (Emsley, 2001). Zinc compounds found at industrial sites, at mines and nearby watersheds, and in sludge spread on agricultural fields include zinc chloride, zinc oxide, zinc sulfate, and zinc sulfide. In field conditions, hyperaccumulator plants may accumulate in excess of  $12\,000 \text{ mg Zn kg}^{-1}$  dry weight (Deng et al., 2006).

Copper (Cu), which has been mined throughout the world for thousands of years, has many industrial uses. Widespread pollution has resulted from mining and smelting, brake dust from automobiles, uses as a marine antifoulant, the spreading of sewage sludge on agricultural lands, and the application of Cu as a fungicide in agriculture (Hutchinson & Whitby, 1974). Soil levels can exceed  $2\,890 \text{ mg Cu kg}^{-1}$ , whereas concentrations in Cu-accumulating plants have been reported above  $1\,300 \text{ mg kg}^{-1}$  (Fernandes & Henriques, 1991). Because of the ubiquitous use in both developing and developed countries, and a long history of smelters releasing Cu as an air pollutant, Cu pollution occurs on nearly all continents and in most countries (Nriagu, 1996). As a result, insects frequently interact with elevated concentrations of Cu either through atmospheric deposition or by uptake and sequestration by plants.

Dissolved inorganic selenium (Se), in the form of sodium selenate, is sequestered by many plants. This material is available directly to aquatic insects, or may be modified into a form bioavailable to herbivores which can be either inorganic (sodium selenite) or organic (selenomethionine and selenocystine). For most plants the total Se concentration rarely exceeds  $50 \text{ mg g}^{-1}$ , but some hyperaccumulators may have total Se levels exceeding  $5\,000 \text{ mg g}^{-1}$

(Galeas et al., 2007). Selenium is a common pollutant in most Pacific Rim countries, and this metalloid is a major pollutant in the western United States where large deposits are leached by rainfall and irrigation practices (McNeal & Balistrieri, 1989). In water collection sites without outlets, such as the Kesterson Reservoir in central California, concentrations can exceed  $1\,400 \text{ } \mu\text{g l}^{-1}$  (Wu, 2004). However, most available studies examine the effects of Se at much lower concentrations. Selenium can also reach high concentrations in vegetation found near coal burning power plants and some industrial sites (McNeal & Balistrieri, 1989; Huggins et al., 2007).

Arsenic (As), commonly found as arsenate, is an important pollutant of groundwater that is often used for drinking and irrigation. Arsenic contamination has become a significant problem in Southeast Asia, where concentrations in well water may exceed  $3\,000 \text{ } \mu\text{g As l}^{-1}$ , and levels in soils can exceed  $30 \text{ } \mu\text{g g}^{-1}$  (Berg et al., 2007). Arsenic contamination results from natural and anthropogenic disturbance of rock, resulting in oxidation and release of inorganic forms of As (arsenate [As(V)] and arsenite [As(III)]), which are available to plants. These form arsenobetaine and arseno-sugars (among other compounds), which may be complexed with phytochelatins, which are important in heavy metal detoxification (Meharg & Hartley-Whitaker, 2002). Some plants reduce arsenate to arsenite, and then further transform it into several methylated forms (Zaman & Pardini, 1996). Thus, insects are likely exposed to a range of As species. Extreme As concentrations in surface waters, soils, and plants have been reported to result from mining effluent (particularly at gold mines) (Eisler, 2004) and as a result of burning coal high in As (Huggins et al., 2007). At industrial sites, As levels can reach up to  $38\,000 \text{ } \mu\text{g l}^{-1}$  in water that is available to plants (Cappuyns et al., 2002). Arsenic tolerant vegetation can sequester concentrations of 500 to nearly  $3\,500 \text{ } \mu\text{g g}^{-1}$  (Porter & Peterson, 1975). However, most reports on crops describe concentrations that are  $75 \text{ } \mu\text{g g}^{-1}$  or less (see references in Meharg & Hartley-Whitaker, 2002).

Another widespread pollutant is cadmium (Cd), with contamination resulting from the application of sludge or urban composts, pesticides, fertilizers, emissions from waste incinerators, waste water irrigation, and residues from metalliferous mining and metal smelting (McGrath et al., 2001). Though unlikely to affect plant growth, Cd negatively influences enzymatic systems of cells in higher organisms as a result of transfer up the food chain (Sanità di Toppi & Gabbriellini, 1999) and has a very long soil residency time. The US Environmental Protection Agency (USEPA) considers Cd a priority toxic pollutant, with an acute exposure limit in freshwater of  $2.0 \text{ mg l}^{-1}$  for up to 10 days and a chronic exposure limit of  $0.25 \text{ mg l}^{-1}$

(USEPA, 2001). In soils intended for agricultural use, acceptable limits range from 1 to 8 mg Cd kg<sup>-1</sup> soil dry weight, depending on pH (Environment Agency, 2002).

Although understanding the individual effects of metals and metalloids is important, most metals occur in combination, and joint effects must be evaluated. Yang (1994) reviewed the literature on the toxicology of metals to all classes of organisms and determined that >95% of all journal articles reported the effects of individual compounds or elements. In combination, effects may not simply be additive, but possibly potentiating or antagonistic. For example, the joint toxicity of mercury and Se to an insect detritivore, the phorid fly *Megasilia scalaris* Loew, was strongly potentiating, with just 5% of the LC<sub>50</sub>'s of the two elements combined producing significantly increased developmental time and significantly greater mortality than the LC<sub>50</sub> of either element alone (Jensen et al., 2006). Where available, we have included the literature that provides information on the joint effects of metals on insect behaviors. However, we recognize that in some cases the concentrations/mixtures will be difficult to replicate exactly (particularly in field studies).

## Methods

ISI Web of Knowledge databases were searched using terminology including metals, metalloids, behavior, insects, and pollution. To be considered, papers were required to meet the following criteria: report quantifiable data regarding insect behavioral responses to metal pollutants, include a control or reference concentration, and include statistical analyses comparing test data. A substantial proportion of papers (>50%) did not include control or reference concentrations, or described behaviors without including data or analyses to verify that behaviors changed as a result of the contaminant. Once suitable papers were obtained, their references were examined, and ISI Web of Knowledge searches conducted for any recent papers citing those already obtained. A total of 75 papers meeting the above criteria were found. Papers from both terrestrial and aquatic systems were considered, evaluating the behavioral responses of first instars through adults. Behaviors were further divided into three categories: ingestion, taxis (locomotion), and reproductive (oviposition) behaviors. See Tables 1 and 2 for a summary of metals, species, and behavioral outcomes for these categories.

## Results

### Terrestrial systems

**Ingestion behavior.** The majority of research concerning feeding behaviors of terrestrial insects has investigated the

effects of metals on feeding preference when individuals were exposed to various concentrations and combinations of metals. For herbivorous insects, this has focused mostly on antifeedant properties of metals on agricultural pests. Zinc, Cu, Ni, Se, and As have been evaluated individually, whereas several other studies examined combinations of metals.

Zinc sulfate has been extensively studied, particularly in experiments involving first-instar lepidopteran pests. Zinc salts are known to cause toxicity in insects and their abilities as feeding deterrents for agricultural pests were quantified. *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae) responded to Zn sulfate treatments in choice experiments by avoiding meridic diet containing concentrations  $\geq 0.1\%$  ZnSO<sub>4</sub> (Gahukar, 1975). Although variability in individual responses was high and not always significant, aversion increased with increasing ZnSO<sub>4</sub> in the diet. These results are consistent with the results obtained by Sell & Bodznick (1971) for *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae), which was deterred by concentrations  $\geq 0.2\%$  ZnSO<sub>4</sub>, and *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), which was deterred by concentrations  $\geq 0.1$  M ZnSO<sub>4</sub> (Salama & El-Sharaby, 1972). Similarly, Pollard & Baker (1997) demonstrated significant preference of *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae) and *Pieris brassicae* (L.) (Lepidoptera: Pieridae) for low Zn treatments over high Zn treatments in choice experiments. Behmer et al. (2005) came to the same conclusion in choice experiments, and further showed that *S. gregaria* learned associatively to avoid Zn-treated foods. Behavioral responses of insect predators and parasitoids to zinc sulfate-contaminated prey have not been reported.

Gustatory perception assays with adult *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) showed that they also prefer low Zn treatments to high Zn treatments (Bahadorani & Hilliker, 2009). These authors observed the same pattern for Fe (II) and Fe (III), while adults preferred control diets to Cd- and Cu-contaminated diets significantly more often. Like adults, larvae also avoided feeding on high concentrations of heavy metals (Bahadorani & Hilliker, 2009).

Copper, as copper sulfate (CuSO<sub>4</sub>), has also been investigated as a feeding deterrent against agricultural pests. Mixing CuSO<sub>4</sub> with lime creates a Bordeaux mixture effective as a fungicide (<http://www.copper.org>). El-Bassiouny (1991) investigated possible feeding deterrent properties for several lepidopteran species. These responded to CuSO<sub>4</sub> feeding deterrents with mixed responses, depending on species. Oligophagous species [*P. brassicae* and *Pieris napi* (L.)] were deterred at lower concentrations (0.05–0.1 M CuSO<sub>4</sub>), whereas polyphagous species

**Table 1** Summary of contaminants and the resultant behavioral outcome observed for insect species in terrestrial habitats

Metal/metalloid	Form	Species	Behavioral outcome	Reference	
<b>A. Ingestion behavior</b>					
Arsenic	Na <sub>2</sub> HAsO <sub>4</sub>	<i>Schistocerca americana</i>	Negative	Rathinasabapathi et al., 2007	
Cadmium	Cd	<i>Chorthippus spec.</i>	Negative	Migula & Binkowska, 1993	
		<i>Lochmaea capreae</i>	No effect	Rokytořová et al., 2004	
		<i>Neochetina bruchi</i>	Negative	Jamil et al., 1989a,b	
		<i>Neochetina eichhorniae</i>	No effect	Kay & Haller, 1986	
		<i>Frankliniella occidentalis</i>	Negative	Jiang et al., 2005	
	CdCl <sub>2</sub> Cd(NO <sub>3</sub> ) <sub>2</sub>	<i>Agasicles hygrophila</i>	Negative	Quimby et al., 1979	
		<i>Bactra verutana</i>	No effect	Quimby et al., 1979	
		<i>Folsomia candida</i>	Negative	Fountain & Hopkin, 2001	
		<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009	
		<i>Folsomia candida</i>	Negative	Filser & Hölscher, 1997	
Copper	CdSO <sub>4</sub> ·2.67H <sub>2</sub> O Cu	<i>Neochetina eichhorniae</i>	No effect	Kay & Haller, 1986	
		<i>Folsomia manolachei</i>	Positive	Filser et al., 2000	
		<i>Folsomia quadrioculata</i>	Positive	Filser et al., 2000	
	CuCl <sub>2</sub> ·3Cu(OH) <sub>2</sub>	<i>Isotomurus palustris</i>	No effect	Filser et al., 2000	
		<i>Onychiurus armatus</i>	Negative	Filser et al., 2000	
		<i>Folsomia candida</i>	Negative	Fountain & Hopkin, 2001	
	Cu(NO <sub>3</sub> ) <sub>2</sub> CuSO <sub>4</sub>	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009	
		<i>Leptinotarsa decemlineata</i>	Negative	El-Bassiouny, 1991	
		<i>Mamestra brassicae</i>	Negative*	El-Bassiouny, 1991	
		<i>Mamestra oleracea</i>	Negative*	El-Bassiouny, 1991	
		<i>Pieris brassicae</i>	Negative	El-Bassiouny, 1991	
		<i>Pieris napi</i>	Negative	El-Bassiouny, 1991	
	Iron	Fe FeSO <sub>4</sub> ·7H <sub>2</sub> O	<i>Orchesella cincta</i>	Negative	Nottrot et al., 1987
			<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
		Fe <sub>2</sub> (SO <sub>4</sub> ) <sub>3</sub> ·xH <sub>2</sub> O	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
Lead	Pb	<i>Chorthippus spec.</i>	Negative	Migula & Binkowska, 1993	
		<i>Folsomia candida</i>	Negative*	Fountain & Hopkin, 2001	
		<i>Lochmaea capreae</i>	No effect	Rokytořová et al., 2004	
	Pb(NO <sub>3</sub> ) <sub>2</sub>	<i>Neochetina eichhorniae</i>	No effect	Kay & Haller, 1986	
		<i>Leptinotarsa decemlineata</i>	Negative	Kwartirnikov et al., 1999	
		<i>Orchesella cincta</i>	No effect	van Capelleveen et al., 1986	
Manganese	Mn	<i>Lochmaea capreae</i>	Negative	Rokytořová et al., 2004	
		<i>Orchesella cincta</i>	No effect	Nottrot et al., 1987	
Nickel	Ni	Aphididae	No effect	Boyd & Martens, 1999; Jhee et al., 2005	
		<i>Delia radicum</i>	Negative	Jhee et al., 2005	
		<i>Evergestis rimosalis</i>	Negative	Jhee et al., 2005	
		<i>Melanoplus femurrubrum</i>	Negative	Jhee et al., 2005	
		<i>Pieris rapae</i>	Negative	Martens & Boyd, 1994	
Selenium	Se	<i>Plutella xylostella</i> G88	Negative	Freeman et al., 2006	
		<i>Plutella xylostella</i> Stanleyi	No effect	Freeman et al., 2006	
		<i>Pieris rapae</i>	Negative	Freeman et al., 2006	
		<i>Spodoptera exigua</i>	Negative	Vickerman & Trumble, 1999	
		<i>Acheta domestica</i>	Negative	Freeman et al., 2007	
	Na <sub>2</sub> SeO <sub>3</sub> Na <sub>2</sub> SeO <sub>4</sub>	<i>Myzus persicae</i>	Negative	Hanson et al., 2004	
		<i>Spodoptera exigua</i>	Negative	Vickerman & Trumble, 1999; Vickerman et al., 2002b	
		<i>Spodoptera exigua</i>	Negative	Vickerman & Trumble, 1999	
	Seleno-cystine Seleno-methionine	Seleno-cystine Seleno-methionine	<i>Spodoptera exigua</i>	No effect	Vickerman & Trumble, 1999
			<i>Spodoptera exigua</i>	No effect	Vickerman & Trumble, 1999

Table 1 (Continued)

Metal/metalloid	Form	Species	Behavioral outcome	Reference
Zinc	Zn	<i>Lochmaea capreae</i>	Negative	Rokytová et al., 2004
		<i>Neochetina bruchi</i>	Negative	Jamil et al., 1989a,b
	ZnCl <sub>2</sub>	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
	Zn(NO <sub>3</sub> ) <sub>2</sub>	<i>Folsomia candida</i>	Negative	Fountain & Hopkin, 2001
	ZnSO <sub>4</sub>	<i>Heliiothis virescens</i>	Negative	Sell and Bodznick, 1971
		<i>Ostrinia nubialis</i>	Negative	Gahukar, 1975
		<i>Pieris brassicae</i>	Negative	Pollard & Baker, 1997
		<i>Schistocerca gregaria</i>	Negative	Pollard & Baker, 1997
		<i>Schistocerca gregaria</i>	Negative	Behmer et al., 2005
<i>Spodoptera littoralis</i>	Negative	Salama & El-Sharaby, 1972		
B. Taxis behavior				
Copper	CuCl <sub>2</sub> x	<i>Folsomia manolachei</i>	Negative	Filser & Hölscher, 1997
		<i>Mesophorura macrochaeta</i>	Negative	Filser & Hölscher, 1997
		Other Collembola	No effect	Filser & Hölscher, 1997; Filser et al., 2000
	3 Cu(OH) <sub>2</sub>	<i>Pseudosinella alba</i>	Negative	Filser et al., 2000
		<i>Pterostichus cupreus</i>	Negative	Bayley et al., 1995
Iron	CuSO <sub>4</sub>	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
	FeSO <sub>4</sub> ·7H <sub>2</sub> O	<i>Drosophila melanogaster</i>	Positive	Bahadorani & Hilliker, 2009
Zinc	ZnCl <sub>2</sub>	<i>Drosophila melanogaster</i>	No effect	Bahadorani & Hilliker, 2009
C. Oviposition				
Cadmium	CdSO <sub>4</sub> ·2.67H <sub>2</sub> O	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
Chromium	Cr(VI)	<i>Megaselia scalaris</i>	No effect	Trumble & Jensen, 2004
Copper	CuSO <sub>4</sub>	<i>Drosophila melanogaster</i>	Negative	Bahadorani & Hilliker, 2009
Iron	FeSO <sub>4</sub> ·7H <sub>2</sub> O	<i>Drosophila melanogaster</i>	Negative**	Bahadorani & Hilliker, 2009
	Fe <sub>2</sub> (SO <sub>4</sub> ) <sub>3</sub> ·xH <sub>2</sub> O	<i>Drosophila melanogaster</i>	Negative**	Bahadorani & Hilliker, 2009
Selenium	Se	<i>Plutella xylostella</i> G88	Negative	Freeman et al., 2006
		<i>Plutella xylostella</i> Stanleyi	No effect	Freeman et al., 2006
		<i>Pieris rapae</i>	Negative	Freeman et al., 2006
	Na <sub>2</sub> SeO <sub>4</sub>	<i>Spodoptera exigua</i>	Positive	Vickerman et al., 2002b
		<i>Spodoptera exigua</i>	No effect	Vickerman et al., 2002a
Zinc	ZnCl <sub>2</sub>	<i>Drosophila melanogaster</i>	Negative**	Bahadorani & Hilliker, 2009

Only individual metals/metalloids are considered for behavioral outcomes because mixtures may lead to synergistic or antagonistic interactions otherwise unaccounted for in the behavioral response. Positive and negative outcomes correspond to stimulation or suppression of the particular behavior as a result of metal presence, respectively, and 'no effect' means the organism was unaffected at the experimental conditions.

\*Indicates the behavioral outcome was only observed at high concentrations and the organism was unaffected at lower concentrations.

\*\*Indicates that there was an initial positive response to low concentrations vs. controls that then became negative as concentrations increased. In choice assays, aversion results in a negative behavioral outcome. See text for the measured concentrations.

(*Mamestra brassicae* L. and *Mamestra oleracea* L.) (Lepidoptera: Noctuidae) were only inhibited by higher concentrations (0.2 M CuSO<sub>4</sub>) (El-Bassiouny, 1991). *Pieris brassicae* took shorter meals before feeding ceased, and experienced an increase in palpation frequency.

Some research has focused on hyperaccumulating plants and documented that high levels of metals in plant tissues may serve to deter herbivory. For example, herbivorous insects preferred *Streptanthus polygaloides* Gray (Brassicaceae) grown in low nickel (Ni) soils (15.6–76.5 μg g<sup>-1</sup>) vs.

high Ni soils (1 820–7 960 μg g<sup>-1</sup>) (Jhee et al., 2005). These included the folivores *Melanoplus femurrubrum* (De Geer) (Orthoptera: Acrididae), *Evergestis rimosalis* Guenée (Lepidoptera: Pyralidae), and the rhizovore *Delia radicum* L. (Diptera: Anthomyiidae). *Pieris rapae* also preferred unamended to treated plants (180 and 7 400 mg Ni kg<sup>-1</sup> soil, respectively) (Martens & Boyd, 1994). The feeding behaviors of aphids and other vascular feeding insects were not altered by Ni accumulation in plants (Boyd & Martens, 1999; Jhee et al., 2005).

The lepidopteran, *Spodoptera exigua* Hübner, exposed to different forms of Se were deterred from feeding by inorganic Se compounds (sodium selenate and sodium selenite) at LC<sub>30</sub> values and greater for first and third instars (Vickerman & Trumble, 1999). By contrast, this same study revealed that organic Se compounds did not serve as feeding deterrents for third-instar *S. exigua*, though first instars preferred controls to these compounds 50–75% of the time. Sodium selenate accumulated by *Brassica juncea* (L.) Czern. (Brassicaceae) also effectively prevented *Acheta domestica* (L.) (Orthoptera: Gryllidae) feeding in choice experiments (Freeman et al., 2007) with 5× as many crickets preferring controls to treated leaves ( $546 \pm 38 \mu\text{g Se g}^{-1}$  dry weight). At 10 mg kg<sup>-1</sup> dry leaf weight, *B. juncea* with incorporated sodium selenate also successfully deterred *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) feeding and prevented colonization (Hanson et al., 2004). When fed alfalfa with incorporated Se, first-instar *S. exigua* were unable to distinguish between low and high ( $2.88 \pm 0.52$  vs.  $305.81 \pm 52.14 \mu\text{g g}^{-1}$  plant dry weight) concentrations of Se compared with controls (Vickerman et al., 2002b). Fourth instars did not differentiate between low Se and controls, but avoided high Se plants. Alternatively, various polyphagous acridid grasshoppers chose low-Se *Stanleya pinnata* (Pursh) Britton (Brassicaceae) significantly more often than high-concentration alternatives (1 vs.  $230 \mu\text{g g}^{-1}$  dry weight) in choice experiments (Freeman et al., 2007). A recently discovered biotype of a lepidopteran, *Plutella xylostella* Stanleyi (Lepidoptera: Plutellidae), was shown to withstand accumulated concentrations of  $2\,000 \mu\text{g Se g}^{-1}$  dry weight on *S. pinnata* and larvae showed no preference for low or high ( $47$  vs.  $792 \mu\text{g g}^{-1}$  dry weight) Se-treated plants in choice experiments, as opposed to *P. xylostella* G88 and *P. rapae* which avoided higher concentrations (Freeman et al., 2006).

Although there are many studies reporting the effects of As on insects, relatively few report behavioral impacts. In terms of ingestion behaviors, only a single paper was found. Rathinasabapathi et al. (2007) reported avoidance by *Schistocerca americana* (Drury) of lettuce contaminated with As when given a choice with low-As treated plants ( $46.14 \pm 22$  vs.  $2.3 \pm 0.2 \text{ mg kg}^{-1}$ ). They showed adult *S. americana* took taste bites before rejecting highly contaminated lettuce, indicating As is detected through gustation.

In polluted areas, metals often exist as simple or complex mixtures. Migula & Binkowska (1993) investigated the ability of populations of *Chorthippus* spp. (Orthoptera: Acrididae) from heavily and weakly polluted sites to distinguish between Cd, lead (Pb), and Cd + Pb exposed diets. They found that grasshoppers locally adapted in weakly polluted sites did not have the ability to distinguish

between leaves with different metal concentrations, whereas those from heavily polluted sites reduced their consumption rate with increasing Cd and Pb concentrations. This may indicate learned avoidance behavior in *Chorthippus* populations living in taxing environments. In a different experiment examining the effects of Cd alone, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) also experienced a significant decrease in feeding, as measured by the 'leaf feeding damage index' for treatment concentrations ranging from 0 to  $300 \text{ mg kg}^{-1}$  in *Thlaspi caerulescens* J. & C. Presl (Brassicaceae) varieties (Jiang et al., 2005).

A subset of research investigating metal impacts on ingestion behaviors examined plant biocontrol agents, with varying results. First-instar *Bactra verutana* Zeller (Lepidoptera: Tortricidae) exposed to purple nutsedge for up to 4 weeks were unaffected by Cd concentrations up to  $18 \mu\text{g g}^{-1}$  (Quimby et al., 1979). *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae) exposed to  $8.7 \mu\text{g Cd g}^{-1}$  alligatorweed showed an inability to distinguish between Cd contaminated and uncontaminated plants, though they did experience feeding depression when fed on Cd-contaminated leaves in choice experiments (Quimby et al., 1979).

*Neochetina bruchi* Hustache (Coleoptera: Curculionidae) is used in the control of water hyacinth, an emergent, metal-accumulating aquatic plant, and spends its life on the leaf surface. When separately exposed to Cd and Zn, Jamil et al. (1989a,b) found a significant decrease in the number of water hyacinth feeding lesions, reflecting a decrease in feeding activity with increasing exposure concentration for both metals. There was no significant difference between numbers of feeding lesions found in plants accumulating up to  $89.5$  and  $165 \mu\text{g Zn}/100 \text{ g dry weight}$ ; however, lesions were significantly fewer when *N. bruchi* were fed on plants accumulating  $232 \mu\text{g Zn}/100 \text{ g dry weight}$  (Jamil et al., 1989a,b). Cd exposure accumulating to levels of 3.78, 6.20, and  $66.70 \mu\text{g}/100 \text{ g dry weight}$  showed the same pattern of feeding depression (Jamil et al., 1989a), with no effect of the lower concentrations on number of feeding lesions. This finding supports results by Quimby et al. (1979).

A different species of water hyacinth beetle, *Neochetina eichhorniae* Warner, had conflicting behavioral outcomes in the presence of Cd when compared with *N. bruchi* (Kay & Haller, 1986). Water hyacinth with  $8.00$  and  $17.20 \mu\text{g Cd g}^{-1}$  leaves did not experience decreased feeding activity of *N. eichhorniae* when compared with controls. *Neochetina eichhorniae* feeding activity when exposed to  $21.62$  and  $44.77 \mu\text{g g}^{-1}$  Cu and  $5.89$  and  $9.84 \mu\text{g g}^{-1}$  Pb was also not significantly different from controls. Kay & Haller (1986) exposed beetles to contaminated water hyacinth for

10 days, vs. Jamil et al. (1989a,b) who exposed beetles for 7 days, and did not report feeding depression at any point during their assays. This implies that *N. eichhorniae* is more tolerant of metals uptake by water hyacinth than *N. bruchi*.

Other studies on the antifeedant effects of metals on beetles showed a consistent decrease in feeding activity as a result of dietary exposure. Third instars of *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) exposed to  $\text{CuSO}_4$  (El-Bassiouny, 1991) and  $\text{Pb}(\text{NO}_3)_2$  (Kwartirnikov et al., 1999) significantly decreased feeding activity compared with controls, which were more pronounced for increasing concentrations of each antifeedant. Adult *L. decemlineata* exposed to  $\text{Pb}(\text{NO}_3)_2$  also showed decreased feeding activity, though this result was less pronounced than for larvae (Kwartirnikov et al., 1999).

Complex preference experiments by Rokytořová et al. (2004) revealed that adult *Lochmaea capreae* L. (Coleoptera: Chrysomelidae) did not alter feeding activity on birch leaves dipped in Cd ( $2\text{--}250 \mu\text{g ml}^{-1}$ ) and Pb ( $4\text{--}500 \mu\text{g ml}^{-1}$ ). For manganese (Mn) and Zn, feeding activity significantly decreased between low and high concentrations ( $100\text{--}500$  and  $10\,000 \mu\text{g Mn ml}^{-1}$ , and  $80\text{--}400$  and  $8\,000 \mu\text{g Zn ml}^{-1}$ , respectively). They also avoided high concentrations of Mn and Zn more often than all concentrations of Cd and Pb. Another chrysomelid, *Melasma lapponica* L. (Coleoptera: Chrysomelidae) showed a preference for very high ( $273.3 \text{ mg Ni kg}^{-1}$  and  $95.4 \text{ mg Cu kg}^{-1}$ ) and very low ( $27.7 \text{ mg Ni kg}^{-1}$  and  $16.9 \text{ mg Cu kg}^{-1}$ ) concentrations of Cu and Ni in willow foliage along a distance gradient from a smelter (Zvereva & Kozlov, 1996). For this species, some feeding was necessary on undamaged leaves before rejection, though damaged leaves with metal exposures were identified and rejected before feeding, possibly due to an increased release of deterrent substances (Zvereva & Kozlov, 1996).

Finally, a handful of studies have examined the effects of metals on soil-dwelling invertebrate feeding behavior. *Orchesella cincta* (L.) (Collembola: Entomobryidae) showed no significant preference for green algae diet contaminated with  $\text{Pb}(\text{NO}_3)_2$  up to  $1\,600 \mu\text{g g}^{-1}$ , and the authors concluded that avoidance was not necessary due to efficient excretion mechanisms already in place (van Capelleveen et al., 1986). Fountain & Hopkin (2001) reported significant avoidance of Pb-contaminated diet at  $2\,170 \mu\text{g g}^{-1}$  for *Folsomia candida* Willem (Collembola: Isotomidae), but no significant avoidance of diet contaminated with  $406 \mu\text{g g}^{-1}$  Pb, consistent with van Capelleveen et al. (1986). *Orchesella cincta* was similarly unaffected by Mn in the diet up to  $9.2 \pm 0.3 \mu\text{mol g}^{-1}$  dry mass, though iron (Fe) caused a significant decrease in feeding activity, especially at higher concentrations (Nottrot et al., 1987).

In a field study, *Sphaeridia pumilis* Krausbauer (Collembola: Sminthuridae), *Parisotoma notabilis* (Schäffer) (Collembola: Isotomidae), and *Mesaphorura macrochaeta* (Rusek) (Collembola: Onychiuridae) gut contents reflected preferential avoidance of the organic horizon where the majority of Cd, Pb, and Zn were concentrated (Gillet & Ponge, 2003).

Copper-contaminated diet significantly deterred *F. candida* at  $1\,500 \mu\text{g g}^{-1}$  dry weight in the laboratory (Filser & Hölscher, 1997), and *Onychiurus armatus* (Tullberg) (Collembola: Onychiuridae) with a 13.5% Cu solution-soaked diet (Filser et al., 2000). By contrast, *Isotomurus palustris* (Müller) (Collembola: Isotomidae) fed on diet with Cu contamination as often as on uncontaminated diet, and *F. quadrioculata* and *F. manolachei* preferred Cu-contaminated diet (Filser et al., 2000). *Folsomia candida* significantly avoided Cu-contaminated yeast at concentrations exceeding  $10 \mu\text{g g}^{-1}$  (Fountain & Hopkin, 2001). *Folsomia candida* also avoided yeast contaminated with Cd at concentrations exceeding  $28 \mu\text{g g}^{-1}$ , and always preferred controls to Zn-contaminated diet (Fountain & Hopkin, 2001).

*Taxis behavior.* Taxis is an oriented movement in response to a directional stimulus or a stimulus gradient. All of the available research investigating locomotory effects of pollution has focused on carabids and collembolans, with the exception of one study investigating pupation-site preference in *D. melanogaster*. Unfortunately, the studies appear to be contradictory, making deduction of patterns impossible. Bayley et al. (1995) found that *Pterostichus cupreus* L. (Coleoptera: Carabidae) larvae exposed to  $500 \mu\text{g Cu g}^{-1}$  in soil and diet experienced severely impaired locomotion as adults. This resulted in decreased prey capture success as adults, despite the absence of antifeedant properties in the larval diet (Bayley et al., 1995). Though collembolans were shown to avoid Cu-contaminated diets, they tended to not avoid Cu-contaminated soils, the exceptions being *M. macrochaeta* and *Folsomia manolachei* Bagnall (Filser & Hölscher, 1997) and *Pseudosinella alba* (Packard) (Collembola: Entomobryidae) (Filser et al., 2000).

By contrast, Lock et al. (2001) sampled seven sites within the vicinity of an abandoned Pb-Zn mine and found no significant relationship between relative activity of carabids and measureable metal concentrations in soils. Activity was measured using pitfall traps in combination with diversity sampling to determine whether certain species were more active given particular soil metal concentrations. The lack of significance despite a gradient in total Pb, Cd, and Cu concentrations was attributed to these metals not being bioavailable to the predatory carabids (Lock et al., 2001).

*Parisotoma notabilis* exposed to a gradient of Cd, Pb, and Zn pollution in the field followed the distribution of its weakly polluted food source by shifting position in the soil from surface to deeper horizons, and thus avoided changing its feeding habits (Gillet & Ponge, 2003). Using methodology identical to that of Lock et al. (2001, 2003) determined that a location with similar contaminants as that of Gillet & Ponge (2003) showed no significant relationship between activity of collembolans and metal concentrations in soils. This difference in collembolan activity may have been caused by the high concentrations of Cd, Pb, and Zn reported in Gillet & Ponge (2003), compared with those in Lock et al. (2001). Other studies examining mixtures of metals in contaminated soils revealed that *F. candida* consistently avoided heavily contaminated soils, though there was high variability in individual response (Natal da Luz et al., 2004). Reporting an overall response of a conglomerate soil insect fauna, Gongalsky et al. (2009) found consistent avoidance of heavily contaminated soils. Collectively, the broadly contradictory results from the available research suggest there are many environmental factors that may influence movement. Thus, substantial opportunities exist for additional research on this topic.

In choice trials, Bahadorani & Hilliker (2009) found no significant difference in pupation-site preference in late-instar *D. melanogaster* when presented with normal food and food with a concentration of 70 mmol Zn l<sup>-1</sup>. Larvae did, however, significantly prefer normal food to Cu-contaminated food (20 mmol l<sup>-1</sup>). They also significantly preferred pupating in Fe (II)-contaminated food (70 mmol l<sup>-1</sup>) to non-contaminated food.

**Oviposition.** To date, only five publications reported the effects of metals on ovipositional response in terrestrial insects. When given a choice between concentrations of ovipositional substrate exposed to hexavalent chromium (Cr VI) (50, 500, 1 000 µg g<sup>-1</sup>), Trumble & Jensen (2004) found that females of *Megaselia scalaris* Loew (Diptera: Phoridae) did not discriminate between control, low, and high concentrations. This occurred despite the observation that the highest level was toxic to the larvae. In a different study on a dipteran, Bahadorani & Hilliker (2009) reported that mated female *D. melanogaster* significantly decreased egg laying at relatively high concentrations of heavy metals (2 mmol l<sup>-1</sup> Cd, 10 mmol l<sup>-1</sup> Cu, 40 mmol l<sup>-1</sup> Fe (II), 20 mmol l<sup>-1</sup> Fe (III), and 30 mmol l<sup>-1</sup> Zn). Interestingly, for both Fe and Zn, oviposition increased significantly relative to controls (0 mmol l<sup>-1</sup> for each) at lower concentrations. This indicates that the female not only senses metals in the environment, but also knows which concentrations will maximize the fitness of her offspring.

Two studies were available that examined oviposition by *S. exigua* in response to Se. Females preferred to oviposit on low concentrations of Se-treated alfalfa (2.88 ± 0.52 µg Se g<sup>-1</sup> dry weight) over controls (Vickerman et al., 2002b). However, adult females were unable to distinguish between low and high (305.81 ± 52.14 µg Se g<sup>-1</sup> dry weight) concentrations of Se for oviposition, despite the fact that the high level was toxic. In a second study examining oviposition on *Atriplex* spp. plants which accumulate Se, *S. exigua* did not distinguish between plants that contained concentrations of Se that were toxic to their offspring (Vickerman et al., 2002a). For both *M. scalaris* and *S. exigua*, the inability to distinguish between lethal concentrations of Cr VI and Se, respectively, puts eggs and larvae at risk at exposed oviposition sites.

Finally, the newly discovered *P. xylostella* Stanleyi biotype does not differentiate between high and low concentrations of Se in *S. pinnata* when ovipositing. This is in direct contrast to a different ecotype, *P. xylostella* G88, and *P. rapae*, which avoided ovipositing on highly Se-contaminated plants (Freeman et al., 2006).

#### Aquatic systems

**Ingestion behavior.** As was the case with CuSO<sub>4</sub> and oligophagous terrestrial herbivores, Hatakeyama & Yasuno (1981) found that aquatic systems with Cu available in concentrations from 0.01 to 0.64 mg Cu l<sup>-1</sup> resulted in reduced food uptake in first-instar *Paratanytarsus parthenogeneticus* Freeman (Diptera: Chironomidae), as measured by the area of deposited feces. Lowered egestion rates were similarly observed for *Chironomus riparius* Meigen (Diptera: Chironomidae) exposed to Zn, Cd, and Fe contaminated sediments (Leppänen et al., 1998). However, this was only the case at one of their treatment locations (2 356.4 µg Cd g<sup>-1</sup> sediment, 38 mg Zn g<sup>-1</sup>, and 17 mg Fe g<sup>-1</sup>). One of the reference locations with minimal contamination also contained chironomids with decreased egestion (7.2 µg Cd g<sup>-1</sup> sediment, 0.9 mg Zn g<sup>-1</sup>, and 42.4 mg Fe g<sup>-1</sup>) when compared with the other reference location (9.0 µg Cd g<sup>-1</sup> sediment, 1.1 mg Zn g<sup>-1</sup>, and 17.4 mg Fe g<sup>-1</sup>). Because of this discrepancy, the authors were unable to conclude whether metal-contaminated sediments had a significant impact on feeding rates of *C. riparius* (Leppänen et al., 1998). A separate field study examining post-exposure feeding depression of *C. riparius* revealed no significant difference between reference, low contamination, and highly contaminated field locations (Faria et al., 2006). Contaminated sites contained a mixture of metals, including As, Cd, Cr, Cu, Fe, Pb, Mn, Ni, and Zn. Post-exposure feeding depression was measured as the amount of algae consumed in an uncontaminated environment after exposure for 6 days, to eval-



uate the effect of acute pollution pulses on long term population viability of *C. riparius* (Faria et al., 2006).

Irving et al. (2003) reported significantly decreased feeding rates for *Baetis tricaudatus* Dodds (Ephemeroptera: Baetidae) exposed to dietary Cd, though they did not preferentially avoid Cd-contaminated diatom mats. Feeding inhibition was apparent after 8 days for both Cd treatments (10 and 84  $\mu\text{g Cd g}^{-1}$  diatoms). Cd concentrations of 0.5–1.0  $\text{mg l}^{-1}$  were further shown to disrupt filter feeding behaviors in fourth-instar *Glyptotendipes pallens* (Meigen) (Diptera: Chironomidae) and result in increased defecation rates, possibly in an attempt to regulate Cd uptake (Heinis et al., 1990).

Only two studies evaluated the impacts of heavy metal contamination on predator hunting behaviors. In a complex factorial design, *B. tricaudatus*, *Kogotus nonus* (Needham & Claassen) (Plecoptera: Perlodidae), and two fish species were placed in a mesocosm and the effects of dietary and waterborne Cd contamination evaluated (Riddell et al., 2005). Because *K. nonus* are predators, only waterborne Cd contamination (0.5 and 5  $\mu\text{g Cd l}^{-1}$ ) was relevant to their behaviors in this experiment. At both concentrations, locomotory activities were significantly reduced, resulting in impaired foraging abilities. Only two of nine attacks on prey were successful, and both occurred at the 0.5  $\mu\text{g l}^{-1}$  treatment, so further extrapolation about effects on predation behaviors could not be made (Riddell et al., 2005). Jensen (2006) evaluated the effects of Se and/or methyl-mercury (MeHg) on consumption rates of *Sympetrum corruptum* (Hagen) (Odonata: Libellulidae) when fed *Culex quinquefasciatus* Say (Diptera: Culicidae). He found that *S. corruptum* in Se treatment solutions consumed significantly more mosquito larvae per day than controls; however, predators eating prey contaminated with Se + MeHg consumed significantly fewer prey per day. Predators' consuming more in Se-treated water with non-treated prey was attributed to the mosquito larvae experiencing a reduction in avoidance behavior. Predators' consuming less in the Se + MeHg treatments was attributed to treatments making the prey unpalatable or suppressing the predator's appetite (Jensen, 2006).

Several studies have evaluated the impacts of metal exposure on the construction of capture nets by *Hydropsyche* spp. (Trichoptera: Hydropsychidae). These nets are used to capture drifting plant and animal materials; therefore, construction anomalies have the potential to negatively impact the efficiency with which nymphs are able to recover food items. Fifth-instar *H. betteni* adapted to either polluted or unpolluted environments were collected from the field and exposed to waterborne (5.4 or 10.7  $\text{mg l}^{-1}$ ) and dietary (113  $\mu\text{g g}^{-1}$ ) Zn (Balch et al., 2000). After 5 and 7 weeks, nymphs from unpolluted and polluted popu-

lations, respectively, exhibited significantly looser net structures with such large openings between net strands that capture efficiency was negligible. Interestingly, larvae exposed to waterborne Zn at 42.1 and 21.7  $\text{mg l}^{-1}$  showed no significant difference in net spinning capabilities (Balch et al., 2000). Third and fourth-instar *H. slossonae* exposed to Cd also exhibited an increase in net anomalies (Tessier et al., 2000). After 5 days, approximately 60% of nymphs exposed to 43.3 and 21.4  $\mu\text{g Cd l}^{-1}$  experienced strand crossover anomalies, with 100% of nymphs showing anomalies after 10 and 20 days, respectively. After 10 days, approximately 60% of nymphs exposed to 11.6  $\mu\text{g Cd l}^{-1}$  experienced strand crossover anomalies, with 100% of nymphs showing anomalies after 15 days. The lowest concentrations tested (1.2 and 0.37  $\mu\text{g Cd l}^{-1}$ ) exhibited approximately 50% of nymphs with net anomalies apparent after 15 and 20 days, respectively. Background anomalies in control treatments were found to be approximately 20% (Tessier et al., 2000).

By contrast, Petersen & Petersen (1983) pooled data for *Hydropsyche* spp. net anomalies after determining that the number of anomalies was independent of species. Specifically, they evaluated the possibility of increased strand crossover frequencies which can result in smaller mesh openings with less uniform strand arrangements. They found that net strand crossover frequency at heavy metal-contaminated field locations was not significantly different from control sites. Metals present at different locations varied and though exact concentrations were not reported, exposure levels were always sublethal. However, the lack of information on metal concentrations in the Petersen & Petersen (1983) report makes direct comparisons with the studies by Balch et al. (2000) and Tessier et al. (2000) impossible. This highlights the critical need for reporting detailed information on metal concentrations which are necessary for documenting potential patterns in insect responses.

*Taxis behavior.* Drift was the most commonly measured response of invertebrates in aquatic systems to pollution, and is defined as an organism detaching from the substrate and swimming or floating downstream. This behavior is used to escape localized pollution, with the tradeoff being greater exposure to predation. It is easily measured in the field just downstream of point sources of pollution and allows for a community-wide assessment of the impacts of contaminants on downstream movements of insects.

For example, aluminum (Al) (0.95  $\text{mg l}^{-1}$ ) caused chironomids to enter the drift column 4–8 times more frequently after exposure for 6 h than controls (Bernard et al., 1990). In this same study, Ephemeroptera and Trichoptera spp. entered the drift column 10–15 $\times$  and 3–5 $\times$

**Table 2** Summary of contaminants and the resultant behavioral outcome observed for insect species in aquatic habitats

Metal	Form	Species	Behavioral outcome	Reference
A. Ingestion behavior				
Copper	CuSO <sub>4</sub> ·5H <sub>2</sub> O	<i>Paratanytarsus parthenogeneticus</i>	Negative	Hatakeyama & Yasuno, 1981
Cadmium	Cd	<i>Hydropsyche slossonae</i>	Negative	Tessier et al., 2000
	CdCl <sub>2</sub>	<i>Baetis tricaudatus</i> <i>Glyptotendipes pallens</i> <i>Kogotus nonus</i>	Negative Negative Negative	Irving et al., 2003; Riddell et al., 2005 Heinis et al., 1990 Riddell et al., 2005
Selenium	Na <sub>2</sub> SeO <sub>4</sub>	<i>Culex quinquefasciatus</i> <i>Sympetrum corruptum</i>	Negative Positive	Jensen, 2006 Jensen, 2006
Zinc	ZnSO <sub>4</sub> ·7H <sub>2</sub> O	<i>Hydropsyche betteni</i>	Negative	Balch et al., 2000
B. Taxis behavior				
Aluminum	AlCl <sub>3</sub>	Chironomidae	Positive	Bernard et al., 1990
		Ephemeroptera	Positive	Bernard et al., 1990; Bernard, 1985
		Plecoptera	No effect	Bernard et al., 1990; Bernard, 1985
		<i>Simulium</i> spp.	Negative	Bernard, 1985
		<i>Simulium</i> spp.	No effect	Bernard et al., 1990
		Trichoptera	Positive	Bernard et al., 1990
		Al <sub>2</sub> (SO <sub>4</sub> ) <sub>3</sub>	<i>Baetis rhodani</i>	Positive
	<i>Dicranota</i> spp.		Positive	Ormerod et al., 1987
	<i>Dixa puberula</i>		Positive	Ormerod et al., 1987
	<i>Elmis aenea</i>		No effect	Ormerod et al., 1987
	<i>Ephemerella danica</i>		Positive	Herrmann & Andersson, 1986
	<i>Ephemerella ignita</i>		Positive	Ormerod et al., 1987
	<i>Heptagenia fuscogrisea</i>		Positive	Herrmann & Andersson, 1986
	<i>Heptagenia sulphurea</i>		Positive	Herrmann & Andersson, 1986
	<i>Leuctra</i> spp.		No effect	Ormerod et al., 1987
	<i>Protonemura meyeri</i>		Negative	Ormerod et al., 1987
	Cadmium	Cd	Simuliidae	Negative
<i>Chironomus salinarius</i>			No effect	Hare & Shooner, 1995
<i>Procladius</i> spp.			No effect	Hare & Shooner, 1995
CdCl <sub>2</sub>		<i>Sergentia coracina</i>	No effect	Hare & Shooner, 1995
		<i>Baetis tricaudatus</i>	Negative	Riddell et al., 2005
		<i>Glyptotendipes pallens</i>	Negative	Heinis et al., 1990
		<i>Hexagenia limbata</i>	No effect	Gosselin & Hare, 2004
3CdSO <sub>4</sub> ·8H <sub>2</sub> O		<i>Hexagenia rigida</i>	Positive	Odin et al., 1995
		<i>Baetis rhodani</i>	Negative	Gerhardt, 1990
		Hydropsychidae	Positive	Vuori, 1994
Copper	Cu	<i>Leptophlebia marginata</i>	No effect	Gerhardt, 1990
		<i>Adenophlebia auriculata</i>	Positive	Gerhardt & Palmer, 1998
		<i>Chimarra</i> spp.	Negative	Clements et al., 1989
		<i>Cinygmula</i> spp.	No effect	Stitt et al., 2006
		<i>Hydropsyche morosa</i>	Negative	Clements et al., 1989
		<i>Paragnetina media</i>	No effect	Clements et al., 1989
		<i>Hydropsyche angustipennis</i>	Negative	van der Geest et al., 1999
	CuCl <sub>2</sub> CuSO <sub>4</sub>	<i>Baetis</i> spp.	Positive	Leland, 1985
		Chironomidae	Positive	Leland, 1985
		<i>Chironomus riparius</i>	No effect	Dornfeld et al., 2009
		<i>Cleptelmis addenda</i>	No effect	Leland, 1985
		<i>Lepidostoma</i> spp.	Positive	Leland, 1985
		<i>Optioservus divergens</i>	Positive	Leland, 1985
	<i>Paraleptophlebia pallipes</i>	Positive	Leland, 1985	
	<i>Simulium</i> spp.	No effect	Leland, 1985	
	<i>Symphitopsyche oslari</i>	Negative	Leland, 1985	

Table 2 (Continued)

Metal	Form	Species	Behavioral outcome	Reference
Iron	FeSO <sub>4</sub> ·7H <sub>2</sub> O	<i>Leptophlebia marginata</i>	Negative	Gerhardt, 1992, 1994
Lead	PbCl <sub>2</sub>	<i>Leptophlebia marginata</i>	Negative	Gerhardt, 1994
Mercury	CH <sub>3</sub> HgCl	<i>Hexagenia rigida</i>	Positive	Odin et al., 1995
C. Oviposition				
Cadmium	CdCl <sub>2</sub> ·2½H <sub>2</sub> O	<i>Chironomus riparius</i>	Negative	Williams et al., 1987
Copper	CuSO <sub>4</sub> ·5H <sub>2</sub> O	<i>Chironomus riparius</i>	No effect	Dornfeld et al., 2009
Mercury	CH <sub>3</sub> ClHg	<i>Culex quinquefasciatus</i>	No effect	Jensen et al., 2007
Selenium	Na <sub>2</sub> SeO <sub>4</sub>	<i>Culex quinquefasciatus</i>	No effect	Jensen et al., 2007

Only individual metals/metalloids are considered for behavioral outcomes because mixtures may lead to synergistic or antagonistic interactions otherwise unaccounted for in the behavioral response. Positive and negative outcomes correspond to stimulation or suppression of the particular behavior as a result of metal presence, respectively, and 'no effect' means the organism was unaffected at the experimental conditions. In choice assays, aversion results in a negative behavioral outcome. See text for the measured concentrations.

more frequently, respectively, while *Simulium* spp. (Diptera: Simuliidae) and *Plecoptera* spp. experienced no significant increase in drift throughout the 12-h study duration. When exposed to Al with varying pH values, Plecoptera nymphs failed to respond by increasing drift when dissolved Al concentration was increased from 31.0 to 40.2 µg l<sup>-1</sup>, and the pH decreased from 7.0 to 5.9 (Bernard, 1985). This may be due to a lack of sensory capacity to detect Al increases within the range tested, or because the chemical was not physiologically stressful at the tested concentration. Trichoptera and *Simulium* spp. both experienced a delayed response at the above concentrations, possibly due to a disruption of physiological processes. Ephemeroptera, the most sensitive order evaluated, showed an immediate response to the Al influx, possibly because they are able to detect this ion in their environment through chemoreceptors (Bernard, 1985). Chironomids became sensitive to Al only after pH had decreased in this experiment. In a different study on pH impacts on Al toxic response, Ormerod et al. (1987) examined a wider range of taxa. Both *Leuctra* spp. (Plecoptera: Leuctridae) and *Elmis aenea* (Müller) (Coleoptera: Elmidae) did not change drift patterns in response to an acid and Al pulse. *Ephemerella ignita* (Poda) (Ephemeroptera: Ephemerellidae) showed significantly increased drift during the episode, and *Baetis rhodani* Pictet (Ephemeroptera: Baetidae) drift density increased 8.4× relative to the control. Simuliidae drift increased 3.6×, and *Protonemura meyeri* Pictet (Plecoptera: Nemouridae) increased 1.6× during treatment and remained high the following day. Both *Dixa puberula* Loew (Diptera: Dixidae) and *Dicranota* spp. (Diptera: Pediciidae) showed significantly increased drift, but only during the episode (Ormerod et al., 1987).

However, not all metals produce a significant drift response. There was no significant difference in drift rate

of *Cinygmula* spp. (Ephemeroptera: Heptageniidae) at concentrations of 78 and 229 µg l<sup>-1</sup> Cu (Stitt et al., 2006), and rates of drift at 3 µg l<sup>-1</sup> Cu were not significantly different from the control. After dosing experimental stream channels with Cu at three concentrations (2.5, 7, and 15 µg l<sup>-1</sup>), Leland (1985) found that *Cleptelmis addenda* (Fall) (Coleoptera: Elmidae) showed no significant increase in drift compared with controls, whereas drift rate of *Optioservus divergens* (Leconte) (Coleoptera: Elmidae) increased slightly at 2.5 and 15 µg Cu l<sup>-1</sup>. *Paraleptophlebia pallipes* (Eaton) (Ephemeroptera: Leptophlebiidae), *Baetis* spp., and *Lepidostoma* spp. (Trichoptera: Lepidostomatidae) increased drift at 7 and 15 µg Cu l<sup>-1</sup>, whereas *Symphitopsyche oslari* Banks (Trichoptera: Hydropsychidae) decreases drift at these concentrations. Drift of chironomids decreased slightly at 7 µg Cu l<sup>-1</sup>, and increased at 15 µg Cu l<sup>-1</sup>, whereas *Simulium* spp. drift was unaffected by Cu (Leland, 1985).

One study documented a decreasing response as pollution levels increased. Riddell et al. (2005) demonstrated that *B. tricaudatus* drift decreased with increasing concentrations of Cd. However, they used a recirculating stream system, so drift behavior did not allow insects to escape to a lower concentration. They suggested that continued exposure could have reduced locomotory behavior, or that an increased energy demand due to contaminant acclimation or detoxification could have reduced the energy available for relocation.

When exposed to multiple metals (2.2 µg Cd l<sup>-1</sup>, 24 µg Cu l<sup>-1</sup>, and 200 µg Zn l<sup>-1</sup>), various aquatic insects (Coleoptera: Elmidae; Diptera: Chironomidae; Ephemeroptera, Plecoptera, and Trichoptera: Hydropsychidae) from populations locally evolved in uncontaminated streams experienced significant increases in drift (Clements, 1999). Because all of the organisms collected in

drift nets were still alive, the authors were able to conclude that drift was a behavioral response to avoid heavy metals in the water. In choice experiments with contaminated sediments, first-instar *C. riparius* exposed to 2 mg Cu l<sup>-1</sup> (Dornfeld et al., 2009) and fourth-instar *C. salinarius*, *Sergentia coracina* (Zetterstedt), (Diptera: Chironomidae) and *Procladius* spp. (Diptera: Chironomidae) exposed to 0.15 µg Cd l<sup>-1</sup> (Hare & Shooner, 1995) were unable to distinguish between treated and control sediments. In choice experiments using sediments collected from five treatments and two reference locations, *C. tentans* preferred control over treatment sediments for the most highly contaminated locations only (774 mg l<sup>-1</sup> Cd, 11 134 mg l<sup>-1</sup> Zn, 1 393 mg l<sup>-1</sup> Cr; 964 mg l<sup>-1</sup> Cd, 16 397 mg l<sup>-1</sup> Zn, 2 129 mg l<sup>-1</sup> Cr; and 1 029 mg l<sup>-1</sup> Cd, 17 262 mg l<sup>-1</sup> Zn, 1 640 mg l<sup>-1</sup> Cr) (Wentzel et al., 1977).

Evaluations of heavy metal impacts on other locomotory behaviors are also common. Cd concentrations ranging from 2.5 to 10 mg l<sup>-1</sup> were shown to significantly increase time spent in inactive states for *G. pallens* (Heinis et al., 1990). Exposure to levels as low as 0.02 mg Cd l<sup>-1</sup> were shown to reduce locomotion in *B. rhodani*, whereas *Leptophlebia marginata* (L.) (Ephemeroptera: Leptophlebiidae), exposed to 0.2 mg Cd l<sup>-1</sup>, showed no difference in locomotory activities compared with controls (Gerhardt, 1990). Based on these results, Gerhardt (1990) concluded that locomotion was a good parameter to measure in cases of suspected subacute chemical stress. He reached the same conclusion when Fe-exposed *L. marginata* decreased motility in proportion to the concentration of dissolved Fe (10, 20, and 50 mg l<sup>-1</sup>) (Gerhardt, 1992). At much lower levels of contamination, female *Hexagenia limbata* (Serville) (Ephemeroptera: Ephemeridae) exposed to 18.9 µg Cd g<sup>-1</sup> in sediment and 5.8 µg Cd l<sup>-1</sup> in water experienced no discernable effect on burrowing activities (Gosselin & Hare, 2004). Similarly, concentrations of 0.05–0.1 mg Cd l<sup>-1</sup> had relatively minor impacts on activity of *G. pallens* (Heinis et al., 1990).

Exposure at concentrations of 0.05–0.296 mg Cu l<sup>-1</sup> led to increased escape behavior by *Adenophlebia auriculata* Eaton (Ephemeroptera: Leptophlebiidae): mayflies searched for stones away from areas of Cu input (Gerhardt & Palmer, 1998). There were more ventilation and abdominal undulations observed at these concentrations as well, possibly in an attempt to rid Cu ions bound in gill membranes. Finally, *A. auriculata* was more prone to climbing on top of rocks instead of maintaining negative phototactic behaviors observed in controls. By contrast, *L. marginata* showed a decrease in escape behavior correlated to increasing exposure time and Fe (10–500 mg l<sup>-1</sup>) and Pb (0.1–5.0 mg l<sup>-1</sup>) concentrations (Gerhardt, 1994). Odin et al. (1995) reported increased bioturbation activity of

*Hexagenia rigida* McDunnough (Ephemeroptera: Ephemeridae), as measured by turbidity in the water column, when nymphs were exposed to sediment concentrations up to 10 mg Cd kg<sup>-1</sup> and MeHg concentrations up to 2.98 mg kg<sup>-1</sup>. Interestingly, nymphs were unaffected when the exposure route was water only (Odin et al., 1995).

For *Hydropsyche angustipennis* (Curtis) (Trichoptera: Hydropsychidae), there was a significant decrease in ventilation, or abdominal undulatory movements, at 20 µg Cu l<sup>-1</sup>, resulting in a proportional increase in other locomotory behaviors and inactivity (van der Geest et al., 1999). Concentrations ranging from 100 to 600 µg Cu l<sup>-1</sup> caused *H. angustipennis* to spend very little time ventilating, and individuals were, for the most part, inactive. When exposed to waterborne Al at 2.0 mg l<sup>-1</sup>, nymphs of *Heptagenia fuscogrisea* (Retzius), *Heptagenia sulphurea* (Müller) (Ephemeroptera: Heptageniidae), and *Ephemerella danica* Müller (Ephemeroptera: Ephemeridae) showed significant increases in respiration (Herrmann & Andersson, 1986).

There are a few studies on combinations of metals and industrial effluents inhibiting locomotory behaviors of insects. Unfortunately, because of the variability, complexity, and unknown constituents of the industrial effluents, analysis of potential synergistic and antagonistic interactions with metals and other non-metals are not possible. However, a few of these studies are included here and will allow the reader to access this literature. Nymphs of *H. angustipennis* exposed to effluent downstream of an industrial area exhibited decreased ventilation, but other locomotory activities increased in frequency (Gerhardt, 1996). Exposed *H. pellucidula* also increased activity relative to controls (Macedo-Sousa et al., 2008). *Choroterpes picteti* (Eaton) (Ephemeroptera: Leptophlebiidae) experienced an initial increase in locomotion, but by the end of the assay, individuals in the control treatment were more active than those exposed to the acid mine drainage (AMD) treatment (Macedo-Sousa et al., 2008). In a similar study, *C. picteti* in AMD treatments increased locomotion in response to heavy metals and lower pH, which had the potential to increase nocturnal drift behavior (Gerhardt et al., 2005).

Inter- and intraspecific behaviors have not been frequently reported, particularly with relation to impacts of metals. When exposed to 0.5 and 5 µg l<sup>-1</sup> dissolved Cd in water and diet, *B. tricaudatus* were more vulnerable to predators as a result of decreased predator avoidance behaviors (Riddell et al., 2005). When crop and stomach contents from *Paragnetina media* (Walker) (Plecoptera: Perlidae) were assessed in Cu-exposed vs. control individuals, Clements et al. (1989) found an increased amount of *Hydropsyche morosa* Hagen and *Chimarra* spp.

(Trichoptera: Philopotamidae) remains, indicating increased susceptibility to predation in 5.5  $\mu\text{g Cu l}^{-1}$  contaminated waters for these species. However, various species of caddisflies exposed to a wide range of Pb, Zn, and Cd concentrations simultaneously in the field showed no difference from controls in amount of time taken to emerge from their cases after a predatory threat (Lefcort et al., 2000). In a factorial experiment, Kiffney (1996) showed that metal-contaminated water (0.7  $\mu\text{g Cd l}^{-1}$ , 6  $\mu\text{g Cu l}^{-1}$ , and 50.3  $\mu\text{g Zn l}^{-1}$ ) had no impact on *B. tricaudatus* and *Rhithrogena hageni* Eaton (Ephemeroptera: Heptageniidae) predator avoidance behaviors, while it increased predation risk to *Hydropsyche* spp. *Prostoia besametsa* (Ricker) (Plecoptera: Nemouridae) predation decreased in metals treatments compared with controls (Kiffney, 1996). Therefore, it would appear that the impact of metals on predator avoidance behavior is species dependent.

In an experiment investigating the impacts of Cd on competition behavior between conspecifics of hydropsychid larvae for optimal foraging habitat, Vuori (1994) found that exposed intruders performed shorter and less fierce attacks when paired with control residents. Exposed residents were surprisingly active during attacks against exposed intruders and fiercer than control residents, though the fights were still shorter. Attacks between control residents and intruders were longer than those involving exposed individuals. Vuori (1994) speculated this Cd-induced behavioral change might have been due to individuals weighing the personal risk involved in combat to the energy that had already been expended in spinning silk to construct a net. Though the animal may be poisoned from Cd exposure, energetically a prime territory is worth defending when a net has already been spun. By contrast, an invading caddisfly may abandon a fight to construct a net in less suitable territory, particularly if they are outmatched.

*Oviposition.* As was the case for terrestrial reproductive behaviors, only a few papers analyzed ovipositional responses of aquatic insects to metal-contaminated environments. Williams et al. (1987) found that when given a choice between water contaminated with different levels of Cd, *C. riparius* adult females distinguished between control and low concentrations (0, 0.3, and 30  $\text{mg l}^{-1}$ ) vs. high concentrations (100 and 300  $\text{mg l}^{-1}$ ). Significantly fewer eggs were laid in Petri dishes with high concentrations of Cd vs. dishes with low or control concentrations. Despite this, female aversion was only sensitive enough to avoid concentrations acutely toxic to eggs; although not toxic to eggs, these concentrations are acutely toxic to first instars (Williams et al., 1987). In another preference study,

Dornfeld et al. (2009) found *C. riparius* females unable to distinguish between control media and treatment media with 1.3  $\text{mg Cu l}^{-1}$  when ovipositing. Though egg hatchability was significantly reduced in Cu treatments, Cu did not affect larval survival (Dornfeld et al., 2009).

Similarly, *C. quinquefasciatus* did not discriminate between water contaminated with sodium selenate (30  $\text{mg l}^{-1}$ ), MeHg chloride (7  $\text{mg l}^{-1}$ ), or a mixture of sodium selenate and MeHg chloride (at the above concentrations) (Jensen et al., 2007). The authors concluded that females were either unable to detect these compounds at the tested concentrations, or did not prefer unpolluted to polluted water when ovipositing.

## Conclusions

A summary of these studies and the observed behavioral outcome for a particular contaminant can be found in Tables 1 and 2. These tables allow for a generic analysis of the broader impacts of metal and metalloid pollution in both terrestrial and aquatic systems, but are not comprehensive and not meant to serve as a quantitative meta-analysis. This qualitative classification is meant to offer the reader a quick summary of the published literature. Further, the designation of positive and negative outcomes does not necessarily confer a fitness advantage or disadvantage, and in some cases a positive behavioral outcome may have negative fitness impacts. For any given study, the outcomes may be dependent on the instar and concentrations tested, as well as exposure routes.

Over 95% of studies (53 of 55) on terrestrial ingestion behaviors reported either no effect or negative impacts as a result of individual pollutant exposure for the various behaviors quantified (Table 1A). In these studies there was some degree of repellency or feeding inhibition. Only 3.6% reported positive effects, equating to a stimulation of feeding behavior as a result of the metal being present. The substantial majority of these studies investigated impacts on lepidopteran pests, Collembola, and Orthoptera; absent or underrepresented orders merit future research. For aquatic taxis behaviors, 40% of studies (18 of 45) reported a positive behavioral stimulation of insects to some form of pollution, with the rest reporting suppressed behaviors or no effects.

Although many insect species were capable of distinguishing contaminated from uncontaminated locations, a surprising number of species evidently cannot detect the presence of metal and metalloid contamination. For purposes of reproduction, an inability to avoid heavily polluted sites would lead to loss of eggs and reduced fitness. Although some species showed a tendency to increase locomotory behaviors to escape from locations with

elevated metal pollution, other species remained and greatly decreased all movements unrelated to feeding. Still other species exhibited behaviors that would result in increased predation, including positive phototaxis that caused immatures to move to exposed positions. Ultimately, for some insects these behaviors result in reduced species fitness at contaminated sites, a general reduction in population sizes as well as species diversity, and a trend toward preponderance of those species that can tolerate pollution.

Due to the paucity of information regarding terrestrial taxis and reproductive behaviors, and aquatic ingestion and reproductive behaviors, further conclusions cannot be drawn about patterns of insect response to metals and metalloids. Analyses by feeding guild, environment (terrestrial vs. aquatic), and systematic classification did not provide evidence for a single dominant response. Additionally, the total number of species that have been investigated is relatively small. Patterns may not become evident until more research is published, particularly as many responses appear to be species-specific. A large number of papers also do not include a comparison with behaviors at uncontaminated sites, or document concentrations of the key pollutants. Although still valuable, these cannot be used as reliable evidence for behavioral changes that occur in response to metals and metalloids.

Because of the extent of the problem with metal and metalloid pollution worldwide, there is considerable opportunity for additional research. Knowledge of the effects of these pollutants at the bottom of the food web will be critical to understanding the true impact of metal contamination and to the potential reconstruction of damaged ecosystems.

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