



Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Selenium exposure results in reduced reproduction in an invasive ant species and altered competitive behavior for a native ant species[☆]

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ARTICLE INFO

Article history:

Received 11 January 2016

Received in revised form

29 February 2016

Accepted 17 March 2016

Keywords:

*Linepithema humile**Dorymyrmex bicolor*

Invasive species

Pollution

Exploitation

Interference

ABSTRACT

Competitive ability and numerical dominance are important factors contributing to the ability of invasive ant species to establish and expand their ranges in new habitats. However, few studies have investigated the impact of environmental contamination on competitive behavior in ants as a potential factor influencing dynamics between invasive and native ant species. Here we investigated the widespread contaminant selenium to investigate its potential influence on invasion by the exotic Argentine ant, *Linepithema humile*, through effects on reproduction and competitive behavior. For the fecundity experiment, treatments were provided to Argentine ant colonies via to sugar water solutions containing one of three concentrations of selenium (0, 5 and 10 $\mu\text{g Se mL}^{-1}$) that fall within the range found in soil and plants growing in contaminated areas. Competition experiments included both the Argentine ant and the native *Dorymyrmex bicolor* to determine the impact of selenium exposure (0 or 15 $\mu\text{g Se mL}^{-1}$) on exploitation- and interference-competition between ant species. The results of the fecundity experiment revealed that selenium negatively impacted queen survival and brood production of Argentine ants. Viability of the developing brood was also affected in that offspring reached adulthood only in colonies that were not given selenium, whereas those in treated colonies died in their larval stages. Selenium exposure did not alter direct competitive behaviors for either species, but selenium exposure contributed to an increased bait discovery time for *D. bicolor*. Our results suggest that environmental toxins may not only pose problems for native ant species, but may also serve as a potential obstacle for establishment among exotic species.

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1. Introduction

Competition between neighboring ants has been implicated as a driving factor in shaping ant assemblages within a given community (Cole, 1983; Rosengren, 1986; Valone and Kaspari, 2005). The coexistence of competing ant species is known to depend on key behavioral characteristics of the species, such as their ability to dominate in exploitative (indirect) or interference (direct) competitive interactions for food and territory (Fellers, 1987; Lebrun and Feener, 2007). These behaviors are considered to be an important factor in explaining successful establishment and expansion of certain invasive species in their introduced ranges, including the red imported fire ant, *Solenopsis invicta* (Porter and Savignano, 1990) and the Argentine ant, *Linepithema humile*

(Holway and Suarez, 1999; Holway et al., 2002). Unlike most native species, the Argentine ant is reportedly dominant in both exploitation and interference competition (Human and Gordon, 1996, 1999). The generation of exceptionally large population densities following introduction into new ranges have also contributed to their competitive success (Holway, 1999). The successful growth in populations of the red imported fire ant has been attributed to their greater ability to engage in mutualistic partnerships for carbohydrates, in their less competitive introduced ranges (Wilder et al., 2011). However, competition alone has been shown to play a relatively minor role in shaping ant assemblages in comparison to other environmental factors, such as resource type and availability (Sanders and Gordon, 2003), habitat complexity (Sarty et al., 2006), or disturbance (King and Tschinkel, 2006).

Anthropogenic disturbances such as fire, tree removal, flooding, and urbanization can alter ant species composition and richness (Hoffmann and Andersen, 2003; Dunn, 2004; Andersen et al., 2006; Nakamura et al., 2007; Pacheco and Vasconcelos, 2007; Graham

[☆] This paper has been recommended for acceptance by Da Chen

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et al., 2009), and thus have the potential to change competitive interactions. In some cases, such disturbances may actually encourage the colonization of invasive ant species (Suarez et al., 1998; King and Tschinkel, 2008), which may further alter dynamics within those communities. Previous studies have also investigated the effects of metal pollution on colony size, density, and species richness, where impacts ranged from neutral to detrimental (Petal, 1978; Hoffmann et al., 2000; Eeva et al., 2004; Grześ, 2009), but few studies have investigated the effects of pollution on competitive behavior and fecundity. There is some evidence for altered behavior among ants following exposure to pesticides. Research into competitive interactions between the red imported fire ant and the Argentine ant, revealed that the aggressive behavior by the red imported fire ant was reduced following ingestion of a pesticide treated bait (Kabashima et al., 2007). Similarly, exposure to a neonicotinoid pesticide resulted in altered aggressive behavior for both a native and invasive species (Barbieri et al., 2013). In an effort to reduce population growth, pesticides have been investigated for their potential to inhibit colony reproduction by specifically targeting the queens of pest species (Lofgren and Williams, 1982). Environmental contaminants may have similar effects on competitive behaviors and reproduction; therefore, more research is necessary to elucidate the mechanisms whereby changes in interspecific interactions among neighboring ant species may occur within a disturbed habitat.

Selenium (Se) is a soil-borne pollutant with particular abundance in the western United States (Brown et al., 1999). Although naturally occurring, soil and plant contamination with Se can increase via human activities (e.g. irrigation, mining and coal burning) that cause Se to become mobilized in the environment (Haygarth, 1994; Ohlendorf and Santolo, 1994). For instance, soil contamination with Se resulting from agricultural irrigation has become a serious problem affecting over 600,000 ha of farmland in eight western states (Brown et al., 1999). Selenium is also an essential dietary component for animals that helps maintain proper growth and development (Council, 1983), but toxicity can also occur following ingestion of Se that accumulates in plants that tolerate seleniferous soils (Eisler, 1985). Such plant species have been documented to contain moderate to high levels of Se in the nectar and pollen (Quinn et al., 2011; Hladun et al., 2011), which are resources consumed by ants (Markin, 1970; Blüthgen and Fiedler, 2004; Czechowski et al., 2008). De La Riva et al. (2014) determined that Argentine ants experienced toxicity to concentrations of Se substantially below those reported in the nectar and pollen. In addition, these ants displayed no aversion to even highly toxic concentrations presented in artificial nectar. Therefore, the objectives of this study were to determine effects of Se on competitive behavior and reproduction in order to document the potential influence of Se pollution on ant community dynamics and establishment/range expansion of the invasive Argentine ant.

2. Methods

2.1. Collection and study organisms

Argentine ant colonies used in both the fecundity experiment and the competition experiment were collected from the same location at the University of California, Riverside, Agricultural Operations (30°57'47"N, 117°20'20"W, 308 m). One excavation was made for each for each experiment, where each excavation is enough to gather several thousand workers and approximately 10–25 queens. Workers of the pyramid ant, *Dorymyrmex bicolor*, were collected a short distance from the UCR campus (33°59'31"N, 117°19'58"W, 314 m). We were unable to use pyramid ants in the fecundity experiment due to the inability in excavating whole

colonies. This species of pyramid ant, also belonging to the sub-family Dolichoderinae, was chosen to act as an opponent for the Argentine ant in the competition experiment, for the following reasons: 1) similar size, 2) the bicolored pattern would allow it to be easily distinguished during observations, 3) similar diet of insects, honeydew and nectar, and 4) overlapping range in southwestern California. *Dorymyrmex bicolor* was also chosen because these native ants are common in Se-contaminated sites (De La Riva and Trumble, unpublished), and have presumably evolved at least some tolerance to Se.

2.2. Fecundity assay

The initial excavated Argentine ant colony was separated into 18 smaller sized colonies. This was done to reduce variability, both genetic and physiological across the 18 sub-colonies as all ants were presumably exposed to the same environment. Each sub-colony contained 1 queen: 100 workers that were placed in small plastic food storage boxes (20 cm L × 15 cm W × 10 cm H) lined with liquid Teflon® (PTFE TE-3859, DuPont Fluoroproducts, Wilmington, DE) to prevent escape. The lids of each box had a hole in the center that was covered with mesh for ventilation. Each box contained a nest, a cotton-plugged vial of 25% sucrose, a vial of water, and approximately 3 g of chopped cockroaches, *Gromphadorhina portentosa*. Nests were composed of a 14.6 cm glass pipet that contained a small piece of cotton inside blocking the tapered end and a piece of foil paper around the outside of the pipet to create darkness (Supplemental Fig.1). Distilled water was added to the cotton weekly at the tapered end of the pipet to maintain humidity within the nest. Colony boxes were placed in an environmental chamber at 28 °C (the optimal oviposition temperature for this species, Abril et al., 2008), 12:12LD and ~60% RH. Ants were given a week to acclimate to their new surroundings before tests were conducted.

After one week of acclimation, boxes were inspected for worker deaths that may have occurred from accidental injury during the colony preparation. Dead workers were removed and replaced with live workers from the original colony. In order to simulate a toxic nectar source, we introduced Se to the colonies by removing the original sucrose solutions and replacing them with one of three different sucrose treatments (0, 5 or 10 µg Se ml⁻¹). We were confident that the ants would ingest the provided diets, because a previous choice experiment revealed that Argentine ants did not avoid sucrose containing 50 µg Se ml⁻¹, regardless of background sucrose concentrations (De La Riva et al., 2014). Selenate was the form of Se tested because it is a predominant form of selenium found in soils and taken up by plants (Pilon-Smits et al., 2013). Treatment solutions were prepared by dissolving sodium selenate powder (Na₂SeO₄, 98% purity, Sigma-Aldrich, St. Louis, MO) in 25% sucrose solutions to yield the target concentration. Cotton-plugged vials were inspected weekly for moisture or microbial growth and replaced, if necessary. Fresh treatments were provided every 4 weeks. There were a total of six replicate colonies per treatment.

In order to track oviposition and development within each box, nests were removed weekly to record the number of eggs, larvae, pupae and newly emerged adults present. Newly emerged adults were easily identified by the typical pale coloration of ant exoskeletons, which may not darken fully until several hours after eclosion. A small piece of plumbers putty was placed on the open end of the pipet to prevent escape during counting. The colony box was also inspected periodically to replace dead workers in order to keep the number of workers constant.

2.3. Competition assay

The experimental design consisted of the addition of 40 worker

ants of *L. humile* or *D. bicolor* added to small plastic colony boxes (species kept separate). These boxes were in all ways similar to those provided for fecundity assays, except for the nests. Nests were made from 9-cm-diameter plastic Petri dishes containing a layer of Plaster of Paris on the bottom half (Supplemental Fig. 2). This layer was kept moist to maintain humidity within the nest by drawing in water from an attached cotton wick that was periodically soaked with ~1–2 mL of DDI H₂O. Cardboard was placed over the top to provide darkness. In order to investigate the influence of Se ingestion on behaviors related to competitive ability, worker ants were exposed to Se treatments of 0 µg Se ml⁻¹ or a sub-lethal level of 15 µg Se ml⁻¹ (De La Riva et al., 2014) for one week before interacting with the opposing species. Treatment sugar solutions were also prepared as in fecundity assays using sodium selenate.

After one week of exposure to treatments, treatment solutions were removed from the colony box and the ants were starved for 24 h. Following this, a pair of colony boxes (one *L. humile* and one *D. bicolor*) was arbitrarily chosen and placed on either side of a central test arena. The central test arena consisted of a larger plastic box (32.5 L x 26.5 W x 9.5cm H), with approximately 2.5 cm layer of sand (Zoo Med Desert White Repti Sand, Petco). A small weigh boat (41 L x 41 W x 8mm H) containing a cotton ball soaked in 25% sucrose was placed at the center of the arena so that its edges were flush with the top of the sand. Ants were then allowed to enter the arena with the use of simultaneously placed cardboard bridges (Supplemental Fig. 3). A video camera recorded all interactions and behaviors that occurred within the arena for 30 min from the time the bridges were added. Assays included combinations of treated and non-treated interspecific and intraspecific pairings, with a minimum of three replicates per combination. The following behaviors were recorded from the videos: 1) latency to bait discovery, the time it took the first ant of each group to find the bait after entering the arena, 2) duration and frequency of wrestling bouts, 3) frequency of neutral behaviors (antennation), 4) frequency of retreats, and 5) frequency of aggressive behaviors (lunges/chase, spasm, bite, gaster tilt). Definitions for each of the interactive behaviors are listed in Table 1 and were categorized based on the methods from Human and Gordon (1999). The initial 10 interactions for each opponent group were those that were scored. In this way, the observer could ensure that behaviors exhibited were not influenced by a previous interaction that an ant had with the opposing species. The number of ants on the bridge was also recorded at the time intervals of 1, 5, 10, 15, 20, 25, and 30 min to determine possible sub-lethal effects on climbing behavior. In addition, the number of casualties (ants that were dead or maimed to the point of immobility) for each species in the arena at the end of each assay was counted. All video reviews were conducted blindly (the reviewer was not aware of the treatments involved).

After reviewing the video recordings for assays in which two different species were interacting, there were several cases in which one species was unable to make it to the bait due to interception by the opposing species. Additional assays (n = 23) were then conducted in which each species was allowed to enter the arena alone. This enabled us to determine if selenium exposure had

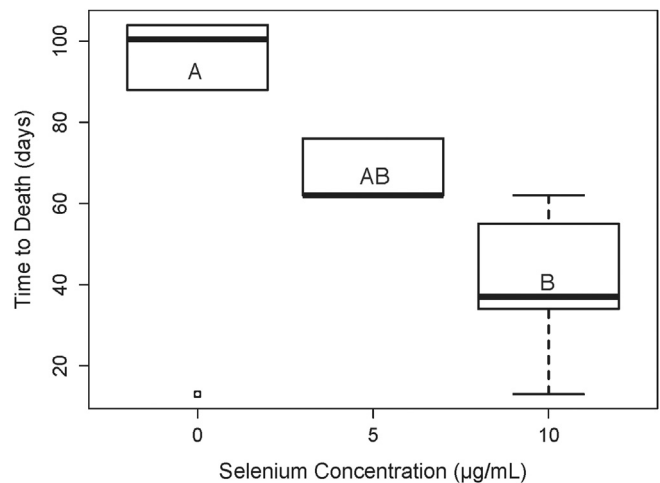


Fig. 1. Time to death (days) for Argentine ant queens across selenium treatments. Different letters represent means that are significantly different from each other (post hoc pairwise *t*-test).

any effect on the latency of each species to the bait in the absence of interspecific competition.

2.4. Statistical analysis

All data analyses were performed using R version 2.14.1 (The R Foundation for Statistical Computing, 2011). A multiple comparison of the time to death of queens across treatments was conducted using a non-parametric Kruskal-Wallis test and post hoc pairwise *t*-test with Bonferroni adjustment ($p < 0.05$). The number of eggs produced by queens across treatments was analyzed using a generalized linear model (GLM) with negative binomial distribution (NB). Model selection was based on the Akaike Information Criterion (AIC), and the final model included the number of eggs as the response variable, treatment as a fixed factor, and the time of death by queens as a co-factor. For exploitation competition, data on latency to the bait was analyzed using a GLM with Gaussian distribution. The model included seconds as the response variable and species, treatment, and competition as the fixed factors. A two-way analysis was carried out for each species separately, when we found no interaction or effect of species. For interference competition, the overall effect of species and treatment on competitive behavior was analyzed with a MANOVA. Subsequent analyses of the frequency of each separate behavior, and the number of casualties for each opponent at the end of the assay, were conducted using GLMs with Poisson distribution. Final models included the behavior or number of casualties as the response variable with species and treatment as the fixed factors.

Table 1

Definitions for direct interactions observed during competition assays. These behaviors are adapted from those defined in Human and Gordon, 1999.

Antennate:	antennating another individual upon face to face contact
Retreat:	running quickly in the opposite direction of opponent after an encounter or chase
Spasm:	twitching or spasm-like movement of body after contact
Lunge/Chase:	jumping towards and moving quickly towards opponent
Bite:	biting any area of the opponent's body
Wrestle:	initiating a full body grapple with the opponent
Gaster Tilt:	bending of the gaster in an effort to direct it towards the opponent

3. Results

3.1. Fecundity

Chronic ingestion of selenium had a negative impact on queen survival and reproduction. Queens in colonies fed $10 \mu\text{g Se mL}^{-1}$ died significantly sooner than queens in control colonies (Kruskal-Wallis: $\chi^2 = 8.6, df = 2, P = 0.01$; Post hoc: pairwise *t*-test with Bonferroni adjustment, Fig. 1). No queens remained alive after 8

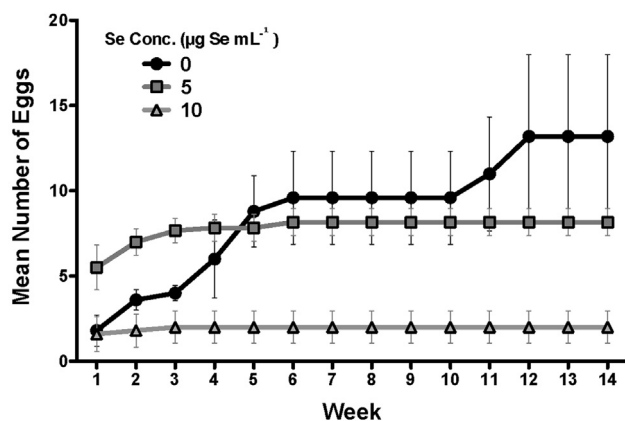


Fig. 2. Comparison of the average number of eggs \pm SEM produced by queens over time (weeks) for each selenium treatment category.

weeks in colonies given $10 \mu\text{g Se mL}^{-1}$ or after 11 weeks for colonies given $5 \mu\text{g Se mL}^{-1}$. One queen from the $0 \mu\text{g Se mL}^{-1}$ died during week 2 for unknown reasons; however, two control colonies still contained healthy reproducing queens when the experiment ended after 14 weeks.

The amount of brood produced by queens was also negatively impacted by selenium ingestion (Fig. 2). Colonies provided 5 and $10 \mu\text{g Se mL}^{-1}$ produced significantly fewer eggs than colonies fed no selenium (GLM.NB, $\chi^2 = 8.5, df = 2, P = 0.01$). In addition, viability and development of their offspring were also affected (Table 2). Offspring from control colonies reached adulthood, with one queen producing as many as six offspring that survived from egg to adult by week 14. In contrast, offspring from selenium treated colonies did not develop beyond the larval stage.

3.2. Exploitation competition

In the absence of selenium and competition, the average time it took Argentine ants to find the bait (171.38 ± 43.27 s) was not statistically different than that for pyramid ants (250.71 ± 58.08 s, species effect: GLM, $\chi^2 = 0.59, df = 1, P = 0.44$). The time it took Argentine ants to find the bait was not affected by the presence of a competitor ($\chi^2 = 0.001, df = 1, P = 0.44$) or treatment ($\chi^2 = 1.02, df = 1, P = 0.31$), nor was there a significant interaction between the two factors ($\chi^2 = 2.05, df = 1, P = 0.15$, Fig. 3A). In contrast,

pyramid ants located the bait faster in the presence of a competitor ($\chi^2 = 6.44, df = 1, P = 0.01$; Fig. 3B). Selenium treatment alone had no effect on latency to bait for pyramid ants ($\chi^2 = 2.82, df = 1, P = 0.09$), but the combination of selenium exposure and a competitor resulted in a slower location of the bait (treatment*competition: $\chi^2 = 4.71, df = 1, P = 0.03$).

3.3. Interference competition

Selenium treatment had no overall effect on any of the behaviors exhibited by either species in direct interactions (MANOVA: $F = 0.47, df = 7, 230, P = 0.86$) nor was there an interaction between selenium treatment and species (MANOVA: $F = 0.26, df = 7, 230, P = 0.96$). There was, however, a difference in the frequency of behaviors exhibited by each species (MANOVA: $F = 10.6, df = 7, 230, P < 0.0001$). Table 3 shows the mean frequencies of the responses for each species upon encountering the opponent, where pyramid ants engaged in significantly more chasing and spasms and Argentine ants displayed significantly more retreats and gaster tilting. Both species had similar counts of antennation, biting, and initiating wrestling bouts. Assays in which the same species was used as the opponent resulted in no wrestling, spasms, biting, chasing or gaster tilting, but only antennation for both species and a single instance of retreating by an Argentine ant. Selenium treatment did not have an effect on the number of deaths/immobile ants remaining at the end of each assay ($Z = -1.338, df = 1, 25, P = 0.18$); however, there was a significant difference in the number of casualties for each species ($Z = 2.09, df = 1, 26, P = 0.04$), where Argentine ants experienced nearly twice as many deaths as pyramid ants.

4. Discussion

Two important intrinsic factors contributing to the success of invasive ant species, such as the Argentine ant are its competitive ability and its numerical abundance (Holway, 1999). Unlike many native species that are subject to a trade-off between discovering and dominating resources such as food and territory, the large numbers and aggressive nature of Argentine ants has allowed them to excel at both (Human and Gordon, 1996, 1999; Holway, 1999; Bertelsmeier et al., 2015). However, other extrinsic components, such as habitat disturbance, should not be overlooked as an important factors influencing invasion and establishment of Argentine ants, because resulting changes in species composition, richness, and abundance (Philpott et al., 2000; Floren and Linsenmair, 2001) within a habitat are likely to leave communities susceptible to invasions (Gibb and Hochuli, 2003; King and Tschinkel, 2006). However, if native species have adapted a tolerance or avoidance to environmental toxins, expansion and establishment by the invasive species will likely be reduced.

Here we found a negative impact for reproduction among Argentine ant colonies fed selenium. Concentrations chosen for this study (5 and $10 \mu\text{g Se mL}^{-1}$) are environmentally relevant and are actually among the lower range of concentrations that can occur in tissues of plants considered non-accumulating (up to $\sim 20 \mu\text{g Se g}^{-1}$); concentrations in selenium 'accumulating' plants

Table 2

Mean number of offspring that reached each developmental stage for each treatment category. The average number is in bold and the ranges are in parenthesis.

Developmental stage	Control ($0 \mu\text{g Se mL}^{-1}$)	Low ($5 \mu\text{g Se mL}^{-1}$)	High ($10 \mu\text{g Se mL}^{-1}$)
Egg	13.2 (4–28)	8.83 (5–10)	3 (0–5)
Larva	6.8 (1–14)	4.67 (2–12)	1.6 (0–8)
Pupa	2.2 (0–10)	0	0
Adult	1.4 (0–6)	0	0

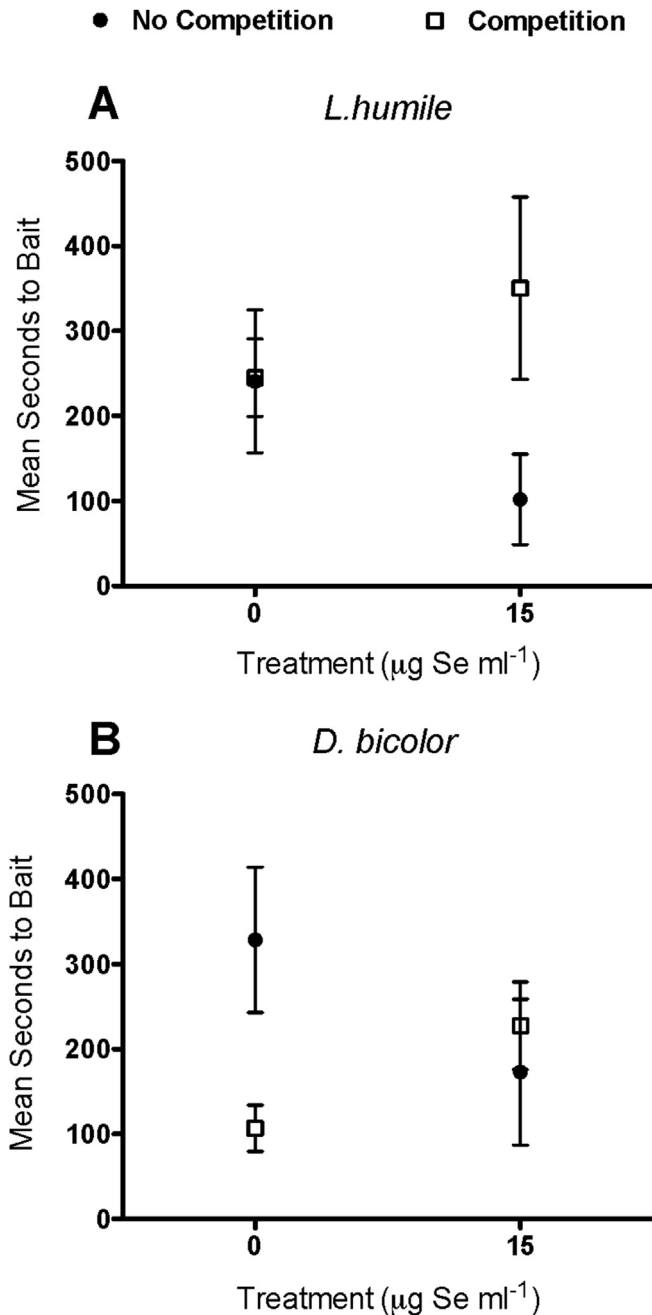


Fig. 3. Interaction plots show the effect of competition and selenium treatment on the average latency to bait (seconds) for *L. humile* (A) and *D. bicolor* (B).

Table 3

Comparison of behaviors exhibited by the Argentine ant (*L. humile*) and pyramid ant (*D. bicolor*). Values shown below each species are means \pm standard error of the means. n = number of encounters.

Response	<i>L. humile</i>	<i>D. bicolor</i>	Z	df	n	P
Antennate	0.66 \pm 0.07	0.70 \pm 0.05	-0.3	1	240	0.76
Retreat	0.80 \pm 0.05	0.36 \pm 0.04	-3.1	1	240	<0.01
Spasm	0.23 \pm 0.03	0.70 \pm 0.05	3.2	1	228	<0.01
Lunge/Chase	0.40 \pm 0.05	0.87 \pm 0.06	2.7	1	240	<0.01
Bite	0.23 \pm 0.03	0.40 \pm 0.04	0.8	1	228	0.41
Wrestle	0.22 \pm 0.03	0.36 \pm 0.05	1.5	1	228	0.13
Gaster Tilt	0.76 \pm 0.07	0.43 \pm 0.04	-2.2	1	274	<0.05
Casualties	8.3 \pm 0.74	4.8 \pm 0.64	2.09	1	28	<0.05

may have up to 1000 $\mu\text{g Se g}^{-1}$ while 'hyperaccumulating' plants may exceed 5000 $\mu\text{g Se g}^{-1}$ (Brown and Shrift, 1982; Terry et al., 2000). Chronic ingestion of selenium was also found to impact queen mortality since queens from all colonies given 10 $\mu\text{g Se mL}^{-1}$ were dead by week 8. The age of the queens at the beginning of the study was unknown and does not serve as a factor in fecundity (Keller and Passera, 1990); however the life expectancy of queens in Argentine ant colonies can extend over a year (Newell and Barber, 1913). Two of the queens from the control group were still alive and seemingly healthy at the end of the assay as they were still producing offspring. It is possible that they may have continued to do so for several more weeks had we not terminated the experiment at 14 weeks. The viability of the brood was also negatively impacted in colonies fed selenium, where offspring did not develop beyond the larval stage. In contrast, queens in control colonies produced brood that developed into adulthood. This developmental time falls within the range expected for Argentine ants (33–114 days from egg to adult; Newell and Barber, 1913).

Previous studies have reported negative effects of metal exposure on ingestion, taxis/locomotion, and oviposition for various arthropods (Mogren and Trumble, 2010), yet few studies have investigated pollution effects on competitive behaviors. For both species in this study, selenium did not alter the behaviors involved in direct competitive interactions. However, the combination of selenium exposure and the presence of a competitor resulted in a greater latency to the bait for the native pyramid ants that was not seen for Argentine ants. An increase in the time required to find resources in the environment could affect acquisition, especially when those resources are ephemeral, and further influence the competitive dynamics between species within a given habitat. The finding that these two species responded differently to the combination of a selenium and competitive pressure is not surprising, because ant species differ in both their competitive abilities (Parr and Gibb, 2010) and their tolerance to pollutants (Grześ, 2010). Insects have been reported to employ various strategies of metal regulation (Dallinger, 1993). Although the presence of such metal binding proteins, detoxifying enzymes and mineral concretions reported for other arthropods (Roesijadi, 1992; Wilczek et al., 2004; Amiard et al., 2006; Eglı et al., 2006) have not been specifically reported in ants, the accumulation of metals in the same target tissues of the midgut and Malpighian tubules (Rabitsch, 1997) also seen in other insects (Humbert, 1978; Brown, 1982; Suzuki et al., 1984), suggests that they possess similar strategies. Furthermore, previous studies have reported differences in the accumulation of metals across ant species collected from the same habitat (Starý and Kubizňáková, 1987; Rabitsch, 1995, 1997). This suggests the possibility for differences in metal regulation physiology across ant species, and may help to explain differences in behavior seen in this study. The selenium levels in this study were enough to inhibit reproduction in Argentine ant colonies, but they were not enough to result in obvious changes in competitive behavior. This is in contrast to other studies that found changes in aggressive behaviors among invasive and native ants following exposure to pesticides (Kabashima et al., 2007; Barbieri et al., 2013) and, in one case, to copper pollution (Sorvari and Eeva, 2010). It is also possible that more significant changes in behavior may have become evident had the experiment been carried out longer than a week. However, longer exposure may have resulted in greater mortality as well.

5. Conclusion

For many ants, there are several possible routes of acquisition of environmental pollutants. For instance, within a contaminated habitat ants may not only acquire toxins from the soil, nectar and pollen, but also seeds, prey insects or insect cadavers, and

honeydew. Each species may also display differences in their feeding preferences, which may result in different degrees of exposure depending on the food sources available. The pyramid ant was not deterred by the concentrations of Se in our tests, and this species has been found nesting in severely contaminated sites where soil concentrations ranged from 7 to 200 $\mu\text{g Se g}^{-1}$ (De La Riva and Trumble, unpublished). This suggests a tolerance for Se. However, even though Argentine ants feed readily on food containing highly toxic concentrations of Se in their diet (De La Riva et al., 2014), our data show they lack a tolerance for even relatively low concentrations in their food source. Thus, the ability of Argentine ants to establish at sites within even low Se contamination would likely be inhibited by a physiological toxicity causing a reduction in queen survival and high larval mortality. This likely would lead to either population elimination or, at a minimum, loss of numerical dominance. The level of reduction in Argentine ant populations that would impact their ability to successfully compete for resources during range expansion is unknown. Regardless, the differential toxicity of Se for these two species appears to play a much more substantial role in mediating interactions than the observed changes in competitive behaviors. Future research is necessary to understand this and other impacts of pollution, as a disturbance, on different stages of an invasion.

Acknowledgments

The authors would like to thank R. Cardé, D. Choe, N. Di, M.B. Jones, G. Kund, M. Pennington, S. Prager and K. Zhang for their reviews of this manuscript. We would also like to thank M.B. Jones and T. Castañeda for their instrumental assistance with colony maintenance, experimental set-up and data collection for the fecundity experiment and competition experiment, respectively. A thank you also goes to B.G. Vindiola for her helpful assistance with ant collections. Student scholarships awarded from the Imperial County Farm Bureau and the University of California, Riverside funded this research.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.envpol.2016.03.045>.

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