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

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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 μg 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 μg 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.

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

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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; Blügthen 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 subfamily 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 (Na_2Se0_4, 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