EFFECT OF FORMICA ASERVA FOREL (HYMENOPTERA: FORMICIDAE) ON GROUND DWELLING ARTHROPODS IN CENTRAL BRITISH COLUMBIA

by

Kendra Gail Schotzko

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ABSTRACT

Carabids and spiders have potential as bioindicators, but may experience niche overlap with some ants. While some studies have uncovered mixed responses by these taxa to ants, negative associations are frequently found. We examined carabids and spiders in a British Columbia clearcut in zones colonized and non-colonized by *Formica aserva* ants. The number of carabids captured in colonized and non-colonized zones differed significantly from expected, and species-specific patterns were observed. While the activity-abundance of most spider species did not differ between zones, the activity-abundances of five species were significantly different in colonized and non-colonized zones. We also investigated behavioural responses by the carabid *Pterostichus adstrictus* to signals of ant presence, and observed that this carabid avoided crushed *F. aserva* gasters. Our results indicate that *F. aserva* may influence the activity-abundance of some carabid and spider species, and that some carabids may be able to detect *F. aserva* chemical signals.

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CHAPTER ONE

Introduction

Increased anthropogenic impacts on natural ecosystems, such as global climate change, introduction of exotic species, urbanization, agricultural land use, and natural resource extraction, coupled with a growing awareness of the need to maintain biodiversity since the Earth Summit in Rio de Janeiro in 1992 (Vicente, 2010), have increased the need for developing methods to monitor changes in the ecology and biodiversity of affected areas (Work et al., 2002, Duelli & Obrist, 2003). Forestry practices, such as timber harvesting, represent a disturbance particularly relevant to central British Columbia. Timber harvesting can have many effects on ecosystem characteristics beyond vegetation structure. Overstory removal can lead to microclimate changes, including soil temperature and moisture, water balance, and airflow patterns (Keenan & Kimmins, 1993). Timber harvesting and other forestry practices can also impact soil properties, biological productivity, and above-ground cycling of organic material (Jurgensen et al., 1997).

The scale, prevalence, and potential ecological impacts of such disturbances have contributed to a high level of interest in development and use of biological indicators, which can aid in monitoring, detecting, or assessing changes in the environment (Langor & Spence, 2006; Rainio & Niemelä, 2003). There are many definitions that describe the functions or characteristics of biological indicators. As defined by McGeoch (1998), a biological indicator is a "species or group of species that readily reflects: the abiotic or biotic state of an environment; represents the impact of environmental change on a habitat, community or ecosystem; or is indicative of the diversity of a subset of taxa, or of wholesale diversity, within an area", while Andersen (1999) describes biological indicators more simply as

"readily measured components of the biota that are used to provide general information about the complex ecosystems in which they occur". In short, the goal of using biological indicators is to describe environmental change without examining all ecosystem features (Rainio & Niemelä, 2003).

Several criteria are usually discussed relative to potential biological indicators, including their distributions, richness, abundances, role in ecosystem processes and sensitivity to environmental changes, simplicity and cost effectiveness of sampling and identification, and how reliably their responses to environmental change can be interpreted (Andersen, 1999). As a group, invertebrates are highly speciose, greatly outnumber vertebrates in nearly all habitats of the world, and are critical to innumerable biotic processes (Wilson, 1987; Maleque et al., 2006). Thus invertebrates, particularly insects and other arthropods, are often discussed as biological indicators (Rainio & Niemelä, 2003; Summerville et al., 2004; Maleque et al., 2006; Scott et al., 2006). Insects are abundant, ubiquitous, ecologically diverse, and involved in many ecosystem processes (Rosenberg et al., 1986); populations of these organisms can also usually be sampled with ease and relatively little expense (Langor & Spence, 2006). Carabids (Coleoptera: Carabidae) and spiders (Araneae) are two groups that have received attention as potential indicator taxa (Pearce & Venier, 2006).

The family Carabidae, commonly referred to as ground beetles or carabids, are widely distributed, species rich, and have a relatively accessible taxonomy (Beaudry et al., 1997; Larochelle & Larivière, 2003). Most adult carabids are relatively easy to identify, can usually be sampled using simple standardized techniques (Beaudry et al., 1997), and are generally sensitive to environmental factors (Larochelle & Larivière, 2003). Adults are typically

considered polyphagous generalist predators or omnivores (Lindroth, 1961-1969), and are often opportunistic in their prey selection (Lövei & Sunderland, 1996). The distribution of carabids is typically limited by abiotic factors such as extremes in temperature or humidity, as well as soil conditions (Lindroth, 1961-1969). Food availability, species-specific life histories, and the occurrence and distribution of competing organisms also influence species distributions (Lövei & Sunderland, 1996). These features, among others including their abundance, size, and often eye-catching appearance, have contributed to carabids becoming a commonly studied family (Lövei & Sunderland, 1996; Larochelle & Larivière, 2003). Carabids have received attention as possible indicators of habitat change (Rainio & Niemelä, 2003), including changes related to forests and forestry practices (Niemelä et al., 1993; Beaudry et al., 1997; Larochelle & Larivière, 2003; Pearce & Venier, 2006).

Spiders have also received attention regarding their potential use as biological indicators (Marc et al., 1999; Pearce & Venier, 2006; Gillette et al., 2008; Cristofoli et al., 2010). The spider fauna is very species-rich and has high functional diversity. Spatial distributions of spiders are typically defined by limiting physical conditions, such as wind, light intensity, temperature, humidity, as well as biological variables including food supply, vegetation types, natural enemies, and competitors (Foelix, 1996). Feeding habits vary among spiders, but most are obligate carnivores and insects constitute the majority of many species' prey (Wise, 1993). Numerous studies have also addressed spider populations and communities across a range of habitats (Turnbull, 1973).

Spider taxonomy is complex (Turnbull, 1973) and roughly 20 different classification schemes have been proposed since 1900 (Foelix, 1996). Taxonomic challenges, however, have not deterred efforts to assess the potential of spiders as biological indicators, including in a forestry context (Pearce & Venier, 2006; Gillette et al., 2008). A preliminary study in British Columbia reported that spider families displayed high habitat specificity (Lindgren et al., 1999). Responses of spider assemblages also appear to vary relative to different types of ecological disturbance (Buddle et al., 2000; Larrivée et al., 2005).

The specific species composition of an area is influenced by many factors, and observed patterns arise from combinations of multiple variables and a hierarchy of intricate interacting processes (Morin, 1999). Interspecific interactions can affect the composition of assemblages and the species abundances within them (Morin, 1999). Detection of interspecific interactions, however, is often difficult despite its recognition as a fundamental ecological process (Parr & Gibb, 2010). Field manipulation of assemblages is often difficult to perform, and consequently much of the evidence supporting the existence of interspecific interactions is non-experimental and is based upon findings of non-overlapping distributions (Parr & Gibb, 2010).

Some carabids, spiders, and ants (Hymenoptera: Formicidae) may occupy similar guilds as surface-active generalist predators (Lövei & Sunderland, 1996), and these groups may experience some degree of niche overlap based on abundance, feeding habits, distribution, and similarity of activity patterns (Lövei & Sunderland, 1996; Hawes et al., 2002; Reznikova & Dorosheva, 2004). Lövei and Sunderland (1996) suggest that failure to account for the presence of ants could result in some community studies forming incomplete or invalid conclusions. Humphrey et al. (1999) also acknowledged the need to identify biotic factors that may influence assemblage compositions, such as ants. Shedding light on the possible relationships between ants, carabids, and spiders may improve the accuracy of these

groups as indicators, enhance our understanding of ground dwelling arthropod hierarchies in disturbed habitats, and increase our understanding of the basic ecologies of these groups.

Given the potential to utilize carabid and spider assemblages as indicators, additional research regarding potential interspecific interactions could help to refine interpretation of changes in their abundance and diversity. In many areas, including British Columbia, relatively little is known regarding the interspecific interactions between ant species and other ground dwelling arthropods. The ecology and diversity of ant species in central British Columbia is also relatively unknown, and little information is available on their specific ecosystem functions (Lindgren & MacIsaac, 2002). In this thesis, I have examined the effects of *Formica aserva* Forel ant colonies on carabids and spiders in a disturbed habitat in the central interior of British Columbia. I have also examined behavioural responses by carabids to possible signals of ant presence in an effort to help explain observed distributions of carabids. My objectives were to: (1) examine carabid assemblages relative to the occurrence of *F. aserva* nests (Chapter 2); (2) shed light on carabid behavioural responses to *F. aserva* glandular chemicals (Chapter 3); and (3) to assess spider assemblages relative to the occurrence of *F. aserva* nests (Chapter 4).

Ants are among the most widely distributed and abundant animal taxa (Hölldobler & Wilson, 1990; Higgins & Lindgren, 2006). Involved in many diverse ecosystem processes, ants are important in shaping soil physical and chemical properties, predation of other invertebrates, facilitation of organic matter decomposition, serving as a food source for vertebrate species, dispersal of seeds, as well as a variety of other roles (Hölldobler & Wilson, 1990 and references therein; Lindgren and MacIsaac, 2002 and references therein).

So called wood ants, specifically of the *Formica rufa* species group, often maintain territories where an area containing food, nest sites, or other resources are defended (Hölldobler & Wilson, 1990). The territories of wood ants are often large (Reznikova & Dorosheva, 2004) and forager densities frequently correlate with forager aggression (Savolainen & Vepsäläinen, 1988). Given this relationship, a relatively small number of dominant ant nests have the potential to appreciably impact local faunas through patrol and defense of extensive foraging areas around nests (Hölldobler & Wilson, 1990).

Numerous studies have addressed the effects of ants on other arthropod fauna (Hölldobler & Wilson, 1990; Niemelä et al., 1992; Karhu, 1998; Laakso & Setälä, 2000; Hawes et al., 2002). For example, Punttila et al. (2004) observed a strong effect of wood ants on the majority of invertebrate groups in mountain birch trees (*Betula pubescens* Ehrh.) (Betulaceae). Gonçalves et al. (2005) also found that predatory ants had a negative effect on termite activity, while non-predatory ants did not, suggesting that predation by ants may be an important disturbance factor in some ecosystems. In some cases, direct interactions with ants may not be required for them to influence other arthropods (Offenberg et al., 2004; Oliver et al., 2008). Artificially low *Formica aquilonia* Yarrow ant densities created by Laakso and Setälä (2000) also resulted in increased activity of other predatory arthropods, which they described as a compensatory shift in the predatory invertebrate guild.

Several studies have also addressed potential interactions specifically between carabids and ants, and mostly negative relationships have been identified (Niemelä et al., 1992; Koivula et al., 1999). Areas of high *Formica rufa* L. densities in mature Scots pine (*Pinus sylvestris* L.) were associated with low carabid abundance and species richness, and this effect was described as the most important variable in determining small-scale carabid

distributions (Hawes et al., 2002). A recent study in central British Columbia also found that the activity-abundance of *F. aserva* had a generally negative effect on the activity-abundance of many carabid species (McColl, 2010).

Ants and some spiders may also be competitors and/or mutual predators (Van der Aart & de Wit, 1971; Wise, 1993; Halaj et al., 1997; Heikkinen, 1999; Sanders & Platner, 2007). Activity of *Formica obscuripes* Forel on sagebrush, *Artemisia tridentata* Nutt. (Asteraceae), near ant nests was determined to have a negative influence on spider abundance (Heikkinen, 1999). Additional studies have also found ants to have negative or mixed associations with spiders in other habitats (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981; Halaj et al., 1997; Punttila et al., 2004; Sanders & Platner, 2007), while other studies have concluded that the presence of ants is inconsequential to spider populations (Van der Aart & de Wit, 1971; Sterling et al., 1979; Brüning, 1991; Neuvonen et al., 2012).

Formica aserva is an ecologically versatile and broadly distributed member of the *Formica sanguinea* species group (Naumann et al., 1999). Often a dominant ant in central British Columbia (McColl, 2010), *F. aserva* (formerly known by the junior synonym *F. subnuda* Emery) shares biological and ecological characteristics with the *Formica rufa* species group (Fisher & Cover, 2007). As a facultative slave taker (Francoeur, 1983), *F. aserva* likely requires suitable slave species to colonize a habitat prior to the establishment of their own colonies through nest parasitism (Higgins, 2010). *Formica aserva* is commonly associated with harvested areas where coarse woody debris is present and open canopy conditions result in increased thermal exposure of the forest floor (Higgins & Lindgren, 2012a). Based on these habitat requirements, the presence of *F. aserva* in cool subboreal

regions of central British Columbia varies with stand age (Higgins, 2010); indicating that in cool environments it is a disturbance specialist (Higgins & Lindgren, 2012a).

In the following chapters I will present the findings of my examination of the effects of *F. aserva* colonies on carabids (Chapter 2) and spiders (Chapter 4) in a disturbed habitat in the central interior of British Columbia, and my observations of the behavioural responses of carabids to *F. aserva* glandular chemicals (Chapter 3). These chapters have been formatted for publication in refereed journals, and are hence written to acknowledge the input, support, and advice of others that have influenced and informed this research.

CHAPTER TWO

Interspecific Interactions of Carabidae (Coleoptera) species and *Formica aserva* Forel ants (Hymenoptera: Formicidae)

Abstract

Carabid beetles have attracted attention as potential bioindicators of forest habitat changes, but relatively few studies have investigated interactions between carabids and other fauna. Some studies have found negative associations between certain ant species and carabids, which may be the result of predation or competitive interactions. This could alter or mask the responses of carabids to habitat features, and consequently influence the interpretation of carabid responses to disturbance. We examined the activity-abundance of carabids in a central British Columbia clearcut in zones colonized and non-colonized by *Formica aserva*, hypothesizing that the activity-abundance of carabid species would vary between these zones. *Calathus ingratus* and *Pterostichus adstrictus* were captured more frequently in non-colonized zones than in colonized zones. The opposite pattern was found for *Pterostichus ecarinatus*, *Pterostichus herculaneus*, and *Syntomus americanus*. Our results supported our hypothesis that the activity-abundance of some carabid species was different between areas colonized and non-colonized by *F. aserva*. Direct observations of carabid responses to aggressive ants and their signals are necessary before specific conclusions can be drawn regarding the nature of effects by ants on carabids.

Keywords: competition, bioindicator, species interaction, Formicidae, ants, Carabidae, ground beetles

Introduction

As a taxonomically and ecologically well-studied insect family, carabids (Coleoptera: Carabidae) have received attention as possible bioindicators of habitat changes (Rainio & Niemelä, 2003), including those associated with forest harvesting practices (Niemelä et al., 1993; Beaudry et al., 1997; Pearce & Venier, 2006) and environmental quality (Eyre et al., 1996). Given the potential to utilize carabid assemblages as indicators of habitat change, it is important to understand the variables that may influence carabid behaviour and distributions. For example, ants (Hymenoptera: Formicidae) may be a complicating factor that could confound other correlations with habitat characteristics (Lövei & Sunderland, 1996; Humphrey et al., 1999). Some carabids and ants appear to experience niche overlap in terms of feeding habits, distributions, and seasonal activity patterns (Lövei & Sunderland, 1996; Hawes et al., 2002). Ants are known to significantly affect other insect fauna (Hölldobler & Wilson, 1990; Karhu, 1998; Laakso & Setälä, 2000; Punttila et al., 2004), and negative interactions observed between some ants and carabids may be the result of competition or predation (Howard & Oliver, 1978; Hawes et al., 2002; McColl, 2010).

Areas of high *Formica rufa* L. densities in mature Scots pine (*Pinus sylvestris* L.) in the United Kingdom were associated with low carabid abundance and species richness (Hawes et al., 2002). It was suggested that the effect of *F. rufa* on the abundance and distribution of most carabid species could override or mask the influence of other habitat characteristics in determining small-scale carabid distributions (Hawes et al., 2002). Other studies have also identified mostly negative relationships between carabids and ants (Niemelä et al., 1992; Koivula et al., 1999; McColl, 2010). The response of carabids to the presence of ants is not, however, always consistent among species (Niemelä et al., 1992; Koivula et al., 1999; Hawes et al., 2002; McColl, 2010).

Formica aserva Forel, a member of the *Formica sanguinea* species group, is ecologically versatile and widely distributed (Naumann et al., 1999). *Formica aserva* are aggressive and omnivorous (Phillips & Willis, 2005; Higgins, 2010) with nests that may include several hundred (Naumann et al., 1999) to a few thousand individuals (Savolainen & Deslippe, 1996). This species is commonly found in British Columbia and frequently nests within coarse woody debris (Lindgren & MacIsaac, 2002; Higgins, 2010). A facultative slave taker (Francoeur, 1983), *F. aserva* colonies usually establish through nest parasitism, which requires that suitable slave species colonize a habitat prior to *F. aserva* (Higgins, 2010). In a cool, sub-boreal region of central British Columbia, *F. aserva* was absent in pine stands that were mature or recently (2-3 years) harvested. It was common in stands 8-10 years postharvest with populations peaking at 13-15 years before decreasing in 23-25 year old stands (Higgins, 2010). This indicated that in cool environments, while not a pioneer species, it is a disturbance specialist dependent on high solar radiation heating available prior to canopy closure in regenerating stands (Higgins & Lindgren, 2012a).

In the same area of British Columbia, McColl (2010) found a decrease in carabid activity-abundance in areas with high (>150 workers/pitfall trap) *F. aserva* activityabundance, compared to areas with no or low (0-50 workers) *F. aserva* activity-abundance. Interestingly, carabid activity-abundance was not significantly different between areas with no *F. aserva*, low (1-50 workers), or moderate (51-150 workers) *F. aserva* activityabundances. Significant species-specific responses to *F. aserva* activity-abundance were not identified (McColl, 2010).

To expand upon McColl's (2010) correlative studies, we selected a recently disturbed habitat that appeared to be in a period of *F. aserva* population establishment and growth based on nest density and distribution. This characteristic allowed us to examine the potential effects of *F. aserva* on carabid beetles by directly comparing catches in areas with similar habitat characteristics but different *F. aserva* presence. We hypothesized that the activity-abundance of carabid species in a central British Columbia clearcut would be different between areas colonized and not colonized by *F. aserva*.

Materials and Methods

Study Area and Field Data Collection

Five replicates were established in the wet cool subzone of the sub-boreal spruce biogeoclimatic zone (SBSwk1) (Meidinger et al., 1991; Government of British Columbia, 2008) approximately 40km east of Prince George, British Columbia (elevation 740m, located approximately 53.901° N, 122.219° W). The replicates were within a five year post-harvest block (Government of British Columbia, 2011). We selected this area based on a preliminary survey that indicated patchy colonization by *F. aserva*. The harvest block had a maximum length and width of approximately 2400m and 650m, respectively. The long axis of the block had a generally north-south orientation. Replicates were spaced at least 100m apart along the long axis of the block, and selected based on apparent habitat homogeneity.

Two zones, with (colonized) or without (non-colonized) *F. aserva* nests, were delineated within each replicate. Colonized and non-colonized zones were determined by a 100% survey of the replicates to detect and mark visibly active *F. aserva* nests (based on the presence of workers and/or thatching material). Due to the highly unpredictable activity-abundance of *Formica obscuripes* Forel workers relative to nest location (Higgins &

Lindgren, 2012b), *F. aserva* worker activity-abundance was not used to delineate colonized and non-colonized zones, only to verify the accuracy of our selection criteria. Colonized zones were parallel to the long axis of the harvested area along a forestry road that bounded the west side of the harvest area. Non-colonized zones were located east of the colonized zones, and farther into the harvest area away from the road. Within each replicate, two pitfall trap lines were established, one in each zone. Trap lines in colonized zones were oriented to maximize exposure to nests, *i.e.*, foraging worker ants, and trap lines in non-colonized zones were positioned at least 25m from any *F. aserva* nest. Trap lines had approximately northsouth orientations, were at least 50m apart, and at least 25m from roads or habitat edges.

Each trap line consisted of six modified Nordlander pitfall traps (Nordlander, 1987; Lemieux & Lindgren, 1999; Higgins & Lindgren, 2012b) spaced at 10m intervals. Pitfall traps measure the activity-abundance of ground active invertebrate species because their capture is dependent both on the species density and the rate at which individuals travel (Greenslade, 1964). Pitfall traps were constructed as described by McColl (2010) using 8oz translucent multipurpose plastic containers with lid (VWR International) 7.5cm deep and 8cm in diameter with 12mm by 6mm entrance holes punched below the container rim using a standard paper hole punch. A second cup served as a sleeve to enable trap servicing with minimal soil and organic litter disturbance. Each pitfall trap was filled to a depth of approximately 2-4cm with 25:75 propylene glycol:water solution (Pearce et al., 2005; McColl, 2010). Pitfall traps in the colonized zones were set May 26, 2010 with closed inner cups to prevent collection. Pitfall traps in non-colonized zones were set May 27, 2010. All pitfall traps were active May 27, 2010 to September 2, 2010; contents were collected and propylene glycol:water solution refilled every 14 days.

Site Assessment

On July 14, 2010 the number of active *F. aserva* nests within 5m of each pitfall trap was measured. On August 9, 2010 two relative soil moisture and two soil pH measurements were taken at each pitfall trap using a moisture and pH meter (Gardena Canada, Ltd., model #RLM4444 RMOTE) inserted approximately eight centimeters into the ground on opposite sides of each pitfall trap. On August 14, 2010 a Canon Powershot A640 ten megapixel digital camera was used to take a photograph from approximately 1.75m above of each pitfall trap to assess ground cover within a $1m^2$ frame.

Using methodology adapted from Daubenmire (1959), plots were assessed for ten types of ground cover: in-ground stumps with an approximate diameter greater than 10cm; coarse woody debris (CWD); fine woody debris (FWD); wood in advanced decay (WAD); surface litter; mineral soil or sand; grass; shrubs; forbs; and conifers. Pieces of solid dead wood greater than 10cm mean diameter estimated from the photo plot were classified as CWD, pieces less than 10cm diameter were identified as FWD, and fragments of broken or rotting wood were considered WAD (McColl, 2010). Ground cover such as fallen needles, moss, dead vegetation or leaves, and other decomposing organic matter on the soil surface were categorized as surface litter. Shrubs and forbs were differentiated based on stem characteristics, overall growth form, and personal knowledge. Photographs of each plot were imported into Microsoft® Office PowerPoint® 2007 and divided into a grid of 16 cells. The percent cover was estimated for each cell. Estimates were based on 0%, 25%, 50%, 75%, or 100% cover of up to four cover types. The 16 cover estimates of each photo plot were averaged to create a mean estimated percent cover for each pitfall trap.

Specimen Identification

Pitfall trap contents were sorted into general taxonomic categories and stored in 70% ethanol. Initial carabid species identifications were made at the University of Northern British Columbia using Lindroth (1961-1969) and Noonan (1991). Identifications were verified with the assistance of D. Shpeley¹. Voucher specimens will be deposited at the E.H. Strickland Entomological Museum, University of Alberta.

Analysis

Data from pitfall traps that were disturbed by adverse weather conditions (flooding), animal interference, or trap malfunction (trap entrance holes not at ground level) were not included in analyses. Data were standardized to total trapping effort (98 trapping days) to adjust for trap disturbance. Captures of individual pitfall traps within each replicate zone were summed. The two measurements of soil moisture and soil pH, respectively, were averaged for each pitfall trap and then averaged within replicate zone. The soil moisture and soil pH of the colonized and non-colonized zones were compared using a Mann-Whitney U test. Mean estimates of cover types for each pitfall trap were averaged within replicate zone, and differences in estimated cover percentages between colonized and non-colonized zones were evaluated with Mann-Whitney U tests. *Formica aserva* activity-abundance and the number of *F. aserva* nests were summed within replicate zone, and colonized and noncolonized zones were each compared using Mann-Whitney U tests. All Mann-Whitney U tests were calculated using SYSTAT 11(©2005 SYSTAT Software, Inc.).

Relatively rare carabid species (defined as those with fewer than five specimens captured in either zone) were not analyzed. Differences in the activity-abundance of

¹ Assistant curator, E.H. Strickland Entomological Museum, Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

relatively common carabid species (five or more specimens captured in either zone) were assessed by a Log likelihood test using a 1:1 expected ratio (Zar, 1984).

Results

Neither mean relative soil moisture (Mann-Whitney U test statistic=16, N=5, 5, P=0.465) nor mean soil pH (Mann-Whitney U test statistic=11.5, N=5, 5, P=0.834) differed significantly when comparing the colonized and non-colonized zones (*i.e.*, with and without *Formica aserva* nests) (Figure 2.1). Similarly, the estimated mean percent cover of the ten cover types did not differ significantly between colonized and non-colonized zones (Table 2.1). Significantly more *F. aserva* workers, however, were captured in the colonized zones than in the non-colonized zones (Mann-Whitney U test statistic=25, N=5, 5, P=0.009). Significantly more *F. aserva* nests were also found in the colonized zones compared to the non-colonized zones (Mann-Whitney U test statistic=22.5, N=5, 5, P=0.018) (Figure 2.2).

One hundred and thirty nine carabids representing seven genera and eleven species were captured. Five species were categorized as relatively rare (*Agonum retractum* LeConte (1 captured in colonized zone, 0 captured in non-colonized zone), *Harpalus laticeps* LeConte (0,1), *Harpalus solitaris* Dejean (2,3), *Pterostichus riparius* (Dejean) (2,0), and *Trechus chalybeus* Dejean(2,0)). Six species were categorized as relatively common, including *Calathus ingratus* Dejean, *Pterostichus adstrictus* Eschscholtz, *Pterostichus ecarinatus* Hatch, *Pterostichus herculaneus* Mannerheim, *Syntomus americanus* (Dejean), and *Synuchus impunctatus* (Say) (Table 2.2).

The number of relatively common carabids captured in colonized and non-colonized zones differed significantly from expected (Log-Likelihood: G=59.33, df=5, P<0.001) (Table 2.2). Calathus ingratus and P. adstrictus were captured more frequently than expected in

non-colonized zones compared to colonized zones. The opposite was found for *P. ecarinatus*, *P. herculaneus*, and *S. americanus*. *Synuchus impunctatus* was caught in similar numbers in both colonized and non-colonized zones and did not differ from expected ratios.

Discussion

Our results support our hypothesis that the activity-abundance of carabid species would differ between areas colonized and not colonized by *Formica aserva*. Four species, *Pterostichus ecarinatus*, *Pterostichus herculaneus*, *Syntomus americanus*, and *Synuchus impunctatus* did not appear to be negatively affected in habitats where *F. aserva* colonies were present, and all but *S. impunctatus* had higher activity-abundance in areas with *F. aserva* nests compared to areas without nests (Table 2.2). The significant differences in *F. aserva* activity-abundance and nest number between the colonized and non-colonized zones confirm that our selection criteria for these zones were valid. The lack of differences between colonized and non-colonized zones for any other factor measured (soil moisture, pH, and ground cover) indicate that the presence of *F. aserva* is a possible explanatory variable for our results.

The different responses found among carabid species in our study was in agreement with variation among other species responses recorded in earlier studies. Other studies have found some carabid species, including *Calathus micropterus* (Duftschmid) (Niemelä et al., 1992), *Amara brunnea* Gyllenhal (Koivula et al., 1999), *Notiophilus biguttatus* (Fabricius) (Koivula et al., 1999; Hawes et al., 2002), and *Carabus regalis* Fischer von Waldheim (Reznikova & Dorosheva, 2004) in close proximity to areas populated by *Formica* spp. ants, generating hypotheses that such species may be able to coexist with ants by avoiding direct encounters or even by utilizing dead ants as a resource (*e.g.*, for food).

Knowledge gaps in the life histories of the species identified in this study make it difficult to explain specific mechanisms responsible for the observed species distributions. At a coarser scale, however, general hypotheses about the causes of species distributions may be possible. For example, Hengeveld (1981) found the remains of Formicidae (mainly *Myrmica*) in guts of four out of five *Pterostichus* species examined. Dorosheva and Reznikova (2006) observed that *Pterostichus magus* (Mannerheim) and *C. regalis* consumed dead ants in a laboratory. *Pterostichus magus* (Mannerheim) and *C. regalis* consumed dead ants in a laboratory. *Pterostichus magus* was also captured more often in pitfall traps containing either dead *Formica aquilonia* ants or *F. aquilonia* nest material compared to pitfall traps containing forest litter (Dorosheva & Reznikova, 2006). These findings suggest *P. magus* may be attracted to cues associated with ants, or that they may utilize dead ants removed from their nest by nest mates (Dorosheva & Reznikova, 2006). Many ant species exhibit necrophoresis, either disposing of corpses in distinct piles, or distributing their dead more or less randomly away from the nest site (Hölldobler & Wilson, 1990). It may be that *P. ecarinatus*, *P. herculaneus*, and *S. americanus* were able to utilize such resources.

The differences in the autecology of *P. ecarinatus*, *P. herculaneus*, and *S. americanus*, however, suggest that these species should interact with *F. aserva* in different ways. *Pterostichus ecarinatus* and *P. herculaneus* are moderate runners incapable of flight; both are also nocturnal species that shelter under or within woody debris during the day (Larochelle & Larivière, 2003). *Syntomus americanus* on the other hand is a mostly diurnal, swift-running carabid, but also typically lacks the ability to fly (Larochelle & Larivière, 2003). It is possible that some species utilize dead *F. aserva* directly as a resource (*e.g.*, the nocturnal *P. ecarinatus* and *P. herculaneus*), while other species that have similar foraging patterns to *F. aserva* may benefit indirectly (*i.e.*, overlap of foraging periods and locations

may benefit some carabids if they are able to take advantage of prey flushed from their cover by *F. aserva* activity).

Our finding that the activity-abundance of *S. impunctatus* did not differ from expected ratios (*i.e.*, 1:1) between *F. aserva* zones (Table 2.2) raises interesting questions about the life history and behaviour of this species. *Synuchus impuncatus* is primarily nocturnal, and is described as a moderate runner with omnivorous feeding habits (Larochelle & Larivière, 2003). It is also a habitat generalist (Pearce & Venier, 2006) and may be able to adapt to the presence of ants, *e.g.*, by effectively avoiding negative encounters with individual ants, which would be consistent with our results.

Formica aserva workers are reported to consistently attack intruders within their territory, including foreign ants and non-ant aphid predators (Phillips & Willis, 2005). They do, however, distinguish between different threats and are not equally aggressive to all perceived intruders (Phillips & Willis, 2005). Given this, it is possible that *F. aserva* may not respond equally to all carabid species. Savolainen and Vepsäläinen (1988) commented that forager density is positively correlated with forager aggression. In west-central British Columbia the occurrence of *F. aserva* is greatest in areas 13 to 15 years post harvest and relatively uncommon 2-3 years post harvest (Higgins, 2010). Thus it is possible that the *F. aserva* colonies in our study (five years post-harvest) were not yet of sufficient size to defend their territories as aggressively as would have been expected based on findings of other studies which included more established ant populations (Niemelä et al., 1992; Hawes et al., 2002; McColl, 2010). Dorosheva and Reznikova (2006) also proposed that the aggressiveness of an ant encountering a carabid may influence the behaviour of the carabid. Relationships between the behaviour of colony workers, which may change over time as a

result of colony growth, and the behaviour of different carabid species may be important variables in determining the effect of F. aserva nests on overall carabid assemblages.

Conversely, the similar activity-abundances of *S. impunctatus* in colonized and noncolonized zones could indicate that this species had a lower abundance in the former but was captured more frequently due to a behavioural response to *F. aserva* presence (McColl, 2010). Reznikova and Dorosheva (2000) proposed that some carabids present in what they termed "ant-controlled territory" were more likely to be observed running quickly, making turns, and were less likely to pause than carabids in areas with reduced ant activity. They also proposed that these behavioural trends were species-specific because other species spent more time motionless (with legs and antennae held underneath their bodies). If the activity of *S. impunctatus* was influenced by *F. aserva* presence or disturbance, then it is plausible that captures of *P. ecarinatus*, *P. herculaneus*, and *S. americanus* were similarly affected. If this were the case, our sampling methods could have masked negative effects associated with *F. aserva* presence experienced by the species we captured more frequently in colonized areas.

Two species, *Calathus ingratus* and *Pterostichus adstrictus*, had lower activityabundance in zones with *F. aserva* colonies compared to non-colonized zones (Table 2.2). Both *C. ingratus* and *P. adstrictus* are nocturnal and can be found in a wide variety of habitats (Larochelle & Larivière, 2003). Given that both species had lower than expected activity-abundances in zones with *F. aserva* nests, it is possible they may be more negatively affected by the presence of *F. aserva* than the four other common species in our study. Possible explanations could include greater niche overlap or lower behavioural plasticity in interactions with *F. aserva*. It is also possible, however, that the activity-abundance patterns

of *C. ingratus* and *P. adstrictus* were the result of reduced activity, rather than abundance, in response to the presence of *F. aserva* (Reznikova & Dorosheva, 2000).

Hawes et al. (2002) found that carabids of different size classes responded differently to various *F. rufa* density levels. The activity-abundances of the carabid species in our study did not show clear differences based on body size. *Pterostichus ecarinatus, S. impunctatus, C. ingratus*, and *P. adstrictus* are moderately sized beetles 7-13mm in length (Lindroth, 1961-1969) and had different activity-abundance patterns relative to the presence of *F. aserva*. The smallest (*S. americanus*) and largest (*P. herculaneus*) of the common carabid species, 2.7-3.5mm and 13.5-17mm respectively (Lindroth, 1961-1969), were both captured more than expected (*i.e.*, > 1:1) in colonized zones. Given the low number of carabids captured, and apparent inconsistency in body length and activity-abundance patterns of common species, we are unable to determine whether body size is related to the activity-abundance patterns we observed. It should also be noted that the ant densities of Hawes et al. (2002) were much greater than those of our study.

The attention carabids have received as potential bioindicators increases the need for continued research into their relationships with abiotic and biotic habitat components. There is a growing body of literature supporting the value of addressing possible interactions between carabids and ants (Niemelä et al., 1992; Lövei & Sunderland, 1996; Oliver & Beattie, 1996; Humphrey et al., 1999; Koivula et al., 1999; Hawes et al., 2002; McColl, 2010). Ant presence and species composition within a habitat change over time (Higgins, 2010) and different ant densities and species have unique effects on carabids (McColl, 2010). Complex interactions involving responses to habitat changes, interspecific pressures, and behavioural characteristics may all act in combination with species-specific seasonal patterns

and niche requirements to create distribution patterns. Greater understanding of these variables may help to improve the reliability of carabids as bioindicators.

Our results indicate that *F. aserva* may affect the activity-abundance of some carabid species. The mechanisms of such effects, however, are not known. Aggressive behaviour, *e.g.*, as shown for the negative effect of *Lasius niger* L. ants on cocinellid beetles (*Adalia bipunctata* L.) (Oliver et al., 2008), is one possible mechanism. Some insects may also have the ability to detect the chemical signals associated with ants. For example, *A. bipunctata* beetles are able to adjust their behaviour in response to *L. niger* semiochemicals (Oliver et al., 2008), and Offenberg et al. (2004) found that chrysomelid beetles (*Rhyparida wallacei* Baly) preferentially fed on leaves collected from trees absent of *Oecophylla smaragdina* (Fabricius) ants compared to the leaves of trees with *O. smaragdina*. Direct observations of how different carabid species respond to aggressive ants or their semiochemicals would be valuable in improving our understanding of the effect of ants on carabid assemblage structure and species abundance.

 Table 2.1. Mean and standard error of estimated percent ground cover surrounding pitfall

 traps in the colonized and non-colonized zones. The results of estimated percent ground

 cover comparison between colonized and non-colonized zones are shown (Mann-Whitney U

 test, SYSTAT 11, ©2005 SYSTAT Software, Inc.).

Formica aserva zone	Cover Type									
	Stumps	CWD	FWD	WAD	Litter	Mineral Soil	Grass	Shrubs	Forbs	Conifers
Colonized Mean (± SE)	1.146 (0.827)	9.635 (1.733)	33.073 (3.027)	7.188 (1.193)	18.698 (1.871)	1.042 (0.577)	0.729 (0.333)	16.771 (3.225)	10.104 (1.825)	1.615 (0.611)
Non-colonized Mean (± SE)	1.667 (0.974)	7.656 (1.602)	34.896 (2.656)	6.979 (1.576)	22.240 (1.996)	0.469 (0.250)	1.719 (0.852)	14.010 (2.486)	7.865 (1.241)	2.500 (0.898)
<i>P</i> value	0.435	0.295	0.602	0.917	0.249	0.519	0.461	0.754	0.402	0.600

 Table 2.2. Activity-abundance (standardized to 98 trap-days) of carabid species for which at

 least five individuals were captured in zones colonized or non-colonized by *Formica aserva*.

 Data in table rounded to nearest whole number.

Formica aserva zone	Number of Carabids Captured								
	Calathus ingratus	Pterostichus adstrictus	Pterostichus ecarinatus	Pterostichus herculaneus	Syntomus americanus	Synuchus impunctatus			
Colonized	1	7	16	24	19	13			
Non-colonized	6	26	1	2	3	10			



Figure 2.1. Mean measurements of relative soil moisture (Mann-Whitney U test statistic=16, N=5, 5, P=0.465) (a) and soil pH (Mann-Whitney U test statistic=11.5, N=5, 5, P=0.834) (b). Measurements were taken at each pitfall trap and averaged for each trap line in zones colonized and non-colonized by *Formica aserva*. Box boundaries indicate the 25th and 75th percentiles, the solid line within each box is the median, the dashed line represents the sample mean, and outer bars show the 5th and 95th percentiles (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).



Figure 2.2. Mean *Formica aserva* activity-abundance (Mann-Whitney U test statistic=25, N=5, 5, P=0.009) (a) and mean number of *F. aserva* nests located within five meters of pitfall traps (Mann-Whitney U test statistic=22.5, N=5, 5, P=0.018) (b) in zones colonized and non-colonized by *Formica aserva*. Box boundaries indicate the 25th and 75th percentiles, the solid line within each box is the median, the dashed line represents the sample mean, and outer bars show the 5th and 95th percentiles (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).

CHAPTER THREE

Response by *Pterostichus adstrictus* Eschscholtz (Coleoptera: Carabidae) to crushed gasters of *Formica aserva* Forel workers (Hymenoptera: Formicidae).

Abstract

Pheromones are used in the intraspecific communication of ants, and some other insects also have the ability to detect these chemical signals. Our study examined responses of the carabid Pterostichus adstrictus to chemicals associated with Formica aserva ants. We hypothesized that if carabids could detect the presence of F. aserva prior to direct encounters, then their behaviour would be different in the presence of crushed F. aserva gasters. Using live P. adstrictus we conducted choice bioassays in plastic rectangular arenas. For each beetle two bioassays were conducted, a treatment and control. Treatment bioassays examined possible behavioural responses to the crushed F. aserva gasters. Control bioassays were conducted to assess for side bias associated with the experimental setup or other unaccounted-for variation. In treatment bioassays P. adstrictus spent less time near the crushed gasters compared to an area without crushed gasters. By comparison, beetles displayed no side bias in the control bioassays. Our results support the hypothesis that some carabid species may be able to detect the presence of F. aserva prior to direct encounters. The potential for *P. adstrictus* to detect chemical signals associated with ants may help explain activity-abundance patterns of this species in habitats were F. aserva are present. Keywords: behaviour, species interaction, semiochemicals, Formicidae, ants, Carabidae, ground beetles

Introduction

In ants (Hymenoptera: Formicidae), communication is conducted through the use of pheromones, a type of semiochemical used specifically in an intraspecific context (Parry & Morgan, 1979 and references therein). Most ant species use pheromone trails (Offenberg et al., 2004), which they typically detect and follow when they're in a gaseous state, creating what Hölldobler and Wilson (1990) described as "vapor tunnels". In the sub-family Formicinae these trails are emitted from the hind gut of workers (Parry & Morgan, 1979) and in red wood ants these signals can persist for long periods (Rosengren & Fortelius, 1987 and references therein). In *Formica polyctena* Förster, these trails are used to recruit and direct conspecifics to a food source (Rosengren & Fortelius, 1987 and references therein).

Chemical communication is also used among ants in defensive or alarm situations (Blum & Brand, 1972). Formic acid has been described as an alarm signal in the genus *Formica*, and is a common secretion of venom glands in formicine species (Ayre & Blum, 1971; Blum & Brand, 1972; Parry & Morgan, 1979). A second alarm pheromone common in formicine species is *n*-undecane, which is produced in the Dufour's gland (Ayre & Blum, 1971; Blum & Brand, 1972), and is a large component of *Formica sanguinea* Latreille Dufour's gland secretions (Parry & Morgan, 1979; Ali et al., 1988). For three *Camponotus* species, Ayre and Blum (1971) stated that activity stimulated by formic acid and *n*-undecane declined after eight minutes and was generally absent after 32 minutes. The hind gut, venom gland, and Dufour's gland are located in the gaster of ants (Hölldobler & Wilson, 1990).

Some other insects also have the ability to detect the chemical signals associated with ants. The leaf beetle *Rhyparida wallacei* Baly (Coleoptera: Chrysomelidae) feeds preferentially on leaves collected from trees not occupied by *Oecophylla smaragdina*
(Fabricius) weaver ants compared to the leaves of occupied trees (Offenberg et al., 2004). The ladybird beetle *Adalia bipunctata* L. (Coleoptera: Coccinellidae) also adjust their behaviour in response to *Lasius niger* L. ant semiochemicals, and the spatial distribution of ants may influence the distribution of predatory cocinellids (Oliver et al., 2008). Similarly, Van Mele et al. (2009) found that for *Ceratitis cosyra* (Walker) and *Bactrocera invadens* Drew-Tsurata & White (Diptera: Tephritidae) fruit flies, the number of landings and the time spent on fruits that had been exposed to *Oecophylla longinoda* (Latreille) ants was lower than the number of landings and time spent on fruits with no previous ant exposure. In their study, fewer attempts to oviposit in fruits exposed to *O. longinoda* were also recorded compared to non-exposed fruits, and fewer puparia emerged from *O. longinoda* exposed fruits (Van Mele et al., 2009). Van Mele et al. (2009) proposed that the behavioural changes of *C. cosyra* and *B. invadens* indicated that these species were possibly responding to predator avoidance cues associated with *O. longinoda* presence.

Given the ability of some beetles to perceive and respond to ant pheromones or other signals of ant presence, it is possible that carabids (Coleoptera: Carabidae) that occur with or near aggressive ant species may perceive and respond to similar signals. Several studies have identified mostly negative relationships between carabids and ants (Niemelä et al., 1992; Koivula et al., 1999; Reznikova & Dorosheva, 2004; McColl, 2010), and it has been proposed that negative interactions observed between some ants and carabids may be the result of competition or predation (Howard & Oliver, 1978; Hawes et al., 2002). Where such interactions occur, selective pressures may favour carabids with the ability to detect and respond to ant semiochemicals.

The responses of different carabid species to ants vary, however (Niemelä et al., 1992; Hawes et al., 2002; McColl, 2010), and the precise nature of interactions between ants and carabids are largely unknown. This type of information is of particular value if carabids are to be used as bioindicators (Niemelä et al., 1993; Eyre et al., 1996; Beaudry et al., 1997; Rainio & Niemelä, 2003; Pearce & Venier, 2006). Lövei and Sunderland (1996) suggested that carabid community studies should account for the presence of ants in order to avoid forming invalid conclusions, because the apparent response of some carabids to habitat changes may differ depending on whether or not dominant ants are present.

Our study was designed to examine whether carabids respond to chemicals associated with the common ant species, *Formica aserva* Forel in central British Columbia. A member of the *Formica sanguinea* species group (Naumann et al., 1999), *F. aserva* are aggressive omnivores (Phillips & Willis, 2005; Higgins, 2010) with nests that may include several hundred (Naumann et al., 1999) to a few thousand individuals (Savolainen & Deslippe, 1996). To our knowledge, nothing is known about the chemical composition of *F. aserva* semiochemicals. We hypothesized that if the carabid species in central British Columbia are affected by *F. aserva* colonization, then these carabids may be able to detect the presence of *F. aserva* prior to direct encounters, and that we would be able to assess this ability through changes in the behaviour of carabids in the presence of crushed *F. aserva* gasters.

Materials and Methods

Ant Nest Collection and Maintenance

Two Formica aserva ant nests in coarse woody debris were collected from the Prince George Forest District east of Prince George, British Columbia, Canada. This species was selected due to the dominance of *F. aserva* in many open or disturbed habitats in central British Columbia (McColl, 2010), and because the coarse woody debris in which this species often nests is relatively easy to collect for laboratory bioassays (Lindgren & MacIssac, 2002). Both nests were taken from an area nine years post-harvest (Government of British Columbia, 2011) in the wet cool subzone of the sub-boreal spruce biogeoclimatic zone (SBSwk1) (Meidinger et al., 1991) approximately 40km east of Prince George, British Columbia (located approximately 53.881° N, 122.240° W). One nest was collected June 8, 2010 and a second nest was collected August 14, 2011 due to the collapse of the first colony. Both colonies were kept indoors at the University of Northern British Columbia campus.

Each colony was contained in large plastic bin approximately 94cm long by 54cm wide, depth varied depending on the size of the nest material. The upper rim of each large plastic bin was painted with fluoropolymer resin (DuPont, Product Type TE3893) to prevent ants from escaping. Through clear plastic tubing (1.27cm diameter) ants were able to access two feeding areas made of smaller plastic containers (204cm² floor area) outside of the main nest container. Ants were fed a mixture of canned tuna (Solid White Tuna in Water, Low Sodium, Western Family), raw egg, honey (Liquid Organic Honey Grade No.1 Amber, Western Natural) and multivitamin (Adult Chewable Multi Vitamin & Mineral, Swiss Natural Sources) (adapted from Bhatkar & Whitcomb, 1970 and Fellers, 1987) and a 20% honey-water solution. A 100watt light bulb (EcoVantage Natural Light, Philips Lighting) on a 12hr timer was mounted above the main nest container to provide light and a small amount of heat to the nest.

Carabid Beetle Collection

Carabids were collected from three disturbed habitats on the outskirts of Prince George, British Columbia (53.959° N, 122.815° W, 53.968° N, 122.897° W, and 53.924° N, 122.887° W). Live carabids were captured using clusters of shallow pitfall traps made of round plastic containers (11cm diameter, 4cm height) (GenPak). Clusters were created by arranging pitfall traps in an X-pattern and installing plastic fences (Lawn Edging 10.16cm, Canadian Tire Corporation, Limited) between each trap to increase capture rates. Pitfall traps were covered with bent pieces of sheet metal to shelter traps from direct sun and rain (Figure 3.1a). The upper inside rim of pitall traps were also painted with fluoropolymer resin to prevent escape of specimens. A small amount of surface litter material from the surrounding area was added to each pitfall trap to help increase the survivorship of captured specimens (Figure 3.1b). Pitfall traps were checked for carabids every two to three days.

Trapped live carabids were placed in small plastic containers with mesh-vented lids along with a small amount of litter material from where the beetles were collected. Captured carabids were brought back to the University of Northern British Columbia campus and kept in a room separate but adjacent to the room where the *F. aserva* nests were located. Carabids were under a low-heat light (13w Daylight Mini Twister Compact Fluorescent, Philips Lighting) to provide a 12hr light cycle. Containers holding carabids were misted with water and provided a piece of pre-cooked ham (Western Family, Overwaitea Food Group LP.) every 24-48hrs, following Tomlin (1975). Carabids were kept in captivity for eight to 12 months prior to experimentation, during which they had no direct interactions with ants. *Bioassay Materials*

Bioassays were conducted in the room where the carabids were maintained. Experiments were recorded using a Canon FS20 Digital Video Camcorder mounted to a tripod and positioned above the experimental arena. A 900 lumens fluorescent light (13w, Daylight Mini Twister Compact Fluorescent, Philips Lighting) located behind the tripod and

directed at a shelf above provided indirect lighting for the recorded video (Figure 3.2). Rectangular arenas with a 218cm² floor area, and partitioned by interior partial walls (Figure 3.3) were constructed out of white corrugated plastic sheet material (Plaskolite, Inc.) and assembled using hot glue sticks (Adhesive Technologies, Inc., Multi Temp). Glue was allowed to fully dry after arena construction, and each arena was then washed by hand with soap (Ultra Concentrated Dish Soap, Great Value), towel dried, and heavily rinsed with 70% ethanol:water solution and allowed to air dry (at minimum overnight).

For each carabid beetle two behavioural choice bioassays were conducted, a treatment and control. Treatment bioassays examined possible behaviour responses of carabids to crushed *F. aserva* gasters. Control bioassays were conducted to assess for side bias associated with the experimental setup or other unaccounted-for variation. Each type of bioassay was conducted in separate, but identical arenas. All bioassays included the use of three filter papers (Whatman 2 Qualitative Circles, 90mm), one in each compartment of the arena. All filter papers were initially stored in the room where bioassays were conducted. Filter papers were designated as either neutral (placed in the center compartment, untreated), treatment (assigned to one of the outer compartments – see below), or control (placed in either both of the outer compartments, or in one outer compartment opposite from the treatment filter paper). Treatment bioassays included one neutral filter paper, one control filter paper, and one treatment filter paper (Figure 3.4a). Control bioassays, conducted in a dedicated control arena, included one neutral filter paper and two control filter papers (Figure 3.4b).

Neutral filter papers were not altered. Treatment filter papers were created in a separate but adjacent room by pressing five *F. aserva* gasters onto a filter paper using a

gloved finger (Textured Nitrile Medical Examination Gloves, Fisherbrand) in an approximately X-shaped pattern (Figure 3.4a). Ants were collected from the feeding areas a laboratory nest and refrigerated at close to 0°C for approximately 20 minutes in order to reduce their activity. Ants were removed from the refrigerator 4-5 minutes prior to the beginning of a treatment bioassay. This time was used to cut the gasters off the ants with a scalpel, place the gasters onto a filter paper, and crush them by pressing them onto the filter paper. Treatment filter papers were then immediately transferred back into the room where behavioural experiments were conducted and placed in a treatment arena. Control filter papers remained in the bioassay room at all times, and a gloved finger was used to mimic the motion and pressing pattern applied to treatment filter papers.

Bioassay Protocol

To account for possible asymmetrical influence of the room where the bioassays were conducted, the position of the treatment filter paper in treatment bioassay was alternated from the left to the right side between tested beetles. The sequential order of control and treatment bioassays was also alternated between tested beetles in an attempt to account for variation bioassay order might have on beetle behaviour. The duration of the different bioassays were not exactly equal due to slight variations in transitional times (approximately one minute) between the sequential steps of each bioassay.

All bioassays began by placing a carabid beetle by hand on the neutral filter paper under a 5cm glass Petri dish (Pyrex®, Corning, Inc) for 10 minutes. Control, or treatment and control, filter papers were then placed in the outer compartments of the arena and the glass Petri dish was removed by hand, allowing the beetle access to the entire arena area for 15 minutes. The carabid was then transferred by hand to the second arena where it was again isolated on the neutral filter paper under the same glass Petri dish for 10 minutes. Again control, or treatment and control, filter papers were placed in the outer compartments of the arena and the glass Petri dish was then removed by hand allowing the carabid access to the entire arena area for 15 minutes. The duration of the 15 minute access period was based on bioassays conducted by Ayre and Blum (1971).

After each bioassay was completed the carabid was killed and preserved in a 70% ethanol:water solution. Each beetle was identified to species using Lindroth (1961-1969) and compared to reference specimens previously verified by D. Shpeley². Additionally, *Pterostichus adstrictus* Eschscholtz was distinguished from *Pterostichus pennsylvanicus* LeConte using Bousquet (1986). Voucher specimens will be deposited at the E.H. Strickland Entomological Museum, University of Alberta. Between each set of bioassays both arenas and the isolation Petri dish were washed by hand with soap (Ultra Concentrated Dish Soap, Great Value), towel dried, and heavily rinsed with 70% ethanol:water solution and allowed to air dry.

Analysis

Only trials using *Pterostichus adstrictus* beetles that showed a measurable response (*i.e.*, moved out of the neutral zone) during at least one of the bioassays (either control or treatment) were included in the analysis. Based on these requirements, 11 out of 16 *P*. *adstrictus* beetles were analyzed. The Observer XT 9.0 Software Package (Noldus Information Technologies) was used to quantify the amount of time a beetle spent in the compartments of each arena. Any time the beetle spent on the walls dividing the compartments was excluded from analysis.

² Assistant curator, E.H. Strickland Entomological Museum, Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

Three indices of movement within the arena were used to assess behavioural patterns. These indices were the total amount of time (seconds) a beetle spent in each of the outer compartments during the treatment and control bioassays, the latency (seconds) of each beetle to enter each of the outer compartments, and the time (seconds) spent in each of the outer compartments upon the beetle's first entry into that compartment. Each of these indices were compared within the treatment and control bioassays, respectively, using Wilcoxon Signed-Ranks Tests (Statistica 6.0 StatSoft, Inc.). Due to our small sample size, T values were compared directly against the critical values of the Wilcoxon T distribution as presented by Zar (1984), rather than using the normal approximation of the T distribution (Z). This was due to the normal approximations being less robust at both small sample sizes and smaller alpha levels (Zar, 1984).

Results

Pterostichus adstrictus beetles spent significantly less total time in the compartment containing the treatment filter paper than in the compartment containing the control filter paper (T=10, n=11, P=0.05) during treatment bioassays (Figure 3.5a). There was also a non-significant tendency by beetles to enter the control compartment more quickly than the treatment compartment (T=11, n=11, 0.10 > P > 0.05) (Figure 3.6a). Additionally, beetles spent significantly less time in the treatment compartment upon their initial entry than when they first entering the control compartment (T=9, n=11, 0.05 > P > 0.02) (Figure 3.7a) of the treatment bioassays.

By comparison, beetles displayed no significant side bias patterns in the control bioassays. Beetles spent similar total amounts of time in the outer compartments during control bioassays (both of which contained a control filter paper) (T=22, n=11, 0.50 > P >

0.20) (Figure 3.5b). Likewise, no significant difference was detected in the amount of time it took for a beetle to enter either of the outer compartments (T=20, n=11, 0.50 > P > 0.20) (Figure 3.6b). The amount of time a beetle spent in the outer compartments upon its first entry into those compartments in control bioassays was also non-significant (T=15, n=11, 0.20 > P > 0.10) (Figure 3.7b).

Discussion

Our results support the hypothesis that some carabid species may be able to detect the presence of *Formica aserva* prior to direct encounters. We were able to detect differences in how carabids utilized the outer compartments of our arenas when crushed *F. aserva* gasters were present versus absent. It took longer for *Pterostichus adstrictus* to enter the treatment compartment, they spent less time in this compartment upon first entry, and less overall time in this compartment during trials, compared to the control compartment. These behavioural patterns may support the findings of other studies that have found negative associations between ants and some carabids (Niemelä et al., 1992; Koivula et al., 1999; Reznikova & Dorosheva, 2004; McColl, 2010). Our findings are also in agreement with other studies that have found that some insects are able to perceive and respond to signals of ant presence (Offenberg et al., 2004; Oliver et al., 2008; Van Mele et al., 2009).

That *P. adstrictus* spent significantly less total time near the crushed gasters may indicate that these beetles avoided this area, which is also supported by our finding that beetles spent significantly less time in these areas when they first entered them. Based on these results it would appear that *P. adstrictus* may not be completely deterred from approaching the crushed gasters, but does not remain near them. This may be supported by the non-significant trend of beetles taking more time to enter the compartment with crushed

gasters. No side biases were found in bioassays in which both outer compartments contained control filter papers, suggesting that patterns detected in treatment bioassays were not the result of extraneous stimuli in the testing area and were the direct result of the crushed gasters.

As previously noted in Chapter 2, one possible explanation for the reduced activityabundance of *P. adstrictus* in areas colonized by *F. aserva* (compared to non-colonized areas) (Table 2.2) was reduced activity rather than abundance. Our present study, however, suggests that *P. adstrictus* may be able to actively select for habitats where *F. aserva* are absent. If such behavioural responses are present in naturally occurring *P. adstrictus* populations, it could be the result of a learned or innate response.

Based on laboratory experiments, Reznikova and Dorosheva (2000) stated that most carabids "learned" to avoid encounters with a tethered ant after one or two direct encounters. This was accomplished by changing their behaviour as they approached the ant (*e.g.*, going around the tethered ant, remaining motionless in a protected posture, or turning away from the ant) or by avoiding the area with the ant altogether. Reznikova and Dorosheva (2000) also observed that the strategies used by the carabids in their experiment differed among species. Dorosheva and Reznikova (2006) later proposed that the behavioural patterns carabids used to avoid ants were "switched on" directly by proximity or contact with ants. In laboratory experiments, Gridina (1994) provided descriptive statistics of *Pterostichus spp*. behaviour in the presence of *Formica polyctena* Förster workers (*e.g.*, percent time spent inactive for "long" periods in the presence or absence of *F. polyctena* workers), which they interpreted as changes in carabid behaviour resulting from the ant presence.

It may also be possible that competitive pressures and/or mortality associated with interspecific interactions with *F. aserva* could have selected for *P. adstrictus* to avoid direct encounters with aggressive ants by detecting cues associated with their presence. Kolbe (1969) made field observations of *F. polyctena* workers attacking the extremities and antennae of *Abax ater* (Villers) and *Pterostichus oblongopunctatus* Fabricius placed on an active ant trail. Kolbe (1969) also found that *F. polyctena* attack on *A. ater* and *P. oblongopunctatus* increased beetle mortality compared to individuals not subjected to attack by *F. polyctena*, and that injury caused by these ants led to premature mortality of some of the carabids studied.

For carabids in central British Columbia, injury frequency was higher in areas with moderate *F. aserva* activity-abundance (51-150 workers) compared to areas with no, low (1-50 workers), or high (more than 150 workers) *F. aserva* activity-abundance (McColl, 2010). McColl (2010) suggested that at moderate activity-abundance levels carabids were more likely to be captured with injuries that resulted from unsuccessful predatory attacks or interference interactions with *F. aserva*, while at high *F. aserva* activity-abundance level these attacks were more successful resulting in increased predation and fewer carabids escaping with injuries. If this interpretation is correct, it would seem that carabids able to avoid encounters with aggressive ants, rather than learning to avoid them post attack, would be most successful.

Different carabid species may respond in unique ways to aggressive ants (Niemelä et al., 1992; Gridina, 1994; Reznikova & Dorosheva, 2000; Hawes et al., 2002; McColl, 2010), reinforcing the need for additional research regarding the detection and response abilities of carabids to *F. aserva* and other aggressive ant species. Research into the interactions between

ants and carabids are also important to understanding the underlying cause of observed patterns such as those in Chapter 2. For example, we do not know what chemical or chemicals the *P. adstrictus* in our study may have responded to, nor do we know how the chemical signals they may have detected compare to semiochemicals they might encounter in a habitat colonized by *F. aserva*.

Our study examined the response of carabids to crushed *F. aserva* gasters and their associated chemicals. To our knowledge this is the first study to examine the ability of carabids to perceive and respond to ant semiochemicals in British Columbia. We detected patterns that suggest at least one carabid species, *P. adstrictus*, may be able to detect and respond to *F. aserva* semiochemicals, which may help explain activity-abundance patterns of this species in habitats were *F. aserva* are present.



Figure 3.1. Arrangement of pitfall traps with metal covers and plastic fences (a). Collection of specimens from pitfall traps, illustrating the fluoropolymer resin painted rims and surface litter material of each pitfall trap (b). Photos © Kendra G. Schotzko.



Figure 3.2. Behavioural bioassay setup with empty arena. Photo © Kendra G. Schotzko.



Figure 3.3. Dimensions of arena used in behavioural bioassays. Diagram produced in Microsoft® Office PowerPoint® 2007.



Figure 3.4. Experimental layout of arenas used in behavioural bioassays. Arena (a) shows the arrangement of filter papers in treatment bioassays, and arena (b) illustrates the arrangement in control bioassays. Image produced in Microsoft® Office PowerPoint® 2007.



Figure 3.5. Total time (seconds) that *Pterostichus adstrictus* beetles spent in each of the outer compartments of treatment (a) and control (b) bioassays. In the treatment bioassays, less total time was spent in the treatment compartment compared to the control compartment (T=10, n=11, P=0.05) relative to the control bioassays where greater similarity occurred between the total amount of time spent in the outer compartments (T=22, n=11, 0.50 > P > 0.20). Box boundaries indicate the 25th and 75th percentiles, the solid line within each box is the median, the dashed line represents the sample mean, and outer bars show the 5th and 95th percentiles (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).



Figure 3.6. The amount of time it took *Pterostichus adstrictus* beetles to enter each of the outer compartments of the treatment (a) and control (b) bioassays. In the treatment trials, beetles trended to enter the control compartments more quickly than the treatment compartments (T=11, n=11, 0.10 > P > 0.05). In the control bioassays the latency of entry into the outer control compartments were more similar (T=20, n=11, 0.50 > P > 0.20). Box boundaries indicate the 25th and 75th percentiles, the solid line within each box is the median, the dashed line represents the sample mean, and outer bars show the 5th and 95th percentiles (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).



Figure 3.7. The amount of time *Pterostichus adstrictus* beetles spent in an outer compartment upon its first entry into that compartment was less for the treatment compartment than the control compartment of the treatment bioassays (a) (T=9, n=11, 0.05 > P > 0.02), and more similar between the control compartments of control bioassays (b) (T=15, n=11, 0.20 > P > 0.10). Box boundaries indicate the 25th and 75th percentiles, the solid line within each box is the median, the dashed line represents the sample mean, and outer bars show the 5th and 95th percentiles (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).

CHAPTER FOUR

Interspecific interactions of spiders (Araneae) and *Formica aserva* Forel ants (Hymenoptera: Formicidae)

Abstract

Some spiders and ants appear to experience some degree of niche overlap. If competitive or predatory interactions between these terrestrial generalist predators occur, the interpretation of spider responses to habitat disturbance may be influenced by the presence or absence of ants. We compared the activity-abundance of spiders in a central British Columbia clearcut between zones colonized and non-colonized by Formica aserva. We hypothesized that the activity-abundance of epigaeic spider species would be different between these zones. While the activity-abundance of most spider species analyzed did not differ between colonized and non-colonized F. aserva zones, the activity-abundances of Pardosa mackenziana, Alopecosa aculeata (Lycosidae), Robertus vigerens (Theridiidae), and Xysticus ellipticus (Thomisidae) were higher in colonized zones, and the activity-abundance of Zelotes puritanus (Gnaphosidae) was higher in non-colonized zones. Our findings support our hypothesis and suggest that the presence of F. aserva can be associated with changes in the activity-abundance of some spider species. Additional long-term studies investigating possible interactions between individual spider species and aggressive ants are needed to clarify the temporal scale, intensity, and nature of possible interactions between these abundant predators.

Keywords: competition, species interaction, Gnaphosidae, Lycosidae, Theridiidae, Thomisidae, Formicidae

Introduction

Ants (Hymenoptera: Formicidae) are known to significantly affect other arthropods (Hölldobler & Wilson, 1990; Niemelä et al., 1992; Karhu, 1998; Laakso & Setälä, 2000; Hawes et al., 2002; Punttila et al., 2004). Spiders (Araneae) are abundant in many habitats, and because many species potentially overlap with ants in terms of niche characteristics and seasonal activity patterns (Van der Aart & de Wit, 1971; Turnbull, 1973; Hölldobler & Wilson, 1990) it has been proposed that ants and some spiders may be competitors and/or mutual predators (Van der Aart & de Wit, 1971; Wise, 1993; Halaj et al., 1997; Heikkinen, 1999; Sanders & Platner, 2007). The potential for interspecific interactions to occur between these groups is important given the attention spiders have received as possible bioindicators of environmental conditions (Marc et al., 1999; Cristofoli et al., 2010), including those associated with forest disturbances (Pearce & Venier, 2006; Gillette et al., 2008). In a preliminary study in British Columbia, spider families displayed high habitat specificity (Lindgren et al., 1999), and spider assemblages responded differently relative to different types of habitat disturbances in other areas (Buddle et al., 2000; Larrivée et al., 2005).

Laakso and Setälä (2000) removed *Formica aquilonia* Yarrow ants from selected areas in a Finnish boreal forest, and observed a positive response by other predatory arthropods, indicating a compensatory shift in the arthropod predatory guild where ants were removed. Cherix and Bourne (1980) also found differences between arthropod predator assemblages within and outside an area occupied by a *Formica lugubris* Zetterstedt super-colony in the Swiss Jura. In their study, large spiders (especially Lycosidae) were less abundant in areas near the super-colony compared to outside the colony's foraging boundary. Cherix and

Bourne (1980) concluded that pressure from the aggressive super-colony limited populations of large spider species.

Fink (1987) made direct field observations of *Formica* sp. ants on the surface of, or within unguarded *Peucetia* spp. Thorell (Oxyopidae) egg sacs, and noted ants removing eggs or spiderlings through holes they had chewed in the sac. Group foraging behaviour of the ants enabled them to completely empty discovered egg sacs in a relatively short period of time (Fink, 1987). The presence of *Formica obscuripes* Forel on sagebrush, *Artemisia tridentata* Nutt. (Asteraceae) near ant nests also had a negative influence on spider abundance (Heikkinen, 1999). Abundance of arthropod prey also increased in the canopies of Douglas-fir trees, *Pseudotsuga menziesii* (Mirbel) Franco (Pinaceae), where ants (primarily *Camponotus* spp.) were excluded (Halaj et al., 1997). Despite ants and some spiders consuming similar prey items, ants in their study did not strongly affect spider species diversity or richness, either through exploitative competition or predation pressure. Aggressive behaviour of foraging *Camponotus* spp., however, did appear to disturb hunting spiders (Halaj et al., 1997). Both Heikkinen (1999) and Halaj et al. (1997) concluded that interference competition may be an important component of interactions between ants and spiders.

Sudd and Lodhi (1981) found that the number of spiders, beetles (Coleoptera), and springtails (Collembola: Arthropleona) were reduced in areas with relatively numerous *F*. *lugubris*. Their study also found indications of species-specific responses and year-to-year variation of those responses. Sanders & Platner (2007) found that ants had a negative effect on ground dwelling web building spiders in a German grassland habitat, particularly Linyphiidae. The abundance of wandering spiders (primarily Lycosidae) was not affected by the presence of

ants, and the abundance of *Formica* spp. workers was greater in areas where spiders had been removed (Sanders & Platner, 2007). Variation among the responses of spider to ants has also been reported in other studies (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981).

Other authors have argued that interactions between ants and spiders are inconsequential (Sterling et al., 1979). Brüning (1991) found no significant difference in overall spider species composition or density between areas within or outside of a *Formica polyctena* Föerster colony, despite observations of ants returning to their nest with a variety of dead spiders. Van der Aart and de Wit (1971) concluded that the presence of *Formica rufa L*. did not influence the species composition or abundance of hunting spiders (including Lycosidae, Pisauridae, Ctenidae, Gnaphosidae, and Clubionidae) in a meadow. While certain species were more (*Aulonia albimana* (Walckenaer), *Pardosa nigriceps* (Thorell), and *Drassodes lapidosus* (Walckenaer)) or less (*Pardosa pullata* (Clerck) and *Pardosa monticola* (Clerek)) numerous in areas with *F. rufa*, Van der Aart and de Wit (1971) proposed that these patterns were due to differences in vegetation structure and humidity between the sampling areas with and without *F. rufa*. As described above, several correlative and some experimental studies have been conducted; yet study of interactions between ants and spiders is still limited considering the ubiquity and wide diversity of these groups. As a result the importance of interactions between these groups remains unclear (Wise, 1993).

In Canada, some spiders may utilize coarse woody debris for foraging, overwintering or shelter, or as access points to direct sunlight for basking and/or accelerating egg development (Buddle, 2001). The diversity of spiders on dead wood in Alberta was also higher than that of the forest floor (Buddle, 2001), and in Québec more spiders and spider species were found on

the surface of downed dead wood than on the forest floor (Varady-Szabo & Buddle, 2006). These findings are relevant to central British Columbia where timber harvest areas (and their associated woody debris) are often dominated by *Formica aserva* Forel ants (Higgins, 2010).

Formica aserva, a member of the *Formica sanguinea* species group, is ecologically versatile and widely distributed (Naumann et al., 1999). *Formica aserva* workers are aggressive and omnivorous (Phillips & Willis, 2005; Higgins, 2010). Their nests are frequently in coarse woody debris (Lindgren & MacIsaac, 2002; Higgins, 2010), and may include hundreds or thousands of individuals (Savolainen & Deslippe, 1996; Naumann et al., 1999). A facultative slave taker (Francoeur, 1983), *F. aserva* colonies likely establish through nest parasitism, and require that suitable slave species colonize a habitat before them (Higgins, 2010). In a cool, subboreal region of central British Columbia, *F. aserva* was absent in mature or recently harvested (2-3 years) pine stands, but common in stands 8-10 years post harvest, with populations peaking 13-15 years post-harvest before decreasing in 23-25 year old stands (Higgins, 2010). This indicated that in cool environments it is a disturbance specialist dependent on solar radiation heating and initial colonization by a suitable pioneer slave species (Higgins & Lindgren, 2012a).

We selected a recently disturbed habitat that appeared to be in a period of *F. aserva* population establishment and growth based on nest density and distribution. This characteristic allowed us to directly compare areas with similar habitat characteristics but differing in *F. aserva* presence. We hypothesized that the activity-abundance of ground active spider species in a central British Columbia clearcut would be different between areas colonized and not colonized by *F. aserva*.

Materials and Methods

Study Area and Field Data Collection

Five replicates were established in a clearcut five years post-harvest (Government of British Columbia, 2011) east of Prince George, British Columbia (elevation 740m, located approximately 53.901° N, 122.219° W) in the cool wet subzone of the sub-boreal spruce biogeoclimatic zone (SBSwk1) (Meidinger et al., 1991; Government of British Columbia, 2008). The selected harvest block had a maximum length and width of approximately 2400m and 650m, respectively, and appeared to be under colonization by *Formica aserva* based on a preliminary survey of the abundance and distribution of nests (Chapter 2). The long axis of the harvest block had a generally north-south orientation. Replicates were established along the long axis of the harvest block, and selected based on apparent habitat homogeneity and spaced at least 100m apart. Two zones, with (colonized) or without (non-colonized) *F*. *aserva* nests, were delineated within each replicate as described in Chapter 2. Use of modified Nordlander pitfall traps (Nordlander, 1987; Lemieux & Lindgren, 1999; Higgins & Lindgren 2012b) and assessment of field site characteristics (*F. aserva* nests, soil moisture and pH, and ground cover) were also as described in Chapter 2.

Specimen Identification

Pitfall trap contents were sorted into general taxonomic categories at the University of Northern British Columbia, and stored in 70% ethanol. Identifications of adult spider specimens were made at the Royal British Columbia Museum, Victoria, BC, by R. G. Bennett³. As identification of spider species is largely dependent on unique reproductive structures only evident in adults, data for juvenile spider specimens were recorded, but not

³ Research Associate, Royal British Columbia Museum, Victoria, British Columbia, Canada

included in analyses. Adult voucher specimens have been deposited at the Royal British Columbia Museum.

Analysis

As in Chapter 2, data from pitfall traps that were disturbed by adverse weather conditions, trap malfunction, or animal interference were not included in analyses. Data were standardized to total trapping effort (98 trapping days) to adjust for trap disturbance. Spider captures for individual pitfall traps were summed within each replicate zone. Soil moisture, soil pH, mean estimates of percent cover type, and *F. aserva* activity-abundance data were handled and analyzed as in Chapter 2.

Spider species data were analyzed by linear mixed effects ANOVA (α =0.05) using R (version 2.14, © 2011 The R Foundation for Statistical Computing). When necessary, data were transformed to satisfy model assumptions based on visual assessment of residual plots. When assumptions could not be met, a Mann-Whitney U test was used (SYSTAT 11, ©2005 SYSTAT Software, Inc.). Only relatively common spider species (defined as species captured in four or more replicates and with five or more specimens captured in either ant-colonization zone) were analyzed. Zone (colonized and non-colonized) and the sex of adult spiders were modeled as fixed effects and replicate as a random effect. Sex by zone interaction was tested, and if non-significant sexes were pooled.

Results

As noted in Chapter 2, neither mean relative soil moisture (Mann-Whitney U test statistic=16, N=5, 5, P=0.465) nor mean soil pH (Mann-Whitney U test statistic=11.5, N=5, 5, P=0.834) differed significantly when comparing the colonized and non-colonized zones (Figure 2.1). Additionally, the estimated mean percent cover of the ten cover types did not

differ significantly between colonized and non-colonized zones (Table 2.1). Significantly more *Formica aserva* workers were captured in the colonized zones than in the non-colonized zones (Mann-Whitney U test statistic=25, N=5, 5, P=0.009), and significantly more *F. aserva* nests were also found in the colonized zones compared to the non-colonized zones (Mann-Whitney U test statistic=22.5, N=5, 5, P=0.018) (Figure 2.2).

In total, 1726 adult spiders comprising 64 species were collected (Table 4.1). All but 29 specimens were identified to the species level, and all unidentified specimens fell into the genus *Agyneta* (Linyphiidae). Twenty-seven species (including the unidentified *Agyneta* species) were classified as common, ranging in capture frequency from six *Robertus vigerens* (Chamberlin & Ivie) (Theridiidae) to 331 *Pardosa moesta* Banks (Lycosidae). Significant differences between the numbers of male and female spiders were found for many species, but there were no significant sex by zone interactions.

The activity-abundance of most spider species analyzed did not differ significantly between *F. aserva* zones. For five species, however, significant differences were detected. *Pardosa mackenziana* (Keyserling) (Lycosidae) ($F_{1,4}$ =15.61653, P=0.0168), *Alopecosa aculeata* (Clerck) (Lycosidae) ($F_{1,4}$ =13.93325, P=0.0202), *R. vigerens* (Theridiidae) (Mann-Whitney U test statistic=22.5, N=5, 5, P=0.018), and *Xysticus ellipticus* Turnbull et al. (Thomisidae) (Mann-Whitney U test statistic=24, N=5, 5, P=0.012) had significantly higher activity-abundance levels in colonized zones compared to non-colonized zones (Figure 4.1). The activity-abundance of *Zelotes puritanus* Chamberlin (Gnaphosidae) was significantly higher in non-colonized zones than in colonized zones ($F_{1,4}$ =29.35472, P=0.0056) (Figure 4.1). One additional species, *Gnaphosa parvula* Banks (Gnaphosidae), showed a nonsignificant trend ($F_{1,4}$ =6.6089, P=0.0619) of higher activity-abundance in non-colonized zones.

Discussion

The significant difference in *Formica aserva* nest number and activity-abundance between the colonized and non-colonized zones, and the lack of differences between these zones for any other factor measured (soil moisture, pH, and ground cover), supports our selection criteria for these zones. Our findings support our hypothesis and suggest that the presence of *F. aserva* can be associated with changes in some spider species populations. The species-specific responses found among spiders in our study were also in agreement with the variation recorded in earlier studies (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981). The majority of common spider species showed no significant difference in activity-abundance between colonized and non-colonized zones, which also agrees with the findings of other studies that recorded no difference in overall spider assemblage or abundance relative to the presence of ants (Van der Aart & de Wit, 1971; Sterling et al., 1979; Brüning, 1991). The species in our study that had significantly different activity-abundances between colonized and non-colonized zones may highlight the value of examining individual species rather than pooling all spiders together when investigating possible interactions with ants.

Pardosa mackenziana, Alopecosa aculeata, Robertus vigerens, and Xysticus ellipticus all had higher activity-abundance in colonized zones compared to non-colonized zones. This may indicate that these species were either able to benefit from the presence of low/moderate ant populations (McColl, 2010), or that the presence of ants increased the activity of these species and thus increased their propensity to be captured in pitfall traps. In some cases the

anatomy and autecology of a species may help explain the differential captures. *Pardosa mackenziana* and *A. aculeata* are widely distributed lycosids, which are considered active predators of ground dwelling invertebrates (Dondale & Redner, 1990). Diurnal and usually dark-bodied, many lycosids are swift visual hunters and active runners (Dondale & Redner, 1990). The genus *Pardosa* is characterized by species with long slender legs and high body carriage, a trait believed to help these species pursue prey. The genus *Alopecosa* differs in appearance from *Pardosa* most notably by thicker bodies and legs (Dondale & Redner, 1990). The Theridiidae *Robertus vigerens* is widely distributed in western North America and has been observed in vegetative litter and under stones; though little additional information is available (Dondale et al., 1997). Like lycosids, thomisids are also primarily diurnal, but differ from the former in hunting strategy (Bennett, 1999). Thomisids have laterigrade legs and dorso-ventrally flattened bodies (Dondale & Redner, 1978; Bennett, 1999). *Xysticus* species are relatively slow moving sit-and-wait ambush predators (Bennett, 1999), and their cryptic coloration and powerful forelegs enable them to capture prey at close range (Dondale & Redner, 1978).

Given the diurnal activity of some lycosids and thomisids, these species may have been able to utilize *F. aserva* either directly as a food resource or indirectly by capturing prey flushed from the litter by the foraging activity of *F. aserva* workers. In a list of ant predators, Pętal (1978) includes the order Araneae, and specifically Thomisidae. Hölldobler (1976) reported *Misumenops coloradensis* Gertsch (Thomisidae) preying upon female harvester ants (*Pogonomyrmex maricopa* Wheeler and *Pogonomyrmex desertorum* Wheeler). Sanders and Platner (2007) also observed lycosids and thomisids preying on ants, and suggested that *Formica cunicularia* Latreille and *Formica fusca* L. workers were negatively affected by high

densities of wandering spiders. Neuvonen et al. (2012) also found that lycosids were positively associated with ants (*Formica rufa* species group), and captured more lycosids near wood ant nests than at greater distances. Neuvonen et al. (2012) suggested that these patterns were not related to direct benefits associated with ant presence, however, but rather the result of habitat preferences or indirect effects related to other arthropod responses. This study did not specify how individual lycosid species may have been affected by wood ants.

Due to the relatively recent clearcutting of our study area (five years post-harvest), it is unlikely that the *F. aserva* colonies in our study had reached their peak density (Higgins, 2010). In ants, forager density can be positively correlated with forager aggression (Savolainen & Vepsäläinen, 1988), and in west-central British Columbia *F. aserva* is relatively uncommon in areas 2-3 years post-harvest and greatest in areas 13-15 years postharvest (Higgins, 2010). This may have increased the vulnerability of foragers to predation by spiders in our study, and hence favoured some spider species.

While Brüning (1991) noted the presence of lycosids within their study area, *Formica* polyctena workers were never observed returning to their nest with lycosids, indicating that these spiders were not a regular prey item of the colony. *Pardosa lugubris* Walckenaer were frequently seen on the litter layer near the *F. polyctena* colony, and Brüning (1991) noted that these individuals avoided *F. polyctena* workers when they came too near with "a short jump," apparently unnoticed by the worker ant. When spiders were detected by *F. polyctena* workers, Brüning (1991) observed that spiders had little difficulty escaping the ant unless the spider ran towards the ant. Based on these observations, *F. polyctena* workers seem ineffective in detecting agile prey, and may be more successful in capturing unsuspecting or injured prey that are more or less randomly encountered (Brüning, 1991). If *P. mackenziana*

and *A. aculeata* were able to effectively avoid foraging workers with strategies similar to those described by Brüning (1991), they might not have been adversely affected by *F. aserva* and may in fact have benefitted from the presence of the ants. Mature lycosid females carry their egg sac (and later spiderlings) on their abdomen (Bennett, 1999), which may also reduce the potential for ant predation of immature lycosid spiders.

The reduced activity-abundances of *Zelotes puritanus* in areas colonized by *F. aserva* suggest that this species may be negatively affected by *F. aserva* in our study. While the ecology of many gnaphosids is poorly understood, this group is generally described as "stealthy hunters"; members of *Zelotes* are also generally nocturnal and possess dark coloration (Platnick & Dondale, 1992). Many of these species live within the litter layer or under stones, coarse woody debris, and other debris, and utilize these microhabitats as refuges during the day (Platnick & Dondale, 1992).

Brüning (1991) observed *F. polyctena* workers returning to their nest with juvenile spiders, including a ghaphosid. Thus the lower activity-abundance of *Z. puritanus* may, at least in part, have been the result of local population reduction by ant predation of juveniles. In contrast to diurnal spider species, nocturnal gnaphosids hiding in the litter may be less able to avoid ant disturbance (or even predation) if their daytime hideaways are encountered by foraging ants. Disturbance of hiding *Z. puritanus* by ants may lead to these spiders selecting for habitats away from ant activity. Halaj et al. (1997) found that aggressive behaviour of foraging ants disturbed hunting spiders, and displacement resulting from interference interactions may be another possible explanation for the activity-abundance pattern of *Z. puritanus*.

Species that had similar activity-abundance levels between colonized and noncolonized zones may not have been equally abundant in these areas. Varied behavioural responses to ant presence could have influenced capture rates between *F. aserva* zones regardless of abundance (Sudd & Lodhi, 1981), and it is plausible that captures of *P. mackenziana, A. aculeata, R. vigerens*, and *X. ellipticus* were higher in the colonized zones as a result of increased activity and not increased abundance. Likewise, it is possible that *Z. puritanus* were not less abundant in areas associated with *F. aserva*, but simply less active. If this was the case, our sampling methods could have mischaracterized the effects experienced by these species. Our methods also prevented us from separating negative effects associated with *F. aserva* from potential effects resulting from interactions among spider species. The lack of information on the ecology and behaviour of most Canadian spiders (Bennett, 1999) also limits our ability to explain the mechanisms behind our findings, and emphasizes the need for continued study of Canadian spider species biology and ecology, in addition to direct observations of how different species interact with aggressive ants.

Our study suggests that the presence of *F. aserva* can have favorable, detrimental, or negligible consequences depending on the spider species. Spider species responses may also vary from year-to-year (Sudd & Lodhi, 1981), possibly relating to fluctuations in ant presence, density, and assemblage composition over time (Higgins, 2010). Additional long-term studies investigating possible interactions between individual spider species and aggressive ants are needed to clarify the temporal scale, intensity, and nature of possible interactions between these abundant predators. Greater understanding of these variables will not only increase our knowledge of spider species, but may also improve the reliability of spiders as bioindicators.

Table 4.1. Spider species captured listed by family and total number captured in colonized

 and non-colonized *Formica aserva* zones. Species in bold had significantly different activity

 abundance in colonized and non-colonized zones.

FAMILY	SPECIES	TOTAL NUMBER CAPTURED	
		Colonized	Non-colonized
AGELENIDAE	Agelenopsis utahana (Chamberlin & Ivie)	0	1
CLUBIONIDAE	Clubiona trivialis C.L. Koch	0	1
CYBAEIDAE	Cybaeus morosus Simon	29	23
GNAPHOSIDAE	Drassodes neglectus (Keyserling)	4	2
	Gnaphosa muscorum (L. Koch)	26	23
	<i>Gnaphosa parvula</i> Banks	57	102
	Haplodrassus signifer (C.L. Koch)	1	1
	Micaria aenea Thorell	2	1
	<i>Micaria pulicaria</i> (Sundevall)	1	0
	Micaria rossica Thorell	4	0
	Zelotes puritanus Chamberlin	1	13
	Zelotes fratris Chamberlin	32	16
HAHNIIDAE	Cryphoeca exlineae Roth	16	13
	Hahnia cinerea Emerton	0	1
	Neoantistea agilis (Keyserling)	3	5
LINYPHIIDAE	Agyneta sp.	20	9
	Agyneta olivacea (Emerton)	34	33
	Bathyphantes alascensis (Banks)	0	1
	Bathyphantes pallidus (Banks)	1	0
	Centromerus longibulbus (Emerton)	0	2
	Ceraticelus fissiceps (O. PCambridge)	2	2
	Ceraticelus laetabilis (O. PCambridge)	0	1
	Ceratinella brunnea Emerton	23	21
	Collinsia ksenia (Crosby & Bishop)	0	1
	Diplocentria bidentata (Emerton)	2	1
	<i>Grammonota gigas</i> (Banks)	0	12
	Hypselistes florens (O. PCambridge)	1	1
	Lepthyphantes intricatus (Emerton)	7	5
	Mermessus trilobatus (Emerton)	4	5
	Oreonetides filicatus (Crosby)	1	0
	Pelecopsis sculpta (Emerton)	58	101
	Pocadicnemis pumila (Blackwall)	2	1
	Scotinotylus sacer (Crosby)	4	3

 Table 4.1 (continued). Spider species captured listed by family and total number captured in

 colonized and non-colonized Formica aserva zones. Species in bold had significantly

 different activity-abundance in colonized and non-colonized zones.

FAMILY	SPECIES	TOTAL NUMBER CAPTURED	
		Colonized	Non-colonized
LINYPHIIDAE (cont.)	Sisicottus nesides (Chamberlin)	2	0
	Sisicus apertus (Holm)	2	1
	<i>Symmigma minimum</i> (Emerton)	99	84
	<i>Tunagyna debilis</i> (Banks)	1	0
	Tachygyna vancouverana Chamberlin & Ivie	1	0
	Walckenaeria atrotibialis (O. PCambridge)	8	6
	Walckenaeria directa (O. PCambridge)	1	1
	Walckenaeria exigua Millidge	11	3
	Walckenaeria tricornis (Emerton)	8	5
LIOCRANIDAE	Agroeca pratensis Banks	0	1
LYCOSIDAE	Alopecosa aculeata (Clerck)	37	9
	Arctosa alpigena (Doleschall)	1	0
	Pardosa fuscula (Thorell)	0	4
	Pardosa groenlandica (Thorell)	0	2
	Pardosa hyperborea (Thorell)	72	65
	Pardosa mackenziana (Keyserling)	62	27
	Pardosa moesta Banks	129	202
	Pardosa wyuta Gertsch	4	5
	Pardosa xerampelina (Keyserling)	19	12
	Trochosa terricola Thorell	32	15
PHILODROMIDAE	Thanatus coloradensis Keyserling	1	1
SALTICIDAE	Neon reticulatus (Blackwall)	1	0
	Pellenes montanus (Emerton)	2	1
	Talavera minuta (Banks)	1	0
TELEMIDAE	Usofila pacifica (Banks)	4	0
THERIDIIDAE	Crustulina sticta (O. Pickard-Cambridge)	1	0
	Robertus fuscus (Emerton)	0	1
	Robertus vigerens (Chamberlin & Ivie)	6	0
THOMISIDAE	Xysticus ellipticus Turnbull et al.	9	1
	Xysticus emertoni Keyserling	5	7
	Xysticus luctuosus (Blackwall)	0	1
	Xysticus montanensis Keyserling	8	9
	TOTAL	862	864



Formica aserva zone

Figure 4.1. Significant (α=0.05) differences in the activity-abundance (mean total number captured) of *Zelotes puritanus*, *Alopecosa aculeata*, *Pardosa mackenziana*, *Robertus vigerens* and *Xysticus ellipticus* (standardized to 98 trap-days) between zones colonized and non-colonized by the ant *Formica aserva* (SigmaPlot® 11.2 © 2009-2010 SYSTAT Software, Inc.).

CHAPTER FIVE

Synthesis

Both carabids (Coleoptera: Carabidae) and spiders (Araneae) have received attention as potential indicator taxa (Niemelä et al., 1993; Beaudry et al., 1997; Marc et al., 1999; Larochelle & Larivière, 2003; Rainio & Niemelä, 2003; Pearce & Venier, 2006; Gillette et al., 2008; Cristofoli et al., 2010). Lövei and Sunderland (1996), however, have also suggested that failure to account for the presence of ants (Hymenoptera: Formicidae) in some community studies could result in the formation of incomplete or invalid conclusions. This suggestion is based on observations that these taxa may occupy similar guilds and experience niche overlap (Lövei & Sunderland, 1996; Hawes et al., 2002; Reznikova & Dorosheva, 2004).

Several studies have addressed potential interactions between carabids and ants (Niemelä et al., 1992; Koivula et al., 1999; Hawes et al., 2002; McColl, 2010) and spiders and ants (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981; Halaj et al., 1997; Heikkinen, 1999; Punttila et al., 2004; Sanders & Platner, 2007). These studies have uncovered mixed responses to ants, and additional research regarding potential interactions between ants, carabids and spiders could help to refine their use as indicators. We examined the effects of *Formica aserva* Forel ant colonies on carabids (Chapter 2) and spiders (Chapter 4) in a disturbed habitat in the central interior of British Columbia, and investigated behavioural responses by carabids to possible signals of ant presence (Chapter 3).

The field components of our research were conducted in a disturbed habitat that was partially colonized by *F. aserva*. Our initial study area selection was based on the presence or absence of active *F. aserva* colonies in areas that were apparently otherwise homogeneous

(Chapter 2). We hypothesized that the activity-abundance patterns of carabids and spiders would differ in these areas relative to the presence or absence of *F. aserva* colonies. When we compared habitat measurements between zones that were either colonized or non-colonized by *F. aserva* we found no significant differences in mean soil moisture (Figure 2.1a), mean soil pH (Figure 2.1b), or the estimated mean percent of different ground cover types (Table 2.1). We did detect a significant difference in *F. aserva* activity-abundance between colonized and non-colonized zones (Figure 2.2a), which validated our initial selection criteria. These results indicate the presence of *F. aserva* could provide a plausible explanation for the differences in carabid and spider activity-abundance between colonized zones.

Of the 11 carabid species captured, six were examined in terms of their activityabundance patterns in colonized and non-colonized zones (Chapter 2). We found that the activity-abundance of these carabids differed significantly from expected (*i.e.*, 1:1) between colonized and non-colonized zones, and that individual species displayed unique patterns (Table 2.2). *Calathus ingratus* Dejean and *Pterostichus adstrictus* Eschscholtz were captured more frequently than expected in non-colonized zones compared to colonized zones. The opposite was found for *Pterostichus ecarinatus* Hatch, *Pterostichus herculaneus* Mannerheim, and *Syntomus americanus* (Dejean). *Synuchus impunctatus* (Say) was caught in similar numbers in both colonized and non-colonized zones, and was thus similar to expected ratios.

We also examined the carabid P. adstrictus in laboratory behavioural bioassays in an effort to determine if this species was able to detect glandular chemicals from crushed F. aserva gasters (Chapter 3). In the treatment bioassays P. adstrictus appeared to avoid the area

of the experimental arena where the crushed F. aserva gasters were located (Figures 3.5a, 3.6a, and 3.7a). By contrast, in control bioassays we detected no significant side-bias in the behaviour of P. adstrictus (Figures 3.5b, 3.6b, and 3.7b). These observations indicate that P. adstrictus may be able to detect F. aserva semiochemicals, and it follows that P. adstrictus may have the ability to detect the presence of F. aserva prior to direct encounters. The results of bioassays with P. adstrictus are consistent with the patterns we observed for this species in our field study, where P. adstrictus had lower activity-abundance in zones with F. aserva colonies compared to non-colonized zones (Table 2.2). Thus it may be possible for P.

Compared to the carabid assemblage of our study, the spider assemblage was both more abundant and species rich. Sixty four species were collected, and all but 29 of the 1726 adult specimens were identified to the species level. The activity-abundances of 27 species were compared between the colonized and non-colonized zones. While differences were found between the numbers of males and females captured, no significant sex by zone interactions were detected, indicating that the differences among sex were due to inherent differences in behaviour among males and females rather than differential effects by ants. The activity-abundance of most spider species did not differ between zones, but for five species significant differences were detected (Figure 4.1). *Pardosa mackenziana* (Keyserling) (Lycosidae), *Alopecosa aculeata* (Clerck) (Lycosidae), *Robertus vigerens* (Chamberlin & Ivie) (Theridiidae), and *Xysticus ellipticus* Turnbull et al. (Thomisidae) had higher activity-abundance levels in colonized zones. *Zelotes puritanus* Chamberlin (Gnaphosidae), on the other hand, had lower activity-abundance in colonized zones.
Variation among the responses of spider to ants has also been reported in earlier studies (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981).

While many studies have examined possible interactions of carabids and spiders with different ant species, the results have been mixed for this group of generalist, surface-active predators. Most studies addressing ant-carabid interactions have found primarily negative relationships, but some carabid species occur in close proximity to areas populated by *Formica* spp. ants (Niemelä et al., 1992; Koivula et al., 1999; Hawes et al., 2002; Reznikova & Dorosheva, 2004; McColl, 2010). It has been proposed that some carabid species may be able to coexist with ants by avoiding direct encounters with aggressive ants or utilizing dead ants as a resource.

Knowledge gaps in the life histories of the carabid species in our study limit our ability to explain the specific mechanisms responsible for our findings, and we can only speculate as to the causes of species distributions. For the species we identified with higher activity-abundance in areas colonized by *F. aserva*, it may be that these carabids were able to capitalize on the necrophoresis of the ant colonies (Hengeveld, 1981; Dorosheva & Reznikova, 2006) or benefited indirectly from the foraging activities of *F. aserva* (*i.e.*, overlap in foraging periods/locations might allow some carabids to take advantage of prey flushed from their cover by *F. aserva* activity). Other explanations are also possible, *e.g.*, *F. aserva* may not be equally aggressive to different carabid species. Some carabids may also be less susceptible to ant attack or disturbance, or the size of the *F. aserva* colonies in our study may not have been sufficiently large to negatively influence some carabid species (McColl, 2010). The lower activity-abundance of some carabid species in zones with F. aserva nests is equally open to interpretation. These species may have been negatively affected by the presence of F. aserva due to greater competitive and/or predation pressures. Our observations of carabid response to F. aserva crushed gasters indicates that some carabids may be able to detect the presence of ants prior to direct encounters, and could potentially select for habitats where aggressive ants are absent. While we have no information on the experiences of the beetles in our study prior to their collection, their eight to 12 month captivity before experimentation may have lessened the likelihood of prior interactions with aggressive ants influencing their behaviour.

While the root cause of the behaviours we observed is still unclear, other studies have suggested that direct encounters with ants may lead carabids to "learn" to avoid ants (Reznikova & Dorosheva, 2000). It may also be possible that competitive pressures and/or mortality associated with interspecific interactions with *F. aserva* could have resulted in some carabid species evolving the ability to avoid direct encounters with aggressive ants by detecting cues associated with their presence. Kolbe (1969) reported that *Formica polyctena* Förster workers readily attacked carabids and that such attacks increased beetle mortality. For carabids in British Columbia, McColl (2010) suggested that at moderate ant activity-abundance levels carabids were more likely to be found with injuries, which may have resulted from unsuccessful predatory attacks or interference interactions with *F. aserva*. At high *F. aserva* activity-abundance levels these attacks were thought to be more effective and result in successful predation of carabids, and hence fewer carabids were observed with injuries.

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As with the carabid species captured more frequently in colonized zones, spider species that had higher activity-abundance in zones with *F. aserva* colonies may have also been able to benefit from the presence of these colonies. Lycosids and thomisids are predators of ground dwelling invertebrates (Dondale & Redner, 1990; Bennett, 1999), and these species may have been able to utilize *F. aserva* either directly as a food resource or indirectly by capturing prey flushed from the litter by foraging workers. Several studies have identified Thomisidae (Hölldobler, 1976; Pętal, 1978; Sanders & Platner, 2007) and Lycosidae (Sanders & Platner, 2007) as ant predators. It is likely that the *F. aserva* colonies in our study were recently established (Higgins, 2010) and may have been vulnerable to predation by spiders. It is notable that three of the four species that had higher activity-abundance in colonized zones were either lycosids or thomisids. Other studies have offered descriptions of the ease with which lycosids are able to avoid direct encounters with ants (Brüning, 1991), and similar strategies may have been used by some of the lycosids in our study as well, allowing these spiders to avoid aggressive encounters with *F. aserva* workers.

The reduced activity-abundances of *Z. puritanus* relative to *F. aserva* suggest that this species may have been negatively affected by *F. aserva* colonies. Gnaphosids often live within the litter layer or under stones, coarse woody debris, and other debris (Platnick & Dondale, 1992). Nocturnal gnaphosids hiding in the litter may be less able to avoid ant disturbance (or even predation) if their daytime hideaways are discovered by foraging ants. Disturbance by ants may lead some spiders to select for habitats away from ant activity. Predation by ants is yet another possibility, as Brüning (1991) observed *F. polyctena* workers returning to their nest with a juvenile gnaphosid.

Our study suggests that the presence of F. aserva may have favorable, detrimental, or negligible consequences depending on the carabid or spider species in question. The fact that we identified species (both among carabids and spiders) with different activity-abundance patterns relative to F. aserva presence highlights the value of examining individual species rather than pooling species together when investigating possible interactions with ants. While we have focused our attention on the species that appeared to respond to F. aserva presence, our results also raise interesting questions about the species for which no response was detected, and the significance of responsive species in terms of assemblage composition and ecological importance.

For species that were apparently not affected by *F. aserva* colonization, it is also important to note that activity-abundance patterns are the result of both behaviour and abundance. Varied behavioural responses to *F. aserva* could have disproportionately affected a species' activity-abundance (Sudd & Lodhi, 1981). Additionally, *F. aserva* may not have been equally aggressive to all species in our study, as they do distinguish between different threats and are not equally aggressive to all intruders (Phillips & Willis, 2005). Our methods also prevented us from separating negative effects associated with *F. aserva* from those potentially resulting from interactions within or between the carabid and spider assemblages.

The effects of competitive and predatory interactions can be difficult to separate, as they may occur simultaneously (Wissinger, 1989). Currie et al. (1996) suggested that food limitations could lead to higher predation pressures among carabids as a result of more time spent foraging leading to increased frequency of interspecific encounters. Similarly, the limitation or abundance of resources could influence interactions between ants and other ground dwelling arthropods (*e.g.*, carabids and spiders). Other authors have emphasized the

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role of behavioural responses in determining the relationships between carabids, spiders, and ants (Gridina, 1994; Dorosheva & Reznikova, 2006). Undoubtedly, interactions between these groups are not only complex, but also variable across different ecological conditions.

Habitat change, interspecific pressures, species-specific behavioural traits, biological requirements, and seasonal activity patterns may all contribute to the distribution patterns of these organisms. The species composition of ant assemblages and the relative dominance of specific species change over time within disturbed habitats (Higgins, 2010), and these fluctuations may have different effects on carabids and spiders. It is also possible that effects of *F. aserva* change as their populations build and they become more dominant in a habitat. Additional studies investigating potential interactions between carabid and spider species with aggressive ant populations of different densities could help to clarify possible interactions between these groups. The ability of a carabid species to detect ant semiochemicals may also indicate these signals have some connection to the survival and reproductive success of some carabids. Future studies addressing the ability of other carabid species to detect and respond to signals of ant presence could improve our understanding of the relationships between carabids and ants.

The attention carabids and spiders have received as potential bioindicators (Pearce & Venier, 2006) increases the need for continued research into their relationships with abiotic and biotic factors in various ecosystems. There is a growing body of literature supporting the value of addressing possible interactions between carabids and ants (Niemelä et al., 1992; Lövei & Sunderland, 1996; Oliver & Beattie, 1996; Humphrey et al., 1999; Koivula et al., 1999; Hawes et al., 2002; McColl, 2010) and spiders and ants (Howard & Oliver, 1978; Cherix & Bourne, 1980; Sudd & Lodhi, 1981; Halaj et al., 1997; Heikkinen, 1999; Punttila et

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al., 2004; Sanders & Platner, 2007). Greater understanding of these variables will not only increase our knowledge of carabid and spider species, but may also improve their reliability as bioindicators.

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