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**FEAR AND LOATHING IN THE SUPER-ORGANISM:
FORAGING STRATEGY DOESN'T CHANGE FORAGER RESPONSE IN A LANDSCAPE OF
FEAR.**

by:

PHILIP SCHADEGG
B.S, UNIVERSITY OF WISCONSIN, EAU CLAIRE, 2015

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Sciences
from the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

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2019**

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ABSTRACT

Understanding how predators impact keystone species, like ants, is very important for our understanding of ecology because of ants' importance in shaping community dynamics and ecosystem functions. In this thesis I present research investigating the role of the ant-specialized spider *Anasaitis canosa* in influencing the foraging behavior of four ant species (*Formica pallidefulva*, *Odontomachus ruginodis*, *Pheidole obscurithorax* & *Solenopsis invicta*). Collectively, these four species use foraging strategies exhibited by most ants. I conducted two experiments to quantify the impacts of spider predation on ant prey. The first used forty colonies of four ant species to investigate how *A. canosa* changed foraging behavior at both the individual and colony level. The second used 27 lab-reared *S. invicta* colonies to see if there was any evidence for innate predatory avoidance in foragers and if predatory avoidance was influenced by learning. A field study observed the density and prey choices of *A. canosa* in 3 sites within the UCF arboretum. In sum, no consistent change in foraging occurred in the presence of *A. canosa*, over time scales sufficient to detect colony-level impacts and thus colonies as a whole appear to be risk insensitive. Naïve colonies had more ants beginning foraging before a single ant would return in their first trial compared to the second trial. This suggests forager learning occurs as foragers respond to the perception of a predator, and that *S. invicta* can reduce individual risk through increasing forager numbers. *A. canosa* predation rates and density were calculated and based on these estimates an approximate impact upon a colony was made. Most importantly, 13 foragers/m² inside each foraging cohort can be expected to have prior experience with the spider.

Dedicated to those figures to whom I consider myself eternally indebted: My parents, for making the miles between school & home disappear, Dr. David Lonzarich, for your invaluable commitment of time & energy to foster my love of science & teaching, and Dr. Becky Nichols, for your patience in teaching me proper techniques and protocol. Thank you all for encouraging me to continue my education.

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CHAPTER ONE: INTRODUCTION

Our understanding of invertebrate ecology is shaped by the interaction of top down and bottom up effects forming a network of relationships within a food web (Cummins & Klug, 1979). Ecology as a whole is moving towards a more nuanced understanding of how behaviors in a food web structure communities and landscapes: two examples are fear and disgust. These overarching theories explore how perceptions regarding the likelihood of a lurking disease or predator can influence decisions made by an organism. These decisions result in behavior-driven outcomes, called non-consumptive effects, which can cause profound and cascading trophic changes not just locally but across the entire ecosystem (Terborgh *et al.* 2001). These theories change our understanding of how communities are structured and how we look at species dynamics.

Models of animal distributions are traditionally based on the availability of, and competition for, food (Rosenzweig and MacArthur, 1963) under what is popularly called patch theory (Pickett & White, 1985). However, non-consumptive effects have a new method of species distribution modeling (Laundré *et al.* 2010. Laundré *et al.* 2014). This is the landscape of fear; a theory modeling a population's distribution across micro-habitats (discrete units within a continuous habitat). The landscape of fear uses the perception of a predator's presence as a 'risk factor' to explain a species distribution across microhabitats prior to information about food and competition (Laundré *et al.* 2010). This risk factor incorporates alterations in behavior, where the prey animal exchanges food for increased safety from predators, usually involving reduction in foraging or avoidance of an area. This theory has focused on large roaming predators and their prey (Laundré *et al.* 2001. Miller *et al.* 2014).

It is likely that ants have not been studied as prey in the landscape of fear because ants are typically considered predators of other arthropods and even some vertebrates (Hölldobler & Wilson, 1990). Ants still have many predators, and if these predators influence ant behavior in subtle ways, it

would have dramatic consequences for ecosystems. Ants are highly abundant in most terrestrial ecosystems (Hölldobler & Wilson, 1994) where they impact nutrient cycling (Hölldobler & Wilson, 1990. Folgarait, 1998.) and distribution of countless species (Hölldobler & Wilson, 1994. Zelikova *et al.* 2011.). Studies of the competitive impacts of ants and their role as predators have shown that ants can and do shape communities (Nelson *et al.* 2005. Offenberg *et al.* 2004. Sendoya *et al.* 2009.), but little attention has been given to how predators may affect an ant colony's behavior and distribution. This makes ants a compelling subject to study within the landscape of fear.

Ants possess a trait that makes them even more important to study within the landscape of fear; a trait which has been almost entirely ignored in studies of non-consumptive effects: social interaction. Though ants, bees, and other eusocial and social organisms have been studied for non-consumptive effects, they have been observed and studied as individuals rather than a group. Ants and other eusocial organisms achieve their dominance in an ecosystem through their complex societies. Eusociality is defined by three features: cooperative care of young, an overlap of generations and division of labor within the group (particularly reproductive division of labor) (Hölldobler & Wilson, 1994). In ants, the queen only produces offspring which typically sterile daughters care for as well as performing all other tasks in the colony. Ant colonies as a whole act through combined decision making (Conradt & Roper, 2005). This is the result of complex behavioral interactions between group members mediated through the exchange of chemical signals (Conradt & Roper, 2005. Jeanson *et al.* 2012.). One of the most common interactions among ants is recruiting foragers to food sources. This interaction varies slightly between the many methods used by ant species; the three most common are mass recruiting, solitary foraging and trunk trails. Because ants with trunk trails have received more attention in how predation affects foraging (Whitford & Bryant, 1979. Porter & Jorgenson, 1981. Shaffer Jr & Whitford, 1981.

Mackay, 1928. Munger 1984. Gentry, 1974. Kwapich & Hölldobler, 2017), I will focus on the two other common strategies in the foraging spectrum: mass recruitment and solitary foraging.

This dissertation aims to discover the relationships between ants and a ubiquitous, widespread ant-predator, the twin-flagged jumping spider, *Anasaitis canosa*. To do this, two lab experiments and a field observation were conducted.

CHAPTER TWO: LITERATURE REVIEW

The Landscape of Fear

Trophic ecology is placing a growing emphasis on understanding non-consumptive effects. Non-consumptive effects are any of the ways a predator influences prey without actually eating them. These effects are important because they can result in trophic cascades, including dramatic changes across food webs, that can ultimately impact ecosystem function (Terborgh *et al.* 2001). A subfield devoted to non-consumptive effects called the ‘biology of fear’ arose following the landmark reintroduction of wolves into Yellowstone National Park in 1994-1995, reversing their total disappearance since 1970 (Wolf Restoration). To avoid wolf predation, deer populations changed their feeding habits, spending less time in areas where wolves frequented, as well as areas where wolves could easily catch them, such as riverbanks (Laundré *et al.* 2001). This prevented deer over-browsing in these areas and plant communities were altered, which eventually changed river dynamics (Ripple & Beschta, 2004. Ripple & Beschta, 2007. Ripple *et al.* 2001). Because the introduction of wolves had impacts that changed major features of the landscape, the study of how predators shaped the surrounding communities by their presence is often referred to as ‘the landscape of fear’ (Laundré *et al.* 2014. Laundré *et al.* 2010).

Though ‘the landscape of fear’ is a relatively new topic in ecology, the concept of risk being physically manifest in the environment is older (Tuan, 1979). Research documenting the responses of prey to predation has occurred in biology prior to emergence of the landscape of fear in biology (Lima and Dill, 1990) when ecologists observed phenotypic alterations to physical traits triggered by direct interaction with a predator which they called ‘trait-mediated indirect interactions’ (Abrams, 1995). Although these are non-consumptive effects, these studies are not directly related to the landscape of

fear, which is largely concerned with pre-emptive decisions prey make to avoid or reduce predation risk. Thus, the landscape of fear focuses on understanding behavioral traits which are changed due to the risk of predation.

Much of the research in the landscape of fear has focused on large mobile vertebrate predators and their prey (Laundré *et al.* 2001. Miller *et al.* 2014. Wirsing & Ripple, 2011), commonly mammals (Brown, 1988. Laundré, 2010. Laundré *et al.* 2001) and fish (Geraldi & Powers, 2011. Hammerschlag *et al.* 2015.). Research has shown non-consumptive effects influence invertebrates (Dicke & Grostal, 2001. Schmitz *et al.* 2010) especially aquatic ones (Barry, 1994, Ram *et al.* 2008. Denno *et al.* 2008. Culp *et al.* 1991. Trekels & Vanschoenwinkel, 2016. Davenport *et al.* 2014. Ngai & Srivastava, 2006. Mccauley *et al.* 2011.). Invertebrates are shown to spend less time in areas where predators are introduced and will avoid regions where they perceive specific signals associated with predators. Terrestrial invertebrates studied within the landscape of fear have primarily been plant pests (Hawlana *et al.* 2012. Hawlana & Schmitz, 2010 [1&2]. Schmitz, 2005. Rosenheim *et al.* 1993. Denno *et al.* 2003. Jandricic *et al.* 2016) and spiders (Hodkinson *et al.* 2001. Schmitz, 2006. Mestre *et al.* 2014. Hawlana *et al.* 2012. Hawlana & Schmitz, 2010 [1&2], Schmitz, 2005. Tahir *et al.* 2017). Eusocial insects, like ants, are typically studied as predators to be avoided rather than prey (Li *et al.* 2014 [1]. Nelson *et al.* 2005. Offenberg *et al.* 2004. Sendoya *et al.* 2009. González & Rodríguez-Gironés, 2013. Harmon & Andow, 2007. Buchanan *et al.* 2017), sometimes impacting larger vertebrates (Haemig, 1996. Haemig, 1994. Young *et al.* 2008. Holtcamp *et al.* 1997. Dáttilo *et al.* 2016). Recent findings by Gonçalves *et al.* (2017) suggest that ants can even influence adjacent ecosystems they are not directly present in. Ants present within bromeliads changed the composition of the aquatic communities, despite not having a physical presence under the water. However, the role that the landscape of fear

plays in the distribution of ants has still not been studied, and it is the goal of this research to fill the gap. Collectively, ant colonies make up a large portion of the animal biomass in most habitats on earth and their activities can have far-reaching impacts on community structure and ecosystem functions (Hölldobler and Wilson 1990).

The potential ecological impact of predators on ants have been largely ignored except for species-specific, nest associated web-building spiders. Studies investigating the interactions between ants and spiders have had mixed findings, showing that ants react to spider presence under species specific circumstances (Mackay, 1982. Bucher 2014) but also that spiders are generally reactive to the presence of ants (Mestre *et al.* 2014. Halaj *et al.* 1997.). Here I further explore this dynamic, focusing primarily on determining whether ants perceive predator risks that affect whole-colony responses, investigating them as prey within the landscape of fear rather than a predator. As I am investigating the response of a whole ant colony, the most appropriate behavior to measure is foraging.

Ant Foraging

Broadly speaking, ants are central-place foragers, where individual workers forage away from the nest (the “central place”) and return with food. Ants begin foraging haphazardly searching on their own. Once food has been located, they recruit others, following the relative path of the original scout who discovered the food resource. Ants recruited to a food source will in turn enlist other ants and eventually all foragers will transition from disarray into an ordered pattern (Li *et al.* 2014 [2]). Making foraging both an individual and colony behavior. The exact mechanics eliciting ants to join the recruitment process varies across ant species (Hölldobler & Wilson, 1990) and can involve physical stimulation and/or chemical cues from a diverse number of glands (Hölldobler & Wilson, 1990). The diverse mechanics of communication between ants, results in a plethora of foraging strategies used by

different species of ants. These different strategies are hypothesized to maximize resource acquisition, minimize energetic costs, and reduce exposure of workers to predation albeit using different mechanisms (Hölldobler & Wilson 1990. Dukas & Edelman-Keshet, 1998. Pearce-Duval *et al.* 2011.). At opposing ends of the foraging spectrum are mass recruiting and solitary foraging ants. Solitary foraging is the simplest and most primitive foraging strategy (Hölldobler & Wilson, 1990), with ants scouting, capturing and returning food to the nest on their own without the aid of nestmates. Solitary foragers do not directly recruit others to food sources, (although workers in the nest sometimes start foraging after sampling food gathered by returning foragers [Wallis, 1964]).

Mass recruiting, on the other hand, is a more complex method of foraging that recruits nestmates to food resources (Hölldobler & Wilson, 1990). As a scout returns from a food source, they lay down a chemical trail back to the nest. When workers encounter this chemical trail, they are stimulated to follow it. In this way a scout rapidly attracts large groups of their nestmates to follow a trail using chemical secretions instead of direct communication or contact (Hölldobler & Wilson, 1990). Each worker then ‘weighs in’ on the route by laying down another trail on their return, strengthening the path and making that option more attractive to other ants (Detrain & Denenbourg, 2006. Beckers *et al.* 1990). This helps ants make decisions if presented with multiple paths to take (Pratt *et al.* 2002. Beckers *et al.* 1990). If the colony is blocked from food, foragers returning empty-handed will shut down the path with another chemical signal (Dussutour *et al.* 2009. Robinson *et al.* 2005).

Foraging behavior has been shown to be affected by many factors which potentially impact whole colonies (Gentry, 1974. Whitford & Bryant, 1979. MacKay, 1982. Munger, 1984. Gordon, 1986. Shaffer & Whitford, 1981.). But, a working hypothesis is that foragers within a colony are

expendable (Porter & Jorgenson, 1981), making ants risk insensitive. That is, dangers to individual workers (and the loss of individual workers) are not a strong enough selective force to drive adaptive behaviors that alter collective foraging. Individual workers are thus “disposable” and foraging behaviors will only be shaped by factors that for example, impact large numbers of foragers (Porter & Jorgenson, 1981). Competition is one of the more frequently studied, as both the distribution and behavior of an ant colony is affected by its neighbors. These neighboring colonies are in direct competition for food and space (Hölldobler and Wilson, 1990). A colony’s hostility towards other ants can range from harassment (Gordon, 1988), to seemingly mundane (Gordon, 1992. Gordon, 1989.), all of which influence foraging behavior (albeit in different ways). For foraging behavior to exhibit these nuanced responses, recruitment must either convey information about the environment or individual ants need to be cognizant of these factors. Other factors impact foraging behaviors as well. Ants with experimentally shortened life spans take more risks than those with unaltered life spans (Moroń *et al.* 2012. Miler, 2016.), and the primary foragers in an ant colony tend to be workers nearing the end of their lifespans (Wilson, 1985). The “expendability” of workers appears to have limits as foragers do detect and respond to risk from both environmental dangers, such as overheating (Cerdea *et al.* 1998.), as well as inter and intraspecific competitors (Tanner, 2006. Tanner, 2008. Tanner & Adler, 2009.). These are factors that potentially affect many or most foragers leaving the nest and thus avoiding or reducing these risks appears to be adaptive. There is also an abundance of evidence that ants perceive predatory risks, often with dramatic consequences. Nonacs & Dill (1988) found that if *Lasius pallitarsis*, a mass recruiter, merely sees a predatory ant (either along the way to a food source or on the return trip back to the colony), then fewer ants recruit to those food patches. Early studies with species-specific nest-associated spiders observed spider-induced foraging changes in *Pogonomyrmex sp.*

(MacKay, 1982. Macmahon *et al.* 2000. Gentry, 1974, Kwapich & Hölldobler, 2019) and *Pheidole sp.* (MacKay, 1982). These have been classified into four responses to spider predation/visual recognition (Gastreich, 1999. for a detailed summary and the cases where these were discovered, see MacKay, 1982): blocking the nest entrance, posting guards, direct attack of the spider, and halting foraging at resources near the spider. Perhaps the best example of non-consumptive effects in ants is the behavioral response of *Solenopsis invicta*, the red imported fire ant, to the parasitic phorid fly. When encountering a phorid fly, *S. invicta* greatly reduces all foraging (Morrison, 1999. Porter *et al.* 1995), and after the encounter, the next groups of workers that are born tend to be smaller (Mehdiabadi & Gilbert, 2002.). In addition, phorid flies alter the way that a colony competes with other ant species (Feener, 1981). These responses to phorid flies are also found in leaf cutter ants (Orr, 1992), *Pheidole dentata* (Feener Jr, 1988) as well as related ants that are not typically parasitized by phorid flies (LeBrun & Feener Jr. 2002). However, these collective behavior changes have not been shown to impact whole colony function (Morrison & Porter, 2005).

Experimental Overview

Most of the work on understanding ant forager responses to risk have been focused on mass recruiting species. An important gap is understanding risk response across different foraging strategies. Here I use a comparative approach to understand how ant foragers utilizing different foraging strategies respond to the same risk. This research addresses a critical gap in investigating what role the landscape of fear plays in social insect biology. While the fights and clashes between ant species have been documented in thrilling detail (e.g. McCook, 1887) there is much less information about how ants are impacted by their predators. It is hypothesized that the evolution of foraging behavior was shaped, in part, by diverging strategies of predator avoidance (Hunt, 1983). Therefore, different foraging strategies

in ants should change the individual and colony-level responses to predation risk exhibited by the colony.

Of ants' natural predators, spiders represent the best starting point for our understanding of foraging response to predation. Spiders exhibit 'classic' traits of predators in the 'landscape of fear'; they have discrete territory (a retreat) which they roam around, and a distinct scent/markings inside that territory (webbing [Tahir *et al.* 2017]). As their attacks on prey can fail, their prey can learn avoidance behaviors using these two traits (Laundré *et al.* 2010). As an added benefit, simple modification can prevent a spider from being able to successfully feed upon its prey without major inconvenience. There is much prior research investigating spiders triggering non-consumptive effects in insects (Hodkinson *et al.* 2001. Schmitz, 2006. Mestre *et al.* 2014. Hawlena *et al.* 2012. Hawlena & Schmitz, 2010 [1&2]. Schmitz, 2005. Bucher, 2014). Ants have also been shown to influence spiders (Mestre *et al.* 2014. Halaj *et al.* 1997). My focus is on a spider's potential to change foraging dynamics of multiple ant species, and if foraging strategy changes how ants interact with the landscape of fear, greatly expanding this prior work on spider-ant dynamics.

Study System

The specific predator used in my experiments was *Anasaitis canosa*, the twin-flagged jumping spider (Order: Salticidae), a widespread and ubiquitous generalist myrmecophagous spider (Hill *et al.* 2006) whose specialized hunting methods and precise attack behaviors render an ant's otherwise potent defenses useless (Edwards *et al.* 1974). *A. canosa*'s behavior contrasts with other jumping spiders which avoid ants (Edwards & Jackson, 1994.), as well as being a generalist while other myrmecophagous spiders are specialist predators of specific ant species with complex predator-prey relationships (Heller, 1974). *A. canosa* has a diverse diet but favors ants over other prey items, although

it is not always successful in capturing prey (Edwards *et al.* 1974). A diverse group of four ant species that display either mass recruiting or solitary foraging were selected from the list of known prey items for *A. canosa* (Edwards *et al.* 1974. Common names are from Deyrup, 2017). Three of the species I selected are introduced/invasive (MacGown *et al.* 2014. Wilson, 1962) from outside the range of *A. canosa*, but since all these ants are abundant and conspicuous and have been present in Florida for decades, the fact they are invasive ants seems unlikely to impact the results. I used two species of solitary foraging ants, *Formica pallidefulva* Latreille, the variable fleet formica ant, and *Odontomachus ruginodis* M. R. Smith, the rough petiole snapping ant. Both *F. pallidefulva* and *O. ruginodis* are large monomorphic ants ~8 mm in length with widespread distributions across Florida and the southeastern US. *O. ruginodis* is a specialized predator of springtails (Order: *Collembolla*) whose ‘spring-loaded’ jaws (Gronenberg, 1995) also are a formidable defense (Patek *et al.* 2006. Carlin and Gladstein, 1989), while *F. pallidefulva* is a swift generalist predator that also gathers honeydew. I also used two mass recruiting ants, *Pheidole obscurithorax* Naves, the large imported big-headed ant, and *S. invicta* Buren, the red imported fire ant. Both of these ant species exhibit polymorphic workers. *P. obscurithorax* is the largest *Pheidole* in Florida with workers and majors measuring 3 and 3.5 mm in length respectively. *S. invicta* workers range from 2 mm minors to 6 mm majors (Hedges, 1997).

Predictions

These four ants occupy opposing ends of the foraging spectrum and my work will compare their responses to the same predation in one experiment, while investigating if the observed responses are learned vs innate in a second experiment. Solitary foragers seek for and capture food resources as individuals without recruiting nestmates whereas mass recruiting species actively recruit nestmates to food resources, rapidly increasing the number of workers to food resources after discovery. My

overarching hypothesis for the project is that foraging ants are cognizant of and react to predation risk from *A. canosa*; changing their behavior to reduce the time they spend in areas of perceived risk and there will be differences in risk aversion between species where solitary foraging species will be more risk averse than mass recruiting species.

Field Evaluation of Spider Predation

Anasaitis canosa (Walckenaer, 1837), the twin-flagged jumping spider, (Order: Salticidae) is a pan South-eastern US/Cuban (Richman & Cutler, 2012. Richman & Cutler, 1978. Bryant 1940) generalist myrmecophagous spider (Hill *et al.* 2006) which uses specialized hunting methods and precise attack behaviors to render an ant's otherwise potent defenses useless (Edwards *et al.* 1974). This spider is abundant and widespread, likely across the Caribbean (*Anasaitis* is a Caribbean genera). *A. canosa* has a diverse diet but favors ants over other prey items (Edwards *et al.* 1974), a behavior which contrasts with other jumping spiders which avoid ants (Edwards & Jackson, 1994). In Florida, *A. canosa* is both widespread and ubiquitous (Edwards *et al.* 1974). Researchers have observed *A. canosa* hunting ants in the field (Hill *et al.* 2006) and assessed its prey selection in the lab (Edwards *et al.* 1974). From these observations, *A. canosa* has been classified as exhibiting stenophagy (Pekar *et al.* 2012).

When given the option *A. canosa* prefers ant prey over non-ant prey (Edwards *et al.* 1974), but there are numerous accounts of these spiders eating other plentiful insects such as dipterans, leaf-hoppers and moths. *A. canosa* has been used in laboratory trials as a predator of flies (de la Flor *et al.* 2017).

Until now, no efforts have been made to investigate the number or volume of prey choices that *A. canosa* makes in the field. Meaning that although the fundamental niche is well understood, the realized niche of the spider remains unknown. Only 1.5% of spiders have well documented diets (Pekar *et al.* 2012) despite being the most important groups that eat insects (Nyffeler & Birkhofer, 2017). Completing our understanding of *A. canosa* will contribute to filling gaps in spider ecology. There are still many changes occurring in our understanding of spider realized niches, including the potential of vertebrates to be spider prey (Nyffeler *et al.* 2017. Jackson *et al.* 2005. Nyffeler & Knörschild, 2013.). There is currently only limited documentation of the realized niche of *A. canosa* and needs to be expanded on in order to better evaluate the role this spider plays within the ecosystem.

Experimental Overview

The question of if *A. canosa* is truly a meaningful predator of ants is of great importance for analyzing the results of my laboratory experiments. By pairing existing lab evaluations of fundamental niche with field observations of realized niche we can gain a critical component of studying *A. canosa* as a meaningful predator of ants. My aim is to first understand 3 questions: First, how abundant is *A. canosa*? Second, does *A. canosa* show preference for ants as prey in the field? Third, are there certain species of ants that the spider encounters that are preferred and are some species of ants more readily captured? This field study aims to find approximations to answer these questions, estimating the density of spiders within a patch of representative territory, the rate at which these spiders feed upon different food sources and how successful they are in their attempts to eat each food source.

CHAPTER THREE: METHODOLOGY

Investigating the Landscape of Fear

Two experiments were conducted: the first investigated non-consumptive effects in the foraging strategies of solitary foraging and mass recruiting (Table 1), while the second investigated if the response in *S. invicta* was an innate or learned response (Table 2). Eight colonies of each species (except *S. invicta*) were collected in fall 2018-spring 2019 from the UCF arboretum by nest excavation. Two additional *O. ruginodis* colonies had to be collected in the summer of 2019 to replace two that died prior to completing all trials. Twenty-seven *S. invicta* colonies were reared from queens found post-nuptial flight in the summer 2017. All colonies had their size standardized to reflect the approximate worker population of a first-year colony. As there was no established survey of a first-year colony for three of the chosen ant species, a size approximation was made based on existing surveys of mature colonies (sometimes of related species). *F. pallidefulva* was estimated at 250 workers + queen (King & Trager, 2007), *O. ruginodis* was estimated at 60 workers + queen (Hart & Tschinkel, 2012), *P. obscurithorax* was estimated at ~1,000 workers + queen (Storz & Tschinkel 2004), and a first-year colony of *S. invicta* is known to contain ~1,000 workers + queen (Wilson, 1962. Tschinkel 1988).

Care of Ants

Colonies were housed in a climate-controlled room (photoperiod: 14L/10D, 76 degrees F, 60% humidity) each in a 'colony tray', a 10" x 21.5" photo-developing tray with a 3/8th inch hole was drilled into one wall where a 3/8th inch external diameter tygon tube with a Y- tube at the end was inserted (Appendix A). Each tray had at least five test tubes partially filled with water, stoppered with cotton and covered in aluminum foil. All ant colonies were provided with food (15% sucrose solutions), water

and protein (par boiled crickets or beetle larvae) which were replenished on a weekly basis. When a colony was not involved in a trial a loop of tygon tubing was attached to the Y-tube to prevent ants from escaping. While in a trial, each end of the Y-tube was attached to a separate ‘foraging tray’, an 8.5” x 5.5” cafeteria tray covered by a glass plate (appendix A). Each glass plate had a paper tube taped to the lid to provide a safe hideaway for the jumping spider to construct a retreat. One of the attached arenas contained a spider (the ‘risky’ or treatment arena) and the other did not (the ‘safe’ or control arena). Spider side assignment was randomly chosen by coin flip due to inherent side biases that ants show when exploring (Hunt *et al.* 2014).

Care of Jumping Spiders

A. canosa spiders were collected into falcon tubes by hand from the UCF arboretum one day prior to testing. Upon returning to the lab, the spider was paralyzed with CO₂ gas, then liquid bandage covered either the spider’s chelicera (preventing it from feeding on ants, the shut treatment), or the underside of the cephalothorax (not changing its feeding ability, the risky treatment). This was randomly determined by coin flip for experiment 1 (so the order a colony performed their replicate trials was random), while it had a set order for experiment 2 (the treatment group always started with a spider with the chelicera glued shut while the control group always started with a spider with its mouthparts left unmodified). Jumping spiders were then placed inside one of the two foraging arenas chosen by coin flip.

Experimental Setup

Foraging arenas were not connected to the housing tray until after a 24-hour adjustment period had passed. Immediately prior to connecting the housing tray and foraging arenas, two test tubes (one 15% sugar and one water) were weighted and placed in each foraging arena. Both foraging arenas were

then videotaped using LG Rebel LTE cellphone cameras for 47 minutes (the maximum file size for a video on the camera). After this period, the colony was given 24 hours to continue foraging, and then filmed again. Once filming ended, the number of dead ants were counted in each arena and the test tubes within the foraging arenas were removed and weighed. Foragers were then removed from the foraging arenas, and both the tubing and foraging arenas were cleaned with DI water and given at least one week before re-use to ensure no residual traces persisted. Each colony was given one week between trials (in the case of experiment two colonies went one month between trials). In experiment one each colony had a minimum of four trials (two of with the ‘Shut’ treatment and two with the ‘Risky’ treatment, in random order) in experiment two, half of the colonies had two trials (one ‘Shut, one ‘Risky’) and the others had one trial (‘Risky’).

Table 1: Experimental Design of Experiment One. Trials is number of replicate trials that each colony was exposed to. Treatment is a short hand for where liquid bandage was applied to each spider. Arena denotes the two arenas that each colony was exposed to.

Treatment	Trials	Arena	Notes
Shut	2	Spider w/ Mouth Glued	Perceived risk, non-consumptive effects alone
		Control	observe normal foraging conditions
Risky	2	Spider w/ Cephalothorax Glued	Perceived risk + Predation, “full impact”
		Control	observe normal foraging conditions

Table 2: Experimental Design for Experiment Two. Treatment is a short hand for where liquid bandage was applied to each spider. Arena denotes the two arenas that each colony was exposed to.

Treatment	Arena	Notes
Prior Exposure to spider with mouthparts glued (Treatment)	Spider	Observe behavior with experience
	No Spider	Control
No Prior Exposure to spider (Control)	Spider	Observe innate behavior
	No Spider	Control

Hypotheses

I hypothesized that arenas with perceived risk (a spider present) will see ants forage for a shorter duration and recruit less than the control arena, meaning fewer ants present overall. Colonies

will react similarly to spiders whether their mouthparts or cephalothorax are glued, as the ants react to their perception of danger rather than the loss of individuals. If one caste is more resilient to the threat in question, then mass recruiters divide labor between castes, and the task will be favored by the more resilient caste (Kay & Rissing, 2005). However, more energetically expensive castes within the colony (majors and larger workers) will be more sensitive to risk than the less energetically expensive ones if they are equally at risk of spider predation. In that case, majors will be less common in ‘risky’ areas compared to ‘safe’ ones. Similarly, all species will consume less water when a predator is present, but sugar (as a more energetically valuable resource) will be unaffected.

In my second experiment I hypothesize that these reactions are the result of colony level learning from foragers interacting with the *A. canosa* spider. Therefore, when exposed to a predator, naïve workers will not change their behavior in their first trial but will adopt avoidance behaviors within two replicate trials. As workers acquire and use these behaviors, forager mortality will drop over consecutive trials as laid out in appendix B.

Data Collection

Variables of interest to this experiment are present in table 5. These variables were collected for both experiments by weighing the food and water test tubes before and after the experiment concluded, counting the number of dead ants & extracting critical information from video files. To do this, a scorer watched each video and recorded the time in seconds when the first and second forager entered the arena, when an ant returned to the colony for the first time, and how many ants were in the arena when an ant returned for the first time. In cases where one or more of these events failed to occur during filming, a time of 3,000 seconds was recorded for

the events in question (all videos were less than 48 minutes long, so no overlap occurred between 'none observed' and merely 'late occurring' videos). In videos with a spider, interactions between the ants and the spider were noted (both the time and number of each interaction). In a separate session the number of ants visible in frame at each minute mark were counted, as well as the number of ants seen feeding at the sugar and water test tubes at each minute mark. In trials with *P. obscurithorax*, where majors and minors were visually distinct, the number of major ants, as well as how many majors were feeding at the water and sugar test tubes each minute were also counted.

Time to first explorer, delay to second explorer, delay to first return and number of scouts in the arena all served as measurements of individual ant behavior. Because no recruitment messages were sent back to the colony until *after* the first ant returned all actions taken before that point reflect workers acting solely on their own perceptions. Time to first and second explorers shows how quickly they entered the arena and time to first return shows how quickly they left (approximately). Number of scouts then shows us how many ants were committing to foraging without prior information. The remaining variables were collected to approximate the different ways that avoidance behaviors could manifest at the colony level. Depletion of sugar and water illustrated colony choice, as the food and water were the primary reasons for ants to forage. The number of ants and majors present in the arena showed the degree of recruitment, to compliment colony choice (as fewer foragers could remove more food/water to achieve the same outcome). The proportion of ants at food/water (calculated from the number of ants at food/water divided by the total number of ants) showed the propensity for exploration compared to resource removal.

Table 3: Variables of Interest in Experiment One & Two. Reason measured provides a short description of why the variable was included in the experiment.

Variables of Interest	Type (units)	Acquired from	Calculations/Equations	Reason Measured
Mortality	Count	Counting number of dead workers at experiment end in each arena	None.	Indirect measure of predatory impacts/cost of foraging.
Depletion of Sugar Source	Change in weight (g)	Metler Toledo AB54-S scale.	Δ treatment arena weight - Δ control arena weight	Energetically Valuable Foraging Resource
Depletion of Water Source	Change in weight (g)	Metler Toledo AB54-S scale.	Δ treatment arena weight - Δ control arena weight	Foraging Resource
Number of ants	Count	Video footage (each minute)	Average	Approximation for time individual ants spend in arena
Number of Ants/Majors in Arena/Food/Water	Count	Video footage (each minute)	Average (majors: <i>P. obscurithorax</i> only)	Compares foragers exploring vs gathering resources
Number of Scouts	Count	Video footage (at time of 1 st return)	Average	Additional measure of ant presence in the earliest stages of foraging.
Number of Majors	Count	Video footage (each minute)	Average (<i>P. obscurithorax</i> only)	Number of energetically valuable ants
Time to One Forager Returning	Count (s)	Video footage (continuous)	Time to 1 st Return – Time to 1 st Forager	Approximation of duration spent in the arena.
Delay to Second Forager Arriving	Count (s)	Video footage (continuous)	Time to 2 nd Forager – Time to 1 st Forager	Secondary measure of avoidance
Time until First Forager Arrives	Count (s)	Video footage (continuous)	None.	Measure avoidance of arena

Statistical Analysis

In order to remove correlation between some variables the data were standardized, where the difference between the first and second forager and the difference between the first forager entering and the first return to the tubing were calculated. This is because the time to the first forager was always reflected in all ant related measurements of time (if it took 300 seconds for the first forager to arrive then it would take a minimum of 300 seconds for the second forager to arrive), and by subtracting the time to first forager from the other variables I was able to

standardize the variable to the time to the first ant arriving. The average number of ants per minute was calculated for each video. The average number of ants at food and water were then divided by the number of ants per minute to show the proportion of foragers at each resource. Each trial was analyzed as a single unit (rather than two separate arenas) by subtracting each measured value in the ‘risky’ arena (the one with the spider) from the ‘safe’ arena (the one without the spider). This treatment minus control measurement was used while both constructing graphs and performing analysis in order to treat each experiment as a replicate rather than using an overall ‘average’ response for each colony. By subtracting the raw values for each variable from the control arena This isolated the effect of the predator on foraging behavior from other factors such as humidity, temperature, time of day or species. This allowed for more direct comparisons between the different species and foraging strategies. As a consequence of this transformation, only experimental trials where **both** the treatment and control arena experienced foraging within the filming period were used in analysis.

Figures 1 & 2 confirm that treatment minus control arena is a valid transformation that accounts for colony learning and makes it appropriate to treat each trial as an individual replicate without introducing any new bias. For most of the variables there was little to no divergence from a line of $y=0$ for the effect of treatment number, so no directional learning appears to have occurred. Overall, there was no evidence of ant colonies learning a preference for either arena, nor does variation appear to change with repeated trials.

Because both experiments had nearly identical methodologies. I included results from experiment two trials as replicates for experiment one as long as the colony in question had at

least four trials completed. Each measurement in table 5 was compared using a Welch's two sample t-test ($\alpha = 0.05$), as both sample size and variance were different between each sample. First the data was simply grouped by treatment, (Risky vs Shut for experiment one, three groups: Naïve-Risky Spider, Naïve-Shut spider and Prior Experience-Risky spider for experiment two). Each group was compared with a Welch's two sample t-test ($\alpha = 0.05$), except in experiment 2, as Naïve-Shut and Prior Experience-Risky were compared with a Welch's paired t-test ($\alpha = 0.05$); as these comprised the same colonies. All variables within each treatment was also tested with a one sample t-test ($\alpha = 0.05$) to check for significant difference from zero. For experiment one, the data were partitioned into solitary forager and mass recruiting ant groups, then into each species and compared the data by treatment with a Welch's t-test ($\alpha = 0.05$), this was done to observe if different interactions with the predator occurred in distinct foraging strategies or species. In cases where the data was not normal, or the sample size was small/unbalanced between groups the non-parametric Kruskal-Wallis rank sum test ($\alpha = 0.05$) was used in place of the Welch's t-test, and a one-sample Wilcoxon test replaced the one-sample t-test.

Visual Display of Data

Because experiment one involved multiple replicate trials with each colony of ants, it was important to assess whether learning might have affected behaviors over the duration of the experiment. Line graphs of each variable over trial number were constructed to check if directional learning occurred. A Tukey's boxplot was constructed for each variable and treatment in experiment one and two. In all figures a blue line at $y = 0$ was included indicating no

difference between the treatment and control arena. Any case where there is no overlap between the boxplot and the line $y = 0$ indicates a significant difference from 0 ($p < 0.05$).

Spider Survey

Study Site

In order to assess the impacts of the spider on ant populations, two 15-day surveys were run from 6/24 to 7/8, and 9/6 to 9/21 in 2019. The study site was the Lake Claire natural area on the north side of campus, a semi-disturbed forest, with moderate inundation. During this survey, one or more researchers would walk into the Lake Claire natural area north of UCF's campus and observe 3 sites of varying dimensions (site 1: 2.1 m², site 2: 3.4 m², site 3: 1.212 m²) for around 10 minutes each (Appendix C). During this period, a count of the number of observed spiders, as well as their gender, relative size and any hunting behavior as well as the outcome was noted for each site. Each day of observation, a list of ant species seen foraging was made. Each of the 3 sites occurred within 10m of each other and multiple sites were measured for a more comprehensive measurement of the spider abundance.

Predictions

As this field experiment is strictly exploratory, I have no formal hypotheses going into this study. Prior collections of spiders from the field have suggested that the spider is quite densely populated.

Statistical Analysis

On days when multiple researchers were present in the field, each site had the average number of observed spiders for that day calculated. This was done to account for the fact that

more researchers might count the same spider twice as well as see more spiders than a single researcher. The total number of hunting behaviors was compared to the number of spiders observed, and the average number of spiders noted for each day at each site was calculated. The averages number of spiders noted for each site were compared by a t-test ($df = 28$) to see if spider populations were spread out or concentrated by comparing the sites to each other. If spider populations are spread out across the landscape there should be no significant difference between the sites, conversely if the spiders are concentrated in a small area then the sites should be different from each other. The density of spiders was calculated by averaging the average number of spiders per site per day into an overall average number of spiders per site per day. These averages were then divided by the size of each site in order to gain the number of spiders/day/m² for each site, and an overall average of these 3 site averages. Prey capture rate was calculated by dividing the number of hunting behaviors by 15 to get a number of attacks per hour of observation. This attack/area/hour was multiplied by $12*7$ to gain a rough estimate of how many attacks occurred within daylight hours in each site in roughly one week. The rough estimate was then multiplied by the relative frequencies of observed attacks to determine the number of attacks by prey type as well as the number of successful/unsuccessful attacks.

Visual Display of Data

A line graph using times of start/end of observation as coordinates was created to show when observations occurred as well as the comparative length of observations. By comparing the distribution of points along the x-axis the distribution of when spiders were observed is clearly visible. By comparing how closely the points adhere to a straight line it can be seen if there was major deviance from the 10-minute observation period per site. Pie charts were created using the

number of observed attacks, and what prey types were being attacked. The pie chart was divided into two sections to separate ant prey from non-ant prey.

CHAPTER FOUR: RESULTS

Experiment one found no significant differences between treatments at any of the levels investigated, nor were any of the treatments significantly different from zero. Collectively, these results suggest the presence of *A. canosa* under laboratory conditions has no impact on ant foraging behavior. In experiment 2 there was a single statistically significant difference, namely that scout numbers were higher in the initial trial compared to the second trial. This suggests that there is a response to predation in naïve colonies after first exposure. This pattern appears to be consistent in naïve colonies exposed to either treatment.

Experiment 1

52 colonies (26 *S. invicta*, 8 *P. obscurithorax*, 10 *O. ruginodis* and 8 *F. pallidefulva* colonies) were used in 172 trials (56 *S. invicta*, 30 *P. obscurithorax*, 36 *O. ruginodis* and 30 *F. pallidefulva*) conducted between July 2018-September 2019. 88 arenas had no foraging occur during the 47-minute foraging period (6 *S. invicta* [5.36% of total], 9 *P. obscurithorax* [15% of total], 35 *O. ruginodis* [48.61% of total] and 38 *F. pallidefulva* [63% of total]). Those trials were excluded from subsequent analysis. Nine colonies failed to have two replicate trials within each treatment (one *F. pallidefulva*, two *O. ruginodis* and six *S. invicta*) and were also removed from analysis. Experiment 1 used 86 trials in analysis (38 Shut, 48 Risky treatment [Appendix D]). Line graphs of variable over trial number can be seen in figures 1 & 2.

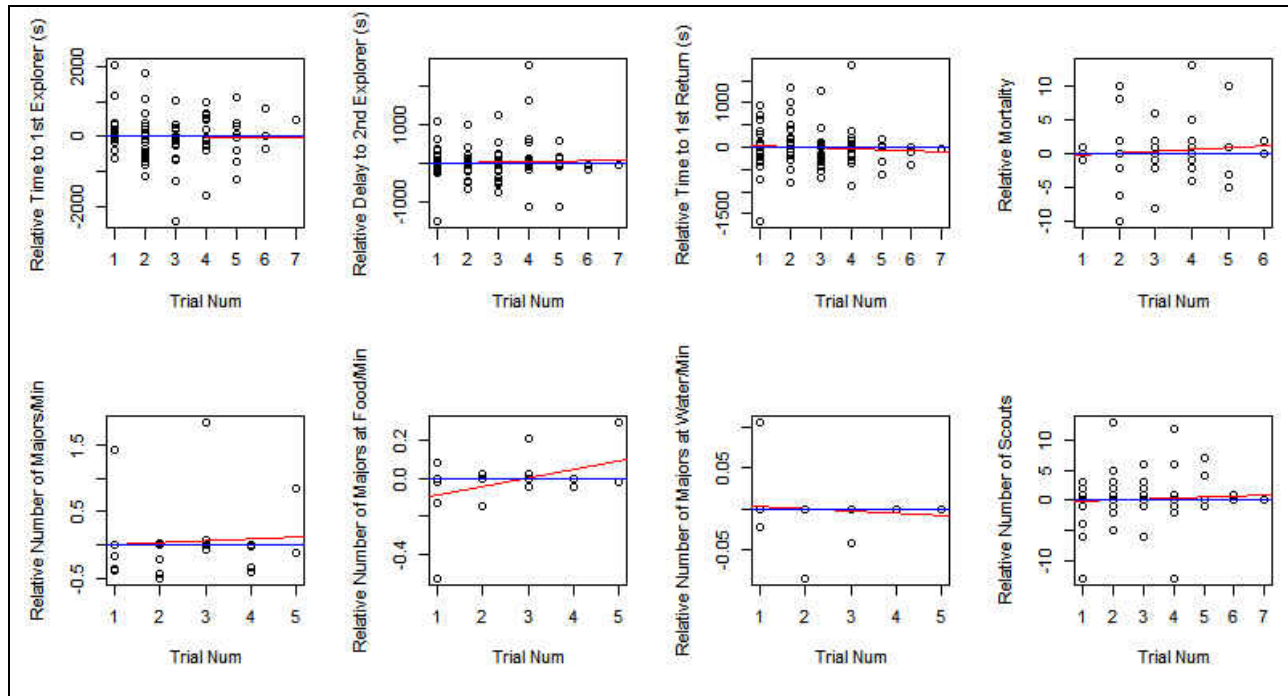


Figure 1: Directional learning across the eight collected variables in experiment 1. Red line indicates change in variable over trial number. There was no evidence any of the variables changes value over trial number

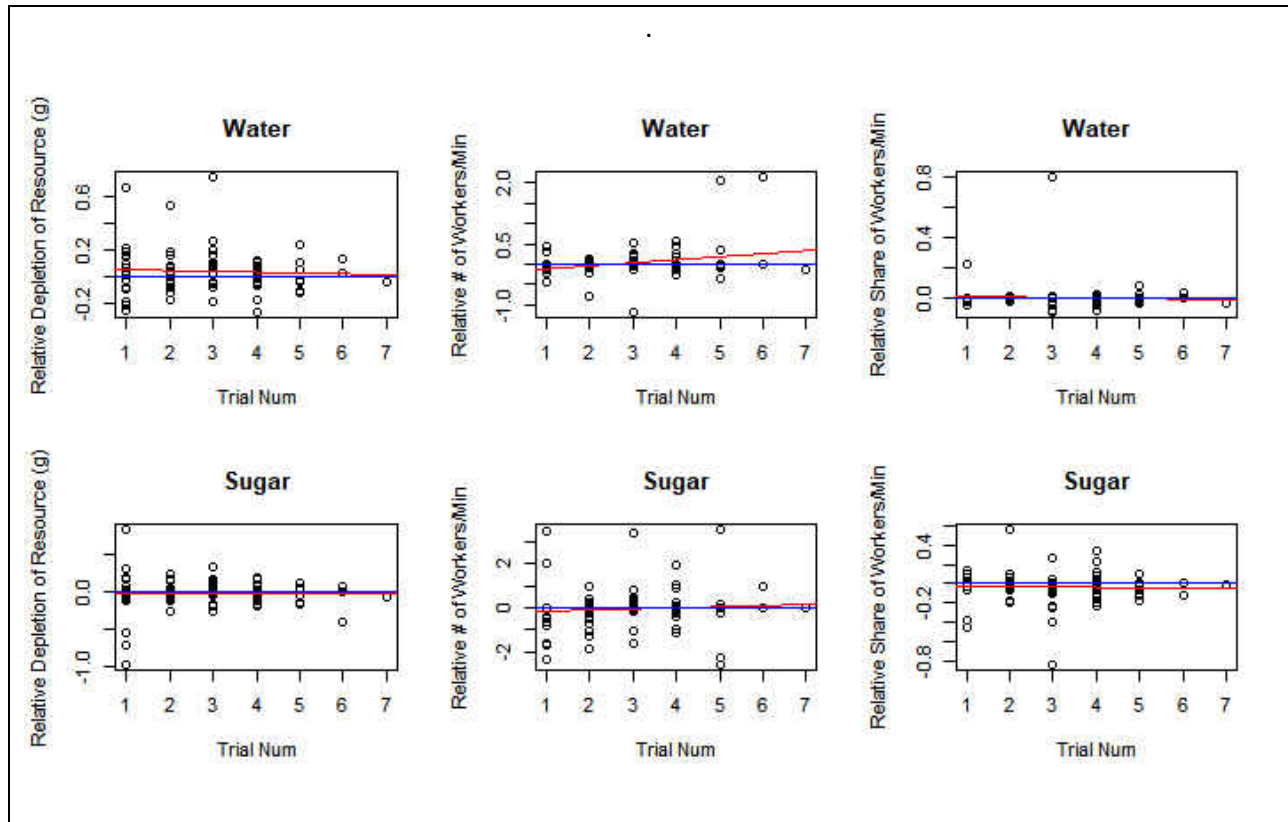


Figure 2: Directional learning in water and food associated variables in experiment 1. Red line indicates change in variable over trial number. There was no evidence any of the variables changes value over trial number.

Treatments

There was no significant difference between treatments in any of the variables of interest (table 4), nor were any of these averages different from 0 (p value > 0.05). There was no difference between treatments in number of *P. obscurithorax* majors in the arena (table 4, fig 3, p-value > 0.05), at water (table 4, appendix E) or at food (table 4, appendix E) nor were any of these values different from 0 (p-value >0.05).

Table 4: Average Values for each Variable of Interest in Experiment One. Means reported are Mean +/- SD. The degrees of freedom for the Welch's T-test is displayed in parentheses after the p-value.

Variable	Risky Treatment	Shut Treatment	Welch's T-test p-value	In:
Ants in Arena	0.9182 +/- 9.913945 ants/min	2.1591 +/- 11.04063 ants/min	0.5914 (df 75.245)	Appendix E
Delay to 2 nd Explorer	-22.19 +/- 581.4471 s	99.39 +/- 433.4937 s	0.27 (df 83.734)	Fig 3
Majors in Arena	-0.1473 +/- 0.186188 ants/min	0.2988 +/- 0.800013 ants/min	0.1155 (df 9.7529)	Appendix E
Mortality	1.027 +/- 3.312321 ants	-0.36 +/- 3.871692 ants	0.1497 (df 46.092)	Fig 3
Number of Ants at Sugar	-0.2102 +/- 0.850067 ants/min	0.13196 +/- 1.202467 ants/min	0.1437 (df 64.474)	Fig 4
Number of Ants at Water	0.08754 +/- 0.463221 ants/min	-0.01203 +/- 0.260677 ants/min	0.2155 (df 74.821)	Fig 4
Number of Majors at Sugar	-0.04255 +/- 0.14792 ants/min	0.02572 +/- 0.139717 ants/min	0.2709 (df 20.038)	Fig 4
Number of Majors at Water	0.00164 +/- 0.39291 ants/min	-0.006383 +/- 0.14361 ants/min	0.5067 (df 15.891)	Fig 4
Number of Scouts	-0.2083 +/- 3.769747 ants	0.6053 +/- 2.964105 ants	0.2657 (df 83.999)	Fig 3
Proportion of Ants at Sugar	-0.04789 +/- 0.198525	-0.02144 +/- 0.154531	0.536 (df 66.874)	Fig 4
Proportion of Ants at Water	0.026638 +/- .13633	-0.006602 +/- 0.022564	0.1472 (df 39.472)	Fig 4
Sugar depletion	-0.02843 +/- 0.223737 g	0.01184 +/- 0.192766 g	0.3787 (df 81.293)	Fig 4
Time to 1 st explorer	-22.6 +/- 575.7437 s	42.26 +/- 734.9788 s	0.6568 (df 68.883)	Fig 3
Time to 1 st return	-68.81 +/- 537.7695 s	79.16 +/- 385.1954 s	0.1413 (df 83.246)	Fig 3
Water depletion	0.1187 +/- 0.144402 g	0.06994 +/- 0.18429 g	0.1215 (df 67.221)	Fig 4

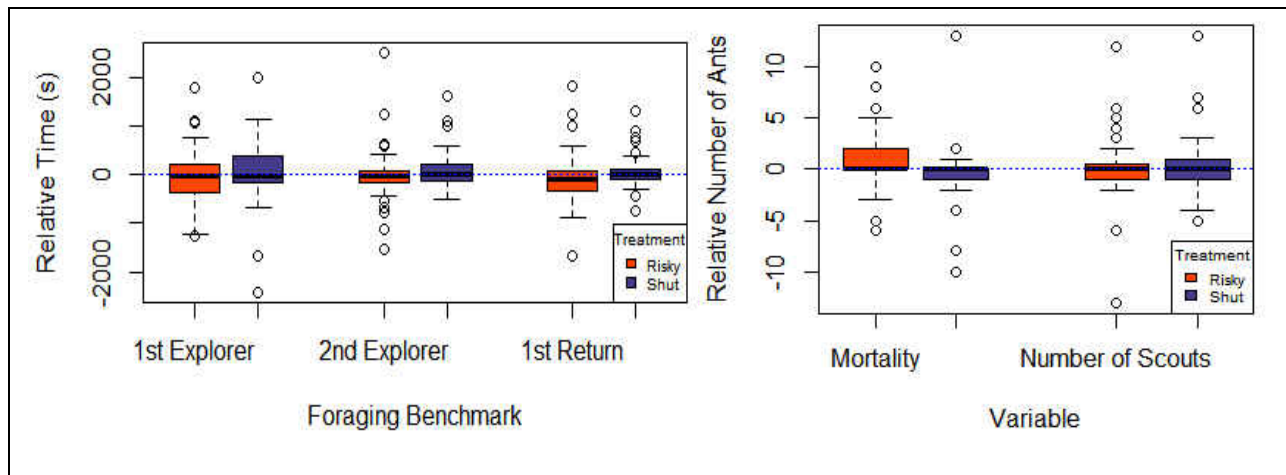


Figure 3: Boxplots of relative time to three foraging benchmarks: time to 1st explorer, delay to 2nd explorer and time to 1st return (left) and number of scouts entering arena prior to recruitment alongside number of ants dead after 24 hours (right) for treatment arena. None of these variables were different

between treatment nor were they different from 0 ($p\text{-value} > 0.05$). Whiskers represent furthest point within 1.5x Interquartile range.

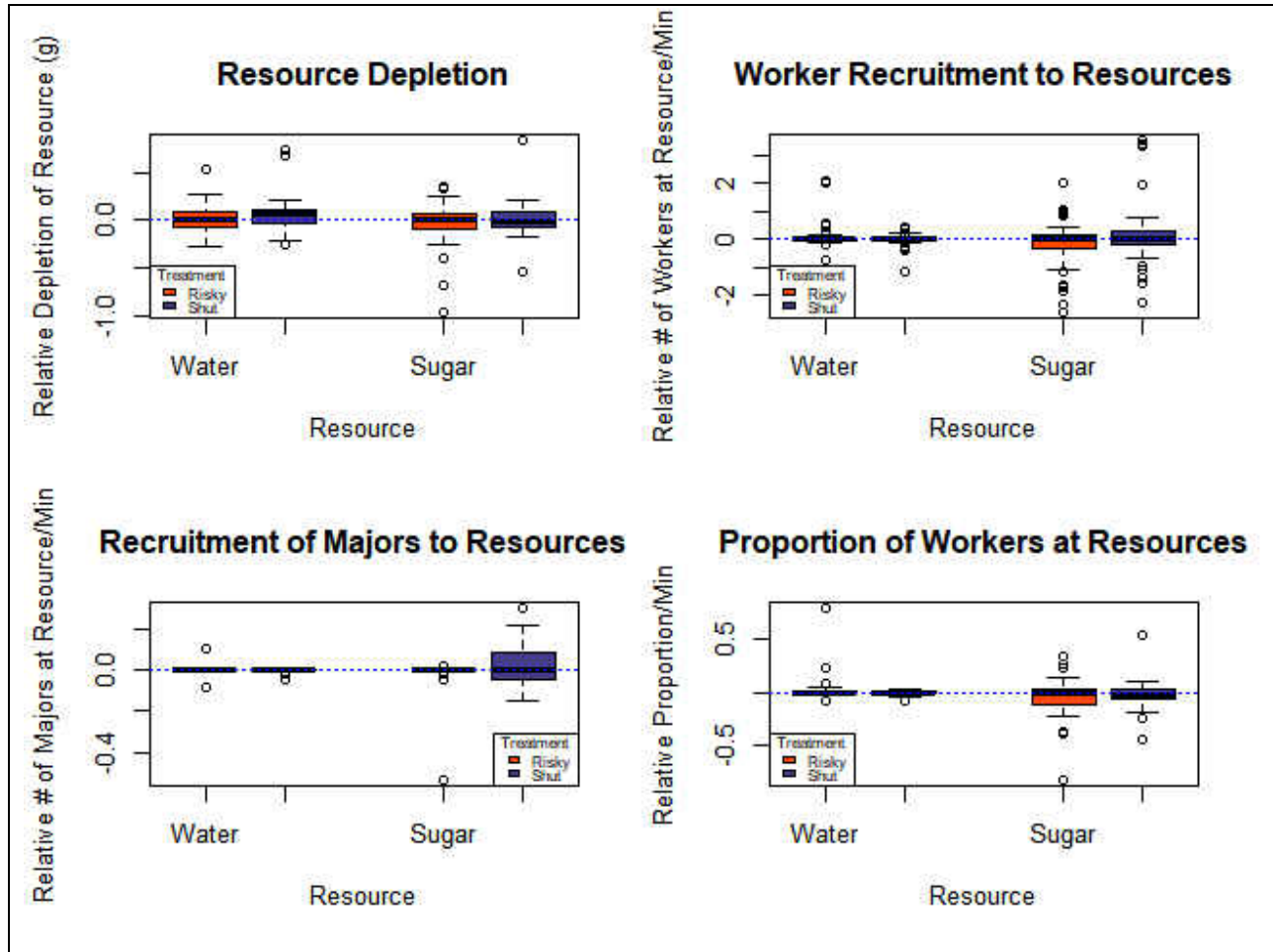


Figure 4: Boxplots of relative depletion of resources (top left), proportional recruitment of workers (top right), recruitment of workers (bottom left) and recruitment of majors (bottom right). None of these variables were different between treatment nor were they different from 0 ($p\text{-value} > 0.05$). Whiskers represent furthest point within 1.5x Interquartile range.

Foraging Strategy

There were 64 experiments with mass recruiting ants (36 with the risky treatment, 28 with the shut treatment), and 22 experiments with solitary foragers (12 with the risky treatment, 10 with the shut treatment). Because of the small sample size for solitary foragers and the

difference in sample size for each treatment the Kruskal-Wallis rank sum test was used to compare the data. With the exception of mortality in mass recruiters, there were no significant differences in any of the investigated variables between foraging strategy nor were any of the means different from 0 ($p > 0.05$) (appendix F). Mortality for mass recruiting ants was significantly higher in the risky treatment compared to the shut, neither of these means were however, different from zero.

Species

Because species was a subset of the foraging strategy dataset, the Kruskal-Wallis rank sum test was used to compare the findings by species. There were no significant differences in any of the investigated variables between treatments or between species or between treatment within species nor were any of the means different from 0 ($p > 0.05$ [appendix G]). Thus, there were no differences among species in their (lack of) response to the presence of a spider predator.

Experiment 2

Experiment 2 constituted 40 trials between 6/2018-8/2019 using 26 lab-reared *S. invicta* colonies (12 colonies receiving one trial, 14 colonies receiving two trials). 11 trials were removed as no foraging occurred in one or more of the foraging arenas, and four additional trials had to be removed since they were lacking a paired trial (due to lack of foraging in the initial trial). In the end 25 trials were analyzed (5 colonies receiving one trial, 10 colonies receiving two trials). When comparing the relative values for each variable measure between treatments in experiment 2, there was no difference between the different experiments (table 5 & 6). There

was a significant difference in the number of scouts (table 6) but only between experiment 1 and 2 (p value 0.02 for paired t-test, p value > 0.05 t-test) (figure 5). However, this significant different was rejected by a post-hoc Benjamini-Hochberg Procedure run to correct p-values given that 4 different variables were measured to observe the behavior of ‘individual ants’ (table 6).

Table 5: Variables of Interest Comparing Naïve Colony Exposure to Each Treatment. Means reported as mean +/- SD. All variables are displayed in Appendix H. The degrees of freedom for the Welch’s T-test is displayed in parentheses after the p-value.

Variable	Naïve exposure- Risky	Naïve exposure- Shut	Welch’s T-test p-value
Number of Scouts	0.6 +/- 0.894427 ants	0.9 +/- 0.994429 ants	0.57 (df 8.9525)
Sugar Depletion	0.09928 +/- 0.198428 g	-0.05643 +/- 0.380788 g	0.317 (12.882)
Time to 1 st Explorer	-167.6 +/- 1356.651 s	242.3 +/- 452.8215 s	0.5433 (df 4.4519)
Time to 1 st Return	309 +/- 829.6948 s	102.8 +/- 347.9798 s	0.6183 (df 4.7183)
Time to 2 nd Explorer	171.8 +/- 853.7428 s	-37 +/- 568.7032 s	0.6388 (df 5.844)
Water Depletion	-0.0175 +/- 0.118275 g	0.01170 +/- 0.158806 g	0.6969 (df 10.624)
Number of Ants	-0.42188 +/- .611042 ants/min	10.23125 +/- 19.27775 ants/min	0.1147 (df 9.0451)
Number of Ants at Sugar	-0.01042 +/- 0.020833 ants/min	-0.26042 +/- 2.256661 ants/min	0.7342 (df 9.0038)
Number of Ants at Water	0 +/- 0 ants/min	0.195833 +/- 0.468449 ants/min	0.22188 (df 9)

Table 6: Variables of Interest Comparing Naïve Colony Exposure to Subsequent Exposure. Means reported as mean +/- SD. The degrees of freedom for the Welch’s T-test is displayed in parentheses after the p-value. A Post-Hoc Benjamini-Hochberg Procedure was run to correct p-values for repeated measurement.

Variable	Naïve exposure- Shut	Prior Experience- Risky	Welch’s Paired T-test p-value	Benjamini-Hochberg Procedure	Displayed in:
Water Depletion	0.01170 +/- 0.158806 g	0.09704 +/- 0.198435 g	0.4512 (df 9)	NA	Appendix H
Sugar Depletion	-0.05643 +/- 0.380788 g	-0.00605 +/- 0.19074 g	0.678 (df 9)	NA	Appendix H
Number of Scouts	0.9 +/- 0.994429 ants	-0.2 +/- 0.788811 ants	0.02426 (df 9)	0.0125	Fig 5
Time to 2 nd Explorer	-37 +/- 568.7032 s	120.6 +/- 390.0861 s	0.5901 (df 9)	0.025	Appendix H
Time to 1 st Return	102.8 +/- 347.9798 s	84.1 +/- 486.2721 s	0.9193 (df 9)	0.0375	Appendix H
Time to 1 st Explorer	242.3 +/- 452.8215 s	249.6 +/- 937.3096 s	0.9759 (df 9)	0.05	Appendix H
Number of Ants	10.23125 +/- 19.27775 ants/min	9.689815 +/- 16.90956 ants/min	0.7604 (df 8)	NA	Appendix H

Number of Ants at Sugar	-0.26042 +/- 2.256661 ants/min	0.12037 +/- 2.669631 ants/min	0.8403 (df 8)	NA	Appendix H
Number of Ants at Water	0.195833 +/- 0.468449 ants/min	0.523148 +/- 0.812129 ants/min	0.2276 (df 8)	NA	Appendix H

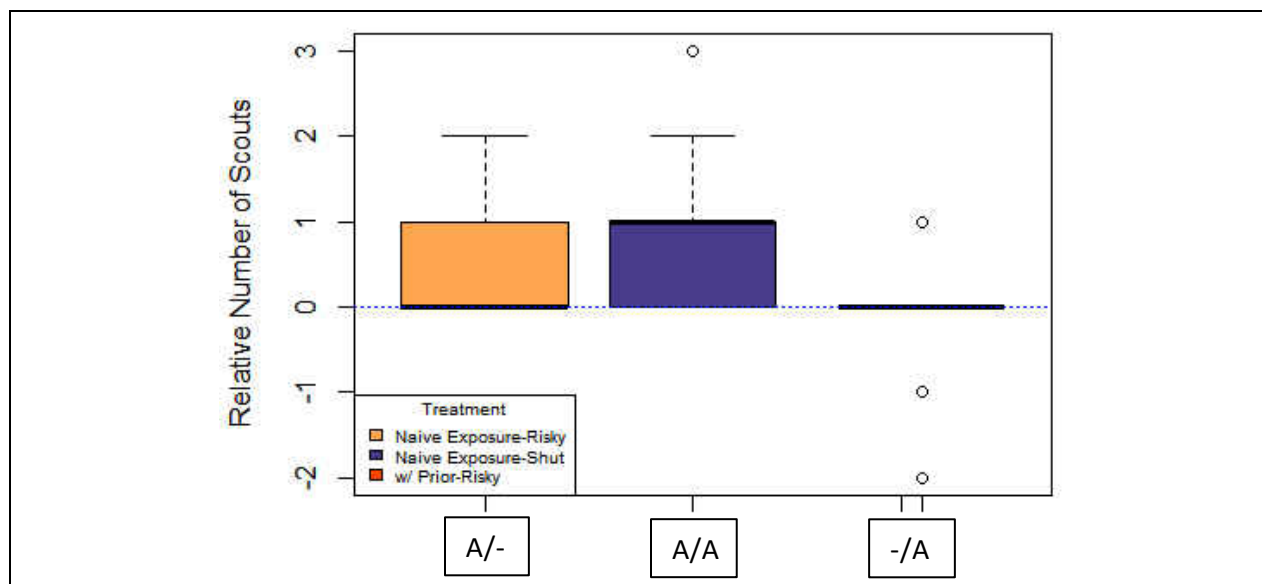


Figure 5: Boxplot of scout number between the 3 groups of trials conducted. Letters below boxplot denote significance groups of $p > 0.05$ for Welch's T-test/paired t-test. There was no difference between Naïve colonies exposed to a risky or shut treated spider (p -value > 0.05) or between a colony's 1st and 2nd trial (Benjamini-Hochburg corrected p -value > 0.0125) Whiskers represent furthest point within 1.5x Interquartile range.

Spider Survey

The spider survey resulted in a total of 484 spiders (70 females, 99 males, 315 unknown sex) observed in ~17.5 hours of observation conducted over 30 days (fig 6, fig 8) and, in the same period, 14 species of ants were observed (appendix I). Across the three sites, there were 3.65 +/- 1.56 spiders/day at the 1st site, 5.29 +/- 1.99 spiders/day at the 2nd site and 4.83 +/- 1.67 spiders/day at the 3rd site (fig 8). As three sites saw no significant differences in number of spiders observed (p -value > 0.05), I observed an average spider density of 2.43 +/- 1.35 spiders/day/m².

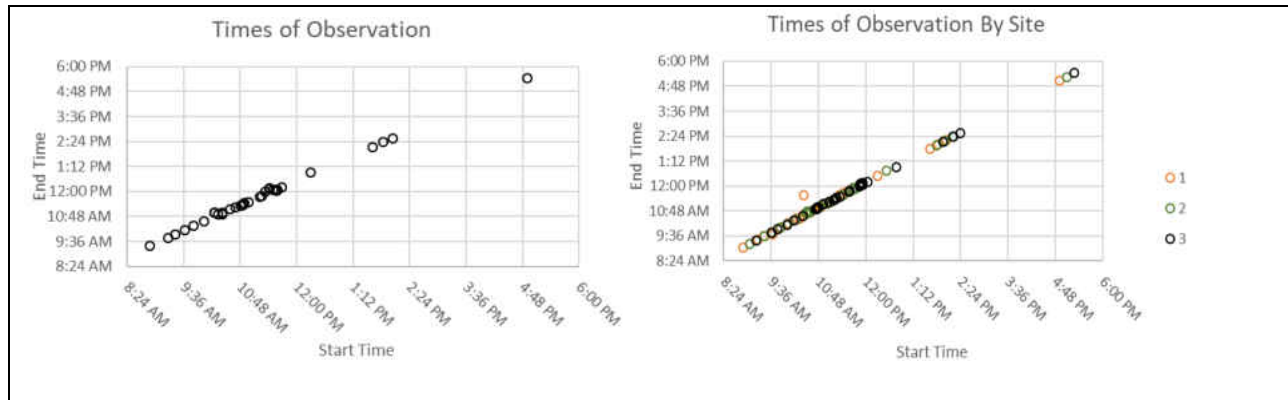


Figure 6: Spider observation period. Range of observation period (left) and range of site observation period (right). Deviation from the clustered line indicates longer or shorter observation periods (30 minutes on left graph, 10 minutes on right graph). Color indicates site number on the right side. Times of observation cover morning to early evening, with a higher density of morning observations.

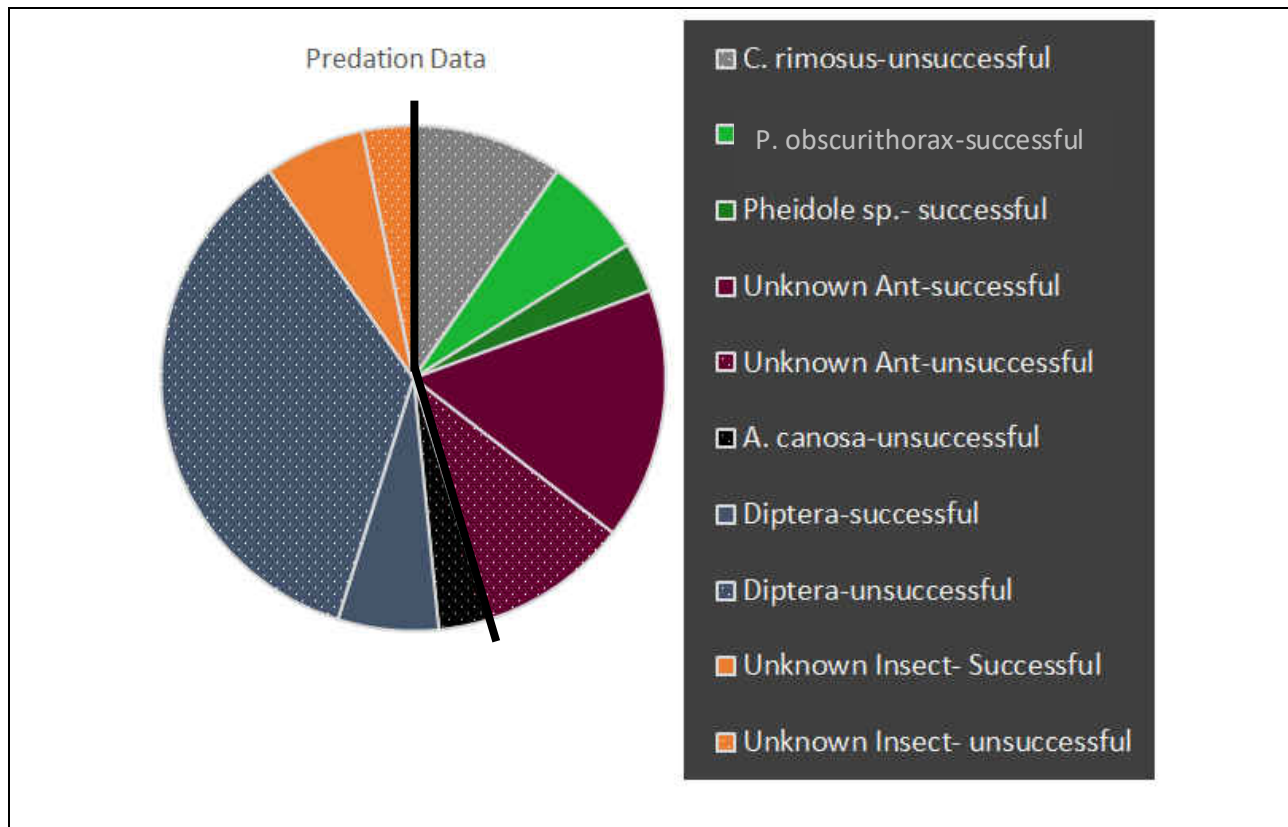


Figure 7: Prey captures from observed spider attacks ($n = 32$). White dots indicate fraction of unsuccessful attacks. The left section of the pie chart represents non-ant prey, the right section indicates ant prey. Ants make up slightly less than 50% of the attacks but were more frequently captured successfully than non-ant prey.

Over this period 32 attacks (1.83 per hour of observation, 6.61% of spiders attacking prey) were observed on a variety of prey, as shown in figure 7, with 40.63 % overall success rate. 15 attacks were observed on ant foragers, 60% of which were successful (9 attacks successful). Attacks on non-ants were also observed, 13 attacks on a variety of dipterans, 15.39% of which were successful (2 attacks successful) and 3 attacks against an unidentified insect, with 66% of those attacks being successful (2 attacks successful). Finally, there was 1 attack against another *A. canosa* which was not successful.

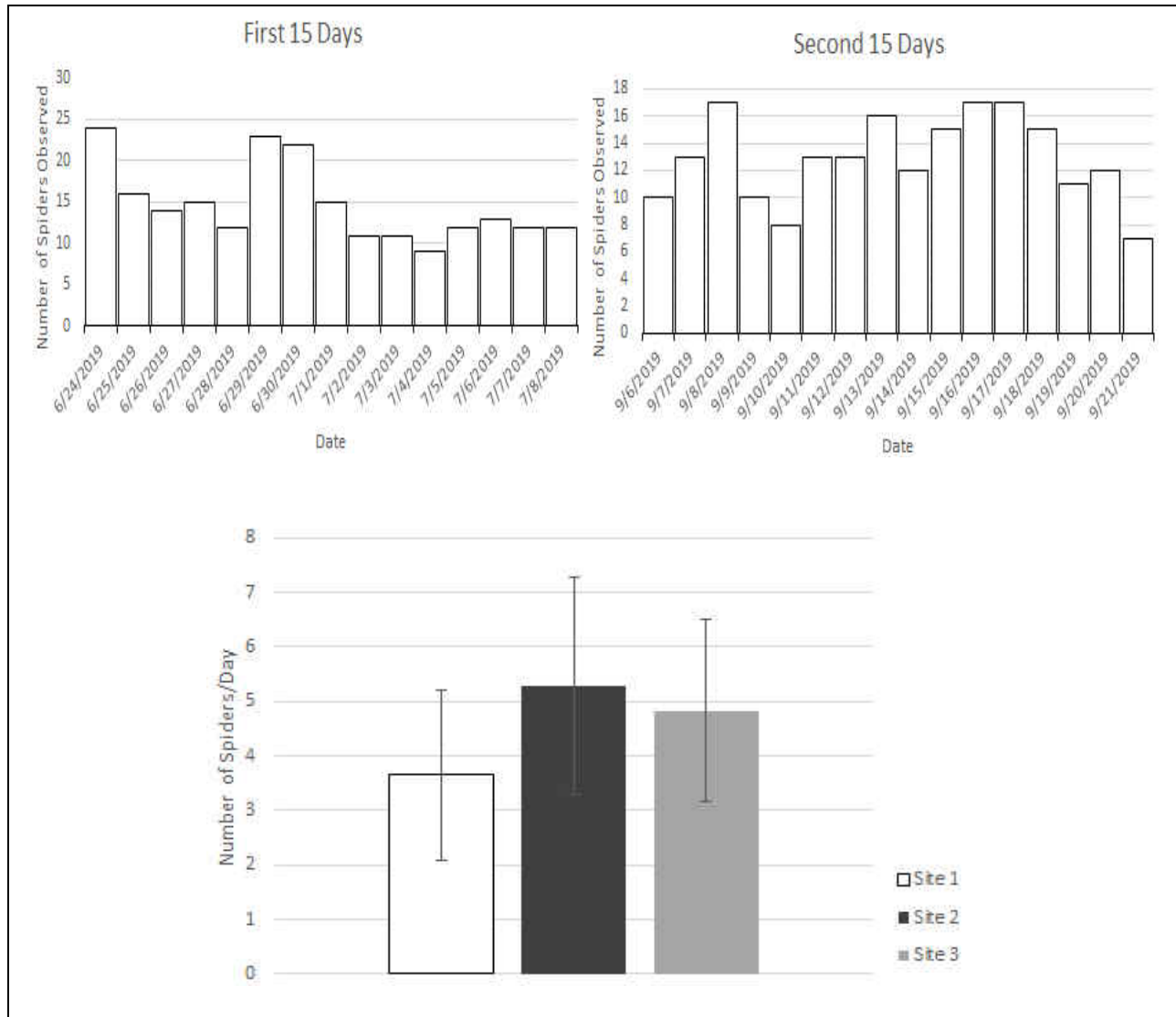


Figure 8: Total number of spiders observed between three sites per day of observation for the first (top left) and second (top right) observation period. The number of spiders over time was relatively consistent during each observation period, but the first fifteen days had much more variation. Average number of spiders present at each site (below), calculated by combining both observation periods. None of the sites were different from each other (p -value > 0.05). Error bars show Standard deviation.

Assuming that spiders are active for 12 hours of a day, I estimate 21.94 attacks occur per day between these 3 sites. Attacks on different prey would be estimated as 10.29 (46.88%) attacks per day would be on ants and of these 6.17 (60%) are successful kills. Over a week, this means

that 43.2 foraging ants would be killed inside the 6.71 m² area I surveyed, or 6.44 ants killed/m²/week.

CHAPTER FIVE: DISCUSSION AND CONCLUSIONS

Ants in the Landscape of Fear

In answer to the central question “do ants respond to predatory risk posed by an ant-specialist spider”, I conclude that, as a colony, they do not. The main indicators of a large-scale foraging change (the actual depletion of resources or significant shift in forager number sustained over time) were not different between treatments or between treatment and control for either sugar or water resources (fig 4), nor did the overall number of ants per minute have any significant difference between the treatments or the treatment vs control (appendix E). For mortality data (fig 3), mortality should be pulled away from 0 by the spiders with the ability to eat ants feeding upon foragers. But this does not appear to be the case, and the hypothesis that mortality would be reduced as ants had repeated exposure to a predator was not supported by the data. Specifically, the number of ants that died in 24 hours did not change with repeated trials (fig 1). There was no significant difference for any of the variables measured among the treatment groups when assessed across foraging strategy or species. No significant divergence from 0 in any of the figures means that the presence and activities of a spider predator did not alter ant prey behaviors associated with any measured variables. More specifically, a result of no significant difference between the risky vs shut treatments means that the spider’s ability to feed upon foragers didn’t have any impact in the way ants responded to the spider. Additionally, because there was no difference detected between the foraging strategies or the different species, it appears that ants are not impacted by predation risk from *A. canosa* regardless of foraging strategy or species.

In sum, foraging ants appear to have **no consistent behavioral alterations** when they perceive a generalist predator's presence, or even as a consequence of *A. canosa*'s predation of other foragers. Although it is possible that there are other individual level behaviors that may have been altered by the spider's presence, these behavioral changes do not appear to lead to any large-scale changes in the outcome of colony foraging that would have been detected in this experiment. Additional analyses did not detect any difference from treatment or species (appendix J). These findings lend some support to the hypothesis of foragers as an expendable caste, insensitive to risk as individuals (Porter & Jorgenson, 1981). This means that *A. canosa* likely does not have cascading impacts from widespread changes in ant foraging due to its arrival or persistence in habitats (Pekar *et al.* 2010). The hypothesis that majors will be more risk averse as a more valuable caste was not supported but Figure 4 does show what may be an interesting difference in variation, where the shut treatment had a much wider range compared to the risky trial. Likewise, figures in appendix E shows the same pattern of much higher variation in the shut compared to risky treatments. Fifteen of the trials failed to see majors at one or both food and water sources however, so the sample size is quite small and more specific testing, focused on the behaviors of foraging majors may be warranted. Further replication is necessary (preferably with more species of *Pheidole*) to really establish the relationship between majors and risk of *A. canosa* predation. Similarly, when comparing the mass recruiting ants to the solitary foragers (appendix E), mass recruiting ants appeared to have more variation compared to the solitary foragers, but the large difference in number of trials (67 vs 22) seems the most likely reason for this difference.

In experiment 2, given that no difference was seen in experiment 1, I did not expect to see evidence of an innate aversion to a predator. It is of particular interest then, that naïve colonies had

more scouts enter the arena containing a predator, but in the second trial, had no difference between the two arenas (fig 5), meaning behaviors which influenced their interactions with the spider appear to be *lost* in one trial rather than gained. This significant difference appears to be a consequence of the number of variables collected in this experiment rather than a truly significant effect (table 6), so a concrete conclusion is not possible. But these results did not support my hypothesis that predator avoidance is a rapidly acquired behavior. The control group showed the same scouting bias towards the arena with a predator (fig 5), which provides further evidence that having prior experience with the predator did change the response of individual foragers. It is important to note however that there was not a significant difference between the treatment and control groups in the second half of experiment 2, but this fact is likely due to a reduction in degrees of freedom comparing a paired and independent samples t-test, as well as the much smaller sample size of the control group. These results suggest that *S. invicta* foragers could be responding to predatory risk by increasing the number of scouts in the arena, likely lowering the risk which an individual ant experiences; a herd effect (Ioannou, 2017). Given the reduction in number of initial scouts between trial 1 and 2 in experiment 2 (fig 12) experience may play an important role in how scouts respond to this risk, and this makes biological sense. As scouts are the oldest and most vulnerable foragers in fire ant colonies (Tschinkel, 2010), having additional scouts appear when there is a perceived threat may be a response to the likelihood that predation could reduce the number of scouts present within the territory. Future studies into this topic should verify these results.

One concern with the experimental design was that although brood was collected and present in all colonies some species (especially *F. pallidefulva*) may not have had enough brood to stimulate foraging. Brood number and hunger drives the foraging behavior of ant colonies (Cook *et al.* 2010).

Thus, small colonies of solitary foraging species sometimes failed to forage in both arenas (or in some cases struggled to forage at all). All the *S. invicta* colonies were queenright but the majority of the other species were not, as no queen was collected during a typical colony excavation. While collecting colonies in the field polygyne colonies of *O. ruginodis* were found, as *O. ruginodis* is not noted as polygyne, these colonies were split into monogyne colonies with appropriate worker numbers. Future work using similar methodology should increase the size of solitary foraging colonies (and to be sure that ample brood are present to stimulate colony hunger).

The spider may have been attractive as a potential food item for the ants, as during seven trials (one *F. pallidefulva*, three *S. invicta* and three *P. obscurithorax*) ants attacked the spider and brought some or all of it back to the colony (probably to be eaten as protein). The fact that ants may successfully perceive and capture these spiders as prey may contribute to the lack of avoidance of spider predators, especially if colonies are hungry. There were other factors that impacted data availability for some of the experiments. For example, in some cases after day 1 filming had concluded, the ants broke through the cotton ball on either the water or sugar test tube and flooded the arena, preventing accurate measurement of mortality and resource depletion. Finally, there was an assumption that all but the lab-reared *S. invicta* colonies had prior experience with *A. canosa*. The result of the spider survey suggest that this is likely true, however, and even if field collected colonies had no experience, they could nevertheless learn within 1 to 2 trials that the spider was a predator. Based on the significant difference found in scout numbers in experiment 2 after 1 trial, this appears to be an appropriate assumption (fig 5).

Spider predation did not manifest in a significant difference in the number of dead ants in the arena after 24 hours overall (figure 3) but it was significant in the case of mass recruiting ants (appendix F), and there is a larger range of mortality in mass recruiting ants compared to solitary foragers (appendix F). This is not surprising as scouts and foragers are older individuals and mortality occurs at a regular rate in this behavioral caste (Tschinkel, 2006). Predation did occur during the experiment and was observed by filming for each species on at least 1 occasion. Deprived of other food sources, the spider attacked and successfully ate foraging ants of all four species during the initial 50-minute observation period (one *F. pallidefulva*, three *O. ruginodis*, 12 *P. obscurithorax* and 28 *S. invicta* [appendix K]). The fact that only mass recruiting ants ended up being a significant result (and taken individually, neither *S. invicta* nor *P. obscurithorax* had a significant difference in mortality, [appendix G]) seems to indicate a fundamental difference in the spider's willingness to eat different ant species. In nature *A. canosa* may exhibit prey preference that does not put foragers of the species I chose routinely in danger from this particular predator. Unfortunately, there was no observed interactions between *A. canosa* and 3 of my four species in the field (fig 7), despite the presence of most of my ant species within the sites (appendix I).

Understanding how predators influence the distributions and behavior of their prey remains a critical goal in ecology. Because ants play a large role in the environments they live in as both ecosystem engineers and predators, it is very important that we, as ecologists understand the role that predators play in mediating how ants interact with the environment. From this experiment it would appear that foragers can be responsive to predation risk, but these impacts are not collectively sufficient to impact colony-level foraging. This distinction suggests that solitary predators like jumping spiders do not create a landscape of fear for ant colonies. This differs from collective responses of foraging ants

in response to web-building spiders that may capture and kill large numbers of foragers (Kwapich & Hölldobler, 2019).

Future directions for our understanding of how ant colonies, and other eusocial and social groups operate in the landscape of fear are: to expand species list to include a greater variety of species, colony sizes and foraging strategies. Additionally, accounting for worker age would verify the assumption that older workers take more risks, and also see if the age cohorts of foragers is altered by the perception of risk.

Spider Survey

My field survey results indicated *A. canosa* is not only abundant but likely densely populated (fig 8). My results also show that spiders capture many ants as prey, and that a large number of foraging ants likely survive encounters with this spider at regular intervals. Although my estimate suggests that 6.44 ants are killed each week/m² area of spider territory, it also suggests that 4.48 ants are exposed to a spider and survive the encounter every week/m². Thus, *A. canosa* represents a small, but consistent predatory threat to a variety of ant species and that most ant colonies should have prior experience with these spiders in the field.

Ant colonies cover a variable sized patch of ground, but foraging ranges routinely span 50 cm to many meters from the nest (Hölldobler and Wilson, 1990). The total space a colony considers its territory also is variable but estimates of at least 2 m² are likely conservative for all but the smallest of ant species. Worker ants live for a few months to more than 1 year (Gordon & Hölldobler, 1988), and typically forage towards the end of their lifespan, typically a time span of 1-2 months, although higher turnover is also common during periods of stress (Schmid-Hempel,

1984). Under an assumption of 1-month turnover inside a colony, that would mean that each foraging cohort within a colony should contain approximately 13 ants that have prior experience with *A. canosa* for every m² of exclusive foraging territory where the spider is found. Although ant colonies are territorial, they sometimes overlap in foraging areas with non-competitive species, so they will in all likelihood not be the only species experiencing spider predation within that space, reducing the number of foragers that would have prior experience. However, even a small number of ants are able to spread knowledge effectively through information sharing (Franks & Richardson, 2006), and age is not a factor in the ability to share information with nestmates (Franklin *et al.* 2012). This means that colonies in regions where *A. canosa* is found should have ample opportunity for foragers to learn and respond to the spider's presence. One important point remains in the feeding data for *A. canosa*, namely that the overall number of ants killed by the spider is somewhat small (over 1 month a colony should have ~19.32 foragers killed/m² of spider habitat that the colony exclusively forages in) and this may mean that *A. canosa* isn't a major impact on foragers themselves, meaning that even if ants were not behaving under the disposable caste hypothesis, perhaps *A. canosa* is not a threat workers need to be aware of. Another critical factor in my estimates, is that the hunting data I observed included 3 attacks on *C. rimosus*, a heavily armored ant, which has been concluded to not be a possible food source for *A. canosa* (Edwards *et al.* 1974). This provides further evidence that the spiders, as an opportunistic forager, don't turn down opportunities to attack any insect.

My observations were conducted across the length of a day (fig 6) but were heavily concentrated in the mid-morning (10-11 am). This may have introduced a bias into my data since only 4 observations occurred in the afternoon.

Pekar *et al.* (2012) noted that on average 7% of spiders observed should have prey, meaning that 500 spiders are a sufficient number to gain an understanding of the spiders foraging behaviors. In my study I observed slightly fewer than 500 spiders but observed only 6.612% of spiders with prey. This difference in rate of feeding is could be due to the methodology applied in this experiment, although there is a close match between my observations and Pekar *et al.*'s (2012) predictions.

Since jumping spider behavior and feeding in the wild are typically different between male and female spiders (ex: Scheidemantel, 1997), being unable to distinguish between male and female spiders due to immaturity poses a very important drawback to this research, as it leaves the realized prey niche for *A. canosa* slightly uncertain. *A. canosa* is an indirect hunter (Hill, 2019) which means that determining the spiders food preference is more challenging than for other spiders, due to the difficulty in determining where a spider 'misses' a chance to feed, or distinguishing preparations to attack a moving prey item (such as a fly or foraging ant) from the spider simply moving from place to place. In addition to the highly distinctive attacks, there were also numerous cases of spiders showing stalking behavior of an ant or dipteran that failed to result in an attack which were not included in the attack data. Finally, not all the insects attacked could be accurately identified or identified beyond order, and a few of the observed attacks were inferred from spiders observed carrying prey, rather than observing them catching it.

From this field study, I am uncertain if *A. canosa* is truly a stenophageous spider. A sizeable chunk (40.6%) of the attacks observed targeted flies (fig 7), and the spider seemed to be more of an opportunist (even scavenging dead insects placed before it) than a true specialist.

Although *A. canosa* has evolved specialist hunting behaviors that make it more successful at hunting ants (60% success rate against ant prey vs. 25% success rate against non-ant prey), spiders seems to stalk and attack anything that gets close to where they wait.

An observation period of 30 minutes appears to have been sufficient time to locate spiders, however, spiders are very prone to vibrational cues (Virant-Doberlet *et al.* 2019) and my walking through the habitat could have driven many spiders into hiding. Given that spiders were typically located within 2 minutes of starting to collect data, this does not appear to have been a major concern in this project. My estimates for spider numbers and predation rates are then likely underestimates due to vibrations from my movement changing spider behavior within the sites. Certainly, this vibrational cue altered the personality of spiders I saw in the field, as bolder spiders would emerge from hiding faster, or not hide at all, so the most conspicuous spiders were also likely the boldest. This personality skew should not have impacted the feeding rate data, as research in other jumping spiders has not seen changes in feeding choices based on personality (Chang *et al.* 2017).

First and foremost, other researchers must duplicate these results across the range of *A. canosa* to increase our understanding of both the spider's ecology and its relationship to ants and other local fauna. This project is relatively short, requires minimal training and would be an excellent way to expose students to the natural environment. Replicating this work in local habitats wherever *A. canosa* can be found would be an excellent project for citizen science or students at either the high school or college level. Subsequent surveys should use random sites to assess true spider abundance.

Overall Conclusions

Drawing upon both studies I completed, there is limited that interactions between ant foragers and an abundant generalist spider predator mediated foraging patterns at the level of the colony, although there was some evidence that prior experience in mass recruiters may affect scouting behavior. *A. canosa* maintains a diverse diet of ants and dipterans in the field (appendix I) and can be expected to be a known threat to ant colonies which maintain medium to large foraging territories in semi-natural areas in Florida. Further study is necessary to explore the process of how workers convey information about risk, best accomplished using the strongly selective competitive threats of other ants (Gordon, 1989). Once this has been done a comparison can be performed to see how the risk of spider predation is either conveyed differently or not conveyed to other mass-recruiting ants. It would also be beneficial to preform experiment two again using naïve colonies of solitary foraging ants to see if the same herd effect is seen. Overall, ant colonies do appear to be risk insensitive and foragers (even if they have changes to behavior to protect themselves) are disposable.

APPENDIX A: EXPERIMENTAL HOUSING AND TEST SETUP



Figure 9: Mock Experimental Setup for Laboratory Studies. One arena at random receives a randomly treated spider in each experimental trial.

APPENDIX B: PREDICTIONS FOR LABORATORY EXPERIMENTS

Table 7: Predictions for Experiment One. All predictions are for the treatment arena compared to control arena.

Treatment	Regular Spider	Glued Shut
Number of Ants in Arena	Greatly reduced	Slightly reduced
Number of Ants at Food	Greatly reduced	Slightly reduced
Water Depletion	Reduced	Reduced
Number of Majors	Reduced	Reduced
Sugar Depletion	No Change	No Change

Table 8: Predictions for Experiment Two. All predictions are for the treatment arena compared to control arena.

Treatment	Prior Exposure	No Prior Exposure
Food/water Depletion	Reduced	No change
Mortality	No change	Higher

APPENDIX C: MAP OF FIELD SITES



Figure 10: Map of Field Sites for Field Survey, Stars Indicate Field Sites.

Original map from: UCF Arboretum, Landscape & Natural Resources.

Retrieved from: <https://arboretum.ucf.edu/resources/trails/> 10/5/2019.

APPENDIX D: TABLE OF TRIALS CONDUCTED

Table 9: Estimation of Power for One-tailed T-test in Experiment.

Level of Analysis	Power Estimate (medium effect size)	Power Estimate (high effect size)
by Treatment	0.7386582	0.9777591
Solitary Forager by Treatment	0.3027321	0.5634899
Mass recruiter by Treatment	0.624657	0.9325567
<i>S. invicta</i> by Treatment	0.46666665	0.8031083
<i>P. obscurithorax</i> by Treatment	0.310511	0.5774244
<i>F. pallidefulva</i> by Treatment	0.1750403	0.3051127
<i>O. ruginodis</i> by Treatment	0.2013883	0.3620295
Experiment two: Paired t-test.	0.2931756	0.7544248
Experiment two: t-test.	0.2179579	0.397235

Power estimates in the table 9 were made in r with the 'pwr' package using only medium and high effect sizes because non-consumptive effects were expected to be amplified in a colony level response. Power under medium effect size used 0.5 for effect size while under high effect size calculations used 0.8 following Cohen's suggested effect size at those levels.

**APPENDIX E: ADDITIONAL GRAPHICAL REPRESENTATION OF
EXPERIMENT 1 DATA**

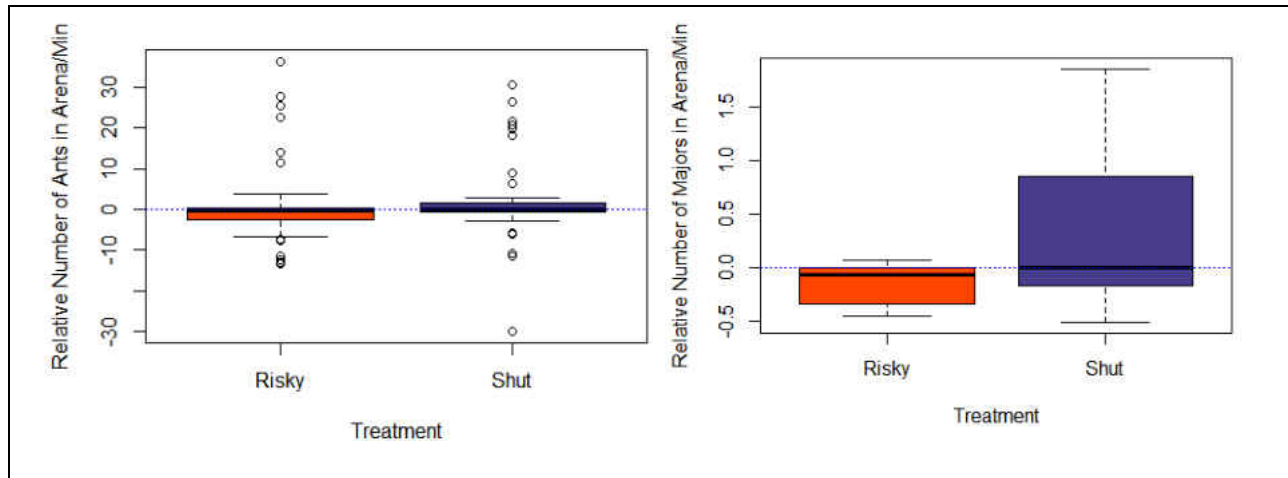


Figure 11: Boxplots of relative recruitment of worker ants (left) and majors (right) into treatment arena. Neither of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

APPENDIX F: BY-FORAGING STRATEGY DATA FROM EXPERIMENT ONE.

Table 10: Comparing Treatment by Foraging Strategy. Due to small sample size which differed between treatments, p-value is for a Kruskal-Wallis rank sum test. * indicates a value is different from 0 according to a Wilcoxon signed rank test ($p < 0.05$).

Variable	Solitary Foraging-Risky	Solitary Foraging- Shut	p-value	Mass Recruiting-Risky	Mass Recruiting- Shut	p-value
Water	-0.003858	0.05272	0.4683	0.01742	0.07632*	0.131
Sugar	-0.03619	-0.00436	0.8951	-0.02557	0.01783	0.8703
Explorer 1	-220.8	265.1	0.1661	43.47	-37.32	0.9407
Explorer 2	180.2	237.1	0.7416	-89.67	50.21	0.6166
Num-Food	-0.25675	-0.04043	0.7915	-0.1942	0.19352	0.6309
Num-Water	0.05014	-0.0383	0.6569	0.10036	-0.002643	0.8934
Pro-Food	-0.09664	0.07174	0.5136	-0.030474	-0.058555	0.5064
Pro-Water	0.095517	-0.005807	0.5898	0.002038	-0.006927	0.2814
Scouts	-0.25	-0.2	0.4537	-0.1944	0.8929	0.6349
Num	-0.5082	-0.3505	0.9474	1.4072	3.0554	0.279
Return	-196.0	56.8	0.1468	-26.42	87.14 +/- 435.9769	0.1916
Mortality	-0.3333	-0.1111	0.6403	1.68 +/- 3.848376*	-0.50 +/- 4.885352	0.02458*

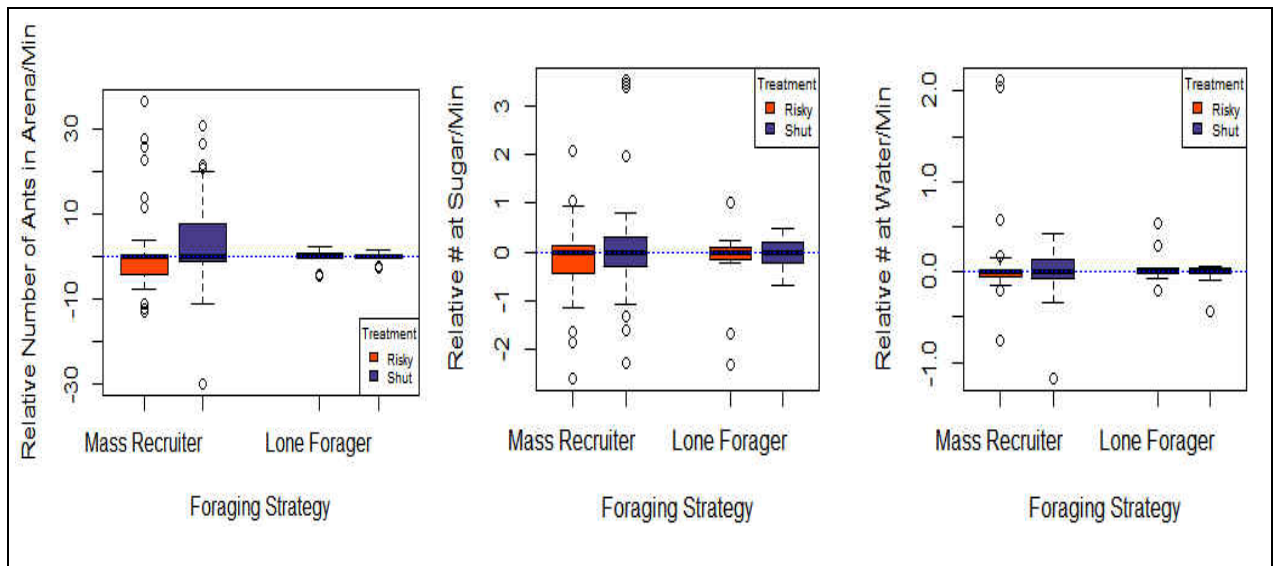


Figure 12: Boxplots of number of ants per minute in treatment arena (left), at sugar (center) and at water (right) for each foraging strategy. None of these variables were different between treatment nor were they different from 0 ($p\text{-value} > 0.05$). Whiskers represent furthest point within 1.5x Interquartile range.

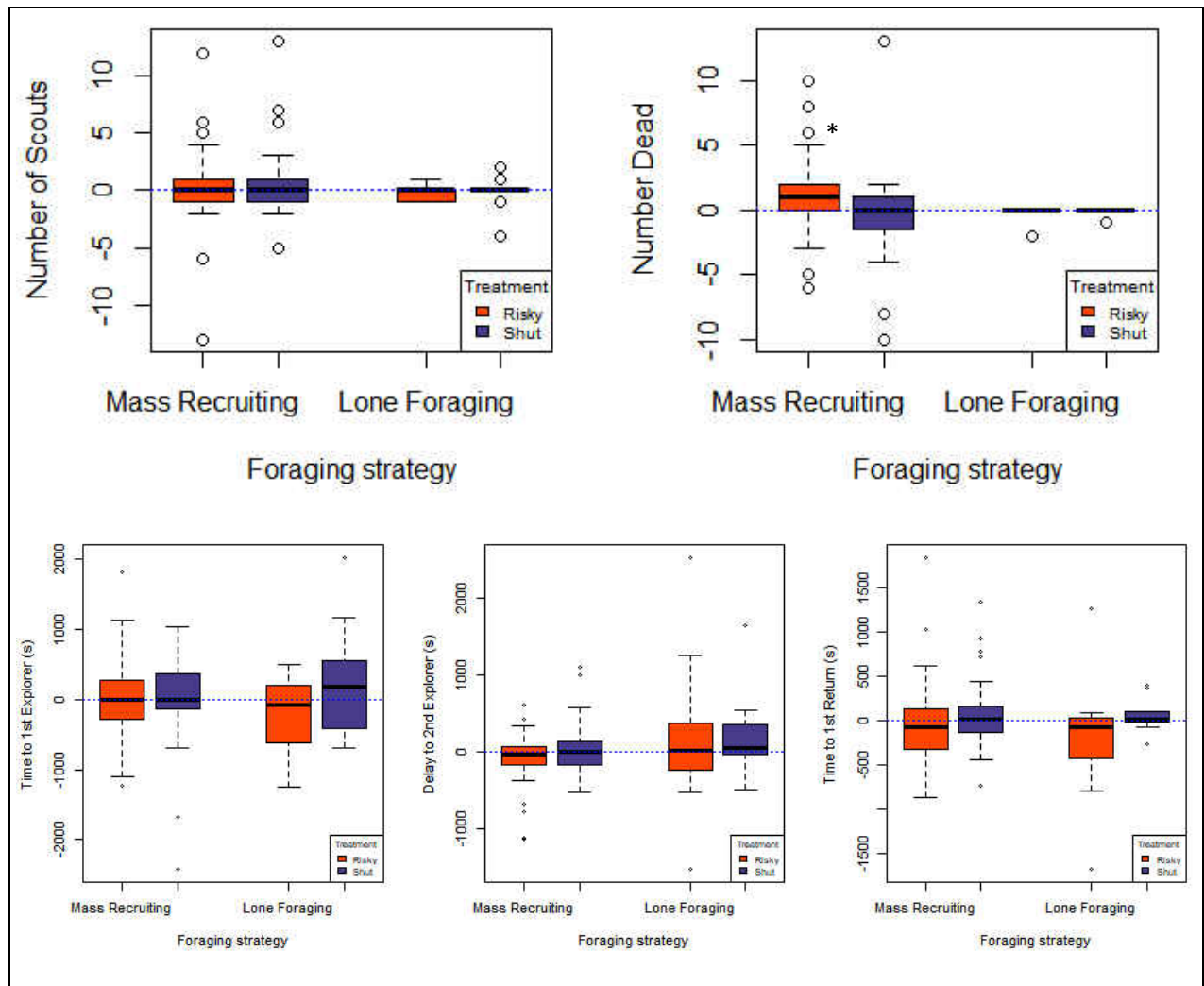


Figure 13: Boxplots of relative number of scouts (top left), total mortality (top right), time to first explorer (bottom left), delay to second explorer (bottom middle), and time to first return (bottom right) in treatment arena for each foraging strategy. * indicates difference between treatment and control (p -value < 0.05). Of these variables, only mass recruiter mortality was different between treatment (p -value < 0.05 [appendix 8]) and no variables were different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

APPENDIX G: BY SPECIES RESULTS FROM EXPERIMENT ONE

When comparing the species data, a major hurdle was the very small sample sizes (especially for the solitary foraging species). To compensate for this, and the different sample sizes between the two treatments a non-parametric Kruskal-Wallis rank sum test was used.

Table 11: Comparing the Means of Solitary Foraging Species. P-value is for a Kruskal-Wallis Rank Sum Test.

Variable	<i>F. pallidefulva</i> - Risky	<i>F. pallidefulva</i> - Shut	p- value	<i>O. ruginodis</i> - Risky	<i>O. ruginodis</i> - Shut	p- value
Water	0.02707	0.02453	0.6698	-0.03478	0.07152	0.2002
Sugar	0.04225	-0.002975	0.5224	-0.11463	-0.005283	0.631
Explorer 1	-370	-32.75	0.3938	-71.67	463.7	0.2002
Explorer 2	-13.17	387.2	0.5224	373.67	137.0	1
Num-Food	-0.24044	-0.14362	0.5224	-0.27305	0.02837	0.4217
Num- Water	0.13475	-0.09043	0.4951	-0.03447	-0.003546	0.8703
Pro-Food	-0.1059	0.12058	0.6242	-0.08739	0.03267	0.6015
Pro-Water	0.20040	0.007058	1	-0.009368	-0.0161	0.6752
Scouts	-0.1667	-0.25	0.5066	-0.3333	-0.1667	0.5228
Num	-0.4526	-0.68617	0.6698	-0.5638	-0.12666	0.7488
Return	-195.3	-52.25	0.6698	-196.67	129.5	0.1495
Mortality	0 +/- 0	-0.25	0.2207	-0.6667	0 +/- 0	0.1736

Table 12: Comparing the Means of Mass Recruiting Species. P-value is for a Kruskal-Wallis Rank Sum Test.

Variable	<i>S. invicta</i> -Risky	<i>S. invicta</i> -Shut	p-value	<i>P. obscurithorax</i> -Risky	<i>P. obscurithorax</i> -Shut	p-value
Water	0.03872	0.03061	0.6491	-0.017	0.15404	0.121
Sugar	-0.007727	0.008182	0.8874	-0.05629	0.03424	0.8041
Explorer 1	-111.8	-39.61	0.4306	318.2	-33.2	0.3211
Explorer 2	-62.35	87.94	.4005	-138	-17.7	0.6641
Num-Food	-0.0595	-.02079	0.5137	-0.4223	0.5793	0.3211
Num-Water	0.18384	-0.04728	0.28519	-0.04092	0.07771	0.3657
Pro-Food	-0.021758	-0.032746	0.5157	-0.042095	-0.091727	0.5978
Pro-Water	0.002726	-0.007246	0.5459	0.0011203	-0.006545	0.3532
Scouts	0.3043	0.2778	1	-1.077	2	0.367
Num	4.072	1.5142	0.8687	-3.1031	5.83	0.1724
Return	-16.39	48.67	0.713	-44.15	156.4	0.1724
Mortality	2.5*	-.6667	0.09219	0.6364	-0.2857	0.1237

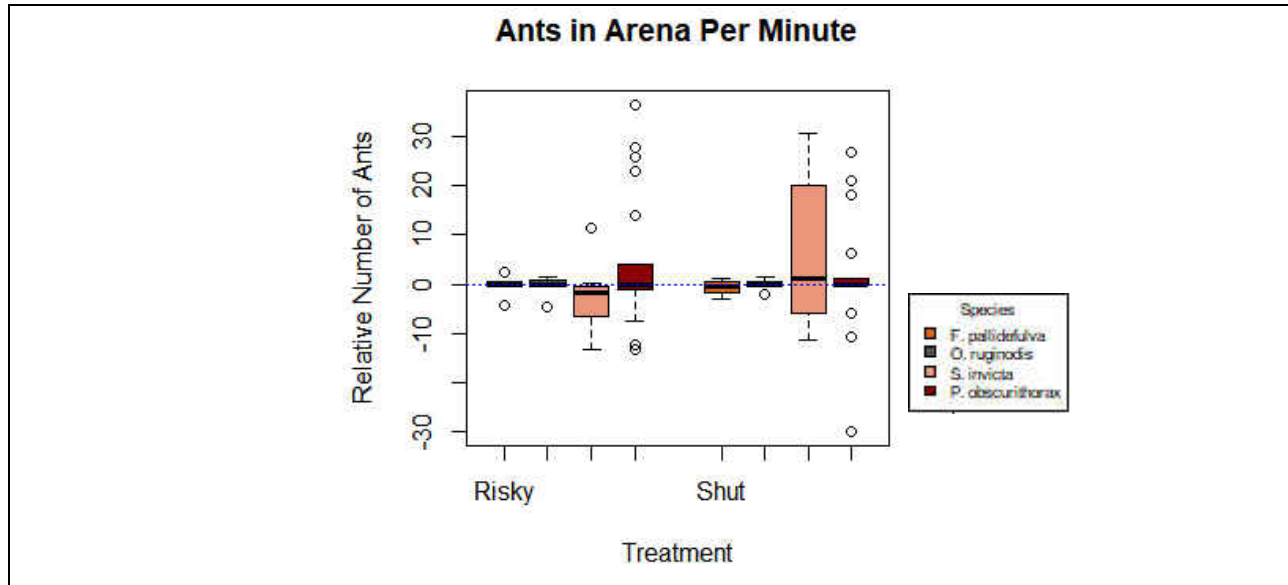


Figure 14: Relative number of ants per minute in treatment arena by species. None of these variables were different between treatment nor were they different from 0 ($p\text{-value} > 0.05$). Whiskers represent furthest point within 1.5x Interquartile range.

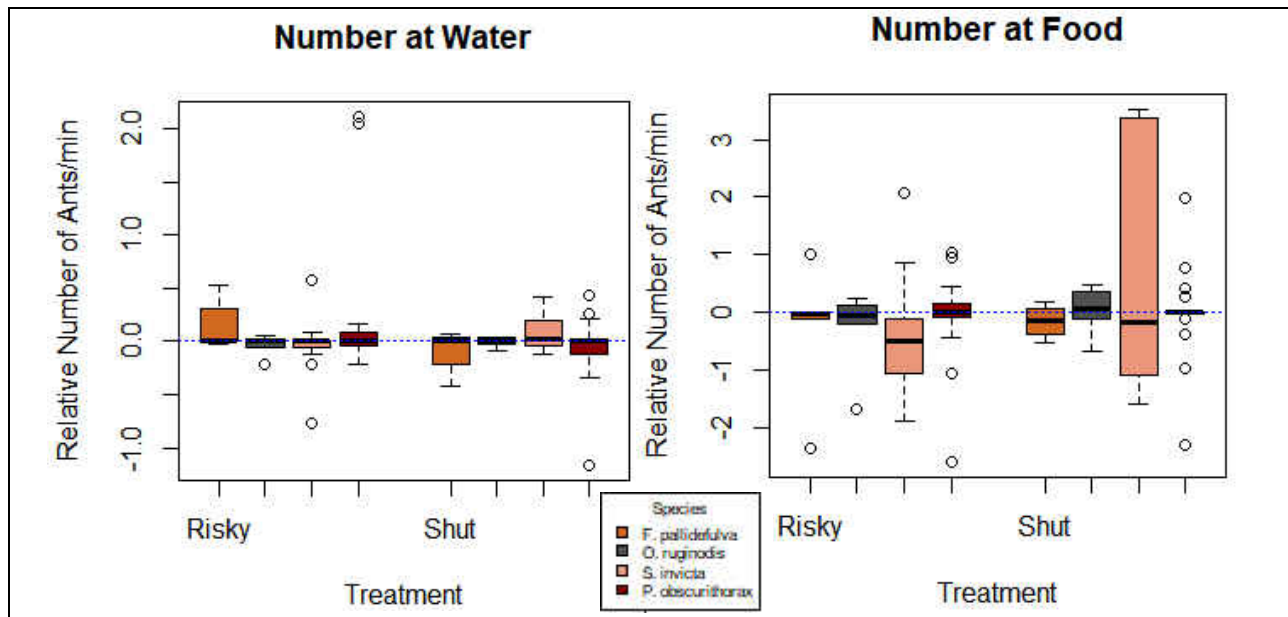


Figure 15: Relative number of ants per minute at water (left) or sugar (right) in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

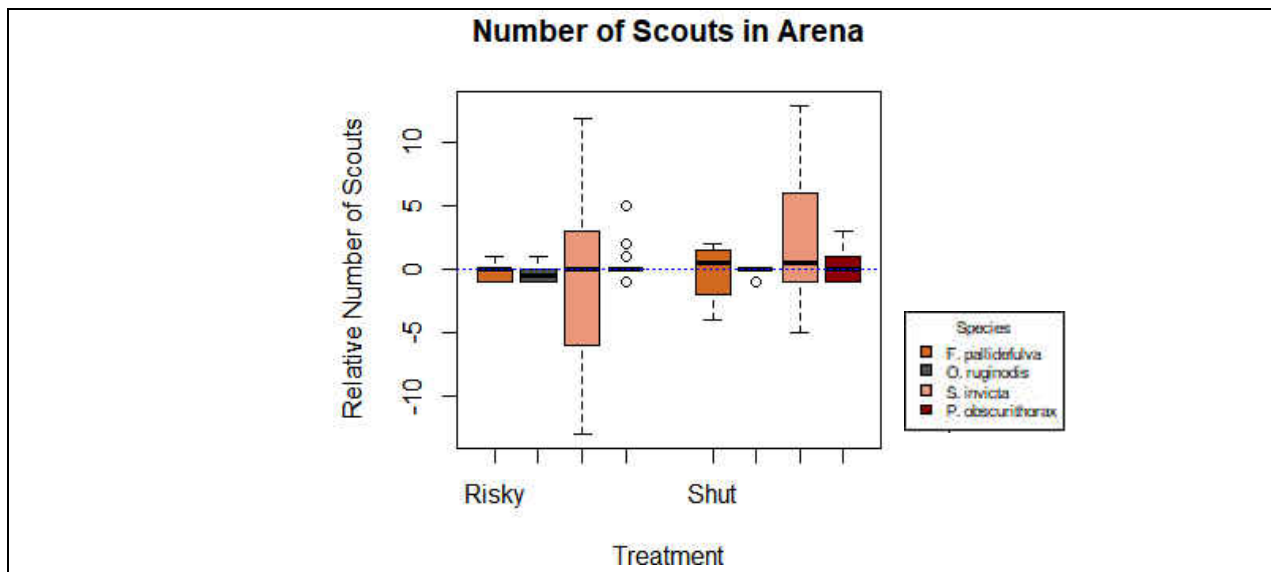


Figure 16: Relative number of scouts in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

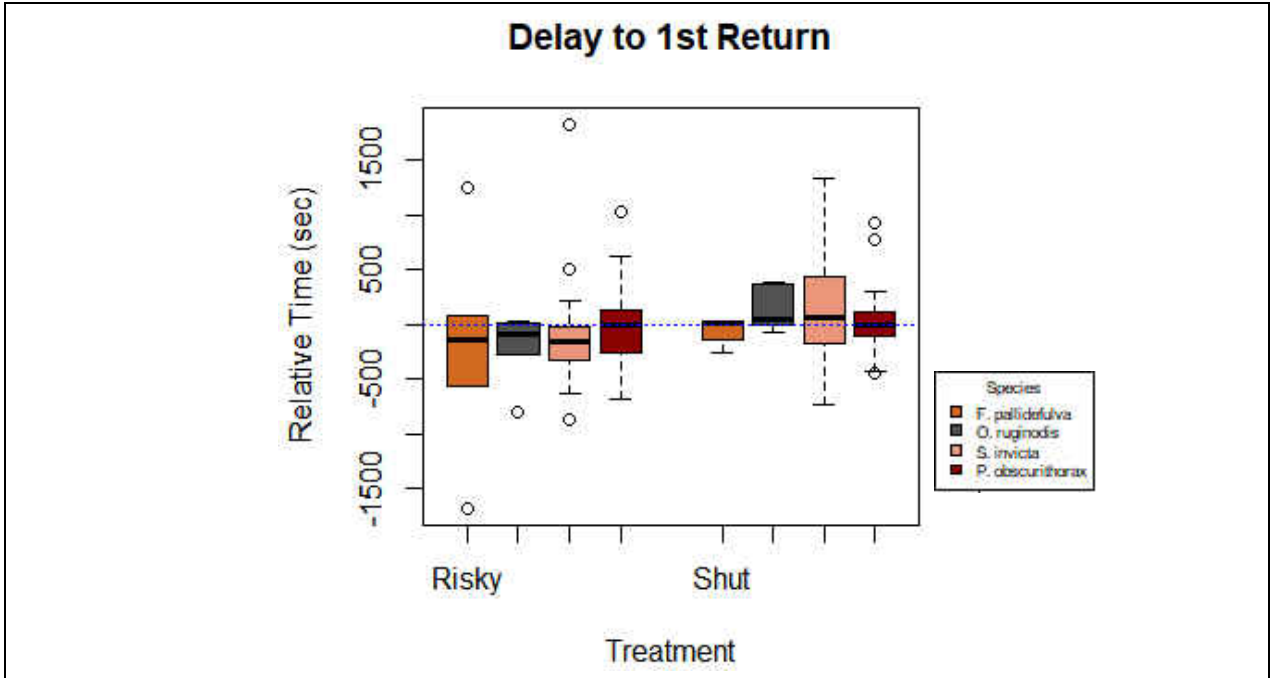


Figure 17: Relative delay to 1st return in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

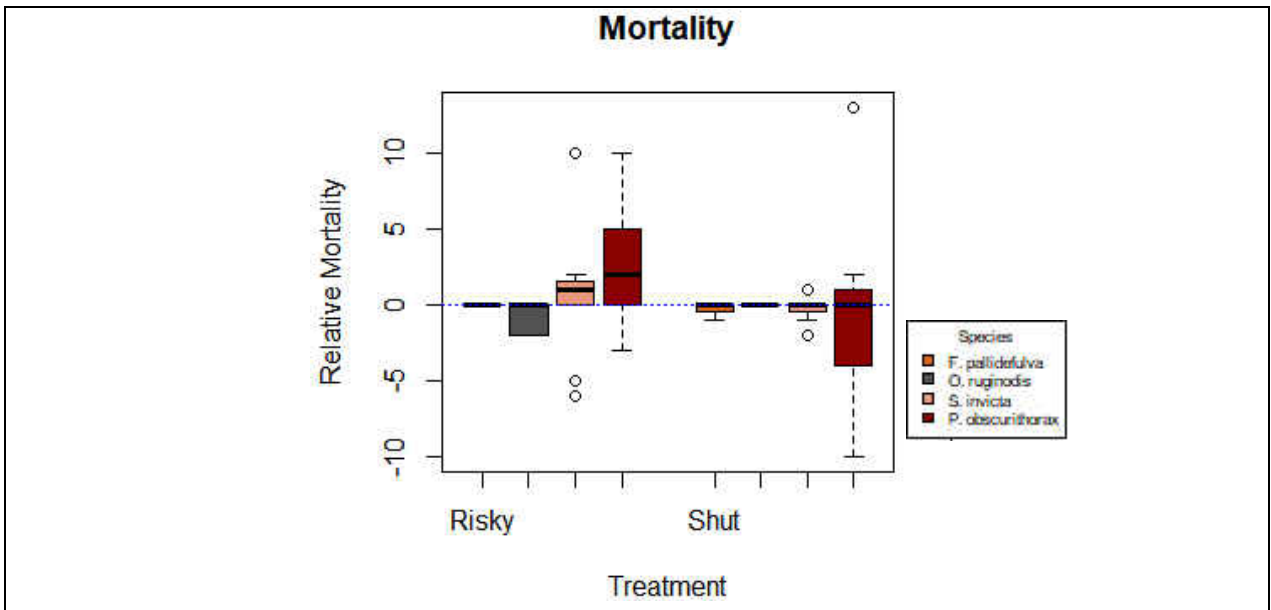


Figure 18: Relative mortality in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

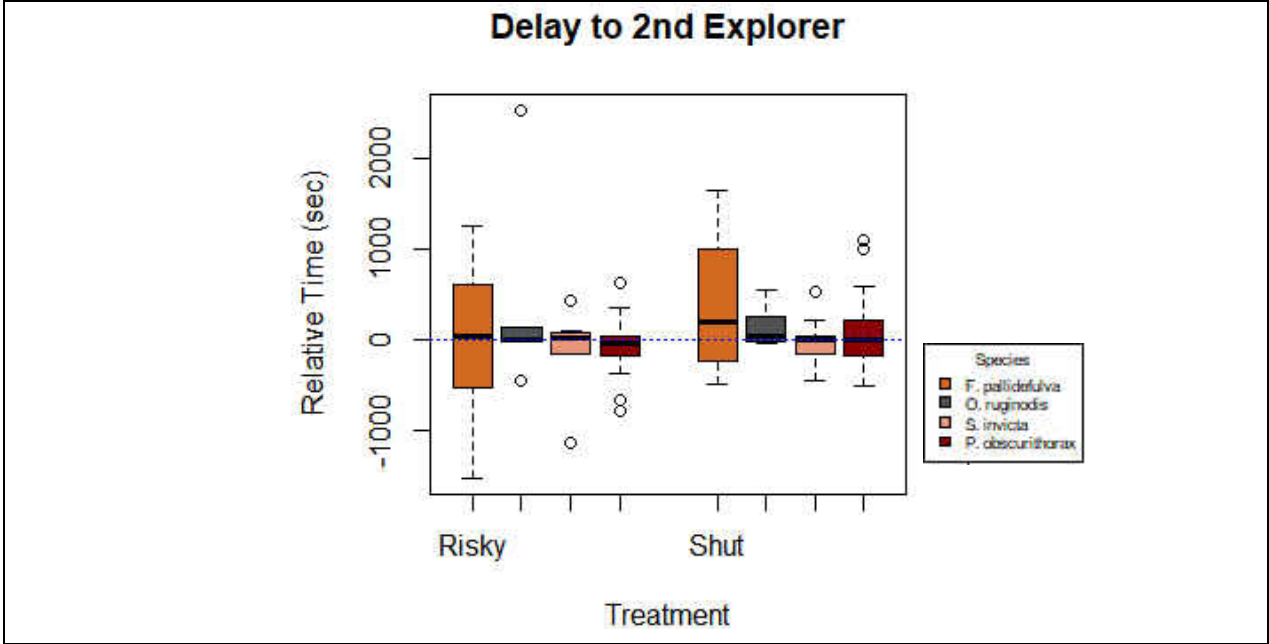


Figure 19: Relative delay to 2nd explorer in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

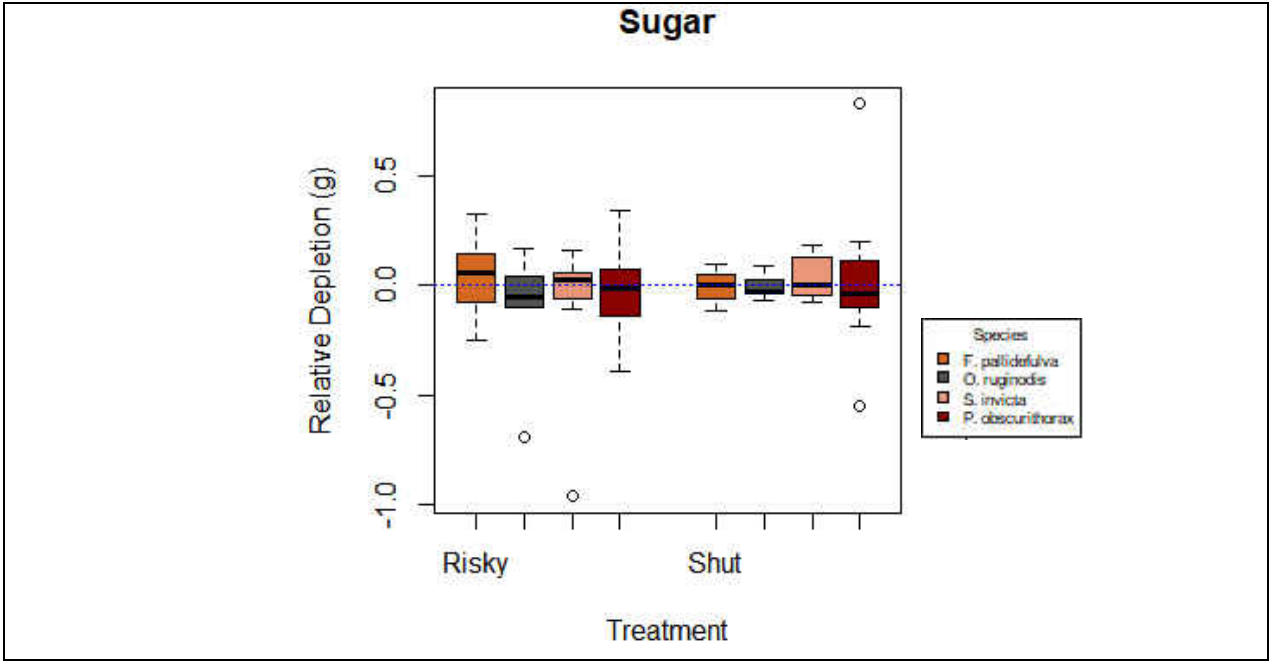


Figure 20: Relative depletion of sugar water in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

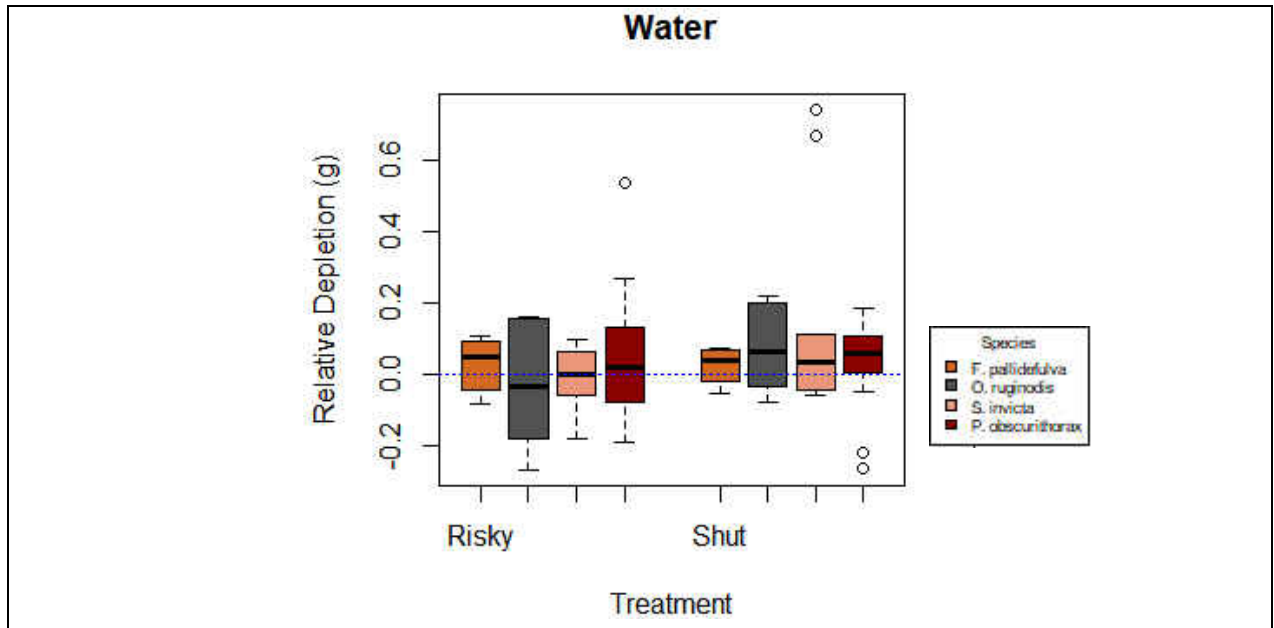


Figure 21: Relative depletion of water in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

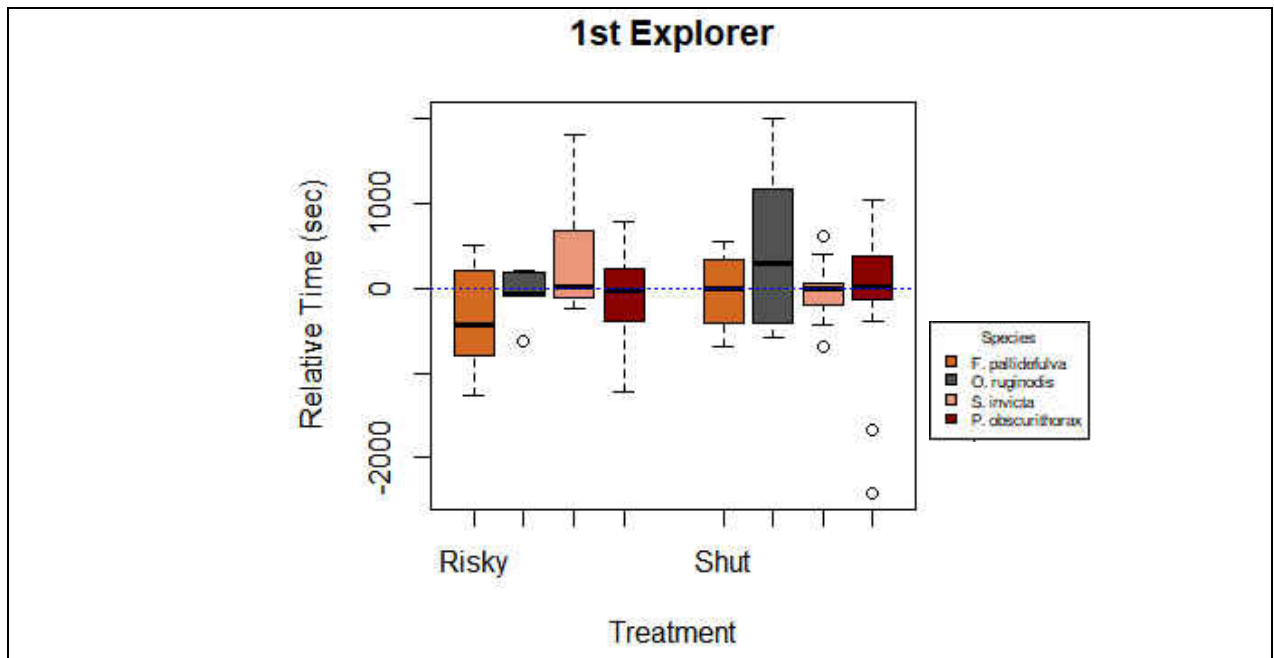


Figure 22: Relative time to 1st explorer in treatment arena by species. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

**APPENDIX H: ADDITIONAL GRAPHICAL REPRESENTATION OF
EXPERIMENT 2 DATA**

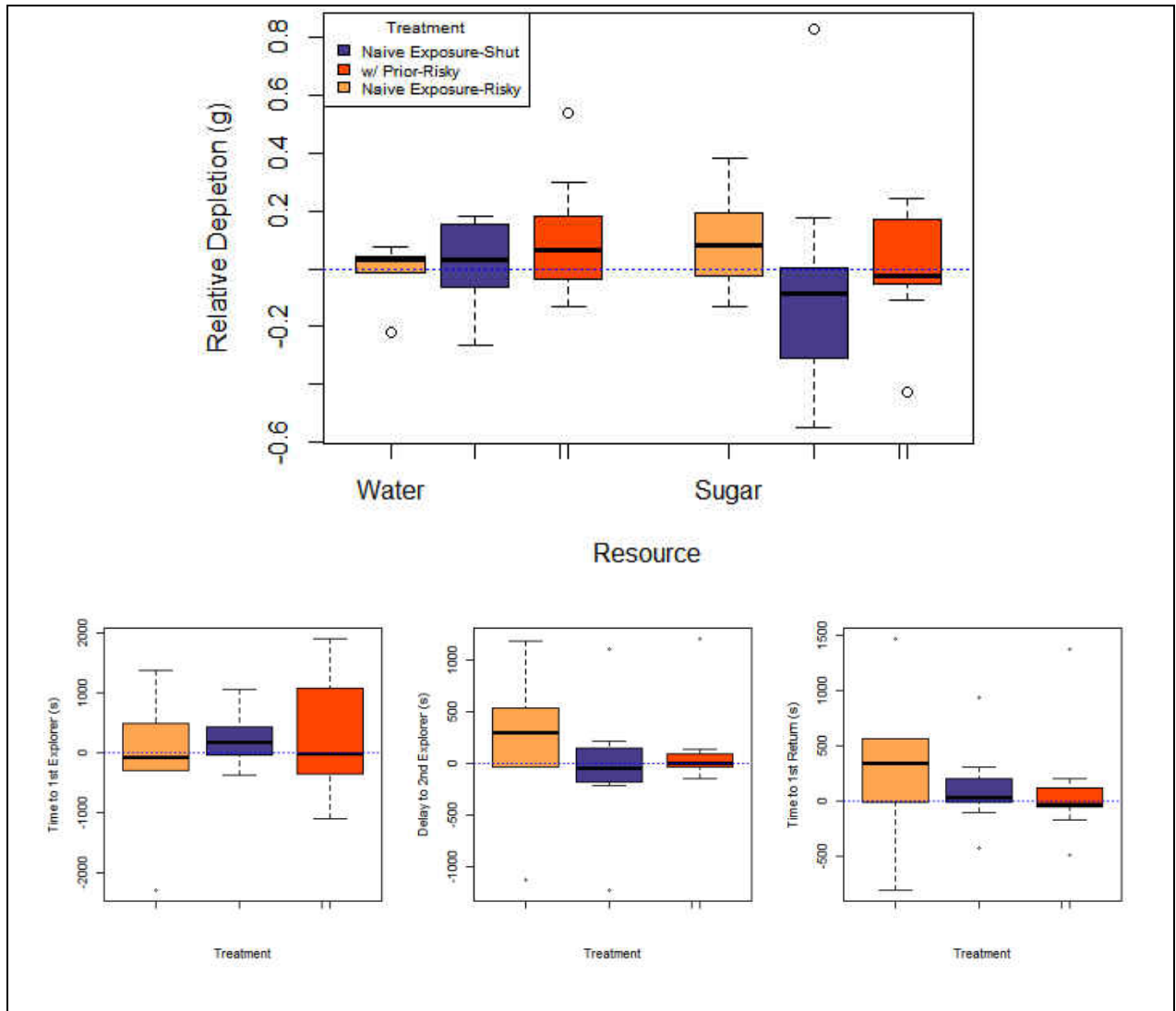


Figure 23: Boxplots of relative resource depletion (top), time to first explorer (bottom left), delay to second explorer (bottom center) and time to first return (bottom right) in experiment 2. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

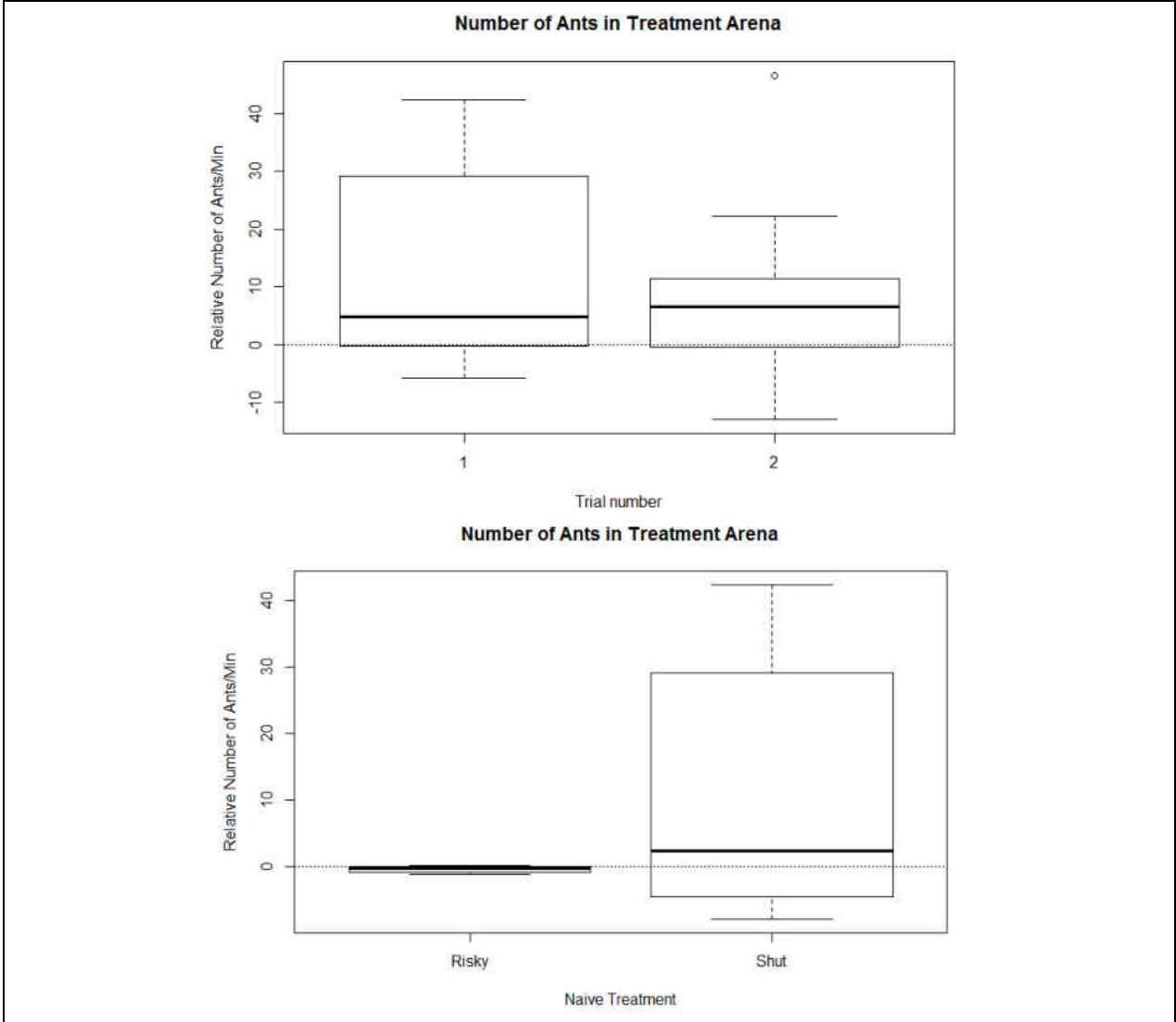


Figure 24: Boxplots of relative number of ants in treatment arena comparing naïve exposure to subsequent exposure (top) and comparing naïve exposure with a risky spider to naïve exposure with a shut spider (bottom) in experiment 2. None of these variables were different between treatment nor were they different from 0 ($p\text{-value} > 0.05$). Whiskers represent furthest point within 1.5x Interquartile range.

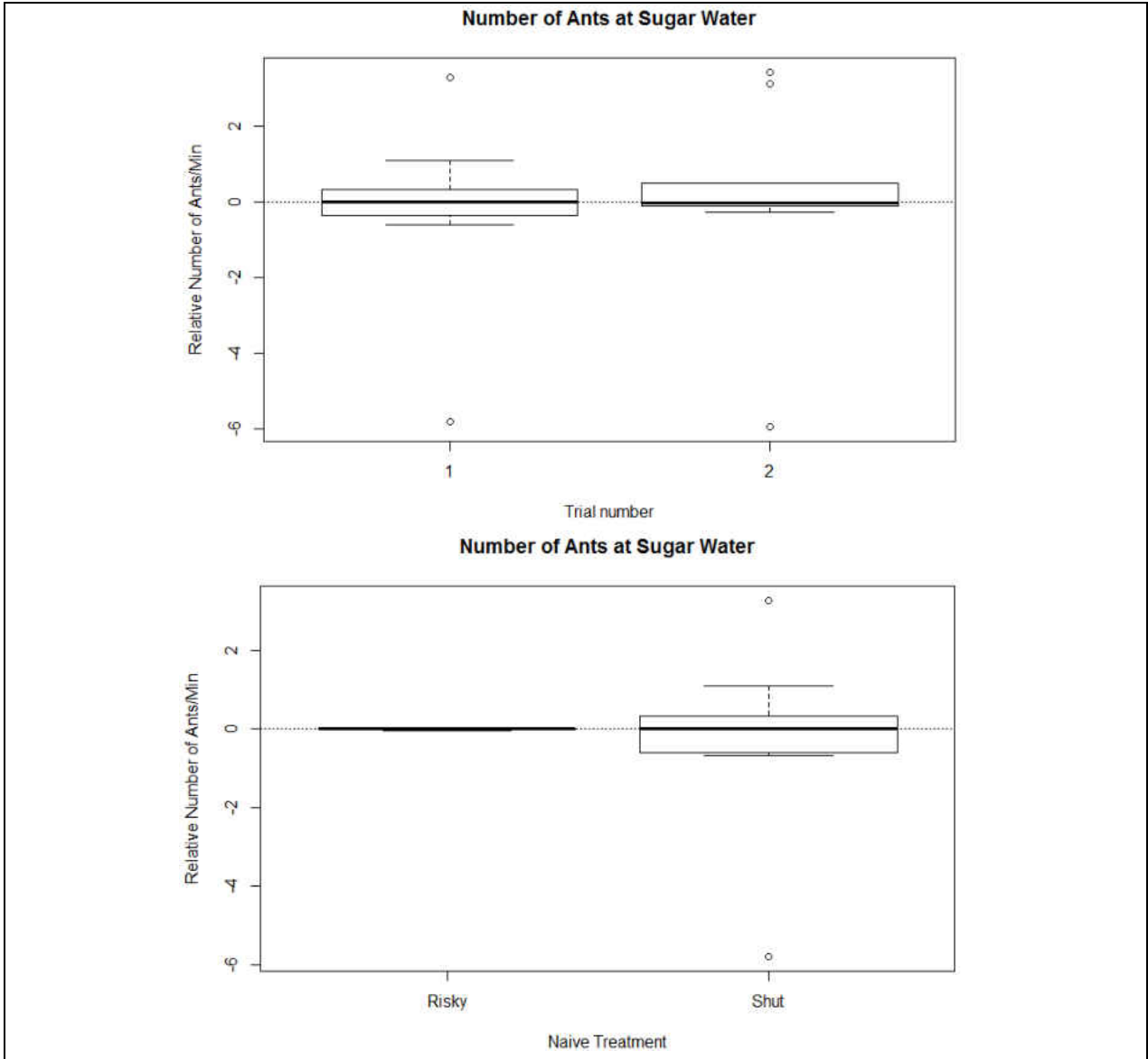


Figure 25: Boxplot of relative number of ants at sugar resources in treatment arena comparing naïve exposure to subsequent exposure (top) and comparing naïve exposure with a risky spider to naïve exposure with a shut spider (bottom) in experiment 2. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

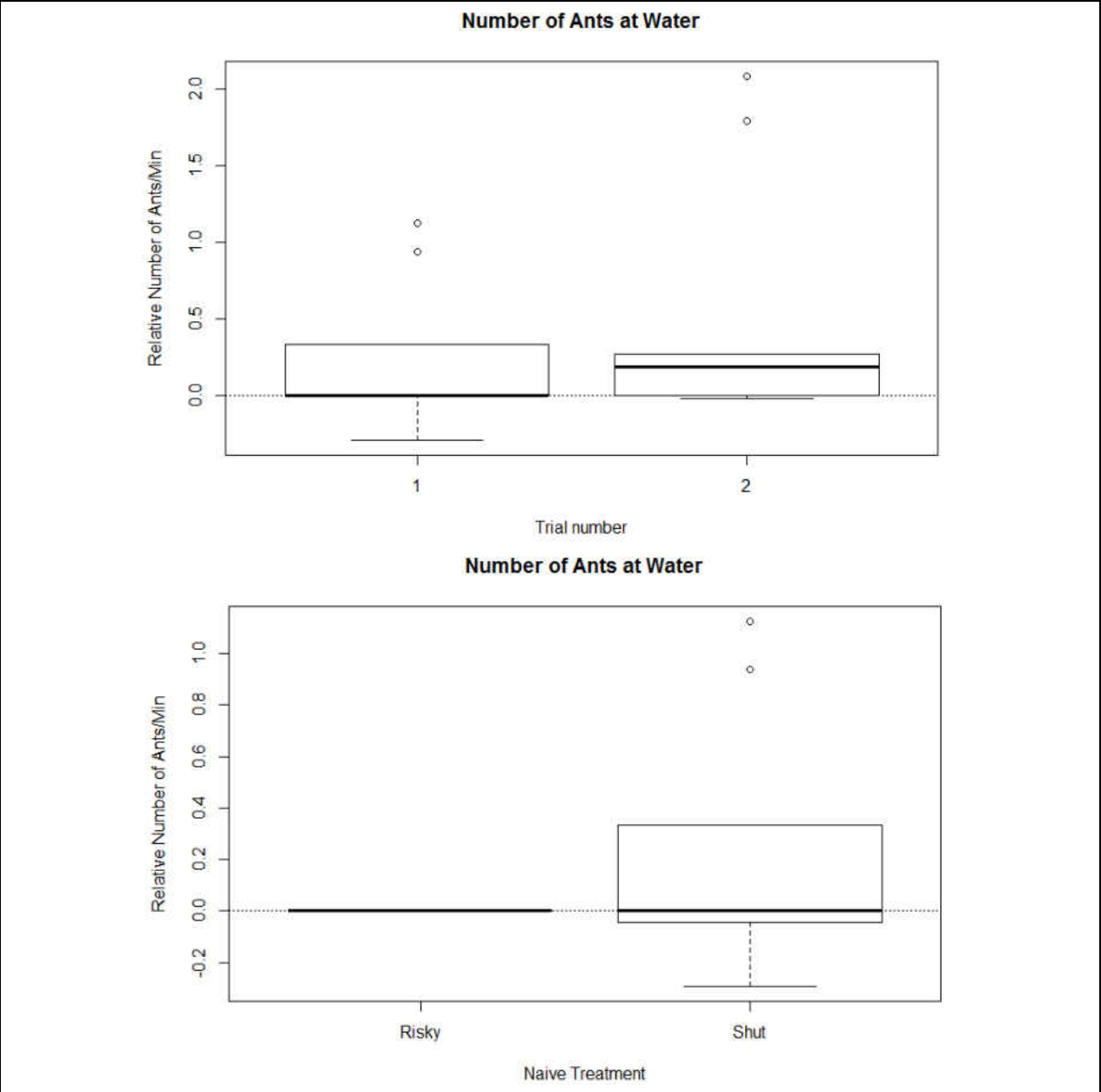


Figure 26: Boxplot of relative number of ants at water resources in treatment arena comparing naïve exposure to subsequent exposure (top) and comparing naïve exposure with a risky spider to naïve exposure with a shut spider (bottom) in experiment 2. None of these variables were different between treatment nor were they different from 0 (p -value > 0.05). Whiskers represent furthest point within 1.5x Interquartile range.

APPENDIX I: ANT SPECIES IN FIELD OBSERVATION

Table 13: Ant Species List from Field Observations. Highlighted rows were species used in laboratory experiments.

Species name	Total observed	Per day observation	Relative Abundance	% of all observed Feeding behavior (% of ant behavior)
<i>Brachymyrmex sp.</i>	3	0.1	0.014851	NA
<i>Cyphomyrmex rimosus</i>	43	1.433333	0.212871	9.6774% (21.4286 %)
<i>Camponotus sp.</i>	29	0.966667	0.143564	NA
<i>Crematogaster pinicola</i>	12	0.4	0.059406	NA
<i>Formica palidefulva</i>	3	0.1	0.014851	NA
<i>Nylanderia sp</i>	6	0.2	0.029703	NA
<i>Odontomachus ruginodis</i>	9	0.3	0.044554	NA
<i>Brachyponera chinensis</i>	1	0.033333	0.00495	NA
<i>Pheidole dentata</i>	1	0.033333	0.00495	NA
<i>Pheidole obscurithorax</i>	69	2.3	0.341584	6.4516 % (14.2857 %)
<i>Pheidole sp.</i>	8	0.266667	0.039604	3.2258 % (7.1429 %)
<i>Pseudomyrmex gracilis</i>	9	0.3	0.044554	NA
<i>Pseudomyrmex pallidus</i>	1	0.033333	0.00495	NA
Unknown	8	0.266667	0.039604	25.8065% (57.1429 %)

**APPENDIX J: PRIMARY COMPONENT ANALYSIS OF EXPERIMENT 1
DATA**

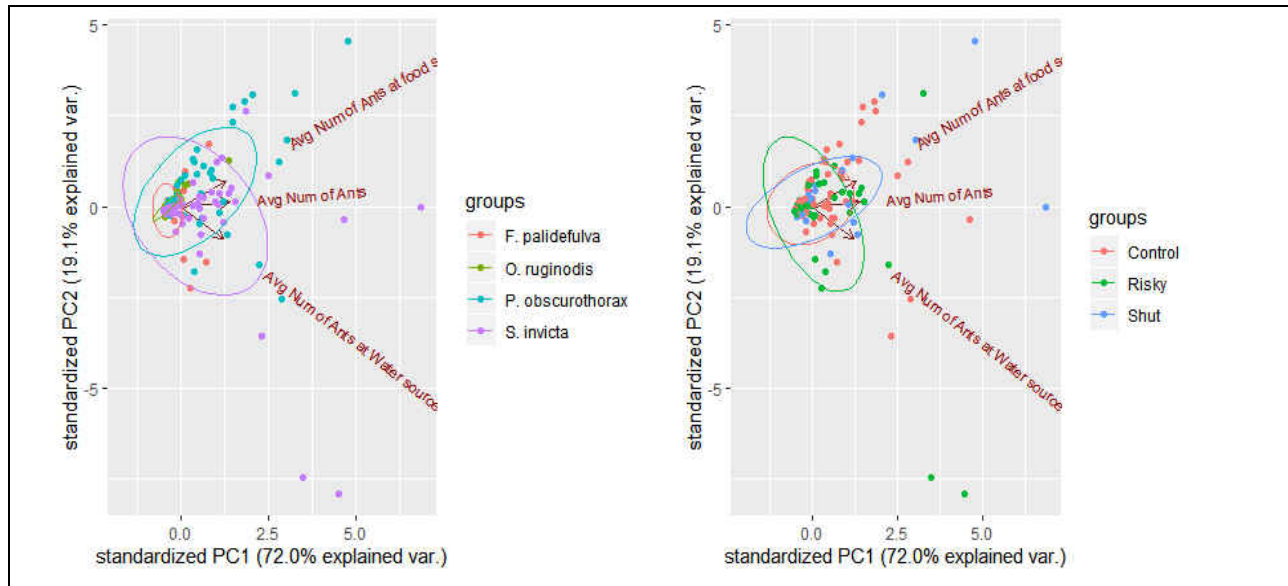


Figure 27: PCA of Raw Average Number of Ants/Minute by Species (Left) and by Treatment (Right). There was no evidence for differentiation of any group from the others.

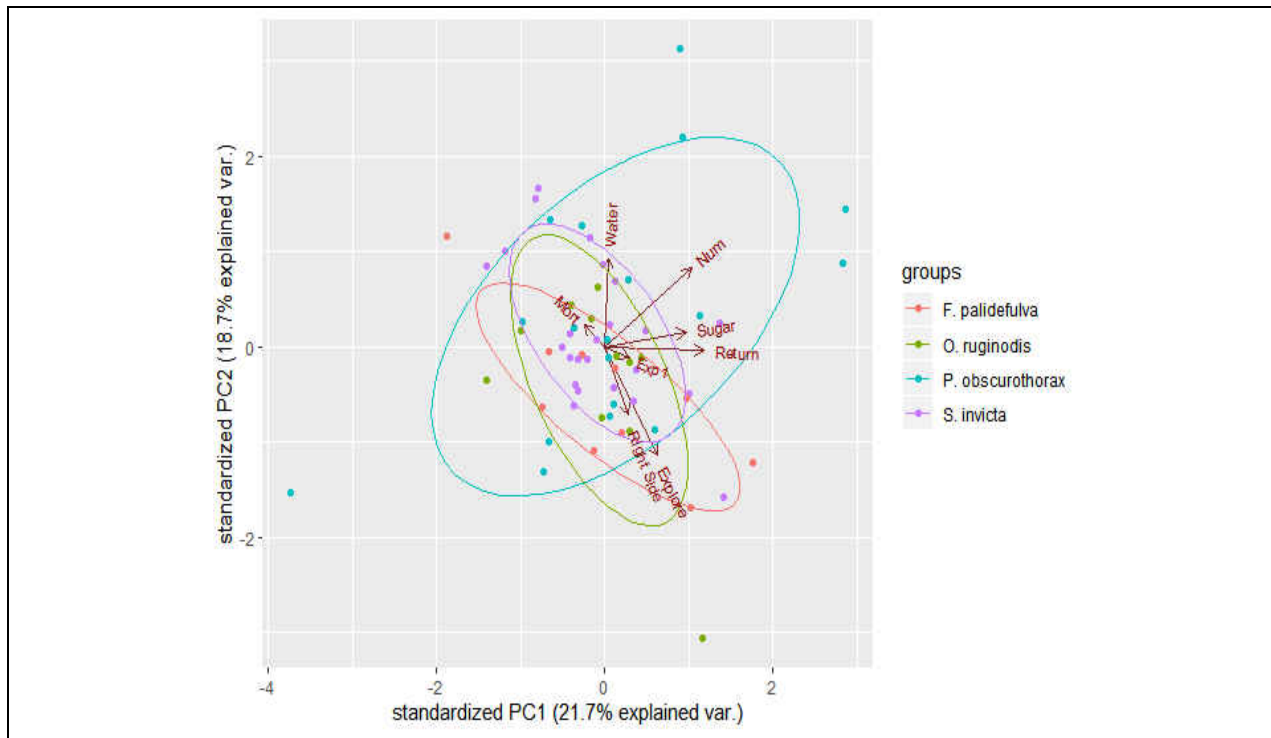


Figure 28: PCA of Transformed Data by Species. All Variables are relative to control arena. There was no evidence for differentiation of any group from the others.

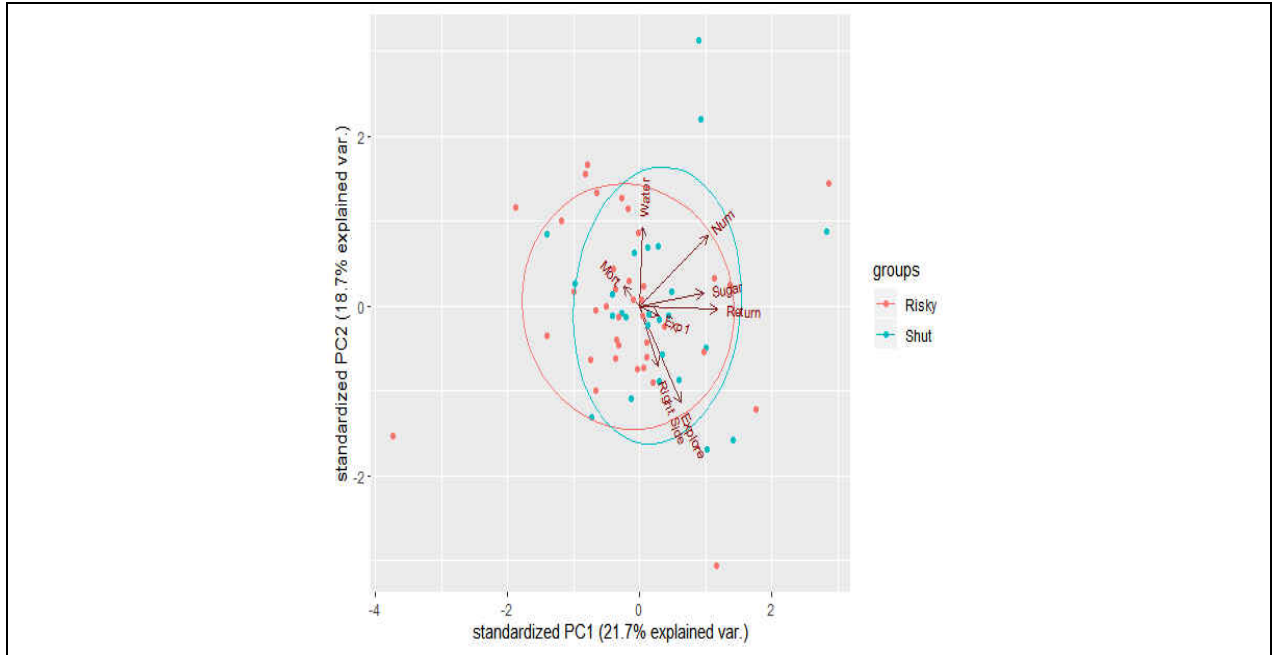


Figure 29: PCA of Transformed Data by Treatment. All Variables are relative to control arena. There was no evidence for differentiation of any group from the others.

For Figure 27 & 28: Num = Number of Scouts, Right side = 0 if left, 1 if right side, Sugar = depletion of sugar, Water = depletion of water, Mort = number dead, Return = delay to 1st return, Exp1 = time to 1st explorer, Explore = delay to 2nd explorer.

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