THE SPATIAL ECOLOGY OF THE COMANCHE HARVESTER ANT POGONOMYRMEX COMANCHE (HYMENOPTERA: FORMICIDAE)

by

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Presented to the Faculty of the Graduate School of
The University of Texas at Arlington in Partial Fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

THE UNIVERSITY OF TEXAS AT ARLINGTON
August 2015

Dedication

This work is respectfully dedicated to

Joe Kuban (1950 – 2009) and Tony Burgess

for the love of place.

Acknowledgements

My dissertation committee consisted of Dr. Esther Betrán (Supervising Professor), Drs. Jonathan Campbell, Paul Chippindale, Sophia Passy, and Walter Tschinkel (Florida State University), supervising committee members. I wish to thank them for their patience and guidance. I also want to thank Dr. Daniel Formanowicz, my original Supervising Professor, for input and feedback on this project as well as lab space and equipment and Dr. Raymond Jones, former manager of the Genomics Core Facility, for use of the dissecting microscope which was essential for ant identification.

I wish to thank Joshua Been and Mitch Stepanovich of the UTA library for assistance with the ArcGIS program and Dr. Colin MacLeod of GIS in Ecology (Scotland) for assistance with the ArcGIS program, spatial ecology methods and spatial analysis.

I wish to thank Dave General of the Museum of Natural History at the University of the Philippines, Dr. Robert Johnson of Arizona State University, Dr. Gail Kampmeier of the Illinois Natural History Survey, and Dr. James Trager of the Shaw Nature Reserve of the Missouri Botanical Garden for providing feedback on drafts of my proposal. I want to thank Dave General, Dr. Danny McDonald of Sam Houston State University, Dr. James Trager, and Chris Wilson of the University of North Texas for help with ant identification.

I wish to thank the city of Fort Worth Parks and Community Services Department and the staff of the Fort Worth Nature Center and Refuge in Fort Worth, Texas for access to the Fort Worth Nature Center and Refuge and the Tandy Hills Natural Area. I especially wish to thank the Staff of the Fort Worth Nature Center for assistance on site. I wish to thank the city of Arlington Parks and Recreation Department in Arlington, Texas for access to the Southwest Nature Preserve and sharing geological and historical information about this site.

I produced most of the maps using ArcGIS® software by Esri (Esri 2012). ArcGIS® and ArcMap™ are the intellectual property of Esri which I used under license, copyright © 2014 Esri, all rights reserved. (For more information about Esri® software, please visit www.esri.com.) I used their World Imagery Basemap in some maps.

I wish to thank Dr. Stephen W. Taber (Saginaw Valley State University) and Texas A & M Press for permission to use Dr. Taber's distribution map of *P. comanche* (Taber 1998).

Finally, I wish to express gratitude to my family and the many friends, both professional and personal, who kept me going.

I couldn't have done it without all of you. Thank you!

May 6, 2015

Abstract

THE SPATIAL ECOLOGY OF THE COMANCHE HARVESTER ANT POGONOMYRMEX COMANCHE (HYMENOPTERA: FORMICIDAE)

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Because of the diverse roles ants play, it has been suggested that ants may be ecosystem engineers and so, may be useful in monitoring ecosystem function and health. Because ant activities are localized around their nests, ant colony spatial patterns may have important ecological impacts on their own populations, other organisms and the environment. While some species in the harvester ant genus *Pogonomyrmex* are well studied, little is known about the Comanche harvester ant, *Pogonomyrmex comanche*.

The goal of this study was to characterize the spatial pattern of local populations of *P. comanche* and investigate possible influences on this pattern. The examination of its local distribution and factors that influence that distribution may contribute to understanding *P.comanche* biogeography, population biology, ecological relationships and because of their movement between prairie and wooded habitats, may contribute to understanding some of the ecosystem processes important in the Cross Timbers Ecoregion.

I hypothesized that the spatial pattern of *P. comanche* colonies is regular. Such a pattern implies the influence of competition and aggression among colonies as a driving force for population organization. I further hypothesized that the important influences on this spatial pattern include habitat characteristics, the presence of other ant species and colony interactions involving nestmate discrimination via aggression.

I assessed the colony spatial pattern by mapping colonies in five areas from 2009 – 2013 and analyzing the pattern with a spatial point process, Ripley's K function. To investigate habitat characteristics and other ant species, I assessed the ground active ant assemblage and environmental variables in 21 sites. I collected ants with pitfall traps in June, July, and August 2012 and measured environmental variables when the ants were collected. I calculated several diversity indices and used a redundancy analysis (RDA) to assess the differences in ant species among sites and ant response to environmental variables. Finally, I used a behavioral assay to test *P. comanche*'s ability to discern nestmates from non-nestmates in order to investigate aggression as a factor influencing the colony spatial pattern.

I found that *P. comanche* colonies are randomly distributed at spatial scales up to 50 m, the ant assemblage differs among sites, species diversity is higher in prairie habitats compared to wooded habitats and *P. comanche* does discriminate nestmates from non-nestmates. However, I found no evidence that aggression is a significant factor in colony location or spatial pattern.

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Chapter 1

Introduction

My original questions concerning the Comanche harvester ant, *Pogonomyrmex comanche* (hereafter, *P. comanche)*, arose from considerations of its basic biology and ecological role with respect to its spatial distribution. The overall goal of this project was to gather basic information about *P. comanche* adding to what is known about the genus *Pogonomyrmex* and specifically, to assess *P. comanche*'s colony spatial pattern and factors that influence this pattern at the population and local habitat levels. This project has important implications for understanding the local distributions of ground nesting ant species and central place animals generally as well as the biogeography of *P. comanche*, for investigating the connectivity between prairie and forest in the Cross Timbers Ecoregion, and for land management in the Fort Worth Nature Center and the Southwest Nature Preserve.

Animal Spatial Patterns

The distribution and abundance of animals create spatial patterns for population and community interactions which influence processes at all ecological levels (Andrewartha and Birch 1954; Blom et al. 1991; King et al. 1991; Stoner and Joern 2004; Eiserhardt et al. 2011). Such patterns and their connections are important in understanding species ecology, community structure, and ecosystem processes as well as patterns of biodiversity and biogeography (Wilson 1958b; Schumacher and Whitford 1976; Gilbert 1979; Crist and Wiens 1996; Schooley and Wiens 2003; Pringle et al. 2010; Silvestre et al. 2011). Animal spatial patterns play unique roles in ecosystems because most animals are mobile. Not only do animals move but they often have the potential to move items (food, other organisms, and nonliving items) within and among habitats, thereby, contributing to resource cycling among habitats. Animals that have a central place – a nest or den – produce such spatial patterns around these central locations.

Many of these central place animals are territorial, defending their nests, foraging and other areas (Hölldobler 1974; Hemmi and Zeil 2003; Fenner and Bull 2011). Because habitats are often heterogeneous, central place animals may experience competition for suitable nesting and foraging sites at the same time experiencing conspecific attraction for finding such suitable sites as well as mates (Stamps 1988). The distributions of these animals are influenced by the environmental spatial structure important for appropriate nesting sites including soil characteristics for burrowing organisms (Meadows and Meadows 1991) and horizontal and vertical vegetation structure for bird and other species (Martin 1988). Other influences include the spatial and temporal pattern of food resources (Martin 1988), the need to avoid predators who may recognize nest structures, and both the attraction and repulsion of conspecifics –attraction for mates and extra pairings (Velando and Freire 2001), for habitat selection (Stamps1988; Kiester 1979; Muller et al. 1997) or to reduce predation (Martin 1988; Velando and Freire 2001) and repulsion to reduce competition (Fisher et al. 2007). The spatial pattern of central place animals often modifies the environment affecting the spatial pattern of other organisms and structuring the ecosystem (Meadows 1991). Such animals are called ecosystem engineers (Bangert and Slobodchikoff 2000; Schooley et al. 2000). These patterns can be quite complicated with patterns within patterns. Jovani and Tella (2007) showed that a distribution of pattern of stork nests consisted of clusters of nests that in turn were clustered involving three spatial scales. Ants as similar central place animals are subject to the same concerns and influences in their distribution patterns.

Ants are nearly ubiquitous in terrestrial environments (Hölldobler and Wilson 1990; Moffett 2010) and play important and diverse roles in communities and ecosystems, including as prey and predators, in symbioses and mutualisms, as recyclers especially important for soil formation and health, and as pest and invasive species (Baxter and Hole 1967; Hölldobler and Wilson 1990; Carlson and Whitford 1991; Brown and Human 1997; Folgarait 1998; Lesica ad Kannowski 1998; Dostal et al. 2005; Bos et al. 2008). Though ants and their activities are often inconspicuous, these species are sometimes considered ecosystem engineers (Eldridge 1993; Jones et al. 1994; Lawton 1994; Lei 2000; MacMahon et al. 2000; Gove et al. 2007) whose distribution patterns may be especially important ecologically. Thus, an evaluation of the spatial organization of ant populations may yield information that is ecologically informative concerning other species and ecosystem function and health as well as useful in land assessments and management (Peck et al. 1998; New 2000; Andersen et al. 2004; Underwood and Fisher 2006; Kilpeläinen et al. 2008).

There are several abiotic and biotic factors that may influence the location, distribution, and density of ground-nesting ant species. On the local spatial scale, both colony distribution within a habitat and population distribution within a region may be considered. Important abiotic habitat variables, such as soil type and structure, may directly influence nest construction (Levings and Traniello 1980; Sudd and Franks 1987; Dean et al. 1997; Catangui et al. 1996; Johnson 1992; Johnson 2001; Ríos-Casanova et al. 2006). Colony spatial patterns may also be affected by biotic factors including queen dispersal and recruitment (Wiernasz and Cole 1995; Cole and Wiernasz, 2002; Johnson 2006), food resource distribution and abundance (Cerdá and Retana 1994), inter- and intra-specific interactions among colonies (Brian et al. 1966; Bernstein and Gobbel 1979; Cushman et. al. 1988), and predation (Crist and Wiens 1996; Johnson 2001; Azcárate and Peco 2002; Johnson 2006; Wiens 2011). The resulting distribution and activity patterns may affect ant population dynamics in ways similar to the spatial patterns of individuals of more solitary animal species (Hölldobler and Wilson 2009) but may require different mechanisms for such common problems as finding mates and resource competition. The location and density of ant nests also creates a spatial structure in which interactions and impacts on habitat are localized (Folgarait 1998; Whiles 2006; Kilpeläinen et al. 2008; Pisani 2009). While these biotic factors may vary in their significance, mated queen dispersal patterns and inter-colonial interactions potentially always influence colony spatial patterns.

Because most ant species are ground nesting and store food resources, their tolerance range for climate may be broad while locally colonies may be more restricted by nest site characteristics, including soil type, shading, and topography (Ricklefs 1987). Appropriate nesting sites are a function of environmental factors derived from climate and plant effects (temperature and drainage) and characteristics of the nesting material in the structural formation of a nest, the maintenance of which provides a hospitable environment for food storage, rearing young, and housing adults.

Species-specific patterns of colony founding and the distance that mated queens disperse define the initial colony distribution pattern which may subsequently be altered by direct and indirect interactions among conspecific colonies. Few studies have directly considered the mated queen dispersal patterns and behaviors, although tools to study these patterns using microsatellites, nuclear DNA and mitochondrial DNA are now being used to address questions of population structure and genetic relatedness among colonies (Chapuisat et al. 1997; Goodisman and Ross 1998; DeHeer et al. 1999; Foitzik and Herbers 2001; Liautard and Keller 2001; Berghoff et al. 2008). Except for a consideration of inbreeding in an ant lek-mating species, *Pogonomyrmex occidentalis* (Cole and Wiernasz 1997), most studies have only partly addressed questions of mated queen dispersal patterns and make little clear connection to such dispersion from a mating lek.

Once a population is established, interactions among spatially-related colonies create neighborhoods and may influence nest distribution patterns especially contributing to regularity (Ryti and Case 1992; Crist and Wiens 1996; Gordon and Kulig 1996; Schooley and Wiens 2003). Intraspecific and interspecific competition among ant species has long been suggested as the primary factor organizing ant populations and communities behaviorally, temporally and spatially (Whitford and Ettershank 1975; Hölldobler and Wilson 1990; Johnson 2000; Albrecht and Gotelli 2001; Gotelli and Ellison 2002; Schooley and Wiens 2003; Dillier and Wehner 2004; Lach et al. 2010). Intraspecific competition is often thought to have a stronger effect arising from limitations of the shared niche (Howe and Estabrook 1977; Levings and Franks 1982; Connell 1983; Johnson 2001). Such intraspecific competition is potentially expressed through discrimination between nestmates and non-nestmates with non-nestmate encounters eliciting aggressive behavioral responses. These behaviors may include threatening displays, harassment, fighting, and death and may involve individual ants, groups, or whole colonies. Competition, therefore, has been hypothesized to produce a regular colony distribution pattern with the nest and associated areas aggressively defended (Bernstein and Gobbel 1979). It has been claimed that such regularity is typical of ants generally and of the genus *Pogonomyrmex* in particular (Bernstein and Gobbel 1979; Kugler and Hincapié 1983). Conversely, such regularity has been interpreted as evidence for neighborhood interactions in general (Crist and Wiens 1996; Ryti 1991; Schooley and Wiens 2003; and Wartburg and Steinberger 1997) and specifically for competition (Bernstein 1975; Bernstein and Gobbel 1979; Cushman et al. 1988; Harrison and Gentry 1981; Kugler and Hincapié 1983; Levings and Franks 1982; Ryti and Case 1984, 1986, and 1988; Wiernasz and Cole 1995). However, random, clustered, and regular distribution patterns have been found and some species exhibit more than one pattern (Whitford et al. 1976; Bernstein and Gobbel 1979; Crist and Wiens 1996; Heinze et al. 1996; Wartburg and Steiner 1997; Keene and Dejean 1999; Schooley and Wiens 2003; de Albuquerque et al. 2005; Kilpeläinen et al. 2008). Ryti (1991) suggested that nest density in the landscape may have a significant impact on colony distribution patterns with increasing numbers of nests producing greater spatial regularity (Cushman et al. 1988). Despite the initial consideration of competition as the most influential factor in spatial structuring of ant populations, other factors are now considered potentially as or more influential, such as mated queen dispersal behaviors (Wiernasz and Cole 1995; Johnson 2006). Patterns of colony distribution and the factors which influence them remain poorly understood due to inconsistencies in assessing colony spatial structure; the limited number of species, habitats, and other variables considered; and assumptions about the roles of aggression and competition.

Seed Harvesting Ants of the Genus *Pogonomyrmex*

Pogonomyrmex species are prevalent in hot, arid regions of grasslands and desert where they are important seed predators (Brown et al. 1979b; Hölldobler and Wilson 1990; Johnson 2000) although some species are found in more moist and montane habitats. Colonies of these species are monogynous, founded by a single queen whose lifespan may be 15 to 50 years (Porter and Jorgensen 1988; MacMahon et al. 2000). Population densities of 20 to 150 colonies per hectare (MacMahon et al. 2000) are not unusual. Some species in the genus, especially *Pogonomyrmex barbatus* (hereafter, *P. barbatus*) and *P. occidentalis*, have been well studied.

Pogonomyrmex ants are ground nesting ants and are typically monodomous with stable nest locations. These nests are often conspicuous and may dominate the landscape (Crist and Wiens 1996). Surface nest diameters are on the order of 0.5 to 2 m and may reach 5.5 m (Schmidt et al. 1986; MacMahon et al. 2000). Nests consist of an internal architecture of tunnels and chambers that house the queen, offspring, seed caches, workers, alates, and various parasites and myrmecophiles (mutualists and commensals; Hendricks and Hendricks 1999; Snyder and Friese 2001). Casts of the internal nest structure of *P. badius* indicate a series of chambers immediately below the soil surface, with tunnels extending downwards, branching off to more chambers (Tschinkel 2003; Tschinkel 2004). The internal nest structure organizes the colony activities vertically. This internal structure can be quite extensive, resulting in the removal and turnover of large amounts of soil (Briese 1982). Though some species entirely lack any external form, there are three typical, external nest forms that are species specific: a flattened disk covered with small pebbles, a flattened disk covered with pebbles and a tall cone of pebbles, or a crater with a central entrance (Dr. Robert Johnson, Arizona State University, personal communication). The species differ in the type of soil in which they nest, some preferring clay-rich soils (generally, the Barbatus and Occidentalis complexes) while others prefer sandy soils (the Californicus complex; Johnson 1992; Johnson 2006). Soil preference may reflect a preference for construction material as well as moisture requirements (Johnson 2000; Johnson 2001; Johnson 2006).

The construction of nests and foraging activities of *Pogonomyrmex* ants may significantly impact other organisms and the environment and some researchers have proposed these ants as keystone species or habitat engineers (Hölldobler and Wilson 1990). In particular nesting activities allow gas and water penetration into the soil (Baxter 1967; Eldridge 1993; Lei 2000; Cox and Blanchard 2000), alter the temperature in the proximity of the nests (Bucy and Breed 2006); concentrate nutrients and minerals (Carlson 1991; Briese 1992; Lei 2000; Nikem et al. 2000; Bardgett and Wardle 2010); and increase the biodiversity of soil organisms in the vicinity of the nest (Snyder and Friese 2001; Nardi 2007; Pinto-Tomás et al. 2009; Bardgett and Wardle 2010; Pirk et al. 2014). *Pogonomyrmex* ants may also have significant direct effects on other organisms, particularly plants. Through the removal of plants from the external nest area, seed harvesting activities, and the deposition of seeds in caches and middens, these ants may influence spatial patterns and recruitment of individual species and thereby, interspecific interactions and the overall plant community (Brown et al. 1979b; Reichman 1979; O'Dowd and Hay 1980; Hobbs 1985; Rissing 1988; Carlson 1991; Crist and MacMahon 1992; Brown and Human 1997; Dean et al. 1997; Guo et al. 1998; Kerley and Whitford 2000; Lei 1999; Mull 2003; Dostal et al. 2005; Bucy and Breed 2006; MacGown et al. 2008; Barton et al. 2009; Bardgett and Wardle 2010; Pirk et al. 2014). They may also compete with other granivorous animals, especially rodents (Brown et al. 1975; Brown et al. 1979b). Through their nesting activities, ants cause local disturbance, which may influence other populations and community diversity (Elmes 1991; Schooley et al. 2000).

To date, the most studied *Pogonomyrmex* species have been desert dwelling and they use trunk trail foraging strategies (De Vita 1979). Kugler and Hincapié (1983) called for ecological studies on less conspicuous *Pogonomyrmex* species and in their ecological review of the genus, MacMahon et al. (2000) called for studies of *Pogonomyrmex* species in different habitats. In his biogeographic review of the genus, Johnson (2001) discusses the pattern of species replacement across regions but is unable to provide references to published information for several species including *P. comanche*. An investigation of the biology and ecology of *P. comanche* would contribute to a fuller understanding of the influences on ant colony spatial patterns and the ecology and biogeography of this genus.

Pogonomyrmex comanche

P. comanche was first described by Wheeler (1902, 1914) but later subsumed into *P. occidentalis* only to be reinstated at the species level in 1934 by Olsen. Some disagreement over the status of *P. comanche* continued until Cole's work on the genus in North America (Cole 1968). *P. comanche* is part of the Californicus complex which includes *P. anzensis*, *P. badius*, *P. californicus*, *P. magnacanthus*, *P. maricopa* and perhaps two other undescribed species (Taber 1990). *P. comanche* nests in deep, very fine-grained sandy soils in prairies which form a habitat mosaic with oak forest (Cole 1968). This species is currently found in Arkansas, Kansas, Louisiana, Oklahoma, and Texas, where it persists especially in electrical power line and other right-of-ways (Figure 1.1; Dr. John Moser, United States Forest Service Southern Research Station, Shreveport, Louisiana, personal communication; A.B.M., personal observation). These areas in Kansas, Oklahoma, Texas, and perhaps some parts of Arkansas are part of the Cross Timbers or Post Oak Savannah Ecoregion (Dyksterhuis 1948). Because of the infrequent occurrence of deep sandy soiled prairies within this prairie-oak mosaic, *P. comanche* has a discontinuous regional distribution (Wheeler 1914; Cole 1968). The external nest form is described as a crater with a single, central entrance (Cole 1968). These ants are active during the day and forage primarily on forb and grass seeds (80% of their diet, A. B. M., unpublished data). Other than a brief note on a mating flight in Waco, Texas by Strandtmann (1941) and identification keys for the genus (Cole 1968; Taber 1998), little published information is available concerning this species.

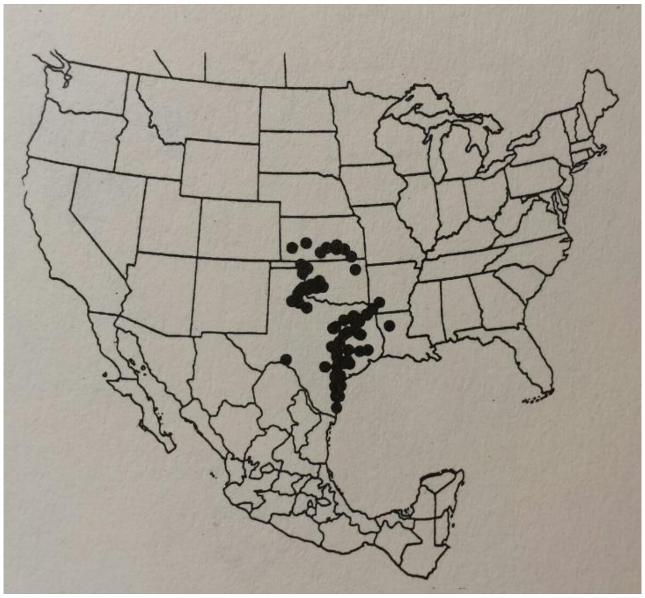


Figure 1.1 Current known range of *P. comanche* (Taber 1998; used with permission)

The goal of this study was to characterize the colony spatial pattern of local populations of *P. comanche* and investigate possible influences on this pattern. The examination of its local distribution and of the factors that influence that distribution is important in understanding *P. comanche* biogeography, gene flow among disjoint populations, ecological relationship to other species, its niche in the tall grass prairie, and may contribute to understanding some of the ecosystem processes important in the habitat mosaic of the Cross Timbers Ecoregion (Crist and Wiens 1996; Mayo 2015).

Hypotheses to Test

I hypothesized that the spatial pattern of *P. comanche* colonies within a population is dispersed, that is, colonies are spaced more regularly than expected. Such a pattern is hypothesized to result in less dense spatial structure in species with individual foraging strategies, as seen in *Pogonomyrmex maricopa* (hereafter, *P.*

maricopa), and implies the influence of competition and aggression among colonies as a driving force for population organization (Hölldobler 1974; Hölldobler 1976). I further hypothesized that the important influences on *P. comanche* spatial patterns include habitat heterogeneity, the presence of other ant species, and colony interactions involving nestmate discrimination via aggression. The null hypotheses tested were:

H_{01}: *P. comanche* colonies are randomly distributed within the landscape.

H_{02}: The ant assemblages (communities) do not differ among local habitats.

H_{03}: The presence of *P. comanche* has no impact on ant species occurrence and abundance.

H_{04}: *P. comanche* does not distinguish nestmates from non-nestmates with an aggressive response.

H_{05}: Any aggressive interaction is equally likely among *P. comanche* ants and colonies, irrespective of distance between interacting colonies.

Study Site Description

P. comanche is found in five prairies at the Fort Worth Nature Center (hereafter, FWNC) in Fort Worth and in the Glen Rose Yucca Prairie (hereafter, SP) and two trails at the Southwest Nature Preserve (hereafter, SWNP) in Arlington, Texas. These prairies are in the Post Oak Savannah or Cross Timbers Ecoregion (hereafter, Cross Timbers Ecoregion; Dyksterhuis 1948; Francaviglia 2000). While not entirely restricted to the Cross Timbers Ecoregion, *P. comanche* has only been found in this kind of habitat mosaic of prairie and oak forest which is typical of the region. The characteristics of this mosaic emphasize the climatic transition between the more mesic forests of the eastern United States and the drier prairies of the American Southwest. Historically, this mosaic was probably maintained by natural disturbance including fire, wind felling of trees, and the activity of large mammals especially bison and antelope. Human control of these areas has virtually eliminated such disturbance. On a local scale, however, the persistence of these prairies may be influenced by feral hogs and the nesting activities of *Pogonomyrmex* and other ant species (Dean et al. 1993) as well as mowing of right-of-ways, pasture and other human land use (Dr. John Moser, United States Forest Service Southern Research Station, Shreveport, Louisiana, personal communication; A.B.M., personal observation). The property of both the FWNC and the SWNP was pasture before becoming public land; currently, these areas lack any management plan. In the absence of natural disturbance, *P. comanche* colonies appear to persist in areas subject to human disturbance such as mowing for right-of-ways, hay fields, and recreational areas. Interestingly, *P. comanche* may not be particularly adversely affected by the mowing and other vehicles which churn up the prairie.

Plant Community

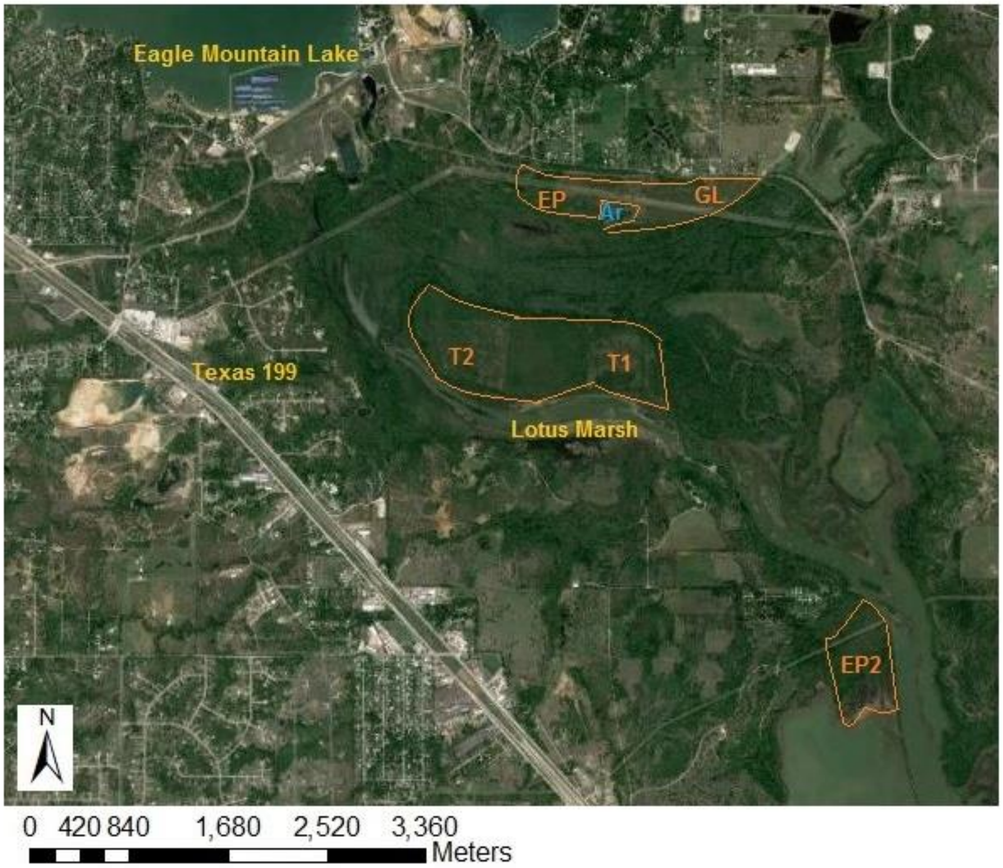
The expected, dominant plants in this prairie system are grasses, especially various grama species (*Bouteloua* spp.) and Texas Stipa (*Stipa leucotricha*; Smith, 1940; Dyksterhuis 1948). While these prairies are dominated by grasses, bull nettle (*Cnidoscolus texanus*), snake cotton (*Froelichia floridana*), sandbur (*Cenchrus* spp.), and prickly pear cactus (*Opuntia* spp.) have a significant presence indicating disturbance, especially overgrazing. This plant community has been described as a disclimax rather than prairie climax community because of the historical importance of disturbance. Wild grape (*Vitis mustangensis*) only occurs at the electrical power-line sites (EP sites in the Fort Worth Nature Center) and Mexican plum (*Prunus mexicana*) only occurs in the Todd Island sites (T1 and T2 sites in the FWNC) and SP in the SWNP where it grows in a single clump rather than throughout these sites. The surrounding woodland is dominated by post oak (*Quercus stellata*), black jack oak (*Q. marilandica*), American elm (*Ulmus* *americana*) and cedar elm (*U. crassifolia*). Light gaps within the woodland are dominated by inland sea oats (*Chasmanthium latifolium*). No *P. comanche* nests are found in the forested areas or light gaps, although *P. comanche* does forage into the woodland for elm seeds (A.B.M., personal observation).

Fort Worth Nature Center Sites (FWNC)

In the FWNC, *P. comanche* nests are found in the Aquilla Sand Formation which has soil particle sizes of 125 – 250 μm and was formed from alluvial sediments with a limestone base (Ressel 1981). There are six prairies on the Aquilla Sand Formation in the FWNC: electrical power line right of way (EP), gas line right of way (GL), a small prairie located on the dirt road that connects EP and GL, Todd Island 1 (T1) and Todd Island 2 (T2), and a second electrical power line right of way (EP2; Figure 1.2). All of these prairies have *P. comanche* colonies except EP2.

The Todd Island prairies were used as pasture until the late 1970s when the land was obtained by the city of Fort Worth (Suzanne Tuttle, Manager of the FWNC, personal communication). Since that time they have not been managed. These areas are fragmented by oak motts consisting of post and black jack oaks. These prairies are surrounded by oak forest which is also on the Aquilla Sand Formation. Some areas within these prairies are dominated by prickly pear cactus (*Opuntia* spp.) rather than grasses. The T1 and T2 prairies have areas of 17.7 ha and 20.0 ha respectively and are separated by 0.5 ha of post-oak forest (T1 lies to the east of T2; Figure 1.2).

Three of the other prairies are connected by a dirt road: an electrical power line right of way (EP) a gas line right of way (GL) with areas of 37.8 ha and 10.0 ha, respectively, and located between these two, a small prairie of 0.894 ha totaling 48.694 ha. Nests of *P. comanche* are found in these prairies as well as in the dirt road. These areas are bounded by post-oak forest also on the Aquilla Sand Formation along the longer sides and prairie of other soil types along the shorter sides. There is a small region of Arents (frequently flooded) soil (related to gravel and sand mining operations) that extends into part of the EP site (noted on the map, Figure 1.2; Ressel 1981). Although the EP site is bounded on its eastern edge by Pulexas Fine Sandy Loam, another well-drained sandy soil, I have not found any *P. comanche* colonies there, including no foundress queens or new colonies. These prairies are separated from the T1 and T2 by 0.08 ha of post-oak forest that is on the Aquilla Sand Formation. The electrical power line right of way 2 (EP2) is located to the south of the other prairies and although it has 0.822 ha of Aquilla Sand Formation, it has no *P. comanche* colonies. The right-of-ways were established prior to the 1960s and are irregularly mowed and disturbed by heavy vehicular traffic so mott development and woody growth are restricted. Due to this human activity, these areas are not further fragmented by oak motts.



World Imagery Basemap source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

Figure 1.2 Map of the FWNC, showing the Aquilla Formation Sites

Southwest Nature Preserve Site (SWNP)

In the SWNP, *P. comanche* colonies are found in SP. The soil in SWNP is the Woodbine Formation of the Birome Soil Series (a mixture of Birome-Aubrey-Urban land complex) with the Crosstell-Urban land complex in SP. These soils are intricately mixed and difficult to map (Ressel 1981). In SP the soil is characterized by a fine sand surface layers with some iron-rich clay and shale and clay horizons below and is considered well-drained (Ressel 1981). This prairie is 0.09 ha in area and was once a pasture but has no oak motts. The northern edge of the prairie appears to be moister with thicker grass and forb vegetation and a stand of Mexican plum (*Prunus mexicana*). No *P. comanche* nests in were found in this area. The prairie is bounded on three sides by post-oak forest and one side by a different soil type. The abundance of sand burr (*Cenchrus echinatus*) indicates that it is a disturbed site. There are a few *P. comanche* colonies in the trail that runs along the western edge of this prairie. A few more colonies are found in another trail farther southwest of SP.

World Imagery Basemap source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, IGN, IGP, swisstopo, and the GIS User Community.

Figure 1.3 Map of the SWNP

SP indicates the Glen Rose Yucca Meadow

Tandy Hills Natural Area (THNA)

The Tandy Hills (THP) and Stradford (STP) Prairies are located in the Tandy Hills Natural Area on the eastern side of Fort Worth, between View Street and I-30 (I-30 is North of View Street). These prairies are separated by 200 m of oak forest and prairie. The soil is the Aledo-Urban complex, a mixture of calcerous soils characterized by clay but is considered well drained (Ressel 1981). There are no *P. comanche* nests in these prairies. These prairies were included in the survey of ground active ants (Chapter 3) to increase the types of prairie sampled and the total number of samples.

World Imagery Basemap source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, AEX, Getmapping, IGN, IGP, swisstopo, and the GIS User Community

Figure 1.4 Map of the Tandy Hills (THP) and Stradford (STP) Prairies in the THNA. No *P. comanche* nest in these prairies.

Chapter 2

The Spatial Pattern of *P. comanche* Colonies

Introduction

Previous studies of ant colony spatial patterns have uncovered an array of factors which may impact nest locations. Such complexity reveals the inherent difficulty in determining a general pattern from just one point in time (Dr. Robert Johnson, Arizona State University, personal communication). All patterns – clustered, random, and dispersed – have been documented, sometimes with the same species exhibiting different patterns in the same areas (Whitford et al. 1976; Bernstein and Gobbel 1979; Ryti and Case 1992; Crist and Wiens 1996; Gordon and Kulig 1996; Heinze et al. 1996; Wartburg and Steiner 1997; Keene and Dejean 1999; Schooley and Wiens 2003; de Albuquerque et al. 2005; Kilpeläinen et al. 2008). Hypothesized influences on colony spatial patterns include colony density (Cushman et al. 1988; Ryti 1991) and queen dispersal and survival (Cole and Wiernasz 2002) but the most frequently hypothesized influences have been competition, the hallmark of ant species (Bernstein and Gobbel 1979; Hölldobler and Wilson 1990; Cerdá et all 2013), as analyzed with first nearest neighbor distances (Crist and Wiens 1996; Sinclair 1985; Yitbarek et al. 2011), and habitat heterogeneity (Levings and Traniello 1981; Sudd and Franks 1987; Johnson 1992; Dean et al. 1993; Catangui et al. 1996; Johnson 2001; Ríos-Casanova et al. 2006; Blanco-Moreno et al. 2014). Competition is expected to produce dispersed spatial patterns as colonies survive better at distances that provide relief from competition while habitat heterogeneity is expected to produce clustered spatial patterns as colonies survive better in optimal habitat and their densities increase in such areas. Because these and other factors may act in concert, the influences on spatial patterns may be difficult to disentangle and the patterns may vary in ways difficult to predict, apart from historical or species level survival strategies such as foraging and territoriality (Levin 1992). Nevertheless, an examination of colony spatial patterns may clarify factors that influence colony location and describe this dynamic character (Besag 1977; Sterner et al. 1986; Kenkel 1988; Dixon 2002).

A better understanding of colony spatial patterns, including patterns through time, is important for understanding the ecological influence of ant species on habitats and ecosystems (Wilson 1958b; Schumacher and Whitford, 1976; Gilbert 1979; Crist and Wiens 1996; Folgarait 1998; Peck et al. 1998; New 2000; Andersen et al. 2004; Schooley and Wiens 2003; Underwood and Fisher 2006; Whiles and Charlton 2006; Fagan et al. 2007; Kilpeläinen et al. 2008; Pisani 2009; Pringle et al. 2010; Silvestre et al. 2011). Even though ants move within habitats and may move among habitats as they forage and mate, most species have stable nest locations around which these activities are organized. Thus, the pattern of colony locations may be informative concerning the impacts of ant ecological relationships.

Despite relative nest location stability, the relocation of nests may pose a difficulty for spatial pattern evaluations since it is difficult to distinguish relocation from death and such movement, especially if frequent, may alter the spatial pattern (Smallwood 1982). Even though location is a relatively unstudied phenomena, it has been hypothesized that colonies relocate due to crowding or competition, changes in the habitat which result in unfavorable internal nest conditions or to a nest problem, such as disease (Carlson and Gentry 1973; Brown 1999; Gibb and Hochuli 2003; McGlynn et al. 2004; McCaffrey and Galen 2011). Some *Pogonomyrmex* species have been observed to move their nests (Hölldobler 1976; van Pelt 1976; De Vita 1979; Droual and Topoff 1981; Harrison and Gentry 1981; Gordon 1992) but relocation by *P. barbatus* and *P.*

badius was not connected to colony density, age or size (Gordon 1989a; Tschinkel 2014). Some colonies have been observed moving to a new location only to move back to their earlier location (Gordon 1992; McGlynn et al. 2004; A.B.M., personal observation). The influences on relocation in *Pogonomyrmex* have been difficult to decipher.

In earlier studies, nearest neighbor distances were a method of choice for determining spatial patterns (Clark and Evans 1954; Sinclair 1985; Cushman et al. 1988; Adams and Tschinkel 1995; Schooley and Wiens 2001). Since Pielou (1960) raised concerns with nearest neighbor analyses, other methods have been developed, notably, spatial point process models which test the divergence of data from random dispersion (Ripley 1997; Dixon 2002; Schooley and Wiens 2003; Baddeley et al. 2006; Illian et al. 2008). Ecologically, a clustered pattern is often expected based on habitat heterogeneity. Such heterogeneity depends on many environmental factors but also on the scale at which the distribution is considered (Levin 1992; Andersen 1997; Braschler and Baur 2003; Schooley and Wiens 2003) since all patterns tend to cluster as scale increases (Illian et al. 2008). In most of these analyses, a border effect, an artifact of choosing an observation window (Dixon 2002; Fortin et al 2002), was controlled by using various forms of correction including the simulation of colony locations beyond the border or artificially choosing a smaller area within the study site (Sinclair 1985; Goreaud and Pélissier 1999; Illian et al. 2008).

In the Cross Timbers Ecoregion, prairies and forests form a mosaic producing natural boundaries which may result in microhabitat or environmental gradient changes. Such an environmental gradient might influence *P. comanche* nest location since these ants do not nest in the forest. Oak motts, an individual oak tree or small island of trees or shrubs within the prairie, may also add to this mosaic producing similar borders. A border effect may limit colony occurrence to prairie large enough to have areas free of microhabitat effects unsuitable for nesting.

The presence of *P. comanche* is readily observable by their conspicuous nests and foraging activities suggesting that they may have an impact on the environment including changes to the physical, chemical and biotic characteristics of soil. If so, this impact would be spatially structured by the colony spatial distribution, that is, impacts would be concentrated at nest locations and within the foraging range. In order to investigate the spatial nature of this possible impact, I sought to determine the typical colony spatial pattern at different spatial scales and to discern factors which may influence this pattern. I expected that colonies would be regularly distributed at smaller spatial scales as a result of competition for nest space and foraging areas. But at larger spatial scales I expected colonies to be clustered because of shared mating leks and dispersal limitation of alates and mated queens.

In this part of my project, I tested the null hypothesis that *P. comanche* colonies are randomly distributed within the landscape (H_{01}) by locating, mapping, and analyzing colony locations with a point process analysis. I considered populations in five sites: EP, GL, SP, T1P and T2P. I have mapped *P. comanche* colonies in the same areas of these sites over several years.

Materials and Methods

Field Methods

I located *P. comanche* colonies by visual searching in areas where they are known to occur and areas with soil and habitat types thought to be suitable for *P. comanche* nesting within the FWNC (Cole 1968; Taber 1998; Johnson 1992; Johnson 2006). I also located colonies by following foragers back to their nests, especially in the

SWNP. I obtained the GIS coordinates for each nest using a Magellan Explorist 600 GPS unit which gave coordinates +/- 3 m error (Thales 2005).

Because *P. comanche* colonies are quite dense in some sites, suitable habitat is extensive in some sites and I was limited in time, I chose to map similarly sized areas based on recognizable landmarks that facilitated mapping the same area repeatedly, such as electrical power line poles and prairie-forest boundaries. I mapped *P. comanche* colonies each year in areas of EP in the spring from 2009 through 2013; for GL and T1P in 2010 through 2013; and for T2P in 2011 through 2013. I mapped all the colonies in SP in 2011 – 2012. In 2012, I included new nests (just dug by a queen with colonies not yet emerged) that I located in EP, GL, T1P and in 2012 in EP, GL, T1P and T2P in 2013. In 2011, I mapped all colonies for each site to assess the total number of colonies in the FWNC. (Figures 2.1 and 2.2; Maps of the colony locations for each site and year are presented in Appendix A.)

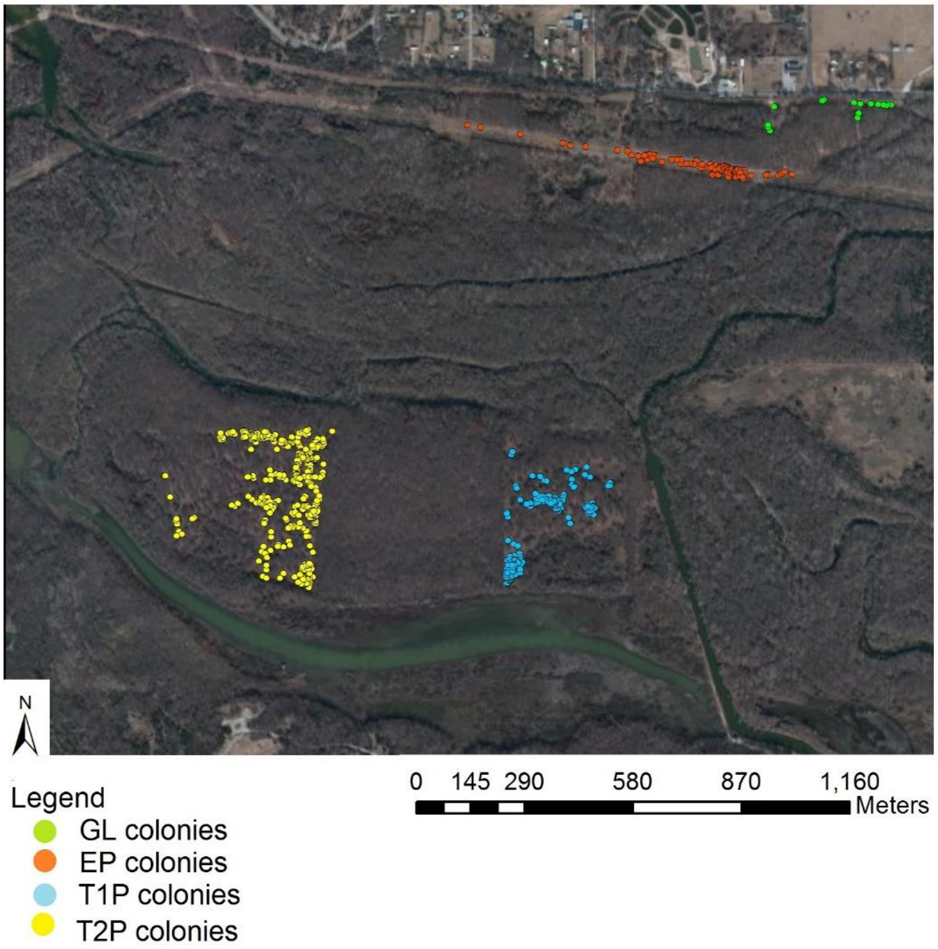


Figure 2.1 *P. comanche* colony locations in the EP, GL, T1P, and T2P sites, FWNC

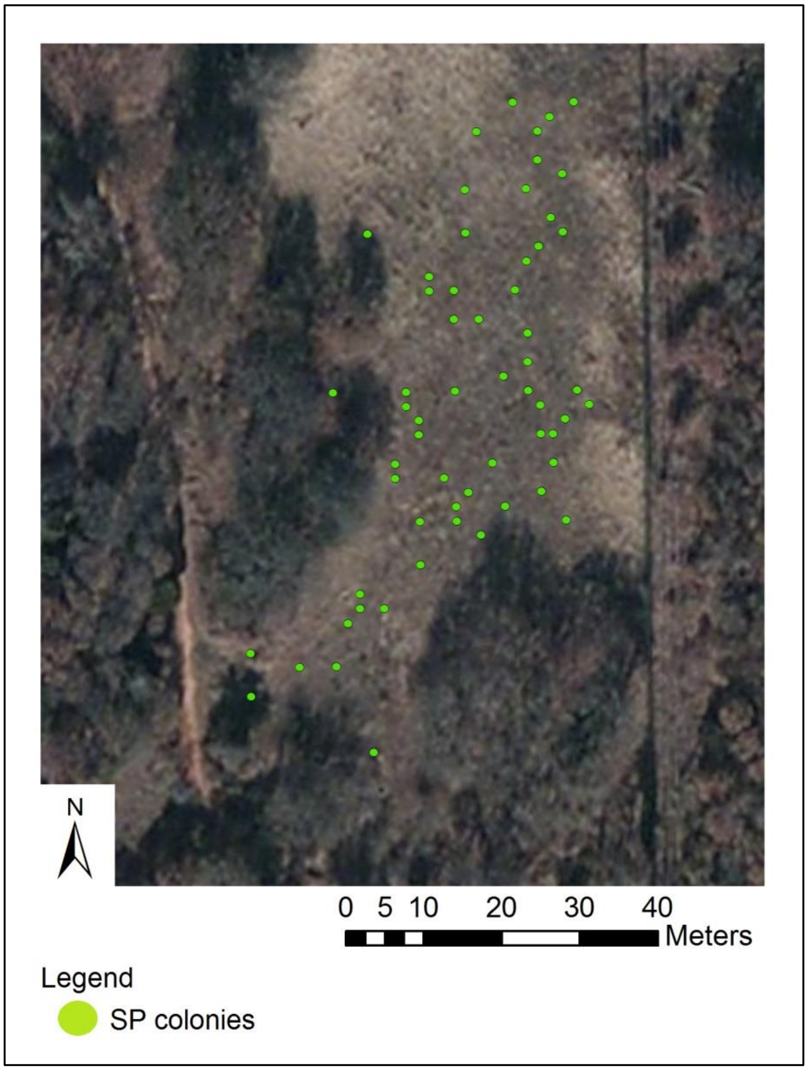


Figure 2.2 *P. comanche* colony locations in the SP site of SWNP

Data Analysis Methods

I converted the GIS coordinates from the GPS format into decimal degrees using the GPS Latitude and Longitude Convertor available on-line (CSG Network) and uploaded these coordinates into the ArcMap (Esri 2012). Because polar coordinates are necessary for spatial statistical analyses, I created shape files using the Lambert Conformal Conic Map Projection (polar coordinates). I chose this map projection because the study sites are near N 34° and this map projection is recommended for middle latitudes and preserves area and distance with minimal distortion close to N 33° and N 45° (standard parallels; Esri 2012). I constructed maps of colony locations in ArcMap (Esri 2012).

I calculated nest abundance (total number of colonies in the defined areas) and densities (colonies per hectare) for the areas sampled for each year and compared these data among sites to assess population stability with a repeated measures Multivariate Analysis of Variation (MANOVA) in SYSTAT (Wilkinson 2009). I assessed the spatial pattern with the L(d) function, a standardized form of Ripley’s K function, using only the established colonies since no new colony survived beyond three months. I used the L(d) function, rather than the nearest neighbor distance analysis because Ripley’s K function is considered more powerful and analyzes spatial pattern at different scales which may have ecological significance (Clark and Evans 1954; Besag 1977; Sinclair 1985; Fisher 1993; Crist and Wiens 1999; Schooley and Wiens 2001; Schooley and Wiens 2003; Baddeley and Turner 2005; Illian et al. 2008).

The L(d) function assesses the spatial pattern based on the average number of points from each point within a distance threshold set by a specified distance increment (Ripley 1976; Besag 1977; Dixon 2002; Illian et al. 2008; Esri 2012). The first threshold is the distance increment, the second threshold is twice the distance increment and so forth. In this way, the L(d) function produces a cumulative average which increases with additional increments. These increasing threshold distances are the scales at which the pattern is assessed. At each scale, the average number of points is compared to the expected average if the pattern were random (a Poisson process; Dixon 2002). A comparison producing a value greater than one has more points than expected and is clustered while a comparison producing a value less than one has fewer points and is regular (or overdispersed; Dixon 2002).

I obtained average nearest neighbor distances and the L(d) function with ArcGIS (Esri 2012). ArcGIS uses the following calculation for the L(d) function.

$L(d) = \sqrt{\frac{A\sum_{i=1}^{n}\sum_{j=1}^{n} w_{i,j}k(i,j)d_t}{\pi n(n-1)}}$ where *A* is the area of the observation window, *i* and *j* are different points (colony locations), *w* is the edge correction, *k* is the weight, *n* is the total number of points in the observation window and *d* is the distance (radius) at each incremental step (scale). The weight *k* equals one when the distance between *i* and *j* falls within that step, otherwise the weight is zero (Esri 2012).

Like any statistical analysis, having a sufficient sample size for significant results is important. Because Ripley's K function is a spatial analysis, not only the number of data points but also the window of observation (shape and size of the area investigated), site heterogeneity, the edge effect and the increment used are important (Dixon 2002; Illian et al. 2008). A sample size of more than 30 points is suggested because smaller samples are subject to greater error and larger standard deviation which hamper meaningful interpretation of spatial analyses (Dixon 2002; Rayburn et al. 2011; Esri 2012). Therefore, I do not report L(d) analyses of the GL site, which had at most 16 colonies. The observation window in the analysis process is defined by the Esri program as the extent of the points (Esri 2012).

All the sites have natural boundaries with forest and while *P. comanche* may nest right up to this boundary, they never nest within the forest. In order to account for a possible edge effect inherent in the analysis process as well as apparent in the sites, I used a correction that simulates outer boundary colony locations based on observed colony locations near the prairie edge (Besag 1977; Dixon 2002; Esri 2012). These simulated points are used as neighbors for points within the sites but the simulated points are not used for their own neighbors.

For the increment, I chose 3 m because this distance is about half the average observed nearest neighbor distance across sites (6.049 m) and is likely to correspond to the typical relocation distance (Gordon 1992; A.B.M. personal observation). I used 25 increments for the cumulative function in order to cover enough scales to observe the transition from one spatial pattern to another. Hence, the scales tested were 3 m, 6 m, 9 m and so forth up to 75 m. Each analysis was completed with 99 permutations to construct confidence intervals which approximated 90% confidence However, the confidence envelope is not included in the diagrams due to a glitch in the program which I was unable to resolve (Esri 2012). Because of this issue with ArcGIS program, I performed a MANOVA in SYSTAT (Wilkinson 2009) with the distance values at which the L(d) function changed from one pattern to another to compare the general pattern across sites. I estimated (by eyeballing the diagrams) the random pattern based on overlap between the red (observed) and blue (null hypothesis) lines.

I was unable to use a post-processing method to correct the spatial data because the GPS unit did not provide the complete raw GIS data necessary for this correction. The measurement error is the spatial data decreases the detection of regularity at small spatial scales and while detecting clustering, overestimates the size of the clusters (Freeman and Ford 2002; Rayburn et al. 2011). The error in the spatial data is of particular concern because the alternative hypothesis is that the colonies are regularly distributed at smaller spatial scales at which the colonies interact and become increasing clustered at greater scales. Thus, the error in the data will make it more difficult to detect regularity and easier to interpret the spatial patterns as random (Type II error).

Results

I mapped *P. comanche* nests in a defined area within EP (2009 – 2013), GL (2010 – 2013) T1P (2010 – 2013), and T2P (2011 – 2013) of the FWNC and SP and in trails of the SWNP (2011 – 2013; Table 2.1). In 2011 when I mapped the entire study sites, I located 719 colonies in the FWNC: 95 colonies in EP, 16 colonies in GL, 150 colonies in T1P, and 458 colonies in T2P. I located 67 colonies in SWNP: 61 colonies in SP and 6 colonies in trails. I also located 21 new nests in EP, 2 new nests in GL and 28 new nests in T1P in 2012 and 29 new nests in EP, 31 new nests in GL, 16 new nests in T1P and 7 new nests in T2P in 2013. The FWNC colonies appear to have a clustered distribution at the level of the entire site (Figure 2.1). However, a clustered pattern is not obvious when looking at individual prairie areas bounded by the forest in the T1P and T2P sites which are also fragmented by oak motts. The area separating T1P and T2P is forested without open prairie. *P. comanche* does not nest in the forest, light gaps or oak motts. GL and EP are connected by a sandy, dirt road in which two colonies nest. This road is about 200 m in length from GL to EP. The colonies are found in a 70 m section lacking canopy cover. (Site abbreviations and details are given in Table 3.1.)

No new colonies (2012 and 2013) survived beyond three months, so recruitment seems poor. Colonies are noticeably more abundant and denser in SP, T1P and T2P than in EP and GL (Table 2.1). This difference may result from the general shape of the sites and the occurrence of oak motts. EP and GL are more elongate without oak motts and SP, T1P, and T2P are more square and fragmented by oak motts. Another potentially significant impact is mowing in EP and GL which are right-of-ways. This seasonal disturbance probably interferes with the survival of new colonies since such new nests are shallow and mowing disturbs the soil to about 12 cm (Tschinkel 2004;

A.B.M., personal observation). There may be other environmental or microhabitat differences which effect colony location as well but this was not tested.

For all of the sites there are a few colonies isolated at great distances from the majority of colonies (by hundreds of meters; hereafter, I refer to these isolated colonies as outliers). In T1P, T2P, and SP these colonies are isolated by expanses of forest. Due to mowing in EP, there are no intervening motts or forest separating these outlier colonies.

Having mapped the same areas over many years, I observed several colonies with stable nest locations (Appendix A). However, at least six colonies in different sites moved their nest locations several times within the study period from 2009 to 2013. These colonies had nest locations in or at edges of dirt roads or paths and moves were within 3 m of previous locations (A.B.M., personal observation). Judging from the nest crater size, none of these nonpersistant colonies were new colonies but I could not determine if they had died or relocated.

Population Stability

Over the years, colony abundance and density have changed in these areas suggesting significant colony turnover (Table 2.1). The MANOVA of colony abundance and colony density by sites and years was significant ($p = 0.000$) with differences between sites and within sites by year (So, EP differed from T1P and EP 2009 differed from EP 2010.) The only exception was that SP and T2P did not differ ($p = 0.196$). Colony turnover may reflect survival as well as relocation outside the study area, though this seems doubtful due to the limited distance of relocation (A.B.M., personal observation).

Table 2.1 Summary of Colony Abundance and Density

Site	Year	Area (ha)	Abundance	Density per ha	Average Abundance (SD)	Average Density per ha (SD)
EP	2009	6.71	54	8.05	46.4 (15.3)	6.9 (2.3)
	2010		43	6.41		
	2011		69	10.3		
	2012		34	5.07		
	2013		32	4.77		
GL	2010	5.82	9	1.6	13.5 (3.11)	2.4 (0.53)
	2011		14	2.4		
	2012		16	2.8		
	2013		15	2.6		
SP	2011	4.43	48	10.8	53.7 (6.66)	12.1 (1.54)
	2012		61	13.8		
	2013		52	11.7		
T1P	2010	3.14	32	10.2	34.3 (8.66)	10.93 (2.77)
	2011		47	15.0		
	2012		30	9.6		
	2013		28	8.9	57.7 (3.21)	11.0 (0.64)
T2P	2011	5.06	60	11.9		
	2012		59	11.7		
	2013		54	10.7		

Spatial Pattern

In the L(d) function diagrams (Figures 2.3 – 2.6), the L(d) function is plotted against threshold distance (m) for observed (red line) and expected (blue line; random pattern) values. When the red line is above the blue, the pattern is clustered. Conversely, when the red line is below the blue line, the pattern is dispersed. I analyzed 15 patterns: five for EP; three for SP, four for T1P and three for T2P. Though the confidence envelope was calculated, I was unable to include a confidence envelope in the diagrams due to a glitch in the program which was not resolved in time to be included in this analysis (Esri 2012).

All the L(d) diagrams have a similar pattern. The MANOVA for threshold distances at which the patterns change across sites was nonsignificant, so the sites show similar spatial patterns with scale (Wilk’s Lambda = 0.129 with p = 0.090). The pattern is random up to spatial scales of about 5 – 10 m, at middle scales (from about 10 m up to about 40 m) the patterns become clustered and at larger scales (from about 50 to 75 m) the pattern becomes dispersed. It is not possible to assess at what scale these patterns significantly depart from random due to problems with the ArcGIS program. Despite this problem, based on how close the observed data appear to follow the expected prediction, I suggest that colony distribution is random (i.e., there is no pattern) up to 50 m.

Because the average first nearest neighbor distance across sites is 6.049 m, there may be few colonies within the five – 10 m scales, so it is not surprising that these patterns are random at these scales (3 m, 6m, and 9 m). Patterns of clustering were observed at about 10 m and continue up to about 50 m. In EP in 2010 – 2013 (Figure 2.3) and T2P in 2011 (Figure 2.6) the departure from random beginning about 10 m is large enough that it may be significant even without the confidence envelope confirming this in EP and T2P.

However, the error in the spatial data raises concerns about the significance of these patterns and at what scale the patterns change (Freeman and Ford 2002; Rayburn et al. 20011). Specifically, the question arises: is the random pattern observed from 0 – 10 m really random or could some regularity be undetected? There are fewer issues with detecting clustering, since the error does not keep clustering from being detected but the error could lead to overestimates of the sizes of the clusters and an increases of the scale at which clustering is detected (Freeman and Ford 2002). So, the threshold spatial scale for the onset of clustering becomes questionable.

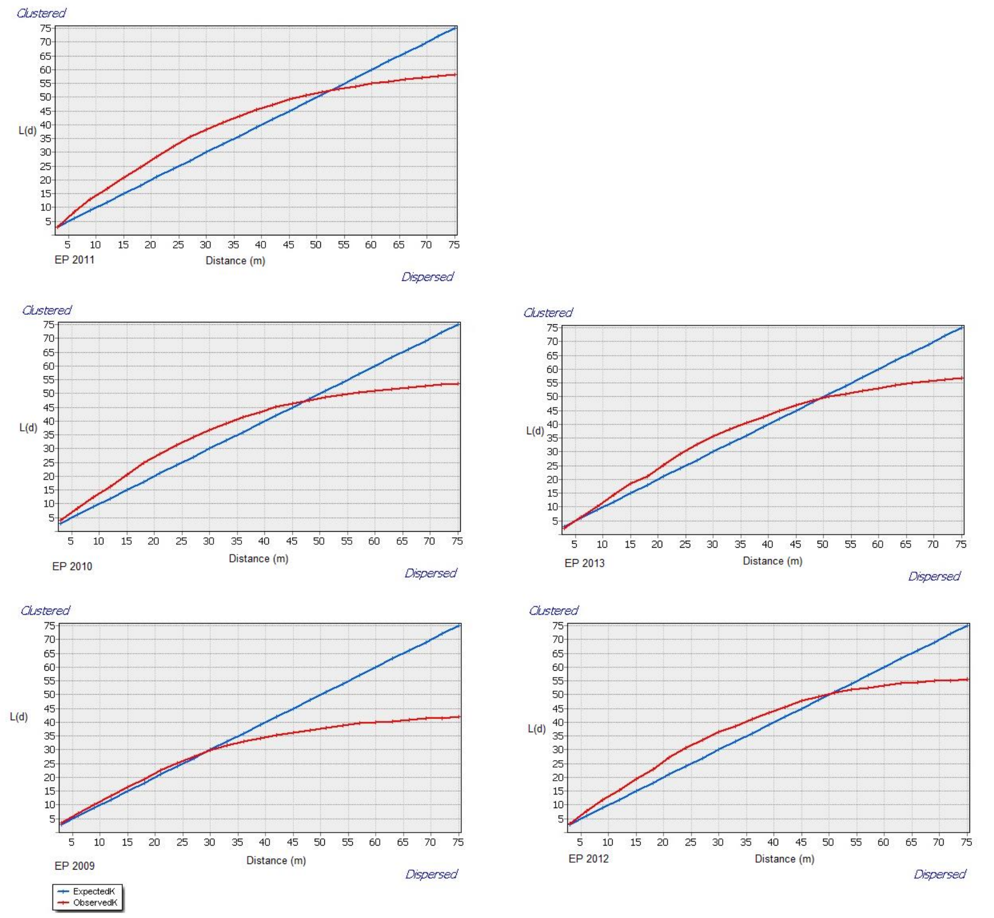


Figure 2.3 Ripley’s K Function Diagrams for EP, 2009 – 2013

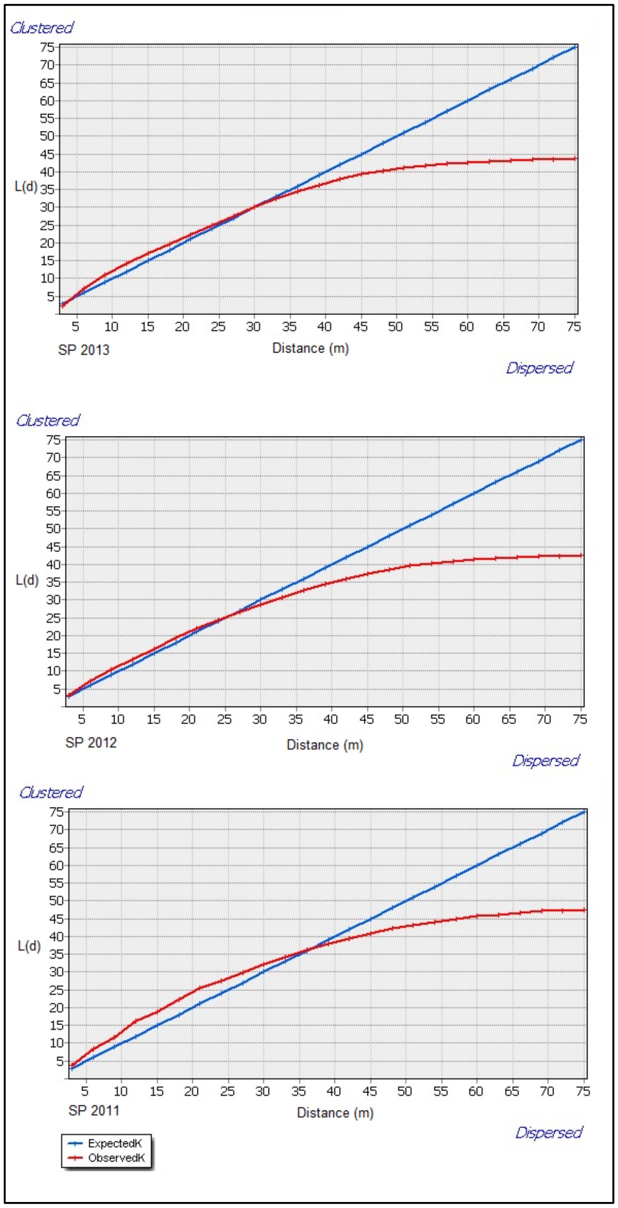


Figure 2.4 Ripley's K Function Diagrams for SP, 2011 - 2013

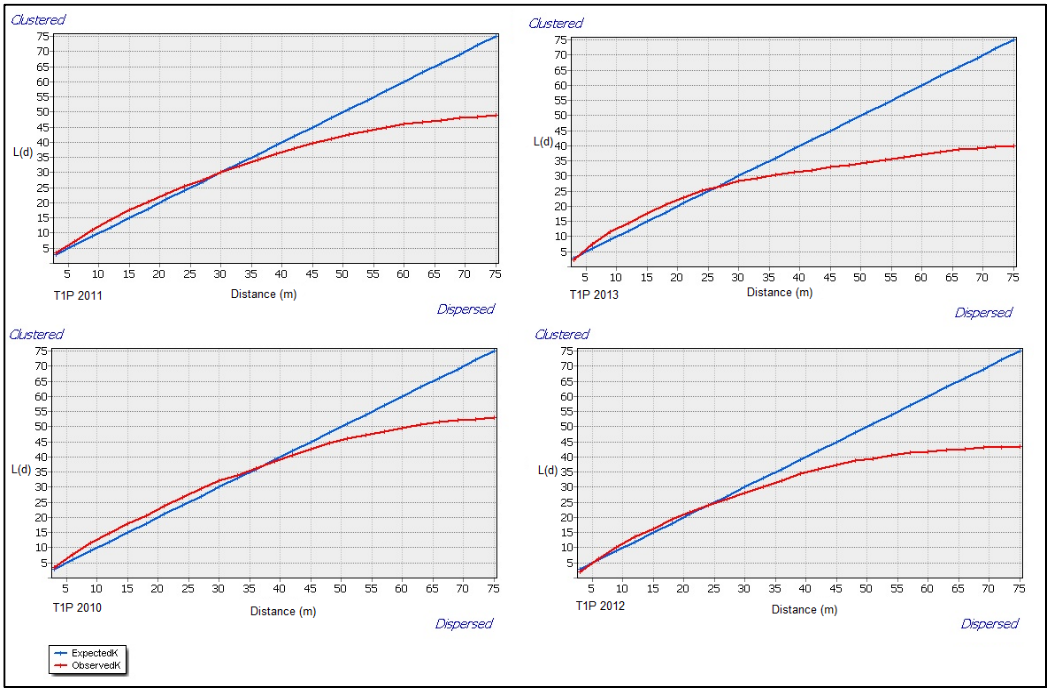


Figure 2.5 Ripley’s K Function Diagrams for T1P, 2010 – 2013

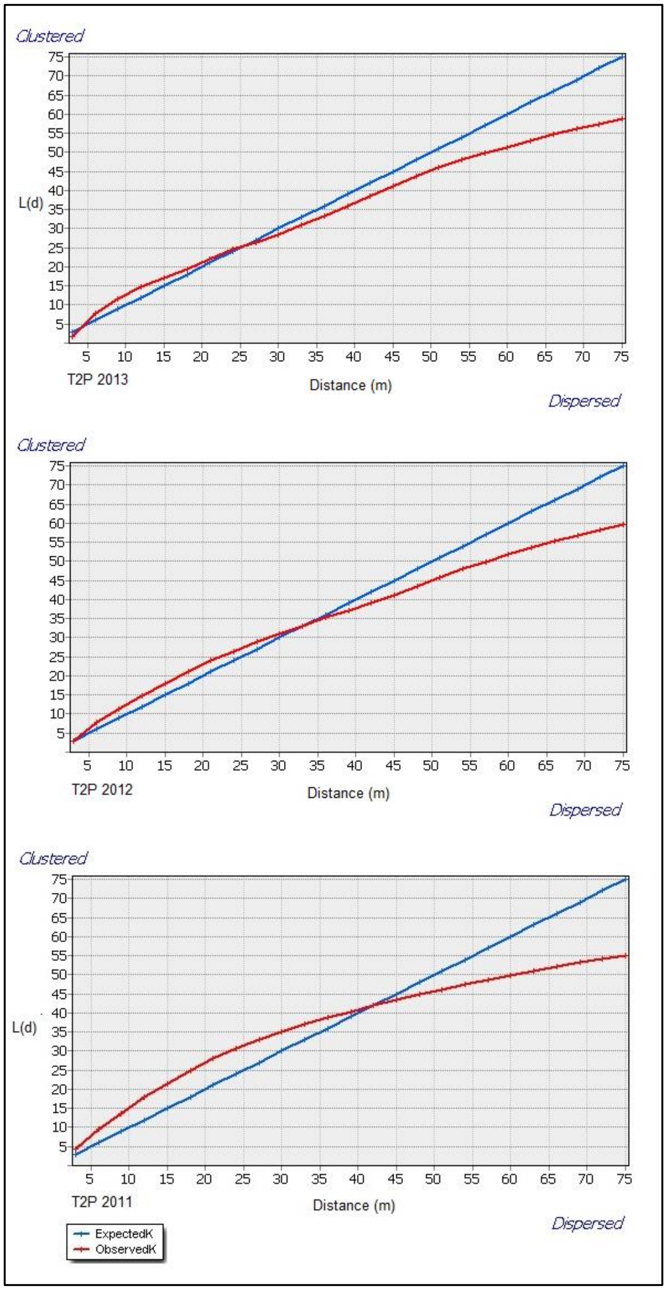


Figure 2.6 Ripley's K Function Diagrams for T2P, 2011 – 2013

Discussion

Population stability appears to be affected by several factors, most of which were observed and not specifically quantified. The changes in nest abundance and density in these areas suggest a substantial level of colony turnover with limited, average colony longevity. Factors which were observed and may affect this turnover include low levels of recruitment, disturbance in the EP and GL sites and colony relocation. The occurrence of several outlier colonies also suggests limited queen dispersal and poor recruitment.

Despite the presence of outlier colonies and extensive, intervening areas free of colonies, the populations do not appear to be expanding into unoccupied areas. Judging by the failure of all observed, newly founded colonies, recruitment is low. In the EP and GL sites, which have the lowest colony abundances and densities, their low recruitment may, in part, be attributed to mowing that maintains these right-of-ways (Schooley and Wiens 2001). The movement of heavy vehicles digs into these sandy prairies disturbing the soil to a depth of 12 cm or more which is likely to destroy recently founded colonies which have shallow nests (A.B.M., personal observation).

The error in the spatial data and the lack of a confidence envelope for the L(d) analyses are problematic for assessing the spatial pattern. However, these issues do not require complete dismissal of the data. Rather, the lack of precision suggests that the data may only be useful for a general estimate of the pattern and the spatial scales at which the pattern changes. From such an estimate, better questions may be raised focused with more appropriate data collection, including tracking of individual colonies.

The most important impact of the spatial data error is the possible failure to detect regularity at small spatial scales (Freeman and Ford 2002). Despite the data and ArcGIS program issues, I hypothesize that the patterns are random at spatial scales up to 50 m as indicated by most of the analyses. I submit this hypothesis for three reasons.

First, the ants cannot be so precise as to have their colony spatial patterns hang on an exact value. Thus, we look for a pattern or average value. Second, the L(d) diagrams do not show strongly divergent patterns from random, except in the EP in 2010 – 2013 and in T2P in 2013 where the pattern becomes clustered in the mid range scales. However, the MANOVA indicated that the sites did not differ in these patterns. So, it might be reasonably expected that the patterns are random not clustered; that is, the clustered pattern for the sites and years is likely to fall within the confidence envelope. Thirdly, I originally hypothesized that the colony spatial pattern would be regular and maintained by aggressive colony interactions (alternative hypothesis). However, my nestmate discrimination test (Chapter 4) gives no indication of aggression playing any significant role in *P. comanche* colony interactions.

Thus, the overall random distribution of colonies at spatial scales up to 50 m suggests that the habitats are homogeneous for factors that influence nest site suitability and that there is little or no intraspecific competition, aggression or territoriality directly affecting colony locations. The perceived high colony turnover rate might contribute to random colony locations by frequent opening of areas for new nest sites as older colonies move or die. This combination of colony turnover and low recruitment seems surprising given that the populations persist. This situation suggests that mature colonies produce large numbers of female alates in order that at least a few establish colonies which live long enough to reproduce. Given that some ant species are known to adjust the sex ratios of alates (male and female reproductive ants), a high production of female alates may have an impact on sex allocation in *P. comanche* (Helms et al. 2000; Hammond et al. 2002; de Menten et al. 2005; Helms et al 2005; Rosset and Chapuisat 2006).

Random colony locations suggest that queen dispersal may be the most significant factor determining colony locations especially if queens disperse from a central mating lek equally in all directions (Cole and Wiernasz 2002). If queen dispersal is limited, such dispersal might contribute to an explanation of the clustered pattern observed in the EP site because this is an elongate site, a shape which limits dispersal in the two long directions and might tend to cluster such dispersal along this axis. This possibility is suggested by colony locations in this site (See the maps of EP in Appendix A).

Finally, the prairie components of the Cross Timbers Ecoregion and other areas where *P. comanche* nests probably have a random distribution, related more to historical accident than any environmental gradient. The nature of this habitat mosaic – inherently mixed with woodland, light gaps and oak motts in which these ants do not nest – may make defining an appropriate observation window difficult or impossible (Dixon 2002; Fortin at al. 2002; Illian et al. 2008). These areas fragment the prairie into various sized areas, some of which appear too small to support a colony (A.B.M., personal observation). The combination of the occurrence of prairie may make any spatial analysis difficult or even inappropriate while also having a significant impact on ant movements, including nest location, foraging areas, mating lek locations and alate and queen dispersal.

Chapter 3

Environmental and Species Impacts on *P. comanche*

Introduction

Species interactions and habitat heterogeneity are often hypothesized to influence species occurrence, abundance and distribution at the local, ecological level. Most ant species are ground nesting with much of their activity taking place at ground level, including foraging, establishing nests and interactions among colonies and species. Therefore, ant species sampled from the ground encompass much of the total species richness and can be used in assessing ant assemblages (communities) and functional roles (Campos et al. 2011). Several factors may contribute to the presence and abundance of these species and therefore, to the structure of their assemblages (Lach et al. 2010). Competition has long been hypothesized to structure ant assemblages (Hölldobler and Wilson 1990; Davidson 1998) and is still considered the most important factor (Cerdá et al. 2013). Ant competition establishes dominance hierarchies in which species may be either numerically or behaviorally dominant (Davidson 1998). Generally, numerically dominant species interact indirectly by finding food resources quickly and removing resources to the nest by a mass of foragers (Lach et al. 2010). Behaviorally dominant species use aggression to control resources such as foraging trails and areas as well as territory around the nest (Fellers 1987; Davidson 1998; Cerdá and Cros 1997; Bestelmeyer 2000). These hierarchies have been described with three levels of interaction: dominant, subdominant, and submissive species (Vepsäläinen and Pisarski 1982; Savolainen and Vepsäläinen 1989; Cerdá et al. 2013). There may be one or a few species in the dominant and subdominant categories and many species in the submissive level. The stronger the dominance of a species, the more restricted is the species richness when the dominant species is present. Extremes in dominance are a key characteristic of invasive species which disrupt communities by excluding many native species (Huxel, 1999; Holway 1999; Sanders et al. 2003; Didham et al. 2005). The dominance hierarchy may be reflected in the shape (line slope) of Whittaker plots.

Although competition remains the most frequent significant factor contributing to the presence and abundance of ant species (Lach et al. 2010), other factors may also play significant roles (Andersen 1990; Neves et al. 2013). Characteristics of soil (mineral content, drainage, or depth of horizons) and dominant vegetation (shading, temperature effects, or structural complexity of the habitat) are considered possible, significant influences on the distribution of ground nesting ant species (Andrewartha and Birch 1954; Schoener 1986; Andersen 1990; Longino and Nadkarni 1990; Andersen 1991; Bestelmeyer and Wiens 2001; Ribas et al. 2003; Boulton et al. 2005; Vasconcelos et al. 2008; Cerdá et al. 2013). Such environmental factors influence survivability and specify a habitat structure within which species interact, in turn influencing community structure.

I tested two hypotheses concerning the relationships among environmental factors, ground active ant species and *P. comanche*. Because of the possibility for species specific soil requirements for nests and the diverse ecological roles ants play, I hypothesized that the ground active ant community would differ among habitats (sites) according to environmental factors and the presence of other ant species (H_{02}; Yek et al. 2009). Because *P. comanche* has an obvious presence in terms of forager size (five - 8 mm), activity level, external nest form (crater form with a 30 cm average diameter but more extensive nest yard area; A. B. M., unpublished data), and appears to have specific soil requirements, I also hypothesized that the occurrence of *P. comanche* would impact the occurrence of other ant species, either in exclusion or co-occurrence, possibly through some form of dominance, competition or other interaction effect (H_{03}). *P.*

comanche presence may be predicted by environmental factors, especially in relationship to soil characteristics which directly affect nest construction and maintenance. The possibility of co-occurring species and of *P. comanche*'s restriction to deep sandy prairies (Aquilla Sand Formation) might define a community with shared preference for environmental conditions. Thus, characterizing *P. comanche* and ground active ant occurrence might shed light on ant assemblages and ecological relationships in the Cross Timbers Ecoregion. Thus, characterizing environmental preferences and co-occurring ant species would be useful for understanding the spatial ecology of *P. comanche*.

In order to test these hypotheses and compare ground active ant occurrence with that of *P. comanche*, I characterized sites by species and taxonomic diversity and tested the environmental response of ant species using ground active ant species and environmental variables sampled from June through August of 2012 in the Fort Worth Nature Center (FWNC) and the Tandy Hills Natural Area (THNA) in Fort Worth, Texas and in the Southwest Nature Preserve (SWNP) in Arlington, Texas. Such characterization may also provide a first step in discerning the structure of ant assemblages and species interactions in this region.

Materials and Methods

Field Methods

I sampled environmental variables hypothesized to be important in ant habitat preferences (Johnson 1992). I collected ants in the FWNC in June, July and August but added the SP, SPW, STP and THP sites in August, so the late summer set of samples includes four additional sites. I conducted analyses on three sets of samples: late summer (all 21 sites), FWNC (17 sites) compiled (all months together as one sample by site) and FWNC monthly (considered as a time series).

I chose sites based on the presence of *P. comanche* colonies*,* soil type, disturbance (managed fire, mowing and vehicular disturbance) and habitat type (prairie and woods). The sites were used as a natural experiment based on the pattern of these characteristics as shared or unshared (Krushelnucky and Gillespie 2010). Because I was interested in the ground active ant species, I collected ants using pitfall traps, a commonly used method particularly suitable for ground active invertebrates (Agosti et al. 2002; Bestelmeyer et al. 2000; Campos et al. 2011). Although representative of the sites, ant samples should not be understood as a complete assemblage for any site due to differences in recruitment behavior and trap bias which may include location bias as well as under sampling of arboreal and army ants (Adis 1979; Marsh 1985; Holway 1998). Rather, these measures were used to assess ground active ant species only.

Site Information

I sampled 21 sites: 7 sites had *P. comanche* colonies, 7 sites were disturbed; and four were wooded (Table 3.1). There were a total of 8 deep sandy prairies where *P. comanche* might nest, all on the Aquilla Sand Formation (Cole 1968; Taber 1998).There were 7 soil types which ranged from alkaline clay soils to acidic sandy soils with the sandiest soils classified as “excessively well drained.” On a drainage scale of one to four, with four being the most well drained, the soils are ranked from “moderately well-drained” (2.5) to “somewhat excessively well-drained” (3.5) as follows: Windthrost (2.5) < Aledo, Aledo-Urban, Bastil; Crosstell-Urban, Silawa (all with 3) < Aquilla (3.5) (Custom Soil Resource Report for Tarrant County, Texas; Ressel 1981; Soil Survey from the Natural Resources Conservation Service). Most of the soil types were well-drained though many contained large amounts of clay in lower horizons and differed in the depth to the restrictive layer. The Aledo and Aledo-Urban soil types are clay soils characterized by gravel which adds to their drainage. All the other soils had surface layers that are sandy or sandy loams. I considered this diversity of soils and habitats an environmental gradient based on ordering the sites with respect to these characteristics (Pacheco and Vasconcelos 2012).

Environmental Variable Sampling

I obtained the following environmental variables from the Custom Soil Resource Report for Tarrant County, Texas (2011) and the Soil Survey from the Natural Resources Conservation Service (accessed 2013): calcium carbonate content, drainage, ecological site designation, expected slope; hydrology, pH, soil plasticity, depth to the restrictive layer, sand depth, percentage of clay, percentage of sand, percentage of silt, soil type and unified soil classification. Each time I sampled ants, I measured soil penetration (an inverse measure of compaction) and the percentage of bare ground, litter/prostrate vegetation, standing plant cover and total cover. I used a penetration hammer to measure soil penetration and estimated the percentage cover variables using the methods of Anderson (1986) and Floyd and Anderson (1987). No specific measure of organic content was included since organic content has not been considered significant in ant nest site choice, although some ant species alter the organic and mineral content of soils in which they nest (Folgarait 1998; Barton et al. 2009). Organic material and its potential impact on soil characteristics are somewhat implicit in the drainage and cover variables.

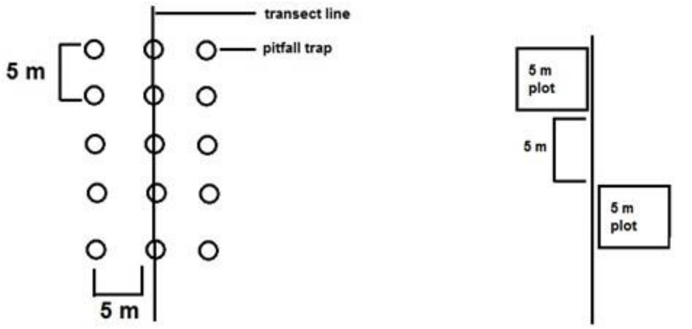
I measured each variable at 20 locations, along a 200 m transect that ran through the sites inclusive of the area where the pitfall traps were located (Engelbrecht and Herz 2001). I made the measurements in five m by five m plots, that were placed five m apart, alternating along the transect line (Figure 3.1). This placement resulted in a total of 20 samples for each variable per site. I averaged the variables for each site for each sampling date and used the averages in the ordination analyses. I also used habitat type (Auqilla Prairie, Other Prairie and Wooded Sites) and presence of *P. comanche* as predictor variables. I conducted the measurement and averaging of environmental variables in this way because I collected ants from a 15 trap arrangement in each site and counted this as one sample (next section). Thus, I likened the individual site samples (ants and environmental variables) to points on a gradient (Pacheco and Vasconcelos 2012).

Table 3.1 Sites Sampled

Habitat Type	Site	Site Abbreviation	*P. comanche*	Soil	Disturbance	Singletons
Aquilla	1 Electrical Power Line, far site, far site, prairie	EPF	present	Aquilla	mow	
Aquilla	1 Electrical Power Line, prairie site, prairie	EPP	present	Aquilla	mow	*Labidus coecus*; *Strumigenys membranifora* (queen)
Aquilla	1 Electrical Power Line, tree site, prairie	EPT	present	Aquilla	mow	*Strumigenys margaritae* (queen)
Aquilla	2 Electrical Power Line, prairie	EP2	absent	Aquilla	mow	
Aquilla	Gas Line prairie	GL	absent	Aquilla	mow	*Strumigenys louisianae* (queen)
Aquilla	1 Todd Island, prairie	T1N	absent	Aquilla	none	
Aquilla	1 Todd Island, prairie	T1P	present	Aquilla	none	
Aquilla	2 Todd Island, prairie	T2P	present	Aquilla	none	
Other	Alice Ashley prairie	AA	absent	Bastsil	none	
Other	Alice Ashley Burn prairie	AB	absent	Bastsil	burn	*Hypoponera opacior*
Other	Bison Range prairie	BR	absent	Aledo	none	
Other	3 Electrical Power Line, prairie	EP3	absent	Windthorst	mow	
Other	Gate House, prairie	GH	absent	Aledo	none	
Other	Hardwicke Center, prairie	HC	absent	Silawa	none	*Formica biophilica*
Other	Southwest Nature Preserve, prairie	SP	present	Crosstel-Urban	none	
Other	Stradford, prairie	STP	absent	Aledo-Urban	none	
Other	Tandy Hills, prairie	THP	absent	Aledo-Urban	none	
Wooded	1 Electrical Power Line Woods	EPW	absent	Aquilla	none	
Wooded	1 Todd Island Woods	T1W	absent	Aquilla	none	
Wooded	2 Todd Island Woods	T2W	absent	Aquilla	none	
Wooded	Southwest Nature Preserve Woods	SPW	absent	Crosstel-Urban	none	*Aphaenogaster carolinesis*; *Temonothorax* sp.

Ant Sampling

I collected ants in pitfall traps over a 72 hour period, once a month for June, July and August in 2012 because this is a standard method for collecting ground active ants (Agosti et al. 2000; King and Porter 2005; New 2000; Schlick-Steiner at al. 2006). In each site, I placed 15 traps, 5 m apart forming a 10 m by 20 m grid and a 200 m^2 sampling area (Figure 3.1). While trap placement may have an effect on capture, Ward et al. (2001) found no difference in ant capture with 1, 5, and 10 m pitfall trap placement. The 15 traps per site constituted one sample. The traps were located at least 10 m from the prairie-forest boundary. Because placing traps disturbs the soil community, I placed the traps for a week prior to the first collection and left them in place for the duration of the collection period (Greenslade 1973). When I was not actively collecting ants, I closed the traps with a plastic lid.



A. Pitfall Trap Array. Traps were arranged in a 3 X 5 m grid with 5 m between traps, producing a total trapping area of 200 square m. The transect line for environmental variable sampling ran through the middle of the trap area and extended for 90 m in each direction.

B. Transect Line. From the transect line 5 m square plots were sampled for environmental variables. The plots alternated along the transect oine and were 5 m apart. The line was a total of 200 m in length.

Figure 3.1 Pitfall Trap Placement and Environmental Sampling Transect

The traps consisted of one plastic cup set within another and with a plastic plate suspended 15 mm above the cups on 2, 5 mm diameter wooden or metal supports. The plate allowed the collection of ants while reducing the amount of rain and debris collected and impeding evaporation of the collecting solution. Each trap was set flush to the soil surface. The collection cup measured 9 cm at the upper diameter tapering 7 cm to a 5 cm diameter bottom with a volume of 275 ml. I filled each trap with 70 ml of propylene glycol as a killing agent (drowning) and preservative fluid. Propylene glycol does not have an odor attractive to ants and is nontoxic (Agosti et. al. 2000).

After collection, I rinsed the samples with water and stored ants in 95% ethanol. I identified the specimens using an AmScope SM-4TP2 trinocular dissecting microscope with 40X maximum magnification. I used the following identification keys: Fisher and Cover (2003), the most current literature, Ants (Formicidae) of the Southeastern United States (MacGown 2013) and AntWeb (2013). I also consulted Dave General (the Museum of Natural History, the University of the Philippines), Dr. Danny McDonald (Texas Research Institute for Environmental Studies – TRIES, Sam Houston State University, Huntsville, Texas), Dr. James Trager (Shaw Nature Reserve, the Missouri Botanical Garden, Gray Summit, Missouri), and Chris Wilson (formerly at TRIES).

I identified ants to species except an unusual *Temnothorax* specimen. I collected two species in the geminata group of the genus *Solenopsis*: *Solenopsis invicta*, the red imported fire ant, and *S. xyloni*, a native fire ant. The key character distinguishing these two species is the presence of a medial tooth on the clypeal margin which is only seen in majors and may not be reliable (D. General, personal communication; Very generally, some ant species show a dimorphism in which one caste is quite large, referred to as majors, and often serves as soldiers in protecting the colony. The other caste is much smaller and often have other morphological differences as well. The smaller caste is referred to as minors and handles more delicate duties, like caring for brood.). Because of this ambiguity, if I found majors with and without this trait, I recorded both species present but did not make a distinction in the count data. Instead I recorded the counts for both species as one count and labeled this count “*Solenopsis* (gem)." I will confirm ant identifications with James Trager and deposit voucher specimens at TRIES.

Data Analysis Methods

Ant Diversity (Point, α and Taxonomic Diversity)

I compiled species lists, species richness and counts for each site and each sampling date. (Although pitfall trap capture may reflect colony abundance, I will be referring to abundance primarily as counts because the number of individuals collected may be more indicative of activity levels and colony size/age; Gotelli et al. 2011) I recorded species occurrence as binary data (absent = 0; present = 1). I standardized species counts by the pitfall trap area of 200m^2 for the diversity measures, Whittaker plots and the ordination analyses. Standardization is necessary for comparison across sites (Whittaker 1965; Magurran 2004). I used the trap sampling area for standardization because the comparison focused on each species across sites and possible bias in pitfall trap sampling, including trapability and species differences in activity levels (Adis 1979; Marsh 1985; Holway 1998).

Because the individual samples were collected without replication in a specific site, each sample is a point diversity, that is, a sampling point within a site rather than a diversity reflective of a site (Lorance et al. 2002; Magurran 2004; Pianka 2014). Based on hierarchical clustering in SYSTAT (using single-linkage with Euclidean distance and confirmed by the validity indices Root Mean Square Standard Deviation and the Dunn validity measure; Wilkinson 2009; Dufrene and Legendre 1997). I grouped the sites as replicates of a habitat type and used these types in order to get an α diversity of the ground active ants (within habitat; Table 3.1). The habitat types constructed were: Aquilla Prairies (Aquilla; Aquilla Sand Formation in which *P. comanche* is known to nest), Other Prairies (Other; prairies with other soil types) and Wooded Sites (Wooded; Table 3.1).

Because species relationships to environments and one another are complex, I calculated several species and taxonomic diversity indices. For species diversity, I chose Simpson's Diversity Index and related measures because I was particularly interested in dominance (Whittaker 1972). I report the reciprocal of Simpson's Diversity Index (1/D) because it is a robust diversity index and its value increases with increased diversity (Gray 2000; Magurran 2004) and the Berger-Parker Index for Dominance (d) which is based on numerical dominance (Berger and Parker 1970; Magurran 2004). I constructed Whittaker (rank-abundance) plots for each habitat type (as described above; Whittaker 1965; Magurran 2004). Because the rank abundance plots are a nonlinear function, I provide the slope values for the line between the first, two highest count species. This slope may be considered the most important slope since it corresponds to the possible impact of the species with the highest count. If the difference between the first and the second most abundant species is particularly great, the most abundant species is often considered to be dominant with a possible repressive effect on other species (Magurran 2004). However, an examination of the entire line is the most informative way to use Whittaker plots. The formulae for the species diversity indices are as follows.

Simpson's Reciprocal of Diversity Index, *1/D*, was calculated as: $\frac{1}{D} = \frac{\sum_{n=1}^{S}(n\,(n-1))}{N\,(N-1)}$ where *n* is the count of a particular species, s is species richness and *N* is the total count of all species in a sample.

The Berger-Parker Index for Dominance, d, was calculated as: $d = \frac{N_{max}}{N}$ where N_{max} is the count of the highest counted species and N is the total number of ants in a sample.

I also calculated taxonomic indices using untransformed count and occurrence data because these indices have been considered more closely related to functional diversity than the traditional species diversity indices and may better capture ecological relationships (Warwick and Clarke 1998; Clarke and Warwick 1999). I calculated four taxonomic indices that are natural extensions of Simpson's Diversity Index. These taxonomic indices are independent of mean values and sampling effort so they are readily compared across sites (Clarke and Warwick 1998).

I calculated taxonomic diversity, taxonomic distinctness and variation of taxonomic distinctness indices using the Linnaean categories of subfamily, genus, and species, categories most important in ant taxonomy (All ant species are in the family Formicidae; Clarke and Warwick 1998; Clarke and Warwick 1999; Clarke and Warwick 2001). The Linnaean categories were used rather than phylogenetic branch lengths based on Clarke and Warwick's recommendation (1988; They obtained the same results using Linnaean and phylogenetic information.) and that the new phylogeny for *Pogonomyrme*x has not been released (This phylogeny is forthcoming. Johnson, personal communication). The taxonomic diversity index, Δ, calculates the average taxonomic distance between two randomly chosen organisms combining relatedness and abundance information within the taxonomic hierarchy. The taxonomic distinctiveness index, Δ^*, measures the average taxonomic distance between two different species without reference to the taxonomic hierarchy (as though all species were in the same genus). For occurrence data, taxonomic diversity and distinctness collapse into the distinctness index, Δ^+ (Clarke and Warwick 1998). The variation in taxonomic distinctness, Λ^+, is an index of taxonomic structure approaching zero as species become more evenly spread among taxonomic levels (Clarke and Warwick 2001). In view of recent work which found that taxonomic indices reveal differences missed by traditional species diversity indices and that ecosystem functioning may be better captured by functional groups than by traditional species based diversity measures, these taxonomic diversity indices may be especially useful (Campbell et al. 2008; Berggren, et al. 2009; Gómez-Anaya et al. 2011; Evtimova and Donohue 2014; Gagic et al. 2015). The formulas for the taxonomic diversity indices are as follows.

The taxonomic diversity index, Δ was calculated as: $\Delta = \frac{\sum\sum w_{ij}x_ix_j}{\sum\sum x_ix_j + \sum x_i(x_i-1)/2}$ where w is the weight of the taxonomic relationship between species i and j and x is the abundance for that species. The taxonomic weights are: w_0 = 0 for the same species; w_1=1 for the same genus but different species, w_2=2 for the same subfamily but different genera and w_3=3 for different subfamilies (Clarke and Warwick 1998).

The taxonomic distinctiveness index, Δ* was calculated as: $\Delta^* = \frac{\sum\sum w_{ij}x_ix_j}{\sum\sum x_ix_j} \equiv \frac{\sum w_kf_k}{\sum f_k}$ where k is the number of hierarchical taxonomic levels; f_k is the cross products from all pairs of species connected at the same hierarchical level; and w_k is the corresponding taxonomic path weights (w_0 = 0 for the same species; w_1=1 for the same genus but different species, w_2=2 for the same subfamily but different genera and w_3=3 for different subfamilies; Clarke and Warwick 1998). This is equivalent to dividing Δ by its value as if all specimens came from the same genus (i.e. without the taxonomic hierarchy).

For occurrence data, taxonomic diversity and distinctness collapse into the distinctness index, Δ^+ which was calculated as: $\Delta^+ = \left[\sum\sum_{i<j} p_{ij}\right]/[s(s-1)/2]$ where p is

the taxonomic pathway between species *i* and *j* and *s* is the species richness of the site (Clarke and Warwick 1998).

The variation in taxonomic distinctness, Λ^+ was calculated as: $\Lambda^+ = \frac{\sum\sum_{i \neq j}(\omega_{ij})^2}{s(s-1)} - (\Delta^+)^2$ where ω is the taxonomic distance between species *i* and *j* and *s* is species richness and Δ^+ is calculated as above (Clarke and Warwick 2001).

Finally, I performed Multivariate Analysis of Variation (MANOVA) with SYSTAT (Wilkinson 2009) on the diversity measures and species abundance to examine differences within and among sites using the summer diversity indices and the monthly samples from the FWNC.

General Ordination Data Preparation Methods

I used ordination analyses to test the hypotheses that the environmental factors measured distinguished sites and that ant species would respond to these environmental factors with differential preferences for sites. I also used the ordination analyses to test the pattern of ant species among habitat types (as described earlier) and that *P. comanche*'s occurrence correlated with specific ant species.

I conducted Detrended Canonical Analysis (DCA) and determined that the appropriate models were linear. I, then, performed Principle Components Analysis (PCA) to confirm underlying patterns in the environmental variables, species occurrence and species count data. A PCA for the environmental variables would also confirm that these variables distinguish sites. If the ant species have environmental preferences for these variables, I expected that these species would reflect this by consistently being found in some sites and not others. The ordination models should demonstrate this.

Because the DCA indicated a linear model, I conducted RDA to compare the ground active ants among sites and determine which environmental variables were significant predictors of these species. I eliminated species that made up less than 1% of the complete count data from the RDA analyses (Dufrene and Legendre 1987). This action removed species which had many zero values and which had single occurrences (singletons), in three cases represented by a single queen. Such queens are likely to represent dispersal into the area rather than established colonies. I transformed the quantitative environmental variables with a Log_{10} transformation to improve normalcy and to accommodate the different metrics. I standardized species count data by the trap sampling area of 200 m^2 to facilitate comparisons among sites (Whittaker 1972). I conducted all ordination analyses with CANOCO (ter Braak and Šmilauer 2002a; ter Braak and Šmilauer 2002b; Lepš and Šmilauer 2003).

Redundancy Analysis (RDA) Methods

In order to test the environmental responses of ant species, I conducted RDA on species presence and count data with all environmental variables as predictors. The models tested were: species presence in late summer for all 21 sites, species counts in late summer for all 21 sites; species presence compiled over June, July, and August for the 17 sites in the FWNC; species presence for the time series of each month (June, July, and August) for the 17 sites in the FWNC; and species counts for the same time series for the 17 sites in the FWNC. I tested a total of five models. I used the RDA results to test habitat type (H_{02}) and *P. comanche* presence effects (H_{03}).

To evaluate each model, I ran a global test that included all environmental variables and tested the significance of the first ordination axis and all the ordination axes together. If the global test were significant, I tested the environmental variables as predictors with a Monte Carlo permutation test and forward selection of the variables. This test evaluated each variable as a sole predictor and tested the additional variation explained as each variable was added to the model. I used this information, the inflation factor and collinearity of predictor variables to manually test combinations of environmental variables and variable interactions in order to select variables for the final model (Blanchet et al. 2008; Gómez-Anaya et al. 2011).

I addressed spatial autocorrelation by constructing a polynomial of the spatial coordinates for the center of the sampling areas and temporal autocorrelation by including a Julian calendar variable (Legendre 1993; Borcard and Legendre 2002; ter Braak and Šmilauer 2002b; Lepš and Šmilauer 2003; Horak 2013). I addressed temporal patterns in the monthly samples by using a whole block, split plot design with each site as a block and the months sampled as plots within blocks as recommended by ter Braak and Šmilauer (2002b). I constructed ordination diagrams to illustrate the species pattern with respect to significant environmental variables in CANOCO (ter Braak and Šmilauer 2002a).

Results

Across all the samples (21 sites), I collected 27,841 individual ants from five subfamilies, 18 genera, and 38 species. More specifically, in the FWNC (17 sites) I collected 26,071 individual ants from all five subfamilies, including singleton specimens from the subfamilies Dorylinae (*Labidus coecus*) and Ponerinae (*Hypoponera opacior*), 18 genera, and 35 species; in the THNA (THP and STP), I collected 1,439 individual ants from 3 subfamilies, 9 genera, and 15 species; and in the SWNP (SP and SPW), I collected 414 individual ants from 3 subfamilies, 10 genera, and 19 species. By far most species were of the subfamily Myrmicinae (24 species), followed by Formicinae (9 species) and then Dolichonderinae (3 species). Of all the ants collected, 8 were singletons, including an unusual *Temnothorax* specimen (unidentified) and one queen from each of three *Strumigenys* species *(S. louisinanae, S. margaritae* and *S. membranifora*). The singletons were all found in different sites, except the *Aphaenogaster* *carolinensis* and the unidentified *Temnothorax* sp. which I collected in SPW. I collected four species from each of the genera *Pheidole* and *Solenopsis* which included the most frequent, highest count species (Figure 3.2: I provide species lists in Appendix B).

I found *Aphaenogaster ashmeadi*, *A. carolinensis, Camponotus pennsylvanicus*, *Prenolepis imparis* and *Temnothorax* sp. only in wooded sites and *Brachymyrmex patagonicus*, *Nylanderia terricola*, *Pheidole bicarinata*, *P. lamina*, *Pogonomyrmex barbatus*, *Solenopsis subterranea*, *Strumigenys louisinanae*, *S. margaritae*, S. *membranifora*, and *Temnothorax texanus* only in prairie sites. Other species were collected in both prairie and wooded sites despite known nesting preferences, such as is known for *P. comanche*. This result probably reflects movement patterns of these species. I used species abbreviations in the Whittaker plots and the RDA (Table 3.2).

Table 3.2 Species Abbreviations

Abbreviation	Species Name	Subfamily
Apcar	*Aphaenogaster carolinensis*	Myrmicinae
Apas	*Aphaenogaster ashmeadi*	Myrmicinae
Aptr	*Aphaenogaster treatae*	Myrmicinae
Brde	*Brachymyrmex depilis*	Formicinae
Brpat	*Brachymyrmex patagonicus*	Formicinae
Camam	*Camponotus americanus*	Formicinae
Camp	*Camponotus pennsylvanicus*	Formicinae
Crli	*Crematogaster lineolata*	Myrmicinae
Crce	*Crematogaster cerasi*	Myrmicinae
Dofl	*Dorymyrmex flavus*	Dolichonderinae
Fomc	*Forelius mccooki*	Dolichonderinae
Fopr	*Forelius prunosis*	Dolichonderinae
Forbio	*Formica biophilica*	Formicinae
Hypopac	*Hypoponera opacior*	Ponerinae
Lab	*Labidus coecus*	Dorylinae
Movir	*Monomorium viridae*	Myrmicinae
Nylare	*Nylanderia arenivaga*	Formicinae
Nylter	*Nylanderia terricola*	Formicinae
Nylviv	*Nylanderia vividula*	Formicinae
Phbic	*Pheidole bicarinata*	Myrmicinae
Phden	*Pheidole dentata*	Myrmicinae
Phlam	*Pheidole lamia*	Myrmicinae
Phmet	*Pheidole metallescens*	Myrmicinae
Pogbar	*Pogonomyrmex barbatus*	Myrmicinae
Pogcom	*Pogonomyrmex comanche*	Myrmicinae
Preno	*Prenolepis imparis*	Formicinae
Sol(gem)	*Solenopsis (geminata group)*	Myrmicinae
Solin	*Solenopsis invicta*	Myrmicinae
Solmol	*Solenopsis molesta*	Myrmicinae
Solsub	*Solenopsis subterranea*	Myrmicinae
Solxy	*Solenopsis xyloni*	Myrmicinae
Strlou	*Strumigenys louisinanae*	Myrmicinae
Strmar	*Strumigenys margaritae*	Myrmicinae
Strmem	*Strumigenys membranifora*	Myrmicinae
Temper	*Temnothorax pergandeia*	Myrmicinae
Temtex	*Temnothorax texanus*	Myrmicinae
Tem_unk	*Temnothorax spp.*	Myrmicinae
Trasept	*Trachymyrmex septentrionalis*	Myrmicinae
Tratur	*Trachymyrmex turrifex*	Myrmicinae

Diversity among Sites

Species and Taxonomic Diversity

I used species and taxonomic diversity measures to test broadly for species differences among sites (I present individual site diversity indices in Appendix C.). Except for Simpson's Diversity Index, the indices were highest for the Aquilla Prairie sites (Table 3.3). The MANOVA uncovered significant differences in diversity among the FWNC samples (Wilk's Lambda = 0.059 with p = 0.007). Post hoc tests revealed this difference between the Aquilla Prairie and Wooded Sites (p = 0.038) with significant effects from Simpson's Diversity Index (p = 0.022) and Berger-Parker Dominance (p = 0.021). The taxonomic indices did not significantly differ indicating similar taxonomic structure across sites.

Table 3.3 α Diversity Indices for the Late Summer by Cluster

Habitat Type	S(SD)	1/D (SD)	d (SD)	Δ (SD)	Δ* (SD)	Δ+ (SD)	Λ+ (SD)
Aquilla Prairie	9.00 (1.41)	3.55672 (1.5451)	0.4324 (0.1588)	1.4745 (0.4397)	2.3561 (0.4440)	0.2503 (0.0823)	0.3370 (0.1017)
Other Prairie	7.89 (2.47)	3.7666 (1.2965)	0.4256 (0.1708)	1.3932 (0.6822)	2.3000 (0.8450)	0.2111 (0.1169)	0.3053 (0.1597)
Wooded Sites	8.50 (2.65)	4.1221 (1.0084)	0.4162 (0.1207)	1.3504 (0.2696)	1.8173 (0.3188)	0.2063 (0.1452)	0.2509 (0.1837)

Whittaker Plots and Dominance

I used the Berger-Parker Dominance Index and Whittaker Plots to compare species count data as a possible indication of community structure and species interactions. While the EPP site had both *Forelius mccooki* and *Solenopsis* (gem) as numerically co-dominant, overall *Solenopsis* (gem) had the most frequent, high counts (Figure 3.2). It is difficult to know what this means since the count includes both *S. invicta* and *S. xyloni*. Moreover, it is not clear from field observation that *S. invicta* is particularly abundant in terms of colonies. It may be best to consider this group as a functional grouping rather than as individual species.

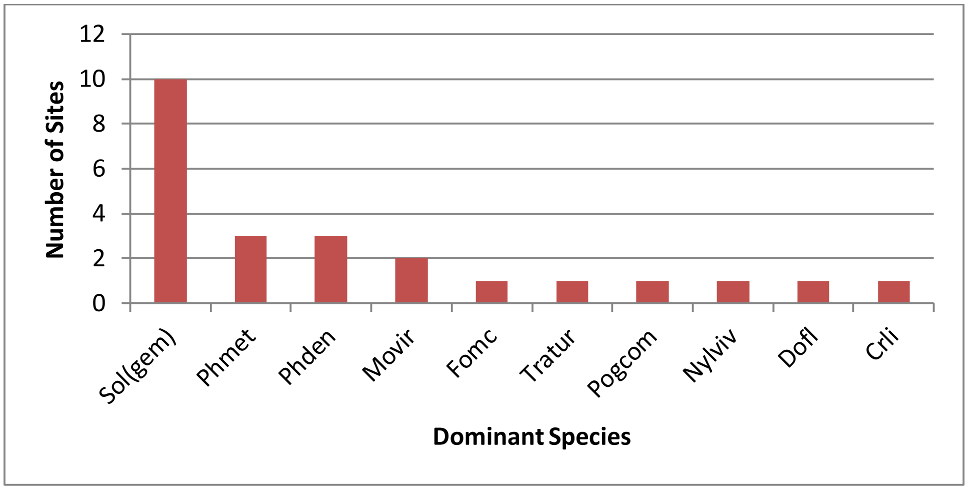
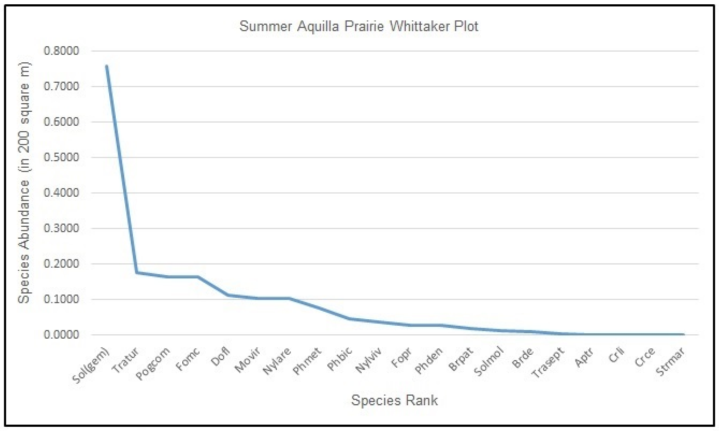


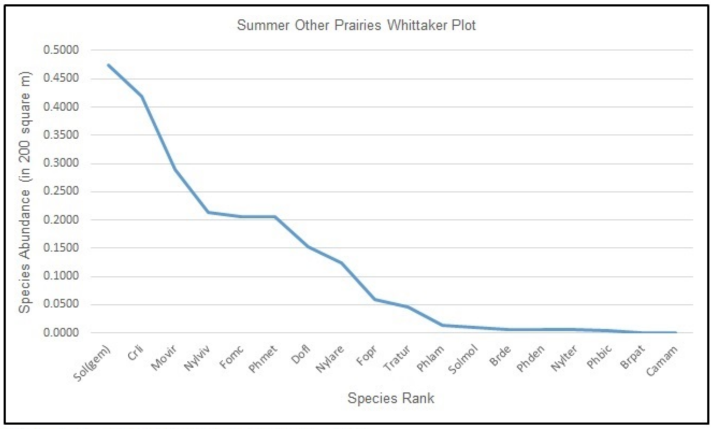
Figure 3.2 Summer Dominant Species Frequency

The Whittaker plots indicate differences in species counts and richness which may reflect community structure and species interactions. Because Whittaker plots, as traditionally understood, may indicate the impacts of most abundant species on lower ranked species, these results are suggestive of dominant, subdominant and submissive functional groups based on numerical and behavioral dominance for ant species (Vepsäläinen and Pisarski 1982; Savolainen and Vepsäläinen 1989; Cerdá et al. 2013).

The Aquilla Prairies show the possible effects of numerical dominance with many low count occurring species (slope = 0.58; Figure 3.4). The Wooded Sites (slope = 0.06; Figure 3.3) have less of such an effect with several subordinate species (moderate counts) and many submissive species (lowest counts) followed by the Other Prairies (slope = 0.06; Figure 3.4) with the most relaxed Whittaker plot indicating greater evenness. Because *Solenopsis* (gem) was the most frequent dominant species, this result may indicate its impact on other ant species with implications for the effects of invasive species – and generally about such hyper-dominant species in general – since there is a similar effect of *Pheidole dentata* in the wooded sites. It is difficult to know what this means since the *Solenopsis* (gem) abundance includes ants from both *S. invicta* and *S. xyloni*. Moreover, it is not clear from being in the sites that *S. invicta* is particularly abundant. However, if *S. invicta* and *S. xyloni* have similar ecological niches, it may be best to think of this abundance in terms of functional group rather than specific species (Campbell et al. 2007; Gagic et al. 2015).



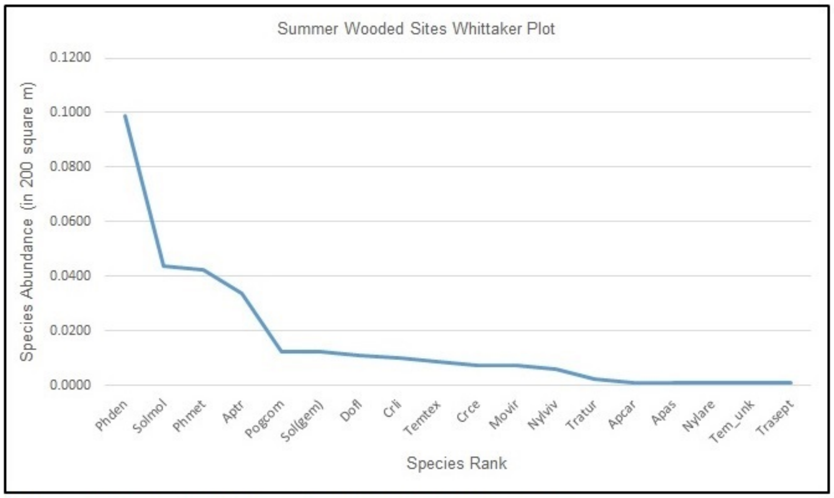
A) Aquilla Prairies: EPF, EPP, EPT, EP2, GL, T1P and T2P
Slope of the first segement = 0.58



B) Other Prairies (O): AA, AB, BR, EP3, GH, HC, SP, STP and THP
Slope fo the first segment = 0.06

Figure 3.3 Whittaker Plots for Aquilla Prairies and Other Prairies

The Whittaker plots suggest that *P. comanche* fits the numerically subordinate functional group (Vepsäläinen and Pisarski 1982; Savolainen et al. 1989; Arnan et al. 2011a; Cerdá et al. 2013).



Summer Whittaker plot for Wooded Sites: EPW, SPW, T1W and T2W
Slope of the first segment = 0.06

Figure 3.4 Summer Wooded Sites Whittaker Plot

Ordination Analysis

The PCA results for the environmental variables confirmed their use as predictors of ant species (First eigenvalue explains 40% and second explains 17% of the variation for a total of 57% explained). The only significant RDA model was the late summer species presence model (hereafter, Late Summer Model) with two significant environmental variables, percent litter cover and drainage. There was no significant interaction between these variables. The first canonical axis explains 16.5% of the variation ($p = 0.020$) and the second axis explains 8.7% ($p = 0.020$ for all the canonical axes), for a total of 25.2% explained variation (goodness of fit based on the eigenvalues, λ, $\frac{\lambda_1+\lambda_2}{\sum\lambda_i} = 47.1$; Jongman et al. 1995). This model explains 22.9% of the variance in *P. comanche* occurrence which was more positively responsive to drainage and less responsive to percent litter cover.

Species occurrence and their level of responses to percent litter and drainage differed as these variables varied among sites (Figure 3.5). The sites are a somewhat complex relationship of these variables despite there being no significant interaction between them.

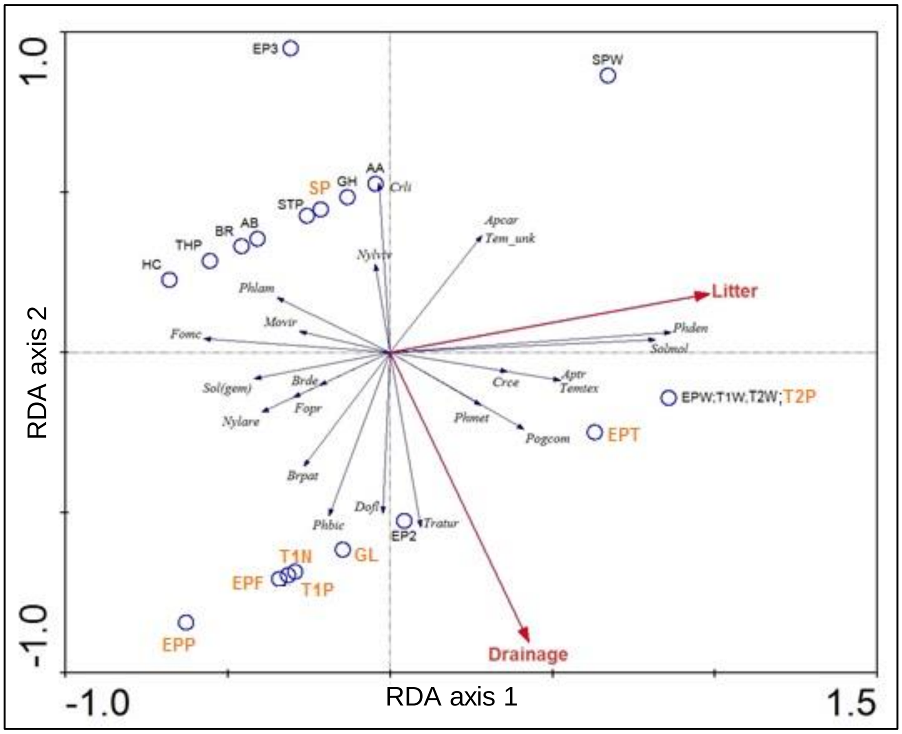


Figure 3.5 Late Summer Model Triplot
Sites with *P. comanche* colonies are designated with orange letters.

Despite the spread of species, there is some indication of an environmental gradient to which some species are particularly allied (indicated by longer species arrows; Figure 3.5). Percent litter cover and drainage significantly influence ant occurrence in the different habitat types – so that the ants present in the woods respond most to percent litter cover and those that are present in the prairie respond most to drainage. Species closely associated with one another may describe distinct ant assemblages with other species less strongly determined by the predictor variables. There are six such closely associated groups: 1) *Brachymyrmex depilis* (Brde), *Forelius prunosis* (Fopr), and *Nylanderia arenivaga* (Nylare) share the same trajectory but with differing levels of negative association with percent litter cover (lower left); 2) *Crematogaster lineolata* (Crli) and *Nylanderia vividula* (Nylviv) share a similar trajectory with a negative association with drainage (upper middle); 3) *Aphaenogaster carolinensis* (Apcar) and a *Temnothorax* species (Tem_unk) completely overlap with a negative association to drainage and a more positive association with percent litter cover (upper right); 4) *Pheidole dentate* (Phden) and *Solenopsis molesta* (Solmol) are closely associated with percent litter cover and less with drainage (middle right); five) *Aphaenogaster treatae* (Aptr), *Crematogaster cerasi*,(Crce) and *Temnothorax texanus* (Temtex) share the same trajectory with a positive association with percent litter cover and a more positive association with drainage; and 6) *Pheidole metallescens* (Phmet) and *P. comanch*e (Pogcom) share the same trajectory with a positive association with percent litter cover and a stronger, positive association with drainage.

Hypothesis Testing

Besides testing for differences among ant assemblages and ant response to environmental variables, I also tested the hypotheses that the ant assemblages could be predicted by habitat type (prairie *versus* woods) and by the presence of *P. comanche* (H_{03}).

The sites generally cluster by habitat types (from the hierarchical clustering analysis): Aquilla Prairies consisting of EPF, EPP, EPT, EP2, GL, T1N, T1P and T2P; the Other Prairies consisting of AA, AB, BR, EP3, GH, HC, SP, STP and THP; and the Wooded Sites consisting of EPW, SPW, T1W and T2W. The MANOVA confirmed significant differences of species among sites (Wilk’s lambda = 0.059 with p = 0.007) with significant differences between the Aquilla Prairies and Wooded habitats (p = 0.038). The RDA indicates that the prairies and their ant species are more strongly predicted by drainage than percent litter cover while percent litter cover is a stronger predictor for ant species in the woods.

The deep sand prairies are characterized by a strong positive relationship with drainage and a less, strong negative relationship with percent litter cover. *P. comanche* nests in most of these prairies (Prairies where *P. comanche* nests are designated with orange type; Figure 3.5). Surprisingly, the SP site, where there are some 60 colonies of *P. comanche*, groups with the non-sandy prairies (upper left) that lack *P. comanche* and although EP2 looks like and shares similar environmental characteristics with other prairies where I find *P. comanche*, there are no *P. comanche* colonies in EP2. The most frequently dominant species are in different areas of the triplot though they co-occur. The presence of *P. comanche* (as a predictor for the ant community) was not significant. There were no significant changes in the ant community correlated with *P. comanche* presence. Clearly, the presence of *P. comanche* does not influence the composition of these ant assemblages.

Discussion

Although most of the ant species were found in most sites, there were some species more closely associated with specific sites, as indicated by the longer species arrows in the RDA plot. This result suggests there may be subtle differences in the assemblages among sites. These differences in species occurrence and community structure may be attributed to prairie and wood habitats (Vance et al. 2007; Fraser et al. 2008; Arnan et al. 2011b). While the ant species do differ by site, the results as a whole indicate significant differences between prairie and wooded habitats, including differences in diversity indices and species occurrence. Though not specifically tested, these results suggest that ant species occurrence is largely impacted by differences between these habitats rather than specific factors (or combinations of factors) unique to individual sites. Although percent litter cover and drainage were the significant RDA factors, there may be other factors (or combinations) which characterize prairie *versus* woodland important in ant response. For instance, factors such as humidity, moisture and surface temperature are likely to impact ant activity and occurrence. These results suggest that many of these ant species may tolerate a broad range of environmental variables, i.e., they are not narrowly specialized.

That several species were collected only in prairie or wooded sites while others were collected in both probably reflects activity and foraging patterns and not necessarily nesting site preferences. Regardless, the species collected are members of those ecologies whether their colonies nest in that area or forage there and so they have some role there. For instance, although *P. comanche* was collected in several wooded sites, they do not nest there. Rather, *P. comanche* forages on elm seeds (*Ulnus* spp.) within the wooded areas (A.B.M., personal observation).

Impacts for P. comanche

P. comanche responded most strongly to drainage which is consistent with a requirement for deep sand nesting sites (Cole 1968; Taber 1998). Therefore, *P. comanche* might be considered an indicator of deep sand, particularly the Aquilla Sand Formation in the FWNC. However, I found that this is not strictly the case. Although *P. comanche* is only found in such prairies in the FWNC, they are not found in all such areas, for instance *P. comanche* is absent from the EP2 site which is an Aquilla soil site. Other ant species found in the Aquilla sites are also found in EP2. What makes a difference for *P. comanche* remains unclear. This may be a random occurrence. However, considering the several outlier colonies in other sites (Chapter 2), it is unclear why *P. comanche* would not have dispersed into and survived in the EP2 area.

Further, *P. comanche* was also found in the Crosstel-Urban soil complex which has a shallow sandy surface horizon (about 10 cm) above clay (up to 3 m below the sand horizon) and is considered a moderately well drained soil (SP site). Despite *P. comanche* being strongly predicted by drainage, *P. comanche* was not found in other soils with a similar soil profile and drainage pattern. If sandy soil is necessary for *P. comanche* nest construction, this result suggests that sand is only required in the top portion of the nest where the foragers and other ants congregate. Preliminary nest casts of *P. comanche* indicate an upper structure of chambers in the top 10 – 12 cm of the nest, probably where the ants congregate near the nest entrance (A.B.M., personal observation). The occurrence of 60 some colonies of *P. comanche* in the SP site suggests that there may be multiple factors affecting their nest construction and survival. *P. comanche* is found only in certain sites in striking comparison to most other ant species. While *P. comanche* absence from the EP2 site and that *P. comanche* colonies do not fill the other Aquilla prairies may be a historical accident or due to some other reason, *P. comanche* is not restricted to deep sand prairies. The local presence and distribution of *P. comanche* remains puzzling.

P. comanche appears to co-occur with *Pheidole metallescens* and *Trachymyrmex turrifex* (i.e., their species arrows in the RDA have the same trajectory and length). Because *Trachymyrmex turrifex* also nests in sandy soils and *Pheidole metallescens* harvests grass seeds, this co-occurrence is probably a result of shared preferences and not a result of any particular species interaction. Despite the suggestion that *P. comanche* may have important impacts on the habitat due to nest construction (i.e., above ground, *P. comanche* clears on average a 30 cm^2 area for the nest mound and up to another 1 m^2 area surrounding the nest) and foraging activities (primarily on grass seeds), there is no indication that *P. comanche* has a strong impact on other ant species. Despite this correlation in occurrence, the ant community did not change in the Aquilla sites with regard to *P. comanche* presence.

Thus, at this localized ecological scale in a humid subtropical climate, local, abiotic factors may be more significant for these populations and assemblages than species interactions (which play a lesser role) or regional scale factors such as climate (Dobzhansky 1950; Fisher 1960; Schoener 1986; Ricklefs 1987). This result probably arises from the broad niche, generalist nature of most of these species and the regional species pool from which local species occurrence is drawn (Dr. James Trager, personal communication; Dr. Kimberly Franklin, Arizona-Sonora Desert Museum, Tucson, AZ, personal communication).

Broader Implications

The finer scale of possibly subtle differences in these ant assemblages among sites presents a challenge to the use of ant species for tracking changes in ecosystems at a local ecological scale (Andersen 1991; Andersen 1992; Andersen 1997; Majer and Nichols 1998; Andersen et al. 2004). In contrast to Andersen's work, Franklin did not find support for such sensitivity or species turnover but rather concluded that ant species are resilient to vegetation changes (2012). Although Andersen did adjust his functional groups for North American systems (Andersen 1997), my different results may arise largely from the difference in specialization of tropical and Australian species in contrast to less specialized species of other climatic areas (Dobzhansky 1950; Fisher 1960). Without more information on the ecology of these species, it is difficult to assess the usefulness of these functional groups, especially with regard to dominance for these sites.

In these Texas sites, the ant species are more generalist probably in part as a response to seasonal environmental variation (Whittaker 1972). Their persistence may be related to their tolerance for a wider range of environmental and climatic conditions supported by their nesting habit where their nest architecture maintains a suitable environment and protects from the adverse conditions aboveground including weather and predation (Franklin, personal communication). The general similarity of species occurrence across these sites is likely the result of broad niches combined with local species occurrence being drawn from the same regional pool. Thus, the evolutionary, phylogenetic, and biogeographic history of the region may be a more significant factor in determining species occurrence with climate and soil type the next most significant factors.

Chapter 4

The Role of Nest Mate Discrimination in the Spatial Pattern of *P. comanche* Colonies

Introduction

The cohesiveness of ant colonies arises from the close kinship of workers, which varies with the number of times queens mate and the number of alate-producing queens in a colony (Hamilton 1964a; Hamilton 1964b; Vander Meer and Morel 1998; Hölldobler and Wilson 1990; Lach et al. 2010). Workers recognize this kinship in a colony specific odor, distinguishing nestmates from non-nestmates (Hölldobler and Wilson 1990). This discrimination ability aids in monitoring and promoting colony survival by the detection of potential intruders, including parasites and other ants which may steal brood (Guerrieri et al. 2009; Fürst et al. 2011). Such discrimination involves the detection of cuticular hydrocarbons by antennal contacts (Le Moli et al. 1983; Gordon et al. 1993; Vander Meer and Morel 1998; Wagner et al. 2000; Lach et al. 2010; Gill et al. 2012). These hydrocarbons are the basis for this odor which also includes chemical influences from the queen, the internal nest environment, diet, and the external environment workers frequent (Wagner et al. 1998; Wagner et al. 2000; van Zweden and d'Ettorre 2010). This odor is expected to vary among colonies but also over time as the environment of the workers changes (Esponda and Gordon 2015). The ability to recognize non-nestmates appears to be learned, an important feature since the turnover of workers happens within seasonal changes which may affect environmental inputs into colony odor (Pamilo et al. 1997; van Wilgenburg et al. 2010).

The discrimination and lack of discrimination of nestmates from non-nestmates has been demonstrated in many ant species (Howard and Blomquist 2005). Because competition expressed in aggression has long been hypothesized to structure ant populations and assemblages, it is generally expected that ants from different colonies will distinguish non-nestmates and interact aggressively based on the perceived level of threat (Hölldobler and Wilson 1990; Hölldobler and Wilson 2009; Scharf et al. 2011). For many species, such discrimination is implicated in maintaining territories, including the control of foraging areas and trails and therefore, may play a significant role in spatial structuring of ant populations including nest locations (Hölldobler 1974; Hölldobler 1976; Roulston et al. 2003). Conversely, the lack of such discrimination facilitates the formation of so-called supercolonies which enhance the invasive qualities of such ants as the Argentine ant (*Linepithema humile*; Chen and Nonacs 2000) and the red imported fire ant (*Solenopsis invicta*; Breed et al. 1991; Jeral et al. 1997; Stuart and Hebers 2000; Schmidt et al. 2010). These species often have multiple, highly fecund queens who have multiply mated, thus, reducing the kinship among workers. This reduction in kinship may contribute to the acceptance of greater variety in odor arising from the diversity of cuticular hydrocarbons of nestmates.

Because colonies of the genus *Pogonomyrmex* are monogynous and typically found in low productivity habitats in which high levels of competition for food resources are likely, nestmate discrimination may be an important mechanism in intraspecific competition (Gordon 1989a; Wagner et al. 1998; Wagner et al. 2000). *P. barbatus* not only distinguishes nestmates from non-nestmates but also distinguishes close neighboring colonies from colonies located at greater distances beyond the typical foraging range (Gordon 1989a). They show higher levels of aggression towards close neighbors with which competition is likely to be greater (This is a reverse of the dear enemy phenomena which proposes that animals are less aggressive with neighbors with whom they are familiar; Jaeger 1981; Lange et al. 2000; Grangier et al. 2007; Newey et al. 2010a; Müller and Manser 2007; Saar et al. 2014). Some *Pogonomyrmex* species move their nests, a trait which might be employed to reduce colony density and relieve competition for food resources and nest locations (Hölldobler 1976). However, colony relocation by *P. barbatus* and *P. badius* was not connected to colony density, age or size (Gordon 1989a; Tschinkel 2014). Besides colony level factors, the disposition of individual ants and the interaction context also influence aggressive behavior in *P. barbatus* (Gordon and Kulig 1996; Scharf et al. 2011). Nestmate discrimination is a multifaceted interaction incorporating individual and colony level aspects typical of eusocial species (Gill et al. 2012).

Because nestmate discrimination has been shown to be important in colony interactions with potential to influence colony survival and spatial patterns, I hypothesized that nestmate discrimination was an important factor in *P. comanche* colony spatial distribution. My null hypotheses were that: *P. comanche* does not distinguish nestmates from non-nestmates with an aggressive response (H_{05}) and that any aggressive interaction is equally likely among *P. comanche* ants irrespective of distance between interacting colonies (H_{06}). On the contrary, if *P. comanche* distinguishes neighbors as a function of distance, such distinction would support frequency of encounter and aggression as possible mechanisms for colony spatial and behavioral organization (Gordon 1989a).

I used a behavioral assay introducing ants and then, observing the occurrence of aggression (Suarez et al. 1999; Roulston et al. 2003; Buczkowski and Silverman 2005). This type of interaction is sometimes used to determine if ants are from different colonies (Dr. Terry McGlynn, California State University Dominguez Hills, personal communication). Because context may influence the response, I carried out two assays to test these hypotheses: one in the neutral context of an artificial arena made of plastic and the other in the context of a nest mound where nestmate discrimination might be important in defense of the colony (Bernstein and Gobbel 1979; Gordon 1989a; Gordon 1989b; Buczkowski and Silverman 2005; Tanner and Adler 2009).

Materials and Methods

Nest Mate Discrimination Assay

I tested nestmate discrimination using the outcome of behavioral interactions of foragers (Suarez et al. 1999; Roulston et al 2003; Buczkowski and Silverman 2005; Esponda and Gordon 2015). As evidence of discrimination, I expected an aggressive response to non-nestmates rather than to nestmates (Hölldobler and Wilson 1990; Hölldobler and Wilson 2009; Lach et al. 2010). The possible aggressive responses included two noncontact displays – a mandible gape and gaster wag – and two types of contact – grabbing a body part and an attempt to sting (Hölldobler and Wilson 1990; Wagner et al. 2000; Lach et al. 2010; van Wilgenburg et al. 2010). A mandible gape is a threat display in which the mandibles are spread apart as one ant faces another (Wagner et al. 2000; Guerrieri and d'Ettorre 2008). A gaster wag is the vibration or movement of the gaster, the posterior portion of the abdomen, which probably involves the release of pheromones. Aggressive, physical contact includes one ant grabbing another with the mandibles. This can be any body part but antennae and legs are common since they project from the body making them easy to grab. In the context of the nest, the grabbing ant may move the offending ant off the nest mound (Hölldobler 1976; A.B.M., personal observation). Grabbing may escalate to a fight of sustained grabbing on the part of both ants including attempts to sting. These aggressive behaviors are non-exclusive aggressive interactions in that noncontact aggression may escalate into contact aggression (Cole 1988; Hölldobler and Wilson 1990; Guerrieri and d'Ettorre 2008; A.B.M., personal observation).

Because response may vary with perceived threat (Hölldobler and Wilson 1990; Hölldobler and Wilson 2009; Scharf et al. 2011) and animals are often reluctant to fight due to the cost (Gordon and Kulig 1996; Starks et al. 1998), I considered the occurrence of any form of aggression as sufficient to establish nestmate discrimination. I conducted interactions in artificial arenas and on nest mounds to account for the importance of context. I used plastic cups measuring 9 cm at the upper diameter tapering 7 cm to a five cm diameter bottom with a capacity of 275 ml as arenas. Though size of arena may not be important (Roulston et al. 2003), it has been suggested that ants perceive each other at distances of one – two cm (Gordon et al.1993; Lahav et al. 1999). I chose this five cm diameter size (bottom of the cup) so that the ants would be close enough to perceive each other and respond (A.B.M., preliminary work). To reduce any chemical cues that might influence subsequent encounters, arenas were thoroughly washed and dried after each use and used only once on any day.

I collected foragers as they returned to the nest mound in the sites where the assays were conducted, placed them individually in small plastic tubes and held them for 20 minutes prior to interactions in order to calm them (Gordon 1989a). To reduce any chemical cues that might influence subsequent encounters, the tubes were washed and dried after each use and used only once on any day. From these tubes, I introduced the ants into the arena simultaneously. I introduced the ants onto the nest mounds within 10 cm of the central nest opening. I recorded the interactions in the artificial arenas with a Canon Vixia HF M400 camcorder and subsequently observed the first minute of these recordings. While a variety of times have been used for this kind of assay (from one – five minutes), I chose a minute because within this time the ants have sensed each other and responded (Dr. Terry McGlynn, personal communication; A.B.M., preliminary work). The interactions on nest mounds were observed until the introduced ant left the mound.

The on-mound interactions were recorded as observational, field notes since I conducted these interactions prior to obtaining the camcorder.

Assay Contexts

The arena was a neutral context in which the ants were expected to respond only to the presence of each other without the influence of any contextual or social cues. The nest mound is the most likely context for aggression since in this context even a non-aggressive, home ant may perceive a threat and defend the nest from the introduced ant.

I conducted the assays on mounds in November 2009 in EPP, SP and T1P. I conducted the assay in arenas using 13 of the 16 colonies in GL during the summer of 2012. Eleven of these were established colonies, one was a newly founded colony (new colony or #8), and one was 211.7 m away from the closest of the other colonies which I designated as the long distance colony (LD or # 13) and considered out of the foraging range of the other 12 colonies and potentially unknown. The three colonies not used were located between colony 12 and LD, 50 m from the other colonies. I considered the first 12 colonies a neighborhood in which colonies were close enough to have overlapping foraging ranges and therefore, to have frequent interactions that I hypothesized would influence their behavior and the colony spatial pattern. This linear, spatial arrangement simplified the possible interactions among ant colonies, since neighbors were found only in one or two directions and not multiple directions. I generated neighborhood maps with ArcMap using GIS coordinates for these 13 colonies (Figure 4.1 and 4.5; Esri 2012).

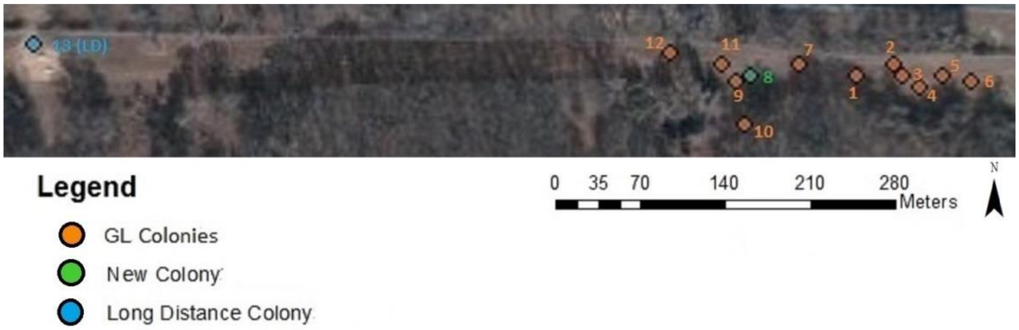


Figure 4.1 Map of the GL Site Neighborhood of *P. comanche* Colonies

Arena Interactions

I set up the arenas on a box in the shade adjacent to the *P. comanche* nesting area. I brought ants to this box in separate vials, let the ants rest for 20 minutes, and simultaneously introduced the ants into the arena. I recorded interactions for just over a minute and wrote notes immediately after the interaction. Each digital recording was given a code which was used to identify the recording and index it to the notes. I later viewed the digital recordings by coded number only, making these blind viewings (van Wilgenburg and Elgar 2013; Esponda and Gordon 2015) and obtained data from the first minute of the recordings for the analyses. I only used recordings that followed this procedure and had no other problems which might influence the interactions (dropping the camcorder, ants climbing out of arenas, etc.).

Nest Mound Interactions

For the mound interactions, I released a forager on an active nest mound within 10 cm of the entrance and observed this ant until she left the mound. For the interactions between colonies, I conducted interactions between workers with their own colony and with other colonies. I also conducted reciprocal interactions, such that colonies from which I collected workers for release became host colonies for interactions with the workers of other colonies. This provided the possibility to detect one colony's response to these different roles as well as to detect if any colony were generally pugnacious.

Analyses

For all interactions, I recorded the occurrence of aggression in any form (gaster wag, mandible gape, grab, sting/fight) as aggression. Because physical contact is necessary to detect nest odor, I used only the recordings of nest mound interactions in which there was physical contact.

In order to test for a distance effect and establish neighborhood interactions in GL, I recorded the distances between and identities of interacting colonies. For the arena interactions in GL, distances between colonies ranged from 0.0 m (self introductions) to 359.7 m (the farthest colony from the LD colony). For the mound interactions distances ranged from 0.0 m (self introductions) to more than 50 m.

From the actual distances between colonies, I constructed distance categories for analysis. In order to avoid categories without any colonies in that distance category and an attempt to spread the actual observations evenly, I constructed 6 categories: S (self) for introduction to the ant's own colony and five categories of neighbor distances, N1 – N5 (Table 4.1; The "# of Colonies" is the number of colonies that are found in that distance category out of the 13 colonies.).

Table 4.1 Distance Categories for *P. comanche* Arena Interactions

Distance Category	Distance	# of Colonies
S	0.0 m	13
N1	0.1 – 11.0 m	5
N2	11.1 – 20.0 m	6
N3	21.1 – 50.0 m	7
N4	50.1 – 106.0 m	12
N5	> 106.1 m	13

In order to test for a distance effect and because the mound interactions were done in 2009, the distance categories were set up differently than those for the neighborhood in GL: S for introduction to the ant's own colony and four categories of neighbor distances, N1 – N4 (Table 4. 2)

Table 4.2 Distance Categories for *P. comanche* Mound Interactions

Distance Category	Distance
S	0.0 m
N1	0.1 – 4.9 m
N2	5.0 – 11.0m
N3	11.1 – 50.0 m
N4	> 50.1 m

To test for colony level aggressive tendencies I examined the occurrence of aggression for each colony. I scored interactions for aggressive responses over a one-minute period. I recorded data as occurrence (binary: 0 for the behavior did not occur and 1 for the occurrence).

I used the X^2 test for independence or Fishers' Exact test to test for a significant association between aggression and distance (Sokal and Rohlf 1981; Whitehouse and Jaffe 1995; Dytham 2011; McDonald 2014). For the analysis of interactions on nest mounds which indicated a significant difference between self introductions and all neighbor interactions, I conducted all pairwise X^2 analyses (10) as post hoc tests and used a Bonferroni correction for the p value to determine the specific distance categories at which aggression was more frequent (McDonald and Gardener 2000; McDonald 2014). This correction spreads the usual α value of 0.05 evenly across the pairwise comparisons. Each pairwise comparison has an α threshold of 0.005 (0.05/10 comparisons). Thus, a post hoc comparison had to have a $p < 0.005$ to be significant. I conducted the X^2 and Fisher's exact test analysis with on-line utilities at http://quantpsy.org (Preacher 2001 and Preacher and Briggs 2001, respectively). For the X^2 analyses I report X^2 and p values for tables larger than 2 X 2 and Yates' X^2 and Yates' p values for the 2 X 2 tables. Yates' correction for continuity improves the accuracy of the X^2 test for smaller tables (with one degree of freedom; Yates 1934; Preacher 2001).

Finally, I brought the results of arena and on mound interactions together to construct neighborhood interactions based on nestmate discrimination and frequency of aggression as a function of distance between colonies.

Results

Arena Interactions

In the arena interactions, I tested nestmate discrimination in a neutral context by comparing the results for the self introductions (Self) with all neighbor distance categories (N1 – N5 considered as Neighbor). I, then, conducted a comparison of aggression occurrence between all distance categories (N1 – N5; Table 4.1). For the general test of nestmate discrimination in this neutral context, I also compared the occurrence of aggression by colony (Table 4.3).

The comparison of self introductions (Self) with all distance categories (Neighbor) gave Yates' X^2 of 1.8050 with Yates' p of 0.1791 (N = 539, $\alpha = 0.05$ and df = 1; Figure 4.4). The comparison of aggression with distance categories gave a X^2 of 3.2880 with a p of 0.5108 (N = 539; $\alpha = 0.05$ and df = 1; Figure 4.5). Neither of these comparisons was significant. These results indicate that *P. comanche* either doesn't discriminate nestmates or doesn't respond with aggression in a neutral context.

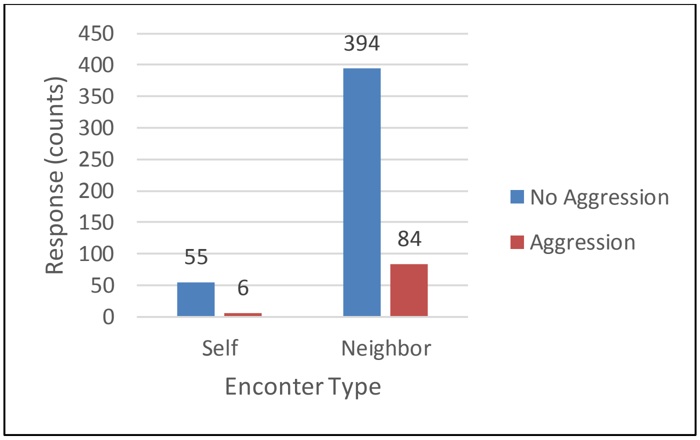


Figure 4.2 Behavioral Response for Arena Interactions of *P. comanche* for Self Introductions and All Distance Categories

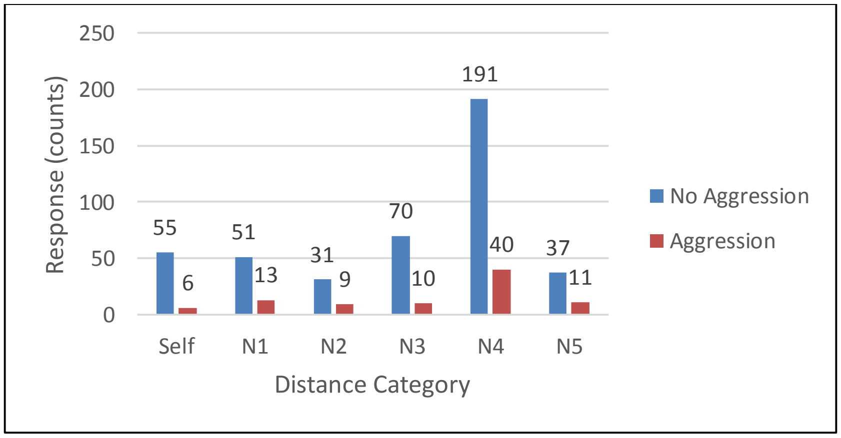


Figure 4.3 Behavioral Response for Arena Interactions of *P. comanche* for Distance Categories

There was no indication of behavioral response differences among colonies in the arena assay. All colonies showed a greater frequency of non-aggressive interactions, ranging from 68.5% – 100% with an average of 80% (Table 4.3). Further, no pattern was detected in looking across the interactions of each colony with all other colonies (Appendix D).

Table 4.3 Behavioral Response by Colony (Percentage)

Colony	No Aggressive Response (%)	Aggressive Response (%)
C1	81.9	18.1
C2	79.6	20.4
C3	89.5	10.5
C4	68.5	31.5
C5	80.2	19.8
C6	86.4	13.6
C7	88.5	11.5
C8	85.0	15.0
C9	83.9	16.1
C10	86.8	13.3
C11	62.3	13.7
C12	81.1	18.9
LD (C-13)	77.1	22.9
Average	80.83	17.33
standard deviation	7.85	5.64

Mound Interactions

The X^2 test for the mound interactions (N = 264) between the self introductions (Self) with all the neighbor distance categories (N1 – N4) was significant with X^2 of 65.9240 and p of 0.0000 (Figure 4.6). In comparison with the lack of significance in the arenas, this result suggests that context is important in the behavioral response.

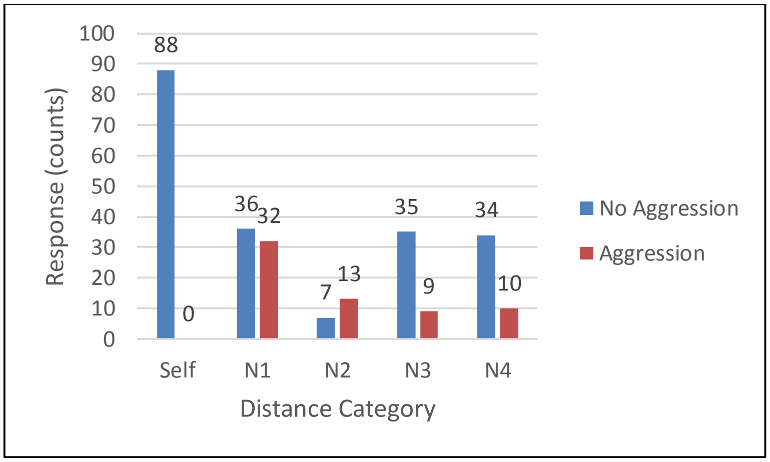


Figure 4.4 Behavioral Response for Mound Interactions of *P. comanche*

Because the X^2 test for the mound interactions was significant, I performed pairwise post hoc X^2 tests to distinguish which neighbor distances had greater aggression.

Post Hoc Tests

With the Bonferroni correction for the p value, the post hoc Yates' X^2 and Fisher's exact tests yielded 6 significant comparisons of the 10 possible pairwise comparisons (p = 0.005; Table 4.4). All the introductions of an ant to its own mound (S) had significantly fewer occurrences of aggression compared to introduction to any other mound for all distance categories (N1 – N4). There were no (0) occurrences of aggression in the S encounters. This result emphasizes the nestmate discrimination ability of *P. comanche* and supports the significance of differences in aggression observed among the distance categories. Because these were all 2 X 2 tables, I report the Yates' X^2 and Yates' p values for the S – N1 comparisons (Table 4.9) Due to low cell values, I report Fisher's exact test for the other S – other distance category comparisons (Table 4.9).

Table 4.4 Significant Post Hoc Pairwise Comparisons for S Interactions

Neighbor Category Comparison	Yates' X^2	Yates' p
S – N1	49.252	0.0000
	Fisher's exact test p	
S – N2	0.0000	
S – N3	0.0000	
S – N4	0.0000	

Only interactions at the N2 distance category (5.0 – 11.0 m) were significantly more often aggressive than those at other distance categories. I report the Yates' X^2 and Yates' p values the N2 – N3 and N2 – N4 comparisons (p = 0.005; Table 4.5).

Table 4.5 Significant Post Hoc Pairwise Comparisons for N2 Interactions

Neighbor Category Comparison	Yates' X^2	Yates' p
N2 – N3	10.2010	0.00140
N2 – N4	8.9150	0.00283

Neighborhood Interactions

Since the on mound assay indicated that aggression was more frequent with N2 distance neighbors (5.0 -11.0 m) I used the N2 distances to evaluate with which colonies each colony might be expected to have a greater frequency of aggressive behavior in the GL site. I included colonies in the first distance category (N1) because that distance must be traversed to get to the second distance category (N2; Table 4.6). The maximum number of such neighbors for each colony was two. Colony 6 had no neighbors within this 11 m distance.

Table 4.6 Aggression Expectations Among Colonies in GL

Colony	#1 Neighbor (0.0 – 4.9 m)	#2 Neighbor (5.0 – 11.0 m)
1	none	Colony 2
2	Colony 3	Colony 1
3	Colony 2	Colony 4
4	none	Colonies 3 and 5
5	none	Colony 4
6	none	none
7	Colony 8	none
8	Colony 7	none
9	none	Colony 10
10	none	Colonies 9 and 12
11	none	Colony 12
12	Colonies 10 and 11	none

I used the information in Table 4.6 to generate an expected aggression map for these colonies (Figure 4.7). The circles indicate the area containing neighboring colonies with which the central colony is expected to act more aggressively (Compare with Figure 4.1). The areas of colonies 3 and 7 duplicate that of other colonies. Colony 3 shares its area with Colonies 2 and 4 and Colonies 7 and 8 share their area. Colony 6 was not within N1 or N2 distance from any other colony. This map indicates extensive overlap in these areas of aggression. Given the border with the oak woodland, these areas have little space in proximity of the established colonies for new colonies to establish outside of these areas of increased aggression. The new colony, #8, did not survive through the summer and may have been adversely affected by aggressive encounters with colony 7.

Figure 4.5 Areas of Expected Aggression Among Colonies in the GL Neighborhood

Discussion

As indicated by the results of the mound assay, *P. comanche* is more likely to interact aggressively with non-nestmates than nestmates. Thus, I reject the null hypothesis that *P. comanche* does not distinguish nestmates from non-nestmates (H_{05}). Further, this assay demonstrates differences in the occurrence of aggression with differences in distance, specifically that aggression is more likely between colonies within 11 m of each other. Thus, I also reject the second null hypothesis that *P. comanche* does not distinguish neighboring colonies by distance (H_{06}). This 11 m distance may indicate an area with frequent encounters between colonies such that foragers learn and continue to maintain the recognition of these neighbors and that at greater distance encounters are not frequent enough to maintain such discrimination.

Yet, the GL neighborhood as structured by this heightened aggression (Figure 4.7) demonstrates overlap of these 11 m areas among colonies. With the exception of the new colony (#8), none of these overlapping colonies were lost or moved during the study period which suggests that aggression is probably not a significant factor in colony location or spatial pattern. The loss of the new colony may reflect some deficiency of this colony or may indicate that such proximity to an established colony adversely affects survival. If the latter, established colonies within this 11 m distance might be expected to be close in age.

Although not impacting the spatial pattern of colonies, this aggression may be a mild form of territoriality contributing to the structuring of social interactions among colonies, perhaps by regulating foraging, nest protection, and the communication of continued existence. For example, territoriality is linked to foraging strategies in many ants including *Pogonomyrmex* spp. (Hölldobler 1974, Hölldobler 1979; Adler and Gordon 2003; Roulston et al. 2003). *P. maricopa* and *P. californicus*, which are in the same species complex as *P. comanche*, have regular colony spatial patterns and aggressively defend foraging territories of about 25 m from the nest (Hölldobler 1976; De Vita 1979). Both these species are found in arid habitats with lower productivity than is likely in the prairies where *P. comanche* is found. Like these species, *P. comanche* is a diffuse forager with little use of foraging trails and poor recruitment abilities (Johnson 2001; A. B. M., unpublished data). The higher productivity of *P. comanche*'s habitat may allow smaller foraging ranges and reduced competition, thereby, contributing to a greater but limited frequency of aggression shown to near neighbors.

Although overall *P. comanche* interactions were non-aggressive, the results indicate that nestmate discrimination may not be a simple behavioral response. Comparison of the occurrence of aggression between arena and mound assays suggests that context plays an important role (Tanner and Adler 2009). Though some species do consistently respond to non-nestmates with aggression even in arenas (Roulston et al. 2003; Tanner and Adler 2009; A.B.M., personal observation). The lack of significant aggression in the arena interactions does not necessarily mean the ants did not discriminate one another but that they did not respond in a recognizable way. The response to non-nestmates may be influenced by the individual ant, the ant's location, the ant's task and the perceived threat (Gordon 1989a; Gordon 1989b; Hölldobler and Wilson 1990; (Buczkowski and Silverman 2005; Hölldobler and Wilson 2009; Newey et al. 2010b; van Wilgenburg et al. 2010; Scharf et al. 2011; Sturgis and Gordon 2012; Norman et al. 2014). Individual ants may not make decisions solely as individuals rather their choices may be confined within a context space given their role in the colony (Gordon 1989; Gordon 1989b). Thus, consideration of both the individual and colony level of response is important in determining nestmate discrimination and the importance of aggression in influencing spatial and behavioral patterns (Roulston et al. 2003).

Chapter 5

Conclusions

Evaluation of Hypotheses

I tested the hypothesis below and obtained the following results:

H_{01}: *P. comanche* colonies are randomly distributed within the landscape.

I accept this hypothesis. *P. comanche* colonies are randomly distributed with scales up to 50 m . They appear to have a high turnover rate and low recruitment. No significant regular or dispersed patterns were detected with scales up to 50 m. This suggests that *P. comanche* populations are probably not significantly structured by competition, aggression or territoriality. Despite large areas in most habitats lacking any colonies, the populations do not appear to be expanding.

H_{02}: The ant assemblages do not differ among habitats (sites).

I reject this hypothesis. Ant assemblages do differ among sites with percent litter cover and drainage being important environmental factors affecting the occurrence of most species. Species occurrence significantly differs between prairie and wooded habitats with several species found only in one or the other habitat.

H_{03}: The presence of *P. comanch*e has no impact on ant species occurrence and abundance

I accept this hypothesis. While the species richness and dominance indices were higher in the Aquilla Prairies, *P. comanche* cannot be considered a dominant species. *Pheidole metallescens* and *Trachymyrmex turrifex* are co-occurring species with *P. comanche* in the Aquilla Prairies but such co-occurrence probably arises from shared habitat and foraging preferences and not from species interactions. Despite *P. comanche* only occurring in the Aquilla formation of deep sand in the FWNC, *P. comanche* cannot be considered an indicator species because of its substantial population in the Crosstel-Urban soil (SP) which has a very different soil profile.

H_{04}: *P. comanche* does not distinguish nestmates from non-nestmates with an aggressive response.

I reject this hypothesis. *P. comanche* does distinguish nestmates from non-nestmates. The aggressive response is context dependent, influenced perhaps by location of the encounter and perceived threat. This result may involve differences among caste as well since only foragers were tested. It might be expected that patrollers would demonstrate the strongest, most consistent aggressive response to non-nestmates because they patrol the nest area (Sturgis and Gordon 2013).

H_{05}: Any aggressive interaction is equally likely among *P. comanche* ants and colonies, irrespective of distance between interacting colonies.

I reject this hypothesis. *P. comanche* does distinguish non-nestmates by distance with aggression occurring more often between colonies within 11 m of each other. This result may be considered a weak territoriality suggesting a possible influence on structuring behavioral interactions among colonies but does not appear to affect colony location.

Implications

These results indicate that *P. comanche* colonies typically exhibit a random spatial pattern at scales up to 75 m. The heightened aggression up to an 11 m distance from each colony suggests a weak territoriality through which colonies may structure their behavioral interactions (in individual encounters) without significantly influencing colony spatial patterns (colony level response). It now seems likely that queen dispersal is the most significant factor in colony location.

In contrast to *P. comanche*, two other members of the Californicus complex, *P. californicus* and *P. maricopa*, found in arid, low productive habitats, are highly territorial and aggressively defend foraging areas. These species have a regular colony spatial pattern which has been attributed to their territoriality in low productive environments where competition is expected to be high (Hölldobler 1976a; De Vita 1979). The lack of such territoriality and the random pattern in *P. comanche* may be influenced by their more productive prairie habitat.

While *P. comanche* is not a dominant nor an indicator species, *P. comanche* may have a role as an ecosystem engineer. They forage into the forest thus transporting materials between the forest and prairie and connecting the nutrient cycling between these two habitats. They also connect the above and below ground habitats by bringing their forage and other items into the nest and bringing refuse and soil to the surface. Their nesting activities clear large areas of surface soil of vegetation (on average 30 cm diameter cleared crater mound and up to 1 m^2 cleared area surrounding the crater mound) which has the potential to impact plant populations, as well as the moisture and temperature soil profile and therefore, the soil biota as well. The internal nest structure opens up avenues for water and gas penetration into the soil and continual excavation of the nest brings soil from deeper horizons to the surface, thus mixing soils (bioturbation). These activities are likely to engineer the soil as has been demonstrated for other ants species (Baxter and Hole 1967; de Bruyn 1999; Folgarait 1998). In turn such engineering is likely to have significant impacts on soil organisms and plants that are rooted in the soil. Because their colonies are not found throughout most of these prairies, these effects would be localized in the immediate area of the nests. The connection that they provide between the forest and prairie habitats is important in this ecoregion which is characterized by a forest and prairie mosaic. When the colonies die or move, these nesting areas may be colonized or used by other organisms, including plants which may benefit from the activities of previous colonies such as nutrient concentration.

Thus, this project on the spatial pattern of *P. comanche* provides some insights into *P. comanche* population dynamics as well as their ecological role and raises many questions for investigation. The results suggest that dominance, competition, and aggression may not be pervasive and significant factors for structuring *P. comanche* populations and perhaps not significant in these ant assemblages. Other factors may be more significant for colony and population responses to intraspecific and interspecific interactions.

Future Work

My field experience and the literature on *Pogonomyrmex* spp. led me to think that *P. comanche* colonies might be relatively long lived, 10 – 15 years, and rather stable in location despite some obvious relocation. However, the changes in colony abundance and density (Chapter 2) suggest a high colony turnover and therefore, a low average colony longevity. My preliminary comparison of the site maps of colony locations over the years leads me to question these ideas. More detailed comparison of the colony location maps could produce estimates of the population age structure by following the survival of colonies through these maps. Further work could be undertaken to establish colony turnover, queen/colony longevity, and the frequency and causes of colony movement. Such investigation would contribute to understanding *P. comanche* population dynamics and sociometrics. Given that *P. comanche* is in the Californicus complex, *P. comanche* shares attributes with many of these species but is also different. More study of *P. comanche* would contribute to greater understanding of this complex and the genus as a whole.

The random spatial nature of these populations suggests that queen dispersal may be the most significant factor determining colony location. My preliminary work and field observations of the behavior of alates and queens do not appear to be in agreement with reviews of *Pogonomyrmex* harvester ants for mating strategy (Johnson 2000; Johnson 2001). Investigation into the mating strategy and queen dispersal behavior including timing of alate release and influencing factors such as weather conditions, location of a lek, queen dispersal limitation and nest site choice would determine the influence of queen dispersal patterns on the colony location and contribute to understanding reproduction and population dynamics.

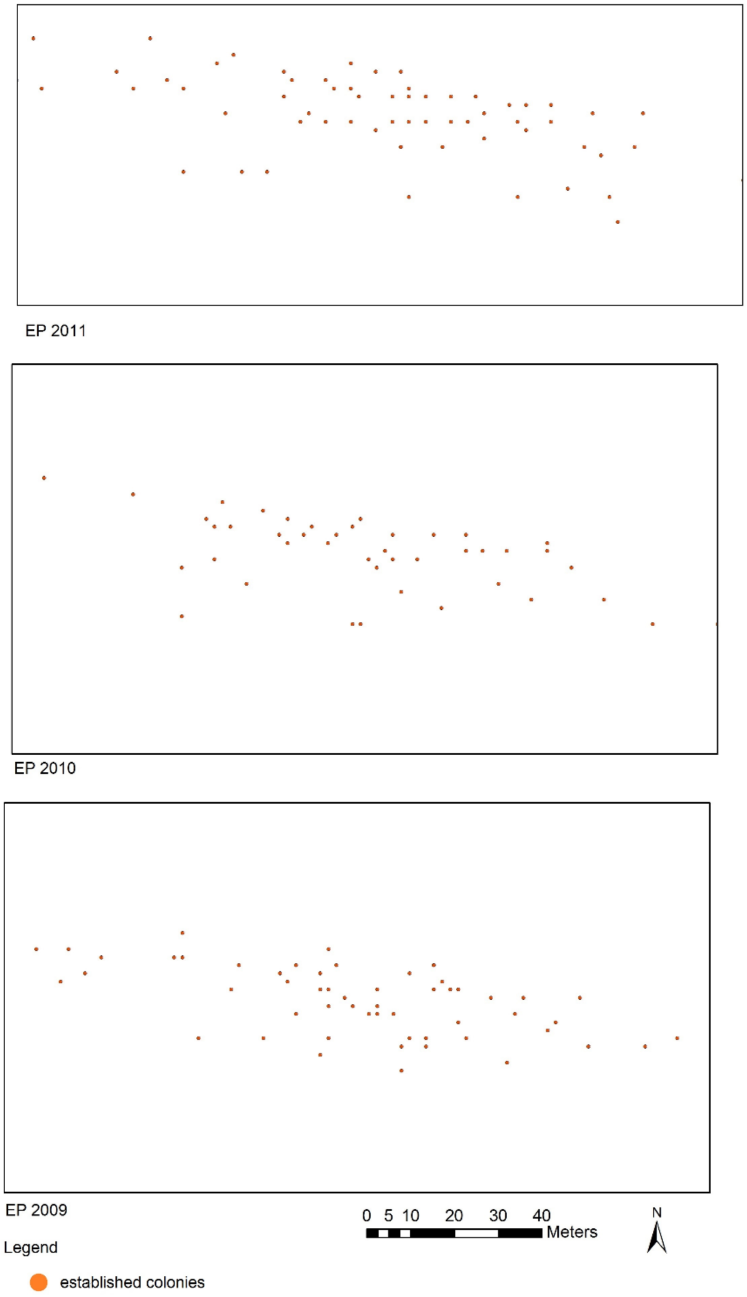
Finally, there remain questions about *P. comanche* as a possible ecosystem engineer and its influence within the habitat. Because of their limited colony locations within most of these sites, their activities and influence are localized. This situation leads to the expectation of a greater influence on soil and soil organisms and plants in these areas as distinct from the whole habitat. A comparison of environmental differences (such as moisture and gas) in nests and in nearby areas without *P. comanche* nests, the quantification of nutrients redistributed between the forest and prairies and the redistribution of materials within the nest and between the nest and the soil surface are needed to assess *P. comanche*'s role in the local environment and the Cross Timbers Ecoregion.

Appendix A

P. comanche Colony Location Maps

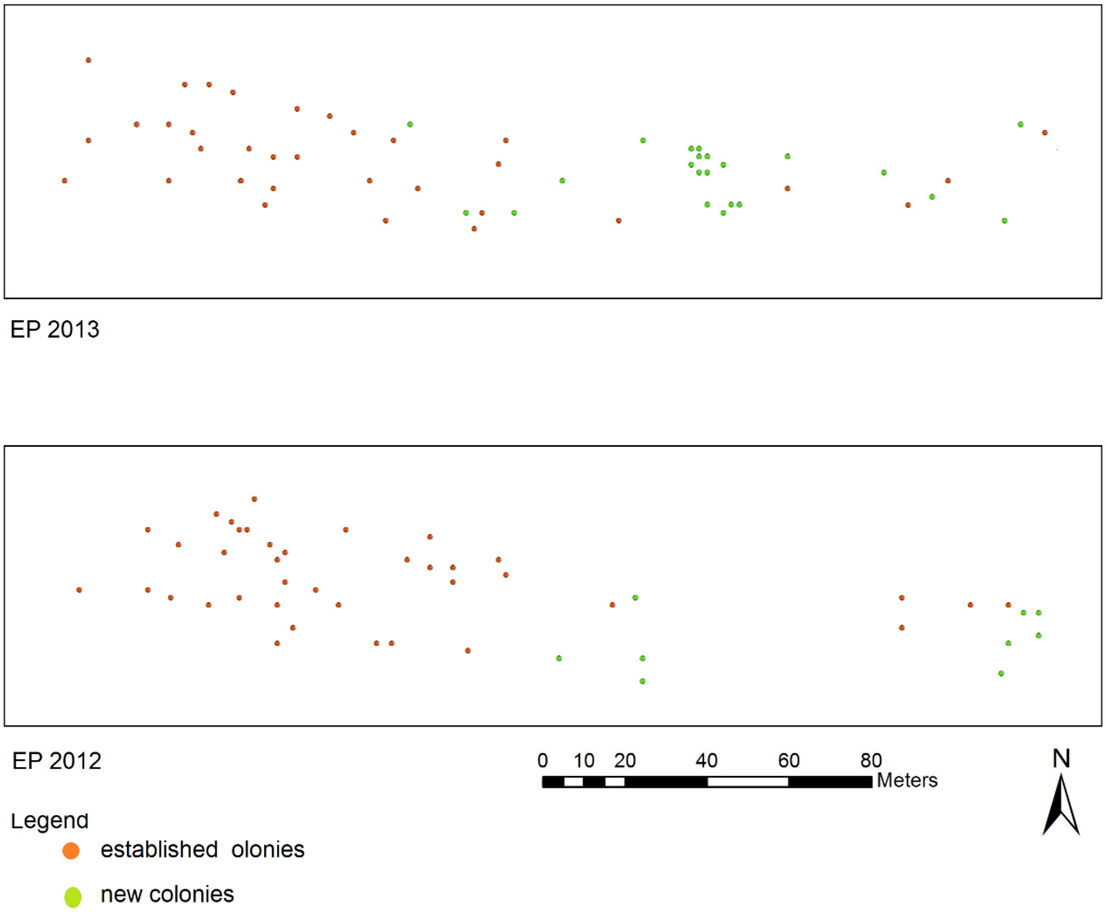
The following maps are a time series of *P.comanche* colonies in the five sites: EP, SP, T1P, and T2P. Each map depicts the locations of established colonies (orange-yellow dots) and in some years, of new colonies (green dots). The area in hectares and colony density for each year based only on established colonies is also given.

I produced all the following maps with ArcMap (Esri 2012) without a satellite map in order to show the pattern of colonies more easily.



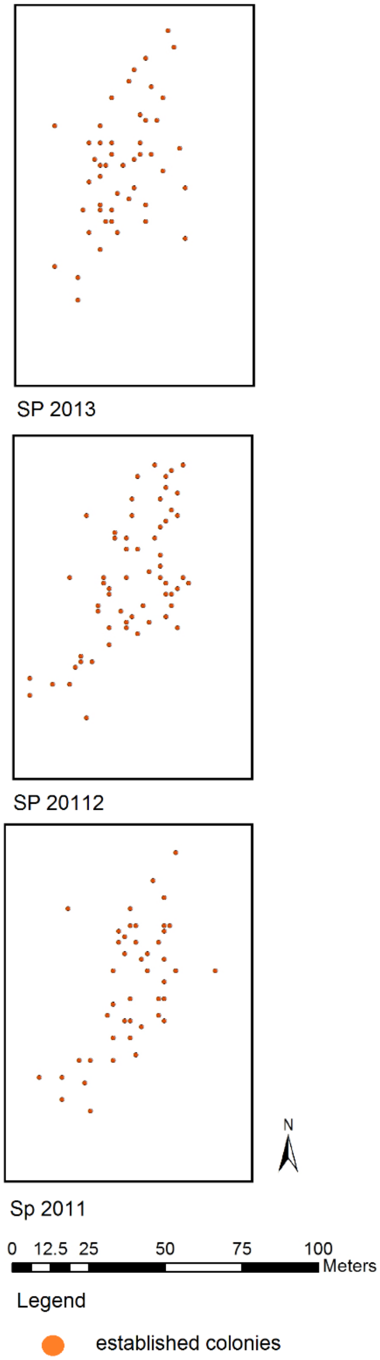
P. comanche colonies in EP (2009 – 2010)

Area: 6.71 ha



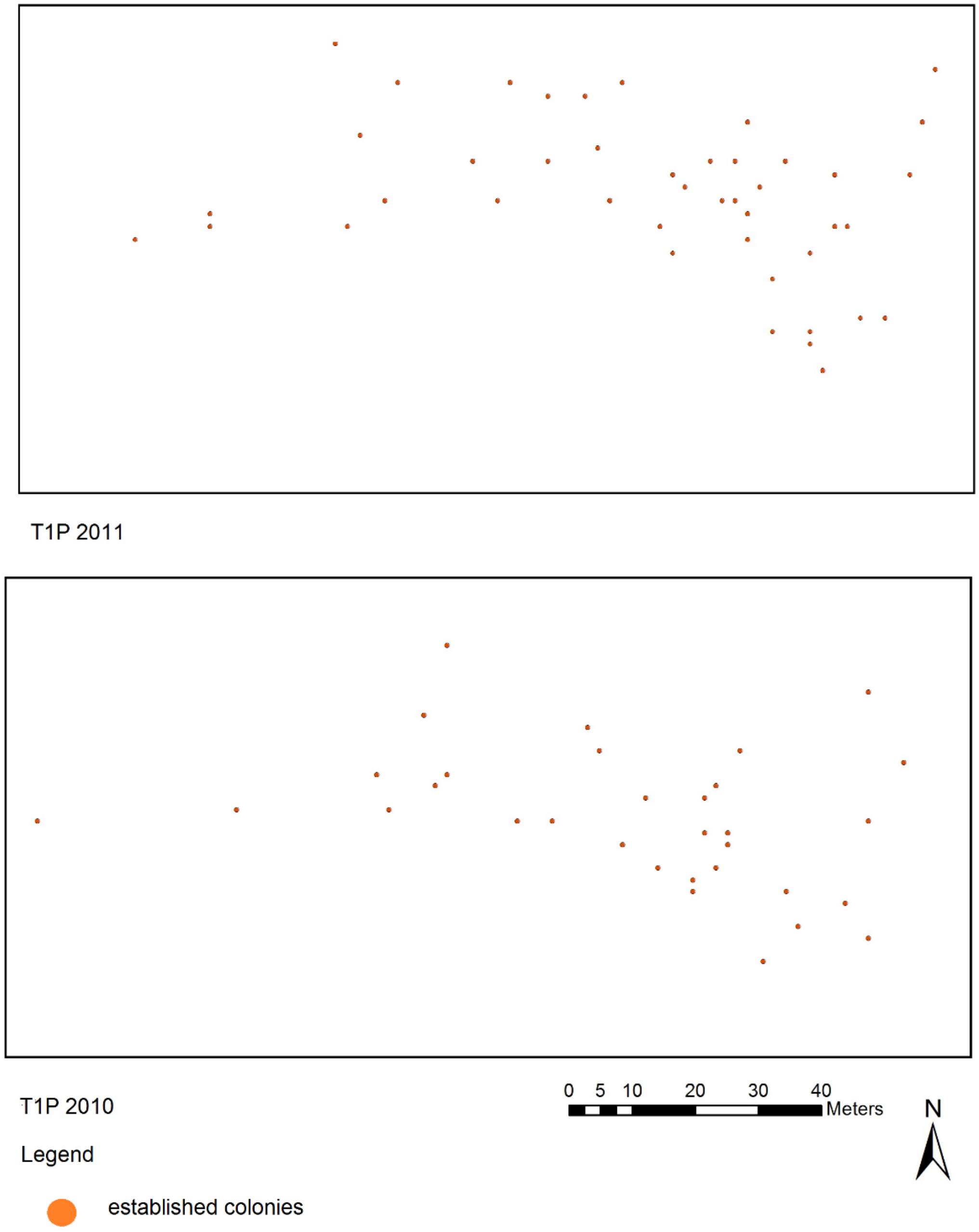
P. comanche colonies in GL (2010 – 2013)

Area: 5.82 ha



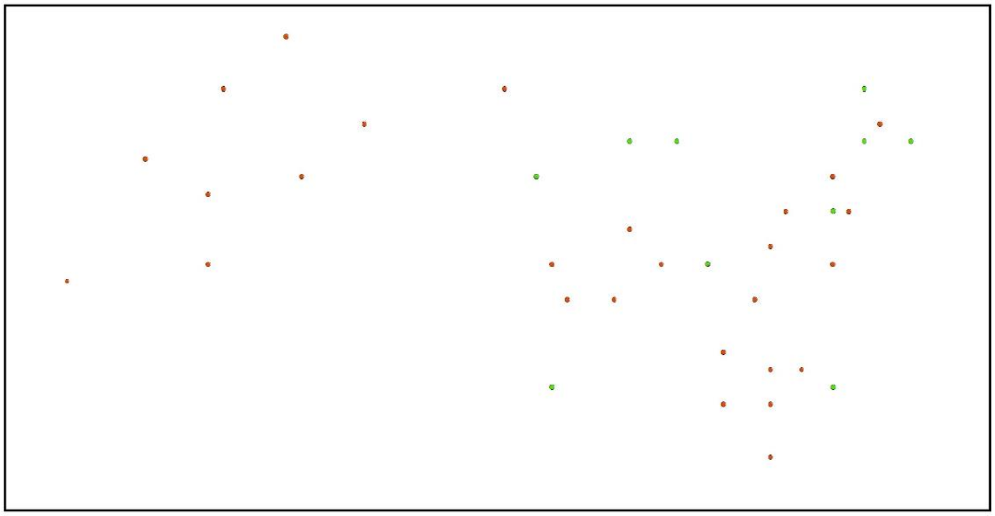
P. comanche colonies in SP (2011 – 2013)

Area: 4.43 ha

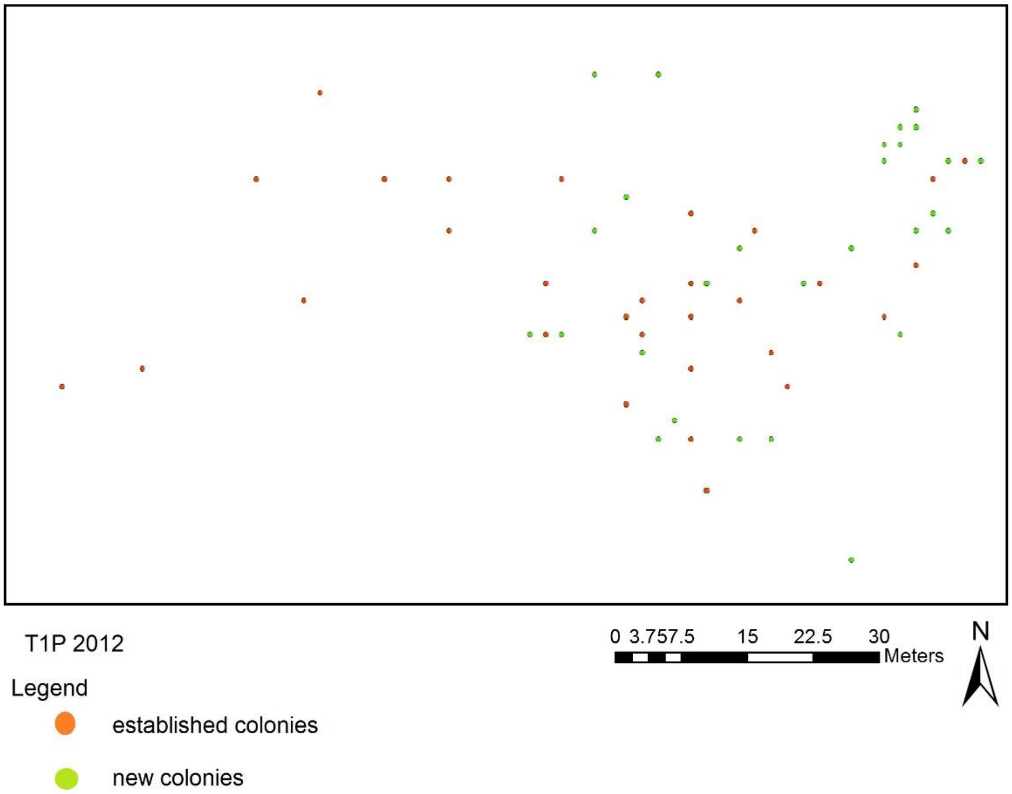


P. comanche colonies in T1P (2010 – 2011)

Area: 3.14 ha

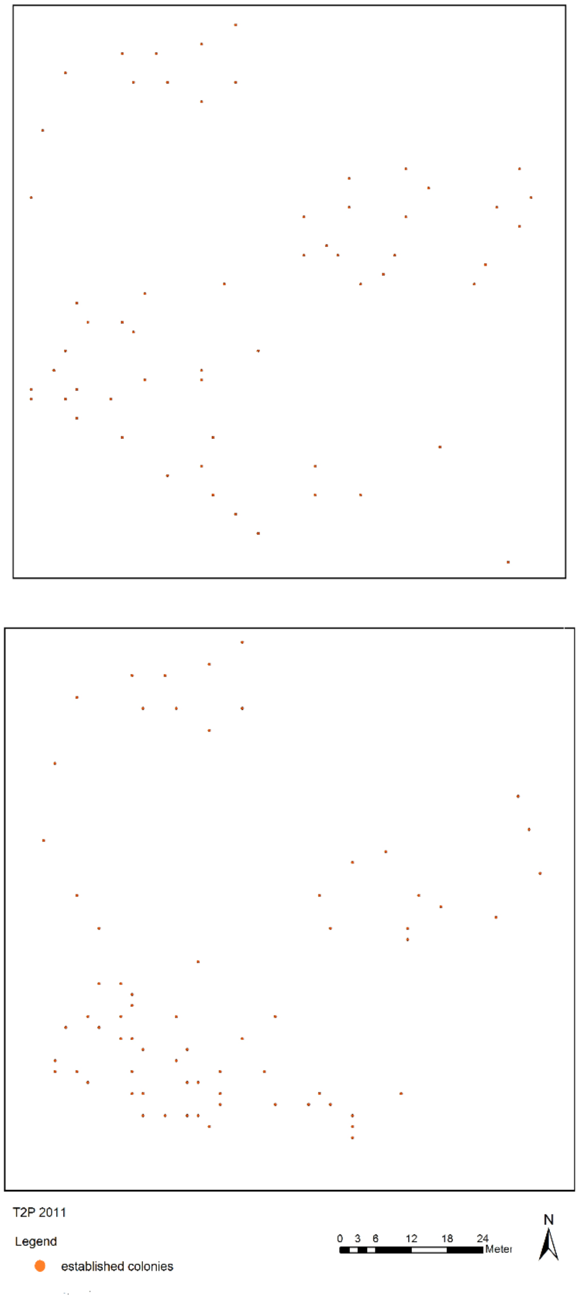


T1P 2013



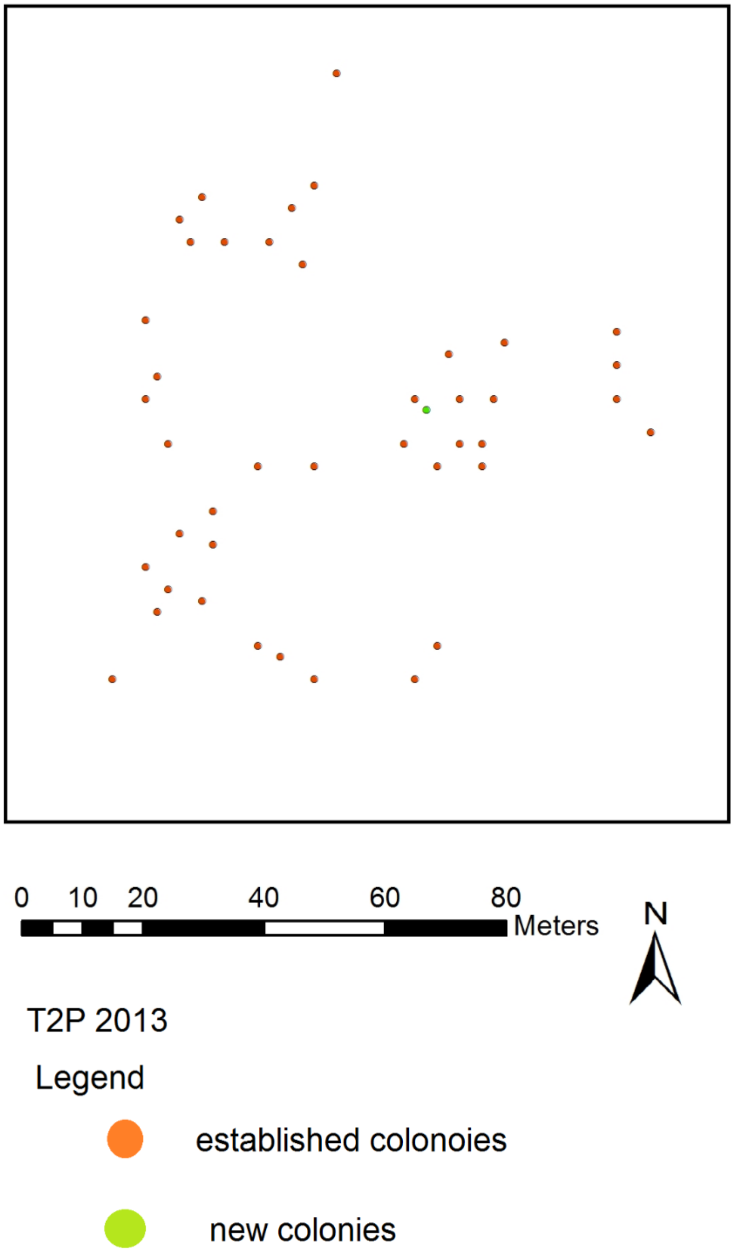
P. comanche colonies in T1P (2012 – 2013)

Area: 3.14 ha



P. comanche colonies in T2P (2011 – 2012)

Area: 5.06 ha



P. comanche colonies in T2P (2013)

Area: 5.06 ha

Appendix B

Species Lists

On the following pages are the species lists for each site (Table B.1), for the late summer samples by habitat group (Table B.2) and compiled over the summer for the FWNC by habitat group (Tables B.3).

Table B.1 Species Collected for Each Site

EPF (11 species)	EPP (17 species)	EPT (16 species)	GL (21 species)
Brachymyrmex depilis	*Brachymyrmex depilis*	*Aphaenogaster treatae*	*Aphaenogaster treatae*
Brachymyrmex patagonicus	*Brachymyrmex patagonicus*	*Crematogaster lineolata*	*Brachymyrmex depilis*
Crematogaster lineolata	*Crematogaster lineolata*	*Dorymyrmex flavus*	*Crematogaster cerasi*
Dorymyrmex flavus	*Dorymyrmex flavus*	*Forelius mccooki*	*Crematogaster lineolata*
Forelius mccooki	*Forelius mccooki*	*Monomorium viridae*	*Dorymyrmex flavus*
Monomorium viridae	*Labidus coecus*	*Nylanderia arenivaga*	*Forelius mccooki*
Nylanderia vividula	*Monomorium viridae*	*Nylanderia vividula*	*Monomorium viridae*
Pogonomyrmex comanche	*Nylanderia arenivaga*	*Pheidole bicarinata*	*Nylanderia arenivaga*
Solenopsis invicta	*Nylanderia vividula*	*Pheidole dentata*	*Nylanderia vividula*
Solenopsis xyloni	*Pheidole bicarinata*	*Pheidole metallescens*	*Pheidole bicarinata*
Trachymyrmex turrifex	*Pheidole dentata*	*Pogonomyrmex comanche*	*Pheidole dentata*
	Pogonomyrmex comanche	*Solenopsis invicta*	*Pheidole metallescens*
	Solenopsis invicta	*Solenopsis molesta*	*Pogonomyrmex comanche*
	Solenopsis xyloni	*Solenopsis xyloni*	*Solenopsis invicta*
	Strumigenys membranifora	*Strumigenys margaritae*	*Solenopsis molesta*
	Trachymyrmex septentrionalis	*Trachymyrmex turrifex*	*Solenopsis xyloni*
	Trachymyrmex turrifex		*Strumigenys louisianae*
			Temnothorax pergandei
			Temnothorax texanus
			Trachymyrmex septentrionalis
			Trachymyrmex turrifex

Table B.1—*Continued*

EP2 (13 species)	T1P (17 species)	T1N (15 species)	T2P (14 species)
Brachymyrmex depilis	*Brachymyrmex depilis*	*Brachymyrmex depilis*	*Aphaenogaster treatae*
Crematogaster lineolata	*Dorymyrmex flavus*	*Crematogaster lineolata*	*Crematogaster lineolata*
Dorymyrmex flavus	*Forelius mccooki*	*Dorymyrmex flavus*	*Crematogaster cerasi*
Forelius mccooki	*Forelius pruinosis*	*Forelius mccooki*	*Dorymyrmex flavus*
Monomorium viridae	*Monomorium viridae*	*Forelius pruinosis*	*Forelius mccooki*
Nylanderia vividula	*Nylanderia arenivaga*	*Monomorium viridae*	*Monomorium viridae*
Pheidole bicarinata	*Nylanderia vividula*	*Nylanderia arenivaga*	*Nylanderia arenivaga*
Pheidole dentata	*Pheidole dentata*	*Nylanderia vividula*	*Pheidole bicarinata*
Pheidole metallescens	*Pheidole metallescens*	*Pheidole metallescens*	*Pheidole dentata*
Solenopsis invicta	*Pogonomyrmex comanche*	*Pogonomyrmex comanche*	*Pheidole metallescens*
Solenopsis xyloni	*Solenopsis invicta*	*Solenopsis invicta*	*Pogonomyrmex comanche*
Trachymyrmex septentrionalis	*Solenopsis molesta*	*Solenopsis xyloni*	*Solenopsis molesta*
Trachymyrmex turrifex	*Solenopsis xyloni*	*Temnothorax pergandei*	*Trachymyrmex septentrionalis*
	Temnothorax pergandei	*Trachymyrmex septentrionalis*	*Trachymyrmex turrifex*
	Temnothorax texanus	*Trachymyrmex turrifex*	
	Trachymyrmex septentrionalis		
	Trachymyrmex turrifex		

Table B.1—*Continued*

SP (10 species)	BR (10 species)	GH (15 species)	THP (9 species)
Crematogaster lineolata	*Crematogaster lineolata*	*Brachymyrmex depilis*	*Dorymyrmex flavus*
Dorymyrmex flavus	*Dorymyrmex flavus*	*Forelius mccooki*	*Forelius mccooki*
Forelius mccooki	*Forelius mccooki*	*Monomorium viridae*	*Monomorium viridae*
Nylanderia arenivaga	*Monomorium viridae*	*Nylanderia arenivaga*	*Nylanderia terricola*
Nylanderia vividula	*Nylanderia arenivaga*	*Nylanderia vividula*	*Nylanderia vividula*
Pheidole bicarinata	*Nylanderia vividula*	*Pheidole bicarinata*	*Pheidole metallescens*
*Pogonomyrmex comanche**	*Pheidole lamia*	*Pheidole dentata*	*Solenopsis invicta*
Solenopsis invicta	*Solenopsis invicta*	*Pheidole metallescens*	*Solenopsis molesta*
Solenopsis xyloni	*Solenopsis molesta*	*Pogonomyrmex barbatus*	*Solenopsis xyloni*
Trachymyrmex turrifex	*Solenopsis xyloni*	*Solenopsis invicta*	
		Solenopsis molesta	
		Solenopsis subterranea	
		Solenopsis xyloni	
		Trachymyrmex septentrionalis	
		Trachymyrmex turrifex	

Table B.1 —*Continued*

STP (10 species)	EP3 (10 species)	AA (13 species)	AB (10 species)
Camponotus americanus	*Crematogaster lineolata*	*Brachymyrmex depilis*	*Forelius mccooki*
Crematogaster lineolata	*Forelius mccooki*	*Brachymyrmex patagonicus*	*Hypoponera opacior*
Dorymyrmex flavus	*Formica biophilica*	*Dorymyrmex flavus*	*Monomorium viridae*
Forelius mccooki	*Monomorium viridae*	*Forelius mccooki*	*Nylanderia arenivaga*
Nylanderia terricola	*Nylanderia arenivaga*	*Monomorium viridae*	*Nylanderia vividula*
Nylanderia vividula	*Nylanderia vividula*	*Nylanderia arenivaga*	*Pheidole metallescens*
Pheidole dentata	*Pheidole metallescens*	*Nylanderia vividula*	*Solenopsis invicta*
Pheidole metallescens	*Solenopsis invicta*	*Pheidole bicarinata*	*Solenopsis molesta*
Solenopsis molesta	*Solenopsis molesta*	*Pheidole metallescens*	*Solenopsis xyloni*
Trachymyrmex turrifex	*Solenopsis xyloni*	*Solenopsis invicta*	*Trachymyrmex turrifex*
		Solenopsis molesta	
		Solenopsis xyloni	
		Trachymyrmex turrifex	

Table B.1—*Continued*

HC (15 species)	EPW (16 species)	T1W (18 species)	T2W (17 species)	SPW (6 species)
Brachymyrmex depilis	*Aphaenogaster treatae*	*Aphaenogaster ashmeadi*	*Aphaenogaster ashmeadi*	*Aphaenogaster carolinensis*
Crematogaster lineolata	*Camponotus pennsylvanicus*	*Brachymyrmex depilis*	*Aphaenogaster treatae*	*Crematogaster lineolata*
Crematogaster cerasi	*Crematogaster lineolata*	*Camponotus americanus*	*Crematogaster cerasi*	*Pheidole dentata*
Dorymyrmex flavus	*Dorymyrmex flavus*	*Camponotus pennsylvanicus*	*Crematogaster lineolata*	*Pogonomyrmex comanche*
Forelius mccooki	*Forelius mccooki*	*Crematogaster cerasi*	*Dorymyrmex flavus*	*Solenopsis molesta*
Forelius pruinosis	*Monomorium viridae*	*Dorymyrmex flavus*	*Forelius mccooki*	*Temnothorax* sp.
Formica biophilica	*Nylanderia arenivaga*	*Forelius mccooki*	*Nylanderia arenivaga*	
Monomorium viridae	*Nylanderia vividula*	*Monomorium viridae*	*Nylanderia vividula*	
Nylanderia arenivaga	*Pheidole dentata*	*Nylanderia arenivaga*	*Pheidole dentata*	
Nylanderia vividula	*Pheidole metallescens*	*Nylanderia vividula*	*Pheidole metallescens*	
Pheidole bicarinata	*Pogonomyrmex comanche*	*Pheidole dentata*	*Pogonomyrmex comanche*	
Pheidole lamia	*Solenopsis invicta*	*Pheidole metallescens*	*Prenolepis imparis*	
Solenopsis invicta	*Solenopsis molesta*	*Pogonomyrmex comanche*	*Solenopsis invicta*	
Solenopsis xyloni	*Solenopsis xyloni*	*Solenopsis invicta*	*Solenopsis xyloni*	
Trachymyrmex turrifex	*Trachymyrmex septentrionalis*	*Solenopsis molesta*	*Temnothorax texanus*	
	Trachymyrmex turrifex	*Solenopsis xyloni*	*Trachymyrmex septentrionalis*	
		Temnothorax texanus	*Trachymyrmex turrifex*	
		Trachymyrmex septentrionalis		

Table B.2 Species List for Late Summer α Diversity by Habitat Group

Aquilla Prairies (8 sites; 21 species)	Other Prairies (9 sites; 19 species)	Wooded Sites (4 sites; 19 species)
Aphaenogaster treatae	*Brachymyrmex depilis*	*Aphaenogaster ashmeadi*
Brachymyrmex depilis	*Brachymyrmex patagonica*	*Aphaenogaster carolinensis*
Brachymyrmex patagonica	*Camponotus americanus*	*Aphaenogaster treatae*
Crematogaster cerasi	*Crematogaster lineolata*	*Crematogaster cerasi*
Crematogaster lineolata	*Dorymyrmex flavus*	*Crematogaster lineolata*
Dorymyrmex flavus	*Forelius mccooki*	*Dorymyrmex flavus*
Forelius mccooki	*Forelius prunosis*	*Monomorium viridae*
Forelius prunosis	*Monomorium viridae*	*Nylanderia arenivaga*
Monomorium viridae	*Nylanderia arenivaga*	*Nylanderia vividula*
Nylanderia arenivaga	*Nylanderia terricola*	*Pheidole dentata*
Nylanderia vividula	*Nylanderia vividula*	*Pheidole metallescens*
Pheidole bicarinata	*Pheidole bicarinata*	*Pogonomyrmex comanche*
Pheidole dentata	*Pheidole dentata*	*Solenopsis invicta*
Pheidole metallescens	*Pheidole lamia*	*Solenopsis molesta*
Pogonomyrmex comanche	*Pheidole metallescens*	*Solenopsis xyloni*
Solenopsis invicta	*Solenopsis invicta*	*Temnothorax texanus*
Solenopsis molesta	*Solenopsis molesta*	*Temnothorax* sp.
Solenopsis xyloni	*Solenopsis xyloni*	*Trachymyrmex septentrionalis*
Strumigenys margaritae	*Trachymyrmex turrifex*	*Trachymyrmex turrifex*
Trachymyrmex septentrionalis		
Trachymyrmex turrifex		

Table B.3 Species List for FWNC (compiled) α Diversity by Habitat Group

Aquilla Prairies (9 sites; 27 species)	Other Prairies (5 sites; 23 species)	Wooded Sites (3 sites; 24 species)
Aphaenogaster treatae	*Brachymyrmex depilis*	*Aphaenogaster ashmeadi*
Brachymyrmex depilis	*Brachymyrmex patagonica*	*Aphaenogaster treatae*
Brachymyrmex patagonica	*Crematogaster cerasi*	*Brachymyrmex depilis*
Crematogaster cerasi	*Crematogaster lineolata*	*Brachymyrmex patagonica*
Crematogaster lineolata	*Dorymyrmex flavus*	*Camponotus americanus*
Dorymyrmex flavus	*Forelius mccooki*	*Camponotus pennsylvanicus*
Forelius mccooki	*Forelius prunosis*	*Crematogaster cerasi*
Forelius prunosis	*Formica* biophilica	*Crematogaster lineolata*
Formica biophilica	*Hypoponera opacior*	*Dorymyrmex flavus*
Labidus coecus	*Monomorium viridae*	*Forelius mccooki*
Monomorium viridae	*Nylanderia arenivaga*	*Monomorium viridae*
Nylanderia arenivaga	*Nylanderia vividula*	*Nylanderia arenivaga*
Nylanderia vividula	*Pheidole bicarinata*	*Nylanderia vividula*
Pheidole bicarinata	*Pheidole dentata*	*Pheidole dentata*
Pheidole dentata	*Pheidole lamia*	*Pheidole metallescens*
Pheidole metallescens	*Pheidole metallescens*	*Pogonomyrmex comanche*
Pogonomyrmex comanche	*Pogonomyrmex barbatus*	*Prenolepis imparis*
Solenopsis invicta	*Solenopsis invicta*	*Solenopsis invicta*
Solenopsis molesta	*Solenopsis molesta*	*Solenopsis molesta*
Solenopsis xyloni	*Solenopsis xyloni*	*Solenopsis xyloni*
Strumigenys louisinanae	*Trachymyrmex septentrionalis*	*Trachymyrmex septentrionalis*
Strumigenys margaritae	*Trachymyrmex turrifex*	*Trachymyrmex turrifex*
Strumigenys membranifora		
Temnothorax pergandei		
Temnothorax texanus		
Trachymyrmex septentrionalis		
Trachymyrmex turrifex		

Appendix C

Point Diversity Measures

The following table shows the point diversity measures for each site (21) in late summer 2012. N is the total number of individual ants collected; S is the total number of ant species; 1/D is the inverse of Simpson's Diversity Index; Evenness is Simpson's Evenness; d is Berger and Parker Dominance Index; Δ is a index for taxonomic diversity; Δ* is an index for taxonomic distinctness based on abundance data ; Δ+ is a taxonomic distinctness index based on occurrence data; and Λ+ is an index for taxonomic structure.

Table C.1: Point Diversity Measures for Late Summer Samples

Site	N	S	1/D	Evenness	d	Δ	Δ*	Δ+	Λ+
EPF	172	9	2.450	0.271	0.610	1.538	2.601	0.257	0.342
EPP	350	9	5.317	0.591	0.283	2.128	2.646	0.257	0.342
EPW	78	9	4.752	0.528	0.321	1.661	2.104	0.193	0.241
EPT	426	11	4.358	0.396	0.383	1.183	2.373	0.344	0.415
GL	101	9	2.202	0.245	0.653	1.206	2.210	0.230	0.284
EP2	559	8	2.537	0.317	0.596	1.453	2.399	0.190	0.248
EP3	260	7	4.820	0.689	0.327	2.056	2.594	0.190	0.258
T1P	675	8	1.722	0.215	0.745	1.021	2.434	0.198	0.269
T1N	240	11	5.835	0.530	0.288	1.129	1.363	0.389	0.503
T1W	11	7	2.784	0.398	0.575	1.142	1.782	0.140	0.131
T2P	428	7	4.116	0.588	0.327	2.138	2.824	0.138	0.175
T2W	74	12	5.03	0.419	0.324	1.108	1.384	0.413	0.481
AA	317	11	5.323	0.293	0.293	2.066	2.544	0.378	0.481
AB	223	6	4.306	0.718	0.314	2.093	2.726	0.103	0.136
HC	502	11	3.953	0.359	0.367	0.188	0.251	0.389	0.503
BR	790	8	3.834	0.479	0.341	1.256	1.699	0.188	0.244
GH	92	3	1.649	0.550	0.750	1.137	2.891	0.021	0.029
SP	396	8	2.59	0.324	0.573	1.755	2.858	0.198	0.267
SPW	18	6	3.923	0.654	0.444	1.490	2.000	0.079	0.078
THP	331	8	5.074	0.634	0.266	0.572	2.673	0.196	0.263
STP	1108	9	2.350	0.261	0.600	1.416	2.464	0.235	0.302

The following table shows the point diversity measures for the monthly compiled samples (June, July, and August) for the FWNC sites (17 sites). N is the total number of individual ants collected; S is the total number of ant species; 1/D is the inverse of Simpson's Diversity Index; Evenness is Simpson's Evenness; d is Berger and Parker Dominance Index; Δ is a index for taxonomic diversity; Δ* is an index for taxonomic distinctness based on abundance data ; Δ+ is a taxonomic distinctness index based on occurrence data; and Λ+ is an index for taxonomic structure.

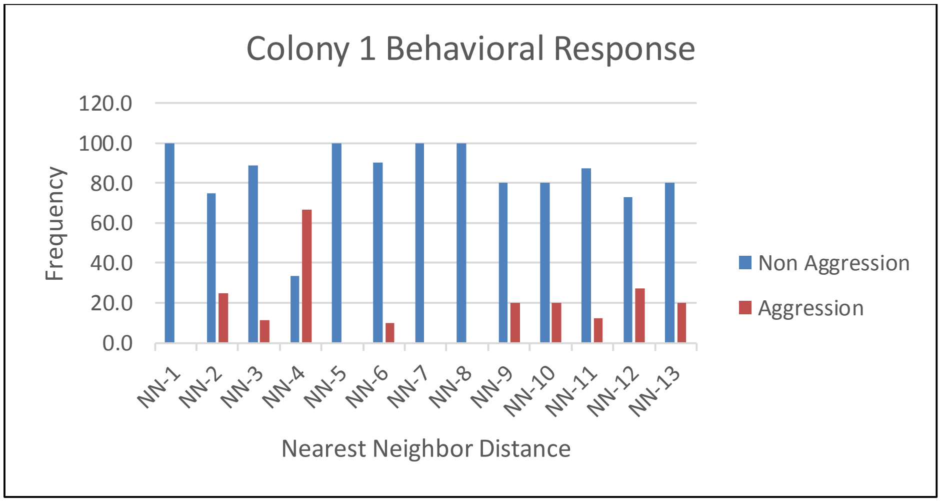
Table C.2 Point Diversity Measures for the FWNC (compiled)

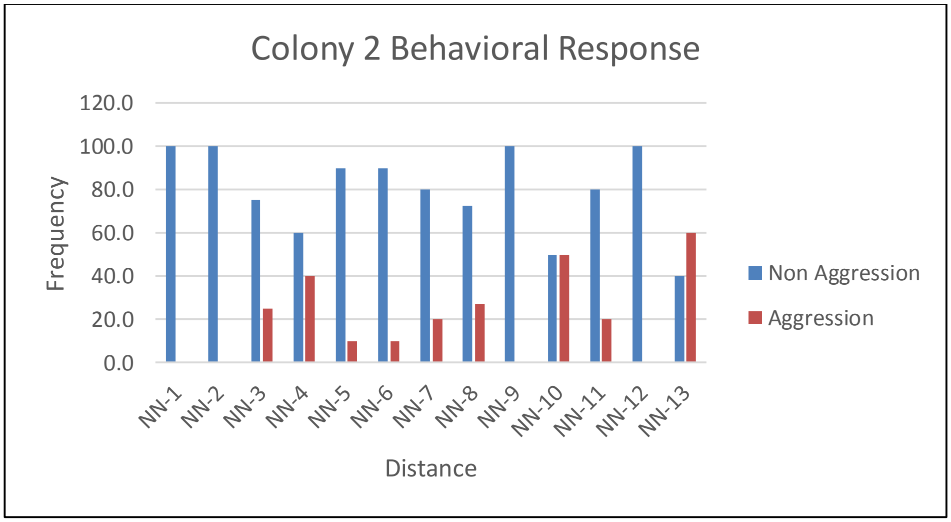
Site	N	S	1/D	Evenness	d	Δ+	Λ+
EPF	2072	10	1.491	0.149	0.813	0.151	0.128
EPP	2075	16	2.296	0.143	0.633	0.526	0.454
EPW	1564	15	2.281	0.152	0.643	0.375	0.292
EPT	2673	15	2.673	0.178	0.564	0.425	0.329
GL	1936	20	2.139	0.107	0.674	0.795	0.595
EP2	2052	12	1.622	0.135	0.778	0.276	0.225
EP3	1061	9	4.030	0.448	0.352	0.156	0.134
T1P	1455	16	3.837	0.240	0.409	0.509	0.424
T1N	978	14	5.756	0.411	0.290	0.437	0.380
T1W	602	17	7.113	0.418	0.241	0.254	0.232
T2P	1823	14	3.982	0.284	0.374	0.356	0.262
T2W	271	16	7.239	0.452	0.229	0.442	0.348
AA	2498	12	2.842	0.237	0.499	0.289	0.252
AB	658	9	4.631	0.515	0.299	0.160	0.141
HC	1500	14	4.732	0.338	0.332	0.402	0.351
BR	1865	9	2.577	0.286	0.587	0.158	0.138
GH	790	14	4.056	0.290	0.434	0.365	0.284

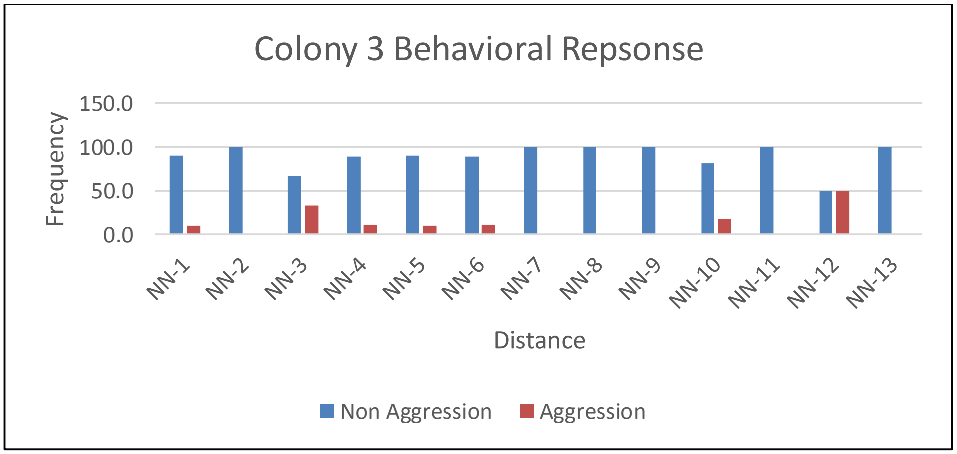
Appendix D

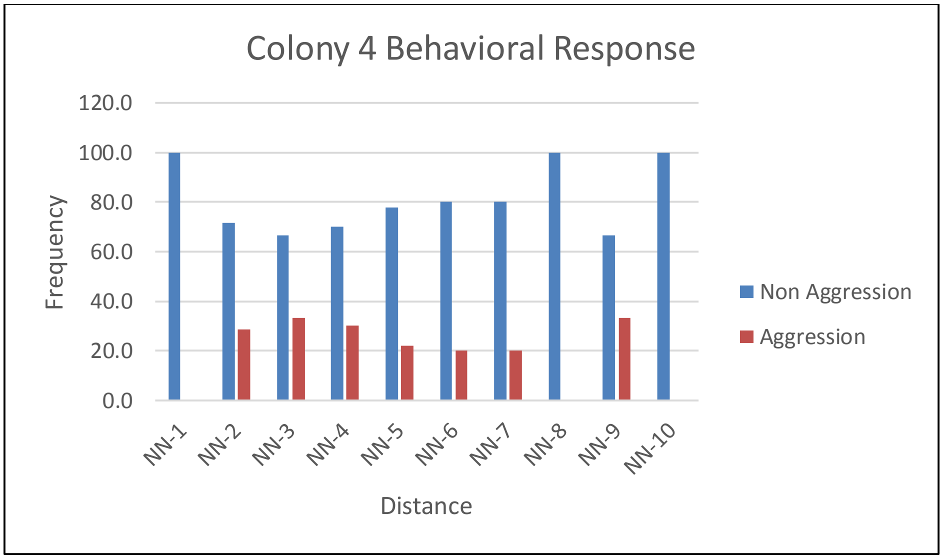
Frequency of Behavioral Response by Colonies

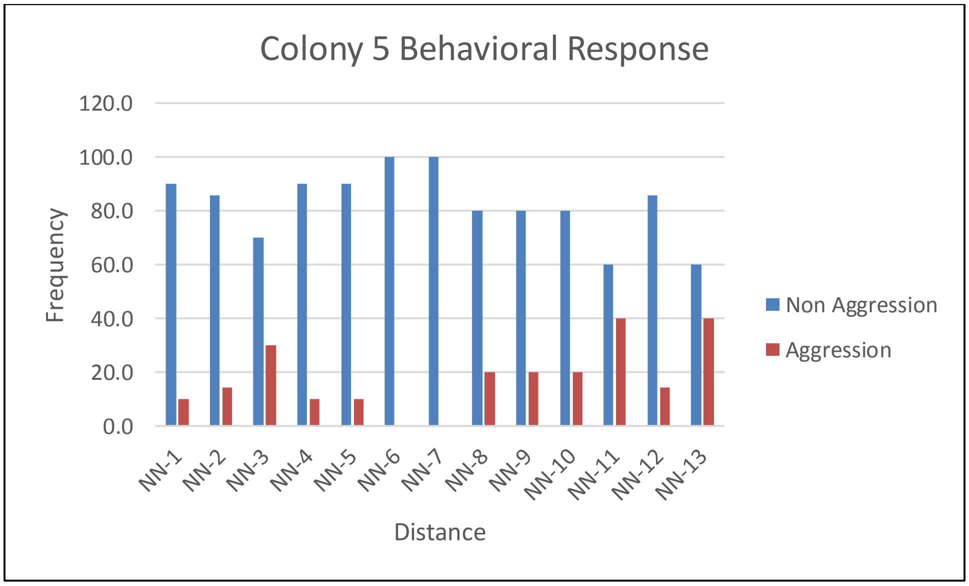
For each colony, I conducted replicate interactions in arenas with 13 other colonies within GL, FWNC. The following bar charts indicate the frequency of aggressive *vs*. nonaggressive behavioral responses for each colony with other colonies as a function of nearest neighbor distance. The x axis is the nearest neighbor distance -- in a ranked order such that NN-1 indicates the closest neighbor, NN-2 indicates the second closest and so forth. I was not able to get interactions between all colonies hence, some charts record fewer than 13 neighbor distances. There is no pattern in behavioral response as a function nearest neighbor distance.

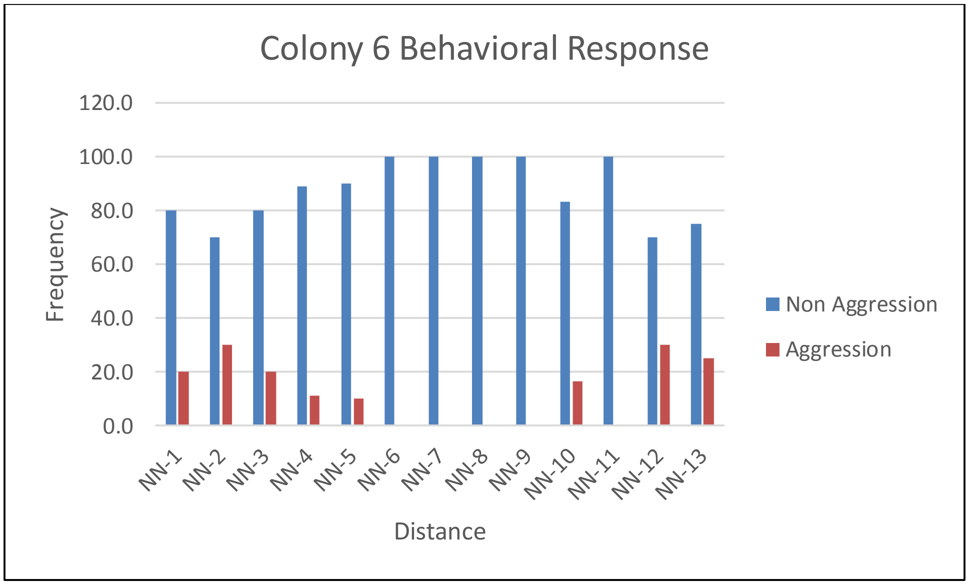


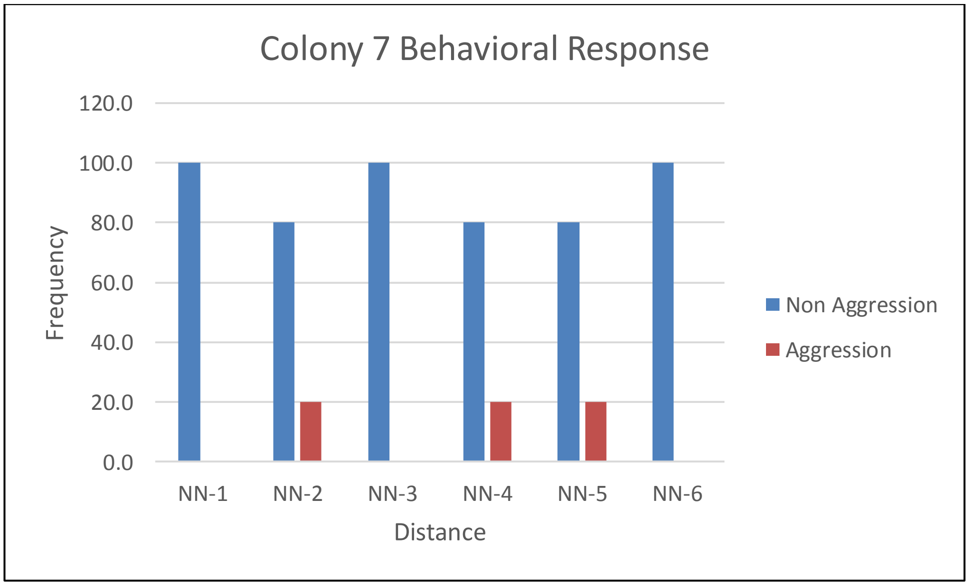

Colony 2 Behavioral Response
Frequency
120.0
100.0
80.0
60.0
40.0
20.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
NN-12
NN-13
Distance
Non Aggression
Aggression

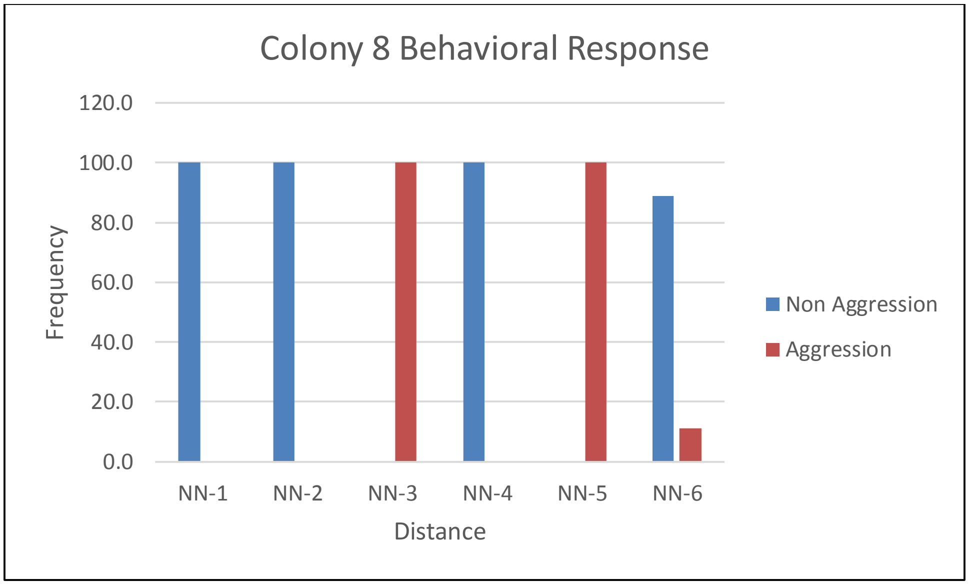

Colony 3 Behavioral Repsonse
Frequency
150.0
100.0
50.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
NN-12
NN-13
Distance
Non Aggression
Aggression


Colony 4 Behavioral Response
Frequency
120.0
100.0
80.0
60.0
40.0
20.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
Distance
Non Aggression
Aggression

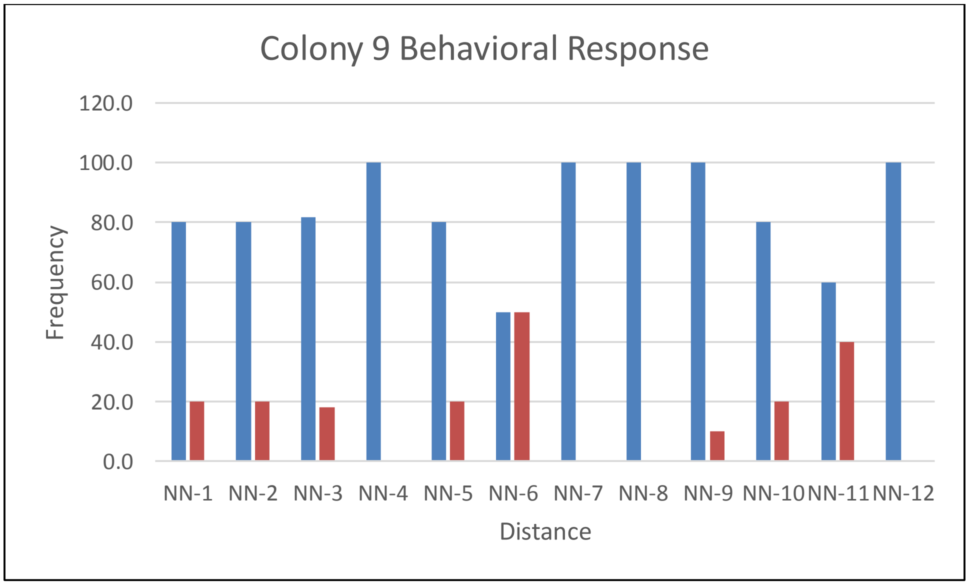

Colony 5 Behavioral Response
Frequency
120.0
100.0
80.0
60.0
40.0
20.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
NN-12
NN-13
Distance
Non Aggression
Aggression

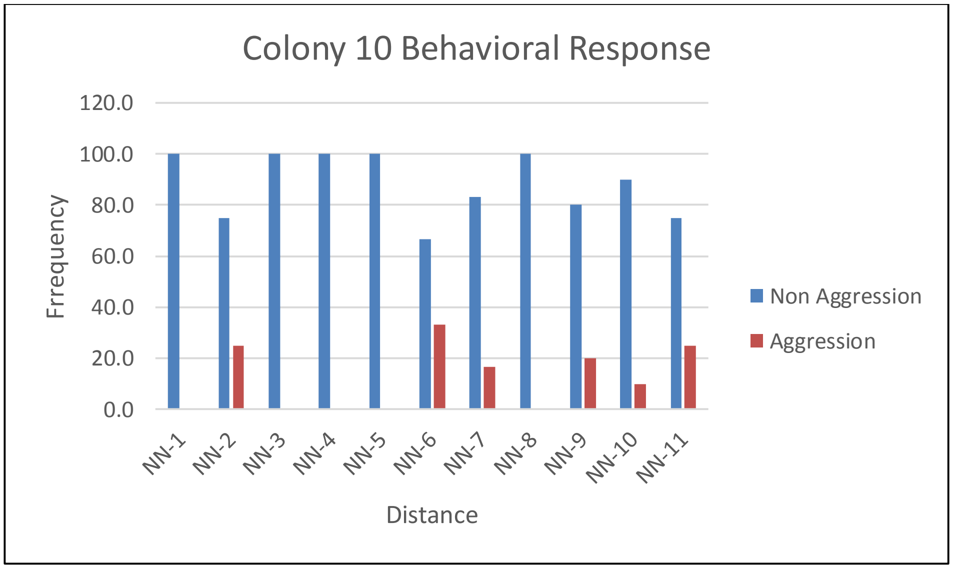

Colony 6 Behavioral Response
120.0
100.0
80.0
60.0
40.0
20.0
0.0
Frequency
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
NN-12
NN-13
Distance
🟦 Non Aggression
🟥 Aggression

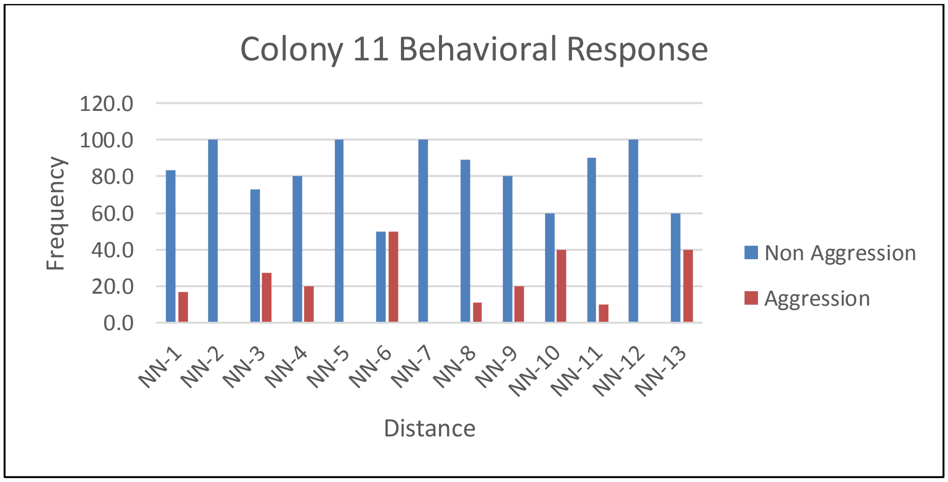

Colony 7 Behavioral Response
120.0
100.0
80.0
60.0
40.0
20.0
0.0
Frequency
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
Distance
🟦 Non Aggression
🟥 Aggression

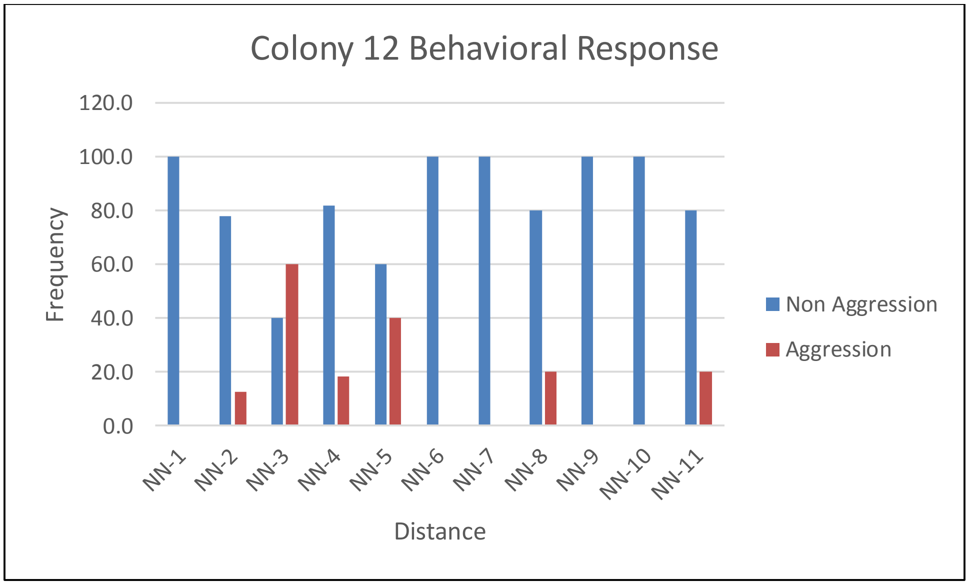


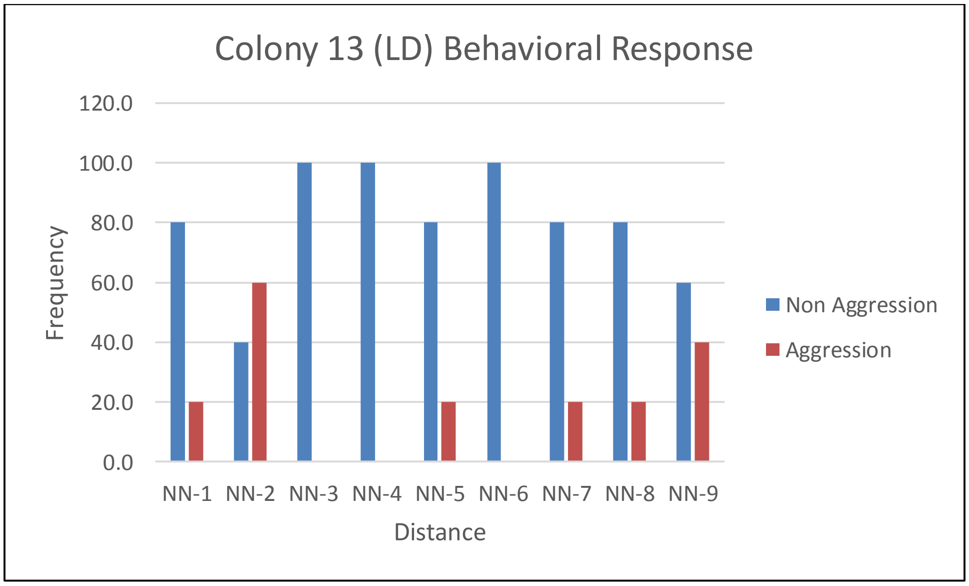
Colony 8 was the newly founded colony and did not survive the entire experimental period.




Colony 10 Behavioral Response
Frrequency
120.0
100.0
80.0
60.0
40.0
20.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
Distance
Non Aggression
Aggression


Colony 11 Behavioral Response
Frequency
120.0
100.0
80.0
60.0
40.0
20.0
0.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
NN-12
NN-13
Distance
Non Aggression
Aggression


Colony 12 Behavioral Response
Frequency
Distance
0.0
20.0
40.0
60.0
80.0
100.0
120.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
NN-10
NN-11
🟦 Non Aggression
🟥 Aggression


Colony 13 (LD) Behavioral Response
Frequency
Distance
0.0
20.0
40.0
60.0
80.0
100.0
120.0
NN-1
NN-2
NN-3
NN-4
NN-5
NN-6
NN-7
NN-8
NN-9
🟦 Non Aggression
🟥 Aggression

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