Temperature variation, resource concentration, and foraging behaviour

influencing the effect of *Monomorium sydneyense* (Hymenoptera: Formicidae)

on the ant community of Tauranga, New Zealand.

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Abstract

Introductions of ants into new areas can dramatically influence resident ant populations. A recent ant introduction to New Zealand is the Australian myrmicine, Monomorium sydneyense Forel. The effects of this ant on the resident ant fauna of Tauranga were assessed, as well as the role of temperature and food concentration on competitive dynamics. Aspects of foraging characteristic and intraspecific behaviour were studied in order to aid management decisions, should population control by toxic baiting be required. There was a significant difference in community structure in M. sydneyense invaded communities compared to uninvaded ones, although the abundance of no individual species was significantly affected or was displaced by *M. sydneyense*. Temperature was found to play a strong role in the competitive dominance of M. sydneyense. Monomorium sydneyense dominated a larger proportion of baits at warm temperatures, however it secured significantly less foods at cooler temperatures. Temperature preference trials in the laboratory supported field observations as M. sydneyense displayed a preference for warmer temperatures, compared to Pheidole rugosula Forel which showed no preference for any of the temperatures tested. *Monomorium sydneyense* showed a distinct preference for the protein based food resources that were offered, including the ant bait X-Stinguish[®]. Foraging distance trials showed that *M. sydneyense* workers were never observed foraging more than 2.8 m from their nest. The probability of only 50% of baits being occupied by M. sydneyense at a distance of 1 m from a nest suggests that intensive baiting would be required

to manage populations of this ant, highlighting that the population management of *M. sydneyense* would be difficult. Aggressive behaviour was displayed between workers from different nests, suggesting that there is a reduced likelihood of this ant attaining high population densities in New Zealand.

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Chapter 1 -General introduction

Invasions

Introduced organisms can have a range of effects in a new area ranging from a mere addition to the flora or fauna, to severe disruption of the host ecosystem (Bond and Slingsby 1984; Christian 2001; Cole et al. 1992). Transportation of these exotic organisms has often been facilitated through their close association with humans (Collingwood et al. 1997; Vitousek et al. 1997), which increases their chance of dispersal past barriers that previously hindered their natural spread (Holt 1996). Dispersal and subsequent arrival of an organism into a new habitat does not automatically equate to successful establishment. Many organisms that arrive fail to establish self sustaining populations (Kareiva 1996; Simberloff and Gibbons 2004). Characteristics of the invader and the new environment must be compatible before the introduced organism becomes a permanent resident (Elton 1958; Heger and Trepl 2003; Holway et al. 2002b; Lester 2005; Moyle and Light 1996; Shigesada and Kawasaki 1997). For species that do establish in the new area, their influence is greatest on species that require similar resources (Andersen 1997; Brown 2000). Consequently the management of some of these exotic species by eradication has been conducted to prevent further disruptions to the flora and fauna of the invaded environment (Causton et al. 2005; Harris 2001).

Ants are particularly successful at establishing populations outside of their native range, as demonstrated by the presence of five species that appear in the '100 of the world's worst invasive species' list (Lowe et al. 2000.). Many species have a suite of characteristics conducive to their establishment outside of new ranges after they arrive. Many have the ability to establish functioning colonies with a low number of individuals, thus only needing a small number of propagules to arrive in the new habitat (Hee et al. 2000). Other invasive species display unicolonial behaviour whereby workers from spatially separate nests show reduced aggression toward each other and cooperate rather than compete with one another for resources, allowing more time and energy to be focused on foraging and worker production than on nest defence (Holway et al. 2002a; Holway et al. 1998). This behaviour can be influenced by genetic variation between and within populations (Suarez et al. 1999; Tsutsui et al. 2003; Tsutsui et al. 2000) and environmental cues (Suarez et al. 2002; but see Giraud et al. 2002) or by a change in the amount of food sources in the environment (Sorvari and Hakkarainen 2004). Furthermore, factors such as escape from enemies, empty niche, omnivory, and general nest site requirements (Herbers 1993; Holway et al. 2002a; Passera 1994; Vega and Rust 2001) can also promote successful establishment of ants outside of their home range.

Generally, the organisms most affected by ant introductions are the resident ant species (Christian 2001; Erickson 1971; Gómez and Oliveras 2003). The numerical superiority of introduced ant species over resident ant species has been cited as a mechanism by which the resident species can be displaced

(McGlynn 1999a). Community composition of ant species is thought to be based on competitive outcomes (Fox et al. 1985; Greenslade 1971; Holway 1999; Morrison 2002; Savolainen and Vepsäläinen 1988), but see (Roughgarden 1983; Schoener 1982) and environmental compatibility (Andersen 2000; Holway et al. 2002b; Human et al. 1998). Ant community structure may not be easily predicted from numerical supremacy or fighting ability alone. Daily or seasonal temperature fluctuations may also affect the outcome of competitive interactions between co-occurring species, due to differences in the temperature tolerances of some species influencing forager number (Campos and Schoereder 2001; Cerdá et al. 1997; Cerdá et al. 1998; Fellers 1989). Additionally, species with low resource needs (Fox 2002; Tilman 1982) or species that have different food utilisation traits, for example epigeic (above ground foraging) or hypogeic (below ground foraging) ants, may be able to maintain populations in the presence of behaviourally dominant species (Palmer 2003; Savolainen and Vepsäläinen 1988).

New Zealand ant fauna

Pacific islands receive a large number of ant introductions (McGlynn 1999b). It is thought that oceanic islands are more easily invaded than continental land masses because of a lack of biotic resistance from the native species (Elton 1958; Wilson 1961; but see Levine 2000; Levine and D'Antonio 1999). New Zealand has a small native ant fauna, most of which are thought to be derived from Australian ant species (Brown 1958). There are an estimated 37 established ant species in New Zealand, 26 of which are considered to be

introduced (Don et al. 2005). One recently successfully established ant is the Australian native, *Monomorium sydneyense* Forel.

Monomorium sydneyense is placed in the Myrmicinae subfamily (Formicidae: Myrmicinae) and is categorised in the Generalized Myrmicinae functional group (Bisevac and Majer 1999). It was found at the Port of Tauranga during an invasive ant survey in 2001 (unpublished MAF 2003) and at the Port of Napier in 2004 (Lester pers. comm.). These are the only two areas known to have colonies of *M. sydneyense*. Monomorium sydneyense is a small monomorphic ant species approximately 1.7 mm long. It is typically a ground nesting species that is found throughout Australia, including Tasmania (Heterick 2001). Currently there are many colour morphologies associated with this species, from dark brown to yellow therefore *M. sydneyense* may be multiple species or sub species under the same species name (Heterick 2001). Therefore, if there is only one *M. sydneyense* colour morph present in New Zealand, it may have a more restricted climatic range than would otherwise be suggested from the distribution records in Australia, which include all of the colour morphologies. *Monomorium sydneyense* has been observed to co-occur with the behaviourally aggressive Argentine ant Linepithema humile (Mayr) and the coastal brown ant Pheidole megacephala (Fabricius) in Australia (Heterick et al. 2000), species that are often regarded as superior competitors with other ants (Bond and Slingsby 1984; Brightwell 2002; Holway et al. 2002a; Vega and Rust 2001).

Research aims

This study was conducted to investigate whether *M. sydneyense* could potentially reduce the abundance of, or even displace, ants in a representative New Zealand environment. My study site was at Sulphur Point in Tauranga because it is where *M. sydneyense* has been recorded at the longest. I examined the role of the spatial dispersion of a food resource and temperature on competitive outcomes at food resources. Additionally, aspects of foraging distance, food preference and aggression behaviour between spatially separate nests of *M. sydneyense* was investigated.

Firstly in Chapter 2 I investigated the effect of *M. sydneyense* on the resident ant species. I compared species richness and abundance in sites with *M. sydneyense* to adjacent sites without *M. sydneyense*. No comparisons could be made at the same site before and after the arrival of *M. sydneyense* as no data has previously been published on the resident ant fauna of Sulphur Point before the introduction of *M. sydneyense*.

In my second research chapter, Chapter 3, I studied possible mechanisms that would promote coexistence of the resident ant species with *M. sydneyense*. I investigated the effect of temperature on the competitive dynamics of the ants present at Sulphur Point and I examined the role of resource concentration on species richness in the area.

In Chapter 4, I studied aspects of the biology of *M. sydneyense*, focussing on foraging behaviour and intraspecific interactions that would be useful for management decisions should there be a need to manage populations of this species.

Finally, in Chapter 5 I discuss the implications of my findings. As I have written chapters two, three and four as individual research papers for publication there is inevitable repetition in the introduction, methods and discussion sections between these chapters.

Chapter 2 -

Changes to the Tauranga ant community composition as a result of invasion by *Monomorium sydneyense* Forel (Hymenoptera: Formicidae).

Introduction

As biological invaders, several ant species rank among the most successful invaders in the world (Lowe et al. 2000). Many ants have managed to overcome natural borders that previously hindered an expansion from their home range due to a close association with humans (Collingwood et al. 1997; Elton 1958; Vitousek et al. 1997). Characteristics such as polyphagy (Holway and Suarez 1999), general nest site requirements (Hee et al. 2000; Herbers 1993), polygyny (multiple queens in a nest) and unicolonality (multiple cooperative nests) (Tsutsui and Suarez 2003) have subsequently contributed to the successful establishment and spread of some exotic ants. Some exotic ant species have had disastrous outcomes on the biology of areas because of their introduction. Effects in their new range have included reducing pollinator efficacy through competition for food (Bond and Slingsby 1984; Buys 1987; Cole et al. 1992; Visser et al. 1996), and displacement of key species causing major changes in ecosystem function (Christian 2001; Cole et al. 1992; O'Dowd et al. 2003).

Commonly, the organisms that are most adversely affected by ant invasions are the resident ant species (Christian 2001; Erickson 1971; Gómez and Oliveras 2003), often accomplished by competitive displacement due to the

numerical superiority of the introduced ant species over the resident species (McGlynn 1999a). Competitive displacement is most likely to occur when cooccurring ants have similar or overlapping dietary or nesting needs (Savolainen and Vepsäläinen 1988), such as ants in the same functional group (Andersen 2000)

The placement of Australian ants into functional groups has aided our understanding of ant community structure and environmental health (Andersen 1995; Brown 2000; Hoffmann and Andersen 2003; Majer et al. 2004). Ants are assigned to groups primarily based on their tolerances to temperature stress and physical disturbance and secondarily by their competitive behaviour (Andersen 1995). Functional group theory predicts that co-occurring ants categorised in the same functional group should have the greatest influence on the behaviour of each other and less influence on ants belonging to different functional groups (Andersen 1995; Andersen 2000; Brown 2000). There have been seven different functional groups distinguished. These groups have been listed in order of the usual competitive superiority over the following groups: 'Dominant Dolichoderinae', 'Subordinate Camponotini', 'Generalized Myrmicinae', 'Opportunists', 'Cryptic species', 'Climate Specialists' and 'Specialist Predators' (Fig. 2.1). 'Dominant Dolichoderinae' are generally found in areas with low temperature and disturbance stress. They are usually behaviourally dominant over the other functional groups. 'Subordinate Camponotini' are often temporally segregated from competitive interactions with other functional groups because of their usual nocturnal habit. 'Generalized Myrmicinae' can often tolerate moderate

temperature stress and physical disturbance. They are occasionally competitively superior to 'Dominant Dolichoderinae'. 'Opportunists' are subordinate to the above groups and are often found in high thermal stress or highly disturbed environments. 'Cryptic species' are often found in low numbers in leaf litter. 'Climate Specialists' are found in environments with large thermal stresses, often categorised into either 'Hot-' or 'Cold- Climate Specialists'. Temperatures may be too high or too low, allowing them to forage without competition from 'Dominant Dolichoderinae' or 'Generalized Myrmicinae' in the area. 'Specialist Predators' often forage singularly and do not interact much with the other functional groups (Andersen 2000).



Figure 2.1 - Functional groups adapted from Andersen (2000). Arrows indicate the general flow of competitive dominance. Dominant Dolichoderinae are competitively superior to all other functional groups. 'Dominant Dolichoderinae' and 'Subordinate Camponotini' are competitively superior to the other functional groups. The bottom box of 'Climate specialists', 'Cryptic species' and 'Specialist Predators' are generally subordinate to all other groups and are not superior to one another.

A recent arrival to New Zealand is the small Australian myrmicine ant *Monomorium sydneyense* Forel (Formicidae: Myrmicinae). It was first recorded at Sulphur Point, Tauranga during an invasive ant survey at the Port of Tauranga in 2001 (MAF 2003 unpublished) and is now established in New Zealand (Lester 2005). It is found throughout its home range in Australia, including Tasmania (Heterick 2001). It can be assumed to tolerate the lower temperatures that are found in New Zealand. Heterick (2001) suggests that there are some different colour morphologies that have been included under the species name *Monomorium sydneyense*. Therefore its Australian distribution may not be a good predictor for its spread in New Zealand.

Lester's (2005) study is the first published record of *M. sydneyense* establishment outside of Australia. Although there are no published data concerning effects that it has had on ants in other countries, it has been found occurring with the invasive Argentine ant, *Linepithema humile* (Mayr) and coastal brown ant *Pheidole megacephala* (Fabricius) in Australia (Heterick et al. 2000). Its ability to survive in the presence of such highly competitive species suggests that it may be a good competitor.

I examined the response of the ant community of Sulphur Point to the presence of *M. sydneynese*. To date, no data have been published on the ant fauna of Sulphur Point before the arrival of *M. sydneyense*. Consequently, in this study, I compare differences between invaded and adjacent uninvaded sites rather than a preferred before and after study. Firstly, I hypothesised that

there would be differences in the ant community diversity and abundances of species in invaded and uninvaded sites. Secondly ants categorised in the same functional group as *M. sydneyense* would be negatively affected by its presence. This result would be indicated by a decline in abundance of these species in invaded sites compared to their abundances in uninvaded sites. The ant community diversity and abundance of species was compared at different times through the year to investigate whether there was an effect of season, indicated by temperature, on the ant communities in the invaded and uninvaded sites.

Methods

Study site

This study was conducted from December 2003 to December 2004 at Sulphur Point, Tauranga, New Zealand (37° 39' S, 176° 11'E) (Fig. 2.2). The majority of Sulphur Point is reclaimed land consisting of the marine sediments dredged up from the adjacent shipping channel. Consequently the soil found on the reclaimed point is a loamy-sand containing portions of shells, which is consistent with the marine sediments of Tauranga harbour (Healy 1994). Sulphur Point has an approximate area of 90 hectares, two thirds of which is occupied by the Port of Tauranga. The remaining land has been set aside for recreational purposes, half of which is grassed and the other half asphalted.

Tauranga experiences a sub-tropical climate, characterised by warm humid summers and mild winters with daytime temperature maxima ranging from 22-26°C in the summer months (December- February) to 12-17°C during the winter months (June- August). On average Tauranga receives 2200 sunshine hours per year (NIWA 2005) and annually precipitation ranges from 1250 to 1500 mm per year, with the monthly average slightly increasing during the winter months (de Lilse and Kerr 1963).



Figure 2.2 - Sulphur Point, Tauranga. Indicating the distribution of *M. sydneyense* captured in pitfall traps from December 2003 – 2004. Monomorium sydneyense present (\bigcirc) *M. sydneyense* absent (\bigcirc) .

Effect of *Monomorium sydneyense* on the resident ant species

I compared an area invaded by *M. sydneyense* with an adjacent uninvaded area for differences in the species abundance and diversity of the ant communities by pitfall trap sampling. I placed pitfall traps along a transect originating from the area that was known to contain nests of *M. sydneyense* in

December 2003. Ensuring that the pitfall trap sites remained constant throughout the course of the survey, I repeated my sampling in March, August, October and December 2004 to determine whether there was any seasonal variation in the abundance of ants. The initial transect contained 13 pitfall traps and of these four were in the uninvaded area. To increase the number of traps in the uninvaded area two extra pitfall traps were added in March 2004 (n = 15), and a further three in August, October and December 2004 (n = 18). Data on the air temperature at a height of four metres, for the different months that the pitfall surveys were conducted, were obtained from the Tauranga Aerodrome's NIWA climate station, 2.7 km from my study site.

The pitfall traps were spaced approximately 60 m apart along the western edge of a planted area. The planted area had a length of 870 m with an average width of 15 m and had a constant orientation of north to south, parallel with the western fence of the Port of Tauranga. The planted area predominantly of Zealand native comprised New coastal plants; Meterosideros excelsa, Dodonea viscosa, Myoporum leatum, and various Hebe and Coprosma spp. Included in this vegetation were some exotic planted species; Araucaria heterophylla and Pinus spp. The pitfall traps were plastic cups that were 65mm in diameter at the top tapering to 43 mm at the base and were 90mm deep. Each trap was filled one third with 30% ethylene glycol and water with 2-3 drops of dishwashing detergent added to break surface tension. They were left in the field for a period of 96 hours after which time they were collected and brought back to the laboratory. All ants in the traps were counted and identified to species level using dichotomous keys

provided by Landcare Research (2005), Heterick (2001) and Brown (1958). Functional groups were assigned to the ants captured (Andersen 1997; Bisevac and Majer 1999; Heterick et al. 2000).

Statistical Analysis

I analysed the similarity in species diversity and species abundances in pitfall traps between invaded and uninvaded sites using an Analysis of Similarities, ANOSIM. This method produced a 'Global R' value with an associated significance value. Significance values (P < 0.05) indicated that Global R values were different from the Null hypothesis, that there was no difference in the diversity and abundance of ants captured in pitfall traps between invaded and uninvaded sites. Many species were absent from pitfall traps throughout the year, consequently, analysis was carried out on log_{10} (x+1) transformed numerical data of the species collected, where x was the count of the species. The data were analysed using Bray-Curtis similarities measure. This method ensured that results were biased toward common ant species captured rather than being strongly influenced by the presence or absence of rare species (Clark and Warwick 2001).

I performed a non-metric multidimensional scaling ordination (NMDS) to graphically illustrate the results of the ANOSIM. NMDS plots are two dimensional graphical representations of ranked pair-wise comparisons between samples. Samples with similar species abundance and diversity are placed as points close together in multidimensional space. Samples that are

increasingly dissimilar to each other are placed further apart. Since the NMDS plots are two dimensional representations of this placement in multidimensional space stress values were associated with the NMDS plots indicating the amount of distortion (stress) needed to create the plot. Stress values ≥ 0.2 imply that the NMDS does not accurately represent the true distances between points in multidimensional space. Values close to 0.1 indicate a good two dimensional representation and values < 0.01 indicate a near perfect two dimensional representation of the ordination (Clark and Warwick 2001).

A Similarities Percentages analysis, SIMPER, was undertaken to determine the contribution of each species to variations in the ANOSIM. Whilst not a statistical test, SIMPER can support other statistical analyses by identifying species that had the strongest influence on results of previous tests. SIMPER evaluates the average similarity within groups and dissimilarity between groups and ranks the contribution that a species makes to an ANOSIM. Additionally, the dissimilarity/ standard deviation (diss/SD) statistic shows the variation within a group, where values \leq 1.4 indicate that there is little within group variation, thus are a good discriminating species (Clark and Warwick 2001). Analyses were performed using Primer v. 5 (PRIMER-E Ltd 2002)

Effect of *Monomorium sydneyense* on individual species

To assess whether ant species diversity and abundance differed between invaded and uninvaded plots and through time, I compared the abundances of the five most commonly observed ant species: *Paratrechina vaga* (Forel),

Tetramorium grassii Emery, *Pheidole rugosula* (Forel), *Iridomyrmex anceps* (Roger), and *Monomorium antarcticum* captured in the invaded and uninvaded pitfall traps. A quasi- Poisson regression, Generalized Linear Model (GLM) was used for comparisons of the counts of the ants in each pitfall trap, using R v. 2.0.1 (The R foundation for Statistical Computing 2004).

Results

A total of 15 ant species, from 11 genera and four subfamilies were collected in the pitfall traps at Sulphur Point (Table 2.1). Thirteen species were classed as exotic species to New Zealand. The most represented functional group was the Opportunist group, followed by the Generalized Myrmicinae, Cryptic, Dominant Dolichoderinae and Specialist Predators (Table 2.1). The pitfall traps captured one worker of the non-established *Paratrechina longicornis* (Latreille) a potential pest species. Species such as *Cardiocondyla minutior* Forel, *Strumigenys perplexa* (Smith), *Monomorium fieldi* Forel (formally known as *Monomorium antipodum* Forel in New Zealand) (Gunawardana 2005) and *Hypoponera eduardi* (Forel) were predominantly or only observed in invaded sites (Table 2.1). *Monomorium sydneyense* was found at 10 of the 18 sites along the pitfall transect (Fig. 2.2). **Table 2.1** Ant species captured in the pitfall traps with their total abundances in invaded and uninvaded sites, including their current origin status in New Zealand. The functional group abbreviations are; DD, Dominant Dolichoderinae; GM, Generalized Myrmicinae; O, Opportunist; C, Cryptic species and SP, Specialist Predators (Brown 2000).

	Status	Functional	Abu	Indance
Species		Group	Invaded	Uninvaded
SUBFAMILY DOLICHODERINAE				
Iridomyrmex anceps (Roger)	exotic	DD	186	79
Technomyrmex albipes (Smith)	exotic	0	0	3
Ochetellus glaber (Mayr)	exotic	0	5	3
SUBFAMILY FORMICINAE				
Paratrechina longicornis (Latreille)	exotic	0	0	1
Paratrechina vaga (Forel)	exotic	0	836	610
SUBFAMILY MYRMICINAE				
Cardiocondyla minutior Forel	exotic	0	52	3
Monomorium antarcticum (F. Smith)	native	GM	28	44
Monomorium fieldi Forel	native	GM	33	0
Monomorium sydneyense Forel	exotic	GM	370	0
Orectognathus antennatus Smith	exotic	SP	0	1
Pheidole rugosula (minor) Forel	exotic	GM	338	507
Strumigenys perplexa (Smith)	exotic	С	7	1
Tetramorium bicarinatum (Nylander)	exotic	0	1	0
Tetramorium grassii Emery	exotic	0	440	299
SUBFAMILY PONERINAE				
Hypoponera eduardi (Forel)	exotic	С	6	0

Effect of Monomorium sydneyense on the resident ant community

The ANOSIM showed a significant difference in species diversity and abundance between invaded and uninvaded sites for the duration of the study (P = 0.010). Analysis of Similarities results differed through time with a significant difference in ant community composition between invaded and uninvaded sites in October (P = 0.009) and December 2004 (P = 0.043) but not in December 2003 (P = 0.066), March 2004 (P = 0.351) and August 2004 (P = 0.811) (Fig. 2.3; Table 2.2).

Table 2.2 Analysis of similarity (ANOSIM) on log(x+1) transformed data of pitfall traps between *M. sydneyense* invaded and uninvaded sites. Global R values outside of the range +0.15 -> -0.15 indicate that groups are not similar to each other as indicated by the significance value. Significant values are in bold

Month	Global R	sig.
December 2003	0.258	0.066
March 2004	0.036	0.351
August 2004	-0.067	0.811
October 2004	0.247	0.009
December 2004	0.202	0.043
All Months	0.283	0.010

SIMPER analysis on all of the months combined, December 2004 and the October samples indicated that *P. rugosula, T. grassii* and *I. anceps* had the strongest influence on the results (Table 2.3). Two thirds of the variation between invaded and uninvaded sites was consistently attributed to these three species. There was little within group variation in the number of these three species captured in the pitfall traps, as indicated by the large values for the dissimilarity/ standard deviation statistic except for *P. rugosula* and *I. anceps* in October and *P. rugosula* in December 2004 (Table 2.3). There appeared to be an influence of air temperature on the abundances of the ants captured in the pitfall traps (Fig. 2.4). Abundances of all of the species included increased with the rise in temperature though there was some variation. *Pheidole rugosula* appeared to have higher abundances in areas without *M. sydneyense*, though *T. grassii* and *P. vaga* showed little variation in the numbers of ants in invaded and uninvaded sites (Fig. 2.4).

Table 2.3 SIMPER analysis on log(x+1) transformed data explaining the percent to which each species had an influence on the differences in ant abundance and diversity observed between the *M. sydneyense* invaded and uninvaded sites. Values of 1.4 and above for Dissimilarity/ sd column indicate that that species is a good discriminating species. SIMPER analysis was carried out on October, December 2004 and all months combined as differences were significant in the ANOSIM analysis.

		Average a pitfall trap	abundance in s		
		•			%
	Species	Invaded	Uninvaded	Diss/sd	contribution
October 2004					
	Pheidole rugosula	4.90	15.63	1.16	26.23
	Tetramorium grassii	4.80	7.75	1.40	24.75
	Iridomyrmex anceps	3.60	2.88	1.36	17.53
	Paratrechina vaga	9.20	11.38	1.40	11.72
	Monomorium antarcticum	0.40	2.13	0.82	10.77
December 2004					
	Pheidole rugosula	9.60	25.75	1.37	26.66
	Iridomyrmex anceps	10.00	3.13	1.66	21.80
	Tetramorium grassii	7.20	8.75	1.50	20.83
	Paratrechina vaga	23.50	24.38	1.38	9.04
	Monomorium antarcticum	1.30	1.00	0.85	8.84
	Monomorium fieldi	3.20	0.00	0.60	8.49
Combined Months					
	Pheidole rugosula	6.81	16.06	1.40	23.68
	Tetramorium grassii	8.81	8.69	1.52	22.63
	Iridomyrmex anceps	3.80	3.03	1.66	16.19
	Paratrechina vaga	17.00	16.61	1.49	9.01
	Monomorium antarcticum	0.06	1.42	1.05	8.81
	Cardiocondyla minutior	1.08	0.11	1.18	8.31
	Monomorium fieldi	0.66	0.00	0.57	4.59



Figure 2.3 Two dimensional non-metric MDS plot of the log(x+1) transformed numerical data. Points represent individual pitfall traps whereby points close to each other are more similar in species diversity and abundance than points that are further away. Figures 3 d, e, and f have significant differences at the <0.05* and <0.01** levels in species diversity and abundance between *M. sydneyense* invaded plots (•) and uninvaded plots (\circ).

Effect of Monomorium sydneyense on individual species

The presence of *Monomorium sydneyense* did not have a statistically significant affect on the abundances any of the individual species tested (Fig 2.5; Table 2.4). There was a significant effect of month on the abundances of *P. vaga* (P < 0.001), *T. grassii* (P < 0.001), *I. anceps* (P = 0.003) and *M. sydneyense* (P = 0.020) caught in the pitfall traps (Fig. 2.5; Table 2.4). Densities of *P. rugosula* did not change significantly through time (Fig. 2.5 f; Table 2.4). A significant *M. sydneyense* x time interaction on the abundance of *M. antarcticum* indicated that the effects of *M. sydneyense* on the

abundance of *M. antarcticum* differed over time, although no clear effect of *M.*

sydneyense on M. antarcticum abundances was observed as dynamics in

December 2003 were very different from December 2004 (Fig. 2.5 b).

Table 2.4 Poisson regression (GLM) on the effect of the presence of *Monomorium sydneyense* and sample time on the abundances of five most common ant species collected in pitfall traps from December 2003 to December 2004. Included is the effect of sample time on the abundance of *M. sydneyense*. Degrees of freedom are in parentheses. Significant values are highlighted in bold.

			Interaction
Species	Time (4)	M. sydneyense (1)	Time x <i>M. sydneyense</i> (4)
Paratrechina vaga	0.001	0.620	0.520
Tetramorium grassii	0.001	0.420	0.750
Pheidole rugosula	0.170	0.130	0.950
Iridomyrmex anceps	0.003	0.980	0.210
Monomorium antarcticum	0.586	0.377	0.032
Monomorium sydneyense	0.002	-	-



Figure 2.4 The mean number of ants (\pm S. E.) captured in invaded areas and uninvaded areas compared with the mean temperature measured during the pitfall surveys. Points represent surveys that are ordered left to right: August, October, December, March 2004 and December 2003.



Figure 2.5 Abundances of ants caught in pitfall traps each month in *M. sydneyense* invaded sites (\bullet) and uninvaded sites (\circ). Bars represent ± 1 standard error. The large variation between the two December surveys may be due to the low sample size in December 2003.

Discussion

Effect of *Monomorium sydneyense* on the resident ant community

Comparisons of ant species abundance and diversity between invaded and adjacent uninvaded areas showed that there were differences between the two areas throughout the study period. This was not continuous throughout the year as demonstrated by differences only observed in October and December 2004 but not in December 2003, March or August. This may be a result of differences in sample size, but it seems likely that weather conditions influenced the ant communities (Gordon et al. 2001). There were a smaller number of pitfall traps in December 2003 (n = 13) and March (n = 15) than in the other months (n = 18) and 12 hours of rainfall was recorded during the pitfall trapping in December 2003. These two factors, sample size and rainfall would have influenced the results by reducing ant foraging activity. Had these issues not have arisen, I would have expected differences to be detected in the December 2003 survey. Differences were significant at the P < 0.10 level when all of the months were considered. Similar species diversity and abundances between invaded and uninvaded sites in August may have been due to the lower number of ants foraging at that time, likely related to the low mean temperature recorded during the survey (Briese and Macauley 1980).

Previous studies have revealed that temperature can strongly regulate the diversity and abundance of foraging ants (Andersen 1992; Bestelmeyer 2000; Campos and Schoereder 2001; Cerdá et al. 1997; Markin et al. 1975; Whitford 1999). There was a large seasonal variation in the numbers of *P. vaga, T. grassii, I. anceps* and *M. sydneyense* captured in the pitfall traps, as indicated by the GLM. This may have been influenced by differences in the mean temperature for each sample period. Greater abundances of foraging species in the summer months may have allowed for differences in species diversity and abundances to be detected between invaded and uninvaded sites in December 2004 and October 2004 but not in March and August, whilst the small sample number could have influenced the December 2003 data.

Effect of *Monomorium sydneyense* on individual species

There was no difference in the abundances of the five most common species in invaded and uninvaded areas. *Paratrechina vaga* and *T. grassii* are categorised as 'Opportunists', therefore are not likely to be influenced by the presence *M. sydneyense* (Brown 2000). The abundances of these species varied seasonally but did not vary between invaded and uninvaded areas. They are likely to be competitively subordinate to *M. sydneyense*, though their tolerances to temperature stress, which may allow them to escape from competitive interactions with *M. sydneyense* (Andersen 2000; Briese and Macauley 1980; Brown 2000). *Iridomyrmex anceps* (Roger), as a Dominant Dolichoderinae is predicted to be competitively dominant over all functional groups (Andersen 2000; Brown 2000), therefore should not be influenced by the presence of *M. sydneyense*. This result appears to be the case as the abundances of *I.* anceps did not differ between invaded and uninvaded sites.

Since functional group theory predicts that ant species categorised in the same group to compete the most intensely for resources (Andersen 2000; Brown 2000), I hypothesised that the presence of *Monomorium sydneyense* would have the greatest effect on resident ant species that were categorised its functional group, the Generalized Myrmicinae group. In Tauranga there were three other species categorised in this group: *P. rugosula, M. antarcticum* and *M. fieldi. Pheidole rugosula* exhibited decreased abundances in the pitfall traps in invaded areas consistently throughout the study, though the effect of *M. sydneyense* was not significant on this species. *Monomorium antarcticum* did show some differences in abundance between present and

absent sites however, this effect was dependent on the month that the sites were sampled. *Monomorium fieldi* was only found in *M. sydneyense* invaded areas, though with the low numbers of this species it is difficult to conclude whether this indicates co-existence.

The influence of *P. rugosula, T. grassii* and *I. anceps* on the dissimilarity between invaded and uninvaded sites in the SIMPER analysis would suggest that *M. sydneyense* is having an effect on their abundance. Only *P. rugosula* showed some reduction in abundance in invaded sites, although this reduction was not statistically significant. The abundances of *T. grassii* and *I. anceps* showed no pattern between invaded and uninvaded sites. There may be other factors not taken into account that have influenced the abundances of these species, such as variations in the availability moisture in the area (Holway 1998).

There were disparities between the ANOSIM and GLM on the influence of *M. sydneyense* on the ant community of Sulphur Point. Differences were found between invaded and uninvaded area in the ANOSIM but not in the GLM. All species captured in the pitfall traps, except *M. sydneyense*, were included in the ANOSIM analysis. This ensured that all differences in abundance and diversity between the invaded and uninvaded areas were influencing results, unlike the GLM, which only focussed on the five most common species, one at a time.

Monomorium sydneyense has only recently been discovered in New Zealand however, it is not known when it arrived in this country. My results suggest that *M. sydneyense* is having an influence on ant community composition, but has not significantly reduced the abundances of any one ant species at Sulphur Point. Introduced organisms can have a 'lag phase' early in their introduction, when the organism adjusts to the new environment and consolidates its establishment before spreading (Crooks and Soulé 1999; Simberloff and Gibbons 2004). After such time it may have a negative effect on some of the resident organisms (O'Dowd et al. 2003; Simberloff and Gibbons 2004). If *M. sydneyense* does have a lag phase there is potential for larger impacts of this species after some time has passed. There were large variations in the numbers of ants captured in pitfall traps seasonally. Generally there were differences in ant abundance captured with temperature. This was expected as often the temperature can influence ant foraging activity (Fellers 1989; Whitford 1999).

Monomorium antarcticum and *M. fieldi*, two native species were found coexisting with *M. sydneyense*. Neither species were displaced or showed consistently reduced abundances in the presence of *M. sydneyense*. My results suggest that *M. sydneyense* will have a limited influence on these two species in ecosystems similar to Sulphur Point. Since this is likely to be the early stages of the *M. sydneyense* introduction to New Zealand there is potential to reassess its influence on the resident ant community by surveying the uninvaded ant community adjacent to the invaded area before, and if it spreads, after invasion.

Chapter 3 -

Influence of temperature and spatial dispersal of food resources on the coexistence of competing ant species at Sulphur Point, Tauranga.

Introduction

Intra- or inter- specific interactions between ants from different colonies frequently occur when workers are foraging for food. If the species occur at the same food they can either; share the resource, fight for it, or relinquish such resources (Fellers 1987; Wilson 1971). Behaviourally dominant ants will often overwhelm subordinate ants at an existing food resource and displace them from food (Holway 1999; Human and Gordon 1996). Alternatively some species can coexist in small numbers at the food in the presence of a more dominant species (Wilson 1971). Ants are often better at either finding and removing foods, or displacing other species from the foods, otherwise known as the dominance discovery trade- off theory (Davidson 1998; Hölldobler and Wilson 1990; Holway 1999). Some invasive ants, such as the Argentine ant (Linepithema humile (Mayr)) have the ability to break this trade-off often finding food quickly and displacing other ants due to their high abundances (Holway 1999; Human and Gordon 1996). Abiotic factors such as a change in temperature can influence the competitive dynamics between ants in an area (Cerdá et al. 1997; Cerdá et al. 1998; Fellers 1989). The dominance hierarchy can change from one where the behaviourally dominant ant is at the top of the hierarchy to one where the most heat tolerant ant species is at the top of the
hierarchy because it is the only ant able to forage at extreme temperatures (Cerdá et al. 1997).

The concentration of food resources in an area can influence species diversity and abundance (Root 1973). Root's (1973) resource concentration hypothesis states that herbivores that find a concentrated resource will be likely to remain at that resource, consequently there may be a decrease in herbivore richness due to displacement by specialist herbivores. Cain et al. (1985) found that the dispersion of a food affected the ability of cabbage white larvae (*Pieris rapae* (L.)) to find collards (*Brassica oleracea* L.). *Pieris rapae* were able to find more collards when they were spaced at regular intervals than when they were aggregated.

Foraging activity due to temperature differences differs between species (Briese and Macauley 1980; Campos and Schoereder 2001; Cerdá et al. 1997; Hölldobler and Wilson 1990). Species diversity and abundance at foods can fluctuate diurnally and seasonally because of temperature differences allowing subordinate ant species access to foods due to the reduced foraging activity (Andersen 1992; Briese and Macauley 1980; Cerdá et al. 1997; Fellers 1989). Holway et al. (2002b) found through a series of temperature mortality experiments that species had different tolerances to high temperatures. Consequently, ants such as the Argentine ant have the ability to dominate food resources at warm temperatures, but when temperatures become too hot other ants that can tolerate those higher temperatures can

access those foods without competition from *L. humile* (Thomas and Holway 2005).

In this chapter, I tested the effect of food dispersion and temperature on competitive ability of ants in the field, particularly in relation to the competitive characteristics of *Monomorium sydneyense* Forel, a recent ant arrival to New Zealand. Additionally, I examined the temperature preferences of species by allowing ants to move between chambers with differing temperatures in the laboratory. The hypotheses tested were that with an increase in the spatial dispersion of a food resource a greater number of ant species would be present during trials because more foods would be free from competitors thus allowing them to be discovered by less competitive species. Secondly, the numerically dominant ant species present at a food resource would change with increasing temperature. Finally, I predicted that different ant species would show a preference for different temperatures, as indicated by a short time to food discovery in a laboratory experiment.

Methods

Field work was undertaken at Sulphur Point, Tauranga, New Zealand (37° 39' S, 176° 11'E), from December 2003 until December 2004. Tauranga has a sub-tropical climate with warm humid summers and mild winters. The average daily temperature ranges from 22-26°C in the summer, with the hottest months being January and February, to 12-17°C during the winter, with July being the coldest month (NIWA 2003), rainfall however, is spread evenly

between all months of the year (de Lilse and Kerr 1963). This part of the point is reclaimed land made up from the dredged harbour channel.

The experiments were conducted in a grassed area 70 x 40 metres in area located less than 100 metres from the sea. It is bordered by the Port of Tauranga, the Tauranga Yacht Club, a Marina and a retail store. Trials were conducted on ant colonies that were located along the edge of the grassed area were it came into contact with asphalt, as nests were easier to find along the grass edge.

Effect of food concentration and temperature

Differences in the proportion of food baits occupied by resident ants due to a change in the spatial dispersion of the food and changes in temperature were investigated. The species tested were *M. sydneyense, Pheidole rugosula* Forel, *Paratrechina vaga* (Forel) and *Iridomyrmex anceps* (Roger) as these four species were observed to co-occur at multiple sites (n = 5). In each trial, approximately six grams of peanut butter (see chapter 4) was placed in a 50 cm radius half circle from the edge of the asphalt. The number of spots of the peanut butter was either 1 (n = 29), 8 (n = 31) or 64 (n = 29). A spatial dispersion of '1' meant that all six grams of the peanut butter was clumped in one spot, whereas a rate of '64' meant that the six grams of peanut was spread out between 64 spots within the 50 cm radius half circle. All of the food items were uniquely identified so that the presence or absence of ant species at the individual food items could be recorded every 10 minutes for two hours.

Soil surface temperature was also recorded every 10 minutes for the two hours. Temperatures were recorded using an electronic thermometer with a probe that was placed under grass next to the trial site. All trials were performed on the grass and not on the asphalt.

Predictions were made regarding the proportion of baits occupied from the response; binary, presence/ absence (1/ 0) data, at the end of the two hour trials due to independent explanatory variables; ant species, dispersion rate, trial site and temperature. These predictions were made using a binary logistic regression in SPSS v. 11.0 (Lead Technologies Inc. 1991- 2000).

Binary logistic regression models the data to give predicted values 'exponent of beta' Exp (β) due to the deviation of modelled data from a reference category. For the categorical variables of species, spatial dispersion and site, the reference categories, from which all deviations are measured against are; species = *M. sydneyense*, dispersion rate = 1 and site = 1. For example, if the predicted odds ratio (EXP (β)) is 15 for one of the ant species, when comparisons are made between the proportion of baits occupied between the species only, the odds that it is present at the food is 15 times as large as the odds of *M. sydneyense* being present. An Exp (β) value of one implies that the predicted proportion of foods occupied by the species is not different from the reference species, *M. sydneyense*. Conversely, an Exp (β) value of 0.5 means that the odds are half that of *M. sydneyense* of being present at the food.

A quasi- Poisson regression was done to test for differences in ant species richness during a trial due to the spatial dispersion of the food by comparing the maximum number of species recorded during each dispersion trial at the five sites R v. 2.0.1 (The R foundation for Statistical Computing 2004).

Temperature preference

The temperature preference of *M. sydneyense* and *P. rugosula* was assessed using laboratory colonies in an experimental temperature gradient setup. Iridomyrmex anceps and P. vaga were not tested as colonies of these species suffered high mortality in the laboratory before the experiments started. I tested temperature preference by modifying Walter's (2003) experiment, allowing ants to move freely between different temperature chambers instead of humidity chambers. A gradient of temperatures (20, 24, 28, 32, 36 °C) was offered to the ants by connecting five chambers of different temperatures with 10 cm lengths of 4 mm diameter plastic tubing (Fig. 3.1). Each temperature chamber was a sealed plastic specimen jar 54 mm deep by 41 mm in diameter that was partially encased and sealed into a water tight piece of PVC drainpipe. There were five plastic pipes that served as extensions of separate water baths for the temperature control in each chamber. Humidity in the temperature chambers was kept above 80% RH for the duration of the trial by adding 10 mL of a saturated salt solution of sodium chloride to the base of each chamber (O'Brian 1948). A plastic cap, 12 mm deep by 25 mm in diameter, was placed into the saturated salt solution in each chamber. It was filled with silica gel to prevent water vapour from condensing on the inside of

the plastic. Gauze mesh was put in each chamber above the liquid to prevent ants from drowning in the solution.



Figure 3.1 Temperature preference setup. A saturated salt solution is at the base of each chamber with a gauze platform above to stop the ants from drowning in the liquid

Fifty ants from a parent colony were spread evenly between the five temperatures. In addition to this one queen from the parent colony was placed randomly into one of the temperature treatments at the beginning of the trial. All ants were able to move freely between the temperature chambers. I recorded the number of live ants in each chamber after eight hours. All queen ants were returned to their nests at the end of the trial to ensure the survival of the laboratory colonies. Therefore queens had the potential of being used more than once in the trials. Trials were replicated eight times for each species, using new ants from their respective parent colonies for each trial.

To test for different temperature preferences between the species, comparisons were made between the percent of live ants in each temperature chamber between species by a two- way ANOVA on angular (Arc-sin) transformed percentage data (Dytham 2003). The preferred temperature for

an individual species was assessed by a one- way ANOVA on angular transformed percentage data on the percent of live ants in each chamber. This was followed with post hoc Tukey tests. I used SPSS v. 11.0 (Lead Technologies Inc. 1991- 2000) for the analysis.

Results

Effect of food concentration and temperature

The odds, Exp (β), that *Pheidole rugosula* (Forel) and *Paratrechina vaga* (Forel) would occupy a bait were significantly greater than the odds for *M. sydneyense* (*P. rugosula*; Exp (β) = 47.2, P = 0.003; *P. vaga*, Exp (β) = 29.0, P = 0.037) (Table 3.1). There were differences in the proportion of foods that were predicted occupied with increasing surface temperature (P < 0.001), dispersion rate of food (P = 0.003), and site (P < 0.001). There was a significant interaction of species, temperature and dispersion rate on the predicted proportion of a food being occupied (P = 0.003) (Fig. 3.2). The odds of bait occupation by different species at different bait dispersion rates did not differ from odds that reference species (*M. sydneyense*) would occupy a food at the dispersion rate of '1' (All P > 0.05) (Table 3.1).

	β	S.E.	Wald	df	sig.	Exp(β)
Temperature	0.153	0.012	170.124	1	0.000	1.166
Species	-	-	11.747	3	0.008	-
P. rugosula	3.854	1.300	8.789	1	0.003	47.183
I. anceps	0.456	2.028	0.51	1	0.822	1.578
P. vaga	3.369	1.618	4.338	1	0.037	29.053
Dispersion	-	-	11.921	2	0.003	-
8	-0.710	0.487	2.128	1	0.145	0.492
64	-1.177	0.459	6.571	1	0.010	0.308
Site	-	-	158.711	4	0.000	-
Site 2	-0.829	0.116	51.261	1	0.000	0.436
Site 3	-0.202	0.106	3.678	1	0.055	0.817
Site 4	0.015	0.113	0.017	1	0.895	1.015
Site 5	-1.485	0.145	104.359	1	0.000	0.226
Species* temperature	-	-	11.805	3	0.008	-
P.rugosula * temperature	-0.136	0.057	5.752	1	0.016	0.873
I. anceps * temperature	-0.062	0.083	.559	1	0.455	0.940
P. vaga * temperature	-0.189	0.077	6.026	1	0.014	0.828
Species * dispersion	-	-	21.076	6	0.002	-
P. rugosula * 8	0.396	1.360	0.085	1	0.771	1.486
I. anceps * 8	3.432	2.216	2.399	1	0.121	30.946
P. vaga * 8	-1.570	2.182	0.518	1	0.472	0.208
P. rugosula * 64	0.763	1.290	0.350	1	0.554	2.145
I. anceps * 64	-1.388	2.118	0.429	1	0.512	0.250
<i>P. vaga</i> * 64	0.982	1.891	0.270	1	0.604	2.669
Species*dispersion*temperature	-	-	19.696	6	0.003	-
P.rugosula * 8 * temperature	-0.016	0.059	0.075	1	0.784	0.984
I. anceps * 8 * temperature	-0.167	0.093	3.218	1	0.073	0.846
P. vaga * 8 * temperature	0.005	0.100	0.002	1	0.964	1.005
<i>P. rugosula</i> * 64 * temperature	-0.016	0.056	0.086	1	0.770	0.984
<i>I. anceps</i> * 64 * temperature	0.023	0.086	0.073	1	0.787	1.024
<i>P.vaga</i> * 64 * temperature	-0.184	0.098	3 507	1	0.061	0 832

Table 3.1 Binary logistic regression on the predicted probability that a species would occupy a bait dependant on temperature, site and dispersion rate of the food item. Significant values are in bold.

There was a significant interaction of species and temperature (P = 0.008) indicating that there were differences in the proportion of baits occupied by the ant species with a change in surface temperature (Fig. 3.2). The odds of bait occupation dropped for *P. rugosula* and *P. vaga* with the increase in

temperature compared to *M. sydneyense* (*P. rugosula*, Exp (β) = 0.87, P = 0.016; *P. vaga*, Exp (β) = 0.83, P = 0.014). *Iridomyrmex anceps* (Roger), however, was not predicted to occupy a proportionally different amount of foods than *M. sydneyense* with an increase in temperature (Table 3.1). In one trial *M. sydneyense* and *P. rugosula* were observed to repeatedly displace each other from baits when there was a change in the amount of insolation. With cloud cover *P. rugosula* quickly displaced *M. sydneyense* from the peanut butter, however, when the cloud was not in front of the sun *M. sydneyense* rapidly returned to the foods that it occupied by displacing *P. rugosula*.



Figure 3.2 Mean proportion (\pm S.E.) of baits occupied by the four main species at different temperatures and spatial dispersal rates. All trials have been combined for two ranges of temperatures recorded during each trial. Some ant species occupied baits simultaneously thus proportions are greater than 1 for some dispersion rates.

There were a significantly lower proportion of foods predicted to be occupied as the food dispersion rate increased from '1' to '64' (Exp (β) = 0.3; P = 0.010) (Fig. 3.3 a), but the proportion predicted to be occupied at a spatial dispersal rate of '8' did not differ from those at a dispersal rate of '1' (Table 3.1, Fig. 3.3 a). These effects were different for the different species indicated by the interaction of species and dispersal rate (P = 0.002). Although predicted occupation by each species did not differ from expected occupation by *M. sydneyense at* a dispersion rate of '1' (Table 3.1).



Figure 3.3 The effect of concentration of the food on (A) the proportion of foods occupied (\pm S. E.) by any ant at the conclusion of a trial and (B), the number of species (\pm S. E.) present during a trial. 1- All food clumped at one site, 8- partially dispersed between 8 sites within the trial area, 64- fully dispersed between 64 sites within the trial area.

Poisson regression on the maximum number of species recorded during the dispersion trials showed that there was a significant effect on the species richness recorded during the trials (P < 0.001) (Fig. 3.3 b, Table 3.2). An average number of 2.0 \pm 0.20 (\pm S. E.) species occurred during the trials when all of the food was clumped at one spot, but an average of 2.7 \pm 0.24 and 3.3 \pm 0.24 species were present when the food was dispersed between 8

and 64 sites respectively. There was a site effect on the number of ant species present, but there was no interaction of dispersal rate and site (Table 3.2).

Table 3.2 Quasi- Poisson regression on the number of ant species present during a trial dependant on the site that the trial was done and the spatial dispersal of the food. Significant values are in bold

	df	deviance	sig.
Dispersal	2	9.43	< 0.001
Site	4	15.821	< 0.001
Dispersal * site	8	1.403	0.932

Temperature preference

The percentage of ants in each of the temperature chamber after eight hours differed between *M. sydneyense* and *P. rugosula* (two- way ANOVA: $F_{(4, 70)} = 3.993$, P = 0.006) (Fig. 3.4, Table 3). *Monomoria sydneyense* showed a preference for the 36°C chamber as a higher percentage of ants were observed in that chamber (one- way ANOVA: $F_{(4, 39)} = 6.172$, P = 0.001) than in the 20, 24 and 28°C chambers (post- hoc Tukey tests, all P < 0.05). *Pheidole rugosula* on the other hand showed no clear preference for any of the temperatures (one- way ANOVA: $F_{(4, 39)} = 2.336$, P = 0.075) (Fig. 3.4). The workers had variable responses due to the presence of a queen in a chamber. In both species observations were made of large numbers of the workers staying close to the queen, however, other trials indicated that the workers were not influenced by the queen's presence.

Source	Type III SS	df	mean sq	F	sig.
Temperature	2159.75	4	539.937	4.586	0.002
Species	12.859	1	12.859	0.109	0.742
Temperature*species	1880.312	4	470.078	3.993	0.006

 Table 3.3 Two way ANOVA on angular transformed percentage data of the percent of ants in each temperature chamber at the end of the trial. Significant figures are in bold.



Figure 3.4 Mean proportion (\pm S.E.) of ants in each temperature chamber in the laboratory after 8 hours

Discussion

The spatial dispersion of the food resource and changes in the surface temperature had an influence on the proportion of food items in the area that were occupied by the different species. The increase in the spatial dispersal of the food in the area led to a higher number of species being present during the trials consistent with Root's resource concentration hypothesis (1973). A higher proportion of foods were unoccupied as a result of the food being spread out within the area. There was a difference in the proportion of foods predicted to be occupied with an increase in temperature. As the temperature increased in the field trials *M. sydneyense* was predicted to occupy more of the foods that were present than *P. rugosula* and *P. vaga*. Laboratory data from temperature preference trials supported this as *M. sydneyense* had a preference for the warm, 36 °C, temperature chambers.

Effect of food concentration and temperature

The resource concentration hypothesis (Root 1973) suggests that as a resource is spread out, becoming less aggregated, there is an increase in species diversity because non- specialist herbivores are displaced from the food resource. I found that there was a higher mean number of ants present during trails where the bait was very spread out '64' than when the food was clumped '1'. Disregarding species dominance an increase in the spread of a resource increases the likelihood of it being found (Cain et al. 1985). The actual abundance of food can influence species richness (Margues et al. 2000). Increasing the dispersion resulted in proportionately less of the food resource being occupied. This may have lessened the impact of competition for behaviourally subordinate ants by dominant ants in the area because there was an abundance of food available for the subordinate species to acquire. Ants have different foraging strategies, some recruit a large number of foragers to discovered food resources and others do not (Andersen 1995; Fellers 1987; Wilson 1971). With an increase in the spread of the food resource more ant species were able to discover the food because species such as *M. sydneyense* and *P. rugosula* that recruit in large numbers to food

resources close to the nest were concentrating foraging on the foods that they had discovered (Andersen 2000). There was however, an effect of site on the number of ant species present during the trials suggesting that there were some differences in the species richness between the sites. I did observe a *Monomorium antarcticum* (F. Smith) at one of the sites and *Tetramorium grassii* Emery was observed at another site.

Pheidole rugosula and *P. vaga* were predicted to occupy significantly more food items than *M. sydneyense*. With an increase in temperature they were predicted to occupy proportionately less of the food items. Only *I. anceps* had a similar response as *M. sydneyense* to a rise in the temperature. This suggests that there is a change in the numerically dominant ant species due to differences in foraging activity at different temperatures, similar to (Campos and Schoereder 2001; Cerdá et al. 1997), from *P. rugosula* and *P. vaga* at cooler temperatures to *M. sydneyense* and *I. anceps* at warmer temperatures.

Temperature preference

Results from the temperature preference trials suggest that *Pheidole rugosula* did not have a preference for any of the temperatures tested, though it may be limited by temperatures above 32 °C. *Monomorium sydneyense* on the other hand, may have higher foraging activity at around 36 °C. There was a variable response in the number of workers in chambers that contained a queen. Observations were made of both high and low abundances of workers present in chambers containing queens. It is possible that the reproductive ability of

the queen could account for these observations. It is less likely that a sterile or unmated queen will be as attractive to workers as an egg laying queen.

Daily and seasonal temperature differences have been suggested as a mechanism by which the observed ant community composition can change (Briese and Macauley 1980; Campos and Schoereder 2001; Cerdá et al. 1997; Fellers 1989; Thomas and Holway 2005). It is likely that subordinate ants in Tauranga would not face as much competition from *M. sydneyense* if they foraged at cool temperatures when the foraging activity of *M. sydneyense* is likely to be lower. In Chapter 2, I found that there were differences in the abundances and diversity of ant species foraging in the warmer months, but not in the cooler months. An increase in the foraging activity of *M. sydneyense* at warmer temperatures may account for these observed differences.

Multiple food resources rather than aggregated resources in the Tauranga ecosystem may allow subordinate ants to coexist with dominant species, as resources not being used by the dominant ant were available for subordinate species. Different ant species have different food preferences (Hölldobler and Wilson 1990; Sanders and Gordon 2003). This is a mechanism by which ants can coexist with dominant species as they do not compete for food (Campos and Schoereder 2001). It is possible that these trials were influenced by differences in food preference.

The results presented here suggest that the resident ant species are coexisting with *M. sydneyense* because of the inability of *M. sydneyense* to

secure all of the food in an area when dispersed rather than when it is clumped. Additionally, *M. sydneyense* appears to have a higher foraging activity at warmer temperatures that would allow other species to find and use food at cooler temperatures. It is apparent that the concentration of food and differences in foraging activity due to differences in temperature is influencing the competitive dynamics of ants in Tauranga.

Chapter 4 -

Foraging characteristics and intraspecific behaviour of *Monomorium sydneyense* (Hymenoptera: Formicidae): Implications for population management.

Introduction

Many ant species are successful invaders. They can threaten the native biodiversity (Christian 2001; O'Dowd et al. 2003). They can also cause economic losses (Mooney 1999; Williams 2001) in the areas that they invade. When the biological or economic costs by the invading species are deemed to be too great, control options of the organism may be sought. These range from management of population sizes of the organism to the eradication of the organism from the area (Cromarty et al. 2002). Eradication, where feasible, is often considered a better option because of a reduced impact on the other organisms in the eradication area (Clout and Veitch 2002). New Zealand has had many introduced organisms that have been subject to population management, such as possums (Jolly 1993) and goats (Parkes 1993) or eradication as in Argentine ants *Linepithema humile* (Mayr) (Harris 2001) and Australian giant bulldog ants *Myrmecia brevinoda* Forel (Lester and Keall 2005).

New Zealand has a predominantly exotic ant fauna. Twenty six of the 37 established species are considered to be introduced (Don et al. 2005). Two of the five ant species that are listed on the 100 of the world's worst invasive

species list (Lowe et al. 2000) are established in New Zealand; the Argentine ant, *Linepithema humile* and the coastal brown ant, *Pheidole megacephala* (Fabricius). Species such as the red imported fire ant, *Solenopsis invicta* Buren and the yellow crazy ant, *Anoplolepis gracilipes* (Smith) have been found in New Zealand but have failed to establish (Lester 2005). These species have had devastating effects on the flora and fauna in the areas that they have invaded (Holway et al. 2002a; O'Dowd et al. 2003; Porter and Savignano 1990). The success of these species has been aided by factors such as unicolonality, whereby different nests of these ant cooperate, rather than compete for resources (Holway et al. 2002a; Holway et al. 1998). The flow on effect of this is that a larger amount of energy is used towards further food procurement instead of food defence leading to greater densities of these ants (Holway et al. 2002a). This numerical dominance has been cited as a major factor influencing positive competitive outcomes for the more numerous species (McGlynn 2000; Wetterer et al. 1999).

The best option for control of an exotic organism, short of keeping it out of the area, is to detect it early and act quickly (Simberloff 2002b). Ants, such as *P. megacephala* and the tropical fire ant *Solenopsis geminata* (Fabricius) have been successfully eradicated from Australia Kakadu National Park by toxic baiting (Hoffmann and O'Connor 2004) and currently an eradication attempt of the little fire ant *Wasmannia auropunctata* (Roger) is taking place on Marchena island in the Galápagos Islands (Causton et al. 2005). A previous successful eradication of an ant in New Zealand was carried out on *M. brevinoda*, by using Chlordane® a persistent organochlorine pesticide

followed by sealing of the area with asphalt (Lester and Keall 2005). The most recent eradication attempt of an exotic ant in New Zealand was undertaken on a 10 ha infestation of the Argentine ant on Tiritiri Matangi, an island near Auckland. A toxic protein based bait, poisoned with fipronil was used (Harris 2001).

Monomorium sydneyense Forel, an Australian myrmicine ant, was discovered in Tauranga in 2001 (NPPRL 2003) and in Napier 2004. The publications that include this ant mostly describe the taxonomy (Heterick 2001) or its occurrence with other species (Bisevac and Majer 1999; Heterick et al. 2000). There are no publications regarding its incursion into other countries, therefore it is not known whether this ant warrants population control or eradication. A recent review of pest status of this ant, based on factors such as incursion rates, invasive history and biological traits to name a few suggested that this ant is not a large threat when compared to other ant species (Harris 2005). Previous chapters have suggested that *M. sydneyense* has the ability to reduce the densities of other ants in invaded sites, however, no ants were ever excluded from the invaded areas. There are no previous data on the food preference, foraging distance or the intraspecific behaviour of *M. sydneyense* and such data would be required for management by density control or a successful eradication if it was found to be needed (Simberloff 2002a; Simberloff 2002b).

Here, I assessed the food preference, foraging distance and the intraspecific behaviour as well as 24 hour foraging activity of *M. sydneyense*. This work

was achieved through a series of experiments in the field, thus providing realistic data due to the inclusion of factors related to its interactions with the other ant species present in the area. Specifically, I asked the following questions; firstly, what is the preferred food type of *M. sydneyense*, carbohydrate or protein based and is the bait X-stinguish® developed for the Argentine ant, *Linepithema humile* (Mayr) suitable for this species? Secondly what is the foraging range of this ant in field conditions and finally do workers from separate nests of *M. sydneyense* act aggressively toward each other?

Methods

The trials were carried out in Tauranga, New Zealand (37° 39' S, 176° 11'E). Trials were undertaken at Tauranga because it has the longest history of *M. sydneyense's* incursion. Tauranga has a sub-tropical climate, characterised by warm humid summers and mild winters. Daytime temperatures range from 22-26°C in the summer to 12-17°C during the winter (NIWA 2005). The annual rainfall average ranges from 1250 mm to 1500 mm of rain each year with the monthly averages fairly constant throughout the year (de Lilse and Kerr 1963).

The study area was in a grass field 70 by 40 metres in area, situated 100 m from the sea. There was little shade offered by trees in the area thus spatially there was little variation in weather conditions within the area.

Monomorium sydneyense nests in Tauranga were examined in March and December 2004. Site observations were made during the collection of the

nests including the amount of shading and nest characteristics. Queen number and the presence of brood in the nest were also recorded. There were no counts of worker number in the nests made at the time of collection.

Food preference

Nests for food preference trials were located in soil along an asphalt verge by following workers of *M. sydneyense* back to their nests. Choice experiments, similar to the cafeteria experiments by Sanders and Gordon (2003) were performed in December 2003 to examine the preferred food resource of M. sydneyense. I offered four foods to the ants; sugared smooth peanut butter and tuna in oil as predominantly protein based foods and 25% sugar water as a carbohydrate. I also offered the non-toxic form of X-Stinguish® ant bait (Landcare Research) which contains both protein and carbohydrate and could be of use for control of these ants in New Zealand. These four foods were simultaneously placed on the ground 10cm from the colony entrances in a random order in direct contact with the asphalt. Bait cards were not used because preliminary trials showed that these were disturbed by the windy conditions at Sulphur Point. The foods all had a diameter of 1 cm to reduce the effect of food size on the trials. Since the sugar water was a liquid it was offered in a test tube that was 1 cm in diameter. The liquid was held in the tube by stopping the end with cotton wool plug, through which the ants could consume the sugar water. I recorded the number of ants present at the four baits every 10 minutes for two hours. Ants that were touching the food were included in the counts. This was replicated 10 times. At the end of each trial I removed and cleaned off any remaining food and removed any residue with

water. A one- way ANOVA was performed on log_{10} (x+1) transformed counts of *M. sydneyense* at the four foods offered to determine if there was a difference in numbers of workers present at the different baits after two hours.

Foraging Distance

The proportion of foods occupied and the predicted probability of a M. sydneyense nest finding and recruiting to a food at known distance from the nest after one and four hours was examined in December 2003. March and October 2004. The preferred food from the preference trial (peanut butter) was used to attract the ants. The distances tested were 0.15m, 0.25m, 0.5m, 0.75m, 1.0m, 1.5m, 2.0m, and 3.0m. Two of these distances, which were assigned randomly for each trial, were tested simultaneously to increase the rate of data collection. The direction of the placement of each food was randomly assigned in a 180° half circle from the asphalt to ensure that the food was always placed in the grassed area. Distances were measured from the nest entrance for nest with a single entrance. Distances for nests with multiple entrances were measured from the approximate mid point between all entrances found. Distances between nest entrances of a colony ranged from 2 cm up to 40 cm. The food was placed against the soil and covered with grass to reduce the amount of interference by birds in the area. Each trial started when the food was placed on the ground and the foods were examined after one hour and four hours. Ants were deemed to have recruited to the food if there were more than 10 individuals touching the food. To ensure that the ants had recruited from the trial colonies I followed foraging trails back to the nest. Foods that were recruited to by other *M. sydneyense*

nests or other ant species were recorded as not found by *M. sydneyense*. At the conclusion of each trial the remaining food, grass and soil with traces of peanut butter were removed. The trials were repeated 24 times for all of the distances except for 0.75 m, which was only repeated 12 times because this distance was added after the first sampling month. Due to rain the total number of completed trials for each distance were; 0.15m (n = 23), 0.25m (n = 22), 0.5m (n = 24), 0.75m (n = 12), 1.0m (n = 23), 1.5m (n = 23), 2.0m (n = 22), and 3.0m (n = 21) Binary logistic regression was performed on the probability of *M. sydneyense* being present or absent at the food. Factors included in the analyses were distance, month, time of day (am or pm) and the site at which the trial was conducted.

Intraspecific behaviour

Intraspecific behaviour between workers for *M. sydneyense* from different nests at Sulphur Point and the surrounding area, up to 6.3 kilometres, away was examined to elucidate whether the Tauranga population displays multicolonial (competitive) or unicolonial (cooperative) behaviour. Unicolonial behaviour allows inferences to be made on whether workers from different nests will compete for, or cooperate at, food resources. The behavioural assays between the colonies were conducted following methods by Suarez et al. (1999), whereby aggression levels between pairs of worker ants from different colonies are scored every two minutes for a total of 10 minutes. Scores ranged from zero to four. A score of 0 indicated that the ants ignored each other and a score of 1 was assigned to ants that stopped and there was

some antennation or feeding observed. I scored a 2 to pairs where one or both of the ants touched each other then ran away (avoid). A score of 3 indicated that pairs locked mandibles, bit or held the others appendages and a 4 indicated that pairs fought intensely including stinging or prolonged biting. Tests between nest pairs were replicated five times for all but four of the pairs which were only replicated four times due to time constraints. I considered scores of 2 and above to be signs of aggression.

Ants for the behavioural trials were collected by aspirating them up on the outward journey from the nest, ensuring that the ants were actually from the target nest and that they were fresh and less likely to be transporting food which could have influenced the assays. Collected ants from each nest were held in separate fluon coated (Australian Entomological supplies, Bangalow, NSW, Australia) plastic vials (52mm tall 25mm diameter). They were held for five minutes before the behavioural trials began. One ant from each colony was put into one plastic fluon coated vial as above. The fluon created a slippery surface, inhibiting the climbing ability of the ants and increasing the chance of interactions occurring between the individuals. The maximum aggression score was recorded for every two minute block. At the end of each trial the ants were discarded and the chambers were cleaned out with 70% ethanol and left for five minutes to dry before using again. Trials between ants from the same nest were done as above as controls to test for an effect of the trial setup on the interactions observed. I tested whether aggression level between pairs of colonies was related to distance apart by using a linear regression. Testing both the maximum aggression level attained for any pair

within the nest replicates and the average of the maximum aggression levels between all worker pairs within a nest pair. All of the above statistical analyses were performed using SPSS v. 11.0 (Lead Technologies Inc. 1991-2000).

Diel foraging behaviour of the ants

Monopolisation of food by *M. sydneyense* during a 24 hour period was investigated in December 2003, March, August, October and in December 2004 by monitoring the species abundance at a continuous food resource for a period of 24 hours. Peanut butter was placed 10 cm from *M. sydneyense* nest entrances in direct contact with the soil surface. As birds interfered with the peanut butter in preliminary trials, it was placed under flagging tape and loose grass to prevent bird interference with the trials. Trials began at 17:00 and ant abundance and soil surface temperature at the baits was recorded every two hours for 24 hours so that a total of 12 counts were made at each food. As there were a large number of Pheidole rugosula Forel workers interacting with *M. sydneyense* I recorded their abundances also. No statistical analyses were performed as there were a small number of samples December 2003 (n = 2), March (n = 2), August (n = 2), October (n = 3) and in December 2004 (n = 6). Soil surface temperature was recorded using an electronic thermometer with the probe of the thermometer placed under grass next to the trial area. Food was not replenished during the trials.

Results

Location of nests

Monomorium sydneyense nests were most often collected in areas where there was little shading by trees, although one nest was dug up between roots of a *Hebe* spp shrub that shaded the nest from the morning until midday. In areas not shaded by vegetation nests were discovered at the soil surface under a circular lid of a tin can lid approximately 10 cm in diameter and under a small rock 20 cm long 10 cm wide and 7 cm deep. A colony of M. sydneyense was discovered nesting in a piece of bark with similar dimensions to the small rock above on the soil surface and one nest was found under a 5 mm thick piece of hard board, 6.3 km from Sulphur Point. Monomorium sydneyense workers were observed foraging on bare earth, halfway up the north-western side of Mt. Maunganui, though no nests were found. All five nests collected in March and December had brood present and six queens were present in one of the nests. There were multiple queens present in four of the nests collected and no queen was found in the fifth nest. This queenless colony had approximately 500 workers present one month after it was collected. Winged *M. sydneyense* queens were observed in one of the laboratory colonies in February that had been collected in December 2003.

Food preference

Large numbers of *M. sydneyense* foragers were observed during the food preference trials. Up to 387 ants were counted foraging at one time from one nest. The peanut butter attracted the most ants (202 workers). *Monomorium*

sydneyense was observed defending the foods from *Pheidole rugosula* by raising their gasters and exuding at the tip of their stings. Significant differences were observed in the numbers of *M. sydneyense* foragers attracted to the multiple foods offered ($F_{3, 428} = 40.105$, P < 0.001). There were larger numbers of foragers at the peanut butter, X-Stinguish® and tuna than at the sugar water (Tukey, P < 0.001) (Fig. 4.1). Peanut butter and X-Stinguish® attracted similar numbers of foragers (Tukey, P = 0.188) and they both attracted more foragers than the tuna (Tukey, P < 0.001). There was a decrease in numbers of ants present at the X-Stinguish® and tuna baits after one hour as both baits had dried out (Fig. 4.1).



Figure 4.1 The preferred food of *Monomorium sydneyense* based on the mean number of workers (± S. E.) at the foods every 10 minutes.

Foraging distance

Some nests were found to have up to three entrances that were up to 0.6 m apart, though whether they were entrances to one nest or entrances to separate nests was unknown as I could not dig up the nests. Workers were observed running between the different entrances. The predicted probability from the binary logistic regression that *M. sydneyense* would be present at the peanut butter, after one hour was significantly dependent on the distance that the food was from the nest (P < 0.001). There was no effect of month (P =0.347), time of the day (P = 0.161), or site (P = 0.512) on the proportion of foods occupied by *M. sydneyense* after one hour. After four hours both the distance that the peanut butter was from the nest (P < 0.001) and month that the trial was done (P = 0.015) had an influence on the proportion of the foods being recruited to by *M. sydneyense*. Distance was the main predictor of presence at the food after four hours for both March (P < 0.001) and October (P = 0.014), however, the day the trial was conducted, not the distance that the food was from the nest was the most significant predictor of presence at the food in December (P = 0.013). Monomorium sydneyense was never recorded recruiting to the food placed 3.0 m from the nest entrance (Fig. 4.2). Even at close distances such as 0.15 m away *M. sydneyense* did not find the food all of the time (Fig. 4.2). It was estimated that 0.60 - 0.80 of the baits would be occupied at 0.15 m after one hour and 0.80 - 0.85 occupied after four hours (Fig. 4.2) for all of the months combined. When the peanut butter was approximately 1 metre away from the nest only 50% of the baits were predicted to be occupied.



Figure 4.2 Probability of recruiting to peanut butter at increasing distance after 1 hour (a-c) and 4 hours (d-f) hours (\pm S. E.). The predicted logistic regression response modelled from the data is displayed as a curve (-). No predictions were made for December four hours (d) as distance was not the main predictor of probability of finding the food.

Intraspecific aggression

Substantial levels of intraspecific aggression were observed between *M.* sydneyense colonies (Fig. 4.3) There was no relationship between distance between colonies and the level of average aggression ($r^2 = 0.007$; P = 0.604) or maximum aggression ($r^2 = 0.037$; P = 0.347) attained. Maximum aggression data showed that there was aggressive behaviour between 12 of the 18 pairs, a score of two or higher, observed between colony pairs as close as 0.9 m apart and up to 6.3 km apart (Fig. 4.3 b, Table 4.1 b). Averaged data, however, showed that consistent aggression was only displayed between two colony pairs. One pair were 5.7 m apart and the other 131 m apart (Fig. 4.3 a, Table 4.1 a) and one nest was involved in both of the trials. No aggression was displayed between the control colonies, aggression between separated individuals collected from the same nest during the trials (Fig. 4.3 Table 4.1).



Figure 4.3 Paired aggression assays between *Monomorium sydneyense* colonies. Distance C represents controls where individuals from the same colony were paired against each other after 5 minutes apart. Aggression score of 0- ignore, 1- antennation or trophallaxis, 2- avoid each other, 3- pulling and biting, 4- prolonged fighting and stinging.

Table 4.1. Average aggression scores between worker ants between nest pairs. An asterisk (*) indicates that pairs of ants were collected from the same nest. Numbers in parentheses indicates the distance in metres between the nests tested.

-															
	S													0.8 ± 0.8 (6308)	
	J											2.8 ± 0.5 (131)	3.1 ± 0.3 (5.7)		
															0.8 ± 0.8 (4)
	F							1.7 ± 0.7 (3.2)							
d.	ŋ					*0	0.3 ± 0.3 (45)						0.3 ± 0.3 (5.4)		
nests teste	A				*0				0.4 ± 0.4 (5.7)						
etween the	В			*0	0 (13.6)										
in metres b	Е		0*	1.5 ± 1.5 (73.8)	0 (73)							0 (10.3)			
e distance	D	*0	0 (107)	0 (36.4)	0 (46)	0.4 ± 0.4 (12)									
indicates th	Т	0.5 ± 0.5 (49.2)								0.4 ± 0.4 (0.9)					
eses	A	D	ш	В	۲	Ð	ш	_	٩	0	ſ	Я	Т	Л	z

Table 4.1 b Maximum scores between nest pairs. An asterisk (*) indicates that pairs of ants were collected from the same nest. Numbers in parentheses indicates the distance in metres between the nests tested

in Se	metres betv	ween the ne	ests tested							
В	Н	D	Ш	В	A	ŋ	Щ	_	ſ	S
	2									
D	(49.2)	•0								
Ш		0 (107)	*0							
۵		0 (36.4)	3 (73.8)	*0						
		(46)	0 (73)	0 (13.6)	*0					
G		4 (12)				*0				
ш						2 (45)				
_							4 (3.2)			
٩					4 (5.7)					
0	2 (0.9)									
ſ										
R			0 (10.3)						4 (131)	
T						2 (5.4)			4 (5.7)	
Л										3 (6308)
z								3 (4)		

Diel foraging behaviour of the ants

Monomorium sydneyense was observed foraging on foods offered for the entire 24 hour period in December 2003, October and December 2004 (Fig. 4.4 a, d and e). *Pheidole rugosula* was observed foraging for the entire 24 hour period in March, October and December 2004 (Fig. 4.4 b, d and e). No *P. rugosula* nests were observed at the sites examined in December 2003. Soil surface temperature appeared to be lowest at approximately 05:00 and warmest at around 13:00. Unexpectedly foraging activity of both ant species did not increase with temperature in October and December 2004. Food was found to be quite dry at the end of the 24 hour period. There were a very low number of ants recorded in August (Fig. 4.4 c).



Figure 4.4 The mean number (± S. E.) of *M. sydneyense* and *P. rugosula* foraging on peanut butter every 2 hours for 24 hours. The food was placed approximately 15 cm from nests of both species. *Pheidole rugosula* was not present at the sites tested in December 2003.

Discussion

Many of the *M. sydneyense* nests that were collected were discovered in the open because they were easier to see and excavate. It appears that *M. sydneyense* has general nesting preferences as they were discovered on the soil surface under a metal lid, a rock and under cardboard, as well in a piece of bark and in soil. Multiple queens were found in the majority of the nests though it is unknown whether they all contributed to the worker population, or whether they were related to each other. Findings from the temperature preference trial in chapter 3 suggests that not all of the queens were contributing to the worker population as occasionally workers did not assemble around the queen unlike other trials. The occurrence of winged females in the *M. sydneyense* one of the laboratory nests and the occurrence of nests up to 6.3 km in Tauranga suggests that this ant may have winged dispersal, however human mediated transport cannot be ruled out.

Food Preference

By committing larger numbers of foragers, *M. sydneyense* displayed a preference for the protein- based foods of peanut butter, and tuna over the carbohydrate based sugar water. X-Stinguish® ant bait, which also contains protein, attracted a larger numbers of workers than the sugar water. One *M. sydneyense* colony had 387 ants foraging on all of the four baits offered simultaneously, 202 of which were on the peanut butter. X-Stinguish® and tuna baits often dried out after one hour which resulted in fewer ants attending those foods. *Monomorium sydneyense* was observed actively defending the

foods from *P. rugosula* suggesting that they may have similar food preferences, as predicted by functional group theory (Andersen 1997; Andersen 2000) and could compete for a toxic bait if laid. Hartley and Lester (2005) also found that *M. sydneyense* had a preference for protein based foods (peanut butter, soy bean oil mixture and fatty sausage meat) over a carbohydrate one (20 % sugar water). Moreover they found that M. sydneyense had a strong preference for X-Stinguish®. The ant bait X-Stinguish® may be suitable for baiting of *M. sydneyense* as in my trials it attracted the same number of ants as the peanut butter and the most ants in Hartley and Lester's (2005) trials. They offering the X-Stinguish® in plastic pottles which would have slowed down the rate at which it dried out increasing the time available for retrieval. An advantage that X-Stinguish® has is that it also contains carbohydrates therefore if *M. sydneyense* changed its protein/ carbohydrate preference during the year, as has been observed in other ant species (Hölldobler and Wilson 1990), X-Stinguish® would still be likely to attract *M. sydneyense* foragers.

Foraging Distance

The relatively short foraging distance of *M. sydneyense*, no further than 3.0 m from the colony, means that food must be fairly close to the nest for *M. sydneyense* to find it, however, *M. sydneyense* was not always predicted to find the food at the short distance of 0.15 m. The probability that *M. sydneyense* would occupy the peanut butter at a distance of 0.15 m was 0.8. This was a surprising result as it is not a great distance from a nest. I
observed nests of *P. rugosula* that were as close as 10 cm from *M. sydneyense* nests. There were trials where food was situated closer to *P. rugosula* nests than it was to *M. sydneyense* nests and *P. rugosula* was observed controlling nine of the foods in the foraging distance trials. Simultaneous placement of two baits may have had an effect on the probability of *M. sydneyense* finding food at large distances.

There were large differences in the probability that *M. sydneyense* would still be at the peanut butter after four hours even though it was recorded as being present after one hour in December (Fig 2 a and d). The weather at this time of the year was characterised by warm days with peaks in heat from midday to early afternoon. As many of the trials started around 09:00, the final count after four hours was at 13:00, which coincided with the warmest part of the day. Temperatures up to 45° C were recorded on the soil surface at this time. Studies have shown that hot surface temperatures can limit the foraging behaviour of some species (Cerdá et al. 1997; Thomas and Holway 2005; Whitford 1999). Only Iridomyrmex anceps (Roger), another Australian ant species, was observed although in low abundances on the surface during this period. When artificial shading of *M. sydneyense* nests was performed at this temperature workers were observed exiting the nest and running along previous foraging trails until the artificial shading was removed. This result is similar to findings by Markin et al. (1975) on the foraging behaviour of Solenopsis invicta. It appears that the foraging activity of *M. sydneyense* may be limited by high surface temperatures.

If control of *M. sydneyense* by toxic baiting such as X-Stinguish® was to be undertaken, the bait would have to be spread at a rate so that all of the nests would be able to find the bait. The data suggest that placing baits at a distance no greater than 0.30 m apart so that *M. sydneyense* nests in the baiting area are no more than 0.15 m from the bait should ensure that at least 60% of the baits will be occupied by *M. sydneyense* after one hour if the baiting was conducted in spring. In summer (December) the probability of bait occupation is 0.7 when the food is 0.5 m from the colony, therefore baits could be placed every metre at this time of the year with a large proportion expected to be occupied by *M. sydneyense*. It is apparent that, even with such a high density of baits, multiple baiting dates would be needed to control this ant.

Intraspecific aggression

The aggression assays conducted between individuals from different nests of *Monomorium sydneyense* suggests that there is some intraspecific aggression within this population, but that aggression is not correlated with distance, a result similar to introduced populations of the Argentine ant (Suarez et al. 1999). Aggression was recorded at least once between workers from 12 of the 18 colony pairs implying that colonies may not cooperate at food sources (Holway et al. 1998). Consistent aggression was only displayed between workers from two nests pairs, one pair was 0.9 m apart the other nest pair was 6.3 km apart. Workers from one nest were involved in both of those interactions which could be an indication that that nest is genetically different to the other two nests (Tsutsui et al. 2003). Previous work by Suarez

et al. (1999) and Tsutsui et al. (2000) have linked a lack of intraspecific aggression with low genetic variation within introduced populations (Tsutsui et al. 2003; Tsutsui et al. 2000). This has lead to increases in population densities because of instead of fighting for resources they cooperate saving energy that would have been used for defensive behaviours (Holway et al. 1998).

Harris (2001) suggested that since the Argentine ants from one nest cooperate with Argentine ants from other nests, the concentration of the poison in a bait could be reduced because the ants would live longer allowing them to consume more of the poison therefore distribute more of it throughout the cooperating nests. The fact that *M. sydneyense* workers from separate nests displayed aggression towards each other, suggests that poison would not be spread by workers to separate nests. Therefore bait would have to be placed close together to ensure that every nest is likely to be close to the bait.

Diel foraging behaviour of the ants

Monomorium sydneyense was observed foraging for the entire 24 hour period during October and December surveys, though the abundance of this ant did not increase with an increase in temperature. Since the food was not replaced during the trials by the end of the trials it was noticed that there was often little of the food left and that what was left was often dry. This would have had an influence on the number of foragers present at the baits during the warmer hours of the day 18 hours after the start of the trial.

Conclusions

If baiting was required for the control or eradication of *M. sydneyense* a protein based attractant would be the best medium by which to transport a poison to colonies. I would recommend that baiting be carried out in the summer months when the surface temperature is likely to rise above 20° C as foraging activity appears to be greatest then. It appears that X-Stinguish® is a suitable ant bait if the desiccation rate can be reduced, for example offering it in containers as was done by Hartley and Lester (2005). Bait could also be placed out in the late afternoon as *M. sydneyense* should be active during the night, dependant on the temperature. Small distances between bait applications would be required to ensure that the bait would have a high chance of being discovered. At a distance of 0.5 m from the nest the bait would have approximately 0.7 chance of being occupied by *M. sydneyense* in December. Larger distances between bait placements would not be recommended as there is less chance of the food being occupied by M. sydneyense as they do not forage great distances. Since *M. sydneyense* does not appear to display coexistence between separate nest it would be unlikely that a toxic bait would be spread from one nest to another again suggesting that a lot of bait would be required to control this species.

Chapter 5 -

General discussion

In this thesis, I investigated whether *M. sydneyense* has had an influence on the ant community of Sulphur Point Tauranga by comparing ant community structure at sites invaded by *M. sydneyense* to adjacent sites not invaded by *M. sydneyense.* Additionally, I examined the role of food concentration and temperature differences on the competitive dynamics of ants in the area by manipulating the concentration of a resource and measuring temperature. I related the proportion of the foods occupied by different species to differences in the spatial dispersion and temperature. I also researched aspects of the population biology and nesting characteristics of *M. sydneyense*. Specifically, I measured the foraging distance of workers from a nest and predicted the probability of ants from a nest occupying a food resource related to the distance that the food was from the nest. I also offered multiple food resources, including an ant bait currently used for ant population control, X-Stinguish ® (Harris 2001), to reveal whether *M. sydneyense* has a preference for either protein or carbohydrate based food resources. Additionally, I examined the 24 hour foraging behaviour of this species to investigate whether it forages for food throughout the entire night. Finally I tested whether workers from separate nests of *M. sydneyense* display aggression toward each other. The results presented in this thesis should aid population management decisions of this species should it be needed.

The influence of *Monomorium sydneyense* on the Tauranga ant community composition

Introduced ants generally have a strong influence on the resident ant species (Christian 2001; Gómez and Oliveras 2003). In chapter two, I found that there were differences in the species diversity and ant abundances of ant communities where *M. sydneyense* was present compared to ant communities where *M. sydneyense* was absent. This effect was only apparent in the warmer months of the year. I expected the greatest differences of abundance of resident ant species to displayed by ants categorised in the same group as *M. sydneyense* because these ants should all have similar resource requirements (Andersen 1995). Ants categorised in the same functional group as *M. sydneyense* (Generalized Myrmicinae) were not significantly negatively influenced by the presence of *M. sydneyense*. In fact no ant species at Sulphur Point had significantly reduced abundances from areas where *M. sydneyense* was present or was absent form invaded areas.

The influence of temperature and spatial dispersal of food resources on competitive dynamics

Variations in the temperature tolerances of dominant ant species can allow for coexistence of other ant species (Andersen 1992; Cerdá et al. 1997; Thomas and Holway 2005). Concentration of food resources can influence both the species richness (Root 1973) and the likelihood of an organism finding a resource (Cain et al. 1985). I investigated the influence of temperature and the effect of food concentration on competitive dynamics in chapter three. An

increase in the surface temperature led to increases in the proportion of foods that were predicted to be occupied by *M. sydneyense*. Without an effect of temperature *M. sydneyense* was predicted to occupy a lower proportion of baits than *P. rugosula* or *P. vaga*. Temperature preference trials also showed that *M. sydneyense* had a preference for warmer temperatures, whilst *P. rugosula* showed no distinct preference for any temperature examined in this study. Species richness increased as the food resource was dispersed at a greater rate, likely due to a lower proportion of those foods being occupied with the increased dispersion.

The lower foraging activity by *M. sydneyense* at cooler temperature, as indicated by a reduction in the number of workers at foods at lower temperatures may act as a mechanism by which other ants can coexist as there is a reduction in competition by *M. sydneyense*. Increasing the spatial food dispersion of a food resource may allow more ant species to coexist as there is a greater number of foods that are unoccupied that can be utilised by subordinate species.

Foraging characteristics and intraspecific behaviour of *Monomorium sydneyense*

Knowledge of the population biology of an organism is essential for successful population management (Simberloff 2002a; Simberloff 2002b). In my final research chapter I studied aspects of the foraging characteristics and intraspecific behaviour of *M. sydneyense*. I found that *Monomorium sydneyense* had a preference for the protein-based food items that were

offered and they did not forage far from the nest to find the food. *Monomorium sydneyense* was observed actively defending the foods from *P. rugosula* suggesting that they may have similar food preferences, therefore would be likely to compete for food resources. There was evidence of polygyny (multiple queens in a nest) from the collected nests. It also appeared that *M. sydneyense* has general nesting requirements as nests were discovered in full sun and part shade, under solid objects, in soil and in bark pieces on the soil surface. There is evidence that populations of *M. sydneyense* at Sulphur Point are multicolonial. Aggression was recorded between 12 of the 18 colony pairs. This could reduce the chance of *M. sydneyense* attaining large population numbers because of more time and energy would be spent defending resources (Holway et al. 1998; Holway et al. 2002b; Passera 1994).

The overall implications of this work are that *M. sydneyense* has the strongest influence on the ant community of Sulphur Point in the warmer months due to the increased foraging activity of this ant. In December it is active for the majority of the 24 hour period, the exception being the hottest part of the day around 13:00. During the warmer months it is likely that *M. sydneyense* would procure a large portion of food resources by numerical dominance due to their heightened foraging activity. Although the majority of these resources would need to be close to the nests as it does not forage far. As the temperatures cool subordinate ants may experience reduced competition from *M. sydneyense* allowing them to satisfy their resource needs. Additionally the

short foraging distance of this ant ensures that food will be available to other ants in the ecosystem at the current nest density of *M. sydneyense*.

Since aggression was displayed between the majority of the nest pairs tested, *M. sydneyense* colonies may not cooperate for resources and instead will fight with each other for them. If toxic baiting of this ant was conducted, baits would need to be placed short distances apart to ensure that at least 70% of the baits would be occupied by *M. sydneyense*. It is likely that *P. rugosula* would compete with *M. sydneyense* for the bait. Since foraging activity of *M. sydneyense* was greater in December population control by toxic baiting would be best conducted at this time.

This study suggests that *M. sydneyense* may not be a serious threat to the ant fauna of Sulphur Point, Tauranga. The ant fauna of Sulphur Point is predominantly exotic so possible effects on New Zealand native ant fauna are not known. Monitoring the responses of native ants to the presence of *M. sydneyense* is required to predict influences that this introduced species may have on the native ant populations

Is population management of Monomorium sydneyense feasible?

The current distribution records of *M. sydneyense* show that it has only been recorded in two areas of New Zealand, Tauranga and Napier. It is quite possible that this ant is already present in other areas throughout New Zealand though has yet not been recorded. I quickly found nests of

Monomorium sydneyense 6.3 km from the port of Tauranga, which is the likely incursion point for this infestation. These nests were located within 10 m of the East Coast main trunk railway line suggesting that they may have spread further via the railway system. The presence of *Monomorium sydneyense* workers on north western slope of Mount Maunganui, Tauranga suggests that *M. sydneyense* nest foundation may be via nuptial flight, whereby at least one queen has crossed the Tauranga harbour, an approximate 2 km wide body of water and established a new nest, however, it is also possible that a queen, or part of a *M. sydneyense* nest may have been transported there by humans inadvertently.

Functional group theory predicts that *M. sydneyense* and *P. rugosula* will have similar environmental tolerances because they are both categorised in the same functional group (Andersen 2000; Brown 2000). *Pheidole rugosula* has been present in New Zealand approximately 50 years (Berry et al. 1997). It has had time to spread throughout the country. Current records indicate that there are populations of this ant in Christchurch and Nelson (Landcare-research 2005). Theoretically *M. sydneyense* also has the potential to occur in temperate climates of New Zealand as it has been found in Tasmania, Australia (Heterick 2001), especially if it has a close association with humans because climatic limitations may not apply (Gordon et al. 2001).

My data suggest that *M. sydneyense* has had an impact on the ant fauna of Tauranga. This impact has not resulted in significant decreases of any particular species, rather all of the species present have been influenced

through its introduction. No ant species were found to be extirpated by *M. sydneyense*. If *M. sydneyense* invades other areas similar to Sulphur Point, it may not have a negative impact on the resident native ant species. Though if it invades native forest, it is possible that *M. sydneyense* will have different effects to those that were observed at Tauranga.

Based on the data that I have collected the population management or eradication of *M. sydneyense* by toxic control is not a viable option. It appears that it is already well established in New Zealand and probably has wider distribution than is currently recorded. Undiscovered populations would serve as source populations from which reinvasion would occur if an eradication attempt was performed. An intensive baiting program would need to be implemented. Baits would need to be placed no more than 1 m apart preferably in containers of some description to prevent desiccation of the bait. It is likely that this baiting would need to be performed multiple times to ensure that all of the nests in the baiting area are exposed to the poison. Such baiting would expose many invertebrates to toxins and would likely be an expensive undertaking. Similarly, for the population management of *M. sydneyense* an intense amount of baiting would be required.

Future Directions

Further information on the population biology of *M. sydneyense* is needed. Information on the dispersal method of this ant could influence the feasibility of baiting. If *M. sydneyense* nests are founded by budding, where one or more

queens and some workers walk to a new place ant start a nest, the natural dispersal rate may be slow (Suarez et al. 2001), increasing the viability of baiting. Conversely, if new nest foundation occurs by nuptial flight, whereby queens are mated and fly a distance before starting a new nest, the dispersal rate of this ant may be quite fast, further reducing baiting success. A study into the temperature- dependant development of *M. sydneyense* eggs through to adults (degree day models) would allow assumptions to be made on the potential future New Zealand distribution of *M. sydneyense* as well as its potential of invading intact native forests (Hartley and Lester 2003).

Assessing the influence of *M. sydneyense* on the native ant fauna is essential to accurately predict the outcome of *M. sydneyense* invasion on these species. Coupled with degree day models, laboratory trials whereby *M. sydneyense* and native ant colonies with the same number of workers compete for food resources at different temperatures would aid this assessment.

It is likely that a low number of propagules of *M. sydneyense* arrived and established the current population. Interestingly, it would be expected that the ants would be highly related, so why do workers from different nest act aggressively towards each other? Genetic insights into the relatedness between queens and workers within and between nests in New Zealand and in Australia would be valuable in assessing whether all queens present in a nest contribute to the worker number in the colonies and whether there has been any loss in genetic variability as a consequence of *M. sydneyense's* dispersal to New Zealand.

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