The effects of decentralisation on foraging and organisation in social insect colonies

Zoe Cook

PhD

University of York
Department of Biology

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Abstract

Social insect colonies demonstrate some of the most striking social behaviours that are seen in nature. Social interaction in these species defines their behaviour and has a large impact on their success.

A number of ant species organise their colony over several socially interacting, but spatially separated nests. This behaviour is known as polydomy. I used simulation modelling to investigate the costs and benefits of this behaviour. The results showed that colony organisation interacts with both foraging strategy and resource distribution to determine the effect of polydomy on foraging success. Importantly, I show that there are previously undiscussed costs to polydomy.

I also addressed questions of how the social connections between the nests in a colony are organised. Complex interacting systems such as the trail system formed between nests in a polydomous colony can be represented as a network. I review the use of this representation in studies of social insects and provide suggestions for future studies on how social insect systems may provide insight into the construction and use of effective network systems in general.

By representing the trail systems found between nests as networks I show that the systems formed by ants are highly efficient for the transportation of resources but balance this efficiency with the cost of producing trails. A number of simple mechanisms have been proposed for the construction of these networks. I test these theories and show that the simplest mechanisms suggested may not be sufficient to replicate the natural systems.

This thesis contributes to the understanding of the behaviour of ants in polydomous colonies and to the understanding of distributed biological systems more generally. The work also provides a basis for future research on how efficient systems can be constructed using simple rules.

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List of Accompanying Material

Disk containing code files for the models used in Chapters 2 and 5. Each .zip file contains the following c# source files:

Ant.cs - class representing a single ant including methods for ant movement and feeding

CMDLineParser.cs - class for passing command line parameters to main program. Created by Christian Bolterauer 2009

Colony.cs - class representing a colony.

FastRandom.cs - class for generating random numbers. Created by Colin Green 2005

Food.cs - class representing food sources

Form1.cs - class for showing visualisation of ants

Nest.cs - class representing nests

Output.cs - convenience class for outputting results of model to text files

Pheromone.cs - class representing pheromones

Program.cs - main program class. Run simulations based on input parameters

World.cs - environment class holding other objects. Also keeps track of time within model.

In addition 'Chapter 5 Code Files.zip' includes the following file:

Path.cs - class for saving path between nests and food sources.

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Declaration

I hereby declare that this submission is entirely my own work except where due acknowledgement is given.

Chapter 2 has been published in the Journal of Theoretical Ecology (Cook et al. 2013) and is presented as published.

Chapters 4 has been published in Behavioural Ecology and Sociobiology (Cook et al 2014) and is presented as published.

Chapters 3 and 5 are currently being written into manuscripts for submission.

Chapter 1

General Introduction

A large variety of species in nature live in social groups. Group living may provide a number of benefits to the individuals within the group, for example individuals may be better protected from predators. This may be in the form of better detection of predators within a group, group defence behaviour or from dilution of risk from predators (Krause and Ruxton 2002). Individuals within a group may benefit also from being able to locate mates more easily or from gaining access to shelter or protection. There may also be a range of foraging benefits to living in a group, for example an individual that gains information from other individuals may improve its own chances of successfully finding resources or a group may be able to more successfully catch difficult prey (Krause and Ruxton 2002).

1.1 Social insects as a model system for behaviour

Some of the most extreme examples of social behaviour are found within insects. The most striking feature of social behaviour found in social insects is reproductive division of labour extending to in some cases worker sterility. In addition, societies of social insects may be huge, for example colonies of driver ants may have more than 20 million individuals (Raignier and van Boven 1955). Within their colonies social insects are also able to communicate effectively with each other, in some cases using impressive communication systems. For example the honeybee uses the waggle dance to indicate the position of food sources (Von Frisch 1967; Dyer 2002) and in other species communication can take place by using systems of multiple chemicals known as pheromones (Hölldobler and Wilson 1990). Social insect colonies are also able to collectively construct large structures, for example termite mounds several meters high, and to also to collectively overcome prey items much larger than any individual. The extreme sociality found in social insects means that in many cases selection can be considered to take place at the level of the colony rather than at the level of the individual. It also allows the social behaviour of these insect colonies to be considered as a behaviour at the level of the whole colony as well as at the level of the individuals within the colony.

Social insects are found throughout the world in a wide range of environments; they also have a large variety in their life history strategies and also in their behaviours. For example army ant species are nomadic and do not form permanent nests (Mirenda and Topoff 1980), while other species of ants bees and wasps construct complex nests in canopy (Seeley and Morse 1976; Holldobler and Wilson 1977), and some species of ants and termites construct large mound nests (Scherba 1961; Korb 2011). There is also wide variation in resource acquisition. For example some species of ants carry out farming behaviour, this may be farming of fungus in leafcutter ants (Cherrett et al.), or farming of other insects such as the farming of aphids by wood ants (Buckley 1987; Phillips and Willis 2005). Other species of ant carry out social parasitism and rely on the foraging of other species (Hölldobler and Wilson 1990).

A range of social insect species can be easily reared in laboratory as well as being readily observed in the field. Of particular interest to the study of social behaviour are recent studies that have developed technology allowing the social behaviour and interactions of individual insects to be tracked automatically over long periods of time (e.g. Otterstatter and Thomson 2007; Sumner et al. 2007; Pinter-Wollman et al. 2011; Jeanson 2012; Mersch et al. 2013). This means that the social behaviours found in social insect colonies can be tracked in both natural environments and in laboratory environments in which the environmental conditions can be manipulated and hypotheses can be tested.

Since social insects provide an extreme example of social behaviour and collectively carry out a wide range of complex types of behaviour that can be studied at a range of levels in both the laboratory and in the natural environment they are an ideal system for studying social behaviour. In addition some species of ant have a complex colony organisation in which the individuals that are part of a single colony are distributed across the environment. These colonies are composed of two or more socially connected nests; this is known as polydomy (Debout et al. 2007). Within polydomous colonies we can examine social behaviour at a larger scale by studying how insects from different nests interact with each other and the effects that this has on the success of the colony as a whole.

1.2 Polydomy

1.2.1 What is polydomy?

There have been several terms associated with the occupation of several nests by a single ant colony (reviewed by Debout et al. 2007). Here a polydomous ant colony is, as defined by Debout *et al.* (2007), one in which the in which the population exists in at least two, spatially separated but socially connected nests. According to this definition for a structure to be considered as a nest it must house both workers and brood, but not necessarily a queen. This excludes several types of structure such as those described by Anderson and McShea (2001) as outstations or shelters which are used solely for foraging. Spatial separation is defined as separation by a distance greater than that between chambers within the main structure. Multiple nests are considered to be a single colony if, as defined by (Pedersen and Boomsma 1999), individuals from the constituent nests function as a cooperative unit (have non-aggressive communication) and there is exchange of individuals between the nests. In particular for the work presented here, I use a functional definition of polydomy in which the nests are considered to be a single colony if they are linked together by trails at the time of observation. An example of a polydomous colony is shown in Figure 1-1.

Polydomy is found in all of the major subfamilies of ants and has been recorded in at least 49 genera and 166 species of ant (Debout et al. 2007). Several highly successful, dominant and invasive species are polydomous, for example the argentine ant *Linepithema humile*, the pharaoh’s ant *Monomorium pharaonis*, the yellow crazy ant *Anoplolepis gracilipes* and the red imported fire ant *Solenopsis invicta*. The effects of invasive ant species can be wide ranging. Recorded impacts include: displacement of native ant species, decline of invertebrates, decline of vertebrates, disruption of mutualisms including interference with seed dispersal, and

Figure 1-1 Photograph of polydomous *Formica lugubris* colony. Located in the Longshw Estste, Derbyshire, UK. The colony has visible trails between a number of the nests. Photograph copyright S.Ellis 2013

effects on soil chemistry and structure (Holway et al. 2002). Specifically, *S. invicta* has negative impacts on the survival of a range of vertebrates including reptiles, birds and mammals (Allen et al. 2004) and *A. gracilipes* has been shown to negatively affect native flora and fauna in several different areas (Hill et al. 2003; Hoffmann and Saul 2010). It has been proposed that part of the success of these species is due to the flexibility in social structure which is associated with polydomy (Holway and Case 2001).

1.2.2 Why be polydomous?

The evolutionary benefits and social consequences of polydomy are not well understood. The species in which polydomy has been recorded are diverse in their ecology and represent species from a wide range of families, with a wide range of life history traits (Debout et al. 2007). Added to this diversity in polydomous species, polydomy is facultative in 84% of species in which it has been recorded and seasonal in 10% (Debout et al. 2007) suggesting that the benefits of polydomy do not always outweigh the costs.

There are a number of proposed causes of polydomy. In the following paragraphs I discuss the published hypotheses of: polygyny, queen-worker conflict, temperature regulation, risk spreading, population pressure, nest site limitation, and increased foraging efficiency.

In **polygynous colonies**, which have more than one queen, new nests can be produced by the process of budding. Budding is a process in which new nests are established by local dispersal of a queen with a group of workers from the natal nest (Hölldobler and Wilson 1990). The new nest is therefore very closely related to the old nest and contains some proportion of workers from that nest. In some cases interchange of workers between the nests will remain and a polydomous colony will be formed at least temporarily. Despite this, the association between polydomy and polygyny is weak (Hölldobler and Wilson 1977), and half of recorded polydomous species are monogynous (Debout et al. 2007). The association between polygyny and polydomy may be due to them being beneficial in similar conditions.

A polydomous colony may benefit from **spreading the risk of predation** among a number of nests; as nest number increases the probability that one or more of the nests avoids damage will also increase. This may ensure the survival of some portion of the colony brood and may allow individuals from damaged nests to relocate to undamaged nests more easily (Rosengren and Pamilo 1983; van Wilgenburg and Elgar 2007b; Dahbi et al. 2008). A similar risk spreading strategy is proposed for polydomy in *Leptothorax nylanderi* in which nest sites have a high rate of decay in the summer months; by spreading their population they may be able to move more easily when existing nests become uninhabitable (Foitzik and Heinze 2001). The advantages of multiple nests in relation to predation have also been described for other species such as wasps (Strassmann 1981).

There is potentially a **conflict between the queen and the workers** of a colony over the allocation of energy to growth of the colony and reproduction due to differences life expectancy of queens and workers and differences in the relatedness of queens and their daughters and the relatedness of sisters (Pamilo 1991; Backus 1993; Bourke and Chan 1999; Herbers et al. 2001). There is evidence that that queens have some level of control over the production of reproductive ants (Brian 1980). The advantage in polydomy may, therefore, in some cases lie in allowing the formation of queenless nests in which workers can escape the influence of the queen and bias the brood development towards their own interests. Reproductive allocation is linked to sex-ratio conflict, a number of other within colony conflicts, and other life history traits (Herbers et al. 2001). It can be difficult to separate these effects and so there is little direct empirical evidence for the escaping of conflict between the queen and the workers in polydomous colonies. The hypothesis is however supported by studies of *Myrmica punctiventris* in which reproductive females were shown to be produced only in queenless nests, a difference which could not be explained by ecological variation between nests (Snyder and Herbers 1991). Additional studies on the same species provide further support for this (Banschbach and Herbers 1996).

It has been proposed that seasonally polydomous colonies may disperse during summer months to **regulate the temperature of the nest**, dispersing to find warmer sites for brood rearing (Banschbach et al. 1997) or aggregating in winter to maintain higher temperatures (Heller and Gordon 2006). However, in lab tests of temperature choice and field observations of nest movement in *Myrmica punctiventris* Banschbach *et al.* (1997) found no evidence for seasonal polydomy acting as a thermoregulatory mechanism. Activity in ants is highly linked to temperature (e.g. Vogt et al 2003) and in some seasonally polydomous species temperature is likely to be a proximate cause of polydomy.

Several studies have highlighted the importance of suitable nest sites and **population pressure** on the social organisation of colonies. Rosengren and Pamilo (1983) suggest that migration between nests in *Formica polyctena* may be an attempt to even out population pressure in summer especially when nest sites are limited. Stuart (1985) found that larger colonies of *Leptothorax curvispinosus* were more likely to split when nest sites were provided, suggesting that space limitation may be a factor controlling polydomy in this species. Levings and Traniello (1981) also report that polydomy reflects a response to nest size and available nest sites. The effect of nest-site limitation could be especially relevant for seasonally polydomous species, where nest site abundance may be linked to seasonal environmental conditions. For example, *Leptothorax nylanderi* nests in natural cavities such as branch hollows and grass stems. In autumn nest sites become limited due to decay which leads to the fusion of colonies. If extra nest sites are provided the colonies will take advantage of them by splitting the population (Foitzik and Heinze 1998). In a related species, *Leptothorax longispinosus*, Herbers (1986) found a similar effect: the addition of nest sites leading to increases in the fractionation of the colony.

Linked to nest site availability is the hypothesis that polydomy acts to increase the available space for **seasonal brood rearing**. For example, the brood of *Myrmica sulcinodis* is reared in small tussocks of grass known as solaria, which are dispersed throughout the habitat. By having a polydomous structure more of these spaces can be utilised for brood rearing in the summer, increasing the reproductive output of the colony as a whole (Pedersen and Boomsma 1999). Another example of seasonal conditions affecting the suitability of nests is seen in *Formica uralensis* where colonies split into several nests over the winter months. High levels of ground water make the conditions unsuitable, forcing the colony to break up and move to new sites (Rosengren and Pamilo 1983).

The benefits of a dispersed colony may also lie in the **defence of a territory**. In contests between competing colonies (interference competition) numerical advantage is often important (e.g. Adams 1990) . Distributed nests allow workers to reach sites of confrontation more quickly since the average distance between the nest and the location of the contest will be reduced.

There are possible **foraging benefits** to polydomy. A polydomous structure may allow the colonies to decrease the energetic costs of food collection by allowing shorter individual foraging trips while maintaining the same foraging range (Hölldobler and Lumsden 1980). This hypothesis is supported by an individual-based model by Schmolke (2009) which suggests that polydomous colonies can exploit food sources more effectively than monodomous colonies when they are scattered throughout the environment. In addition several studies have shown establishment of new nests in response to food sources (Holway and Case 2000; Lanan et al. 2011). For example In *L. humile* new nests establish close to food sources in both lab and field experiments (Holway and Case 2000) and there is an association between the nest locations of *Iridomyrmex purpureus* and the location of stable food sources (van Wilgenburg and Elgar 2007a). This behaviour also supports foraging as a driver of polydomy.

Although there are many proposed benefits of polydomy it is also important to consider the costs of having a dispersed population. The transport of resources and the movement of individuals between nests may be costly in terms of energy use while travelling, increased predation risk on individuals and increased risk of loss of resources such as brood. There may also be a cost associated with splitting the ant population between multiple nests since, for a colony of the same size, a polydomous nest will contain fewer individuals. With a reduced number of ants within each nest there may also be a risk that there will not be sufficient numbers of individuals for defence of the nest. To combat this and to defend each nest adequately, it may be necessary that a larger proportion of the total colony worker population carries out defence. This behaviour may come at a cost since these workers will not be carrying out other tasks such as foraging.

Although the exact effects will depend on the resource distribution and the type of foraging carried out the foraging benefits of polydomy should apply to any species which is polydomous. In addition foraging success provides clear and testable signal of the effect of polydomy on success meaning that any theoretical benefits may be able to be experimentally tested. For these reasons, when considering the benefits of having a polydomous colony, I concentrate on the possible foraging benefits to the colony.

1.3 Foraging

The acquisition of resources is essential for all life. In animals food resources are gathered by the process of foraging. A wide body of theory has been developed and tested in relation to foraging and in general foraging theory tests how foraging objectives should be maximised given a set of constraints (Stephens et al. 2007). Studies of animal foraging address a wide range of questions including issues of where to forage, how selective individuals should be, how long to remain foraging in a productive area, and many others (Stephens et al. 2007). The best strategy for foraging has been shown to be dependent on elements such as the probability of finding food, the quality of food items and predation risk.

Many of the studies of foraging focus on the success of an isolated individual however, many species including certain species of fish, birds, mammals and insects carry out social foraging. In such species the behaviour of other group members is expected to influence the behaviour and success of an individual (Giraldeau and Caraco 2000). A good example is how the trade-off between exploring the environment to locate food sources and exploiting known food sources is affected by group behaviour. For individuals, theory predicts that time spent exploring the environment at the expense of exploiting known food sources should be related to factors such as quality of known food sources, quantity of food sources and environmental predictability (Stephens 2007; 2008). Several studies show how organisms can balance this trade-off (e.g. Kramer and Weary 1991; Latty and Beekman 2009). However in social species this balance may be modified by the behaviour of others, for example information collected by an individual may be shared with other members of the group possibly reducing the need for other members of the group to explore the environment (Giraldeau and Caraco 2000).

1.3.1 Foraging in ants

In ants, as in most eusocial insect species, social foraging is taken to an extreme level. Ant colonies usually have a specialised subclass of individuals that carry out foraging and provide food to the colony. Many individuals within the colony (up to 80%) do not forage for themselves and so rely on the foraging done by others (Porter and Jorgensen 1981; Robinson et al. 2009; Nobua-Behrmann et al. 2013). Also within an ant colony, division of labour means that different aspects of foraging can take place at the same time. For example foragers from a colony can explore the environment while at the same time others exploit a known resource. This means that, when we consider the foraging of social insect colonies, in many cases the foraging can be seen to take place at the level of the colony rather than the level of the individual.

Classical central-place foraging theory, in which individuals are assumed to forage away from the home site and return with resources, can be applied to ant colonies. Predictions of the types of resource that should be collected by individuals and the time spent foraging have been tested in a number of studies of ant colonies (Holder and Polis 1987; Bonser et al. 1998; Morehead and Feener 1998; Detrain et al. 2000). For example harvester ants can carry out a foraging strategy that minimises the total travelling time with seeds (Morehead and Feener 1998) while several other species are shown to feed for longer on food sources that are more distant or better quality (Bonser et al. 1998). These studies suggest that ants are able to maximise their energy intake according to theoretical predictions. However being part of a cooperative colony, where a large number of nestmates are often found at resources may also affect the strategy of individual insects. The presence of a large number of individuals at a resource leads to crowding and individual strategy may be altered to maximise the whole colony intake (Ydenberg 2007). Recruitment, defined as communication which assembles nestmates in a place where they are needed for work (Wilson 1971), is found in a large number of ant species. Recruitment may allow rapid exploitation of a discovered food source but may also change the optimal strategy for individual foragers. This means that an important component of a foraging strategy is the method by which nestmates are recruited to a food source and needs to be accounted for when considering the theoretical optimal foraging strategy.

A number of species carry out what appears to be individual foraging, with **no recruitment** to food sources (e.g. Fresneau 1985; Nielsen 2001). Although there may be no recruitment in these cases the decision of an individual to forage will be based on the influence of the colony. For example colonies of the red harvester ant *Pogonomyrmex barbatus* respond to the availability of food in the environment by reacting to the return of successful foragers (Schafer et al. 2006).

Other species use **direct recruitment** to food sources including tandem running and group recruitment (Hölldobler and Wilson 1990). In these cases individuals that have discovered a food source can lead other individuals directly to the location. In a tandem run, a single nestmate is recruited to the food source. Nestmates may be attracted to the leading ant by a calling pheromone. Physical contact initiates the tandem run and during travel the pair remain closely linked with the following ant maintaining periodic antennal contact with the leading ant (Wilson 1959; Hölldobler et al. 1974; Möglich et al. 1974). During group recruitment a recruiting ant directly leads up to 30 ants to a food source, this process may involve the use of pheromones for orientation however the presence of a leader ant is essential (Hölldobler 1971). Although there are clear ecological differences between the two methods of recruitment, tandem running can be considered to be a special case of group recruitment in which the size of the group is one (Planqué et al. 2010).

The use of **indirect recruitment** via pheromone trails is common within ants species including polydomous species (Hölldobler and Wilson 1990). Ants which discover a food source are able to lay a trail of pheromones as they are returning to the nest site, nestmates can follow this trail to food sources even in the absence of the individuals which have discovered the food (Hölldobler 1976). A network of trails can be established carrying information on the location of food sources, these trails can recruit foragers which are already searching for food as well as those which are in the nest.

Colonies may also use a **combination of recruitment methods** dependent on the situation. For example *Messor rufitarsis* will carry out recruitment to persistent food sources but otherwise forages with no recruitment (Hahn and Maschwitz 1985). The decision to recruit to a food source may be dependent on a number of factors such as food size or food quality (Cerdá et al. 2009). There are also a number of species which carry out group recruitment initially after finding a food source but move to mass recruitment over time as a trail is built up (Beckers et al. 1990; Collignon and Detrain 2010).

While recruitment can allow the rapid exploitation of a discovered food source there may also be costs to this behaviour, in particular there is a trade-off between the amount of resource benefit gained by sharing information and the amount of opportunity lost in time spent sharing information. Therefore the optimal strategy for recruitment within a colony is dependent on the situation of the colony. Factors that can determine the optimal strategy include the colony size, the resource distribution and the costs involved in transferring information between nestmates (Beekman et al.

2001; Dechaume-Moncharmont et al. 2005; Dornhaus et al. 2006; Planqué et al. 2010).

1.3.2 Optimal recruitment strategy in ants

Recruitment to food sources is often assumed to increase the foraging efficiency of the colony. Recruitment may reduce the search time of individuals, increasing the probability that they will find a profitable food source. However, theoretical models of recruitment in both ants and bees suggest that recruitment may not always be beneficial (Dechaume-Moncharmont et al. 2005; Dornhaus et al. 2006; Beekman and Lew 2008). The optimal method of recruitment may be dependent on factors such as the number of ants in the colony and the foraging environment.

The type of recruitment which can be successfully employed may be limited by the number of ants within a colony. Planqué *et al* (2010) show theoretically that in small colonies no recruitment will be the most competitive strategy and that as colony size increases recruitment should move towards pheromone recruitment with the possibility of tandem running or group recruitment at intermediate stages. There is some empirical support of an association between colony size and the type of foraging employed with larger colonies tending to have foraging systems which rely more on mass recruitment (Beckers et al. 1989). Beekman *et al.* (2001) have also shown both theoretically and experimentally that a minimum population size is needed to establish a pheromone trail to a food source however they point out that the use of group recruitment or other mechanisms can reduce this effect. There is also a cost to sharing information and in certain environmental conditions individual foraging may be more beneficial for the colony as a whole due to these costs. Dechaume-Moncharmont *et al.* (2005) show that the probability of finding a food source and particularly the duration for which food sources are available are important factors in determining the number of foragers which should forage individually. The time spent inactive while waiting for information from successful foragers can offset the benefits of the information even when the probability of finding food is increased by the information received.

1.4 Polydomy and foraging

While there have been a range of studies investigating the optimal foraging strategies and optimal recruitment strategies in ant colonies (e.g. Morehead and Feener 1998; Detrain et al. 2000, Dornhaus et al. 2006; Planqué et al. 2010) there have been few studies that have considered polydomy as part of the foraging strategy of a colony. However, foraging has been suggested as one of the major reasons for polydomy. Having a polydomous colony will disperse the population of foragers over a wider geographical area and so have effects on the foraging success of the colony as a whole.

In particular, in contrast to a colony with a single nest, polydomous colonies can theoretically carry out dispersed central-place foraging in which food is collected locally and then distributed between nests (McIver 1991). This should allow the colony to decrease the energetic costs of food collection by allowing shorter individual foraging trips while maintaining the same foraging range (Hölldobler and Lumsden 1980). There is some empirical support for this: localised foraging has been shown a number of species including *Tapinoma sessile* (Buczkowski and Bennett 2006) and *Lasius neoniger* (Traniello and Levings 1986). *L. neoniger* has been shown to forage in the immediate vicinity of the nest entrance suggesting spatial specialisation, reduced foraging distance, and reduced search time (Traniello and Levings 1986). Distribution of resources between nests is evident in species such as *Camponontus gigas* (Pfeiffer and Linsenmair 1998).

While having a polydomous colony may reduce the search time for discovering new resources, the search time can be reduced further in ant colonies by recruitment. Foraging and recruitment strategy in polydomous ant species is as diverse as it in ant species generally. However, for a polydomous colony carrying out recruitment, the population from which recruits can be found will be dispersed. This could make the colony size effectively smaller than it would otherwise be if the colony occupied a single nest. This may lead to interactions between recruitment and the success of polydomous colonies. While theoretical studies have suggested that a polydomous structure may increase foraging success of a colony (Hölldobler and Lumsden 1980; Schmolke 2009), these studies do not include any assessment of the effects of different foraging strategies. In particular recruitment to food sources is not considered. I address the question of how recruitment type, colony organisation (monodomy or polydomy) and colony size interact in **Chapter 2**.

1.5 Organisation within polydomous colonies

The nests within a polydomous colony are, by the definition used in this work, socially linked in some way. Therefore, while the foraging benefits of polydomy may not be clear in all cases, a polydomous organisation will have an effect on the resource acquisition of a colony. Resources collected by foragers from one nest within the colony will impact on the colony as whole and therefore on individuals from other nests. In particular, resources that are collected by foragers from one nest may be transported to other nests. Once transported they could be used by workers from these nests or possibly transported further though the colony. This transportation between nests may provide additional benefits to the colony. The movement and redistribution of workers between nests may also be adaptive for the maintenance of colony cohesion (Cerda et al. 1994; Dahbi and Lenoir 1998) or provide an alternative to transporting food.

Given the possible benefits of efficient movement between the nests in the colony the way that individuals move between the nests may have a large effect on the success of a colony. To assess how individuals move between nests, detailed observation of colonies is needed. There have been a number of field studies which have mapped the extent of polydomous colonies. The recording of polydomous colonies can be difficult since colonies can be constantly changing structures. Nest moving is extremely common in some species. For example, a large proportion of *L. humile* nests may be occupied for less than one month, be occupied at different times of year or be temporarily abandoned and reoccupied (Heller and Gordon 2006). Other examples include *Cataglyphis iberica* in which the lifetime of over half of nests has been recorded as between one and three months (Cerdá et al. 2002). In other species however nests may be occupied for a much longer time period. For example nests of *F. polyctena* have been observed to persist for up to 5 years (Mabelis 1979). In many polydomous colonies the nests of the colony are linked together with clear trail systems along which individuals move and food is transported (e.g. Holt 1990; McIver 1991; Buczkowski and Bennett 2006; Heller et al. 2008). In colonies with long lived nests the colony may reuse trail systems they construct over several years.

Maps of polydomous colonies that include detailed recording of the trail system that links the nests together are relatively rare. Within the studies that map the trail system of polydomous colonies there is generally no analysis of the structure of these trail systems (Holt 1990; Pfeiffer and Linsenmair 1998; Boudjema et al. 2006). However, in more focussed laboratory studies Aron *et al.* (1990) and Latty *et al.* (2011) have studied the inter-nest trail systems in small colonies of *L. humile*. In their study Aron *et al.* (1990) arranged nests in squares or triangles with fixed bridges as possible paths between them and studied the use of bridges. Their results show the colony will neglect one bridge, producing a trails structure that resembles a minimum spanning tree network. This type of organisation of trails connects all nests in the colony while minimising the total length of paths. A similar result was found by Latty *et al.* (2011) who carried out a similar experiment using an open arena. In this case no restrictions were placed on connecting paths and the trails linking the nests were found to be arranged in a way similar to Steiner minimum trees or minimum spanning trees. These results suggest that colonies minimise the cost of trail construction while connecting all nests. The trail systems produced in these experiments are however much smaller than those that would be created by this species in natural situations where colonies have been recorded as sharing food between over 14 nests and between nests up to 50m away from each other (Heller et al. 2008). In other species polydomous colonies have been recorded with over 100 nests connected within a single component (e.g. Cherix 1980). Within natural colonies the transportation networks produced by polydomous colonies may also be strongly affected by environmental conditions such as food distribution.

In **Chapter 4** I address how the trail systems in natural polydomous colonies are structured. I compare the results of analysis of field colonies to those found in lab colonies and ask how efficient the natural networks could be for transportation of resources around the system of nests.

1.5.1 Constructing trail systems

While there are some studies that record the structure of the networks of trails found between nests in polydomous colonies (e.g. Cherix 1980; Holt 1990; McIver 1991; Andersen and Patel 1994; Pfeiffer and Linsenmair 1998; Heller et al 2008) there is very little data on how these systems are constructed, maintained and put to use for transportation. It has been suggested that food is redistributed by foraging ants that treat nests as food sources, taking food from them to the discovered nest and returning it to the nest they are foraging from (McIver 1991). However, the best documented mechanism of food distribution throughout a colony is transportation by a special class or group of ants. This behaviour has been described in several species including *Camponotus gigas* (Pfeiffer and Linsenmair 1998), *Iridomyrmex purpureus* (van Wilgenburg and Elgar 2007a) and others (McIver 1991; Lanan et al. 2011). In these cases food is collected locally and subsequently moved to neighbouring nests along trails by ants that act as transporters.

The formation of transportation networks is of interest particularly if the systems have properties that might be desirable in human systems. The formation of efficient transportation systems has been studied in a number of natural systems including fungal systems (Nakagaki et al. 2004; Bebber et al. 2007). In their study of laboratory colonies of *L. humile* Latty *et al* (2011) show that a trail system is formed with a large number of trails and that the number of trails is subsequently reduced to connect the nests with a minimal distance of trail. This mechanism of formation is similar to the mechanism that has been studied in fungal networks (Nakagaki et al. 2004; Bebber et al. 2007). Increased understanding of the mechanisms of formation may be more widely applicable to other biological systems and also to human systems. In **Chapter 5** I use a simulation of a polydomous colony to investigate whether simple behaviours can produce trail networks with the properties that are observed in natural colonies.

1.6 Modelling framework

1.6.1 Agent-based modelling

In chapters 2 and 4 of this thesis I use an agent-based (or individual-based) model to represent a polydomous ant colony. It has been stated that there is no clear definition of an individual based model (DeAngelis and Mooij 2005). However, it is generally understood that within this type of model, individual entities such as animals, plants or cells within the population are represented explicitly in the model of the system. The individuals have their own state and history of behaviour and can typically interact with each other and with the environment based on a set of simple rules (Macal and North 2010).

A review by DeAngelis and Mooij (2005) identifies over 900 models that could be considered to be individual based. From the examples in this study it can be seen that individual based models have been used to a address a wide range of biological issues including animal migration (e.g. Huse et al 2002), seed dispersal (e.g. Jongejans and Schippers 1999), foraging (e.g. Nolet and Mooij 2002), host-parasite interactions (e.g. Jeltsch et al 1997), competition (e.g. Weiner et al 2001), and species invasions (e.g. Higgins et al 1996).

There are a number reasons to use agent-based models over more traditional, equation-based mathematical models. In particular, agent-based models can be used to represent complex systems, that cannot be easily represented. This approach also makes possible study of how system level properties are linked to local properties and local interactions with both other individuals and with the environment. Feedback between local changes in the environment and both the individuals and the system as a whole can also be assessed. The effects of variation between individuals can also be included and investigated in these models including variation in the past interactions of individuals. For the work in this thesis one of the main advantages of using an agent-based modelling approach is that it allows us to link small scale, local interactions and simple behavioural rules at the level of the individual ants to larger scale, emergent behaviours at the level of a colony.

While individual based models are a powerful tool for studying complex, emergent behaviour there are a number of issues with this approach that must be addressed. Individual based models may become more difficult to analyse due to their complexity. The model must be carefully designed to enable the results to be analysed and carefully implemented to avoid errors. In some cases it may be difficult to determine the cause of an emergent behaviour or process and a through sensitivity analysis may need to be carried out to determine which parameters have a large effect on the outcomes of the simulations. It can also be easy to make the assumption that what we see in these types of models is 'real' behaviour. When communicating the results of these models it must be made clear that the model is designed to address specific questions and that simplifying assumptions have been made about conditions and behaviours.

Individual based models have been used to represent ant colonies and other social insect colonies in a range of studies. These studies address a range of questions including questions about collective nest choice (Pratt et al 2005), formation of droplets of ants in experimental conditions (Theraulaz et al 2001) trail formation (Jackson et al 2004), recruitment strategy (Dornhaus et al 2005) and movement and foraging (Haefner and Crist 1994). It is also interesting to note that models based on the behaviour of ant colonies have also been used to solve problems in other fields. A particularly well studied and extensively used example is the ant inspired 'ant-colony optimisation algorithm'. This algorithm can be used to investigate a wide range of problems that can be reduced to the problem of finding the shortest route through a network (e.g. Bonabeau et al 2000, Sim and Sun 2003, Blum 2005, Mandala et al 2013).

The individual based model I use in this work is based on a previously published model produced by Schmolke et al. (2009). The model consists of a spatially explicit environment, within which ant colonies and resources exist. Ant colonies are made up of nests which have a location and a number of ants that are associated with them. The ants are the individuals (or agents) within the model. The ants have their own state and are able to interact with the other entities that exist within the environment. This is shown graphically in Figure 1-2. The modelled ants have their own state and behaviour based on their previous behaviours and interactions. The possible

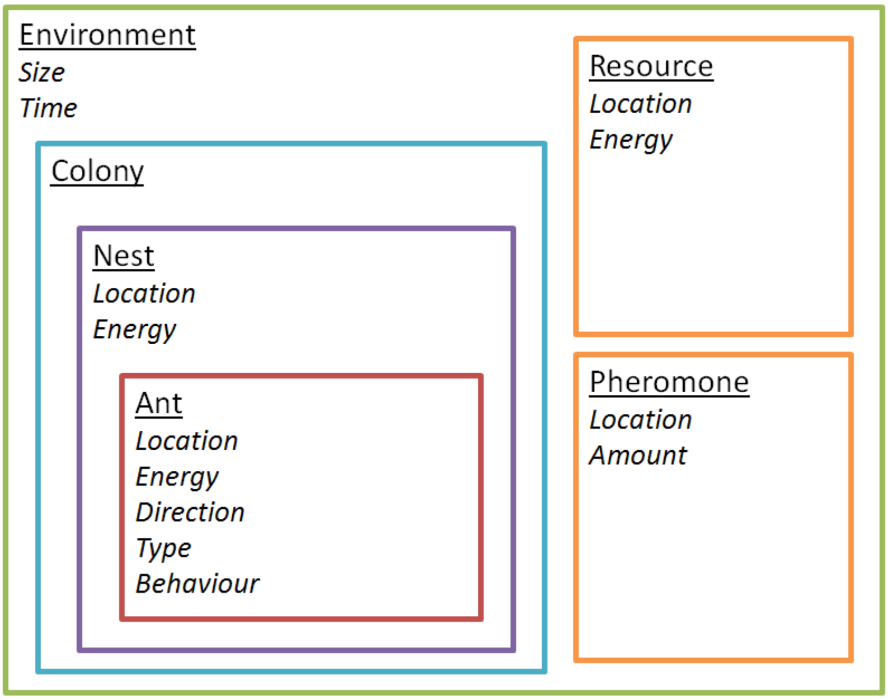

Figure 1-2 Graphical representation of the structure of the model used in Chapters 2 and 5. Each box represents an entity in the model and contains the name of that entity and its key properties.

behavioural states of the ants and the transitions that can take place between these states are shown in Figure 1-3.

The detailed behaviour of the ant agents within the model and the parameters used are described in more detail in Chapters 2 and 5. While care has been taken to ensure that the behaviour of ants within the model is representative of real ants it must be noted that it is a model. It is good practice to produce a model that is as simple as possible (Grimm 1999) and the model used here is not designed to perfectly reproduce the behaviour of any ant colony. Instead it is designed to be only as complex as is needed to address the specific questions raised in the chapters where it is used.

The model is implemented as a C# application and the code for the implementation is included electronically.

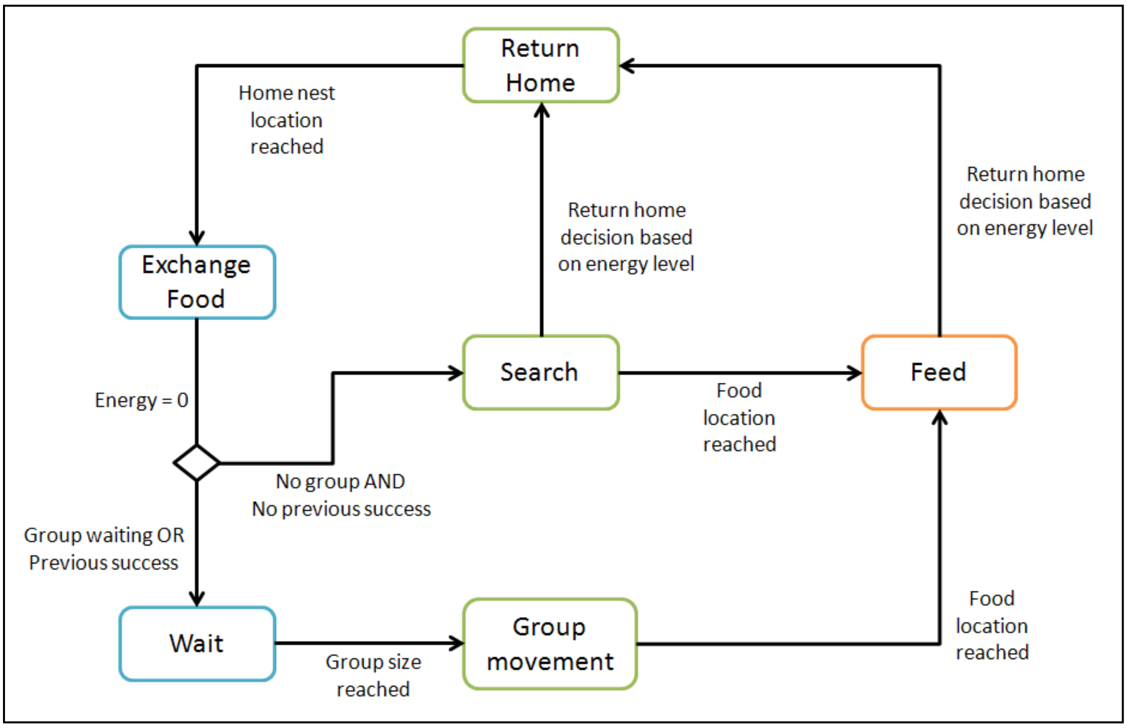

Figure 1-3 Graphical representation of the behaviour of ants within the model used in Chapters 2 and 5. The behavioural states of ants are shown in the boxes and transitions can take place in the direction of the arrows. Labels on the arrows indicate under what conditions the ant will change state. The colour of the box indicates where that behaviour takes place. Blue boxes indicate behaviours that take place at the home nest location, green boxes anywhere in the environment and orange boxes at a food source location. A detailed description of the behaviour that takes place in each of these states is in Chapter 2. Details of the parameters that determine the change decisions are also in Chapter 2. The 'wait' and 'group movement' behaviours only take place in simulations with group recruitment.

1.6.2 Networks

In Chapters 4 and 5 I use networks to represent the trail systems formed between nests in polydomous ant colonies. The use of networks to represent biological systems has increased greatly in recent years. Much of the work on networks has concentrated on the analysis of social networks, in which social connections or interactions between individuals within a population of animals are recorded and analysed (see Croft et al 2008). Applications of network theory include previous studies of the trail system of polydomous ant colonies (Aron et al. 1990; Buhl et al. 2009; Latty et al. 2011).

A network representation can be used for any system that is made up of discrete parts that may be connected in some way. The parts of the system are usually known as nodes and the connections between them as edges. A network can be represented by a matrix in which the element *(i, j)* of the matrix details the connection between node *i* and node *j* of the system. Networks are often represented graphically as shapes connected by lines. In the most simple networks the edges within the network are recorded as being present or not. However, more complex networks can also be constructed; edges within a networks can be directed, edges may also be weighted based on the strength of the connection or given other properties.

The methods of network analysis allow quantitative description of the structure of interactions (Wasserman and Faust 1994; Croft et al. 2008). Analysis is possible on the level of the individual nodes within the network or at the level of the network as a whole. The most simple property of a network is the number of connections it contains. The number of connections is referred to as the degree in most network literature. While it is a simple measure, the number of connections is arguably one of the most important properties of a network as it has effects on many other properties.

Most analyses of networks will also include some analysis of centrality in the network. Centrality can be measured at the level of the whole network or the nodes. It is often used as a measure of the importance of single nodes within the network. Centrality can be measured in a number of ways: by examining degree or more specialised measures such as betweeness and closeness. Both betweenness and closeness are measured using shortest paths. A path is defined as a sequence of edges that connect two nodes and so the shortest path between two nodes is the path that uses the least number of edges (or in some cases has the least combined edge weight). Betweenness measures of how many of all of the shortest paths through the network a node lies on and closeness measures the average distance of the shortest path from that node to every other node in the network.

There are numerous other, more complex, analyses available for the analysis of networks (Wasserman and Faust 1994; Croft et al. 2008). For example, some studies also look for the presence of particular sub-graphs (or motifs) within a network. Others analyses allow the study of clustering within a network, flow through a network, or features such as assortativity (whether connections are linked to other features such as size, location or age). A glossary of some of the terms associated with network analysis is included in Appendix A.

Networks have been used to represent social insect colonies a number of times. Network representations of social insect colonies vary in scale from representing interactions between individual insects (Otterstatter and Thomson 2007; Naug 2009; Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Mersch et al. 2013) to representing colony level trail systems (Aron et al. 1990; Buhl et al. 2009; Latty et al. 2011). The representation of social insect systems as networks is reviewed in **Chapter 3**.

In Chapters 4 and 5 I use a network to represent the trail system of polydomous colonies. In this representation the edges of the network are the trails created by the colony between nests and the nests are the nodes. In Chapter 4 I analyse the trail systems produced by natural colonies and in Chapter 5 I use network analysis techniques to compare the trails created by the modelled colony to the trails in the corresponding natural colonies. In these analyses I use relatively simple analysis of

1.7 Thesis structure

In **Chapter 2** I use an individual-based model of a polydomous colony to study how the foraging success of an ant colony is affected by it being polydomous. In particular I include two types of recruitment within the model and investigate how polydomy interacts with the type of foraging strategy used, the colony size, and the distribution of resources in the environment. For the remainder of the thesis I look at the organisation of polydomous colonies by using a network representation of the colony, where the nests of the colony are represented as nodes in a network and trails join these nodes. I introduce this approach in **Chapter 3,** which reviews how social insect colonies have been represented as networks in different ways. In **Chapter 4** I carry out an analysis of the structure of the trail networks formed by eight natural polydomous ant colonies. In particular I examine whether the structures formed are efficient for the transportation of resources and compare the colonies' networks to networks that minimise total distance or are created by connecting to their nearest neighbours. In **Chapter 5** I use a modification of the model used in Chapter 2 to study the possible processes involved in the construction of polydomous trail networks. I investigate the effects of the inclusion of a class of ants that carry out only transportation of resources between nests and discuss the behaviours that ants may perform to produce the networks observed in natural colonies. I conclude in **Chapter 6** with a general discussion which highlights the contributions of the work in this thesis to the understanding of the causes, consequences and organisation of polydomy in ant colonies and distributed systems in general. I also address questions that are remaining and the possible directions of future work to address these questions.

Chapter 2

Exploration versus exploitation in polydomous ant colonies

2.1 *Abstract*

In socially foraging species resource information can be shared between individuals, increasing foraging success. In ant colonies, nestmate recruitment allows high exploitation rates at known resources. However, to maximize foraging efficiency this must be balanced with searching for new resources. Many ant species form colonies inhabiting two or more spatially separated but socially connected nests: this type of organization is known as polydomy. Polydomous colonies may benefit from increased foraging efficiency by carrying out dispersed-central place foraging. However, decentralisation of the colony may affect recruitment success by limiting interaction between ants based in separate nests. We use an agent-based model which compares the foraging success of monodomous and polydomous colonies in different food environments, incorporating recruitment through pheromone trails and group foraging. In contrast to previous results we show that polydomy is beneficial in some but not all cases. Polydomous colonies discover resources at a higher rate, making them more successful when food is highly dispersed, but their relative success can be lowered by limitations on recruitment success. Monodomous colonies can have higher foraging efficiency than polydomous colonies by exploiting food more rapidly. The results show the importance of interactions between recruitment strategy, colony size, and colony organisation.

2.2 *Introduction*

Traditional optimal foraging models assume complete knowledge of the distribution and quality of the food sources in the environment (Charnov 1976; McNair 1982). However, knowledge of the environment often must be obtained through sampling and this can affect the predicted behaviour of foragers (McNamara and Houston 1985).

Gathering information can conflict with other activities such as exploitation of known food sources meaning that the balance between resource discovery and resource exploitation can be an important factor in success. Optimal foraging theory predicts that time spent exploring the environment should be related to factors such as quality of known food sources, quantity of food sources and environmental predictability (Stephens 2007; 2008). Both acellular slime mold (Latty and Beekman 2009) and chipmunks (Kramer and Weary 1991) have been shown to increase exploration effort when food quality is low.

Social foraging has been described in many species including fish, birds, mammals and insects (reviewed in (Giraldeau and Caraco 2000)). In such species, information is communicated between members of the group, and the information gained from the group can change the predicted behaviour of an individual forager. In the social insects, foragers provide both for themselves and for non-foraging nestmates. This allows us to analyse foraging dynamics such as exploration and exploitation from the level of the individual and the level of the colony. Information about food is shared with nestmates during recruitment (Hölldobler and Wilson 1990); allowing individual foragers to find profitable food sources with higher probability.

Previous studies have looked at the balance between individuals which primarily explore the environment (scouts) and those which primarily exploit known food sources (recruits) within colonies (Jaffe and Deneubourg 1992; Biesmeijer and de Vries 2001; Dechaume-Moncharmont et al. 2005). However, few studies have examined how this balance is affected by colony nesting strategy.

At least 166 species of ant in 49 genera have colonies that are polydomous (Debout et al. 2007). A polydomous colony is one in which the colony consists of at least two spatially separated but socially connected nests (Debout et al. 2007). Exchange of individuals and food may take place between nests (McIver 1991; Pfeiffer and Linsenmair 1998; van Wilgenburg and Elgar 2007a; Lanan et al. 2011). In polydomous colonies, there may be additional costs or benefits to collecting and sharing information.

The evolutionary benefits of polydomy are not well understood (Debout et al. 2007). Polydomous species are diverse in their ecology and represent species from a wide range of subfamilies, with variable life history traits. In addition, polydomy is facultative in 84% and seasonal in 10% of all species in which it has been recorded (Debout et al. 2007), which suggests that the benefits of polydomy do not always outweigh the costs.

There are a number of proposed causes of polydomy including: polygyny (Rosengren and Pamilo 1983), queen-worker conflict (Snyder and Herbers 1991), temperature regulation (Banschbach et al. 1997), risk spreading (Foitzik and Heinze 2001; Dahbi et al. 2008), population pressure and nest site limitation (Rosengren and Pamilo 1983; Traniello and Levings 1986; Foitzik and Heinze 1998), and increased foraging efficiency (Hölldobler and Lumsden 1980; Schmolke 2009). In this study we focus on the foraging benefits of polydomy, using an agent-based model to compare the success of monodomous and polydomous colonies under a variety of conditions. The possible foraging benefits of polydomy should be applicable to a wide range of species.

Polydomous colonies can carry out dispersed central-place foraging in which food is collected locally and then distributed between nests (McIver 1991). This allows the colony to decrease the energetic costs of food collection by allowing shorter individual foraging trips while maintaining the same foraging range (McIver 1991; Debout et al. 2007). Empirical support that foraging drives polydomy includes the suggestion that foraging can be a driver of polydomy (Traniello and Levings 1986; Pfeiffer and Linsenmair 1998) and new nests have been shown to establish close to food sources in both lab and field experiments (Holway and Case 2000; van Wilgenburg and Elgar 2007a; Lanan et al. 2011). The results of a previous individual based model suggest that polydomous colonies can exploit food sources that are scattered throughout the environment more effectively than monodomous colonies, and that there is no difference in the success of polydomous and monodomous colonies when food sources are clumped (2009). However, these results contrast with lab experiments which suggest that polydomy decreases the success of colonies feeding on resources which are clumped (Holway and Case 2001).

A diverse range of foraging strategies are found in ants, including recruitment behaviour (Carroll and Janzen 1973). While some ant species show no recruitment to food sources (Beckers et al. 1989; Dean 1989), recruitment to food sources is observed in many species including polydomous species (Hölldobler and Wilson 1990; Hölldobler and Wilson 2009). Colonies can carry out recruitment through tandem running or group recruitment (e.g. *Leptothorax curvispinosus* (Beckers et al. 1989), *Camponotus socius* (Hölldobler 1971)) and via pheromone trails (i.e. mass recruitment) (e.g. *Linepithema humile (Deneubourg et al. 1990), Polyrhachis muelleri* (Liefke et al. 2001)). The prevalence of recruitment behaviour in polydomous colonies strongly suggests that this behaviour should be included in foraging models. However, previous models of the costs and benefits of polydomy (Hölldobler and Lumsden 1980; Schmolke 2009) are based on a single foraging strategy in which ants forage independently and do not incorporate alternative recruitment strategies.

In this study we use an individual based model to investigate the effect of recruitment strategy on the relative success of monodomous and polydomous colonies. We test monodomous and polydomous colonies of three sizes (125, 250 and 500 ants) using three recruitment strategies (none, group recruitment and pheromone recruitment), under clumped and dispersed food distributions (single large food source, three large food sources, 100 small food sources). We address the possible causes of differences in colony success by looking at the ability of monodomous and polydomous colonies to locate and exploit food sources of differing spatial distributions.

2.3 Model description

We use an agent-based model which includes recruitment to food sources and is based on Schmolke (2009). Our model is implemented as a C# application. Ants are modelled as individual agents which exist in a two-dimensional continuous space. Time passes in discrete steps. All ant agents are updated in a random order in each time step.

In each time step ants are engaged in one of several behaviours: searching, feeding, returning home, waiting or exchanging energy with nestmates at the nest. Ants search for food (searching) and upon discovering food transfer energy from the food to their own budget at a fixed rate (feeding). After feeding ants return to their home nest where they exchange energy and subsequently are recruited or return to searching for food.

Stochasticity is introduced into the model by using random numbers as part of the processes described below which determine when an ant switches behaviour.

2.3.1 Initialisation

At initialisation food and nests are located randomly within a 1000mm x1000mm area. Although the food and nests are placed within this area, ants are unrestricted in their movement; they are able to take any position, including positions outside of this area. We do not use a toroidal surface.

We use a random distribution for nest locations. In empirical studies nest locations within a colony have been described as overdispersed (Traniello and Levings 1986), aggregated (Cerdá et al. 2002), and random (Snyder and Herbers 1991). Although Schmolke (Schmolke 2009) used an overdispersed distribution, we use a random distribution as gives the same results and is a neutral distribution which does not require additional parameterisation. 500 units of energy are evenly distributed among food sources (one, three or 100 items). We choose random food locations from a uniform distribution in all cases. The food distributions with one or three items represent large, relatively stable food sources such as an aphid colony on a single tree, while 100 small food items represent dispersed ephemeral food sources such as dead insects.

We model both monodomous colonies and polydomous colonies with five nests. Simulated ants are located within their home nest at initialisation. In a monodomous colony all ants are in a single nest, in a polydomous colony the same number of ants are split evenly between the five nests of a colony. Although nest sizes within a real colony can be very variable, colonies can also have nests of very similar sizes (Cerdá et al. 2002). We distribute ants in our model evenly between nests within polydomous colonies as this avoids adding additional complexity to the model.

All nests and ants initially have zero energy and energy levels are subsequently compared to this state meaning that net energy levels may be positive or negative.

To incorporate division of labour, a proportion of the ants were designated as ‘nest ants’ which remain in the nest, and a proportion as ‘foraging ants’ which leave the nest and carry out foraging (Oster and Wilson 1978; Porter and Jorgensen 1981; Gordon 1989). We assume that these ants do not switch task throughout the simulation.

2.3.2 Searching

Searching ants look for food using a correlated random walk in which the distance travelled in a time step is drawn from a normal distribution. Negative distances are ignored and a maximum distance of 6mm is travelled per step. The turning angle is drawn from a von Mises distribution with its mean in the previous direction of travel. Parameters for the distributions used are shown in Table 2-1.

The individual ants use energy as they move, the energy used increases linearly with distance travelled according to:

$$E_t = w(M_r + 0.75d_t)$$

where E_t is the energy used at during time step t, M_r is the resting metabolic rate of an ant, d_t is the distance travelled during time step t, and w is the weight of an ant (Vogt and Appel 1999). During searching, ants have a probability of stopping and beginning the return home behaviour based on their energy. Ants with less energy have an increased chance of returning to the nest. In each time step a random number between 0 and -24 is drawn (Schmolke 2009), if this number is less than the energy of the ant then it will begin to return home. The range 0 to -24, determines how long an ant searches for before returning home. At the minimum energy of -24 the ant is guaranteed to begin to return home. Changes to this parameter affect the amount of

Table 2-1 Parameters used in simulations. Parameters marked with * are varied, all others are fixed. Parameter values in brackets were used for sensitivity analysis and results are shown in Appendix B.

Description	Value(s)	Units	Reference
Number of nests in a polydomous colony	5	nests	Schmolke (2009)
Number of ants within the colony *	125; 250; 500; (1000)	ants	
Proportion of ants in each colony which forage	20%	ants	(Bruin et al. 1977; Robinson et al. 2009)
Area over which food and nests are distributed	1000 x 1000; (1414 x 1414)	mm	Schmolke (2009)
Weight of an ant	2.5×10^{-6}	kg	Schmolke (2009)
Resting metabolic rate of ants	4.1	µW	Vogt and Appel (2000)
Rate of exchange of energy with food or nest items	0.0033	µW	Schmolke (2009)
Number of foods in simulation *	1; 3; 100	foods	
Total amount of energy within simulation	500	J	Sufficient food for length of simulation
Distance from which food can be detected	6	mm	Schmolke (2009)
Mean distance travelled by an ant per time step	4.3	mm	Schmolke (2009)
Standard deviation of mean distance travelled by an ant	2	mm	Schmolke (2009)
Maximum distance travelled by an ant per time step	6	mm	Stops unrealistically large steps
Deviation in turning angle distribution ($1/\kappa$)	2.33		Schmolke (2009)
Minimum deviation in turning angle distribution while following pheromones ($1/\kappa$)	0.78		Allows ants to follow trails
Maximum angle change in a single time step when pheromones are detected	PI/4	rad	Prevents ants overcompensating when following trails
Decay parameter for pheromones (λ)	-0.005; (-0.001)		Pheromones persist long enough for trails to form
Initial amount of pheromone laid by ants in single time step	1	Arbitrary units	Pheromones persist for appropriate time
Minimum density of pheromone	0.05	Arbitrary units	For computational efficiency.
Distance from which pheromones can be detected	6	mm	Prevents ants from losing trails Robinson et al (2005)

time an ant searches unsuccessfully; using a higher value range results in ants travelling less far from the nest and therefore not finding food sources as effectively, using a lower value range would allow ants to travel greater distances from the nest. Any changes would affect both monodomous and polydomous colonies equally and therefore would not affect the conclusions of our work. For the value chosen the average outward trip duration is approximately 1500 steps, for ants which do not discover food. This ensures that ants can discover food but do not travel unrealistically far from the nest. Ants that do not search take energy directly from the nest energy.

2.3.3 Feeding

When a searching ant finds a food source, it removes energy from the food item and adds it to its own energy budget at a constant rate (Table 2-1); we assume that this energy is immediately available for the ant to use. Ants vary in the amount of energy they remove from a food source (Mailleux et al. 2000). The exact amount taken in the model is determined by a random process based on the current energy of the ant. In each time step a random number between 0 and 100 is drawn, if this number is less than the energy of the ant then it will leave the food source. This means that ants which have a higher energy are more likely to leave the food source. Ants will also leave food sources in which the energy has been depleted to zero. The range of values used allows comparability to the previous model. The theoretical maximum energy of an ant is 100 however the average amount of food taken from a food source in a single trip is 0.5, meaning that the smallest food items are depleted within 10 visits while larger food sources are more stable in time.

In a polydomous colony ants will treat nests that are not their own home nest as food sources if the energy of the discovered nest is greater than zero (Schmolke 2009). This was designed to simulate a simple method of food exchange between nests of a polydomous colony as proposed by McIver (1991).

Ants that leave food sources begin the return home behaviour.

2.3.4 Return home

Ants that are returning to the nest follow a similar movement to foraging ants. However we assume that the ants are aware of the direction of their home nest and so the direction of travel is drawn from a von Mises distribution in which the mean direction is always the direction of the home nest. Thus returning ants follow a more direct route and always successfully return to their home nest.

2.3.5 Energy exchange with nest

Once home, nest energy and ant energy are exchanged until the ant has an energy of zero. This can involve the nest gaining or losing energy dependent on the success of the returning ant in finding food. Biologically, the exchange of food with the home nest is equivalent to the transfer of food between foraging ants and the ants or brood which are located in the nest. Energy budgets are relative to the initial state of zero so negative energy budgets can occur in both the nests and the individual ants.

2.3.6 Recruitment

Three recruitment models are used: the original ‘solitary foraging model’ (Schmolke 2009), group recruitment, and mass recruitment via pheromone trails.

During group recruitment ants that have completed the energy exchange process in the nest will carry out one of several behaviours. If an ant has been successful in finding food during its previous trip it remains in the nest until there are enough ants to form a group. The size of the group is specified by the recruitment strategy. Previously unsuccessful ants join a group if there are recruiting ants already in the nest, otherwise they return to searching. If there are multiple successful ants in the nest then one is randomly chosen to lead the group. If there are more than the required numbers of ants in the nest, the group members are randomly chosen. Once a foraging group has formed this group move to the discovered food source following the path the discovering ant used to return home.

During pheromone recruitment ants that are returning home from feeding lay pheromones at their location in each time step. Pheromone points are initially laid at a density of one and decay exponentially (Jeanson et al. 2003) according to

$$P_t = P_0 e^{\lambda t}$$

where P_t is the amount of pheromone at time t and λ determines the rate of pheromone decay. Pheromones are deleted once they reach a minimum density (0.05).

We used the following to model the ant's reaction to pheromones: Pheromone concentration is detected with two antennae modelled as detecting within two circular regions with radius of 10 units located 10 units away from the ant at 45° to the left and 45° to the right of the direction of travel. The ant turns stochastically towards the region with the highest concentration of pheromone. The degree of turning is dependent on the ratio of the pheromones detected by the left and right antenna. Noise is added by drawing from a von Mises distribution with mean of the new direction and kappa which is increased linearly (to a maximum) dependent on the total amount of pheromone detected (Table 2-1). This means that ants on weak trails are subject to high noise levels and thus are more likely to leave the trail.

2.3.7 Parameterisation

For consistency, the parameterisation of movement, feeding and energy exchange with the home nest was unchanged from the ‘solitary foraging model’ (Schmolke 2009). Pheromone decay rates are extremely variable both between and within ant species, lasting from a few minutes to several days (Hölldobler and Wilson 1990). In our model we aim to represent relatively short-lived pheromones used solely for recruitment to food. Pheromones can be detected for 599 time steps: this is approximately half of the mean outward trip length of an ant which does not find food (mean = 1468, sd = 715, n = 1000).

All parameters used are shown in Table 2-1

2.3.8 Data collection and analysis

We examined the success of polydomy versus monodomy under a range of food environments, colony sizes and recruitment strategies. The success of a colony is measured by its energy budget at the end of the simulation. For each recruitment strategy the number of food items and the number of ants were varied according to the values shown in Table 2-1. For all combinations of food numbers, ant numbers and recruitment strategies, 100 replicates of 10000 time steps were run.

At the end of each simulation the energy budgets of each nest and each colony were recorded; these values are relative to the initial value of zero and hence can be negative. The energy budget of the colony includes the energy of all nests belonging to the colony. The energy of individual ant agents is small enough to be ignored (Appendix B).

The time at which each colony discovers food for the first time was recorded for each run. Survival analysis was used to account for the effects of colonies which did not find food within the maximum 10000 time steps of a run. The effect of colony organisation on time to find food was analysed using Cox proportional-hazards regression found in the R package 'survival’.

In group recruitment simulations we recorded the time it took for groups of foragers to form in each of the ‘group foraging’ simulations. This is based on the maximum time spent waiting in the nest by a member of each group. In pheromone recruitment simulations with a single food source the number of ants arriving at the food source in the first 1000 time steps after it had been discovered was also recorded.

The energy budget and discovery time data do not meet the assumptions of parametric tests and so bootstrap tests of the difference in mean between polydomous and monodomous colonies were used to calculate confidence intervals for the differences in mean energy budget and in mean time to locate a food item (1000 samples).

We use ANCOVA to test for differences between the recruitment rate to food sources. We use ANCOVA to control for the covariation between the initial time to find a food source food and amount of ants arriving in after it has been discovered.

All analysis was carried out using R 2.12.2 (R Development Core Team 2011).

2.3.9 Sensitivity analysis

We test the sensitivity of the results to several parameters of the model. We test for the effects of doubling the colony size and decreasing pheromone decay rate. We also carry out simulations in which the energy of ants is included in the results and simulations in which individual memory of food sources is included. The results of these simulations are shown in Appendix B.

2.4 Results

2.4.1 Effect of recruitment strategy

We measure the success of a colony by its energy budget at the end of a simulation run. All of the variable parameters in the model (colony organisation, number of food sources and number of ants) have an effect on the energy budget of the colony (Figure 2-1).

We are particularly interested in the effect of colony organisation so pairwise comparisons between monodomous and polydomous colonies in each combination of the other parameters are used.

With the 'no recruitment' behavioural strategy, polydomy is more successful than monodomy in an environment with many small food items (Bootstrap tests, 1000 samples, $P < 0.05$ in all cases where 100 food sources are present). There is no difference between polydomous and monodomous colonies in an environment with few, large food items. These results match those of (Schmolke 2009) qualitatively and are unchanged by varying the colony size (Figure 2-1 A-C). The same result is also found when ants are given individual memory of the location of food sources (Appendix B). Confidence intervals for bootstrap tests are available in Appendix C.

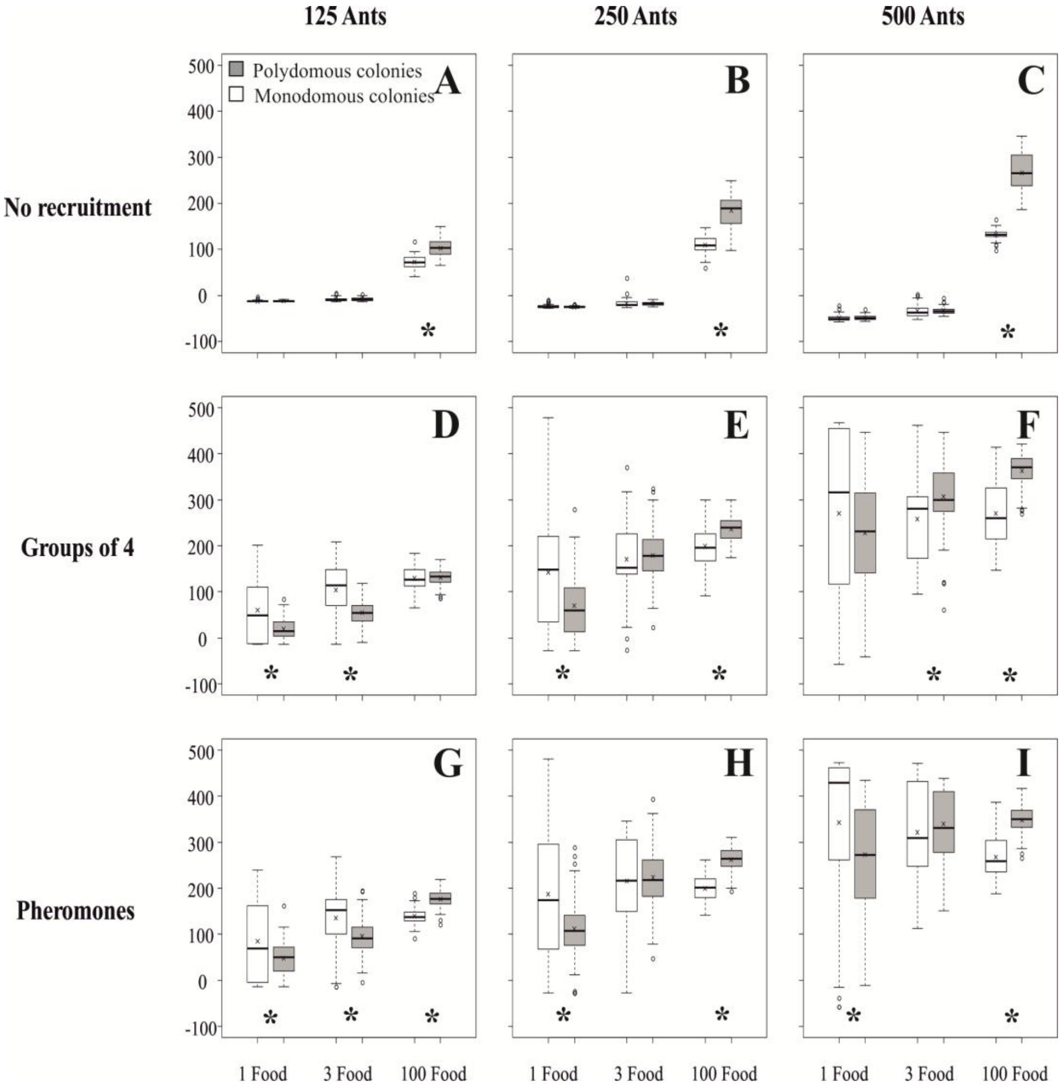

Figure 2-1 The success of colonies under a range of experimental conditions.

In each case the vertical axis shows the colony energy budget at the end of simulation. The results for monodomous and polydomous colonies under each condition are represented as white and grey boxes respectively. Cross symbols (×) indicate the mean, dark horizontal lines represent the median value, the box represents the 1st and 3rd quartiles, and outliers (defined as points lying outside 1.5 times the inter-quartile range) are represented by dots. Where a significant difference between monodomous and polydomous colonies is found (bootstrap tests of difference in mean, 1000 samples, $p<0.05$) this is indicated by a star (*) underneath the pair of boxes

In simulations in which individuals used pheromone recruitment polydomy is more successful than monodomy in an environment with many small food items. When a single, large food item is present polydomy is less successful than monodomy (Bootstrap tests, 1000 samples, $P < 0.05$ in all cases) and when three food items are present monodomy is more successful when colony size is small and not significantly different from polydomy as colony size is increased (Figure 2-1 G-I).

In the case of group recruitment colony size becomes an important factor. Increasing the colony size leads to increases in the relative success of polydomous colonies; there is also an effect of food distribution with monodomy being relatively more successful when food sources are less dispersed (Figure 2-1 D-F).

The results for a colony size of 500 also hold for colonies of double the size over double the foraging area (Appendix B).

2.4.2 Food discovery

The increased success of polydomous colonies in simulations which include no recruitment and have dispersed food sources may be due to the ability of polydomous colonies to locate food sources more quickly than monodomous colonies. To test for this we recorded the first time the colony found a food item during each simulation. Results from all recruitment strategies were pooled for this analysis since during the initial food discovery stage recruitment strategy will not affect behaviour.

Polydomous colonies are faster than monodomous colonies in locating a food source in all cases (Cox proportional-hazards regression. $P < 0.01$ in all comparisons) except when a single food source is available and colony size is 125 ants. In this case there is no significant effect of colony organisation (Cox proportional-hazards regression, $z = -0.498$, d.f = 1, $P = 0.619$). Confidence intervals and the hazard ratio for all tests carried out are available in Appendix C.

2.4.3 Effect of polydomy on group recruitment

During group foraging the time spent by ants waiting in the nest may contribute to the lowered success of polydomous colonies. We recorded the amount of time each foraging group took to form to test for differences in the time spent by ants waiting in the nest.

Polydomous colonies take significantly longer to form groups than monodomous colonies (Bootstrap tests $P < 0.01$ in all comparisons). The same result is found when smaller groups consisting of 2 individuals (tandem running) are used. Confidence intervals for bootstrap tests are available in Appendix C.

2.4.4 Pheromone trail establishment

A polydomous structure may also limit the success of colonies using pheromone recruitment by limiting trail establishment. We recorded the establishment of pheromone trails by the number of ants arriving at a food source in the first 1000 time steps after it had been initially discovered. The previous results show that there is no difference between the food discovery time of monodomous and polydomous colonies of 125 ants when a single food source is available so we use data from these runs to compare trail establishment.

There is co-variation between the time a food source is initially found and the number of arrivals after discovery; this is accounted for in analysis. Monodomous colonies are able to recruit significantly more ants to a food source, especially when a food source is discovered early in a simulation (ANCOVA, $F = 55.289$, d.f. = 162, $p < 0.001$).

2.5 Discussion

Our results show that colony success is affected by the interplay between colony organization and recruitment strategies. In environments where success is determined primarily by the exploitation of large food sources, monodomous colonies can have a higher foraging success than polydomous colonies. The results of our model are supported by lab experiments which suggest that polydomy can have a negative effect on colonies which feed on resources that are clumped (Holway and Case 2001). Previous theoretical considerations of the foraging benefits of polydomy (Hölldobler and Lumsden 1980; Schmolke 2009) however, suggest that polydomy does not decrease the success of colonies under these conditions.

The results highlight a trade-off between the discovery of food items during initial exploration and the exploitation of previously discovered food sources. Polydomous colonies have an advantage when there are a large number of scattered food items due to their ability to find food sources more quickly. However, their relative success is reduced when recruitment is used and when food is clumped. Under these circumstances, the exploitation rate of food sources becomes a limiting factor for polydomous colonies. Monodomous colonies are able to better exploit food sources by having a concentrated population available for recruitment.

Several studies have shown that information about food sources is more valuable in environments in which food is clumped (e.g. Barta and Szép 1992; Dornhaus and Chittka 2004). For example, Dornhaus and Chittka (2004) show in bees that accurate information is more important in environments which have few rich food sources than in environments where food is homogeneous. It has also been shown that the use of public information by colonial birds should be dependent on the distribution of food (Barta and Szép 1992) and that the behaviour of fish in response to food discovery by others can be dependent on food distribution (Ryer and Olla 1995). Our model produces similar results, increasing information use and exploitation (via recruitment and having a monodomous structure) increases success when food is clumped while increasing exploration (via polydomy and large colony size) increases success when food is distributed. We show that the effectiveness of resource discovery and exploitation is affected by colony structure and therefore when considering social systems which are spatially distributed this should also be accounted for.

Hypothetically there can be a cost to sharing information. Time spent inactive while waiting for information from foragers which have discovered food can offset the benefits of the information even when the probability of finding food is increased by the information received (Dechaume-Moncharmont et al. 2005). Our results for group recruitment reflect this cost. Monodomous colonies can be more successful than polydomous colonies of the same size because a larger number of ants are located within a single nest and time spent waiting for information is lower. However, the validity of these results is dependent on the cost of recruitment being the time spent waiting in the nest. There is little data on the behaviour of unsuccessful scouts within a nest however, in experiments with C*amponotus socius*, Hölldobler (1971) reports that most scouts which fail to recruit nestmates will remain in the nest for some time before changing behaviour.

The success of the polydomous colonies in our study is limited by recruitment success. It has been shown both theoretically and experimentally that small populations are less able to establish pheromone trails to food sources (Beekman et al. 2001) and that in small colonies individual foraging is likely to be the most competitive strategy (Planqué et al. 2010). Larger colonies tend to have foraging systems which rely more on mass recruitment (Beckers et al. 1989). Within our model, when the colony is decentralised the number of ants which return to each individual nest is decreased and so, for colonies of the same size, a polydomous colony cannot establish trails as efficiently.

Although we use relatively small colony sizes in this study, increases in forager arrival rate in both monodomous and polydomous colonies show that pheromone trails are established by both types of nest distribution. We also show that the results hold when larger colonies are used in an appropriately larger environment (Appendix B). Additionally, within real polydomous species, a large number of species use pheromones for recruitment to food sources, including species such as *Polyrhachis muelleri* (Liefke et al. 2001) and *Aneuretus simoni* (Jayasuriya and Traniello 1985) (which have a maximum colony size of fewer than 500 individuals (Debout et al. 2007)).

In a comparative analysis of the interaction between the distribution of resources, recruitment mechanism and polydomy, we would expect that polydomy would be common in circumstances where food is highly distributed, regardless of recruitment strategy used and less common in species that primarily exploit larger stable food sources via pheromone trails.

Examples of polydomous colonies which employ pheromone recruitment to exploit a small number of relatively large and stable food sources, include several highly successful, invasive species such as *Linepithema humile* and *Myrmica rubra* (Dreisig 1988) . The success of these species may not be due to benefits derived from polydomy (Holway and Case 2001). Some species may however, be able to overcome the recruitment costs of having a dispersed population. Long range recruitment of ants from several nests to a single large food source has been recorded in several polydomous, pheromone recruiting species (Hölldobler and Wilson 1978; Pfeiffer and Linsenmair 1998; Holway and Case 2000). The results of Holway and Case (Holway and Case 2001) and the presence of this behaviour suggests that the costs of polydomy on recruitment, as shown in this study, exist in real colonies which are much larger than those simulated.

It is also important to consider that there are other potential benefits of polydomy which are not considered in our model including relieving population pressure if nest size is limited (Levings and Traniello. 1981; Stuart 1985), resolving queen-worker conflict (Snyder and Herbers 1991) and spreading the risk of nest predation (Foitzik and Heinze 2001; Dahbi et al. 2008). There are also a number of other possible costs to having a polydomous colony such as the energetic costs of building and maintaining nests and costs involved in recognition of nestmates.

Within our model the movement of ants and also resources between nests is limited; Transfer of energy occurs only when a foraging ant locates a nest which has a positive energy budget. Discovered nests are treated as food items, however no recruitment occurs to nests. Although limited movement is observed in some species (Traniello and Levings 1986), in several other species, workers, food and brood are frequently exchanged between nests (McIver 1991; Holway and Case 2000). This behaviour may help the colony overcome the costs of having a smaller population of ants within each nest relative to a monodomous colony of the same size.

Our model does not incorporate complex or social search strategies, competition between colonies, variation in recruitment effort, or the use of mixed recruitment strategies or varied food types. Future expansion of the model may be able to address some of these complexities.

The inclusion of recruitment in the discussion of polydomy represents a substantial step forward in understanding the costs of polydomy and may explain why monodomy is so common among ant species. While polydomous colonies can benefit in environments where success is determined by the effectiveness of exploration, these benefits can be offset by reductions in recruitment efficiency in some circumstances.

2.6 Acknowledgements

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Chapter 3
The use of network analysis in the study of social insect colonies

3.1 Abstract

Social insect colonies provide an ideal system for the study of biological networks at different scales. Networks can be observed within social insect colonies at scales ranging from interactions between individuals within the colony to trail networks formed between nests and food sources. We review the use of network analysis to address questions about the varying types of networks found within social insect colonies. Network analysis provides tools that can be used to study these complex interactions at all levels. A wide range of network methodologies can be used to analyse the effectiveness of these systems. We address how the data can be collected and represented as networks and also summarise the results of analyses carried out on the networks. We show that networks across all scales of social insect colonies have properties that maximise their efficiency but that the networks also balance trade-offs between properties such as efficiency, robustness and cost successfully. We also summarise results that show how both space and time can have a strong effect on the interactions of individuals and also on larger scale behaviours. We provide suggestions for future studies that may contribute to the understanding of how cooperative behaviour within social insect colonies is organised and suggest how work on social insect systems may provide insight into the construction and use of effective network systems in general.

3.2 Introduction

Network analysis is a powerful tool that is increasingly being used to examine the relationships within social species (Croft et al. 2008). Network analysis allows a wide range of properties of the patterning of interactions between elements in a large system to be addressed using quantitative techniques. Studies of social networks have addressed questions such as the roles of individuals within social groups (Lusseau and Newman 2004), or the effects of social structure on transmission of disease or parasites (Godfrey et al. 2009; Drewe 2010). More recently, network analysis has been used to examine the effectiveness of other structures formed by biological organisms, for example the transportation networks found within fungal and slime mould systems (Nakagaki et al. 2004; Southworth et al. 2005; Bebber et al. 2007; Tero et al. 2010).

A network is a set of nodes which are linked together by edges; network analysis allows the quantitative analysis of the patterns of interactions between these nodes (Wasserman and Faust 1994; Croft et al. 2008). It provides detailed information about the interactions between individual parts of the system and also allows us to look at not only direct links but also the indirect effects of other connections within the system. This places connections between individual parts within the context of the whole system and allows us to understand better the system as a whole. Features of networks that can be quantified include the efficiency of the network, the amount of clustering within a network and the robustness of the network to disruption of either nodes or edges. The comparison of real world biological networks to theoretical networks which are constructed to be optimal in different ways can also allow analysis of the types of constraints that have shaped the networks. A glossary of some terms associated with network analysis is included in Appendix A.

Social insects provide an extreme example of social behaviour; they live in cooperative colonies that may be very large, can carry out complex behaviours such as division of labour and can have complex communication systems. The extreme sociality found within social insect colonies makes them ideal systems for the application of network analysis in order to understand the structure and behaviour of groups of individuals and the effects of interaction structure on behaviour. Social behaviour within the colony can be determined by interactions between individuals which can lead to behaviour that in turn results in the construction of larger scale structures. Behavioural interactions within social insect colonies are particularly interesting since there is no central organisation within a colony and larger scale features of the colony emerge from the interactions of simple, individual behaviours (Hölldobler and Wilson 1990).

Networks can be used to represent different levels of organisation within social insect colonies, from the interactions of individual insects to the large scale networks of trails formed by many individuals as a result of these interactions. As well as allowing the quantification of the interactions within a colony, using a network approach allows studies of these different levels of organisation within the colony to be carried out using similar methods.

In this review we provide a description of the types of networks that have been studied within social insect colonies and discuss how the colony is represented at different levels of abstraction. We show how these networks have been constructed from observation of the colonies and how, once constructed, they can be used to answer a wide range of ecological questions. We also discuss how spatial and temporal effects have been addressed in the analysis of these networks. Throughout, we provide suggestions for additional studies, highlight the benefits of using network analysis, and make suggestions for approaching the associated challenges.

3.3 Types of networks within social insect colonies

Network structures have been observed within social insect colonies at a number of levels. These can be split broadly into (i) networks of interactions between individual insects are and (ii) larger scale network structures that are formed by the colonies. These larger scale networks include trail systems found outside of social insect nests and physical network structures within the nest of a colony. At different scales different parts of the social insect colony are considered as the nodes and edges of the network: the different representations are summarised in Table 3-1.

On a small scale, individual insects are considered as the nodes of the network and the edges in these networks are interactions between the insects in the form of close contact or communication**.** The individual insects within the colony can also be grouped by their behaviour or task within the nest and networks created based on these groups. Within such networks the groups of individuals are represented by the nodes within the network and the transitions of individuals between tasks as edges (Table 3-1).

Species	Network type	Method of identifying connections	Time period of observation	Reference
Linepithema humile	Nests	Manual counting of movement of ants	10 minute observations	(Aron et al. 1990)
Linepithema humile	Nests	Manual observation of composite photos	1 minute for static networks. Recorded for period of 6 hours for formation study	(Latty et al. 2011)
Odontomachus hastatus	Association	Ants within 2cm are associated.	7 days. Repeated 3 times consecutively	(Jeanson 2012)
Camponotus fellah	Association	Angle between ants >70° duration of >1s ants could reach each other	10 or 11 days. Repeated 4 times consecutively	(Mersch et al. 2013)
Pogonomyrmex barbatus	Association	Physical contact between antenna and another ant. Ants within 55 pixels for 0.2 seconds	5 minutes	(Pinter-Wollman et al. 2011)
Temnothorax rugulatus	Association	Antenna to body contact.	30 minutes. Repeated twice 3 weeks apart	(Blonder and Dornhaus 2011)
Pogonomyrmex californicus	Association	Both antennae touch another ant.	26, 52, 78, 104, and 130 seconds	(Waters and Fewell 2012)
Apis melifera	Association	Food transfer between bees (manual observation of video)	1 hour	(Naug 2008)
Bombus impatiens	Association	1cm threshold for contact	12 hours	(Otterstatter and Thomson 2007)
Cubitermes sp.	Chambers	Empty regions and corridors identified automatically	N/A	(Viana et al. 2013)
Messor sancta	Chambers	Branch points identified manually	Static networks recorded after 3 days. Recorded throughout.	(Buhl et al. 2004b)
Cubitermes sp.	Chambers	Empty regions and corridors identified automatically	N/A	(Perna et al. 2008a)
Temnothorax albipennis	Association	Trophalaxis event (manual analysis of video)	30 mins	(Sendova-Franks et al. 2010)
Ropalidia marginata	Association	Manual observation of interaction between two individuals	5 mins repeated 15 times consecutively. Repeated over 16 or 8 days.	(Naug 2009)
Formica aquilonia	Foraging	Visible trails	Recorded over 2 months in Summer for two years	(Buhl et al. 2009)

Table 3-1 Summary of studies of social insects that use a network representation of the colony as and carry out network analysis. The network types represent what entities are represented as nodes. In 'association' networks individual insects are the nodes, in 'nests' networks nests are the nodes, in 'chambers' networks either nest chambers or nest branching locations are the nodes, and in' foraging' networks trails branching points are the nodes.

Social interaction networks that take place within a colony are the most studied networks within social insect colonies and have been applied to a wide range of questions. Issues addressed include pathogen flow through a colony (Otterstatter and Thomson 2007; Naug 2008), food flow through a colony under varying conditions (Sendova-Franks et al. 2010), information flow through a colony (Blonder and Dornhaus 2011), and also investigations of task allocation (Fewell 2003; Naug 2009).

Larger scale structures formed by social insect colonies can also be represented by networks. Many species of ants and termites create nests which consist of a series of tunnels and connected chambers. The nest structure can be represented as a network in which nodes represent either chambers or branching points within the nest and edges represent tunnels (Table 3-1) Outside of the nest, resources such as food, brood, and workers are often transported over longer distances. The foraging trail systems of ant colonies and the systems of trails which are formed between nests in multiple nest (polydomous) ant colonies can be readily observed and represented as networks (Cook et al. 2014). Within these networks, nodes are used to represent nests, food sources or points at which the trail branches. Edges represent the trails that insects use to travel between these features (Table 3-1).

Larger scale networks, in particular trail systems found outside of nests, are similar in structure to human transportation systems such as rail, air travel and road networks. A number of these human systems have been analysed (Latora and Marchiori 2002; Sen et al. 2003; Guimera et al. 2005; Buhl et al. 2006b). Within both social insect colonies and human systems, the success of the system relies on the construction of an efficient transportation network. Analysis of these systems therefore concentrates on determining the quality of the network in terms of the distances over which resources must be transported, the time it takes for resources to flow though the network and the robustness of the network to disruption. The similarity between human and social insect transportation systems allows the results to be compared between systems (e.g. Buhl et al. 2009)

3.4 Constructing network representations

Before any analysis can be carried out, a network representation of the system must be produced. This process starts with the collection of field or experimental data. These data must then be interpreted and converted into a format suitable for network analysis. The variation in the scale of the networks that are observed means that a number of different approaches have been taken, both to the collection of data and to conversion for analysis.

3.4.1 Interaction networks

Within social insect colonies, individuals can communicate by a wide range of mechanisms including close contact. It is these close contact interactions that allow the direct passage of information or food that are the focus of studies of associations between individuals. However, these interactions between individual insects cannot easily be observed in natural colonies where they are hidden within a nest. In a number of studies, the properties of the networks of interactions between individual ants have been by tracking the spread of radioactively labelled food (Markin 1970; Gordon and Mehdiabadi 1999; Feigenbaum and Naug 2010). However, these approaches do not provide information about which individuals interact with which others since individuals are not identifiable. This level of detail is required to allow detailed network analysis to be carried out.

In contrast, in some recent studies highly detailed representations of association networks between individuals within a colony have been constructed (Otterstatter and Thomson 2007; Naug 2008; 2009; Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Jeanson 2012; Waters and Fewell 2012; Mersch et al. 2013). Communication in social insect colonies often takes place via interactions involving close contact between individuals. This allows the network of interactions to be determined from individual-specific marking of ants combined with either close manual observation of the colony (Naug 2008; 2009; Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Waters and Fewell 2012) or identification of interactions automatically by software (Otterstatter and Thomson 2007; Pinter-Wollman et al. 2011; Jeanson 2012; Mersch et al. 2013).

In studies that use automatic tracking, the positions of individual ants or wasps are recorded and this information is used to identify when two individuals meet the criteria given for an interaction. Within all of these studies an assumption is made that there is a direct correlation between the association of two insects in space and an interaction occurring between those two insects. A number of different definitions of a spatial association have been have been used; these are detailed in Table 3-1.

The variation between studies in defining an association between two individuals means that in studies that use automatic tracking of individuals an assessment of whether the associations that are measured relate to a meaningful interaction between individuals is needed. This is particularly relevant when using network representations to address questions about the flow of resources, information, or pathogens where spatial association may not be sufficient for transmission. It is also a key issue to consider if the results of studies are to be compared. In current studies tracking software is parameterised using behaviour observed on video recordings to reduce false positive interactions being recorded to low levels (Otterstatter and Thomson 2007; Pinter-Wollman et al. 2011; Mersch et al. 2013). Pinter-Wollman et al (2011) report low rates of false positive interactions (0.75% and 3.75%) when interactions were checked manually in their study, however this type of information is rarely provided.

The development of new tracking technology that can identify the interactions of a large number of individuals over a long time period opens up many possibilities for testing hypotheses about the social interaction between individuals. In particular, much larger, more natural colonies can be studied than previously and questions of how interactions are variable over time and space can be addressed more easily.

3.4.2 Trail networks

Observation of trail networks formed by ant colonies has been carried out in both laboratory studies and in the field. Within lab studies conditions can be controlled and the networks can be observed more easily. The trail structure can be determined either from counts of ants on trails (Aron et al. 1990) or by observation of composite photos taken of an extended period of time (Latty et al. 2011). There are a number of field studies which record the foraging trail system of ant colonies or the trail system between nests in a polydomous colony (e.g. Holt 1990; Pfeiffer and Linsenmair 1998; Boudjema et al. 2006). Within these studies, the data are often presented graphically without detailed information on how these systems are recorded. We recommend that when presenting trail networks, as a minimum the following information should be given: i) details of how the presence of a trail is decided, for example were a specific threshold number of ants observed on trails within the recording period or were physical trails visible ii) details of the time period over which the network was observed. In addition, observations of the directionality of ants travelling on trails or records of the number of ants travelling on trails would allow more complex analysis to be carried out. The inclusion of such details, even in studies that do not aim analyse trail systems, would improve the usefulness of the data in comparative work.

3.4.3 Nest structure networks

When considering the networks found within the physical structure of social insect colonies, the 3-dimensional structure of the nests adds complexity to the collection of data and construction of network representations. Several studies have used excavation, along with the creation of casts of nests, to allow them to describe the structure of nests (e.g. Wang et al. 1995; Mikheyev and Tschinkel 2004; Tschinkel 2004). However, although these studies could use a network approach to analyse the structure within the nest they do not, instead concentrating on the size, shape and distribution of chambers in the nest. Within studies that address questions related to the network structure of the nest two different methodologies have been used to collect data on the network structure within nests: using 2-dimensional lab colonies and x-ray tomography of natural nests.

Within studies using a 2-dimensional approach, lab colonies of ants or termites are placed into an arena between two sheets and allowed to create a nest which can be observed more easily (Buhl et al. 2004a; Buhl et al. 2004b; Buhl et al. 2006a; Jost et al. 2012). The processing of the data to create networks is carried out manually by visual inspection of the tunnel structure and placement of the nodes by eye. While this method is carried out more easily than extraction of nests from natural environments care must be taken to consider how the shape of the arena used may affect the types of networks that are constructed (Buhl et al. 2006a)**.** An alternative approach is to use X-ray tomography to build a 3-dimensional image of natural nests (Perna et al. 2008a; Perna et al. 2008b; Perna et al. 2008c; Valverde et al. 2009; Viana et al. 2013). This method has been applied solely to termite nests and defines nodes as small empty spaces (chambers) within the nest which are connected by thinner tunnels. Identification of these features is carried out automatically by software and, after this process has been carried out, the resulting network is checked against the visualisation of the nest structure and any mistakes in the structure are corrected manually.

3.4.4 Collection of additional data

During the process of recording the network structure additional useful information about both the nodes and edges can be collected. Measures of the strength of the connection between two nodes and measures the directionality of the interaction between two nodes take place can be incorporated into the network structure. Other information about the nodes of the networks, for example location of interactions or the type of nodes, can also be recorded. This additional information can be used to calculate more detailed properties of the network that take into account this information or to ask more complex questions about the network, for example how the structure of the network is affected by particular types of nodes.

Both trail networks and nest structure networks are inherently spatial and in all studies of these types of networks the spatial position of nodes and edges is recorded. However, additional details about either the edges or nodes are rarely recorded. For example in trail networks, information such as the amount of movement along an edge, the direction of flow, the size of nests, or quality of food sources would greatly increase the range of questions that could be addressed. A study that records these features is found in Cerda et al (1994) in which the number of transports between nests were recorded, as well as the direction of transport, changes in the network over a period of four months, and properties of the nests. This approach allowed the authors to identify the role of the queenright nest, the changes in the network over time and the possible reasons for adult transport between nests in a polydomous colony. We would recommend that future studies of trail networks record the strength and directionality of trails and node properties including, for example, the size of the nests or the amount of foraging the nest performs, to provide insight into how the trail networks created by social insects are used and maintained.

Many studies of association networks between individual insects within a colony record additional information about these interactions. Interactions are often weighted by either the number of times individuals were associated with each other (Otterstatter and Thomson 2007; Pinter-Wollman et al. 2011) or by the length of time individuals spent associated (Otterstatter and Thomson 2007; Naug 2008; Sendova-Franks et al. 2010; Jeanson 2012). Within these networks recording of some level of the strength of a connection is often essential for analysis since it provides definition within association networks in cases where all individuals within a colony are connected to each other (e.g. Otterstatter and Thomson 2007).

The association networks of individuals within a colony are not inherently spatial and many studies of association networks do not consider where interactions take place. However, if information is collected on the location of interactions within the colony this allows additional analysis to be carried out on how spatial properties affect the networks produced. While they are not inherently spatial, most of the recent studies of association networks within social insect colonies record the location where interactions take place; this location may either be a region of the nest or an exact location within the colony. Studies which use automatic tracking of individuals can also track the location of individuals throughout the study allowing analysis of how the movement behaviour of individuals affects the networks produced (Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Jeanson 2012)**.**

Within all types of networks the timing of interactions can also be recorded. In nest structure networks and trail networks, recording video footage during the formation of the network the order of construction of the nodes and tunnels or trails can be identified within experimental nests (Buhl et al. 2006a; Latty et al. 2011). The trail networks of natural colonies are rarely recorded over long periods of time. In association networks the timing of interactions, along with the direction of interaction where recorded (e.g. Naug 2008), can allow the flow of resources or a pathogen to be modelled more accurately

The collection of more detailed data on systems that are represented as networks allows more complex analysis to be carried out on the resulting networks and may allow more detailed behaviours to be studied. The types of additional data that may allow advanced studies to be carried out include: information on edge weight, edge direction, the location of nodes and interactions, the timing of interactions and information on the properties of the nodes. The collection of this type of data should be encouraged in studies at all levels of social insect colonies.

3.5 Answering questions with networks

The methods and types of analysis used to analyse the networks that are observed is dependent on the questions being asked and the types of networks that are being analysed. Here we discuss the main questions that have been asked about the different networks found within social insect colonies and how using a network approach helps to answer these questions.

3.5.1 Are natural networks efficient for flow of information, resources, or pathogens?

Questions about the ability of the network structure to transport information, resources, or pathogens through it are the most asked within the social insect network literature. Analysis of efficiency within a network uses the characteristics of the shortest paths between nodes within a network to determine how effectively things can flow around the network. This could be how information or pathogens are passed to nestmates within an association network or how food is transported from where it is found to where it is needed using a foraging trail network. While the ease of flow through the network is normally referred to as the efficiency of the network although it may be calculated using a variety of measures. The measures used are dependent on the type of network under analysis.

Flow within association networks

When individuals within a colony interact they are able to pass information or resources through the colony. Pathogens may also be passed through the interaction of individuals. Network analysis allows for quantitative measurement of how easily substances can flow throughout a whole network and also to particular individuals within a network. The ability of association networks to transmit different substances through the colony has been measured in a number of ant and wasp species (Naug 2008; Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Waters and Fewell 2012; Mersch et al. 2013). Where the time of interactions has been recorded or colonies have been observed closely the ability of a signal to propagate through the individuals within the colony can be measured directly. This is achieved by introducing a signal to the network representation and examining the nodes that this signal can reach within a specified time period (Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Mersch et al. 2013). Using a different approach, Waters and Fewell (2012) use motif analysis to assess the possible flow through the network. This analysis looks for the presence of particular local, sub-graph structures such as triangles within the network and can be used to infer the efficiency of flow through the network.

The results of these studies suggest that the properties of the association networks are adapted for the flow of information. In particular motif analysis of *Pogonomyrmex californicus* shows that feed forward loops are common, suggesting that the association network structure has been selected for efficiency of information flow throughout the colony (Waters and Fewell 2012). Within association networks of *Temnothorax rugatulus* information is able to propagate quickly locally but spreads more slowly than might be expected over a longer time period (Blonder and Dornhaus 2011) and in *Camponotus fellah* information is potentially able to flow faster to local individuals carrying out the same task than to other groups within the colony (Mersch et al. 2013). Similar results in the honeybee *Apis mellifera* show that pathogens with a short infectious period are contained locally while those with a longer period of infection can infect the entire colony (Naug 2008). This pattern of flow may provide adaptive benefits for the colony. This structure allows rapid information flow locally for control of common, local tasks but has slower global flow that may help to protect the colony somewhat from pathogen infection (Blonder and Dornhaus 2011).

Flow within transportation networks

Both nest structure networks and trail networks are spatially embedded, meaning that the position of the nodes in space plays an important role in their properties. As a consequence, the efficiency of these types of network is calculated in terms of the distances over which resources must be transported and the time it takes for resources to flow though the network. Varying methods are used to determine the efficiency.

Most measures of the efficiency of a network are based on the average path lengths between nodes and in some studies the path lengths within the network have been used directly as a measure of efficiency (Perna et al. 2008a; Perna et al. 2008c). In these cases the path lengths within the network are compared to the path lengths of maximally connected networks and found to be similar. Other studies (Buhl et al. 2004b; Valverde et al. 2009; Cook et al. 2014) use a more slightly complex measure of global efficiency as defined by Latora and Marchiori (2001). This is a standardised version of path length that compares the inverse of the path length in the network to the inverse of the path length in a maximally connected network. In foraging trail networks the speed of transport from a resource location to the nest is the most important factor in measuring efficiency. For this reason Buhl et al (2009) use the measure of 'route factor' to determine the efficiency of transport within the network: this measure is a comparison of the direct distance from the food source to the nest with the distance of the path taken by the trail.

In general, the efficient movement of individuals or resources is one of the main roles of the networks studied and the efficiency is shown to be relatively high. In particular the inter-nest networks of polydomous colonies have a higher efficiency than a minimum spanning tree (MST), in which all nodes are connected with the minimum possible trial distance, due to the presence of extra trails (Cook et al. 2014), and the foraging trail networks of *Formica aquilonia* are close to star graphs, which minimise travel time to resources, in their efficiency (Buhl et al. 2009). Within nest structure networks Perna et al (2008a; 2008c) show that path lengths are close to optimal. In the 2-dimensional nest structure networks of *Messor sancta* the efficiency is higher than a MST and importantly, does not decrease as much as a MST or a maximally connected graph as network size increases (Buhl et al. 2004b).

The maintenance of high efficiency in larger nest tunnel networks may achieved by increasing meshedness in the network. Meshedness is a measure of clustering within a planar network (at network that is embedded in space and in which edges cannot overlap) which compares the number of faces (enclosed spaces) of the network with the maximum number of faces that can be formed without adding any edges that intersect. This measure is particularly useful for spatial networks in which the edges cannot overlap. Increases in meshedness are achieved by the merging of simple networks to produce cycles (closed loops). It has been suggested that this mechanism may also be found in other natural systems to create networks that are highly efficient (Buhl et al. 2004b).

Although most studies of efficiency concentrate on an analysis of the network as a whole, it is also possible to use measures based on edge-level properties to look at how easily substances might travel through a network. For example Viana et al (2013) uses accessibility, a measure of how many nodes can be reached from a particular node within a set number of steps, given a set of movement rules. This analysis shows that within the termite nests studied there are bottlenecks within the network and suggests that the structure is designed to limit the access of predators to the central parts of the nest. The efficiency of flow through a network is clearly a key feature of the networks within social insect colonies. However, there are costs to the colony in creating and maintaining the network and the networks may also have selective pressures acting on them other than the pressure to be efficient for transportation of information or resources. Most studies therefore consider a number of other factors that may affect how effective a network is for its’ purpose.

3.5.2 Is efficiency balanced with other factors?

The most efficient networks for flow are those that connect all nodes to all others directly; however a network with this structure would contain a large number of connections. There is a trade-off between maximising conflicting properties of the network including efficiency of transport, robustness to disruption, and the costs of building and maintaining a network. Even in networks in which efficient transportation is the main purpose there may be disadvantages to creating a highly connected network.

Cost

There are costs to a colony in constructing and maintaining trails and so it might be expected that the total distance of trails within trail networks will be reduced and balanced with the efficiency of transport. In an extreme example, polydomous lab colonies have been shown to create inter-nest networks that minimise the total distance of trails while linking all nests, creating a minimum spanning tree or Steiner tree (Aron et al. 1990; Latty et al. 2011). These results suggest that the cost of trail production and maintenance is the determining factor in network creation. Other studies show that the cost of the network is balanced with efficiency of transport. For example in larger, natural, polydomous colonies, while the total number of trails remains low, having a larger number of trails than the MST increases efficiency significantly (Cook et al. 2014) and in foraging trail networks while networks are closer to Steiner trees in their total length, they are closer to star graphs in their efficiency indicating balance between the two extremes of minimising total length within the network (Steiner tree) and minimising travel time to resources (star graph) (Buhl et al. 2009).

Nest defence

A low number of connections, as well as reducing the cost of the network, may also provide other adaptive benefits. An example is found within nest structure networks of termites: the chambers within these networks have a low average number of connections. It has been hypothesised that the low connectivity within these networks may provide a defence against predators entering the nest (Perna et al. 2008a; Perna et al. 2008c; Valverde et al. 2009). This hypothesis is consistent with the results of analysis of movement through nest networks from Viana et al (2013) showing that accessibility to the centre of the nests is limited by bottleneck regions within the nest.

Robustness

Networks may need to be robust to disruption of either edges or nodes. For example, nests within a polydomous colony nests may need to remain connected to maintain colony cohesion (Cerda et al. 1994), or a nest structure network may need to remain connected to allow insects access to all parts of the nest. Therefore robustness may play a role in determining the adaptive value of the network and so the structure of the networks formed. The robustness of a network often reflects the efficiency of the network and, as mentioned previously, while both the cost of networks and some defensive properties of nests may benefit from a low number of connections within the network, both efficiency and robustness may be decreased in networks with a lower number of edges.

The robustness of a network to disconnections of pathways is considered in several studies and can be quantified in a large number of ways. Perna et al. (2008a) and Cook et al (2014) use the simple measure of the proportion of single edge removals that will create a disconnected network, while Buhl et al. (2004b) use a more complex analysis that assesses the proportion of node removals that are required for the largest remaining component to reach 50% of the size of the original network. In association networks Naug (2008) assessed the effect of removing the five most connected individuals on the properties of flow within the network.

The results of analysis of robustness suggest that the nest structure networks of *M. sancta* are relatively robust to removal of random nodes (Buhl et al. 2004b) while in polydomous colonies the trail structure is also relatively robust to the disruption of trails, being substantially higher than the MST of the network (Cook et al 2014). In association networks the removal of a small proportion of nodes had only a small effect on the flow of a pathogen with a long infectious period (Naug 2008). In this case the trade-off between a network that is robust and efficient and one that is less efficient and less robust is made clear. While a robust network may be beneficial for flow of substances or information around a colony, infections may be harder to control in a robust network where removal of infectious individuals has a small effect (Naug 2008).

3.5.3 How do networks change with environmental conditions?

Most of the studies examining networks within social insects a specific set of conditions. However, we might expect that under different environmental or social conditions the network that is formed would be different. A study by Sendova-Franks et al. (2010) provides a clear example of how a colony's state can affect the interaction of the individuals within it. By creating detailed association networks this study shows that starved *Temnothorax albipennis* colonies are able to increase the rate of food transfer by an order of magnitude by changing their behaviour to become more well-mixed. This allows more workers to both receive and donate food. In contrast Jeanson (2012) demonstrates that the removal of the queen from colonies of *Odontomachus hastatus* does not affect the interactions of workers.

These studies show the effects of different conditions on the network, however there may also be changes in the networks more generally over time. In particular the period over which the network is observed may have an effect on the properties of the network that is observed. The way these issues have been addressed is discussed separately later in this review.

3.5.4 What role do individuals play?

A number of studies have aimed to determine whether certain individuals within a colony have a greater effect on the colony than others. To address this question many of the studies of the association networks within colonies describe the (weighted) degree distribution of the network. This measure indicates whether there are some highly connected individuals, which interact with a large number of different individuals, within the colony or whether connections are shared equally between individuals.

The degree distribution of colonies has been reported as exponential in a number of studies (Naug 2008; Pinter-Wollman et al. 2011; Jeanson 2012) suggesting that a few individuals are highly connected and play a major role in information flow while most have fewer connections. It has been suggested that this variation between individuals can accelerate flow through the networks (Pinter-Wollman et al. 2011).

However in small colonies of *Bombus impatiens*, while the queen has significantly more contacts than workers, the workers do not differ in their degree (Otterstatter and Thomson 2007). There is also disagreement on the longevity of particular roles within the nest; while in *T. rugatulus* highly connected individuals do not remain so over a 3 week period (Blonder and Dornhaus 2011), in *O. hastatus* the most highly connected individuals are persistently so over a 3 week period (Jeanson 2012). The disagreement between these studies may suggest that there are species specific structures or behaviours in the social networks within colonies. However, the differences in the way studies define associations between individuals, differences in colony size and differences in the time scale over which the colonies are recorded may also have large effects (Jeanson 2012).

Other studies have examined the role of individuals in structuring the social networks within a colony by carrying out experiments in which individuals are removed from the colony and the changes within the networks structure have been recorded. For example it has been shown the removal of the queen from colonies of *O. hastatus* does not affect the interactions of workers (Jeanson 2012).

Within larger scale trail networks and within nest structure networks the role of individual nests, food sources or chambers in structuring the networks has not been addressed. For example we might expect that nodes with specific properties might have specific role in the networks. For example large nests within a polydomous colony or chambers within a nest that contain brood might be expected to be better connected to others or be more central in the network (Ellis et al. 2013 submitted). Tools within network analysis allow such questions to be addressed and information of this type may provide more insight into how the networks produced by social insects are constructed and maintained.

3.6 Spatial effects

In trail networks and nest structure networks the spatial location of the nodes is fixed and therefore the spatial location of nodes is normally incorporated into the analysis of the properties of the networks. However, there is one area of study in which the spatial features of the network are considered separately. Within the dendritic (tree-like) foraging networks formed by some species of ants the branching angles found at junctions within the trails are also considered to be important features (Acosta et al. 1993; Jackson et al. 2004; Buhl et al. 2009). The angles that are observed have been shown to be a compromise between the shortest path to return to the nest and the advantages of travelling on a trail (Acosta et al. 1993). It has also been shown that the spatial properties of the branching points can affect the use of trails by individuals by providing information on the directionality of trails and letting individuals identify in which direction the nest is located (Jackson et al. 2004; Gerbier et al. 2008).

In social insect association networks an association between individuals relies on close contact between individuals and so we would expect that the spatial location of individuals will also affect the properties of these networks. This has been shown to be true in a number of studies that have recorded the spatial location of interactions. In colonies of ants interactions within a colony are clustered around the areas where most individuals are found most often (Pinter-Wollman et al. 2011) and individuals found in areas of high population density are likely to have more contacts (Pinter-Wollman et al. 2011; Jeanson 2012). Individuals are also more likely to be socially connected to other individuals that share the same spatial area of the nest and carry out similar tasks (Naug 2008; Mersch et al. 2013).

In a number of species the movement of an individual also affects the number connections it has; individuals that have reduced movement or increased spatial fidelity are more likely to be highly connected to few individuals consistently while those with higher movement levels contact nestmates more evenly (Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Jeanson 2012).

The results of studies that track the spatial position of individuals within a nest suggest that the spatial arrangement of individuals has an effect on the association networks that are constructed. It has been suggested that the link between spatial structure and the network of association within a colony may have adaptive benefits for example by increasing the flow of information to workers carrying out the same task (Blonder and Dornhaus 2011) or slowing the transmission of pathogens to younger workers within the centre of the nest (Naug 2008). However, under stress the spatial associations may be broken down, for example changes in movement behaviour that affect the spatial structure of individuals can affect the flow of food in starved colonies through changes in the association network (Sendova-Franks et al. 2010).

While the spatial behaviour of individuals is shown to affect the structure of association networks in terms of the number of associations within particular areas of the nest, there is little work on how the spatial behaviour may affect other network properties such as the types of substructure found within a network. It is also not clear how much of the structure of association networks is determined by spatial location and spatial behaviours, for example Pinter-Wollman et al. (2011) suggest that individuals do not seek or avoid contact with any particular individuals suggesting that spatial location, rather than individual/group recognition plays the major role in structuring the network. Using manipulated colonies it may be possible to separate the effects of spatial location from the effects of other behaviours and determine how associations between individuals are regulated.

3.7 Network Dynamics

3.7.1 Formation

The transportation networks that are described in most studies are presented as they were recorded at a particular point in time. However, these networks must be formed initially by some process. After formation the transportation networks found within social insect colonies are generally considered to be stable in time and laboratory studies suggest that networks formed between nests in polydomous colonies are stable in the short term (Aron et al. 1990; Latty et al. 2011). Likewise, the structure of nests is generally considered to be stable once the formation of the nest is completed. However, these networks have been shown to be highly efficient and well adapted for their purpose and are constructed by without central control by social groups of simple organisms, so the process by which they are constructed is of interest. The study of how the network grows over time can provide insight into the types of behaviour and feedback that can create these highly efficient spatial networks.

The formation of networks can be observed directly or can be inferred. Within lab studies of both trail networks and gallery networks colonies have been observed over a period of time, from the initial introduction of ants into the arena to the formation of a stable network (Buhl et al. 2004a; Latty et al. 2011; Jost et al. 2012). Although the networks from natural termite nests represent a snapshot of the colonies' structure when they were collected (Perna et al. 2008a; Perna et al. 2008b; Perna et al. 2008c; Valverde et al. 2009; Viana et al. 2013), the processes that occur during the formation of the colony can be inferred from comparisons of colonies collected at different ages.

The mechanism of the formation of nest structure networks within the laboratory has been inferred from studies of the behaviour of insects within the system. The results of laboratory studies of the growth of tunnel networks within lab colonies of ants and termites show that branches within the network are produced at a constant rate over time (Buhl et al. 2004a; Jost et al. 2012) and that networks with similar features can be reproduced by a model that uses simple probabilistic rules (Buhl et al. 2006a). These models provide insight into how a growth processes may produce networks with a balance of optimal properties and may be useful for the study of a number of natural networks. However, one of the remaining challenges is determining how the simple branching rules in these models are related to the behaviour and interactions of the groups of individual insects which produce these tunnels (Buhl et al. 2004a; Buhl et al. 2006a).

These studies suggest that the networks within these nests are stable immediately and can be reproduced from a growth process alone. However, results from both trail networks and termite nest structure networks suggest that the networks within these systems are formed by a process of link minimisation in which lesser used tunnels or trails are abandoned due to lack of reinforcement. This leads to a reduction in the total number of connections within the system over time until the network becomes stable (Perna et al. 2008a; Perna et al. 2008c; Valverde et al. 2009; Latty et al. 2011). This mechanism has also been observed in other natural systems that create efficient networks (Nakagaki et al. 2004; Bebber et al. 2007) and so understanding of this process may be widely applicable.

3.7.2 Changes over time

The timing of interactions within association networks has been recorded in some studies and can be included within network analysis in order to address questions of how networks change over time. Analysis of the flow of information through the network can be carried out using networks that are time-ordered: within this type of analysis information can only flow forwards in time through the network. The results of this type of analysis show that information can flow through a network to a high percentage of ants (89 ± 14%) within the nest within a short time period (Mersch et al. 2013) and over a short time scale can flow faster than expected from a model of random movement but slower than expected over longer time period (Blonder and Dornhaus 2011).

Although a few studies have used networks including time measurements to analyse the flow through networks it is also important to consider the total amount of time the colony was observed for to construct the network representations since this will also have a large effect on the networks that are observed. Association networks within social insect colonies have been constructed using observations over various periods of time, ranging from observation over 26 seconds (Waters and Fewell 2012), observation over 30 minutes (Blonder and Dornhaus 2011), to observation over 41 days (Mersch et al. 2013) (Table 3-1). This disparity in the time period of sampling the network may affect the comparability of networks since we might expect that networks change over time. Over short time periods Waters and Fewell (2012) show that 26 seconds of recording captures interactions for most of individuals and that increasing the sampling period from 26 to 130 seconds has no effect on the motif distributions found within their network. However, over longer periods results are conflicting. Data from Jeanson (2012) suggests that individuals form associations that are persistent over a 3 week period, while data from Blonder and Dornhaus (2011) suggests individual differences in associations do not persist over time. However, these differences may be due to differences in sampling methods, analysis techniques or species specific behaviours and more studies are needed to determine how association networks change in the long term.

On the larger scale, while formation of trail and nest structure networks has been considered, the possibility of the networks changing over time has not been studied. Analysis of the networks has been carried out only on data that is a snapshot of the network (Cook et al. 2014). While the networks may be stable in the short to medium term, over a longer time period there may be changes in network structure. In particular as food distributions and conditions change we would expect that the networks transporting them would respond. Studies which recorded the trail network over a longer period of time are rare and results are conflicting: the foraging trails in one study of *F. aquilonia* changed very little between study years (Buhl et al. 2009), while in a study of the transportation of *Cataglyphis iberica* workers between nests the network changed considerably over several months (Cerda et al. 1994). The conflicting nature of these results is likely to be due to the variation in the species, the types of networks recorded and the amount of detail recorded. This however highlights that there are questions remaining for future work to determine to what extent and in what ways the transportation networks within social insect colonies are flexible over time.

Ideally future studies of both small scale association networks and larger scale networks should address the effects of sampling period on the resulting networks and/or use the time of interactions to analyse the properties of the networks such as flow of information. The use of time-ordered networks in which the system is observed continuously and time of each interaction is recorded allows extensive analysis of the effects of time on the network (reviewed in (Blonder et al. 2012)). While we would recommend the use of these methods where possible, it is also important to note that the time period of sampling should be selected to be appropriate for the questions being asked. For example, since most studies of association networks concentrate on the flow of information, pathogens or resources through a colony, longer time periods for observation may not be necessary.

3.8 Discussion

3.8.1 Future questions

How are networks used?

The foraging trail networks formed by social insect colonies are constructed primarily for the transportation of resources, therefore these networks should allow for studies of how systems that are already constructed are used to distribute resources effectively around a system. Although the structure of the networks has been studied the behaviour of the individuals within these systems has not. The behaviour of individuals on the network will however affect the effectiveness of the system. In particular, the networks of trails between polydomous colonies have striking similarities to human transportation networks such as road or rail networks. However, there are few studies which examine what resources are being transported between nests.

Within nest structure networks it has been suggested that the behaviour of ants within the nest has a large effect on their suitability for transportation through the network and Garnier et al (2009) suggest that all studies of network efficiency should include both the structure of the network and the behaviour that takes place on that network. Viana et al. (2013) are able to link nest structure networks to their use through models of the behaviour of individuals in them. However, in this study the authors use a model of movement of insects through the nest based on random movement. It is unlikely that insects move through the nest at random and these tests could therefore be improved significantly by future studies which incorporate data from studies on how tunnels are utilised by individuals.

Future studies which link the transport of resources to the structure of the network on which they move would allow better understanding of how distributed systems can be utilised effectively.

What are the effects of network structure on behaviour?

While the network structure within association networks has been shown to be determined by the behaviour of individuals (Sendova-Franks et al. 2010; Blonder and Dornhaus 2011; Pinter-Wollman et al. 2011; Jeanson 2012) there is also a feedback since the interactions between individuals have an effect on their other behaviours. There is a large interest in division of labour and the mechanisms of task allocation and within social insect literature (Robinson 1992; Beshers and Fewell 2001; Robinson 2009) and it has been shown that the number of associations individuals have with others in the colony and how the associations are distributed between individuals affects the task performance of the colony as a whole (reviewed in O'Donnell and Bulova 2007). The number of connections an individual has is just one basic property of the association network of the colony and analysis of other properties of the association network may provide clearer insight into how tasks within the colony are determined by the interactions of individuals.

Can networks at different scales be linked?

A related question that remains unexplored is that of how the networks which occur at different scales can be linked together. In particular, as discussed previously, association networks are intimately linked to tasks carried out by ants within the nest. Within a nest associations are more likely to occur between individual insects that are carrying out same task and that are within the same region of nest (Naug 2008; Mersch et al. 2013). However, as highlighted by Fewell (2003) the important links within these networks may be those that are between tasks. Model networks can be constructed in which the tasks within a colony are the nodes of the network and the transition of insects between tasks are the edges. Models of task networks have been used to investigate the possible mechanisms by which division of labour occurs within a colony (Gordon et al. 1992; Pacala et al. 1996; Beshers and Fewell 2001) . There is an important link between these task networks and the association networks that lie underneath them; the strength of the connections between tasks will be determined by the associations of individuals within the colony. Previous task networks have modelled the interaction behaviour of individuals based on simple rules (Gordon et al. 1992; Pacala et al. 1996) however the detailed data that has been collected recently on the association networks within social insect colonies may provide information that can link the small scale behaviour to these larger scale networks of tasks within a colony.

Similar steps could be made to link together association networks with larger scale transportation networks. For example, simple models using probabilistic rules can be used to reproduce the major features of the larger scale networks such as the nest structure networks (e.g. Buhl et al. 2006a). However, in reality these rules are implemented by an interacting set of individuals with their own association network. For example there have been a number of studies of the social rules concerning the digging of tunnels within nests (e.g. Buhl et al. 2004a; Mikheyev and Tschinkel 2004). This work and future studies on the effect of individual interactions on construction behaviour could provide the link between the association networks observed within a colony and the models of tunnel network construction.

Are networks in different species or groups similar?

Another remaining challenge within the analysis of insect social networks is the comparison of networks across levels and across species. There are relatively few studies of each level of organisation and within these studies the species used, the size of colonies, the methods used to construct the networks and the types of analysis carried out all vary significantly. This means that comparison between studies is difficult and it is hard to identify features that may be linked to different factors. For example factors including foraging strategy, reproductive strategy, colony size, environment, pathogen loads and pathogen risk may play a role in the types of association networks that are formed and similar factors may affect both nests structure networks and trail networks. One of the advantages of being able to compare networks across species and across different levels of organisation is that if similar features are found across a number of species this may suggest widely used fundamental. An example of this can be found in studies of the formation of networks in which a similar mechanism has been found in trail networks (Latty et al. 2011) and nest structure networks (Perna et al. 2008c) in social insect colonies and also in the production of fungal networks (Nakagaki et al. 2004; Bebber et al. 2007).

3.8.2 Summary

Network analysis is an ideal tool for studying the complex interactions within social insect colonies and in turn social insect colonies provide an ideal system for the study of biological networks at different levels. Network analysis provides a wide range of methodologies can be used for analysing the effectiveness of the systems found across scales within social insect colonies. It allows study of the behaviour of individuals within complex societies and also can reveal the selective forces that might be acting on the system. Network analysis has shown that many of the networks within social insect colonies have properties which maximise their efficiency. Across the different scales of networks, the colonies are also able to balance trade-offs between properties such as efficiency, robustness and cost with high levels of success. This suggests that interactions between components of a social insect colony are optimised. Other results show how both space and time have effects on the interactions of individuals and may therefore affect colony behaviour. Future studies examining the behaviour of individuals within the networks, studies linking together the networks found at different scales or studies comparing networks across systems may help to answer complex questions about how cooperative behaviour within social insect colonies is organised. In addition future work on social insect systems using the methods of network analysis may be able to provide insight into how network systems in general can be used and constructed effectively. The highly adaptive properties found in social insect networks and the mechanisms for network construction which are found across levels may also have future applications to the design of efficient human systems.

Chapter 4

Robustness and efficiency in ant transportation networks

4.1 Abstract

Efficient and robust transportation networks are key to the effectiveness of many natural systems. In polydomous ant colonies, which consist of two or more spatially separated but socially connected nests, resources must be transported between nests. In this study, we analyse the network structure of the inter-nest trails formed by natural polydomous ant colonies. In contrast to previous laboratory studies, the natural colonies in our study do not form minimum spanning tree networks. Instead the networks contain extra connections, suggesting that in natural colonies, robustness may be an important factor in network construction. Spatial analysis shows that nests are randomly distributed within the colony boundary and we find nests are most likely to connect to their nearest neighbours. However, the network structure is not entirely determined by spatial associations. By showing that the networks do not minimise total trail length and are not determined only by spatial associations, the results suggest that the inter-nest networks produced by ant colonies are influenced by previously unconsidered factors. We show that the transportation networks of polydomous ant colonies balance trail costs with the construction of networks that enable efficient transportation of resources. These networks therefore provide excellent examples of effective biological transport networks which may provide insight into the design and management of transportation systems.

4.2 Introduction

Transportation networks are vital to the success of many human systems. The effectiveness of these systems is of interest; the structures of railway, subway, road and air travel networks have all been analysed (Latora and Marchiori 2002; Sen et al. 2003; Guimera et al. 2005; Buhl et al. 2006b). Features of transportation networks such as cost of construction, efficiency of movement through the network, and robustness of the network to disruption of either the nodes or edges can determine their effectiveness. Many natural systems also rely on efficient transportation networks for their success; examples of such networks include leaf vein networks, subterranean nest structures, and fungal and slime mould networks (Buhl et al. 2004b; Nakagaki et al. 2004; Southworth et al. 2005; Katifori et al. 2010; Tero et al. 2010). Natural transportation networks balance the competing elements of cost, efficiency and robustness successfully without the need for central control over design (Buhl et al. 2004b; Nakagaki et al. 2004; Bebber et al. 2007).

In this study we use transportation networks within social insect colonies as a model system for the study of natural transportation networks. Within many social insect colonies transportation of resources is essential. A large proportion of individuals within a colony can remain within the nest and do not forage for themselves (Robinson et al. 2009) and so rely on an efficient network of foraging trails (Buhl et al. 2009) to transport resources from where they are found to the nest. In many ant species transportation of resources between nests within a colony is also an important behaviour. Over 150 ant species have a colony that is made up of two or more socially connected but spatially separated nests: this is known as polydomy (Debout et al. 2007). Ants may move between nests frequently and sharing of resources such as food and brood can take place between nests (Debout et al. 2007). An example of a polydomous colony is shown in Figure 1-1. The connected nests of a polydomous ant colony can be represented as a transportation network, in which nests (nodes of the network) are connected by trails (edges of the network). A number of field and laboratory studies have mapped the spatial location of the nests within polydomous colonies and the trails that link them (Cherix 1980; Holt 1990; McIver 1991; Andersen and Patel 1994; Cerda et al. 1994; Federle et al. 1998; Pfeiffer and Linsenmair 1998; Dillier and Wehner 2004; Elias et al. 2005; Boudjema et al. 2006; van Wilgenburg and Elgar 2007a; Buczkowski and Bennett 2008; Heller et al. 2008; Latty et al. 2011).

The location of nests within a colony may play an important role in the network structure and the role of particular nests. Many field studies examine the spatial distribution of nests within an ant community (e.g. Herbers 1989; Wiernasz and Cole 1995; Cerdá et al. 2002) and the existence of polydomy within a species has been inferred from observations of aggregated nest distribution within a population

(Debout et al. 2007; Santini et al. 2011). However, few studies have examined the distribution of nests within a single polydomous colony and conflicting results are reported; the distribution of nests has been described as overdispersed (Traniello and Levings 1986), random (Snyder and Herbers 1991) and aggregated (Cerdá et al. 2002). We address this by quantitatively analysing the spatial distribution of nests within eight colonies from six species.

In lab studies polydomous colonies form networks that are close in structure to a minimal spanning tree (MST) or a Steiner tree (Aron et al. 1990; Latty et al. 2011). A Steiner tree is a network in which all nodes are connected with the minimal total distance of edges, these networks may have additional nodes (Steiner points) added to the network to achieve this minimum distance. This means within a Steiner tree trails branch at points away from the nest. A MST connects all nodes and minimises distance without the addition of extra nodes. These two types of networks may therefore be an efficient arrangement for the trail structure within a polydomous ant colony since the amount of trail that needs to be maintained is minimised (Latty et al. 2011). In this study we analyse the structure of the trail network of eight field colonies of polydomous ants from published maps to determine whether they have a similar MST structure. We expect that in large, natural colonies properties of the network other than total distance, such as robustness to trail disruption and the speed of information or resource flow around the colony may also be important factors. To test this we examine the structure of the ant transportation networks.

We address both and the structure of the network across all the nests in the colony and the role of individual nests. We assess the ability of the networks to transport resources quickly to all parts of the colony by calculating the efficiency of the network. We expect that nests will connect to their nearest neighbours and that this feature will affect the structure of the network. To test the effects of nearest neighbour connections we compare the network structure of the polydomous colonies to the structure of spatially embedded networks and random networks. This analysis allows us to identify the extent to which important properties of the networks such as robustness, cost of network construction and transport efficiency are optimised. Comparisons with spatially embedded networks, formed by connection of nests to their nearest neighbours, also allow us to establish to what extent the structure of the networks is determined by spatial associations between nests and how the relative placement of the nests affects structure of the network which links them.

4.3 Methods

4.3.1 Data

A literature search was carried out to identify published maps of polydomous ant colonies in which the location of nests and the trails connecting nests were recorded. An example of a polydomous colony can be seen in Figure 1-1. We define a polydomous colony as a group of nests that are functionally linked by trails and so we included only colonies in which nests were connected in a single component. To allow meaningful network analysis, only maps which recorded colonies with ten or more nests were included. This provided a dataset for this study consisting of eight maps of colonies. These eight colonies are from six ant species from four genera. The number of nests ranges from ten to 117 (Table 4-1). We assume that within all these studies all nests within the colony were recorded and that colonies were correctly identified and do not contain nests of another colony. The ecology of the species varies; a single species is monogynous, five are polygynous; all species within this study carry out some level of both scavenging and honeydew collection. An example of one of the maps used, from Holt (1990), is shown in Figure 4-1.

ImageJ software (Rasband 1997-2012) was used to record the coordinate position of nests. Adjacency matrices (which indicate which nests have connections between them) were created manually for each of the polydomous colonies. There is no information available about the direction or strength of the connections between nests so analysis is carried out on binary networks: trails between nests are recorded only as being present or not. We also create a distance matrix for each network which contains the linear distance between each pair of nests.

Reference	**Species**	**Number of nests**	**Number of trails**
Andersen and Patel (1994)	*Iridomyrmex sanguineus*	13	12
Boudjema *et al.* (2006)	*Formica lugubris*	35	35
Cherix (1980)	*Formica paralugubris*	117	160
Heller *et al.* (2008)	*Linepithema humile*	14	16
Holt (1990)	*Iridomyrmex sanguineus*	28	35
McIver (1991)	*Iridomyrmex sanguineus*	10	10
Pfeiffer and Linsenmair (1998)	*Camponotus gigas*	17	20
van Wilgenburg and Elgar (2007a)	*Iridomyrmex purpureus*	11	11

Table 4-1 Information about data sources used in analysis.

4.3.2 Network analysis

Mantel tests are used to test for correlation between the binary adjacency matrix of the network and the matrix of distances between nests. The results indicate whether connection presence is related to the distance between nests, i.e. whether nests are most likely to be connected to their nearest neighbours.

To test whether the network structure is influenced by preferential connection to nearest neighbours we compare the empirical networks to the networks produced by two null models: random networks and spatially embedded networks. In both of the null models we preserve the overall degree of the colonies and we also preserve the spatial location of the nests within the colonies. The networks created are similar to the empirical networks in that they are undirected and binary. Nodes are not allowed self-connections and can only have a single connection to each other node.

To produce random networks we select a node randomly and add a connection to another randomly chosen node. This process is repeated until the number of connections matches the empirical network. For the spatially embedded networks the placement of connections is based on the distance to other nests. To produce these

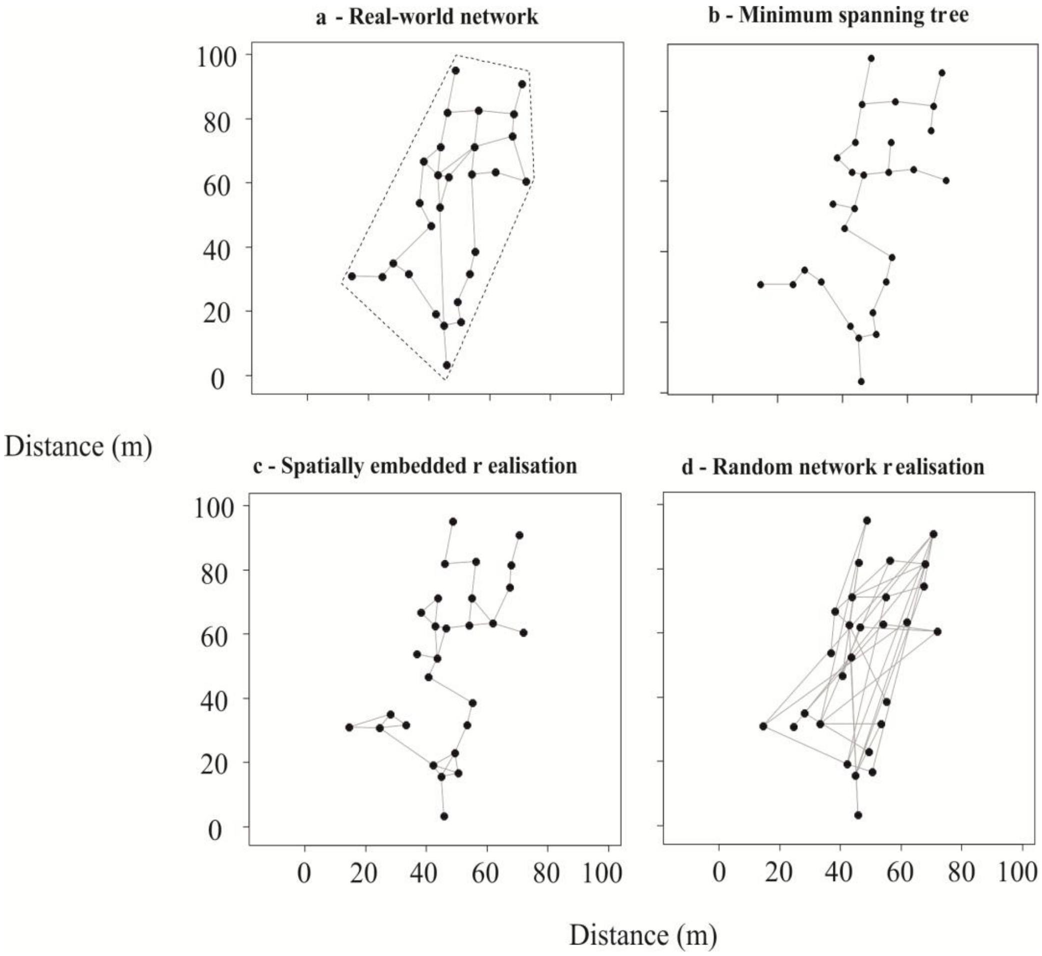

Figure 4-1. Example of an empirical network from Holt (1990) and the corresponding simulated networks. Panel a shows the empirical network and also the Ripley-Rasson estimated boundary used for spatial analysis.

networks a node is selected randomly and a connection is made to the nearest node that is currently unconnected to it. Each node is selected once initially and subsequent nodes are selected randomly. This process is repeated until the number of connections matches the empirical network.

In the empirical networks the nests are connected within a single component, therefore we select only realisations of the null model networks that form a single connected component. In this way we compare networks with the same key features. Two of the networks (Boudjema *et al* (2006) and Cherix (1980), failed to form a single component network in 5000 realisations of the null model networks and so were excluded from analysis of network properties.

We measure features of the networks at both the node level and the whole network level. At the node level, we record the centrality of each node based on two measures: betweenness and closeness. The betweenness of a node is defined as the number of the shortest paths in the network that pass through that node and gives an indication of the importance of the node in linking parts of the network. The closeness of a node is defined as the inverse of the average length of the shortest paths to all the other nodes in the network. Closeness gives an indication of how easily resources flowing through the network can reach the node. These node-based measures of centrality indicate the importance of particular nests to resource flow through the network.

To quantify the number of trails within the networks we calculate the meshedness of the network. Meshedness is defined as the number of faces within the network divided by the number of faces in the maximally connected network that has the highest possible number of edges without those edges intersecting (Buhl et al. 2004b) (for further details see Appendix D). Meshedness gives a value between zero and one which indicates where the network lies in relation to a minimum spanning tree (with a meshedness of zero) and a maximally connected network (with a meshedness value of one). Meshedness values close to zero show a graph is less well connected graph with a structure more similar to a MST. We calculate the robustness of the network by calculating the proportion of single edge removals that result in the network becoming disconnected. The robustness is then one minus this value so that high values of robustness are those that are less likely to become disconnected when an edge is removed. We also calculate the global efficiency of the binary network. Efficiency measures how easily information or resources could pass through the network. Efficiency is, as defined by Latora and Marchiori (2001), a standardised version of the inverse of the average path length, where the average path length is the mean number of trails within all of the shortest paths within the network (for further details see Appendix D). We use the binary path length (number of trails) within our measure of efficiency since loss of resources and changes in ant behaviour will take place at nests; therefore the number of nests resources must pass through is an important characteristic of the network.

These network-level properties give an indication of how easily resources can be transported through the colony. Other standard network measures such as analysis of degree distribution and calculation of clustering coefficients are inappropriate on networks of the size and sparseness of those in this study.

For each network-level measure, we compare the value found in the empirical networks to the distribution of values of the same measures from 1000 realisations of the corresponding null model networks. The empirical network is found to be significantly different from the null model if the empirical value lies outside of 95% of the values from the realisations of the null model. For each of the two measures of node-based centrality measures (betweenness and closeness) we carry out a rank correlation between the centrality value for each node in the empirical network and the mean centrality value of each node from 1000 realisations of the null model. Significant results indicate the centrality of the nodes in the null model is related to the centrality of the nodes in the empirical network.

The MST of the network is calculated using the *spatgraph* package in R. Mantel tests are carried out using the Zt mantel test software (Bonnet and Peer 2002). Network statistics are calculated using the *igraph* package and the *NetworkAnalysis* package in R (Csardi and Nepusz 2006; R Development Core Team 2011).

4.3.3 Spatial analysis

We analyse the point location of the nests within each colony in our study to determine their spatial distribution. To carry out our statistical analysis it is necessary to define the limits of the sampling window. The window for analysis is estimated using the Ripley-Rasson estimator (Ripley and Rasson 1977) which creates an estimated window based on an expansion of the convex hull of the point locations of the nests. An example of this window, for the network from Holt (1990) is shown in figure 4-2.

Within the boundary of the sampling window we test the distribution of points against complete spatial randomness (CSR) using the L-function of the data. The L-function is a transformation of the Ripley's (1976) K-function which characterises the distribution of the points by assessing the average number of points within an area of radius r from a randomly selected point; the function is calculated over a range of values of r. The L-function stabilises variance within this function making it more suitable for analysis. We use Monte Carlo methods (generating multiple simulations of CSR) to construct critical bands for the L-function. If the observed point pattern is random, there is a 5% probability that the observed L-function will fall outside of these bands. Therefore if at any point the L-function of the observed points falls outside the critical bands the spatial pattern is significantly different from CSR. The direction of any deviation from a random distribution (towards randomness or towards aggregation) can be determined from where and in which direction points lie outside the bands.

For further analysis regarding deviations from a random distribution we also use the Kolmogorov-Smirnov test to test the distribution of the points against a Poisson distribution for both the x and y coordinates separately.

All spatial analysis was carried out using the *spatstat* package for R (Baddeley and Turner 2005)

4.4 Results

4.4.1 Network analysis

None of the empirical networks have the same network structure as the MST or the Steiner tree. In all cases the number of connections in the empirical network is higher than found in the MST (see Figure 4-1for example), except for the network from Andersen and Patel (Andersen and Patel 1994) which has the same number of connections. Although the number of edges greater than is found in a MST the networks have low meshedness values (maximum of 0.127) (Table 4-2). This shows that the number of connections within the network is low, being much closer to a MST than to a maximally connected graph. In addition we note that branched trails (which could potentially be equivalent to the formation of Steiner point) are only shown within one of the colony maps (Pfeiffer and Linsenmair 2000) and in this case only two branched trails are shown.

Network	**Meshedness**	**Robustness**	**Mantel tests**		**Betweenness**				**Closeness**			
					Spatial		**Random**		**Spatial**		**Random**	
			R	**p-value**	***ρ***	**p-value**	***ρ***	**p-value**	***ρ***	**p-value**	***ρ***	**p-value**
Andersen and Patel (1994)	0	0	-0.247	**0.020**	0.763	**0.002**	-0.452	0.121	0.731	**0.006**	-0.670	**0.015**
Boudjema *et al.* (2006)	0.016	0.82	-0.344	**0.010**	-	-	-	-	-	-	-	-
Cherix (1980)	0.188	0.86	-0.228	**0.002**	-	-	-	-	-	-	-	-
Heller et al. (2008)	0.130	0.62	-0.272	**0.006**	0.842	**0.000**	0.313	0.275	0.770	**0.001**	-0.011	0.970
Holt (1990)	0.157	0.86	-0.337	**0.002**	0.410	**0.030**	0.163	0.409	0.614	**0.001**	0.164	0.404
McIver (1991)	0.067	0.8	-0.217	0.139	-0.183	0.612	-0.343	0.333	0.006	0.987	0.216	0.549
Pfeiffer and Linsenmair (1998)	0.138	0.75	-0.298	**0.002**	0.654	**0.004**	-0.185	0.478	0.876	**0.000**	-0.369	0.145
van Wilgenburg and Elgar (2007a)	0.059	0.28	-0.281	**0.030**	0.615	**0.044**	-0.343	0.302	0.790	**0.004**	-0.421	0.198

Table 4-2 Robustness of empirical networks, mantel-test results and results of comparisons between the centrality in the empirical networks and realisations of the null model. Robustness is defined as one minus the proportion of single edge removals in the network which result in disconnection. Mantel tests are carried out for each network between the binary adjacency matrix and the distance matrix for all pairs in the network. For the centrality measures of betweenness and closeness, rank correlation is carried out between the centrality value for each node in the empirical network and the mean centrality value of each node from 1000 realisations of the null model indicated (spatial or random). Significant values are shown in bold.

Within the seven networks which contain more edges than the MST the additional edges within the networks lead to increased robustness to disruption of edges. Within a MST removal of any edge results in the network becoming disconnected. Within the empirical networks the proportion of single edge removals which result in a disconnected network is less, ranging from 14% to 72% (Table 4-2).

Mantel tests between the binary adjacency matrix of the network and the distance matrix for all pairs in the network show that the linear distance between nests is related to whether a connection is present in all empirical networks ($p < 0.05$ in all cases) except for the McIver (1991) network in which there is no relationship (Table 4-2). This shows that in general, connections are more likely to be present between nests that are close to each other and that the networks formed do not have a random structure.

Although the nests within the empirical networks do not connect randomly to other nests, the efficiency in the empirical networks is not significantly different from the efficiency in 1000 realisations of random networks in all cases (Table 4-2). The efficiency is significantly higher than in the realisations of the spatially embedded null model in all empirical networks except for the Andersen and Patel (1994) network, in which the efficiency is not significantly different from the spatially embedded null model realisations (Table 4-2). Rank correlation tests of the centrality of nests in null models and in the real-world network show there is no relationship between which nests are most central in realisations of random networks and which nests are central in the empirical network ($p > 0.05$ in all cases) (Table 4-2). There is a significant relationship between the centrality of nests in the empirical networks and the centrality of nests in the realisations of the spatially embedded networks ($p < 0.05$ in all cases) except for in the McIver network (McIver 1991) in which there is no significant relationship (Table 4-2). Nests which are most central within the empirical networks are also most central in the spatially embedded networks, indicating that the nest level properties are strongly affected by the preferential connection to neighbours.

Network	Efficiency				
	Empirical	Spatial 95% CI		Random 95% CI	
Andersen and Patel (1994)	0.395	0.387	0.433	0.380	0.450
Heller et al. (2008)	0.462	0.418	0.460	0.420	0.489
Holt (1990)	0.341	0.281	0.321	0.336	0.383
McIver (1991)	0.495	0.448	0.489	0.465	0.537
Pfeiffer and Linsenmair (1998)	0.422	0.371	0.416	0.394	0.455
van Wilgenburg and Elgar (2007a)	0.493	0.452	0.488	0.442	0.508

Table 4-3. Comparison of efficiency of empirical networks and the 95% confidence intervals of the efficiency for 1000 single component networks formed from null models (spatial and random).

4.4.2 Spatial analysis

The L-function tests show no significant difference from complete spatial randomness in all colonies studied ($p > 0.05$ in all cases). However, we find a significant difference ($p < 0.05$) from a Poisson distribution in the in x-direction for both the Boudjema and Cherix maps. In these two maps the points are more clustered in this axis than would be expected from a random distribution.

4.5 Discussion

Our results clearly show that the colonies in our study form networks that have a topology that would allow efficient transportation of resources and resources. The networks formed are also robust against disruption of edges. The networks we study have a structure that would allow efficient transportation through the colony both locally and globally. Nests are connected to neighbours in a local structure which allows efficient transport of resources or information locally. However, the networks also contain some longer distance connections which bridge the network and increase the efficiency of transportation globally through the entire colony.

In contrast to previous studies of lab colonies (Latty et al. 2011), the networks from the field in this study do not show evidence of forming a minimal spanning tree (MST) or a Steiner tree. Although they have a low number of connections, the field networks, with one exception, have a higher number of connections than a MST and Steiner points are rare. These results indicate that the connection of all nests with the minimum length of trail is not the only driver of trail network structure in these transportation networks. While in lab colonies ants appear to be minimising total trail distance (Latty et al. 2011), in field colonies the larger numbers of ants may be able to maintain trails more easily (Beekman et al. 2001), thus relaxing the constraints placed on the total length of trails within the network. The absence of Steiner points within the network also suggests that a local process such as pairwise interactions between nests is driving the network construction rather than the minimisation of total path length.

Although there is a cost of constructing a larger number of trails, our results show that the robustness of the colony to disruption of trails is increased greatly in comparison to the MST. This may be an important feature of the trail system since in natural situations the nests within a polydomous colony may need to remain connected to each other to maintain cohesion (Dahbi and Lenoir 1998), or for resource flow through all nests (Holway and Case 2000) and disconnection may be disadvantageous.

The presence of extra trails also impacts on the efficiency of the network by providing shorter routes between distant nests. The colonies in our study appear to balance the cost of constructing and maintaining trails with other factors including robustness and efficiency. Similar results have been found in other types of transportation networks found within social insect colonies. For example ant foraging networks (Buhl et al. 2009) balance total trail distance and transportation efficiency effectively, and at a much smaller scale, the network of tunnels between galleries in termite nests have path lengths that are close to optimal length for efficient transportation (Perna et al. 2008c). Although there are differences between these networks in terms of their function and scale the similarity in results suggests that social insect colonies are highly successful in creating structures that are optimised for transportation.

Although the total length of trails is not minimised over the whole network, there is a relationship between the presence of a connection and the distance between two nests. Nests are more likely to be connected to the nests that are their nearest neighbours, forming networks which have spatial properties. Many other transportation networks are spatially embedded (Boccaletti et al. 2006; Gastner and Newman 2006a; b). Shorter trails may be favoured since long trails are harder for colonies to maintain (Beekman et al. 2001; Cook et al. 2013) and moving outside of the nest also carries a predation risk. Although it is unsurprising to find spatial effects in our study, this spatial association of nests does not explain all the features of the networks studied.

When we compare the properties of the network to realisations of spatially embedded networks we find that the empirical networks have higher efficiency than expected due to spatial embedding alone. The combination of local connections with some longer connections and increases the efficiency of the networks. This phenomenon within our data is illustrated in Figure 4-1; the empirical network shows a number of long-distance connections that are not present in the spatially embedded network, and that increase efficiency by decreasing average path length. Polydomous colonies may benefit from this efficiency within their network, as the number of nests that resources flowing through the network must pass through is reduced. This may allow resources to travel further through the network by reducing losses as they pass through nests.

Although spatiality does not explain all of the network features, connections are most likely between neighbouring nests, so the spatial distribution of the nests may play an important role in how the trail network is structured. The spatial distribution of nests within polydomous colonies has been described as overdispersed (Traniello and Levings 1986), aggregated (Cerdá et al. 2002) and random (Snyder and Herbers 1991) in previous studies of single colonies. In our study of eight polydomous colonies, we find a random spatial structure in all colonies. The clustering shown in the x-direction in two colonies can be explained by features of the landscape. Both are *Formica rufa* group species which are reliant on foraging in trees. In Cherix (1980) the wooded areas are distributed unevenly across the mapped area and nests are found mostly within the wooded areas, while in Boudjema et al (2006) nests are associated with a woodland edge shown on the map. To maximise foraging efficiency, the nests of polydomous colonies might be expected to have an overdispersed distribution within their colony boundary. However, sharing of food between nests and lack of competition between nests may lead to distributions which are different to those predicted for competing nests. A large number of factors may affect nest placement, for example microclimate (Heller and Gordon 2006), the placement of food (Holway and Case 2000; van Wilgenburg and Elgar 2007a), and nest site availability (Herbers 1986). These factors may, in combination, lead to the observed pattern within a colony being indistinguishable from random.

Due to the preferential formation of connections to nearby nests, other properties of the colony trail networks are affected by the spatial location of nests. In particular we show that nests that are most central in the empirical networks are the ones that are most central in corresponding spatially embedded networks. This suggests that which nests have high levels of control over flow through the network (high betweenness) or are most easily reached by resources (high closeness) is determined mostly by the spatial location of the nests within the colony. Thus the position of nests relative to other nests could be a significant factor in determining the importance of a nest within the colony network.

We have shown that the spatial positioning of nests has an effect on the construction of the network and on the centrality of the nests; however there are a number of other factors that could influence the transportation network that is formed. In particular the presence of queens within a nest may affect the amount of transport to and from a nest. In this study only a single colony (Pfeiffer and Linsenmair 1998) is monogynous, the remaining five have multiple queens within the colony and these queens are likely to be spread throughout the colony. In their study Pfeiffer and Linsenmair show that the nest in which the queen is located has an effect on the number of ants visiting the nest, however it does not appear to have an impact on the structure of the network as a whole. The size of the colony may also affect the structure of the network. This could be in terms of the number of nests, the number of individuals within nests or the distances between nests. On a smaller scale within 2-dimesional nests ants are able to maintain high efficiency as colony size is increased (Buhl et al. 2004b). It would be interesting to examine whether this is the case in larger scale natural transportation networks such as those in this study.

The data used in this study give only a snapshot of the trail system. However, the mechanisms by which efficient natural networks, such as those found in these polydomous colonies, develop without centralised control over the design have been investigated in several systems (e.g. Nakagaki et al. 2004; Bebber et al. 2007; Latty et al. 2011). Studies of biological systems show the creation of complex and efficient networks by overproduction of connections, followed by a pruning process (Nakagaki et al. 2004; Bebber et al. 2007). This process has also been reported for the establishment of inter-nest trails in polydomous ant colonies in lab experiments (Latty et al. 2011). A similar process may occur in some natural polydomous colonies when trails are re-established after overwintering. However colonies may also have memory of where trails have been previously established. An existing network will also be modified as new nests are established. New nests in polydomous colonies have been shown to establish close to food sources (Holway and Case 2000; van Wilgenburg and Elgar 2007a), where it is likely that foraging trails already exist. The use of existing foraging trails to move to and from newly established nests may lead to the local connections shown in the inter-nest networks.

By analysing several colonies across a range of species we show that the inter-nest networks of polydomous ant colonies have properties that make them both locally and globally efficient for the transportation of resources. Further study on the formation of these biological networks and on the way they function may provide insight into designing and managing effective human transportation systems.

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Chapter 5

Mechanisms for the construction of transportation networks in polydomous ant colonies

5.1 Abstract

Natural transportation systems have been shown to be highly effective for the transportation of resources, yet the mechanisms behind their distributed, self-organised, construction are not well understood. An example of one of these natural transportation systems is found in the trail system found between the nests of polydomous (multiple nest) ant colonies. Previous work suggests that these trail systems may be formed and maintained by the treatment of nests as food sources by foragers. This process could also be carried out by separate classes of ants. With a division of labour between ants known as transporters that carry out only transportation between nests and other foraging ants. In this study we use simulation to determine if these simple mechanisms can replicate the transportation network structure in four polydomous colonies. The results show that adding simple recruitment behaviours to the model does not allow colonies to consistently connect all of the nests in the colony with a low number of edges. This suggests that either more complex behaviours are carried out by ants to allow all of the nests within the colony to connect with a low number of edges or that other factors such as historical connections play a fundamental role in structuring the trail systems. We discuss the possible role of different mechanisms and also suggest several areas for future study.

5.2 Introduction

Linking together hubs of information or resources in a way that is both efficient and cost effective is important for many human activities. Road and rail systems have been designed and constructed in a way that makes them efficient for transportation around the system (Latora and Marchiori 2002; Sen et al. 2003; Guimera et al. 2005; Buhl et al. 2006b). In natural systems, efficient transportation systems are equally as important, for example when providing links between different parts of an organism. These natural networks are often formed without central control but have been shown to be able to balance competing pressures such as efficiency, robustness to disruption, and cheapness of construction with high levels of success (Buhl et al. 2004b; Nakagaki et al. 2004; Bebber et al. 2007). A particularly clear example of a natural transportation system is provided by the trail systems of social insects.

Within a social insect colony, many individuals do not leave the nest to forage and so the success of colonies is reliant on the transportation of resources from where they are found to the nest. Many ant species recruit to food sources resulting in the formation of trails leading to and from food sources and nests. In some cases the trail systems of ants may also link a number of nests. Over 166 ant species form polydomous colonies, in which the colony is distributed across two or more spatially distinct nests (Debout et al. 2007). The nests are socially connected and a system of trails may be formed between nests along which individuals can move and transport resources including food and brood.

The trail system found in polydomous ant colonies can be represented as a network in which the nests of the colony are represented by the nodes and the trails are represented by the edges (Cook et al. 2014). By representing systems as a network, a range of statistical analyses of their properties can be carried out (Croft et al. 2008). Within laboratory colonies, ants appear to connect all nests in the colony with the minimum total distance of trails possible (Aron et al. 1990; Latty et al. 2011). However, natural colonies contain a small number of extra connections that increase robustness and allow the networks to be highly efficient for the transportation of resources across the whole colony (Cook et al. 2014).

The behaviours performed by the ants to form the trail networks are not well understood. One suggested mechanism of food redistribution between nests in a polydomous colony is the treatment of nests as food sources by foragers (McIver 1991). This is the simplest case since it does not require any complex behaviour or memory of nest locations. Other studies suggest that there is a specific class of ants that only carry out transportation between nests. This behaviour has been described in several species including *Camponotus gigas* (Pfeiffer and Linsenmair 1998), *Iridomyrmex purpureus* (van Wilgenburg and Elgar 2007a) and others (McIver 1991; Lanan et al. 2011). These studies suggest that food is collected locally by foragers and subsequently moved to neighbouring nests along trails by the transporter class of ants. Food-collecting ants are shown to have high fidelity to one nest whereas transporting ants move between nests readily (McIver 1991). In *C. gigas*, there is also some level of worker polymorphism related to these classes of ants. The ants that carry out transport are also physically different to ants that carry out foraging. In this species transporter ants are larger and can carry up to five times as much as foraging ants, meaning that transport between nests is more efficient and resources can be transported quickly to where they are needed (Pfeiffer and Linsenmair 1998).

In this study we aim to determine, through simulation, whether simple behavioural rules can form a network structure that replicates the structure observed in natural colonies. We start with a simple mechanism of transport in which all foraging ants treat nests as food sources and recruit others to them using pheromone trails. We also carry out simulations in which the foragers are modified so that a class of ants that only carries out transporting behaviour between nests is added to the model.

For comparison to empirical data, we use the network structure of four colonies taken from maps within published studies. The properties of the networks produced by simulation are compared to these networks allowing us to determine which behaviours are mostly likely to be carried out by ant colonies in producing the transportation networks. In particular we analyse whether a transporter class of ants that carry out different behaviours to foragers is needed to reproduce the features of the natural networks, and explore the role of route fidelity in constructing the networks.

5.3 Model description

We use an agent-based model based on a model used in previous work (Schmolke 2009; Cook et al. 2013). More details of the model are discussed in the Introduction and in Chapter 2. Within the model, ants are represented by individual agents within a two-dimensional continuous space and time passes in discrete steps. In each time step the behaviour of all ants is updated. Ants are selected in a random order for updating. In each time step, ants perform one of several behaviours; the behaviours involve either travelling through the environment (searching or returning home) or exchanging energy with food sources (feeding) or nests (nest exchange). Stochasticity is introduced into the model by using random numbers as part of the processes which determine when an ant switches from one behaviour to another.

5.3.1 Initial forager recruitment model

Ants are initially located within their home nest and leave the nest to search for food. Fifty foraging ants are associated with each nest within a colony. Ants search using a correlated random walk which depletes their energy budget. While searching the ants have a probability of returning home based on their energy levels. This prevents ants from searching for an unlimited period. On discovering a food source ants will add to their energy budget from the food source and return home after a period of time determined by their energy. During the return home behaviour, ants that have discovered a food source will deposit pheromones in every time step. These pheromones can be detected by ants carrying out the searching behaviour and searching ants will move towards the area of highest pheromone concentration. Pheromones decay over time meaning for trails to persist they must be reinforced. Once the ants have returned to the nest they exchange energy with the nest to reset their energy budget to zero. This may involve removing or adding to the nest energy budget dependent on the ant’s energy. All model parameters for the movement of ants and the behaviour of pheromones are shown in Chapter 2 (Table 2-1).

We modify the model used in previous work by adding route fidelity into the forager recruitment model. In nature, ants that exhibit route fidelity travel along the same trails repeatedly, allowing them to revisit successful foraging locations. This behaviour has been demonstrated in a range of ant species (Cherix and Maddalena-Feller 1987; Beverly et al. 2009; Tanner 2009). To achieve route fidelity in our model, ants which have visited a food source or nest site and collected food will subsequently leave the nest in the direction of that food source. This increases the likelihood of them following a trail to that food source since ants only detect pheromones in the direction they are facing. Ants only use route fidelity on leaving the nest and subsequently will follow any pheromone trails they encounter.

To allow sharing of food between nests and the establishment of a trail system, the forager recruitment model is also modified to include recruitment behaviour between nests. Ants which arrive at a nest that is not their home nest and has a positive energy budget will, after carrying out feeding, return home and lay a pheromone trail.

5.3.2 Transporter model

The forager recruitment model described above aims to replicate a method of food sharing as proposed by McIver (1991) in which foraging ants treat nests in an identical way to food sources. In this model a single class of ants exists that carries out movement both between a nest and a food source and also between nests within the colony. An alternative method of food-sharing is tested in the transporter model. In the transporter model the ants within each colony are split into a transporter class of ants specialising in movement of resources between nests and a forager class of ants specialising in transport of resources from food sources to their home nest. The transporter class of ants will ignore any food sources that they discover and the behaviour of the forager class is also modified so that the forager class of ants will ignore any nests they discover. While either class of ants can follow a pheromone trail to a nest or food source, trails to nests will only be reinforced by transporters and trails to food sources will only be reinforced by foragers. By using this method we create a model that includes a transporter class of ants using a very simple mechanism.

5.3.3 Empirical data

To determine whether the simulated behaviours replicate transportation networks in real colonies we compare the networks produced by the simulation to the networks found in real colonies. To select empirical colonies to use for comparison to the model a literature search was carried out to identify published maps of polydomous ant colonies. Maps were only considered if they recorded the location of nests within the colony, the location of at least one food source used by the colony and the trails that connect the nests. In addition, to allow meaningful network analysis, only maps which recorded colonies with ten or more nests were included. This search provided a dataset for this study consisting of four maps of colonies. The four colonies used are from three different species and range in size from ten nests to 28 nests (Table 5-1). In all cases the spatial distribution of the nests is not significantly different from random (Cook et al. 2014). Each of the four colonies was used for testing each of the behaviours. ImageJ software was used to scale the images of the colonies and record the coordinate position of nests in meters from the edge of the image.

Species	Colony name	Number of nests	Number of trails	Number of food sources	Reference
Linepithema humile	L. hum	14	16	1	Heller *et al.* (2008)
Iridomyrmex sanguineus	I. sang A	28	35	3	Holt (1990)
Iridomyrmex sanguineus	I. sang B	10	10	3	McIver (1991)
Iridomyrmex purpureus	I. purp	11	11	4	van Wilgenburg and Elgar (2007a)

Table 5-1. Information about colonies used in simulations

To convert the empirical maps into a suitable format for modelling, several additional steps are taken. Firstly the size of the colony is scaled to fit the whole colony into 1000x1000 unit arena; this allows the model to produce useful output in a reasonable time. The movement speed of the ants is also scaled accordingly. A speed which represents 20mm per second is used for all of the nest layouts. All the species in empirical colonies forage at least in part on honeydew producing homopterans in food sources in the maps represent the locations of these sources in all maps apart from in the *L. hum* colony where a bait was provided. Therefore, in our simulations we assume that food sources are stable and are large enough to be available for the whole simulation. The location of the food sources in the map of the colony are used for food sources in the model. To test the effect of food distribution we also run simulations with four food items located randomly within the 1000x1000 arena rather than at the locations shown within the maps.

5.3.4 Sensitivity analysis and testing additional behaviours

In addition to testing the effect of adding transporter class of ants to the basic model also carry out a sensitivity analysis to test the effects of changing some of the

Name of modified model	Behaviour in forager recruitment model	Behaviour in modified model
Transporters	All foragers visit both nests and food sources	Half of foraging population ignores food sources. Half of foraging population ignores nests.
Double colony size	50 foragers per nest	100 foragers per nest
Lower proportion foraging	200 ants remain within each nest and use energy	400 ants that remain within nests and use energy
Foraging further	Foragers search unsuccessfully for 460 steps on average	Foragers search unsuccessfully for 610 steps on average
Small foods	Food sources located as marked on maps	20 small food sources (with 5 units of energy each) are added to the environment every 500 time steps in addition to including the food sources marked on the maps
Random foods	Food sources located as marked on maps	Four food sources located randomly in the environment
Stronger route fidelity	Foragers follow pheromones at all times when searching	All foragers ignore pheromones in the first 5 time steps when searching
Recruit to all nests	Foragers leave pheromone trails only to nests with positive energy budgets	Foragers leave pheromone trails to all discovered nests regardless of energy status

Table 5-2. Summary of the modified models and the changes made to the forager recruitment model the create these models.

parameters within the model. A summary of the simulations carried out is shown in Table 5-2.

The number of ants and the number of foragers within the mapped colonies is unknown and so we run simulations in which the size of the colony is doubled to have 100 foragers. We also test the effect of changing the proportion of the colony that forages, by doubling the amount ants that remain within the nest and use energy. To test the effects of ant foraging distance within the model we run simulations in which the time that an ant forages for unsuccessfully before returning to the nest is increased from an average of 460 steps in the forager recruitment model to an average of 610 steps in the foraging further model.

Previous studies have shown that the distribution of food within the environment can affect the success of polydomous colonies (Cook et al. 2014). Although the maps we use have stable food items marked and these are used for the main simulations we know that the species in these colonies also carry out some level of scavenging. We investigate the effect of small food items on the results by running simulations in which small random food sources are added periodically to the environment. It is also possible that the stable food sources move between years or are not recorded accurately for all colonies and so we run simulations in which four large, stable food items are placed randomly within the environment.

Within our forager recruitment model we also assume that ants always follow pheromone trials that they encounter. This means that the amount of information gained from route fidelity is limited by the tendency of ants to follow strong pheromone trails close to the nest. To eliminate the effect of this we modify the behaviour of ants so that they ignore pheromones for the first 5 steps after leaving the nest. This behaviour makes the ants more reliant on route fidelity for information about the location of food sources. This represents a situation where, for example pheromone levels around a nest are very high meaning that an ant's detection levels are saturated, and instead it uses memory initially for direction.

In the forager recruitment model, ants do not lay a pheromone trail if they encounter a nest that has a negative energy budget. Although nests with a negative energy budget can occur in our model, in real colonies it is unlikely that nests enter a state where they have no food reserves for long periods. It is also possible that resources other than food may be transported between nests. To test the effect of recruitment to nests for purposes other than food transportation we modify the behaviour of ants so that foragers recruit nestmates to all nests, not only those that have a positive energy budget.

5.4 Analysis

The output of the model is a weighted and directed association matrix, in which the element *(i, j)* of the matrix represents the number of ants travelling from nest *i* to nest *j* within a specified period. This matrix represents the network of the trails between nests. The properties of these networks can be calculated and analysed.

5.4.1 Effects of time and duration of sampling, and edge thresholding

The aim of this work is to compare the model output to the networks constructed by real colonies. Although the output of the model includes details of weight and direction of ant movement, the available data on real colonies are binary networks (edges are recorded as present or not) that are a snapshot of the trail system of the colony at a particular time. To compare between the model output and the real data, the types of data must be similar and so the simulation output must, like the field data, be sampled to create binary networks from a specific time. The networks must also be dichotomised to create networks in which connections are either present or not. This is done by removing all connections with a weight below a threshold and setting all the remaining edge weights to one. Before carrying out sampling of the output of the model I made an assessment of the effect of different sampling procedures on the results.

We use the results from five replicates of the initial forager recruitment model to assess the effect of both sampling time and aggregation of networks (length of time for data collection) on the network created by the model. This model was run for a total of 100,000 time steps with an association matrix being created for the movement between nests every 100 time steps.

Time of sampling

The properties of the network were calculated for each 100 time step network over time and changes in these values were assessed. Plots of the network properties over time show that there are some changes over time. Firstly there is an initial period of instability, during which the number of connections initially increases. After a period of around 1000 time steps the properties of the networks are fairly stable. This pattern of stability is consistent across the different network measures and across the nest layouts used; therefore we use the movement from a time period leading up to 30000 time steps in our sampling. Plots of the changes in the number of edges in the networks produced by a simulation of the *I. sang* B colony are included Appendix E.

Duration of sampling

The length of the time window used for observation also has an effect on the network parameters since collecting movement data over a longer period increases the probability of observing a movement between nests within the sample. As the time window of observation is increased, the number of connections within the network increases and that data is smoothed. Although the data is smoothed, detailed changes in the number of edges over time can still be observed when the time window for sampling is increased to 1000 time steps (Appendix E). For this reason we use networks created from movement over 500 time steps.

Edge thresholding

To test the effect of the value of the threshold used for dichotomising the networks we tested how the mean value of network measures from 50 simulations changes as the threshold was increased from zero to one hundred. Plots of the number of edges against the threshold value show a steep decrease in the number of edges at low thresholds with a decreasing effect as the threshold is increased further (Appendix E). The plots also show that at low thresholds the number of trails within the simulated networks is above the number found in the real world maps. However, the number of edges in the simulated networks drops below the number in the real world networks with only a small increase in threshold (Appendix E). The number of edges within the network is an important biological property and so for further comparison we use a range of thresholds. We choose to use thresholds of zero, two and four as these thresholds give networks that are variable in the number of edges within them.

The number of trails within the network and the number of connected components within the network are key features and so I concentrate on these during this analysis. The number of edges in the network determines the cost to the colony of constructing and maintaining the trail system. The number of edges also has a large effect on other properties of the network such as the robustness to disruption of edges and the efficiency of transportation through the network. The number of connected components within the network is an important biological property since networks may need to remain connected for both sharing of resources and cohesion of the colony.

In summary, the initial analysis of the effect of sampling time and sampling period allowed me to select an appropriate sampling regime for the simulation output. It also allowed me to select an appropriate threshold to convert the networks into a binary form. As a result of the analysis we choose to use networks formed from the movement of ants for the 500 time steps leading up to 30000 time steps. This was chosen as the properties of the network were relatively stable during this time period and an aggregation of 500 time steps retains the detail within the network. By selecting a relatively low total run time and a mid-level aggregation time we were also able to record enough detail in the networks while having a reasonably short run time for the model even for larger colonies.

5.4.2 Similarity to empirical networks

To determine whether the simulations replicated the networks found in the maps of field colonies we compare the properties of the networks produced by the simulations to the properties of the empirical networks. We compare the number of edges within the networks and also calculate the proportion of times that a network was produced that was connected in a single component. For each of the simulated behaviours I calculated the mean and standard deviation of the number of edges for 50 replicates of the simulation.

The values from the 50 simulation runs were compared to the values in the empirical networks the using Wilcoxon tests. To determine if the there was a difference in the number of edges in different simulations Kruskal-Wallis tests were carried out for each map of nests. Within these tests each simulation was a treated as a group. The Kruskal-Wallis tests were followed by post-hoc tests based on Tukeys HSD to determine which pairs of simulations differed.

All analysis was carried out using R statistical software (R Development Core Team 2011). Post-hoc tests were carried out on Kruskal-Wallis tests using the *kruskalmc* function from the R package *pgirmess*.

5.5 Results

5.5.1 Forager recruitment model

We first investigate whether a simulation of a simple behaviour in which foraging ants recruit to discovered nests by laying a pheromone trail can reproduce the networks found in real colonies.

When we consider all of the movement of ants between nests and do not apply a threshold to the model the simulated colonies produce networks with significantly more edges than are found in the empirical networks in all of the four colonies tested ($p < 0.01$ for all comparisons. Wilcoxon tests). (Table 5-4). This shows that the connections produced by the natural colonies are arranged in a way that is more effective at connecting all the nests than the networks produced by the simulations.

The simulated colonies create single component networks with varying levels of success (Table 5-3) Simulations using the *I. purp* colony are most likely to form a single component network (48% of networks), while the simulations using the largest map (Holt 1990) very rarely produce networks in which all of the nests are connected in a single component (4% of networks).

When we apply a threshold to the edges, and therefore consider only stronger edges, the number of edges within the networks decreases. In three of the four nest layouts the number of edges drops to a value significantly below the empirical networks when only edges with more than one ant moving on them are considered (threshold of one) ($p < 0.01$ Wilcoxon test). Simulations using the *I. purp* colony continue to produce networks that have a significantly higher number of edges than the empirical networks when a threshold of one is applied ($p < 0.01$ Wilcoxon test). However, the number of edges drops to significantly fewer than the empirical networks if a higher threshold is applied ($p < 0.01$ Wilcoxon test).

In all of the networks, the decrease in the number of edges as the threshold is increased is accompanied by a large decrease in the proportion of simulations that produce single component networks. This suggests that in these simulations using the forager recruitment model, the number of ants travelling between most of the pairs of nests is low.

The results show that the forager recruitment model is unable to consistently create networks similar to in the real colonies. The networks produced by the model either do not connect all nests in the colony or have a significantly higher number of edges than in the networks produced by real colonies.

5.5.2 Transporter model

The addition of a simple transporter class to the model has an inconsistent effect on the networks that are produced by the simulated colonies.

In simulations of the *L. hum* and *I. sang* B colonies the mean number of edges within the networks produced is increased significantly when a transporter class is added to the model ($p < 0.05$ post-hoc test on KW). Within these networks, once a transporter class is introduced to the model the simulation always forms a network in which all the nests are connected.

	Original Model			**Model With Transporters**		
Map	Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4
L. hum	0.36	0.00	0.00	1.00	0.90	0.30
I. sang A	0.04	0.00	0.00	0.00	0.00	0.00
I. sang B	0.46	0.04	0.00	1.00	0.72	0.08
I. purp	0.48	0.22	0.06	0.68	0.04	0.00

Table 5-3 Proportion of 50 simulated networks that formed a single component connecting all nests within the colony.

Map	**Real Network**	**Original Model**			**Model With Transporters**		
		Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4
L. hum	16	20.34 (3.27)	13.06 (2.123)	10.76 (1.53)	30.98 (3.27)	18.24 (2.12)	14.06 (1.53)
I. sang A	35	37.52 (6.42)	22.88 (5.22)	18.22 (4.85)	36.88 (6.42)	19.66 (5.23)	14.46 (4.85)
I. sang B	10	16.14 (1.74)	9.78 (1.34)	7.12 (1.19)	26.42 (1.74)	13.32 (1.34)	7.42 (1.19)
I. purp	11	18.84 (3.78)	12.64 (3.03)	10.42 (1.92)	21.56 (3.78)	11.96 (3.03)	9.2 (1.92)

Table 5-4 Mean number of edges in 50 simulated networks. Numbers in brackets show standard deviation

The increase in the number of connected networks in these two maps may be due to the increase in the number of edges. However, when we consider only stronger edges within the network by applying a threshold to the edges the number of edges is significantly lower than in the initial model ($p < 0.05$ post-hoc test on KW). Despite this the networks produced are connected in a single component a high proportion of the time (90% of networks in *L.hum* colony simulations and 72% of networks in *I.sang* B colony simulations). This shows that when a transporter class of ants is added to these simulations the stronger trails are produced between nests. This enables the nests to be connected in a larger group. The addition of ants that only recruit to nests strengthens the trails between nests leading to more connected networks.

In simulations of the *I. purp* colony the addition of a transporter class does not significantly increase the number of edges within the network ($p < 0.05$ post-hoc test on KW). However, the proportion of simulations that produced networks that are connected in a single component increases, although to a lesser extent than in the maps from Heller and McIver. In contrast to the maps from Heller and McIver, when a threshold is applied to the edges in these networks the simulations are less likely to form a single component network then in the initial model. This is despite the networks that are produced having a similar number of edges to the initial model.

The addition of a transporter class of ants to the simulations of the *I. sang* A colony has no significant effect on the number of edges in the networks produced ($p < 0.05$ post hoc test on KW) and the simulation does not produce any networks in which all of the nests are connected in a single component.

5.5.3 Additional models

We test the sensitivity of the model to changes in a number of different behaviours. The changes made to the forager recruitment model are summarised in Table 5-2 and the results of these simulations are summarised in Table 5-5. Detailed results showing the mean number of edges with the networks and the results of post-hoc comparison to the forager recruitment model are provided in Appendix F.

The size of the colonies in the real networks is unknown and so we test the sensitivity of the model to the size of the colony. Firstly we modify the forager recruitment model to have double the number of foragers and secondly we modify it to have the same number of foragers but a smaller proportion of the colony foraging. When we double the number of foragers within the model the simulated colonies produce significantly more connections than the model with a smaller colony ($p < 0.05$ post hoc on KW test) and also are more likely to produce networks connected in a single component. When we consider only the stronger connections within the network by applying a threshold to the edges the number of edges drops steeply, as does the proportion of single component networks. Decreasing the proportion of the colony that forages has no significant effect on the number of edges within networks that are produced by the simulation ($p < 0.05$ post hoc test on KW) and does not change the proportion of simulations that connect all nests within a single component.

The colonies we test are highly variable in their size and so we test the possible effect of spatial scale within the model by running simulations in which foragers search unsuccessfully for a longer period before they return to their home nest. In the *L. hum* colony and the *I. sang* B colony this behaviour has no effect on the number of edges in the networks produced by simulations but increases the number of networks in which all nest are connected slightly (36% and 46% compared to 44% and 54% in the *L. hum* and *I. sang* B colonies respectively). In the other two colonies, *I. purp* and *I. sang* A (the largest colony), the number of edges is increased significantly when compared to the forager recruitment model ($p < 0.05$ post hoc test on KW) and the number of networks that connect all nests also increases.

Model	Threshold	Number of edges compared to empirical networks	Number of edges compared to forager recruitment model	Single component networks
Forager recruitment	0	Higher	-	4-48%
	2	Variable (higher in one colony, lower in 2 colonies, no difference in one colony)	-	0-22%
	4	Lower	-	0-6%
Transporters	0	Higher	Variable (higher in 2 colonies, no difference in 2 colonies)	0-100%
	2	Variable (higher in 3 colonies, lower in one colony)	Variable (higher in 2 colonies, no difference in 2 colonies)	0-90%
	4	Lower	Variable (higher in 1 colony, no difference in 3 colonies)	0-30
Double colony size	0	Higher	Variable (higher in 3 colonies, no difference in 1 colony)	10-96%
	2	Variable (higher in 3 colonies, lower in 2 colonies)	Variable (higher in 3 colonies, no difference in 1 colony)	0-44%
	4	Variable (higher in one colony, lower in 3 colonies)	Higher	0-30%
Lower proportion foraging	0	Higher	No difference	8-46%
	2	Variable (higher in one colony, lower in 3 colonies)	No difference	0-18%
	4	Variable (lower in 3 colonies , no difference in 1 colony)	No difference	0-8%
Foraging further	0	Higher	Variable (higher in 1 colony, no difference in 3 colonies)	12-76%
	2	Variable (higher in one colony, lower in 2 colonies, no difference in one colony)	No difference	0-22%
	4	Variable (lower in 3 colonies , no difference in 1 colony)	No difference	0-14%

Table 5-5 Summary of results of simulation model. If a difference is reported this this significant at $p < 0.05$ level. From either Kruskal-Waillis tests (for comparison to empirical data) or from post-hoc analyses on KW tests comparing the number of edges in all simulations to each other. **Table continues on next page.**

Model	Threshold	Number of edges compared to empirical networks	Number of edges compared to forager recruitment model	Single component networks
Small foods	0	Variable (higher in 3 colonies, lower in one colony)	Variable (lower in 3 colonies, no difference in 1 colony)	0-16%
	2	Variable (lower in 3 colonies, no difference in one colony)	Variable (lower in one colony, no difference in 3 colonies)	0-10%
	4	Lower	Variable (lower in one colony, higher in one colony, no difference in one colony)	0-8%
Random foods	0	Variable (higher in 3 colonies, no difference in one colony)	No difference	4-48%
	2	Variable (lower in 2 colonies, no difference in 2 colonies)	No difference	0-14%
	4	Lower	Variable (higher in one colony, no difference in3 colonies)	0-2%
Stronger route fidelity	0	Higher	Variable (higher in 2 colonies, no difference in 2 colonies)	6-94%
	2	Variable (higher in 2 colonies, lower in 2 colonies)	Variable (higher in one colony, no difference in3 colonies)	0-84%
	4	Variable (higher in 3 colonies, lower in one colony)	Variable (higher in 2 colonies, no difference in 2 colonies)	0-62%
Recruit to all nests	0	Variable (higher in 3 colonies, lower in one colony)	Variable effect (higher in one colony, lower in one colony, no effect in 2 colonies)	0-94%
	2	Variable (higher in 2 colonies, lower in one colony, no difference in one colony)	Variable (higher in 3 colonies, lower in one colony)	0-80%
	4	Variable (higher in 2 colonies, lower in 2 colonies)	Higher	0-62%

Table 5-5 Cont. Summary of results of simulation model If a difference is reported this is significant at $p < 0.05$ level. From either Kruskal-Waillis tests (for comparison to empirical data) or from post-hoc analyses on KW tests comparing the number of edges in all simulations to each other. **Table continued from previous page**.

In the initial forager recruitment model we use the locations of food items as marked in the maps of the colonies. However, the distribution of food has been shown to affect the success of polydomous colonies, and the species in the mapped colonies can carry out scavenging in addition to using large stable food sources. Therefore we tested the effect of changing the food distribution within the model. The results of these tests show that food distribution can affect the movement of ants between nests. Firstly, in simulations in which small food items are added to the environment periodically the colonies form significantly fewer connections than in the initial model ($p < 0.05$ post hoc test on KW) and are less likely to form single component networks, with two of the maps never producing networks that connect all of the nests. In simulations with four randomly located food items three of the four colonies produced single component networks less often. The fourth colony produced a similar proportion of connected networks as the initial model (46% of colonies and 48% of colonies respectively).

We also ran simulations in which the behaviour of ants was modified so that they ignored pheromones close to the nest. This allows us to test a situation in which ants are more reliant on route fidelity. In these simulations two colonies produce networks with a significantly higher number of edges than the forager recruitment model ($p < 0.05$ post hoc test on KW). However, in simulations of the other two colonies there is no significant change in the number of edges from the initial model. In simulations of all of the colonies the proportion of networks produced that connect all of the nests is increased in the strong route fidelity model compared to the forager recruitment model. When a threshold is applied to the edges in three of these networks the number of edges decreases and the proportion of colonies that connect all nests together decreases greatly. However, in the *I. purp* colony the number of connections remains significantly higher than in the real networks ($p < 0.05$ post hoc test on KW) and the proportion of networks connected in a single component also remains relatively high (62% of colonies with threshold of 4 on the edges).

To test whether recruitment between nests for purposes other than food distribution may have an effect we ran simulations in which ants recruited to nests that have a negative energy budget as well as to nests with a positive energy budget. The results of these simulations are inconsistent across the colonies. In simulations of the *L. hum* colony the addition of this behaviour to the initial model does not significantly change the number of connections within the colony but decreases proportion of simulations that form connections between all of the nests. In simulations of the *I. purp* colony the addition of this extra recruitment has no significant effect on the number of connections within the networks and also has little effect on the proportion of simulations that connect all nests in a single component (48% of networks in initial versus 54% of networks in model with additional recruitment). In simulations of the *I. sang* B colony the number edges in the model with additional recruitment is significantly higher than in the initial model. The proportion of colonies that connect all of the nests is also increased greatly (46% of colonies versus 94% of colonies). Importantly, in this map when we consider only strong connections by applying a threshold, the number of simulations in which all of the nests are connected remains relatively high (62% of colonies with threshold of 4 on the edges). This is true even though the number of edges is not significantly different from the number in the real networks. This suggests that in simulations of the *I. sang* B colony this behaviour strengthens the connections between nests, allowing the colonies to be better connected. In simulations of the *I. sang* A colony both the number of edges and the number of single component networks is decreased by the addition of recruitment to empty nests to the initial model.

5.6 Discussion

Our results show that a simple model of a polydomous ant colony in which ants treat nests as food sources and recruit to them using pheromone trails does not replicate the structure of the trail network formed between nests. The networks created have significantly more edges than in the empirical network and, despite this, do not consistently connect all of the nests within the colony. This suggests that the real ant colonies are carrying out a more complex behaviour that connects the nests within a colony with a low number of edges. For three of the empirical maps introducing division of labour by the addition of a simple transporter class of ants improves the ability of the colony to produce networks in which all of the nests of the colony are connected in a single component. However, in simulations of the largest colony (*I.*

sang B) none of the behaviours tested were able to consistently connect all of the nests in the colony in a single component.

In all of our simulations except one the number of edges in the simulated colonies is significantly higher than in the empirical networks. This is despite the simulations not consistently connecting all the nests into a single component. When a threshold is applied that reduces the number of edges to a number similar to in the real networks the proportion of simulations that create networks that connect all of the nests is reduced further. These results suggest that the ants in the colony carry out a behaviour that allows them to form trails between nests in a way that is highly effective for joining the colony into a single component.

A number of behavioural studies of polydomous ant colonies report the presence of a transporter class of ants. These ants do not forage, instead carrying out only transportation between nests (McIver 1991; Pfeiffer and Linsenmair 1998). We use a simple modification of forager behaviour to add a class of transporter ants to the model. In three of the colonies this behaviour leads to the trails between nests being reinforced more successfully than in the initial model and creates more systems in which the nests are connected in a single group. The behaviour of this transporter class in reality may be more complex (e.g. Pfeiffer and Linsenmair 1998) and may therefore have a stronger influence than in this model. The behaviour of transporters may also be more flexible in reality than in the model. Ants may, for example, have a partial preference for moving between nests or for foraging rather than performing only one of these tasks.

The simulations that are carried out using the *I. sang* A colony give results that are not consistent with the other three maps in any of the properties tested. We would not expect that this difference from the other colonies is a result of different fundamental behaviour within the colony since two of the colonies are the from this species. The results may be explained by the size of the colony. This colony has 28 nests which is double the size of the next smallest colony in this study. This suggests that the scale of the colony may have an influence on the success of simple mechanisms in joining a colony. There is a possibility that the observed effect of scale is an artefact of the model used. The movement of ants within the model was parameterised for movement within an arena of 1x1m (Schmolke 2009). It is possible that ants found within large natural colonies that do not find food will travel further away from the nest than in the model. We tested whether the effect of spatial scale was an artefact by testing the sensitivity of the model to the distance that the foragers will search unsuccessfully before returning to their home nest. In these tests the success of the colony in connecting all of the nests was increased only slightly suggesting that this is not the primary reason that the colonies do not connect all of the nests together. It is also possible that the model is missing some behaviour that is carried out by ants that is essential to connecting a network and that this is highlighted by the large colony size. The simple mechanism of treating nests as food sources as investigated in this study may be successful in connecting only smaller groups of nests.

The mechanisms of trail formation used in this study rely on the movement of food. We have shown that the spatial distribution of food resources within the environment plays a role in the ability of the colony to form connections between all of the nests. In particular, when small food sources are included in the initial model the colonies are less able to connect all of the nests in the colony. This is caused by the colonies forming more trails between the food sources and nests and therefore fewer of the foragers move between nests. In real species however, there may not be recruitment to small food sources (Cerdá et al. 2009). The effect of adding small food sources may have been lessened if a different type of recruitment was included. In addition, if transporters were also included in the model with small food sources there may have been less of an effect since transporters ignore food sources. In real colonies there may also be movement between nests for reasons other than food distribution.

The effect of the spatial distribution of food sources is also likely to be linked to the behaviour of the model that only allows recruitment to nests that have a positive energy or food budget. The movement of resources other than food between nests is not considered in this model. In particular, brood has been shown to be transported between nests and the transport of workers between nests by carrying has also been observed (Cerda et al. 1994). Additionally, in reality nests may not reach a level of food supply that is low enough to prevent any exchange with visiting foragers. To investigate the effect of behaviour that allows trails to form for reasons other than resource exchange we ran simulations with a behaviour that allowed trails to be laid between nests that did not have excess energy reserves. In all of the colonies, adding this behaviour to the model increased the probability of colonies connecting all of the nests in a single component. Importantly, in one of the maps this behaviour was shown to increase the strength of trails between nests resulting in more connected networks even when only strong trails are considered.

We modify our forager recruitment model to have stronger route fidelity by having ants ignore pheromones close to the nest suggest. The behaviour eliminates the tendency of ants to turn away from the direction of their route fidelity towards areas of strong pheromone concentration. The results of these tests suggest that strong route fidelity may play a role in connecting nests in a single group in some cases. In one of the colonies tested the strong route fidelity behaviour increased the ability of the colony to form connections between all of the nests and also had a particularly strong effect on the strength of the connections between nests.

In this study, we define a trail as being present when a small number of ants have travelled between a pair of nests. None of the studies that map the colonies used in this study included detailed descriptions of the recording of trails between nests. However, it is unlikely that in field studies the recording of trails is based purely on a number of ants travelling between nests over a short period of time. There may be physical evidence of trails or much larger number of ants travelling between nests than are included in the simulations in this study. Field studies that record the strength of trails may allow empirical studies to be compared to models more easily (Chapter 3). This type of information may also provide additional information about how the trail systems between nests are used by ant colonies.

The inconsistency in the results of the simulation across the four colonies highlights the importance of using data from different sources over a range of physical scales. In particular, by using a variety of nest layouts on different scales we see that scale may play a role in the results. Behaviours that may be able to connect nests over a small area are not able to create all of the connections needed to connect a large colony. By combining the results from multiple colony simulations we are able to consider more general behaviour and can form hypotheses that should apply more generally than if a single colony was used. There are however limitations to the dataset used in this study. We use only four colonies from three species and these three species are closely related. Polydomy is found in a much larger range of species (Debout et al. 2007) and there are a recorded maps of a wider range of species. However, the details of colonies that are needed to carry out the simulations in this analysis (nest locations, resource locations and details of trails) are not available.

Throughout this study, we examine the nests and the trail structure between those nests at a particular point in time as they were recorded. This is a limitation of the model as we must assume that the trail system must be re-established at the start of each simulation and that the colony has no memory of previous links between nests. However, the trail system of natural colonies may need to be re-established at certain points in time. For example, a number of species enter a period of inactivity and in the spring they must re-establish the trail system between nests (Hölldobler and Wilson 1990). Our model replicates this type of process. A similar process of establishing a network has been examined in laboratory study by Latty et al (2011). In their study of *L. humile* colonies, the formation of inter-nest trail networks takes place by a process of link-minimisation whereby many trails are formed initially and then the number is reduced by reinforcement of some trails (Latty et al. 2011). This process is not observed in the model used in this study however, the colonies used in this laboratory study were small (consisting of 4 nests less than 30cm apart) and this may account for the differences observed.

It is likely that the trail system between nests in natural field colonies is affected by historical events and in particular, the addition of new nests to the colony as it grows. Many polydomous colonies reproduce by budding: during this process a group of ants leave the nest to establish a new nest close by (Debout et al. 2007). After a new nest is established, the nests may remain connected as part of a polydomous colony. This means that links between nests may form during this period and remain over time due to either fidelity to the original nest or memory of its location. Nests have also been shown to be established close to food sources (Holway and Case 2001; van Wilgenburg and Elgar 2007a). This may lead to the establishment of nests on pre-existing trails that are already linked to the rest of the colony. Food sources may subsequently change but nests may remain connected by a trail. To understand the processes involved in the formation of the internest transportation networks in polydomous ant colonies more long-term studies on both their use and their formation are needed.

Our results suggest that adding simple division of labour by introducting transporter behaviour to a proportion of the ants within a colony can increase the success of a polydomous ant colony in maintaining a trail system that connects all nests. In addition, a mechanism that combines recruitment to nests with strong route fidelity may reinforce trails between nests and also allow nests within a small colony to remain connected. However, these behaviours may not be enough to connect a large colony into a single network. The connection of nests that are distant from each other may require more complex behaviour or a combination of several of the behaviours tested in this model. Trails formed between nests may also be linked to historical events and memory of trail locations. Future studies in the field on the behaviour of ants travelling on the trails between the nests of polydomous colonies and on the history of colonies as they grow might provide more insight into how ants are able to construct highly efficient transportation networks without central control or design.

Chapter 6
Discussion

A wide range of ant species have colonies in which the ants are spread between several socially connected but physically separated nests. This behaviour is known as polydomy (Debout et al. 2007). In this thesis I use polydomy in ant colonies as a model system for investigating distributed social systems. The thesis contributes to the understanding of ant colony organisation and also addresses questions that relate to distributed systems more generally. Chapter 2 discusses the possible benefits to an ant colony of a distributed system of nests and highlights recruitment costs that have not been previously discussed. Chapter 3 introduces and reviews the use of networks for representing social insect systems across a range of scales. Chapters 4-5 use this network approach to examine how the parts of the distributed system of nests in a polydomous ant colony can be linked together. Chapter 4 presents the first analysis of natural trail systems between nests and shows that the networks formed by ant colonies have properties that make them highly efficient. Chapter 5 investigates simple mechanisms and behaviours for the construction of these networks and suggests that strong route fidelity and a class of ants that carry out only transportation may play a vital role in connecting nests in a colony.

6.1 Summary of Chapters

6.1.1 Polydomy and foraging

The benefits to a colony of having a distributed system of nests are not well understood (Debout et al. 2007). Previous studies have suggested that the colony can increase its forage by being polydomous (Hölldobler and Lumsden 1980; Schmolke 2009). This benefit may be gained by carrying out dispersed central place foraging, where ants forage locally from nests and any collected food is subsequently distributed to other parts of the colony (McIver 1991). This type of behaviour reduces the length of individual foraging trips and may allow colonies to forage over large areas more effectively than from a single large nest. In Chapter 2 I use an agent-based model to investigate the consequences of having a polydomous organisation on the foraging success of a colony. The work improves on previous theoretical considerations of the foraging benefits of polydomy by including three different types of recruitment to discovered food sources.

The results show the inclusion of recruitment in the model has an important effect: there is an interaction between recruitment type, food distribution and the relative success of polydomous and monodomous colonies. While polydomous colonies are able to discover randomly distributed food sources faster on average they incur a cost by having their population dispersed. The dispersion of a colony lowers the available recruit population and reduces the exploitation rate of newly discovered food sources. The recruitment costs imposed by polydomy have not previously been discussed within the literature and may play an important role in explaining why many ant species are not polydomous. The results in Chapter 2 are also more generally applicable to studies of foraging strategy in ant colonies. Previous studies have shown that the optimal recruitment strategy for an ant colony is dependent on the colony size and the distribution of resources. The results in Chapter 2 show similar interactions between the success of particular recruitment strategies and both colony size and resource distribution. There is also an additional interaction between these factors and colony organisation. In a polydomous colony the effective population for recruitment is reduced and information cannot flow through the colony as effectively. This suggests that the organisation of a colony (monodomy or polydomy) will also play an important role in optimum recruitment strategy and this effect should be considered in future studies of foraging strategy. This work also provides several testable predictions about the foraging success of polydomous colonies. For example, the results predict that the ability of a distributed colony to both discover and exploit food sources is affected by colony structure. This could be tested in laboratory colonies where both the resources and the colony structure can be manipulated.

6.1.2 Organisation within polydomous colonies

The rest of the thesis explores the organisation of polydomous ant colonies by representing the system of trails that is formed between nests as a network. To introduce this approach, in Chapter 3 I present a review of how network analysis techniques have been used previously to analyse the behaviour of social insect colonies at different levels. Social insect colonies have been represented as networks a number of times at a variety of scales ranging from interactions between individuals within a nest (e.g. Otterstatter and Thomson 2007; Naug 2008; Blonder and Dornhaus 2011; Mersch et al. 2013) to large scale foraging trails (e.g. Holt 1990; Pfeiffer and Linsenmair 1998; Boudjema et al. 2006). The review highlights the benefits of using networks to analyse the effectiveness of systems at different scales and to gain insight into the selective forces acting on them.

Many polydomous ant colonies form a system of trails that link the nests in the colony. These trail systems are used for the transportation of resources between nests (McIver 1991; Pfeiffer and Linsenmair 1998; Heller et al. 2008) and movement between nests along these trails may be necessary to maintain cohesion in the colony and prevent conflict (Cerda et al. 1994). In Chapter 4 I present the first analysis of the transportation networks formed between the nests of natural polydomous ant colonies. The results of this analysis contrast with the results found in studies of laboratory colonies. In particular, in lab colonies the ants minimise the total distance of trails within the network while in natural, already established colonies the ants do not. Natural colonies do not simply connect to their nearest neighbours. They contain some long-distance connections that make the network structure particularly efficient for transportation through the whole colony. This suggests that in natural colonies factors other than the cost of constructing and maintaining trails play an important role. The contrast of these results with previous lab studies also highlights the importance of using both laboratory studies and field studies.

Chapter 5 presents an investigation of the mechanisms by which the highly efficient networks found between nests of polydomous colony can be formed. Previous studies have suggested that the trail systems between nests are formed by the treatment of nests as food sources by foragers (McIver 1991; Holway and Case 2000). In addition, in several species a separate class of ants has been reported that carries out only transportation between nests (McIver 1991; Pfeiffer and Linsenmair 1998). Chapter 5 tests the possibility that nests can be connected using these two simple recruitment behaviours using an extension of the model used in Chapter 2. The results show that adding simple recruitment behaviours to the model does not allow colonies to consistently connect all of the nests in the colony with a low number of edges. This suggests that either more complex behaviours are carried out by ants to allow all of the nests within the colony to connect with a low number of edges or that other factors such as historical connections play a fundamental role in structuring the trail systems.

6.2 General comments

6.2.1 Distributed systems

This thesis focuses on the system of connected nests found in polydomous ant colonies; however there are a wide range of distributed systems found both in nature and in human systems. Network analyses similar to those carried out in Chapter 3 have been carried out on other natural transportation systems. In particular, ant foraging trail systems and the structure of social insect nests have shown to be optimised for efficient transportation (Buhl et al. 2004b; Perna et al. 2008c; Buhl et al. 2009). Other natural systems, in particular slime mould systems connecting areas of high nutrients, have also been shown to produce highly efficient networks (Nakagaki et al. 2004; Tero et al. 2010). Polydomous ant colonies have also been compared to clonal plants (Holway and Case 2000). Transportation between parts of these systems may not be as important as in ant colonies. However, the results found in Chapter 2 relating to exploration and exploitation and in what circumstances these may have applications to these types of systems.

The transportation networks between nests of polydomous ant colonies also have some similarities to human systems and tunnel systems of ants have been directly compared to human systems (e.g. Buhl et al. 2009). However, these human systems are usually designed by looking at the system from a global perspective, where the whole system can be analysed and optimised before it is constructed or used. One of the most striking features of social insect colonies (and other natural systems) is that they can create complex and efficient systems without the need for centralised design. Each individual within these systems carries out simple behaviours and has knowledge of only a small part of the system. However, the results in Chapter 5 suggest that the behaviours carried out by individuals are not the simplest possible behaviours. The ants within polydomous colonies carry out more complex, self-organised behaviours that have been shaped by natural selection to maintain the networks that are formed by the colonies.

6.2.2 Modelling framework and empirical data

Throughout this work I use agent-based simulation models to investigate the behaviour of polydomous ant colonies. This approach allows me to determine how small changes in individual behaviour can affect larger scale, emergent properties of the system. However, there are limitations to creating simulation models of a colony in this way. The more complex a model becomes the more difficult it is to determine which parts of the model are causing an effect. It can also be difficult to observe the outcome of a simulation in a useful way.

This is highlighted in particular, in Chapter 5 where I aim to determine the effect of different behaviours on the construction of intra-nest trail systems. An alternative approach may have provided a more testable model. One possible alternative may have been constructing a model where the trails were fixed in place between nest and testing the effect of different patterns of movement along these trails.

The models presented in this work are intentionally not species specific. This approach is used to try to address question that are relevant to general behaviours and that can be applied across a wide range of ant species. While this approach allows simple predictions to be made about behaviour it also has limitations in addressing the many specific behaviours found across ant species. If needed, the modelling framework presented in this thesis could be used to ask question about polydomy in a specific species. However, modelling a specific species has its own issues. For example, the movement behaviour of individuals (including speed, turning rates, forging distance etc.) may need to be measured to allow accurate parameterisation or models may need to be made more complex to include specific behaviours, for example including behaviours for species that carry out a combination of recruitment methods.

Although the models presented are not representative of specific species, where possible the results are compared to data collected from natural polydomous colonies. Using theoretical models allows testing of behaviours under a wide range of conditions and allows the generation of hypotheses; however this modelling is not useful if it cannot be related to real systems. Several parts of this work have highlighted the need to use field data from a range of sources if this is possible. In particular, the analysis in Chapter 4 was carried out across a range of species and on colonies of different spatial scales. This enabled the discovery of general characteristics of polydomous networks and shows that the results are not simply constraints of a particular species and environment. Similarly, in Chapter 5 by using data from a range of spatial scales we show that this prevents the results of the simulations from suggesting solutions that are applicable only to a small set of circumstances.

Despite the fact that data from a number of sources are used, the analysis in both Chapter 4 and in Chapter 5 would have benefitted from comparison with bigger empirical datasets. Unfortunately, the number of colonies used for analysis in both of these chapters was limited by the amount of empirical data that was available. There are also remaining questions about the quality of the data from these studies. In most cases the purpose of the study was not to record the trail system of the colony and in some cases details which may be important, such as when and how the trails were recorded, is missing.

In my analysis I make the assumption that the maps are comparable to each other and that the data is accurate and reliable. However, a more comprehensive analysis could be carried out if data were available. In Chapter 3 I provide suggestions about the data collection that is necessary in future studies of polydomy to make the data that is collected more widely usable for studies of the structure of colonies.

6.3 Questions remaining and future work

6.3.1 Behaviour of individuals on trails

It is important to note that transportation throughout a polydomous colony must be carried out by insects moving on the network of trails. The specifics of the movement of the insects along these trails will affect the effectiveness of the trail system in allowing transportation through the colony. In the case of the trail networks between nests in a polydomous colony the trails are also constructed and maintained by the movement along them. This means that understanding the behaviour of ants moving between nests is a crucial part of understanding the system as a whole.

There is limited data on the movement of ants on systems of trails found between nests in polydomous colonies, however, it is likely that ants move between nests based on need or some other non-random behaviour. Recent studies on the red wood ant, *Formica lugubris,* suggest that the movement of individuals between nests is based on pairwise interactions and is related to the difference between the amounts of foraging carried out by nests (Ellis et al 2013). In *Camponotus gigas*, transporters have been shown to wait within a nest to collect resources from a number of returning foragers before leaving to another nest. The transporters within this system are larger and able to carry more than foragers and so this behaviour should improve transportation efficiency through the network (Pfeiffer and Linsenmair 1998).

Studies of other transportation networks within social insect colonies suggest that studies of network structure must be combined with observations of the behaviour of individuals on these networks to truly understand the suitability of the network for transportation (Garnier et al. 2009; Viana et al. 2013). This, and the close link between use and construction in these networks, highlights the need for more work documenting the behaviour of ants on the trail systems.

6.3.2 Transport through a colony

A question that is related to the behaviour of individuals on the trails is how the movement between nests of a colony provides a benefit to the colony. Throughout the modelling of the construction of the trail systems in Chapter 5 I assume that the movement of ants between nests is primarily an adaptation of the transportation of food resources across the colony. However, if this is the case then, for the colony to benefit as a whole from being polydomous, resources must be distributed between the individual nests so that all nests receive an appropriate level of resource. In the simulations carried out in Chapter 2, where there is no transfer of resources between nests, some nests may end the simulations with a highly negative energy budget while others build up a large amount. The analysis carried out assumes that the whole colony benefits from any build-up of resources in one nest. Nest moving and nest abandonment has been shown to be common in some ant species (Cerdá et al. 2002; Heller and Gordon 2006) and in reality, nests that do not receive enough resources are unlikely to persist. The models used in Chapter 5 do not consistently recreate networks that are similar in structure to the real colonies' networks and so the distribution of resources in colonies that share resources was not tested in these simulations. However, we would expect that, by transporting food away from nests with excess energy, resources would be shared more equally between nests. It may be possible to create models in which different mechanisms of movement of resources is investigated in relation to environmental factors such as the distribution and persistence of food sources. By adding the trail system between nests from mapped colonies manually, these models could further the understanding of transportation between nests even if construction of the trails is linked closely to historical events that are unknown.

6.3.3 Other benefits of polydomy

Throughout this work I concentrate on the foraging of polydomous colonies. This thesis focuses on the foraging behaviour in the dispersed system of a polydomous ant colony throughout and assumes that foraging success has a large impact on the behaviour of colonies. In particular, Chapter 2 concentrates on investigating circumstances in which foraging success is changed by polydomy and in Chapter 5 the mechanisms of connecting the nests also rely heavily on foraging behaviours and the assumption that the colony is linked together to facilitate the sharing of food resources between nests. Foraging is an important behaviour for all animals and by focussing on foraging the work addresses benefits that are directly measurable and also should be applicable to ant species generally.

However, the focus on foraging in this thesis means that other aspects of polydomy are not addressed as fully. For example, there are several other proposed benefits to having a colony structure that is polydomous. These include: the avoidance of queen-worker conflict, spreading risk from predation, improving territory defence, and the ability to escape from colony size limitations imposed by nest size limits.

Some of these possible benefits of polydomy may interact with each other and also with foraging benefits. For example the effective defence of a territory may enable colonies to take advantage of food sources more successfully. Future work on the other possible benefits and their interactions may provide more insight into when and where it is advantageous to have a dispersed population.

6.3.4 Invasiveness and polydomous ants

Polydomy, as well as providing direct benefits to a colony, may also allow a colony to outcompete other ant colonies within an area. The competitiveness of polydomous colonies is highlighted by a number of highly successful, invasive species that have polydomous colonies. These species include the Argentine ant, *Linepithema humile* and the red imported fire ant *Solenopsis invicta*. These polydomous ant species, and others, have been shown to have wide ranging effects on the flora and fauna of the environments that they invade, including the displacement of native ant species (Holway et al. 2002).

It can be difficult to determine what characteristics make a species a particularly successful invader (e.g. Hayes and Barry 2008). However, the invasiveness of a species could be affected by life history traits such as reproductive strategy, dispersal strategy, competitive ability and also behaviour. It has been suggested that the polydomous nature of colonies may play a role in their success of some polydomous ant species in invading (Holway and Case 2001). In particular it has been suggested that polydomous colonies may be able to break the trade-off between (Davidson 1998; Holway 1999). In Chapter 2 I show that the related trade-off between exploration and exploitation may exist can be affected by having a dispersed population in a polydomous colony.

The ability to outcompete native species may play a major role in the invasiveness of polydomous ant species. Competition could be added into the agent-based model framework used in this thesis by allowing more than one colony to exist within the environment. The success of these colonies could then be judged against each other directly. The results from Chapter 2 show a trade-off between exploration of the environment and the exploitation of discovered food sources, so we might expect that certain types of colony would be more successful in given environments. However, the effect of competitors within the environment may reveal unseen costs to certain types of organisation and may also have more complex interactions with food distribution. In addition, these types of models may need to include behaviour that simulates the interaction between ants from different colonies arriving at the same food source. Another interesting approach would be to carry out this type of competition in combination with allowing recruitment and colony organisation (number of nests in a colony) strategies to evolve within realistic bounds. An evolutionary algorithm approach has been used to investigate a range of biological systems (e.g. Barta et al. 1997; Chaiyaratana and Zalzala 1997; Krink and Vollrath 1997) and use of this approach could add to the understanding of the system.

Analysis of the effects of competition and under what circumstances polydomous colonies can outcompete monodomous colonies could provide more insight into the cost and benefits of distributed systems. Investigation of how resource distribution and environmental variables interact with competition may also provide useful information for the control of invasive species in environments where they have negative consequences. Conversely, when considering conservation of a species understanding of the importance of the connections formed between nests in a colony may be important in informing the management of habitats containing polydomous species.

6.3.5 Growth of a colony

Throughout this thesis, analysis is carried out on static colonies; the position and number of nests does not change throughout the simulations implemented and all analysis is carried out on networks that are snapshots of the trail system. However, in reality, the structure of a polydomous colony is unlikely to be static. Nest moving is common in many ant species and in some polydomous species nests are frequently abandoned and new nests created (Cerdá et al. 2002; Heller and Gordon 2006). Additionally, as a colony grows new nests are likely to be established. The construction or abandonment of nest is likely to be dependent on a number of factors including: the availability and stability of food throughout time, the cost of constructing a nest (which will vary dependent on the type of nest built), the availability of suitable nests sites, predation, and the social structure of the colony (for example whether the colony is monogynous or polygynous). It should be possible to create models in which a colony is able to grow and expand through time. The establishment of nests close to food sources has been shown in several polydomous species (Holway and Case 2000; Lanan et al. 2011) and this could be used as a basis for the position of new nests within a colony.

Theoretical investigations of how networks with the properties of the natural networks might grow over time could be complemented by analysis of the changes in real colonies over time. Recently a number of tools have been developed for the analysis of dynamic networks (Blonder et al. 2012). If data were available on the changes in trail structure over a long time period, this could allow a much more informative analysis of the structure of the colony to be carried out. In particular, information such as the resource use, trail strength and net trail direction were collected in combination with spatial information about whether trails are present between pairs of nests would be useful in determining both the behaviour of individuals and also the function of the system. This type of information can be incorporated into analyses and could add a great deal to the understanding of both how networks develop and how they are used over time to benefit the colony.

Appendix A
Glossary of network analysis terms

Network - Representation of a set of units (nodes) in which pairs of units may be linked or connected together in some way. May also be referred to as a graph.

Node - component of the network that may have connections with other components.

Edge - connection between two nodes in a network.

Association matrix - representation of a network in the form of a matrix in which the element (i,j) represents an edge between nodes i and j. In a weighted network the value of (i,j) represent the weight of the connection.

Path - sequence of edges that links two nodes in a network

Path length - either the number of edge in a path or a combination of

Shortest path - path between two nodes that has the lowest path length.

Degree - the number of edges either within the entire network or associated with the particular node. Can be used as a measure of centrality.

Centrality - an measure of the importance of a node based on the position it holds within the network

Betweenness - centrality measure based on how many of the shortest paths within the network a node lies on

Closeness - centrality measure based on the shortest path distance from this node to all other nodes in the network

Motif - a small, specific sub-graph (typically of less than 6 nodes) that may be found within a larger network. An example is a triangle.

Appendix B
Sensitivity analysis for Chapter 2

8.1 *Colony Size*

Within the main text we use a maximum colony size of 500 ants. To test the effect of increasing the size of the colony we run larger simulations with colony sizes of 1000 ants within a foraging arena of size 1414x1414 units. This is a doubling of the both the highest number of ants used in the main results and also a doubling of the size of the area over which food is distributed. The results are qualitatively the same as those for smaller 500 ant colonies (main text Figure 1 G-I).

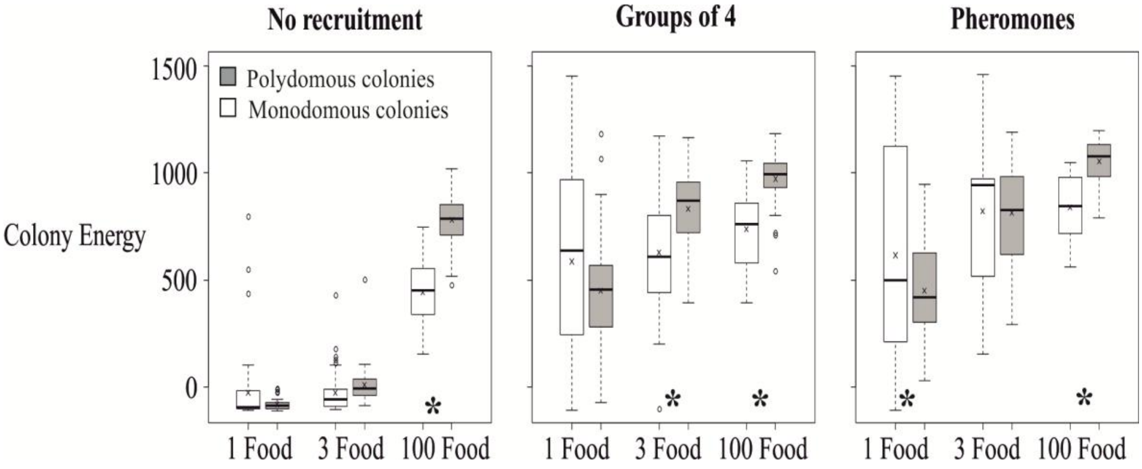

Figure 8-1 The success of colonies under a range of colony sizes.

In each case the vertical axis shows the colony energy budget at the end of simulation. The results for monodomous and polydomous colonies under each condition are represented as white and grey boxes respectively. Cross symbols (×) indicate the mean, dark horizontal lines represent the median value, the box represents the 1st and 3rd quartiles, and outliers (defined as points lying outside 1.5 times the inter-quartile range) are represented by dots. Where a significant difference between monodomous and polydomous colonies is found (bootstrap tests of difference in mean, 1000 samples, $p<0.05$) this is indicated by a star (*) underneath the pair of boxes

8.2 *Pheromone decay rate*

The main text models a short-lived pheromone with a decay rate parameter (λ) of -0.005. Here we use a slower decay (λ=-0.001) which increases the time pheromones can be detected from 599 time steps to 2996 time steps. The results are qualitatively similar to those in which pheromone decay is faster (main text Figure 1 C, F and I). Monodomous colonies are significantly more successful in a single food environment and polydomous colonies are more successful in an environment with 100 small food items.

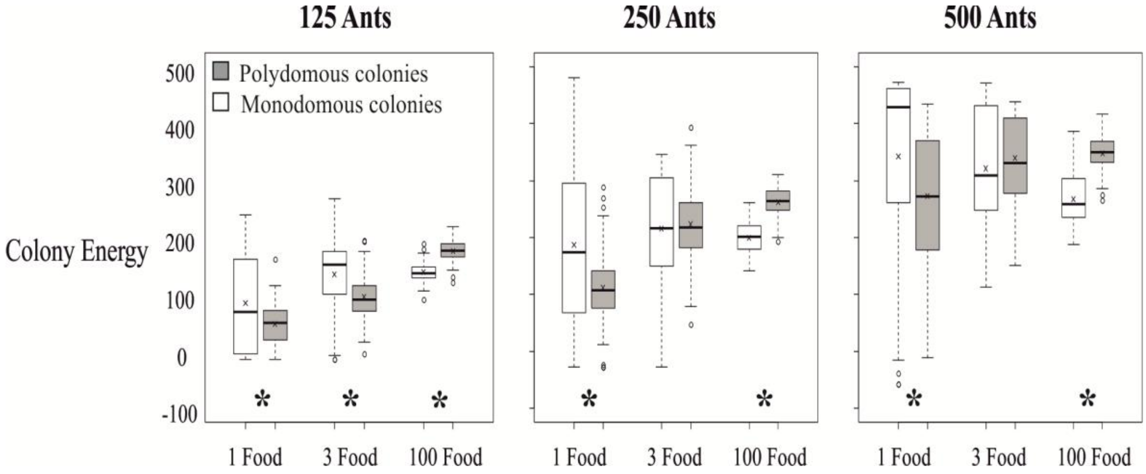

Figure 8-2 The success of colonies under a modified pheromone decay rate.

In each case the vertical axis shows the colony energy budget at the end of simulation. The results for monodomous and polydomous colonies under each condition are represented as white and grey boxes respectively. Cross symbols (×) indicate the mean, dark horizontal lines represent the median value, the box represents the 1st and 3rd quartiles, and outliers (defined as points lying outside 1.5 times the inter-quartile range) are represented by dots. Where a significant difference between monodomous and polydomous colonies is found (bootstrap tests of difference in mean, 1000 samples, $p<0.05$) this is indicated by a star (*) underneath the pair of boxes

8.3 Energy of agents

The results presented within the main text ignore the energy levels of individual ant agents when assessing the success of colonies. Here we present results which include the energy of all agents at the end of the simulations within the total colony energy. The results are qualitatively the same as those without the ant agent energy included (main text Figure 2-1).

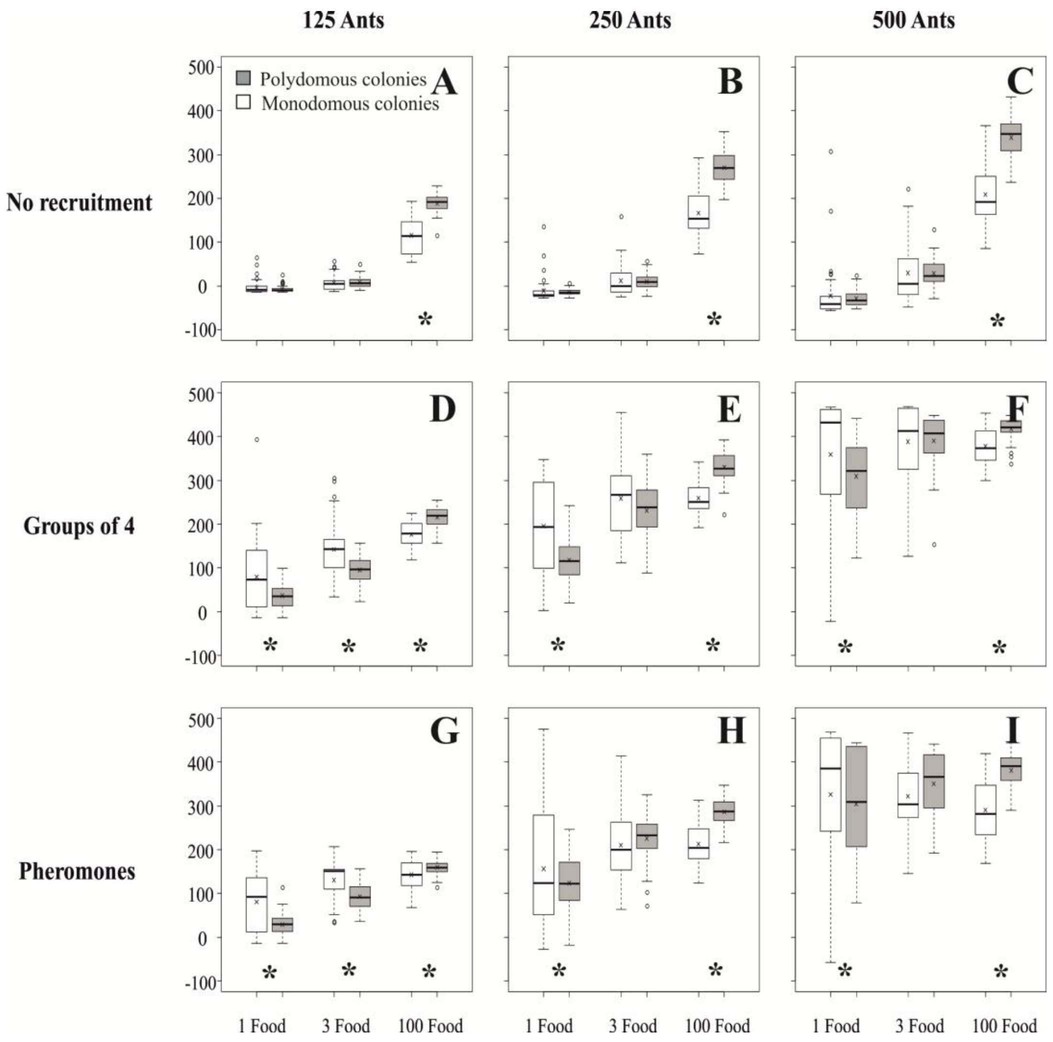

Figure 8-3 The success of colonies under a modified energy regime.

In each case the vertical axis shows the colony energy budget at the end of simulation. The results for monodomous and polydomous colonies under each condition are represented as white and grey boxes respectively. Cross symbols (×) indicate the mean, dark horizontal lines represent the median value, the box represents the 1st and 3rd quartiles, and outliers (defined as points lying outside 1.5 times the inter-quartile range) are represented by dots. Where a significant difference between monodomous and polydomous colonies is found (bootstrap tests of difference in mean, 1000 samples, $p<0.05$) this is indicated by a star (*) underneath the pair of boxes

8.4 Individual memory

The main text tests the success of colonies carrying out individual foraging, group recruitment, and mass recruitment via pheromone trails. Here we test the success of colonies which carry out individual foraging with memory. In this case if an ant has been successful in finding food during its previous trip it will return immediately to this food source once it has completed the exchange of energy with its home nest. The results are qualitatively the same as those for ants which carry out individual foraging without recruitment or memory (main text Figure 2-1 A-C).

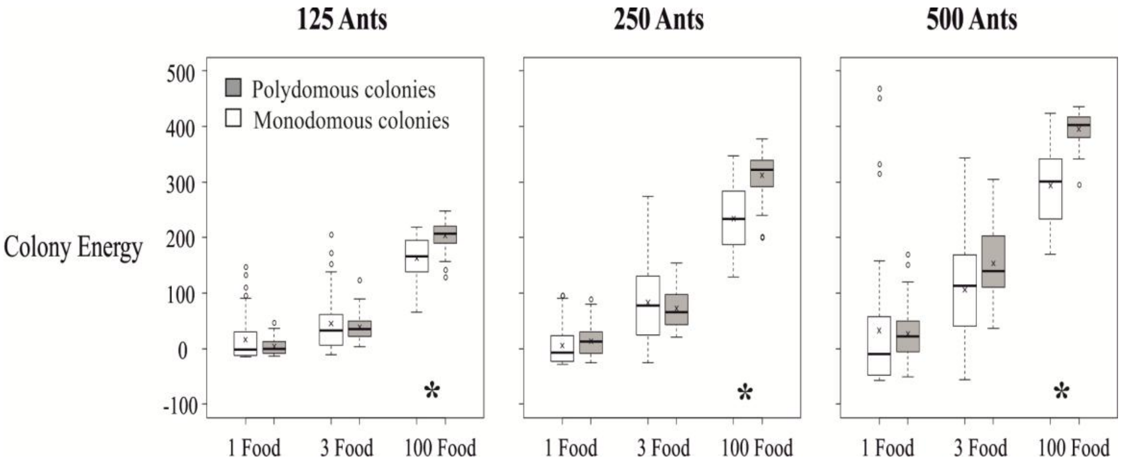

Figure 8-4 The success of colonies with memory.

In each case the vertical axis shows the colony energy budget at the end of simulation. The results for monodomous and polydomous colonies under each condition are represented as white and grey boxes respectively. Cross symbols (×) indicate the mean, dark horizontal lines represent the median value, the box represents the 1st and 3rd quartiles, and outliers (defined as points lying outside 1.5 times the inter-quartile range) are represented by dots. Where a significant difference between monodomous and polydomous colonies is found (bootstrap tests of difference in mean, 1000 samples, $p<0.05$) this is indicated by a star (*) underneath the pair of boxes

Appendix C
Additional statistical details for Chapter 2

The following tables show the confidence intervals for statistical tests carried out for analysis of data. Tables S1 and S2 show 95% confidence intervals for bootstrap tests in which the difference between means of monodomous and polydomous cases was calculated. Table S3 shows 95% confidence intervals for the hazard ratio of time to locate a food item, calculated as part of Cox proportional-hazards regression.

Table 9-1 95% confidence intervals for the difference in mean colony energy (monodomy - polydomy) for all tested conditions.
Intervals which include zero are non-significant. Calculated from bootstrap tests with 1000 samples.

Number of food items	Number of ants	No recruitment	Group recruitment (groups of 4)	Pheromone recruitment
1	125	-1.75, 1.13	24.79, 59.79	20.21, 65.82
	250	-1.63, 3.94	36.14, 107.49	45.78, 112.55
	500	-7.15, 4.94	-13.67, 98.09	5.54, 92.00
3	125	-1.83, 3.60	31.08, 63.66	30.13, 66.00
	250	-4.11, 6.63	-31.26, 15.17	-0.92, 55.67
	500	-7.26, 10.72	-79.15, -15.59	-29.87, 26.41
100	125	-46.47, -24.98	-10.32, 6.03	-51.03, -30.93
	250	-93.78, -65.45	-67.81, -44.02	-83.39, -55.79
	500	-131.76, -86.14	-111.91, -71.24	-52.74, -26.85

Table 9-2 95% confidence intervals for the difference in mean group formation time (monodomy - polydomy) for all tested conditions.
Intervals which include zero are non-significant. Calculated from bootstrap tests with 1000 samples.

Number of food items	**Number of ants**	**Confidence interval**
1	125	-507.01, -498.26
	250	-216.75, -214.95
	500	-98.81, -98.26
3	125	-250.19, -245.60
	250	-204.75, -203.55
	500	-58.33, -57.86
100	125	-34.90, -33.61
	250	-66.00, -65.30
	500	-56.67, -56.30

Appendix D
Additional details on network analysis for Chapter 4

10.1 Efficiency

Efficiency is defined in our paper as defined by Latora and Marchiori (2001). It is a standardised version of the measure of the inverse of the average path length between any two nodes. So for any connected graph G the global efficiency $E(G)$ is defined as:

$$E(G) = \frac{1}{N(N-1)} \sum_{i \neq j \in G} \frac{1}{d_{ij}}$$

where N is the number of nodes within the graph G and d_{ij} is the shortest path length between nodes i and j.

This value is standardised so that $E_G = \frac{E(G)}{E(G_{ID})}$ where $E(G_{ID})$ is the efficiency of the ideal graph for efficiency which is the fully connected graph. However in our case we use a binary fully connected graph and so $E(G_{ID})$ is always 1.

10.2 Meshedness

Meshedness (M) is defined in our paper as in Buhl et al (2004b). It is a measure of cycles within a graph, we use this measure to compare the connections with our networks to the case of a maximally connected planar graph (a graph in which no edges intersect each other). It is defined as

$$M = \frac{f}{f_{MAX}}$$

where f is the number of faces within the graph and is calculated by $m - N + 1$ where m is the number of nodes in the graph and f_{MAX} is the number of faces within a maximally connected planar graph and is calculated by $2N - 5$.

Appendix E
Figures of analysis of networks over time for Chapter 5.

11.1 *Time and duration of sampling*

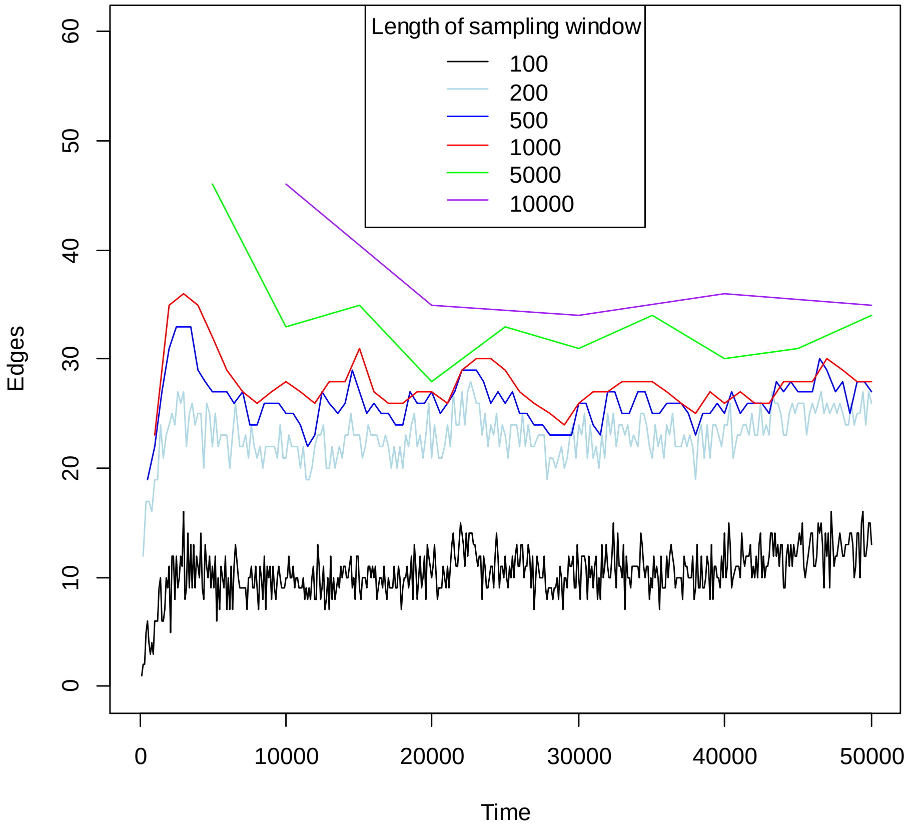

Figure 11-1 The number of edges within the networks produced by a typical run of the forager recruitment model on the *I. sanguineus* B colony. Different lines represent network that are created when different time windows are used for sampling the networks.

11.2 Edge thresholding

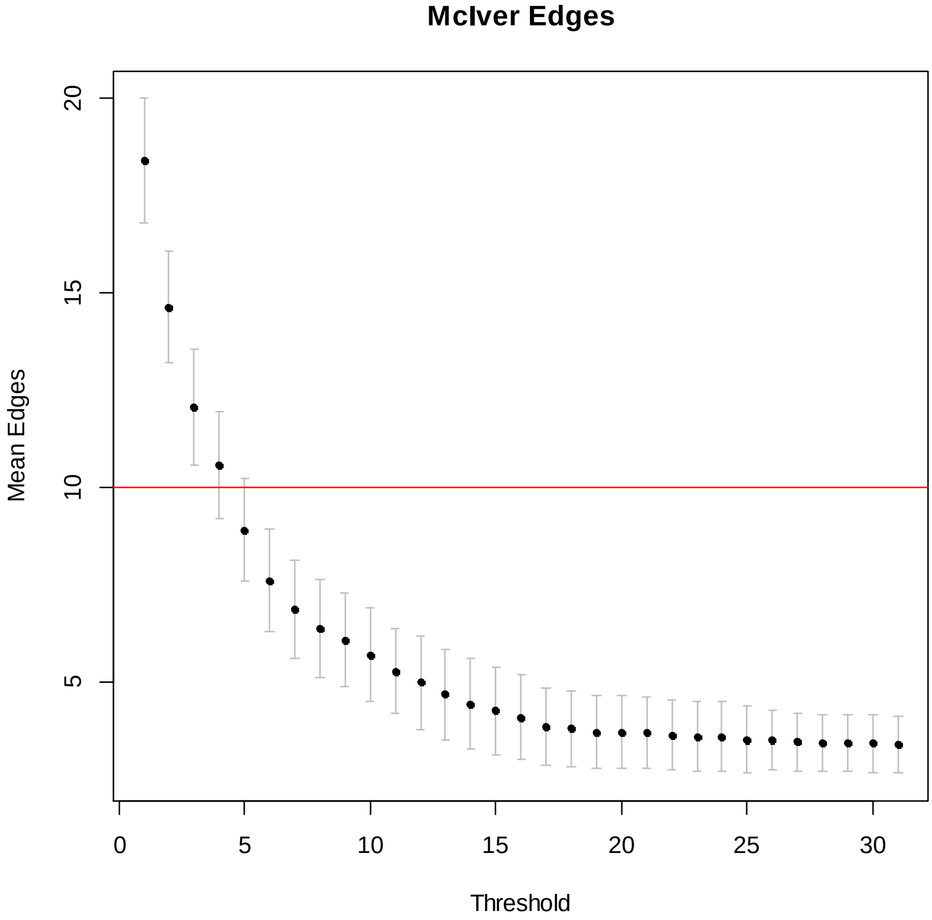

Figure 11-2 Effect of threshold on the mean number of edges within networks produced from 50 simulations of the forager recruitment model on the I. sanguineus B colony. Edges that have less than the threshold value of ants travelling on them are discarded from the network. The Horizontal line represents the number of edges within the empirical colony.

Appendix F

Detailed results of simulations from Chapter 5.

12.1 Mean number of edges within simulations

Table 12-1 Mean number of edges within each model given each threshold tested. Values in brackets show standard deviation. Table continues onto next page

Map	**Empirical Colony**	**Forager recruitment model**			**Transporters**			**Double colony size**		
		Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4
L. hum	16	20.34 (3.27)	13.06 (2.12)	10.76 (1.53)	30.98 (3.27)	18.24 (2.12)	14.06 (1.53)	22.82(3.22)	14.88(2.05)	12.54(1.84)
I. sang A	35	37.52 (6.42)	22.88 (5.22)	18.22 (4.85)	36.88 (6.42)	19.66 (5.23)	14.46 (4.85)	46.88(6.99)	32.00(5.35)	27.12(5.17)
I. sang B	10	16.14 (1.74)	9.78 (1.34)	7.12 (1.19)	26.42 (1.74)	13.32 (1.34)	7.42 (1.19)	18.38(1.59)	12.06(1.49)	8.92(1.32)
I. purp	11	18.84 (3.78)	12.64 (3.03)	10.42 (1.92)	21.56 (3.78)	11.96 (3.03)	9.2 (1.92)	20.82(3.51)	14.34(2.94)	12.54(2.48)

Map	**Empirical Colony**	**Lower proportion foraging**			**Foraging Further**			**Small foods**		
		Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4
L. hum	16	19.32(2.57)	12.70(1.68)	10.88(1.41)	20.10(2.89)	12.82(1.59)	10.86(1.39)	17.60(2.80)	12.94(2.44)	11.06(2.23)
I. sang A	35	41.24(7.57)	24.00(5.22)	19.04(4.59)	44.82(7.89)	26.42(5.15)	20.70(4.81)	31.28(4.74)	25.86(3.77)	23.32(3.07)
I. sang B	10	15.54(1.68)	9.50(1.50)	7.06(1.33)	16.50(1.76)	9.92(1.44)	7.36(1.44)	13.92(2.61)	9.46(1.86)	7.98(1.48)
I. purp	11	20.40(4.65)	13.02(3.17)	10.78(2.23)	19.68(4.27)	13.32(2.57)	11.38(1.96)	13.08(2.41)	9.72(1.80)	8.52(1.57)

Map	**Empirical Colony**	**Random Foods**			**Stronger route fidelity**			**Recruit to all nests**		
		Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4	Threshold 0	Threshold 2	Threshold 4
L. hum	16	17.66(4.06)	11.60(3.23)	9.92(3.19)	20.32(2.52)	13.46(1.69)	11.66(1.29)	21.72(2.99)	15.66(2.28)	13.84(2.26)
I. sang A	35	36.78(9.08)	22.94(5.64)	19.28(5.44)	42.64(6.07)	25.52(5.08)	20.38(4.33)	30.78(2.63)	27.44(1.86)	25.62(1.72)
I. sang B	10	14.78(2.27)	9.96(1.63)	8.18(1.61)	17.38(1.79)	10.80(0.97)	8.92(0.90)	18.16(1.23)	12.74(1.26)	10.54(1.09)
I. purp	11	16.02(3.60)	10.52(2.88)	8.62(2.81)	25.26(2.43)	17.30(2.04)	13.62(1.58)	19.18(2.36)	14.80(1.01)	12.76(0.96)

12.2 Results of post-hoc analysis

The following tables show the results of post-hoc tests to compare the mean number of edges in additional simulations to the mean number of edges in the forager recruitment model. Each table shows comparisons from a different colony. Although comparisons were taken between all models only the comparisons the forager recruitment model are shown. Where a difference is reported this is significant at the 0.05 level.

Table 12-2 Results of post-hoc tests on the L. hum colony

	Threshold 0		Threshold 2		Threshold 4	
Comparison	**Test Value**	**Difference**	**Test Value**	**Difference**	**Test Value**	**Difference**
Transporters	244.15	Higher	252.32	Higher	226.08	Higher
Double colony size	93.47	Higher	108.49	Higher	124.77	Higher
Lower proportion foraging	40.72	NS	22.87	NS	7.33	NS
Foraging further	9.87	NS	15.06	NS	8.18	NS
Small foods	100.83	Lower	3.97	NS	25.27	NS
Random foods	80.87	NS	55.07	NS	21.68	NS
Stronger route fidelity	4.6	NS	24.16	NS	69.56	NS
Recruit to all nests	56.58	NS	143.85	Lower	192.56	Higher

Table 12-3 Results of post-hoc tests on the I. sang A colony

	Threshold 0		Threshold 2		Threshold 4	
Comparison	**Test Value**	**Difference**	**Test Value**	**Difference**	**Test Value**	**Difference**
Transporters	3.83	NS	73.66	NS	91.73	NS
Double colony size	159.76	Higher	224.38	Higher	224.1	Higher
Lower proportion foraging	68.36	NS	37.78	NS	22.22	NS
Foraging further	123.77	Higher	94.72	NS	66.43	NS
Small foods	108.94	Lower	85.6	NS	138.74	Higher
Random foods	11.45	NS	13.79	NS	34.53	NS
Stronger route fidelity	98.95	Higher	72.42	NS	57.19	NS
Recruit to all nests	129.36	Lower	139.24	Higher	211.6	Higher

Table 12-4 Results of post-hoc tests on the I. sang B colony

	Threshold 0		Threshold 2		Threshold 4	
Comparison	**Test Value**	**Difference**	**Test Value**	**Difference**	**Test Value**	**Difference**
Transporters	287.7	Higher	262.39	Higher	30.22	NS
Double colony size	140.16	Higher	190.67	Higher	180.73	Higher
Lower proportion foraging	35.79	NS	14.87	NS	0.19	NS
Foraging further	21.76	NS	15.94	NS	26.31	NS
Small foods	102.82	NS	8.62	NS	94.19	NS
Random foods	66.66	NS	27.46	NS	112.13	Higher
Stronger route fidelity	74.11	NS	89.75	NS	189.49	Higher
Recruit to all nests	134.37	Higher	244.2	Higher	320.75	Higher

Table 12-5 Results of post-hoc tests on the I. purp colony

	Threshold 0		Threshold 2		Threshold 4	
Comparison	**Test Value**	**Difference**	**Test Value**	**Difference**	**Test Value**	**Difference**
Transporters	86.16	NS	30.83	NS	73.22	NS
Double colony size	59.61	NS	76.82	NS	113.3	Higher
Lower proportion foraging	41.6	NS	15.72	NS	16.96	NS
Foraging further	21.08	NS	32.83	NS	56.41	NS
Small foods	175.62	Lower	133.15	Lower	113.37	Lower
Random foods	92.34	NS	93.02	NS	91.42	NS
Stronger route fidelity	200.4	Higher	202.81	Higher	184.98	Higher
Recruit to all nests	7.83	NS	113.69	Higher	149.5	Higher

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