Is predation a driver of polydomy in ants?

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Abstract

Living in groups can confer advantages, such as improved foraging, access to mates, or defence. It may also incur costs, for example through competition for resources. Eusocial species overcome this disadvantage of group living, but groups (colonies) vary in structure. One such structure is polydomy, found in ants, in which a single colony inhabits several nests. It has been hypothesised that polydomous colonies benefit from enhanced defences through:

(1) Dilution of risk: if one nest is destroyed, the colony will persist.
(2) Improved retaliation: inhabitants of a nest targeted by a predator may recruit from connected nests to aid in defence.
(3) Improved evacuation: the inhabitants of a nest have connected nests to flee to.

A dynamic network model of polydomy suggests that stochastic nest destruction favours polydomy over monodomy. This thesis adapts this model to investigate the effect of predator behaviours on the success of polydomy, and to investigate whether polydomous colonies could benefit from colony-level retaliation. We find that the frequency of polydomy in a population increases when a predator would destroy the entire nest, but that the addition of defence by retaliation has no effect on the frequency of polydomy. This suggests that polydomous colonies do benefit from dilution of risk, but not from improved retaliation. Extensions to address evacuation are discussed, as is the potential impact of including further predator behaviours, such as learning.

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Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter 1: Literature Review

Section 1.1: Group Living

Many species in the animal kingdom live in groups. Group living has a wide range of benefits for different species, and different species may benefit differently from this phenomenon. These benefits include improved foraging, improved ability to find a mate, or improved defence. There are also costs to group living, such as the potential for conflict between group members over resources, and potentially increased attack rates on larger groups.

Living in groups can enhance foraging through strength in numbers, or through the transfer of information about resource location. One example of enhanced foraging through strength in numbers is seen in several subsocial crab spider species (*Australomisidia ergandros*, *A. socialis* and *Xysticus bimaculatus*). These spiders have a higher success rate, and capture prey significantly more quickly, when exposed to fruit flies in groups, than when exposed to fruit flies as individuals (Dumke et al. 2018). An example of enhanced foraging through the transfer of information may be seen in black-browed albatrosses, *Thalassarche melanophris* (Grünbaum and Veit 2003). These birds engage in local enhancement, whereby individuals are more attracted to large groups of feeding conspecifics, making it easier for them to find and exploit food sources. Indeed, a model of *T. melanophris* behaviour has predicted that these birds find most of their prey, Antarctic krill (*Euphausia superba*), via local enhancement, rather than by finding their prey themselves (Grünbaum and Veit 2003). Transfer of information may also be more active than this, such as through foragers communicating the location of food to other members of the group. This is seen in *Calloconophora pinguis*, a treehopper, in which scouts vibrate to indicate that they have located a food source, and recruit other members of the group to this food source (Cocroft 2005).

Living in groups can improve defence through a range of means. One such way is the dilution of risk, which means that individuals in larger groups have a lower chance of being singled out by a predator. Large or dense groups of potential prey may also confuse predators, resulting in a decreased success rate for predators attacking prey (Cresswell 1994; Ioannou et al. 2009). Groups of prey may be more vigilant, and therefore more able to identify and quickly respond to potential predators. Finally, some species are more successful at defending themselves, their young or their resources, when defending as a group, either by retaliating against attackers (Fanshawe and Fitzgibbon 1993), or mobbing potential threats that are not currently attacking (Chiver et al. 2017). The defensive benefits of group living are explored in depth in section 1.3.

Living in groups may also pose costs to individuals. Large groups are more conspicuous and provide larger quantities of food, and are therefore often more likely to be targeted by predators than individuals are (Lindström 1989; Cresswell 1994; Krause and Ruxton 2002). Individuals living in groups must also compete for resources, such as food or mates, with other group members. Competition for resources may be costly in itself, and in long-tailed macaques (*Macaca fascicularis*) groups are likely to divide into smaller groups in times of food scarcity (Noordwijk and Schaik 1986). This competition for resources can result in a range of forms of intra-group conflict, such as aggressive fighting over females in males of the fig wasp *Philotrypesis pilosa*, which often results in severe injuries (Murray 1987). These costs may be overcome through different group-living strategies. One such strategy is eusociality, which will be examined further in section 1.4.

Section 1.2: Predation

Predation is an important driver of evolution, both for the predator themselves and for their prey. Predators may select prey for a variety of reasons, such as targeting more familiar prey (Khorozyan et al. 2018) or targeting more vulnerable prey (Cresswell and Quinn 2004). Predators may also end up simply targeting prey that is more easily detectable (Krause and Godin 1995). In many cases, selection of prey involves a trade-off between quality of prey, ease of perception and ease of capture, and these factors influence both predator and prey evolution, and predator and prey strategy.

While large groups of animals are more conspicuous and provide larger quantities of food for predators, they may also be better defended. Some group-living species, such as meerkats or dwarf mongoose, benefit from vigilance behaviours that help them perceive and respond to predators (Rasa 1986; Clutton-Brock et al. 1999; le Roux et al. 2009; Santema and Clutton-Brock 2013). In other cases, larger or denser groups may confuse predators. For example, sticklebacks experienced a reduced success rate when predating upon dense groups of daphnia (Ioannou et al. 2009), cichlids experienced reduced success when predating on larger shoals of guppies (Krause and Godin 1995), and sparrowhawks or peregrine falcons predating upon flocks of redshanks experienced a reduced success rate when targeting larger flocks (Cresswell 1994). Groups of animals may also be able to cooperate to drive predators away, or even inflict harm. Group mobbing behaviours, as well as retaliation, may result in predators being driven off, injured, or even killed (Janzen 1970; Saitō 1986*a*; Arnold 2000). These forms of defence will be discussed further in section 1.3.

Despite this increased defence experienced by larger groups of animals, predators may often preferentially target larger or denser groups of prey. In the cases of sticklebacks predating on daphnia (Ioannou et al. 2009), cichlids predating upon guppies (Krause and Godin 1995), and birds of prey predating upon redshanks (Cresswell 1994) described above, while predators experienced reduced predation success on larger or more dense groups, they also preferentially targeted these groups. This is likely to be because larger or denser groups are easier to perceive, and indeed in some cases predators preferentially target smaller groups. For example, cheetahs preferentially target smaller groups of gazelle, and experience an increased success rate for doing so (Fitzgibbon 1990*a*). This altered strategy likely relies on having senses keen enough to readily perceive smaller groups.

Some prey are more spatially constrained than others. While gazelles or guppies may travel throughout their home range, animals such as meerkats or many species of ants are tied in space to a nest structure. These living arrangements affect how visible and easy to catch prey may be, but also how well defended they may be (Edmunds 1974), and as such have an effect on predation behaviour.

An example of prey that are spatially constrained are the nests of birds. Eggs are unable to move, and parents must remain near their eggs. In these cases, much of the research has been on the density and distribution of nests. There appears to be no significant difference in predation with changes in the distribution of artificial birds' nests (Picman 1988; Reitsma 1992), regardless of the density of nests (Reitsma 1992), or whether the nests are uniformly distributed, randomly distributed, or clustered (Picman 1988). As such, it appears that the density of birds' nests does not have a significant impact upon predation.

These studies showing a lack of impact of the density of birds’ nests upon predation were performed on artificial nests, however. Predation on artificial nests differs from predation on natural nests, and differs from predation on natural nests with artificial eggs, and so these studies may not necessarily reflect actual predation behaviour (Hoset and Husby 2019). For example, when artificial nests were placed in clusters and solitarily, predation was higher on clustered nests than solitary nests, suggesting that predators would preferentially target denser groups of nests (Andersson and Wiklund 1978). However, when real fieldfare parents were present, the reverse was found, and predation was lower when nests were near to a colony (Andersson and Wiklund 1978). If only artificial scenarios had been considered, the effects of parental defence would have been overlooked, and actual predator choice would have been missed.

As well as the distribution of nests, the physical structure of the nest itself influences and is influenced by predation pressure. Nest crypsis (Albrecht and Klvaňa 2004), nest size (Sieving and Willson 1998; Biancucci and Martin 2010) and the medium in which the nest is constructed (Christman and Dhondt 1997) are all factors that may be influenced by predation.

In the case of nest size, predation risk increases as nest size increases in tropical birds, as well as in some temperate species, suggesting that predators are more likely to predate upon larger nests. Similarly, smaller nests in social spider mites (*Stigmaeopsis* spp.) better protect eggs from predators (Mori and Saitō 2004). In the experiment which found this result, females were removed from nests in order to determine the protective capabilities of the nest structure itself. However, social spider mites do defend their eggs (Saitō 1986*b*), the effectiveness of this defence increases with increased density of female spider mites (Saitō 1986*a*), and the population of the nest is proportional to the size of the nest (Mori and Saitō 2004). As such, the removal of females for this experiment means that, while the study found the effects of the size of the physical nest structure, the results are unlikely to be the same when females are present.

Colonial species, such as meerkats or ants, are also often spatially constrained, and are often made up of a range of ages of individuals. In such cases, different group sizes may affect different demographics of the colony differently, based upon the wider pressures of the environment. For example, when meerkats live in areas of high predator density, juvenile mortality decrease as group size increases, while, in contrast, in an area of relatively lower predator density, juvenile mortality increases as group size increases (Clutton-Brock et al. 1999). Adult mortality decreases with increasing group size in both environments. It was suggested that mortality was higher in small groups when predator density was high as there were fewer helpers to guard juveniles, while mortality was higher in large groups when predator density was relatively lower due to competition for resources (Clutton-Brock et al. 1999). In this case, we can see that the size of a group may protect different demographics of individuals differently.

Ants are another group of colonial animals which are consumed by predators, ranging from large mammals such as bears (Noyce et al. 1997; Swenson et al. 1999; Mattson 2001; Auger et al. 2004; Fujiwara et al. 2013; Tosoni et al. 2018), to other colonial animals such as other ants (Lamon and Topoff 1981; LaPolla et al. 2002; Le Breton et al. 2007; Huang 2010), to individual small predators such as spiders (Huseynov et al. 2008; Pekár et al. 2008; Cushing 2012; Rákóczi and Samu 2014; Kwapich and Hölldobler 2019).

Predators may choose to avoid ants which are well defended. Both American black bears (*Ursus americanus*) and Apennine brown bears (*Ursus arctos marsicanus*) appear to avoid consumption of stinging ants (Auger et al. 2004; Tosoni et al. 2018). Both species of bear consumed large quantities of the non-stinging genus *Formica*, with this being the main genus of ant consumed by *U. americanus*. The ant genus mainly consumed by *U. arctos marsicanus* was *Lasius*, another non-stinging genus. Defence is not an equal repellent among all predators, however. Many ants consumed by eastern narrow-mouthed toads, *Gastrophryne carolinensis*, produce some form of chemical repellent, which did not appear to drive *G.*

carolinensis to avoid consuming them (Deyrup et al. 2013). The authors of the study which found this hypothesised that this may indicate that the toads sequester repellents from the ants they consume, in order to bolster their own defences. As such, predators may have their own methods of countering prey defence, and this is likely to influence their prey choice or avoidance.

While defence can influence the way in which predators choose their prey, colony density and nest size may also play a role. Large or densely distributed nests may be more easily detectable, or may be attractive due to providing more food. In the cases of *U. americanus* and *U. arctos marsicanus*, it is possible that both bears mostly consumed *Formica* and *Lasius* due to their conspicuousness, rather than due to avoidance of stinging species. *Formica* inhabits large, conspicuous mounds, and in the habitat of *U. arctos marsicanus*, *Lasius* is common, has high colony densities, and inhabits large underground nests (Tosoni et al. 2018). It has been hypothesised that the size and easy visibility of these mounds contributed to their popularity in the bears' diets (Tosoni et al. 2018). Chimpanzees, *Pan troglodytes ellioti*, may also prefer to predate upon colonies at high colony densities (Pascual-Garrido et al. 2013). Chimpanzees feed on army ants of the species *Dorylus rubellus*, and preferentially targeted ants in forests, where colony density was higher than in savannah-woodland (Pascual-Garrido et al. 2013). However, as this is also the location that chimpanzees were more likely to be, it is possible that chimpanzees are simply more likely to find these colonies, rather than specifically targeting them for predation. While there may be a preference for densely distributed colonies, then, the evidence for this is not strong.

Conversely, some predators may prefer to predate upon less densely distributed nests. Such a preference for less densely distributed nests was found in echidnas predating upon meat ants, *Iridomyrmex purpureus* (Wilgenburg and Elgar 2007). Meat ants are polydomous, meaning that a single colony inhabits multiple nests, a nesting strategy that will be explored in further depth in section 1.4. This means that nests nearby each other are likely to belong to the same colony. It was found that the probability of an echidna predating upon a nest decreased as the number of nests within a 20 mile radius of the nest increased, suggesting an avoidance for densely distributed nests. It has been hypothesised that this is also due to an avoidance of well-defended ants, with more densely distributed nests of meat ants being better defended. This hypothesis will be discussed in depth in section 1.3.

Some predators may also prefer to target ants with smaller colonies, though it is unlikely that this is due to the size of the colony. *Camponotus* is a genus of ants which live in small colonies that are difficult to access, due to living in logs. However, these ants are large, and more nutritious than other ant species in the same location (Mattson 2001). Despite the smaller colony size, both grizzly bears (*Usus arctos horribilis*) and brown bears (*Ursus arctos*) preferred to consume *Camponotus*, suggesting that there is a trade-off between the size or nutritional quality of the ants, and the size of the colony (Swenson et al. 1999; Mattson 2001).

Predation on ants differs in intensity between predators. Despite their size, brown bears in Scandinavia consumed only a fraction of the ants in a mound (Swenson et al. 1999)[1]. Other predators, such as the eastern narrow-mouthed toads (Deyrup et al. 2013) or spiders (Cushing 2012) consume only small quantities of ants at a time. On a similar scale, some parasites impose only minor fitness impacts on nests. For example, the snake *Leptodeira annulata* lays its eggs in the fungus gardens of the ant *Atta columbica*, benefiting from protection from egg predation and good climatic conditions (Baer et al. 2009). Though the impacts of this on the ants is unknown, some fitness impact is likely. In contrast, some predators, like army ants, consume the majority of the brood in the nest, with *Trachymyrmex arizonensis* colonies raided by the army ant *Neivamyrmex rugulosus* containing 90% fewer eggs and brood than unraided colonies (LaPolla et al. 2002). This is also the case in some parasitic species, such as socially parasitic ants, which remove all brood from the nest of a targeted ant (Pamminger et al. 2014).

Prey are not undefended against predators. As discussed here, prey may be defended by living in groups, through vigilance, or through chemical repellents, among other forms of defence. These varieties of defence available to prey will be discussed further in section 1.3.

Section 1.3: Defence

In the book *Defence in Animals: A Survey of anti-predator defences*, Edmunds divides animal defences into two major types: primary defence, which occurs whether or not a predator is present, and serves to reduce the chances of encountering a predator in the first place, and secondary defence, which occurs in response to the presence of a predator (Edmunds 1974).

There are several forms of primary defence described by Edmunds. These include hiding through living in burrows, rather than out in the open, termed anachoresis (Edmunds 1974;

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[1] This is inferred based on the values in this paper (Swenson et al. 1999), but was not explicitly stated in the paper. Calculations are summarised here.

The dry mass of red wood ants eaten per mound is about 13g. The dry mass of red wood ants available per hectare is 9400g. In the study area, there were 3.8 colonies per hectare; this value includes all species, not just red wood ants.

If we assume that all mounds are monodomous colonies, and all colonies are red wood ants, we find a value of 2473.7g dry mass per mound. As the colony density includes more species than just red wood ants, we should actually expect more red wood ants per mound than calculated in the study area. Therefore, less than 0.5% of each mound is actually consumed.

Pekár 2014), hiding through disguising oneself as a part of the environment, termed crypsis (Edmunds 1974; Kuntner et al. 2016), making predators aware of less obvious defences, such as poison or distastefulness, through clear, bright colours, markings or signals, termed aposematism (Edmunds 1974; Mappes et al. 2005), or mimicking the signals of species that have these defences, termed Batesian mimicry (Edmunds 1974; Pfennig et al. 2001; Raška and Pekár 2019).

Secondary defences can be divided into active, and passive. Passive secondary defences include things such as the presence of spines on sea urchins, which require no action on the part of the prey to come into effect. There are several forms of active secondary defences. These include withdrawal to a prepared retreat, an active form of secondary defence often seen in conjunction with the primary defence of anachoresis. It may also include flight - the movement away from a predator, be it through actual flight, running, swimming, and so on (Edmunds 1974; Ford and Reeves 2008). Active secondary defence also includes 'aggressive defence', termed 'retaliation' by Edmunds. This is the situation in which prey attack predators, reducing the efficiency of predation and driving them away (Edmunds 1974; Ford and Reeves 2008).

Species which live in groups often display a mixture of primary and secondary defences, and that these often have to be considered together when discussing group-living species (Edmunds 1974). One of the major forms of defence for those living in groups is the reduced chance of being predated, due to the presence of other prey and the limited hunger of a predator (Krause and Ruxton 2002). Often termed 'risk-spreading' or 'dilution of risk', this form of defence is often supplemented by some other form of defence, such as flight, being aposematic or possessing the ability for retaliation (Edmunds 1974).

One of the ways that living in groups can improve defence is through the dilution of risk (Krause and Ruxton 2002; Morrell and James 2008). The larger the group, the lower the chance that any one particular individual will be attacked. This means that living in groups lowers the chance of an individual being predated, as long as the increased chance of being detected by a predator caused by living in a group is not so much higher than the chance of a single individual being detected that it would, on average, be safer to live alone. This can be observed in the aphid *Aphis varians*. Individuals have a decreased risk of being predated by *Hippodamia convergens*, a species of ladybird beetle, when they are near conspecifics, even though *H. convergens* is more attracted to large aggregations of *A. varians*, and even though *H. convergens* consumes more aphids as the size of the aggregation increases (Turchin and Kareiva 1989).

Groups of animals are also able to more efficiently work together to drive predators off. One strategy is group mobbing, a behaviour which involves aggression towards predators, regardless of whether the predator is hunting or not. This aggression may be in the form of noise or a display, but it may also be in the form of a physical attack. In noisy miners (*Manorina melanocephala*), an Australian species of bird, mobbing can involve groups of over one hundred birds (Arnold 2000), though the number of birds involved in mobbing for the defence of a nest does not correlate with the success of the nest.

Another form of defence found in group living species, termed 'retaliation', or 'aggressive defence', involves prey attacking predators to drive them off, or even kill them. Coatis (*Nasua narica*), for example, have been observed attacking predators in response to an attack on a group member (Janzen 1970). Another group living species, spider mites (*Schizotetranychus celarius*), defend their eggs against predators through counter attacking. In this case predators had a lower chance of survival when the defending groups were larger (Saitō 1986*a*). Such defence is also observed in colonial animals. Colonies of very closely related individuals may benefit more strongly from retaliation than groups of more distantly related through inclusive fitness benefits (discussed further in section 1.4). For example, the clonal aphid *Pemphigus spyrothecae* produces soldiers which defend the galls that the colony inhabits from predators, often dying in the process (Foster 1990). As the aphids are clonal, the soldiers still benefit from retaliation via inclusive fitness, even if they die.

Some prey species prefer to defend through fleeing, rather than attacking the predator. Improved vigilance in group living species may result in a faster reaction to predators, allowing the group to flee earlier. This is observed in groups of white-tailed deer (*Odocoileus virginianus*) responding to approaching humans. Larger groups of deer were more likely to notice and flee than smaller groups (LaGory 1987). However, other benefits of group living, such as the dilution of risk, may mean that there is less of a benefit to fleeing than to remaining in place. A review of flight in group living species found a diversity of responses to predators, including groups fleeing sooner, or later than individuals (Ydenberg and Dill 1986). As such, the effects of group living on flight is likely to depend on the species and its life history traits.

In many animals with colony structures, the group is tied in space to a nest, which may have an effect on their defensive abilities. The 'static' existence of the nest means that they are less able to exhibit defensive behaviours such as flight or predator confusion, but may still benefit from vigilance or retaliation, as well as the protection provided by the physical nest structure via anachoresis (Edmunds 1974). Meerkats, for example, are similarly tied in space, living in extensive burrow networks, and living in groups allows for improved vigilance, as well as burrows to retreat to (Clutton-Brock et al. 1999).

Colonial species can also use retaliation, as observed in an army ant *Dorylus* sp. These ants are predated upon by chimpanzees (Allon et al. 2012), and are often exposed to predators while travelling on the surface during raids (Schöning et al. 2005). Chimpanzees feed on *Dorylus* by inserting a tool fashioned from a stick onto a trail or into nest entrances.

The ants respond by travelling rapidly up the tool, where they are able to bite the predator in order to drive it off (Schöning et al. 2005; Allon et al. 2012).

Some species of ants respond to predators by evacuating the nest, such as seen in *Camponotus festinatus*. When exposed to *Neivamyrmex nigrescens*, a species of army ant, *C. festinatus* responds by evacuation of the entire colony, including brood and the queen (Lamon and Topoff 1981). This evacuation has been described as 'explosive', and involves *C. festinatus* retreating to climb nearby vegetation, remaining still for several hours before returning to the nest. Evacuation is triggered if *N. nigrescens* enters the nest, or if a single *C. festinatus* forager makes contact with *N. nigrescens* and manages to return to the nest.

Ants may respond differently to different predators (Teppei et al. 2019). In Madagascar, *Aphaenogaster swammerdami* ants are preyed upon by *Madatyphlops decorsei*, a snake. Another species of snake, *Madagascarophis colubrinus*, is often found in the nests of these ants, but is not a predator of the ants. A study involved exposing ants to *M. decoresei*, *M. colubrinus*, and *Thamnosophis lateralis*, a sympatric frog-eating snake used as a control. They found that ants responded to *M. decoresei* predominantly by evacuating the nest, while they predominantly responded to *T. lateralis* by attacking (biting it), and did not respond to *M. colubrinus*. It was hypothesised that the ants' response to *T. lateralis* is a generic response to any perceived threat, while the response to *M. decoresei* is a response to a specialised predator (Teppei et al. 2019).

A primitively eusocial (see section 1.4) colonial species of wasp, *Polistes canadensis*, exhibits dilution of risk as a form of defence (Jeanne 1979). This species builds combs consisting of several cells, in which eggs are deposited by the colony's queen. Combs are constructed, and new cells are gradually added to the comb. Eventually, the construction of the comb stops abruptly, and a second comb is constructed a few centimetres away from the first. This is repeated with a third, and so on. A predator for *P. canadensis* brood is moth larvae of an undescribed species, which mostly feed on the waste of *P. canadensis* brood, but may also prey on the brood itself (Jeanne 1979). In addition, the moth larvae may weaken the comb by tunnelling through it, causing the comb to collapse and killing brood. By dividing brood into several combs, *P. canadensis* benefits from dilution of risk (Jeanne 1979). The chance that brood will be affected by moth larvae will be reduced, as infestation cannot spread between combs. This approach to risk spreading, by constructing several combs, is remarkably similar to polydomy in ants. Polydomy, whereby a single colony of ants inhabits several nests, will be explained and discussed in depth in section 1.4.

Section 1.4: The Model System

The model system for this thesis is ants. Ants are a family of eusocial insects, and exhibit a wide range of nesting strategies. In this thesis, I will specifically investigate polydomy, in which a single colony of ants inhabits multiple nests, and monodomy, in which a single colony of ants inhabits a single nest. This section will introduce the model system, and describe how it relates to other comparable systems.

Social groups vary in relatedness. Some groups may be mixed-species, such mixed-species shoaling in various species of fish (Ehrlich and Ehrlich 1973; Krause et al. 2000; Weber et al. 2009; Paijmans et al. 2019), or mixed species groupings in gazelles (Fitzgibbon 1990*b*), while others are groups of animals of the same species. Among same-species groups, some groups may be of unrelated or distantly related individuals, as seen in Natterer's bats (Scott et al. 2018), or mixes of related and unrelated individuals, as observed in mongooses (Creel and Rabenold 1994) and kingfishers (Reyer 1984). Other groups, such as black-tailed prairie dogs (Hoogland 1983) and social spiders (Pruitt and Avilés 2018), tend to be composed of closely related individuals. The extreme in relatedness in social groups is found in eusociality, a phenomenon observed in species including mole-rats, bees, shrimps and ants (Avilés et al. 2012; Chak et al. 2017; Kappeler 2019).

In a 2005 review, Wilson and Hölldobler define eusociality as "an evolutionarily advanced level of colonial existence, *(in which)* adult colonial members belong to two or more overlapping generations, care cooperatively for the young, and are divided into reproductive and nonreproductive (or at least less-reproductive) castes" (Wilson and Hölldobler 2005). This definition has recently been criticised (Boomsma and Gawne 2018), as it does not include the physical differentiation of queen and worker castes. Many eusocial species are also considered to be superorganisms - in which a colony of multicellular organisms are considered to be a level of organisation akin to multicellularity itself. The requirement for the physical differentiation of queen and worker castes is considered important, as it allows eusocial species to also represent an irreversible evolutionary step into superorganismality. However, for the purposes of this thesis the Wilson and Hölldobler definition will be used, as it is a commonly accepted definition that provides a readily understandable insight into the study system.

This thesis will focus on ants as eusocial species. In ants, the differentiation of roles is seen in the existence of castes, with individuals being physically differentiated for acting in different roles in the colony, including a worker caste and a queen caste, with, the queen being the only reproductive female caste in most species (Wilson and Hölldobler 2005). As such, ants are eusocial under both Wilson and Hölldobler definition, and under the definition suggested through Boomsma and Gawne's critique.

Eusocial species often live in physical structures, such as nests or similar cavities, and this has been argued to be important for the evolution of eusociality (Ruxton et al. 2014). Such a structure would be important for providing physical protection for the colony while it grows, and is often expansible (Alexander et al. 1991; Crespi 1994), such as in burrows underground. In addition, these structures provide places for the storage of food and are long lasting, providing the colony with the time it needs to establish itself and grow (Alexander et al. 1991; Crespi 1994). In this way, eusociality provides another form of defence in the form of the nest structure, in addition to the defences seen in other group living animals.

The inclusive fitness benefits of kin selection play an essential role in driving eusociality. Inclusive fitness is the theory that genes will increase in frequency through improving the fitness of the individual with the gene (direct fitness), or through improving the fitness of relatives (indirect fitness), which are likely to also bear the same gene (Hamilton 1964). Eusocial species are an extreme in kin selection, because for the non-reproductive caste, fitness is entirely indirect. This reduces the potential for intra-group conflict, as fitness is not based upon the health or reproductive output of the (non-reproductive) individual, but rather the health or reproductive output of the reproductive caste (Hamilton 1972; Queller and Strassmann 1998). There still remains the potential for reproductive conflict, particularly in species in which workers may be physically able to produce young. In the ant *Harpagoxenus sublaevis*, for example, workers are able to reproduce, but have their reproductive ability suppressed by the queen, and in part reproductive workers suppress the reproduction of subordinate workers (Bourke 1988).

Many of the costs of group living, discussed in section 1.1, are resolved in eusocial species. While group living organisms may experience fitness losses as they compete for resources, eusocial colonies are more able to survive in resource-limited scenarios than other group structures (Fronhofer et al. 2018), as the fitness of an individual in a eusocial colony is based upon the health of the queen. Eusocial colonies are also more able to mitigate the risks of predation or disease, with individuals in eusocial colonies allowing themselves to die in order to reduce the spread of disease, or in order to drive off predators (as reviewed in Sun et al. 2018).

Eusociality itself varies in complexity. In the ants, for example, some colonies may be monogynous - that is, have a single queen. However, in contrast to this, some colonies may have multiple reproductively active queens, and therefore be polygynous. Similarly, colonies may be monodomous, in which a single colony of ants inhabits a single nest. On the other hand, some colonies of ants inhabit multiple nests, termed polydomy.

Polydomy is defined as "an arrangement of an ant colony in at least two spatially separated nests" (Debout et al. 2007). This can be contrasted with monodomy, in which an ant colony inhabits a single nest. For the purposes of this thesis, the ants inhabiting a single nest within a polydomous colony will be referred to as a 'subcolony'. Polydomy can be difficult to identify in the field, as it may be hard to define the boundaries between colonies (Ellis et al. 2017), and each method of defining these boundaries has its limitations.

One way of identifying polydomy in the field may be through the sharing of resources, as this is one of the major aspects of a eusocial colony. However, not all movement of resources may be cooperation - it may be difficult to determine whether exchange of resources is sharing, or stealing food or brood from others of the same species. Appeasement behaviours may also result in subordinate colonies giving resources to a dominant colony (Ellis et al. 2017). Beyond this, it is also difficult to record sharing of resources. It may most easily be recorded through the movement of marked resources through the population, but as this means the point of exchange is not recorded, it is harder to tell whether the transaction is sharing or not.

Another way of identifying polydomy in the field may be through colonies sharing space, either through a lack of aggression between nests, or the clustering of nests in an environment. This implies that there is a level of cooperation between nests, or a lack of competition, as organisms, particularly sessile organisms, may be expected to maintain a distance from other organisms that they are in competition with (Hovanes et al. 2018). However, aggression is costly, and it may simply be more energy efficient for a subcolony to avoid engaging in conflict unless the benefits are great, such as when resources are low. As well as this, different levels of clustering or dispersion may be evident through observing the landscape at different scales, meaning that the scale of study may influence whether or not polydomy is judged to be present (Cook et al. 2013; Ellis et al. 2017).

Finally, we may identify polydomy based on how genetically similar ants in nests are to each other. This makes sense, as a colony is expected to be a genetic unit, but it may not always be effective. Polygynous colonies - colonies with multiple queens - have high within-nest genetic diversity, and in polydomous colonies genetic structure may be better explained by the nest's location in space, rather than the ants being from different colonies (Ellis et al. 2017). Alternatively, recently separated colonies may not have begun to diverge enough to tell the difference.

Overall, while there are a range of methods of identifying polydomy in the field, in practice these methods each have their own flaws. Nevertheless, the ability to identify polydomy is important, as it allows us to observe identified polydomous colonies or species and their behaviours, and from this understand the benefits and evolutionary drivers of polydomy.

There are several hypotheses to explain the evolutionary drivers behind polydomy (Robinson 2014). These include the hypothesis that polydomous colonies are better able to access resources distributed widely in an environment, that polydomous colonies are able to grow in size regardless of nest-size constraints, and that polydomous colonies are better defended against predators.

Polydomous colonies are separated into multiple subcolonies which can be spread widely across an environment, and because of this they have several nodes from which ants can be deployed and to which they can retrieve resources. The colony as a whole may therefore be more able to find resources quickly, and be more able to exploit them. However, polydomous colonies may be easily outcompeted by monodomous colonies when competing for a resource, as each nest in a polydomous colony may have fewer ants to recruit for exploiting a resource (Cook et al. 2013; Robinson 2014). This assumption that nests in polydomous colonies contain fewer ants may not hold true in reality, as will be discussed further in Chapter 4.

In a monodomous colony, the size of the colony is linked to the size of the nest that the colony inhabits. This is particularly relevant when it comes to species that live in physically constrained nests, such as in cavities in wood or rock (Robinson 2014). Polydomous colonies overcome this constraint, as the colony is divided into several nests, meaning that a polydomous colony theoretically has no bounds on its size. In some species, such as *Temnothorax nylanderi*, colonies become polydomous as more nest sites become available, and return to monodomy once the nest sites are no longer available (Foitzik and Heinze 1998). Nest size may also be restricted indirectly by other pressures, such as predators that preferentially target large nests.

It is thought that polydomy also provides defensive benefits to the colony. There are three main hypotheses for how this can be mediated. The first hypothesis, the risk-spreading hypothesis, suggests that the spread of a colony across several nests acts as risk-spreading for the colony (Debout et al. 2007; Robinson 2014). If a single nest is destroyed, by a predator or abiotic phenomenon, a polydomous colony will still persist, while a monodomous colony would be lost. The second hypothesis, the retaliation hypothesis, suggests that polydomous subcolonies may also be better able to retaliate against predators, by recruiting defenders from connected subcolonies - meaning that a given subcolony is relatively better defended for its size (Wilgenburg and Elgar 2007). The third hypothesis is that subcolonies may be able to evacuate either the subcolony itself, or its brood, to connected nests, when the nest is attacked or under threat (Denis et al. 2006). This thesis will focus on the first two of these hypotheses: risk-spreading, and retaliation.

In polydomous ants, risk-spreading is hypothesised to occur in the Argentine ant, *Linepithema humile*. Argentine ants are a polydomous, polygynous species that is frequently referred to as 'unicolonial' (Abril et al. 2013), meaning that the entire population of ants in an area acts as a single colony (Robinson 2014), and that the colony is polygynous (Holway et al. 2002). This means that, if one nest in a colony survives, it will be likely to have at least one queen and survive (Hee et al. 2000). Similarly, many multicolonial polydomous species are also polygynous, or, if not polygynous, have sexual brood in multiple nests (Robinson 2014).

So long as a queen or brood survives, the colony can continue to reproduce after one or multiple connected nests in the colony are destroyed. However, these risk-spreading mechanisms would not be in place in monogynous species that do not have sexual brood in multiple nests, and the evolution of monogynous polydomy is likely to have different drivers to the evolution of polygynous polydomy (Debout et al. 2007; Robinson 2014).

Polydomous colonies may also be more effective at defence than monodomous colonies in the form of retaliation. In the case of the meat ant, *Iridomyrmex purpureus*, echidnas were less likely to predate upon nests in areas of high nest density (Wilgenburg and Elgar 2007). In addition, the proportion of nests in a colony predated upon reduced with increased numbers of nests in a colony. It was hypothesised that this is because nearby subcolonies will defend nests of the same colony that are not their own, increasing nest defence relative to the size of the subcolony actually experiencing predation (Wilgenburg and Elgar 2007).

Based on these hypotheses, we may expect polydomous colonies to increase in frequency, relative to monodomous colonies, when placed under increased pressure from predators. This system and these hypotheses provide us with a good opportunity to test our assumptions about both polydomy in general, and the defensive benefits of polydomy in particular, through the use of modelling. Several models of polydomy exist (Table 1; Schmolke 2009; Cook et al. 2013; Burns et al. 2019), and in section 1.5 I will provide an overview of three of them and their results.

Section 1.5: Models of Polydomy

Previous models of polydomy have been written to investigate specific potential evolutionary drivers. One driver investigated in particular is foraging. Schmolke in 2009 modelled foraging in polydomous and monodomous colonies, and found that, in their model, when food sources were randomly distributed across the environment, polydomy had a higher foraging success rate. When food sources were clustered in a few locations, polydomy and monodomy were equally successful.

Cook et al. adapted Schmolke's model in 2013 to take recruitment into account, and found that while polydomy had a higher foraging success rate when food sources were scattered, it had a lower success rate than monodomy when food sources were clustered. This was because nests of monodomous colonies were larger and better able to recruit large groups of ants for the rapid exploitation of food sources than nests of polydomous colonies.

A different model (Burns et al. 2019), focussing on the nest as the agent, rather than the individual ants, examined the success of polydomy under several foraging scenarios, including manipulating the cost of foraging, and the distribution of food sources through space (clustering or random distribution) and time (fluctuating food source availability). This study found that polydomy has a higher success rate when foraging is costly.

Contrary to Cook et al.'s findings, however, Burns et al. found that polydomy was favoured when food sources were clustered in distribution. They suggested that this may be due to the fact that Cook et al. modelled only a single colony at a time, and therefore did not take into consideration the effect competition between colonies may have. When Burns et al. removed competition from their model, they found that the success rate of polydomy decreases when food is clustered; this matches the findings of Cook et al.

The model by Burns et al. examined the success of polydomy under a range different evolutionary drivers. Beyond foraging, these drivers included the size of the nest (termed 'carrying capacity'), and stochastic nest destruction. There was a clear influence of carrying capacity on the success of polydomy (Burns et al. 2019), with polydomy increasing in frequency at lower carrying capacities. This matches observations of polydomous species in the wild, such as *T. nylanderi,* as discussed in section 1.4. Carrying capacity also had interactive effects with other conditions in the model - food source stochasticity, food source distribution, and stochastic nest destruction.

Most relevant for this thesis, there was also an influence of stochastic nest destruction on the success of polydomy, with polydomy increasing in frequency when there was a chance of nest destruction. This increase was more pronounced when carrying capacity was high. In this model, nest destruction was not modelled in any particular form, such as predation or natural disaster, and nests did not have any active forms of active defence. This suggests that the model’s resulting increase in polydomy under increased predation risk was specifically due to dilution of risk, and aligns with the risk-spreading hypothesis and previous literature.

This thesis involves the adaptation of the Burns et al. model to examine the success of polydomy under the specific pressures of predation. The model was originally written to represent a generic form of stochastic nest destruction, involving the complete destruction of the nest, so there are some key differences from predation in reality. Predators do not randomly target prey (Ioannou et al. 2009), and do not always destroy an entire ant nest or subcolony - even predators as large as brown bears consume only a fraction of the ants in a nest (Swenson et al. 1999), as discussed in section 1.2.

The Burns et al. model was chosen as a starting point as it had already explicitly investigated the influence of stochastic nest destruction, making it effective for further investigation of the phenomenon. By using the Burns et al. model as our basis, we were also able to better understand why the original model had produced the results it did. As part of our model, we investigated the destruction of a range of numbers of ants. By doing so, we would be able to determine whether the improved success of polydomy under the pressure of stochastic destruction found in Burns et al. 2019 was only seen when the entire nest would be destroyed, or whether it was the result in a gradual increase in success as destruction increased.

We ran three versions of the model. The first contained no nest defence, and aimed to test the hypothesis that polydomy may confer advantages to a colony through risk-spreading. The second exhibited defence at the level of the nest, which we hypothesised would result in an increase in the frequency of monodomy, as monodomous nests in the Burns model on which this model is based tend to be larger than polydomous nests (Burns et al. 2019). The final version of the model allowed nests in polydomous colonies to recruit ants from other, directly connected nests in the same colony, increasing the defending population, as has previously been hypothesised to happen in polydomous colonies (Wilgenburg and Elgar 2007), referred to as the retaliation hypothesis in section 1.4. We hypothesised that this would result in higher frequencies of polydomy.

Each of these versions of the model were run under three conditions of predator preferences for nests based on size, with predators in the first condition preferring smaller nests, the second having no preference, and the final preferring larger nests. We hypothesised that polydomy would be less strongly affected by increasing predation intensity than monodomy when predators preferentially target large nests, and that this trend would be reversed when smaller nests were targeted. This is due to the fact that, in the model, monodomous nests tend to be larger than polydomous nests.

We also ran the model at a range of different, consistent levels of predation, with predators removing logarithmically larger numbers of ants at each predation event (referred to as 'predation intensity'), until the carrying capacity of a nest was reached. We hypothesised that there should be a gradual increase in the frequency of polydomy as the intensity of predation increased.

Chapter 2: Methods

Section 2.1: Model Initialisation

The model used in this paper was developed from Burns et al.'s model (2019), a dynamic network model in R 3.4.1. Individual ants are not explicitly modelled, but instead the agents in the model represent nests of ants.

The model simulates an arena, seeded with 10 initial nests (Table 2.1). Each initial nest has a unique colony identification number and a unique nest identification number, and nests are distributed across the arena, with their location selected randomly from a uniform distribution of potential locations covering the entire arena. Half of the colonies are polydomous while half are monodomous. Monodomous colonies always comprise only one nest, and are unable to share food with other nests. Polydomous colonies can consist of several nests, and can share food between nests of the same colony. At the start of the model, each nest represents a unique colony, so that the five initial polydomous nests do not share food. Each nest can house a fixed maximum number of ants (here termed the carrying capacity, *K*). Simulations were run at three carrying capacities (Table 2.2). Forty food sources are generated in the arena with a random uniform spatial distribution (Table 2.1), and with a constant rate of productivity each season (Table 2.2).

Letter	Description	Value	Unit
A	Starting number of nests	10	
C	Starting number of colonies	10	
G	Number of food sources	40	
I	Food source distribution	Random uniform	
X	Length of season	20	timesteps
J	Number of seasons	500	
r	Number of replicates per condition	30	
B	Arena length/width	50	m

Table 2.1: Starting variables for the model. Table adapted from Burns et al. 2019.

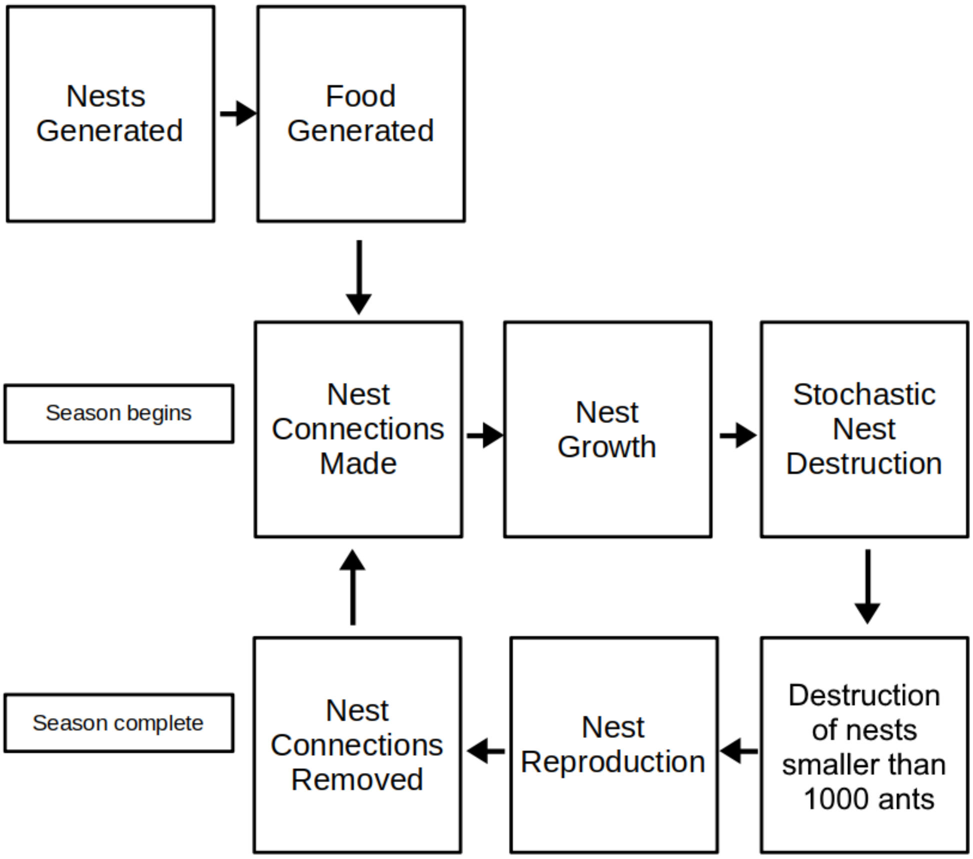

Figure 2.1: Flowchart depicting the structure of the model.

Letter	**Description**	**Value**	**Units**	**Justification**
F_i	Rate of productivity of food source *i*	Constant - 4,000	resources t^{-1}	Constant level of productivity (Burns et al. 2019)
K	Carrying Capacity	Low: 30,000 Medium: 100,000 High: 300,000	ants	Previous work found an interaction between the effects of predation and *K* when comparing *K* = 30,000 with *K* = 300,000; we added an intermediate value of K = 100,000 to increase coverage of this effect.

E_{ij}	Connection cost for a connection from nest *i* to food source *j*	Internest - 0.00001 Foraging – 0.00003	resources t^{-1}	Internest cost is unchanged from Burns et al. 2019. Foraging cost selected as a midpoint of the extreme levels of 0.00001 and 0.00005 used in Burns et al. 2019.
P	Probability of stochastic nest destruction	See Equation 5.		
Y	Number of ants lost to a stochastic nest destruction event	0; 1; 10; 100; 1,000; 10,000; 30,000; 100,000; 300,000 (with max *Y* = K)	ants	Selected as logarithmically increasing values of nest destruction, allowing us to observe the response of the ant population to a range of levels or types of predation.

Table 2.2: Model parameters which have been changed from Burns et al., their values, their units, and justifications for changes.

Letter	**Description**	**Value**	**Units**
Q	Rate at which an ant can transport food to its nest along an outgoing connection	0.1	resources ant^{-1} t^{-1}
H	Rate of population size shared by polydomous nests	0.01	proportion t^{-1}
V	Rate of colony loss	0.05	$proportion^{1}$ t^{-1}
U	Constant to adjust probability of creating new nest	K x 20	ants
S	Proportion of a parent nest that is donated to a new nest	0.1	
D	Minimum population threshold for nest survival to next season	1000	ants

Z	Constant to adjust probability of removing connection based on profitability	0.001	
M	Probability of strategy mutation	0.1	

Table 2.3: Model parameters that remain unchanged from Burns et al., their values and their units. Values and descriptions from Burns et al. 2019.

Section 2.2: Process

The unit of time in the model is a timestep, during which nests are allowed to grow as detailed in section 2.2. A season consists of twenty timesteps of growth plus the creation and destruction of connections between nests and food sources, or between polydomous nests of the same colony, predation on nests, as well as the destruction or reproduction of nests, as detailed in Figure 1 and described further in this section.

At the start of each season, connections are made between nests (internest trails) and food sources (foraging trails). The probability of a given connection being made is proportional to the distance between a nest and a food source:

$$p_{ij} = \frac{L_{ij}^{-2}}{\sum_{n=1}^{\infty} L_{in}^{-2}}$$

(Equation 2.1)

where p_{ij} is the probability that a connection is made from nest *i* to nest or food source *j*, and L_{ij} is the length of a connection between nest *i* and nest or food source *j*.

The number of connections each nest can have, T_i increases linearly with the number of ants in the nest, N_i :

$$T_i = \left\lceil N_i \frac{Q}{F} \right\rceil$$

(Equation 2.2)

where *Q* is the rate at which an ant can transport food to its nest along a connection, *F* is the rate of productivity of the food source (constant of 4000 food units per timestep), and T_i is the number of connections that nest *i* makes. T_i is rounded up to the nearest integer.

In the case of polydomous nests of the same colony, nests will also connect with each other at this point, with the probability of a connection also being relative to the distance between nests and their sizes (Equation 2.1). These inter-nest connections are unidirectional. Inter-nest connections are treated the same as foraging connections, with the exception that the cost of a connection (E_{ij}; Table 2.2) is different for inter-nest and foraging connections. Probabilities for inter-nest and foraging connections are calculated together. The population of the nest, N_i, is divided equally between all connections that a nest has. Each connection has a cost, based on the length of the trail L_{ij}, the number of ants committed to the trail, and a constant connection cost, E_{ij} (Table 2.2). This cost reduces the actual rate at which the nest receives food from the food source or nest, R_{ij}.

Nests grow based on their access to food sources, which may include other nests in the case of nests in polydomous colonies. The growth of the nest is calculated as the sum of the food collected by foraging, subtracting food that would be lost through competition and a constant rate of loss. This occurs throughout the season.

At the end of a season, nest predation occurs, described in detail in section 2.3. In the event of predation, a number of ants (Y) are removed from the nest. The model was tested over a range of values of Y (Table 2.2), allowing us to observe the response of polydomy to a range of levels or types of predation.

After predation, nests containing at least 1,000 ants survive to the next season, and any nests with fewer ants are removed, simulating size-dependent survival over the winter (Kaspari and Vargo 1995). Surviving nests can then create new nests, with the size of each new nest being a proportion, S, of its parental nest, and the parental nest being reduced in size accordingly. The probability of a given nest creating a new nest is proportional to the parent nest's size, with larger nests more likely to reproduce than smaller ones:

$$p_i = \frac{N_i}{U}$$

(Equation 2.3)

where p_i is the probability that nest i reproduces, N_i is the nest size of nest i, and $U = K \times 20$ is a constant. At K, p_i would therefore be 0.05.

Newly established nests have a small chance of having a different nesting strategy to their parent (i.e. polydomous or monodomous). However, if a polydomous nest produces another polydomous nest, these nests are both part of the same colony, though they are not necessarily connected by a trail. New monodomous nests are always new colonies. The final stage is removal of connections, with a probability relative to the connection's profitability, defined as the rate at which a nest receives food from the connection, with more profitable connections being less likely to be removed:

$$p_{ij} = min\left(Z\frac{R_{ij}}{N_i}, 1\right)$$

(Equation 2.4)

where p_{ij} is the probability of a connection between nest i and nest j being removed, and R_{ij} is the profitability of the connection from nest i to nest j and $Z = 0.001$ is a constant. As such, if at least 1,000 profit units per ant in the nest are brought to the nest via the connection, the connection is guaranteed to be maintained.

The new season then begins (Figure 2.1).

Simulations ran for 500 seasons, as preliminary tests showed that this was long enough for the ratio of nesting strategies to reach an equilibrium, and found no notable changes if the simulations were run for longer.

Section 2.3: Nest Destruction

Nest destruction has been adapted from Burns et al. to specifically represent predation. When predation occurs, the size of the predated nest (N_i) is reduced by a number of ants (Y), but not below zero. Unlike Burns et al.'s model, in which nest destruction always involved the loss of the entire nest, our model was tested over a range of values of Y, which increase logarithmically from 0 up until the nest-level carrying capacity, K (Table 2.2).

While in the Burns et al. model nests were destroyed at random, our model allows for predator preference behaviours. The behaviour of predators is represented by the effects that predation has on the number of ants in a nest. As such, individual predators are not explicitly modelled.

Predators may preferentially target nests based on their size (Krause and Ruxton 2002; Ioannou et al. 2009). We modelled nest-level probability of predation as a function of nest size (N_i), represented by a sigmoid function (Equation C2.5, Figure C2.2):

$$f(N_i) = \mu + \frac{\rho}{1+e^{\left(-\left(b-\left({}^{9}/_{K}\right)\right)\times\left(N_i-\left({}^{K}/_{2}\right)\right)\right)}}$$

(Equation 2.5)

where μ = 0.005 is the minimum probability of predation per nest per season, ρ = 0.01 is the interval between minimum and maximum probabilities of predation per nest per season, and b is the predation preference (preference for large nests: 1; no size preference: 0; preference for small nests: -1.

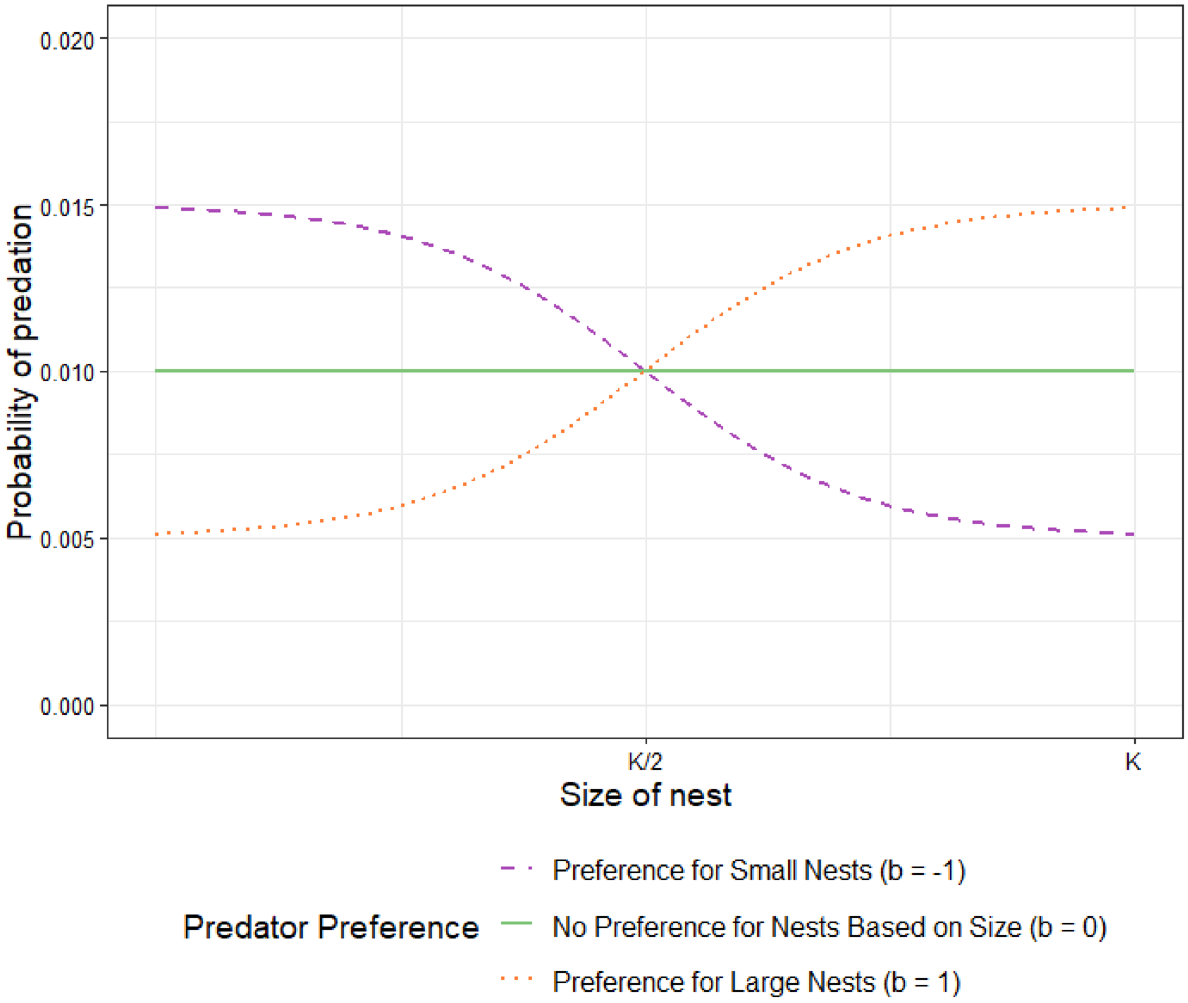

Figure 2.2: Plot of function relating size of nest to probability of predation under three different predation regimes

At the end of each season, each living nest is considered in turn, as in the original model. This was in the same order each season. They have a chance of experiencing predation, with this probability being proportional to the size of the nest, as determined by Equation C2.2. If predation occurs, a number of ants (Y) are removed from the nest.

Section 2.4: Nest Defence

Ants in a nest are likely to defend themselves against predation (Schöning et al. 2005; Allon et al. 2012; Teppei et al. 2019). In the model, nest defence is represented by a two-step function (Equations C2.6 and C2.7, Figure C2.3), which calculates Φ, the probability of successful nest defence (represented as the probability for the cessation of predation). The first step of this function represents recruitment of ants to defend the nest:

$$f(Y_t) = \frac{s}{1 + e^{-h \times (Y_t - m)}}$$

(Equation 2.6)

in which s is the maximum probability of successful defence, defined as 3×10^{-6} in order to allow the number of ants consumed by the predator by the end of predation to cover the range of all possible numbers of ants, h is the gradient of the curve (Figure 2.3), defined as oD_i - W, in which D_i is either the nest size of nest i, or the combined size of defending nests, o is the constant 2.683×10^{-10} and W is the constant 1.783×10^{-6}, with both o and W selected to allow the curve to realistically scale between very low nest sizes and very high nest sizes, Y_t is the number of ants lost at time point t during the predation process, a value between 0 and Y, m is the midpoint of this function, defined as a/D_i, where $a = 1.5 \times 10^{10}$, is a constant, chosen to allow the curve to realistically scale between very low nest sizes and very high nest sizes, and D_i is either the nest size of nest i or the combined size of defending nests.

The probability of successful defence increases with the size of the nest. When successful defence occurs, predation stops and no more ants are lost. The probability of successful defence plateaus at a maximum of 3×10^{-6}, above which the recruitment of further ants will have no effect on the success of defence.

The second step of this function represents the reduction in the chance of successful defence as ants are removed and the nest becomes too small to effectively defend itself. The probability of successful defence rapidly decreases:

$$f(Y_t, D_i) = \frac{s}{1 + e^{0.001 \times (Y_t - D_i)}}$$

(Equation 2.7)

The model draws probabilities from Equation 2.6 until the probability produced by Equation 2.6 is the same as the probability produced by Equation 2.7 at the same number of ants removed from the nest by a predator, at which point probabilities are drawn from Equation 2.7. In this way, smaller nests never reach the optimal level of successful defence (Figure 2.3).

It has been hypothesised that nests in polydomous colonies are also defended by directly-connected nests in the same colony (Wilgenburg and Elgar 2007). We included this scenario by running simulations in which the pool of potential defenders, D_i, comprises not only the targeted nest, N_i, but also nearby nests of the same colony; this increases the rate of recruitment and length of time for which defence can remain at the maximal level before decreasing due to loss of ants to the predator.

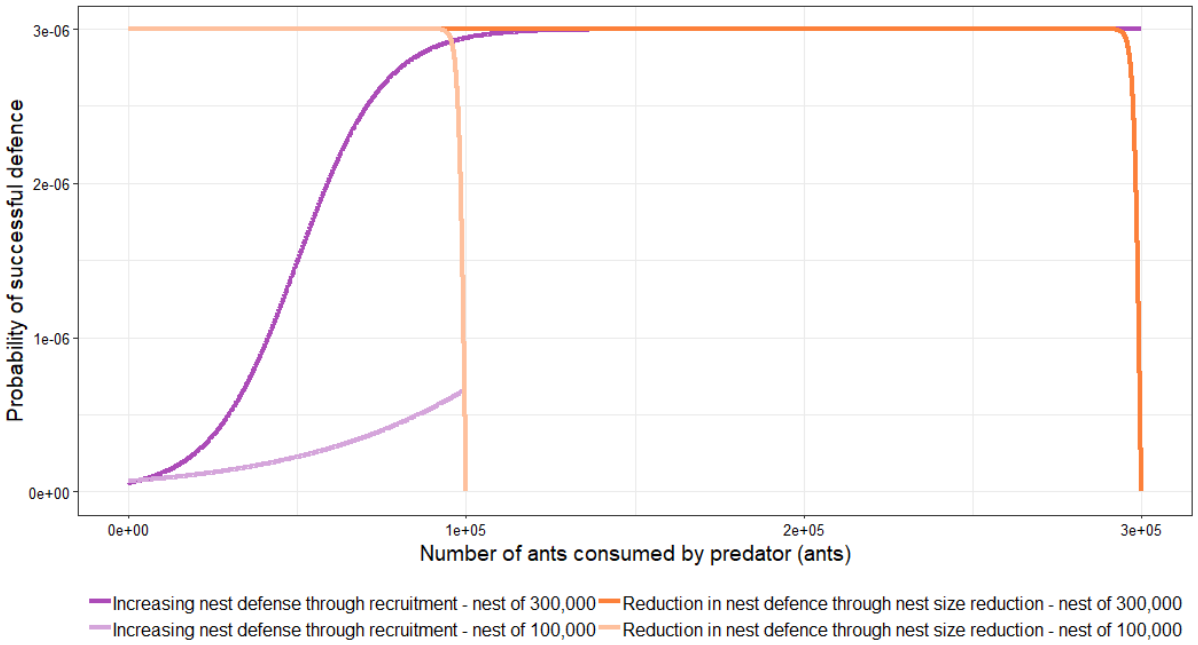

Figure 2.3: Plot of the change in Φ, the probability of successful defence (represented as the cessation of predation) for nests with a defending population of 300,000 ants and a nest with a defending population of 100,000 ants.

Section 2.5. Simulations

The model was run under several conditions (Table 2.4). These included a) no nest defence, b) with defence only on the level of the nest, and c) with nests in polydomous colonies also defended by directly connected nests in the same colony, as detailed in section 2.4. Each of these simulations was run under three different, consistent predator preferences, as detailed in section 2.3. Finally, each of these conditions was also run under a range of different, consistent levels of predation, with predators attempting to consume logarithmically larger numbers of ants at each predation event, until the number of ants consumed was equal to the carrying capacity (Table 2.2).

Variable	**Values**
Nest defence	No defence
	Nest-level defence
	Colony-level defence
Predator preference	Preference for small nests
	No preference for nests based on size
	Preference for large nests
Predation intensity	0; 1; 10; 100; 1,000; 10,000; 30,000; 100,000; 300,000 (with max *Y* = K)

Table 2.4: Variables manipulated in simulations

Section 2.6: Data Analysis

It was decided that statistical analysis would not be conducted on the results of these simulations, and as such we do not report p-values or significance. This is because it is possible to conduct a theoretically unlimited number of independent replicates in a simulation such as this one, and present any effect as significant in this way. As such, p-values or significance are not necessarily meaningful in this scenario, and we did not consider them a good basis for the reporting of any trends found (Wasserstein and Lazar 2016). As trends were clearly observable from the results, we reported on these trends without conducting statistical analysis.

Chapter 3: Results

Section 3.1: No Nest Defence

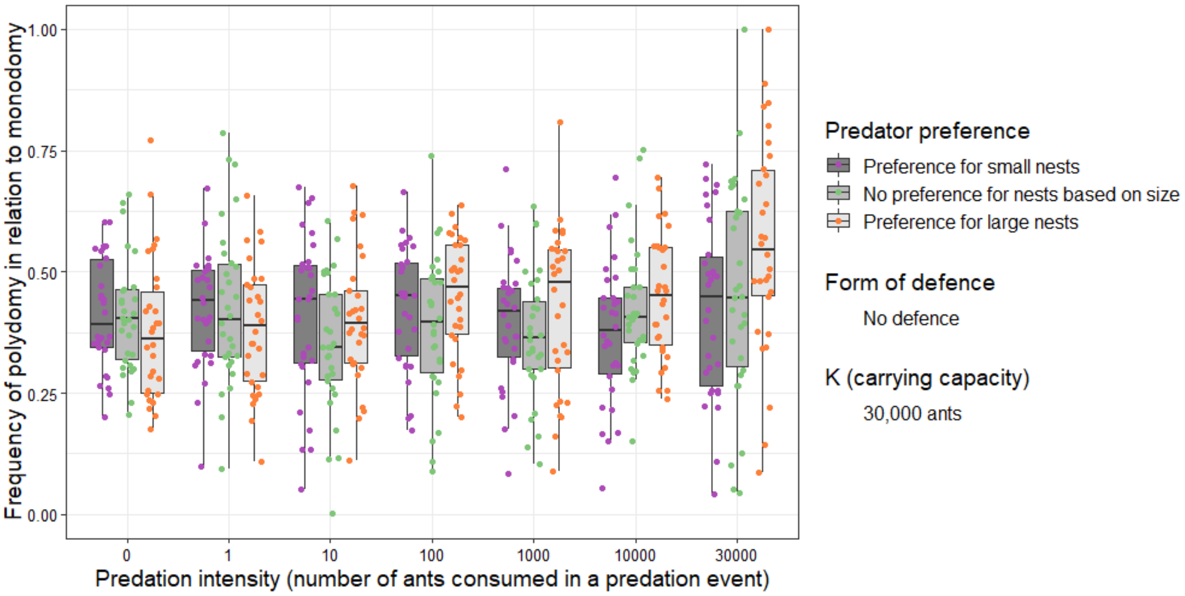

Figure 3.1: Change in frequency of polydomy with increasing predation intensity, when nests exhibit no defensive behaviour. K = 30,000. Top of the box is the 75th percentile, centreline is the 50th percentile, and bottom of the box is the 25th percentile. Top of whisker is the largest value above the 75th percentile, within 1.5 times the interquartile range, and bottom of whisker is the smallest value below the 25th percentile, within 1.5 times the interquartile range.

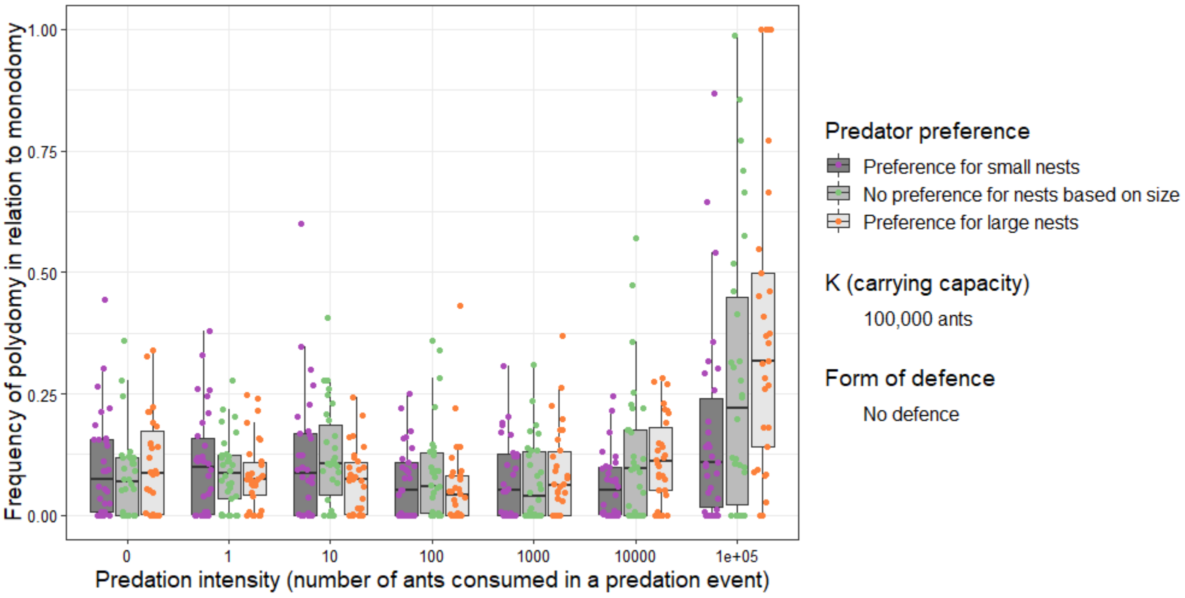

Figure 3.2: Change in frequency of polydomy with increasing predation intensity, when nests exhibit no defensive behaviour. K = 100,000. Box and whiskers as for Figure 3.1.

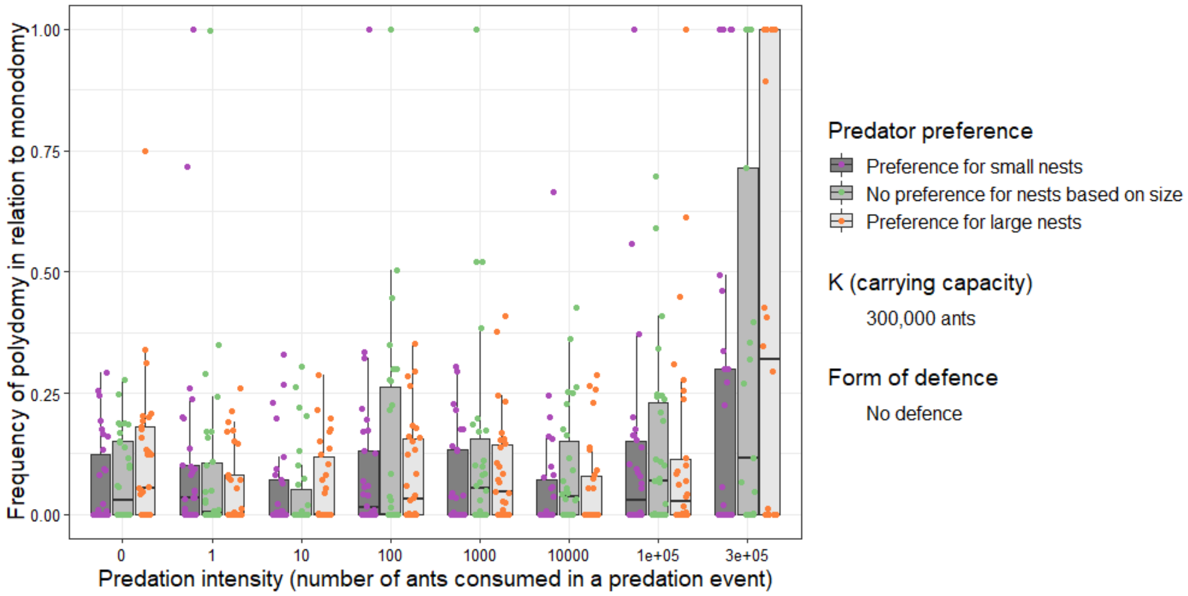

Figure 3.3: Change in frequency of polydomy with increasing predation intensity, when nests exhibit no defensive behaviour. K = 300,000. Box and whiskers as for Figure 3.1.

In these results, frequency of polydomy relative to monodomy refers to the probability of any individual ant belonging to a polydomous colony, as compared to a monodomous colony. It is calculated as the number of individuals in polydomous colonies, divided by the population of all ants in the model.

Contrary to the predictions of the risk-spreading hypothesis, there was no apparent change in the frequency of polydomy with increasing predation intensity when the carrying capacity was 30,000 ants (Figure 3.1). This was regardless of predator preference based on the size of nests predated upon. This is similar to results found in Burns et al. 2019, which found that changes in the frequency of polydomy were small when nest-level carrying capacity was low (K = 30,000).

When carrying capacity was increased to 100,000 ants (Figures 3.2, 3.12), there was an increase in the frequency of polydomy relative to monodomy, but only when the number of ants consumed in a predation event was equal to the carrying capacity, i.e. 100,000. When carrying capacity was further increased to 300,000 ants (Figures 3.3, 3.13), there was again an increase in the frequency of polydomy relative to monodomy, this time only when the number of ants consumed in a predation event was 300,000, again equal to the carrying capacity. In both of these simulation sets there was no apparent effect of predator preference for particular nest sizes. In these simulations, there is no defensive behaviour by ants.

Section 3.2: Nest-Level Defence

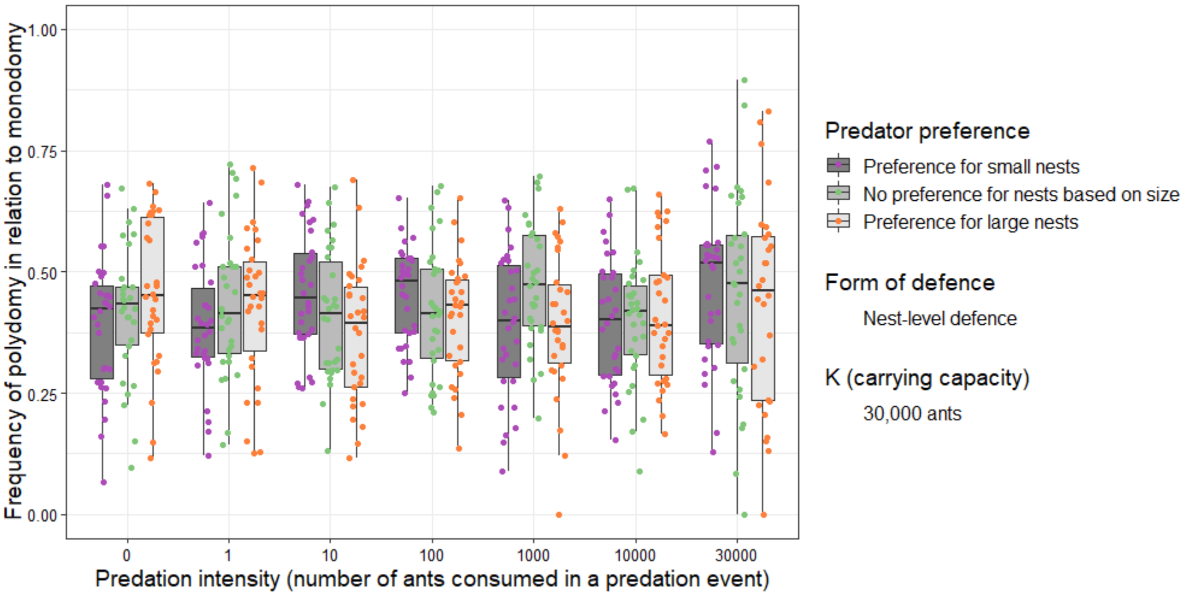

Figure 3.4: Change in frequency of polydomy with increasing predation intensity, when defence is proportional to the size of the nest targeted. K = 30,000. Box and whiskers as for Figure 3.1.

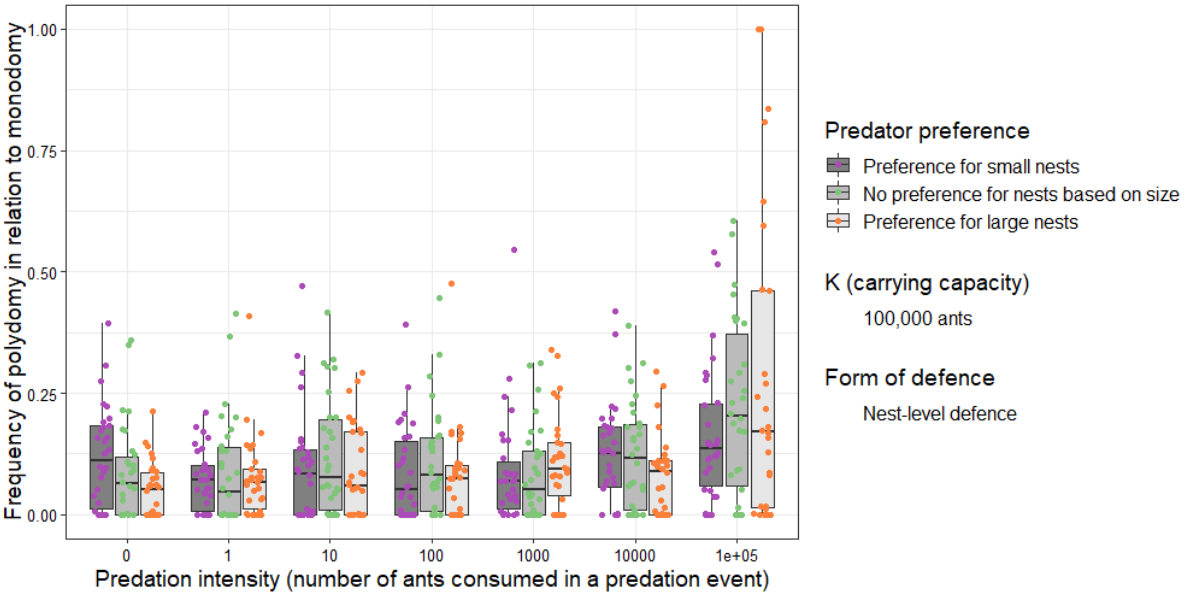

Figure 3.5: Change in frequency of polydomy with increasing predation intensity, when defence is proportional to the size of the nest targeted. K = 100,000. Box and whiskers as for Figure 3.1.

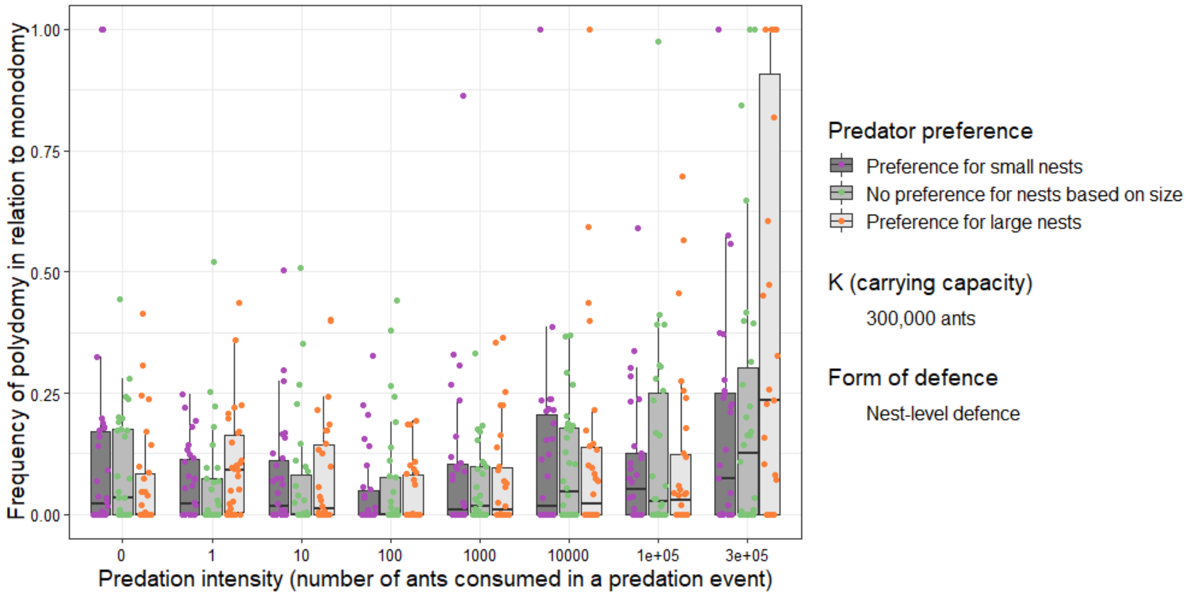

Figure 3.6: Change in frequency of polydomy with increasing predation intensity, when defence is proportional to the size of the nest targeted. K = 300,000. Box and whiskers as for Figure 3.1.

In this version of the model, defensive behaviour was included. The success of defence was proportional to the size of the nest. In the model, monodomous nests tend to be, on average, larger than polydomous nests (Figure 3.10). As such, monodomous nests were expected to increase in relative frequency as predation pressure increased in this version of the model. Contrary to this prediction, there was no apparent change in the frequency of polydomy with increasing predation intensity when carrying capacity was 30,000 ants (Figure 3.4). This was regardless of predator preference based on the size of nests predated upon.

When carrying capacity was increased to 100,000 ants (Figures 3.5, 3.12), there was an increase in the frequency of polydomy relative to monodomy when the number of ants consumed in a predation event was equal to the carrying capacity, i.e. 100,000. When carrying capacity was further increased to 300,000 ants (Figures 3.6, 3.13), there was again an increase in the frequency of polydomy relative to monodomy, this time only when the number of ants consumed was 300,000, again equal to the carrying capacity. This increase was smaller than the increase seen when carrying capacity was 100,000 (Figure 3.5) and also smaller than the increase seen in the corresponding ‘no defence’ simulation (Figure 3.3). At the predation intensity of 100,000 ants, the frequency of polydomy was higher when there was a predator preference for large nests.

Section 3.3: Colony-Level Defence

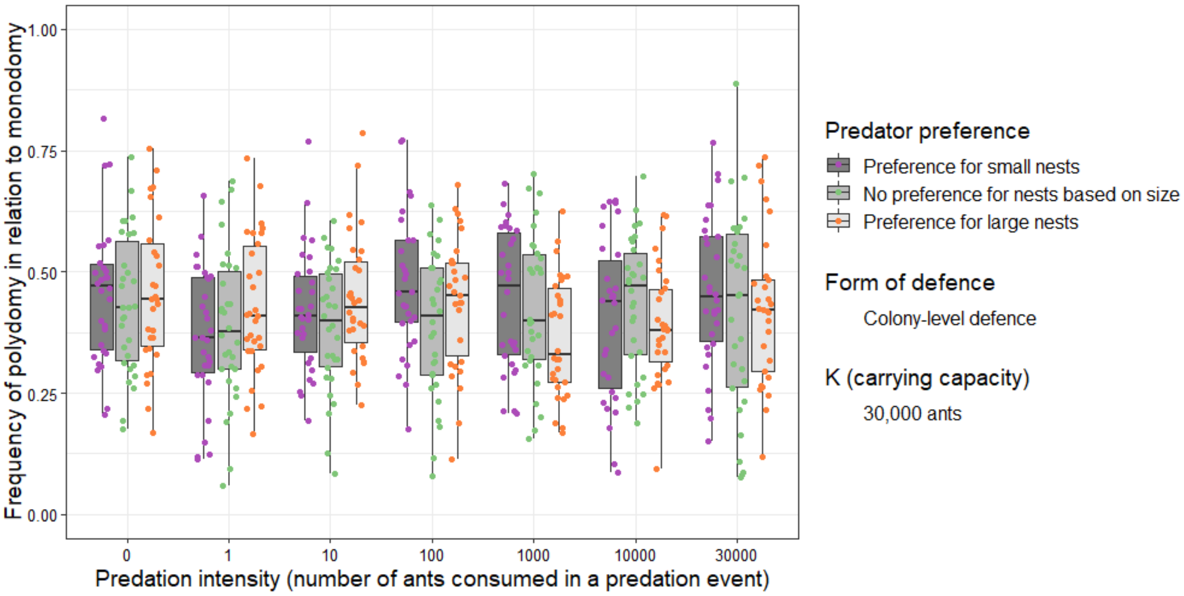

Figure 3.7: Change in frequency of polydomy with increasing predation intensity, when defence is relative to the size of the nest targeted, plus that of connected nests. K = 30,000. Box and whiskers as for Figure 3.1.

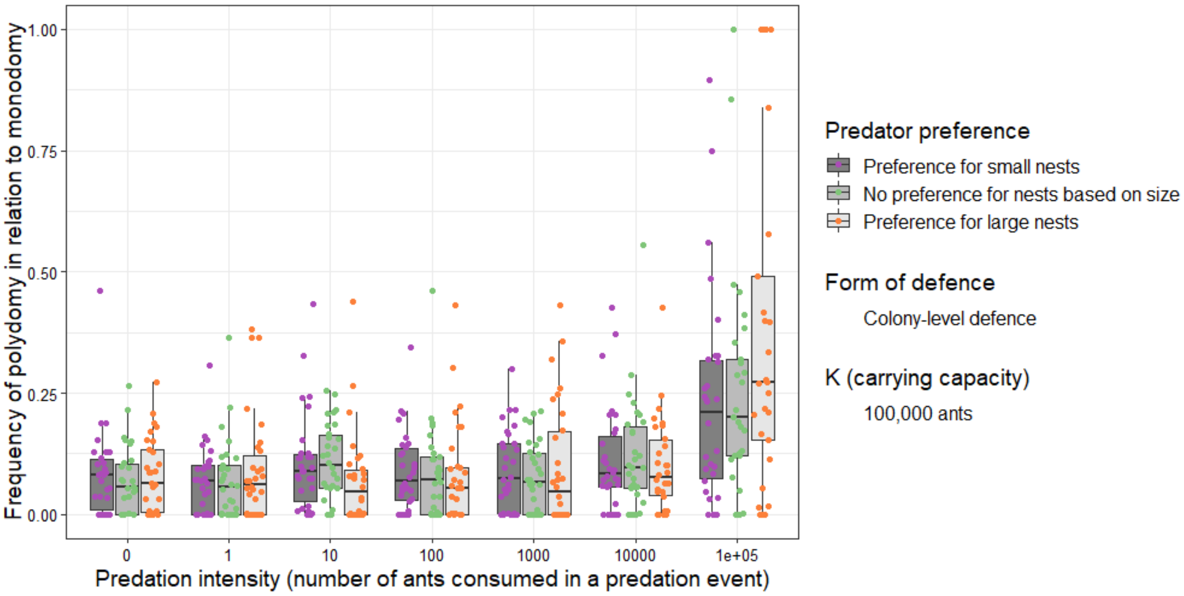

Figure 3.8: Change in frequency of polydomy with increasing predation intensity, when defence is relative to the size of the nest targeted, plus that of connected nests. K = 100,000. Box and whiskers as for Figure 3.1.

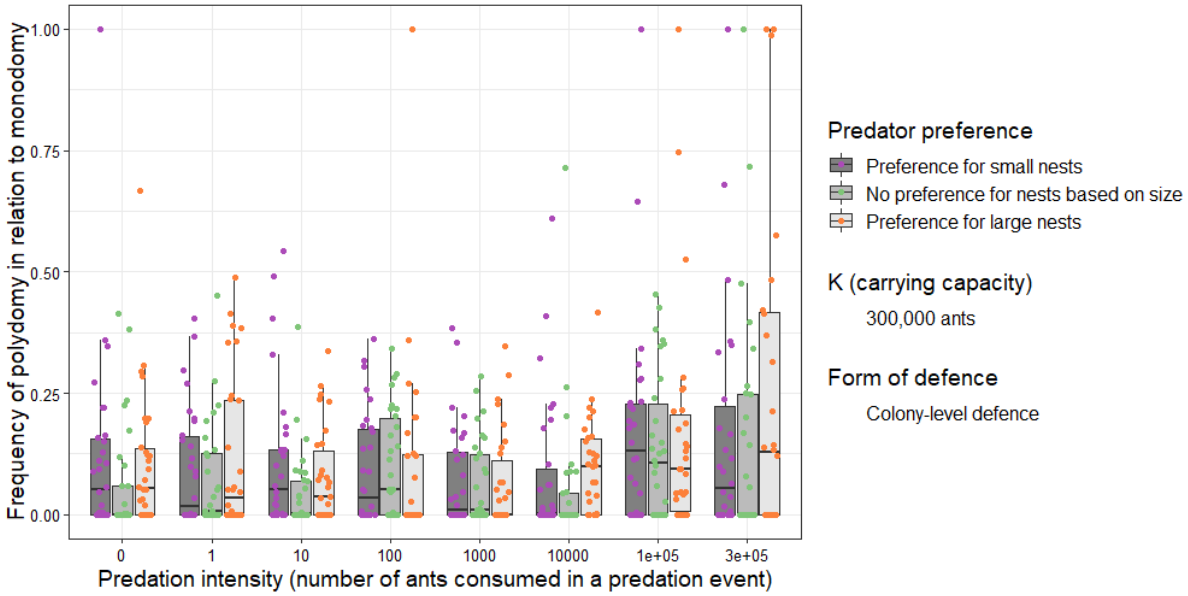

Figure 3.9: Change in frequency of polydomy with increasing predation intensity, when defence is relative to the size of the nest targeted, plus that of connected nests. K = 300,000. Box and whiskers as for Figure 3.1.

The final iteration of the model had polydomous nests also defended by other connected polydomous nests. This defence was such that its effectiveness was proportional to the size of the defending population, rather than the size of the nest under attack, to investigate the retaliation hypothesis.

We predicted that colony-level defence would result in an increased frequency of polydomy over monodomy with increasing predation intensity. Contrary to the hypothesis, there was no apparent change in the frequency of polydomy with increasing predation intensity at a carrying capacity of 30,000 (Figure 3.7). This was regardless of predator preference based on the size of nests predated upon.

When carrying capacity was increased to 100,000 ants (Figures 3.8, 3.12), there was an increase in the frequency of polydomy relative to monodomy but only when the number of ants consumed was equal to the carrying capacity, i.e. 100,000. However, this increase was smaller than the increase seen when defence was on the level of the nest (Figure 3.5) and also smaller than the increase seen without nest defence (Figure 3.2). When carrying capacity was 300,000 ants (Figures 3.9, 3.13), there was again an increase in the frequency of polydomy relative to monodomy, this time only when the number of ants consumed in a predation event was 300,000, again equal to the carrying capacity. In both of these simulation sets there was no apparent effect of predator preference for particular nest sizes.

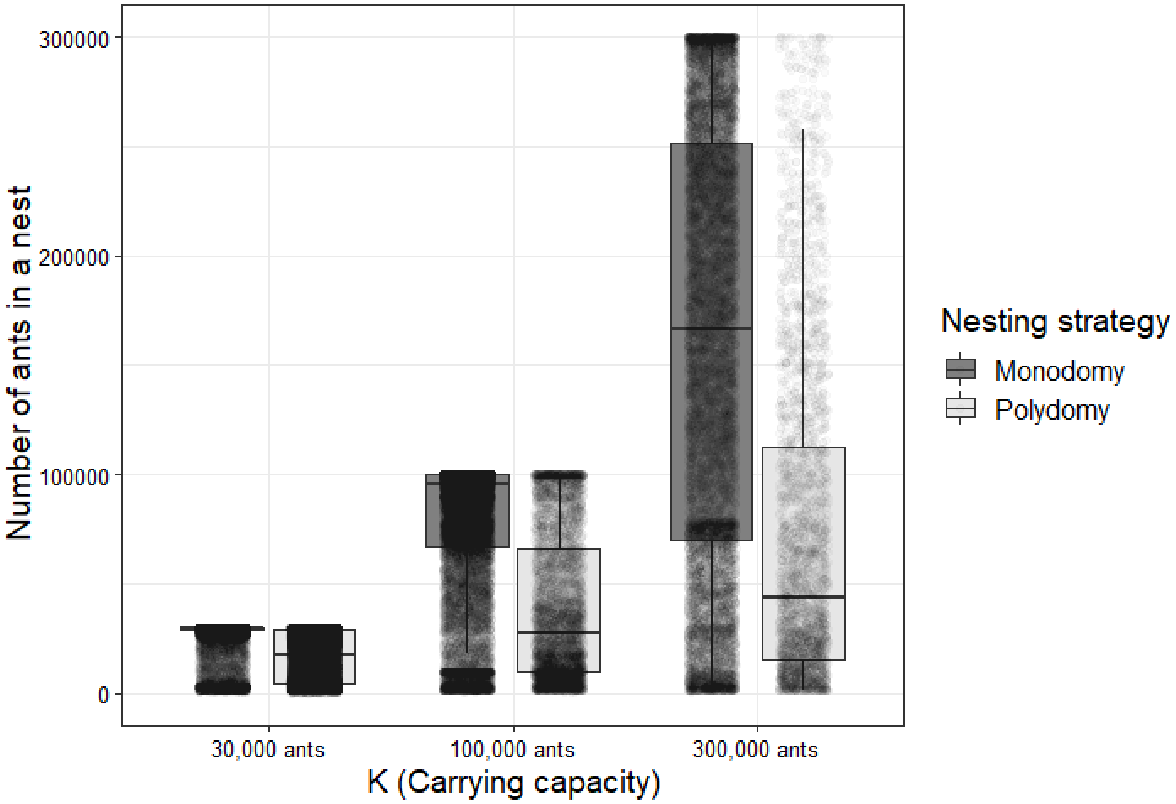

Figure 3.10: Number of ants in a nest for monodomy and polydomy at the end of simulations for defence strategy and nest size preference (season = 500). Box and whiskers as for Figure 3.1.

Section 3.4: Differences between defence strategies

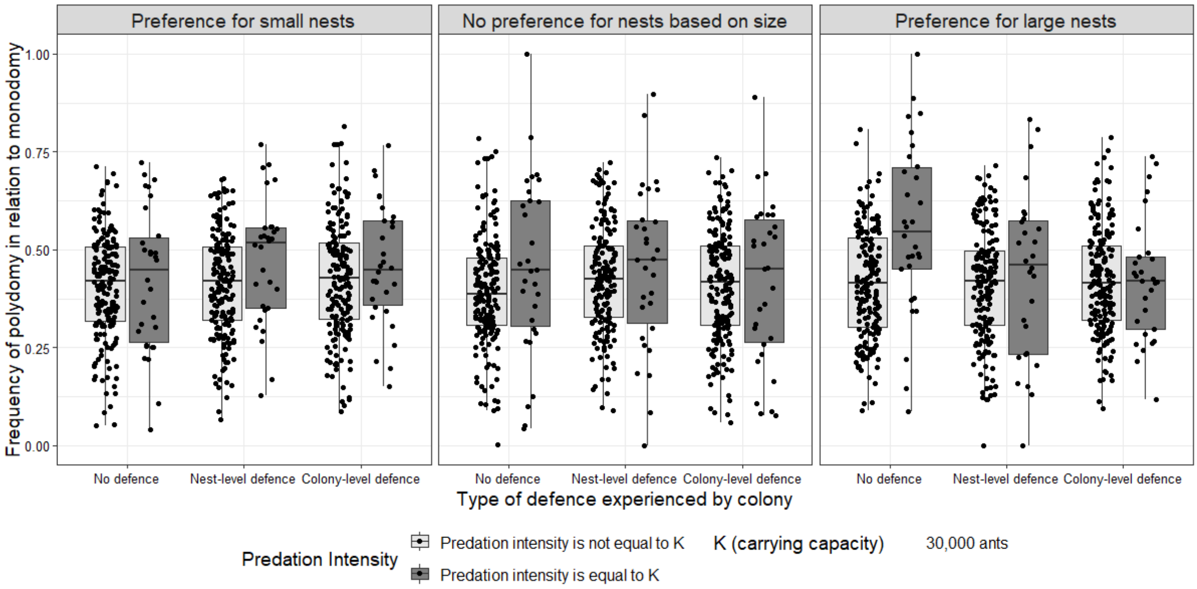

Figure 3.11: Frequency of polydomy between different models of defence. K = 30,000. Box and whiskers as for Figure 3.1.

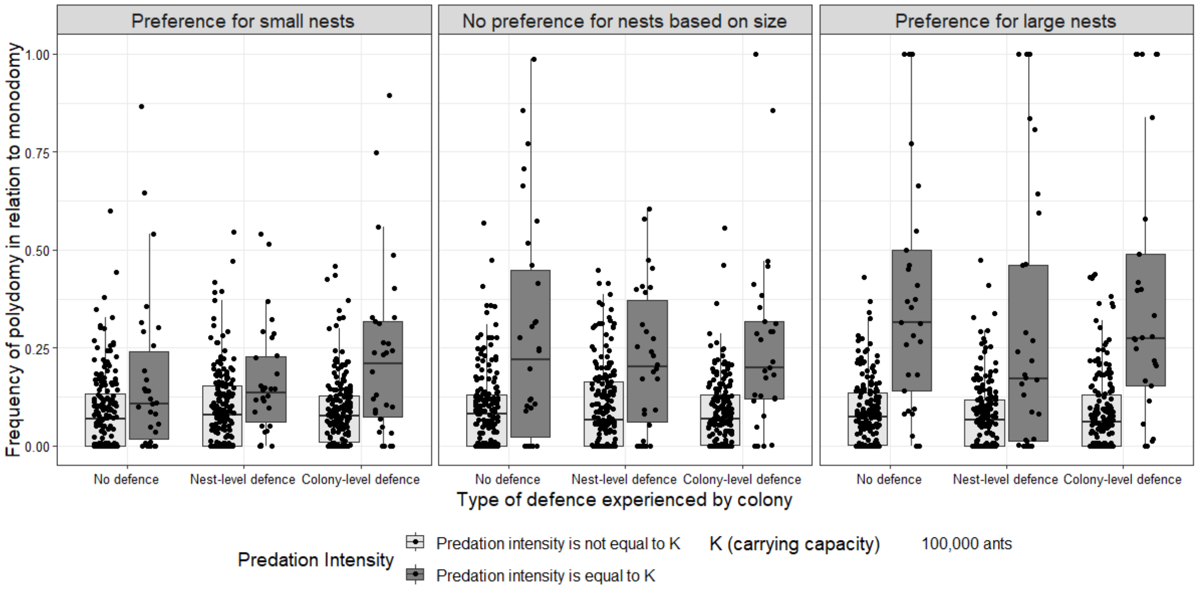

Figure 3.12: Frequency of polydomy between different models of defence. K = 100,000. Box and whiskers as for Figure 3.1.

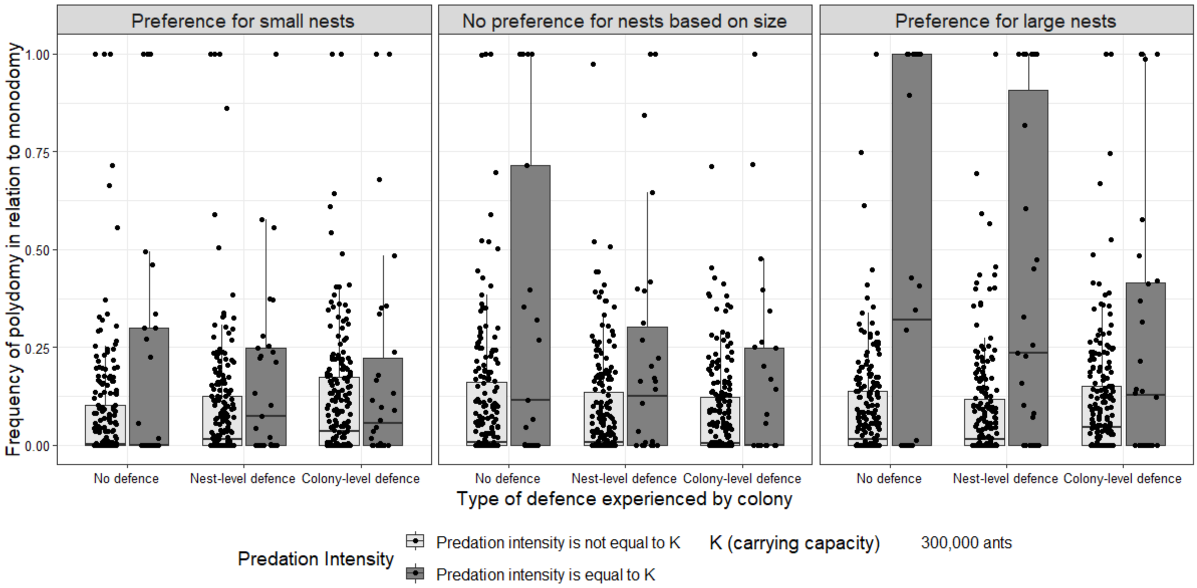

Figure 3.13: Frequency of polydomy between different models of defence. K = 300,000. Box and whiskers as for Figure 3.1.

The retaliation hypothesis predicts that defence on the level of the colony should result in higher frequencies of polydomy, while defence of the level of the nest would result in higher frequencies of monodomy. However, there was no apparent difference in the frequency of polydomy between models of differing defence strategies, regardless of predator preference based on the size of nests predated upon, and regardless of carrying capacity (Figures 3.11, 3.12, 3.13).

When carrying capacity was 30,000, there was no increase in the frequency of polydomy when predation intensity was equal to K (Figure 3.11). However, when carrying capacity was 100,000 and 300,000, there was an increase in the frequency of polydomy when predation intensity was equal to K (Figures 3.12, 3.13). When carrying capacity was 100,000, and when carrying capacity was 300,000, this increase was higher when predators preferentially predated upon larger nests (Figure 3.12, 3.13).

Chapter 4: Discussion

We found that, at medium and high carrying capacities, the frequency of polydomy in our simulated ant population increases when a destructive event, such as predation, would destroy an entire nest. When ants defend themselves or when colonies defend nests collectively this pattern persists; that is, there was no influence of defence on the frequency of polydomy. We also found that the frequency of polydomy increased when nest carrying capacity was low, regardless of the defence strategy, or the intensity of predation. This effect appeared to be stronger than the influence of predation. Taken together, these results suggest that we can support the risk spreading hypothesis, but provides no support for the retaliation hypothesis. It also suggests that predation or nest destruction may not be as strong an evolutionary driver for polydomy as carrying capacity, because of the way that polydomy increased in frequency at low carrying capacity, regardless of predation intensity.

Section 4.1: Analysis of findings

Predation affected polydomy only at medium or high carrying capacities. This is again similar to the results of Burns et al., which showed an interaction between stochastic nest destruction and carrying capacity, with nest destruction having a smaller impact at lower carrying capacities. While predation has a positive effect on the frequency of polydomy, this effect is not as strong as the positive effect that carrying capacity has. As such, any additional positive effects of predation on the frequency of polydomy are masked by the already strong positive effect of carrying capacity. It has also been hypothesised that the interaction may also be due to the fact that polydomous colonies at low carrying capacities consist of more, smaller nests than at medium or high carrying capacities, a fact that is also the case in our model. In such a case, the loss of each nest would have less of an impact on the colony as a whole, so that risk spreading is less necessary for colony health (Burns et al. 2019).

When carrying capacity was medium or high, polydomy increased only when predators consumed the entire subcolony present in a nest, providing support for the risk spreading hypothesis. If the risk of predation also carries with it the risk that an entire nest will be destroyed, polydomy would be an advantageous nesting strategy over monodomy. A polydomous colony would be able to persist through the loss of a nest and its subcolony, while for a monodomous colony the loss of a nest and its subcolony would mean the loss of the colony. Polydomy did not appear to benefit when carrying capacity was high but maximum predation was less than the carrying capacity. This means that polydomy increases in frequency only when predation (or a similar event) would be likely to destroy the entire nest, further providing support for the hypothesis that this benefit is via risk spreading.

The implementation of defence mechanisms for nests and polydomous colonies did not have an impact on the frequency of polydomy (Chapter 3, Figures 3.10, 3.11, 3.12). As such, we found no support for the retaliation hypothesis, i.e. that polydomous colonies benefit from colonial defence of nests. The implications of and reasons behind this will be explored further in section 4.2. However, when defence is modelled, risk spreading still appears to have a strong effect, even though defence is likely to protect the nest from complete destruction. This may be because, even when the nest is defended, it is likely to be much smaller after predation, meaning that it will be less likely to survive the next season, or successfully defend against predators in the future. In this way, the effect of predation may last beyond the specific predation event.

Nest carrying capacity had a clear impact on the frequency of polydomy. When the number of ants that could occupy a nest was low, polydomy was more frequent than when nest carrying capacity was medium or high. This was expected, because it aligns with the results of the model on which this work was based (Burns et al. 2019), which also found that polydomy had a higher frequency at lower carrying capacities.

Section 4.2: Comparison to Empirical Data

Risk Spreading

The results of this model support the risk spreading hypothesis, a phenomenon that has been recorded in *Wasmannia auropunctata* (Le Breton et al. 2007), and hypothesised in other polydomous species, such as Argentine ants, *L. humile* (Robinson 2014). In *W. auropunctata*, specialised attack on the colony by army ants (*Neivamyrmex compressinodis*) still left some surviving nests due to the polydomous nature and opportunistic nesting of the attacked species (Le Breton et al. 2007). *Linepithema humile*, as discussed in Chapter 1, is a unicolonial, polygynous species, and is often invasive. Such species are likely to benefit from risk spreading due to the difficulty in completely eradicating every nest of a colony from an area during pest control attempts (Hee et al. 2000; Abril et al. 2013; Robinson 2014).

An assumption of our model is that polydomous colonies will be polygynous, or have sexual brood in multiple nests, because we assume a colony can survive if any one of its nests survive. There is an association between polydomy and polygyny in many species of ants (Debout et al. 2007; Robinson 2014), but this is not the case in all polydomous species, several of which are monogynous (Debout et al. 2007). *Oecophylla longinoda*, or the weaver ant, is a monogynous species that lives in polydomous colonies spread across several nests. In *O. longinoda*, sexual brood do inhabit multiple nests, however, meaning that the colony would be able to persist even if the queenright nest is destroyed (Way 1954). In some species, such as *I. purpureus* from which the data inspiring the defence aspect of this model was drawn, polygyny is facultative, and colonies are often polydomous and monogynous (Wilgenburg et al. 2006).

It is possible that monogynous and polygynous colonies experience different evolutionary drivers in relation to nesting strategy. For polygynous species, polydomy may reduce competition between different queens in the same colony, so long as the queens inhabit different nests, and this may be one driver of polydomy (Debout et al. 2007). In addition, polygynous species are most likely to benefit from risk spreading, since other nests will be able to act as reproductive units even if a nest containing a queen, and the queen within, is destroyed (Debout et al. 2007; Robinson 2014). For monogynous species, it is possible that carrying capacity is the stronger evolutionary driver, with polydomy first developing from seasonal variation in colony size and nest availability, as seen in *T. nylanderi* (Foitzik and Heinze 1998) and *M. punctiventris* (Snyder and Herbers 1991). This is reflected in *O. longinoda* (Way 1954) and *Tetraponera* sp. (Buschinger et al. 1994). Both species have limited carrying capacity, with *O. longinoda* making nests by binding leaves together, and *Tetraponera* sp. nesting in bamboo stems.

Defence

The results of this model do not support the retaliation hypothesis. Defence through the recruitment of ants from connected polydomous nests to a particular targeted nest, as hypothesised for *I. purpureus* meat ants (Wilgenburg and Elgar 2007) did not increase the frequency of polydomy. While this may be because polydomous colonies do not benefit from improved defence through retaliation, it may also be due to the particular way in which defence itself was implemented in the model, or due to other confounding factors, such as predator behaviour.

This model did not include the ability for predators to learn, or for predators to show a preference based on defence or nest density. Predator behaviour is a key aspect of the hypothesised relationship between meat ants and their predator, the echidna (Wilgenburg and Elgar 2007) because the hypothesised defence behaviour was derived from echidna predation choices. Unpleasant experiences may in some cases drive predators off without learning being necessary, such as in the case of the spider mite *Schizotetranychus celarius* defending against and killing predators (Saitō 1986). However, many predators learn to avoid unpalatable prey, as seen in chicks avoiding coloured crumbs flavoured with quinine sulphate solution (Skelhorn and Rowe 2006). An unpleasant experience with prey by itself may not always be enough to protect the colony, as our model suggests, but the predator's ability to remember an unpleasant experience and alter their behaviour based on it may be. If predators can learn, stronger defence may result in reduced predation through avoidance in future, rather than through the actual process of defence.

Future studies of the meat ant - echidna system (Wilgenburg and Elgar 2007) should focus on meat ant defensive behaviour, and on echidna learning. This species of echidna (*Tachyglossus aculeatus*), does not appear to have the ability to retain spatial memory over long periods of time (Burke et al. 2002). In the short term, they are able to avoid previously rewarding locations, possibly as a way of avoiding nests for which they had already depleted the resources of, or triggered defence, and are less able to learn to return to previously rewarding locations. As such, it may be possible that predator learning is not an aspect of the echidna/meat ant system, or that defence is not the cause of the echidna's avoidance of densely distributed ant nests. Meat ant defensive behaviour will be discussed further in section 4.3.

Carrying Capacity

The increase in the frequency of polydomy at low carrying capacities is supported by observations of facultatively polydomous species in the wild such as *Temnothorax nylanderi* (Foitzik and Heinze 1998). These species live in nests with low carrying capacities, such as acorns or cavities in deadwood. After the ants have awoken from hibernation, many nest sites become available due to reduced decay speeds over the autumn and winter. During this time, colonies become polydomous, and spread across multiple nest sites. During the spring and summer, these nest sites rot, and colonies return to monodomy, or to living in fewer nests.

However, while low carrying capacity is a driver of polydomy in some species, this is not always the case. In some species, such as those in the *F. rufa* (red wood ant) group (Punttila and Kilpeläinen 2009; Ellis and Robinson 2014), or *I. purpureus* (meat ants) (Greaves and Hughes 1974), mound nests are not restricted in size by physical constraints, and can be very large. Drivers for polydomy in these species have been hypothesised to include improved foraging efficiency, monopolisation of resources (Ellis and Robinson 2014), and improved defence of the nest (Wilgenburg and Elgar 2007).

Model assumptions

A key effect that emerged from the model is that there is a trade-off between number of nests, and size of nests. In other words, nests in polydomous colonies in the model tended to be smaller. Because reproductive ability, predator targeting and defensive ability of nests were all related to nest size, this assumption has the potential to have a large impact on the model's results. While this trade-off seems plausible for monogynous cavity-dwelling species (Cao 2013), the evidence that this is a more general pattern is weak , with a preliminary metaanalysis of polydomous colonies finding no significant relationship between nest size and nest number for either polygynous or monogynous colonies (R. Kinsella, unpublished data).

It is possible that removing the trade-off would have no or very little effect on the results of the model. The trade-off was expected to have an impact on the frequency of monodomy when defence was at the level of the nest, and to interact with predator preference based on the size of nests. It was expected that monodomy would increase in frequency when nests, but not colonies, were able to defend themselves. This was not observed (Figures 3.12, 3.13), although it is possible that this is because the frequency of monodomy was already so high that any effects of defence had no impact. It was also expected that polydomy would increase when predators prefer to target larger nests, since monodomous nests tended to be larger. This effect was seen to a small extent at the medium and high level of carrying capacity (Figure 3.12, 3.13).

Another assumption of the model was that a nest and the subcolony within it was treated as a single entity. In reality, the population of ants living in a nest are not the same as the physical structure of the nest itself, and predators may inflict different levels of damage to the nest itself. For example, bears may cause a lot of damage to nests through excavation of mounds (Swenson et al. 1999) or through opening logs to access log-dwelling nests (Mattson 2001)[2]. In other cases, animals may cause damage to the nest without consuming any ants. This is the case with wild boar, *Sus scrofa*, which may wallow in ants nests or excavate them to consume chafer beetle grubs, though they may also eat ants and their brood (Stockan and Robinson 2016).

Differentiation between nest and subcolony is an important consideration when ants are likely to evacuate their nest, a behaviour not included in the simulations covered here. If the physical nest structure is entirely destroyed and slow to repair, this is likely to have a larger impact on a subcolony even if the majority of the subcolony has survived than if the physical nest structure is only partly destroyed or easy to repair. In this model, this was not a major issue, as the hypotheses being tested involved risk-spreading or defence by retaliation. However, a model that allowed ants to evacuate their nests, temporarily or permanently, would need to differentiate between nests and subcolonies. This will be examined more closely in section 4.3.

The model did not consider any response of predators to fluctuations in ant populations. Many ant predators are generalists (Torres et al. 2000; Mouhoub-Sayah et al. 2018), meaning

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[2] Videos of bears excavating mounds and opening logs may be found at:
KB Bear. 2017. A Black Bear Digs Up an Ant Hill (Aug, 2017). YouTube.
DrKUNOmaha. 2009. Black bear rips open log to eat ants. YouTube.

that they predate upon multiple species. Generalist predators are less likely to be affected by fluctuations in prey populations (Mañosa 1994; Maerz et al. 2005; Rutz et al. 2006), and as such the model is appropriate when considering these types of predators. However, some ant predators are specialists (Suarez et al. 2000; Le Breton et al. 2007), and some, such as the specialist army ant *N. rugulosus*, are less successful when predating upon species of ant other than their specialist prey. In this case, a decrease in the population of an ant species could have an effect on the population of specialist predators (Suarez et al. 2000), and therefore affect predation intensity.

Predators attacked each nest in the same order each season, if predation occurred. This is not realistic, and meant that nests in polydomous colonies later in the order of attack than other nests in the same colony are less likely to be defended by connected nests, as there is the repeated probability of the connected nests being destroyed before predation of the nest is considered. Predators were also equally likely to predate upon all nests, as we did not allow for predator learning or make assumptions of predator preference based upon nest density. This means that predators were more likely to predate upon densely distributed nests, an assumption which contradicts with the meat ant - echidna system that this study is partly based upon (Wilgenburg and Elgar 2007).

In addition, only one type of predator was modelled at a time, while in nature a range of types of predators are likely to co-exist and compete for resources. Different predators are likely to align with different combinations of model parameters (Figure 4.1), and it is possible that this range of pressures acting upon colonies at the same time will have an impact on the frequency of polydomy or monodomy.

The model also contains an assumption inherent in Equation 2.1, which suggests that the probability of connections between nests or between nests and food sources is relative to the density of nests and food sources. This means that connections between nests are more likely to form over longer distances when nest density is low. This may not necessarily be realistic, as densely distributed nests may have a higher degree of polydomy than sparsely distributed nests (Ellis et al. 2017), though this may be due to budding as a form of reproduction for polydomous colonies, rather than as a response to nest density (Bernasconi et al. 2005). In our model, it may mean that, at low population frequencies of polydomy, long-distance and expensive connections between nests may form, putting polydomy at a disadvantage as compared to monodomy.

These assumptions mean that the effects of predators found in this model may be more applicable to natural disasters than predators. If ants in nests are particularly vulnerable to natural disasters, it is possible that the spatial distribution of a colony across several nests increases protection from natural disasters. While ants do not defend against natural disasters through retaliation, defence did not change the effects of destruction on the colony, so we find nothing in our results to suggest that any protective benefit of polydomy is specific to active predation, as opposed to passive nest destruction, such as by local flooding or collapse of a cavity.

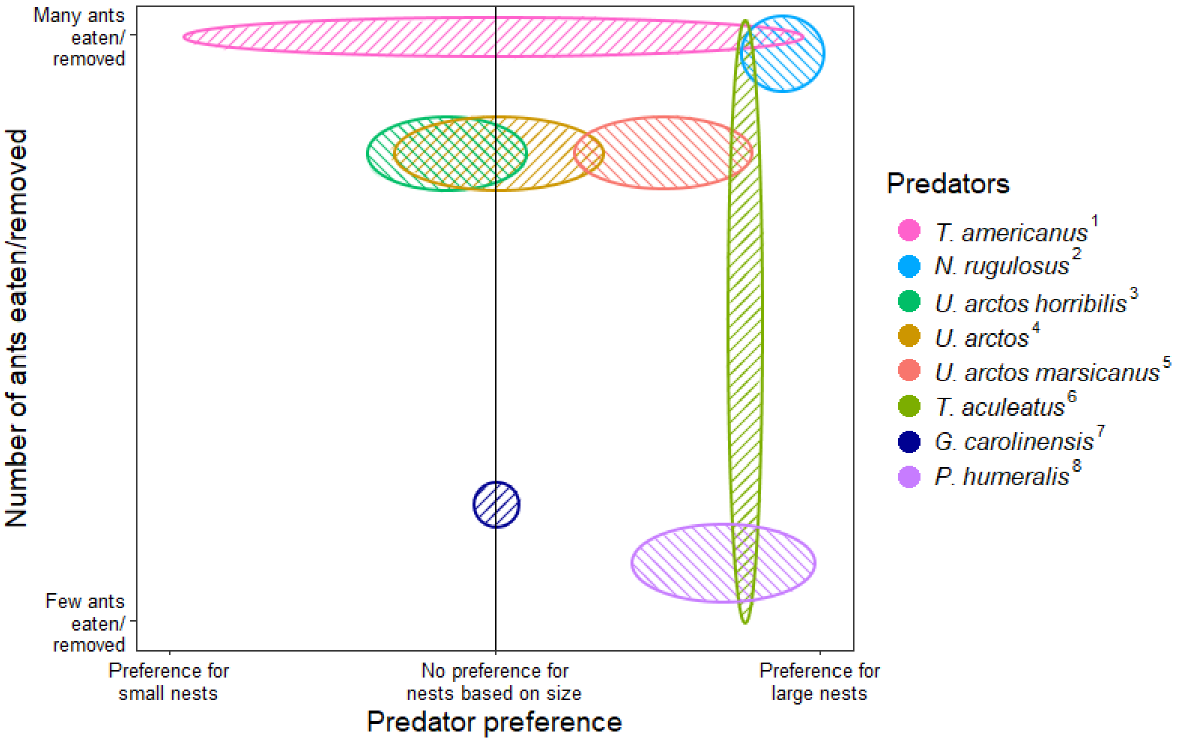

Figure 4.1: Postulated plot of predators in relation to model parameters. Predators used are: (1) *Temnothorax americanus* (Pamminger et al. 2014); (2) *Neivamyrmex rugulosus* (LaPolla et al. 2002); (3) *Ursus arctos horribilis* (Mattson 2001) (4) *Ursus arctos* (Swenson et al. 1999); (5) *Ursus arctos marsicanus* (Tosoni et al. 2018) (6) *Tachyglossus aculeatus* (Wilgenburg and Elgar 2007); (7) *Gastrophryne carolinensis* (Deyrup et al. 2013); (8) *Pella humeralis* (Päivinen et al. 2004)

Section 4.3: Future Work

Future work in the framework of this model should explore the assumptions made by the model, and their impact on the system. As discussed in section 4.2, this model assumes that nests are polygynous, or have sexual brood in all nests, although polygyny and monogyny may experience different selection pressures. A future model should take this into account by providing each nest with a parameter that defines its reproductive status. In this way, a polygynous colony or colony with sexual brood in multiple nests may have several reproductive nests, while a monogynous colony or colony with sexual brood in only one nest would have a single reproductive nest. This would also allow the model to consider the impact of monogyny or polygyny on the survival of polydomous colonies.

Future models should also test the effect of relaxing the trade-off between nest size and nest number. This trade-off may not exist in all polydomous colonies, as discussed in section 4.2. By investigating a model without this trade-off, we can see how much of an impact it has on the success of polydomy, and how much of an impact it has had on the results of this model.

The role of predators as agents is also important to explore in future iterations of this model. This would, firstly, allow predators to learn from their interactions with colonies and change their behaviour to optimise food gained. This may be an important factor to consider when investigating defence in polydomous colonies. A range of types of predators should also be modelled in an environment simultaneously, and may respond to the environment differently. For example, specialist predators' populations would change in response to changes in ant population, while generalists would be less affected.

The model should be adapted to investigate whether polydomous colonies benefit from having nests to evacuate to in response to predation. This is an important part of the investigation initiated by this thesis, as discussed in the literature review. Evacuation has been observed in monodomous colonies, such as *Aphaenogaster swammerdami* (Teppei et al. 2019). When *A. swammerdami* is exposed to the predatory snake *Madatyphlops decorsei*, the ants evacuate their brood from the nest. This evacuation is temporary, and *A. swammerdami* returns to their nest and resumes normal activity by one day after exposure. Evacuation may also be of benefit to polydomous colonies, though the existence of multiple nests that ants can evacuate to. One such case is seen in *Pachycondyla goeldii*. The species is restricted in the size of their nests - a factor known to encourage polydomy by itself (Foitzik and Heinze 1998; Burns et al. 2019), but is also restricted in the speed at which new nests can be created. Their nests are built into the roots of epiphytes, termed 'ant gardens' (Denis et al. 2006); these nests are slow to build, since they must be grown. It is hypothesised that polydomy developed in *P. goeldii* because they are unable to quickly construct a new nest in the case of a nest being destroyed (Denis et al. 2006). Being polydomous allows a single colony to establish multiple nests, providing subcolonies with nests to which they can evacuate, should one nest be destroyed. In a similar way, a single colony of the monodomous species *Pheidole desertorum* may have multiple nests, but a colony only occupies a single nest at a time (Droual 1984). When the currently occupied nest is threatened, such as by army ants, the colony evacuates its nest and move to another unoccupied nest.

During the course of this work, I wrote and prototyped a model that allowed subcolonies that were part of polydomous colonies to evacuate their nests in response to predation (detailed in Figure 4.2). Another iteration of the evacuation model would involve both polydomous and monodomous colonies maintaining ‘outposts’ (Lanan et al. 2011). These would be smaller nest structures, maintained by fewer than 100 individuals. Outposts would allow monodomous colonies to temporarily evacuate, and allow polydomous colonies to have permanent nests that subcolonies can evacuate to in the possibility of predation.

Ideally, a version of the model would be produced that represents the physical nest and the subcolony living in the nest as independent entities. This would allow ants to return to nests that have been recently evacuated some time after a predation event, until the nest decays due to lack of maintenance. It would also allow for more variation in the types of predators present, since predators would also be able to inflict different levels of damage to the physical nest and to the subcolony in the nest. For example, large predators such as bears may have a large impact on the nest structure while only removing a fraction of the colony within (Swenson et al. 1999), while predators such as army ants may effectively eradicate the subcolony without inflicting much damage to the physical nest structure (Le Breton et al. 2007). This may have implications for evacuation or returning to empty nests.

It can be expected that worker traffic on paths between nests of polydomous colonies would increase or otherwise change in response to predation. Ants would be expected to move towards the nest that is under attack if the retaliation hypothesis is correct, and away from this nest if the evacuation hypothesis is correct. If both hypotheses are correct, an overall increase in traffic during or immediately following predation would be expected, though this increase may not have any directionality.

In order to test these hypotheses, we conducted a preliminary field experiment on polydomous colonies of *Formica lugubris*. Worker traffic, including direction of worker movement, on trails connected to a focal nest was recorded. These included internest trails, as well as foraging trails. After recording, the focal nest was manually disturbed, simulating a predation event, and traffic on trails was observed after disturbance. Traffic before disturbance and at two timepoints after disturbance were compared to determine whether there was any response on trails to disturbance at the nest. This preliminary experiment was performed on two focal nests from different colonies. This experiment and its results are explained in further detail in appendix 1.

The field experiment did not show any consistent change in trail traffic after nest disturbance. This included general changes in traffic, and changes in traffic that could correspond with recruitment for defence, or evacuation. However, this experiment is not conclusive due to the small sample size. In addition, while other polydomous systems may exhibit retaliation or evacuation, this may not be the case in wood ants. The retaliation hypothesis, for example, originates from observations of *I. purpureus*, a species which is usually monogynous, while *F. lugubris* is a polygynous species. As polygynous colonies are at lower overall risk from nest destruction due to risk spreading, it is possible that monogynous colonies will respond differently to predation. Finally, in an experiment in which *A. swammerdami* ants were exposed to predatory snakes, the snakes were constantly present during the recording period (Teppei et al. 2019). However, in our experiment, potential reactions to disturbance were recorded only after disturbance stopped. It is possible that trail responses occur only during disturbance, and that these responses were therefore missed by the experiment.

Future work should expand upon this field experiment, and include different intensities and durations of disturbance. It is likely that different polydomous species will respond differently to predation, based on a range of life history traits such as gyny or nest carrying capacity. As such, these experiments should be repeated on a range of polydomous species. This experiment should also be repeated on related monodomous species for comparison.

Box: Evacuation Model

- In this iteration of the model, the nest being attacked (focal nest) is defended as normal, without support from connected nests. This defence continues until a threshold number of ants are consumed (evacuation trigger).
- Once the evacuation trigger is reached, ants evacuate to the nearest connected nest, until this nest is full. The ants then evacuate to the next nearest nest, and repeat this until either all connected nests are full, or until the focal nest is empty.
- Ants will not evacuate to nests that are indirectly connected to the focal nest.
- When evacuation is complete, predation and defence will resume. The predator will still attempt to consume enough ants to sate its previously defined hunger, as described in the methods, but the model will skip forward in the defence curve so that the nest is now as poorly defended as if the ants evacuating the nest had been predated upon.

Figure 4.2: Box detailing evacuation model

Section 4.4: Broader Implications

The results of these simulations suggest that risk spreading may be an important evolutionary driver of polydomy. Risk spreading is an important aspect of group living throughout the animal kingdom, and is one of the key benefits of living in a group. This is not only observed in direct response to predation, however. Several species of bird, including wood ducks (*Aix sponsa*), goldeneye ducks (*Bucephala clangula*) and cliff swallows (*Hirundo pyrrhonota*) engage in intraspecific brood parasitism, in which mothers will lay eggs in the nests of other conspecific birds (Semel and Sherman 1986; Brown and Bomberger Brown 1989; Andersson and Åhlund 2012). This allows the mother to produce a clutch of offspring larger than if she were restricted to her own nest, and also allows the mother to dilute any risks associated with uncertain environments on her offspring. Risk spreading is a passive form of defence, as discussed in Chapter 1. Many species also use active forms of defence, such as fleeing from or fighting predators.

Fight or flight is considered to be an important aspect of prey response to predation, and is reflected in the comparison between the retaliation and evacuation hypotheses in this thesis. Individuals of some species may consistently choose to flee certain predators, or choose to fight them. For example, when responding to killer whale (*Orcinus orca*) predation, some species of baleen whale consistently respond with a fight response, while others consistently respond with a flight response (Ford and Reeves 2008). For other species, the fight or flight response may be variable, dependent on the situation or individuals involved. In the case of baleen whales attacked by killer whales, southern right whales (*Eubalaena australis*) and grey whales (*Eschrichtius robustus*) would sometimes flee from predators, despite being what the authors classed as 'fight' species.

Living in a group is more complex than merely being an aggregation of individuals. The dynamics of group life and structure of the group, as well as the behaviour of the group as a whole plays an important role in determining the overall success of a group living species. Polydomous ants provide an added level of complexity to our understanding of group living, but also provide an important lens through which we can understand how and why different group living strategies may be advantageous or costly.

Throughout this study, we have found that monodomy outcompetes polydomy except under particular conditions - specifically, when risk spreading is able to take effect, and under low nest carrying capacities. Yet, despite these findings, polydomous species are known to be effective at monopolising resources (Cook et al. 2013; Burns et al. 2019), and can become highly successful invasive species (Hee et al. 2000; Abril et al. 2013). It is likely that predation pressure provides very little evolutionary drive for polydomy, as compared to factors such as resource distribution or nest carrying capacity. However, this model has also shown that identifying single, unifying factors for all polydomous species of ant is difficult. Perhaps a better understanding of polydomy will come when we are able to identify the evolutionary pressures and histories that make different groups of polydomous ant different.

Appendix 1: Field Work

Section A1.1: Aim

To perform a preliminary test of the retaliation and evacuation hypotheses under field conditions.

Section A1.2: Study system

We conducted field work on two polydomous colonies of *Formica lugubris*, located in Longshaw Estate, Derbyshire. Many colonies at this site have been mapped and studied for more than 7 years (Ellis et al. 2017; D. Burns, unpublished data).

Section A1.3: Methods

Two polydomous colonies in the area were identified for inclusion in the study on the basis of having a suitable focal nest. A focal nest for each colony was selected, this being a nest that was connected by inter-nest trails to at least two other nests, as well as being connected by a foraging trail to at least one tree. The width, length and height of the focal nest were recorded to ensure that the focal nests for the 2 colonies were of similar size. Three trails were selected for observation, two of these being internest trails, and the final being a foraging trail. These were selected to have length and trail traffic as similar as possible across the 3 trails. The midpoint along these trails was identified, and two coloured glass beads were placed eight centimetres apart nest to the trail. A white bead indicated the direction of the focal nest, and a blue bead indicated the direction away from the focal nest (Figure A1:1).

Video recordings were made for fifteen seconds of the areas of the trails marked by the beads. Ten seconds after these recordings were complete, the focal nest was disturbed through a person excavating part of the nest. Thirty seconds after disturbance, another fifteen second video recording was made of the marked areas of the trails. Recording was repeated 180 seconds after the disturbance.

These video recordings were then blind coded for analysis. Ants that crossed a line drawn as a midpoint between the two beads on the trail were recorded, including their direction of movement. If an ant crossed the line more than once, only its first crossing was recorded. This gave counts of the number of ants travelling in either direction at each time point, which could be compared to determine whether there was any change in traffic or direction of traffic after disturbance.

We hypothesised that if the retaliation hypothesis were correct, there would be an increase in traffic travelling towards the focal nest after disturbance, and that if the evacuation hypothesis were correct, there would be an increase in traffic travelling away from the focal nest after disturbance. If both hypotheses were correct, we expected to see an increase in overall traffic, regardless of direction.

Figure A1.1: Experimental setup

Section A1.4: Results

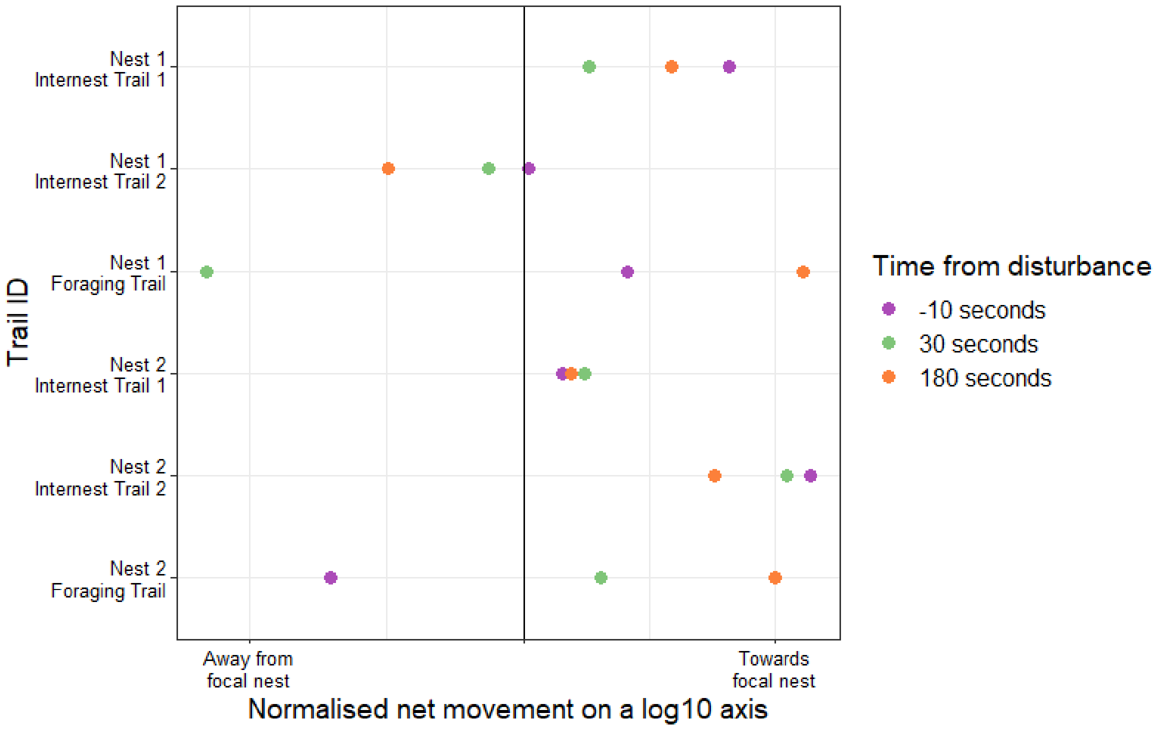

Figure A1.2: Direction of movement before and after disturbance of the focal nests. Net movement was calculated as the number of ants moving towards the focal nest divided by the number of ants moving away from the focal nest. The vertical line represents equal movement to and from the focal nest.

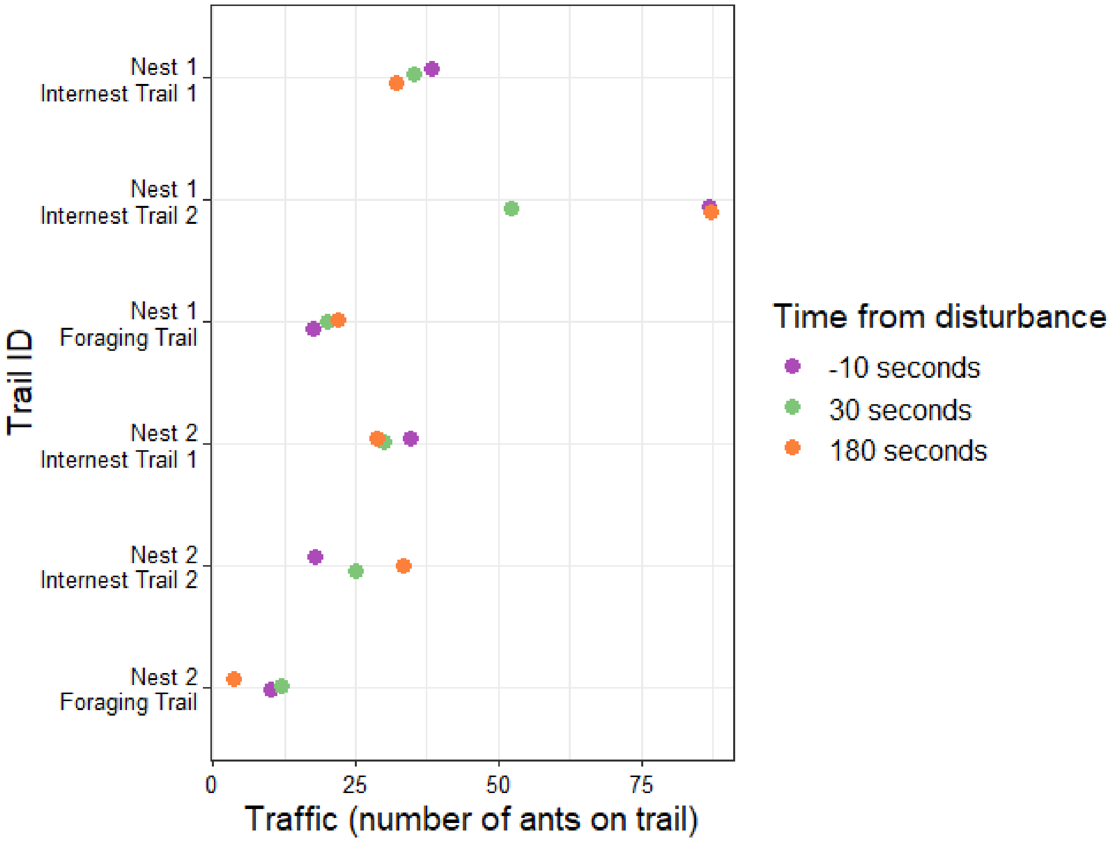

Figure A1.3: Total traffic (both directions summed) before and after disturbance of the focal nests

Section A1.5: Conclusion

We did not observe any change in traffic or direction of traffic after disturbance. The low number of replicates in this experiment means that it is far from conclusive, and further research would be necessary. In addition, traffic was only observed before and after disturbance (not during), and it is possible that ants would only respond with retaliation or evacuation while disturbance is ongoing. While there was a generally greater movement of ants towards the nest than away (Figure A1.2), the data suggest this is irrespective of time before or after disturbance, and may have been an effect of time of day or weather conditions.

Bibliography

Abril, S., M. Díaz, M. L. Enríquez, and C. Gómez. 2013. More and bigger queens: a clue to the invasive success of the Argentine ant (Hymenoptera: Formicidae) in natural habitats. Myrmecological News 18:19–24.

Albrecht, T., and P. Klvaňa. 2004. Nest Crypsis, Reproductive Value of a Clutch and Escape Decisions in Incubating Female Mallards *Anas platyrhynchos*. Ethology 110:603–613.

Alexander, R. D., K. M. Noonan, and B. J. Crespi. 1991. The Evolution of Eusociality. Pages 3–44 *in* The Biology of the Naked Mole-Rat. Princeton University Press.

Allon, O., A. Pascual-Garrido, and V. Sommer. 2012. Army ant defensive behaviour and chimpanzee predation success: field experiments in Nigeria. Journal of Zoology 288:237–244.

Andersson, M., and C. G. Wiklund. 1978. Clumping versus spacing out: Experiments on nest predation in fieldfares (*Turdus pilaris*). Animal Behaviour 26:1207–1212.

Andersson, M., and M. Åhlund. 2012. Don't Put All Your Eggs in One Nest: Spread Them and Cut Time at Risk. The American Naturalist 180:354–363.

Arnold, K. E. 2000. Group Mobbing Behaviour and Nest Defence in a Cooperatively Breeding Australian Bird. Ethology 106:385–393.

Auger, J., G. L. Ogborn, C. L. Pritchett, and H. L. Black. 2004. Selection of ants by the American black bear (*Ursus americanus*). Western North American Naturalist 64:166–174.

Avilés, L., G. Harwood, and W. Koenig. 2012. A Quantitative Index of Sociality and Its Application to Group-Living Spiders and Other Social Organisms. Ethology 118:1219–1229.

Baer, B., S. P. A. den Boer, D. J. C. Kronauer, D. R. Nash, and J. J. Boomsma. 2009. Fungus gardens of the leafcutter ant *Atta colombica* function as egg nurseries for the snake *Leptodeira annulata*. Insectes Sociaux 56:289–291.

Bernasconi, C., A. Maeder, D. Cherix, and P. Pamilo. 2005. Diversity and genetic structure of the wood ant Formica lugubris in unmanaged forests. Annales Zoologici Fennici 42:189–199.

Biancucci, L., and T. E. Martin. 2010. Can selection on nest size from nest predation explain the latitudinal gradient in clutch size? Journal of Animal Ecology 79:1086–1092.

Boomsma, J. J., and R. Gawne. 2018. Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation. Biological Reviews 93:28–54.

Bourke, A. F. G. 1988. Dominance orders, worker reproduction, and queen-worker conflict in the slave-making ant *Harpagoxenus sublaevis*. Behavioral Ecology and Sociobiology 23:323–333.

Brown, C. R., and M. Bomberger Brown. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial cliff swallows. Animal Behaviour 37:777–796.

Burke, D., C. Cieplucha, J. Cass, F. Russell, and G. Fry. 2002. Win-shift and win-stay learning in the short-beaked echidna (*Tachyglossus aculeatus*). Animal Cognition 5:79–84.

Burns, D. D. R., J. W. Pitchford, C. L. Parr, D. W. Franks, and E. J. H. Robinson. 2019. The costs and benefits of decentralization and centralization of ant colonies. Behavioral Ecology 30: 1700–1706.

Buschinger, A., R. W. Klein, and U. Maschwitz. 1994. Colony structure of a bamboo-dwelling *Tetraponera* sp. (Hymenoptera: Formicidae: Pseudomyrmecinae) from Malaysia. Insectes Sociaux 41:29–41.

Cao, T. T. 2013. High social density increases foraging and scouting rates and induces polydomy in Temnothorax ants. Behavioral Ecology and Sociobiology 67:1799–1807.

Chak, S. T. C., J. E. Duffy, K. M. Hultgren, and D. R. Rubenstein. 2017. Evolutionary transitions towards eusociality in snapping shrimps. Nature Ecology & Evolution 1:0096.

Chiver, I., C. A. Jaramillo, and E. S. Morton. 2017. Mobbing behavior and fatal attacks on snakes by Fasciated Antshrikes (*Cymbilaimus lineatus*). Journal of Ornithology 158:935–942.

Christman, B. J., and A. A. Dhondt. 1997. Nest Predation in Black-Capped Chickadees: How Safe Are Cavity Nests? The Auk 114:769–773.

Clutton-Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. Maccoll, R. Kansky, P. Chadwick, M. Manser, et al. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology 68:672–683.

Clutton-Brock, T. H., M. J. O'Riain, P. N. M. Brotherton, D. Gaynor, R. Kansky, A. S. Griffin, and M. Manser. 1999. Selfish Sentinels in Cooperative Mammals. Science 284:1640–1644.

Cocroft, R. B. 2005. Vibrational communication facilitates cooperative foraging in a phloem-feeding insect. Proceedings of the Royal Society B: Biological Sciences 272:1023–1029.

Cook, Z., D. W. Franks, and E. J. H. Robinson. 2013. Exploration versus exploitation in polydomous ant colonies. Journal of Theoretical Biology 323:49–56.

Creel, S. R., and K. N. Rabenold. 1994. Inclusive fitness and reproductive strategies in dwarf mongooses. Behavioral Ecology 5:339–348.

Crespi, B. J. 1994. Three conditions for the evolution of eusociality: Are they sufficient? Insectes Sociaux 41:395–400.

Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. Animal Behaviour 47:433–442.

Cresswell, W., and J. L. Quinn. 2004. Faced with a choice, sparrowhawks more often attack the more vulnerable prey group. Oikos 104:71–76.

Cushing, P. E. 2012. Spider-Ant Associations: An Updated Review of Myrmecomorphy, Myrmecophily, and Myrmecophagy in Spiders. Psyche: A Journal of Entomology. Research article.

Debout, G., B. Schatz, M. Elias, and D. McKey. 2007. Polydomy in ants: what we know, what we think we know, and what remains to be done. Biological Journal of the Linnean Society 90:319–348.

Denis, D., J. Orivel, R. R. Hora, S. Chameron, and D. Fresneau. 2006. First Record of Polydomy in a Monogynous Ponerine Ant: A Means to Allow Emigration Between *Pachycondyla goeldii* Nests. Journal of Insect Behavior 19:279–291.

Deyrup, M., L. Deyrup, and J. Carrel. 2013. Ant Species in the Diet of a Florida Population of Eastern Narrow-Mouthed Toads, *Gastrophryne carolinensis*. Southeastern Naturalist 12:367–378.

Dumke, M., M. E. Herberstein, and J. M. Schneider. 2018. Advantages of social foraging in crab spiders: Groups capture more and larger prey despite the absence of a web. Ethology 124:695–705.

Edmunds, M. 1974. Defence in Animals: A Survey of Anti-predator Defences. Longman.

Ehrlich, P. R., and A. H. Ehrlich. 1973. Coevolution: Heterotypic Schooling in Caribbean Reef Fishes. The American Naturalist 107:157–160.

Ellis, S., and E. J. H. Robinson. 2014. Polydomy in red wood ants. Insectes Sociaux 61:111–122.

Ellis, S., D. S. Procter, P. Buckham-Bonnett, and E. J. H. Robinson. 2017. Inferring polydomy: a review of functional, spatial and genetic methods for identifying colony boundaries. Insectes Sociaux 64:19–37.

Ellis, S., D. W. Franks, and E. J. H. Robinson. 2017. Ecological consequences of colony structure in dynamic ant nest networks. Ecology and Evolution 7:1170–1180.

Fanshawe, J. H., and C. D. Fitzgibbon. 1993. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour 45:479–490.

Fitzgibbon, C. D. 1990*a*. Why do hunting cheetahs prefer male gazelles? Animal Behaviour 40:837–845.

———. 1990*b*. Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. Animal Behaviour 39:1116–1126.

Foitzik, S., and J. Heinze. 1998. Nest site limitation and colony takeover in the ant *Leptothorax nylanderi*. Behavioral Ecology 9:367–375.

Ford, J. K. B., and R. R. Reeves. 2008. Fight or flight: antipredator strategies of baleen whales. Mammal Review 38:50–86.

Fronhofer, E. A., J. Liebig, O. Mitesser, and H. J. Poethke. 2018. Eusociality outcompetes egalitarian and solitary strategies when resources are limited and reproduction is costly. Ecology and Evolution 8:12953–12964.

Fujiwara, S., S. Koike, K. Yamazaki, C. Kozakai, and K. Kaji. 2013. Direct observation of bear myrmecophagy: Relationship between bears' feeding habits and ant phenology. Mammalian Biology 78:34–40.

Greaves, T., and R. D. Hughes. 1974. The Population Biology of the Meat Ant. Australian Journal of Entomology 13:329–351.

Grünbaum, D., and R. R. Veit. 2003. Black-Browed Albatrosses Foraging on Antarctic Krill: Density-Dependence Through Local Enhancement? Ecology 84:3265–3275.

Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. Journal of Theoretical Biology 7:1–16.

Hamilton, W. D. 1972. Altruism and Related Phenomena, Mainly in Social Insects. Annual Review of Ecology and Systematics 3:193–232.

Hee, J. J., D. A. Holway, A. V. Suarez, and T. J. Case. 2000. Role of Propagule Size in the Success of Incipient Colonies of the Invasive Argentine Ant. Conservation Biology 14:559–563.

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The Causes and Consequences of Ant Invasions. Annual Review of Ecology and Systematics 33:181–233.

Hoogland, J. L. 1983. Black-Tailed Prairie Dog Coteries are Cooperatively Breeding Units. The American Naturalist 121:275–280.

Hoset, K. S., and M. Husby. 2019. Are predation rates comparable between natural and artificial open-cup tree nests in boreal forest landscapes? PLOS ONE 14:e0210151.

Hovanes, K. A., K. E. Harms, P. R. Gagnon, J. A. Myers, and B. D. Elderd. 2018. Overdispersed Spatial Patterning of Dominant Bunchgrasses in Southeastern Pine Savannas. The American Naturalist 191:658–667.

Huang, M. H. 2010. Multi-Phase Defense by the Big-Headed Ant, *Pheidole obtusospinosa*, Against Raiding Army Ants. Journal of Insect Science 10.

Huseynov, E. F., R. R. Jackson, and F. R. Cross. 2008. The meaning of predatory specialization as illustrated by *Aelurillus m-nigrum*, an ant-eating jumping spider (Araneae: Salticidae) from Azerbaijan. Behavioural Processes 77:389–399.

Ioannou, C. C., L. J. Morrell, G. D. Ruxton, and J. Krause. 2009. The effect of prey density on predators: conspicuousness and attack success are sensitive to spatial scale. The American Naturalist 173:499–506.

Janzen, D. H. 1970. Altruism By Coatis in the Face of Predation By Boa Constrictor. Journal of Mammalogy 51:387–389.

Jeanne, R. L. 1979. Construction and utilization of multiple combs in *Polistes canadensis* in relation to the biology of a predaceous moth. Behavioral Ecology and Sociobiology 4:293–310.

Kappeler, P. M. 2019. A framework for studying social complexity. Behavioral Ecology and Sociobiology 73:13.

Kaspari, M., and E. L. Vargo. 1995. Colony Size as a Buffer Against Seasonality: Bergmann's Rule in Social Insects. The American Naturalist 145:610–632.

Khorozyan, I., S. Ghoddousi, M. Soufi, M. Soofi, and M. Waltert. 2018. Cattle selectivity by leopards suggests ways to mitigate human–leopard conflict. Ecology and Evolution 8:8011–8018.

Kinsella, R. unpublished data. Colony Structure in Ants: How does the Number of Nests Relate to Worker Population in Polydomous Colonies? Unpublished.

Krause, J., and G. D. Ruxton. 2002. Living in Groups. OUP Oxford.

Krause, J., and J.-G. J. Godin. 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. Animal Behaviour 50:465–473.

Krause, J., D. J. Hoare, D. Croft, J. Lawrence, A. Ward, G. D. Ruxton, J. J. Godin, et al. 2000. Fish shoal composition: mechanisms and constraints. Proceedings of the Royal Society of London. Series B: Biological Sciences 267:2011–2017.

Kwapich, C. L., and B. Hölldobler. 2019. Destruction of Spiderwebs and Rescue of Ensnared Nestmates by a Granivorous Desert Ant (*Veromessor pergandei*). The American Naturalist 194:395–404.

LaGory, K. E. 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Animal Behaviour 35:20–25.

Lamon, B., and H. Topoff. 1981. Avoiding predation by army ants: Defensive behaviours of three ant species of the genus *Camponotus*. Animal Behaviour 29:1070–1081.

Lanan, M. C., A. Dornhaus, and J. L. Bronstein. 2011. The function of polydomy: the ant *Crematogaster torosa* preferentially forms new nests near food sources and fortifies outstations. Behavioral Ecology and Sociobiology 65:959–968.

LaPolla, J. S., U. G. Mueller, M. Seid, and S. P. Cover. 2002. Predation by the army ant *Neivamyrmex rugulosus* on the fungus-growing ant *Trachymyrmex arizonensis*. Insectes Sociaux 49:251–256.

Le Breton, J., A. Dejean, G. Snelling, and J. Orivel. 2007. Specialized predation on *Wasmannia auropunctata* by the army ant species *Neivamyrmex compressinodis*. Journal of Applied Entomology 131:740–743.

le Roux, A., M. I. Cherry, L. Gygax, and M. B. Manser. 2009. Vigilance behaviour and fitness consequences: comparing a solitary foraging and an obligate group-foraging mammal. Behavioral Ecology and Sociobiology 63:1097–1107.

Lindström, Å. 1989. Finch Flock Size and Risk of Hawk Predation at a Migratory Stopover Site. The Auk 106:225–232.

Maerz, J. C., J. M. Karuzas, D. M. Madison, and B. Blossey. 2005. Introduced invertebrates are important prey for a generalist predator. Diversity and Distributions 11:83–90.

Mañosa, S. 1994. Goshawk diet in a Mediterranean area of Northeastern Spain. J Raptor Res 28:84–92.

Mattson, D. J. 2001. Myrmecophagy by Yellowstone grizzly bears. Canadian Journal of Zoology 79:779–793.

Mori, K., and Y. Saitō. 2004. Nest-size variation reflecting anti-predator strategies in social spider mites of *Stigmaeopsis* (Acari: Tetranychidae). Behavioral Ecology and Sociobiology 56:201–206.

Morrell, L. J., and R. James. 2008. Mechanisms for aggregation in animals: rule success depends on ecological variables. Behavioral Ecology 19:193–201.

Mouhoub-Sayah, C., H. Djoudad-Kadji, F. Kletty, A. Malan, J.-P. Robin, M. Saboureau, and C. Habold. 2018. Seasonal variations in the diet and food selection of the Algerian hedgehog *Atelerix algirus*. African Zoology 53:1–10.

Murray, M. G. 1987. The closed environment of the fig receptacle and its influence on male conflict in the old World fig wasp, *Philotrypesis pilosa*. Animal Behaviour 35:488–506.

Noordwijk, M. A. V., and C. P. V. Schaik. 1986. The Hidden Costs of Sociality: Intra-Group Variation in Feeding Strategies in Sumatran Long-Tailed Macaques (*Macaca fascicularis*). Behaviour 99:296–314.

Noyce, K. V., P. B. Kannowski, and M. R. Riggs. 1997. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Canadian Journal of Zoology 75:1671–1686.

Paijmans, K. C., D. J. Booth, and M. Y. L. Wong. 2019. Towards an ultimate explanation for mixed-species shoaling. Fish and Fisheries 20:921–933.

Päivinen, J., P. Ahlroth, V. Kaitala, and J. Suhonen. 2004. Species richness, abundance and distribution of myrmecophilous beetles in nests of *Formica aquilonia* ants. Annales Zoologici Fennici 41.

Pamminger, T., S. Foitzik, D. Metzler, and P. S. Pennings. 2014. Oh sister, where art thou? Spatial population structure and the evolution of an altruistic defence trait. Journal of Evolutionary Biology 27:2443–2456.

Pascual-Garrido, A., B. Umaru, O. Allon, and V. Sommer. 2013. Apes finding ants: Predator–prey dynamics in a chimpanzee habitat in Nigeria. American Journal of Primatology 75:1231–1244.

Pekár, S., S. Toft, M. Hrušková, and D. Mayntz. 2008. Dietary and prey-capture adaptations by which *Zodarion germanicum*, an ant-eating spider (Araneae: Zodariidae), specialises on the Formicinae. Naturwissenschaften 95:233–239.

Picman, J. 1988. Experimental Study of Predation on Eggs of Ground-Nesting Birds: Effects of Habitat and Nest Distribution. The Condor 90:124–131.

Pruitt, J. N., and L. Avilés. 2018. Social spiders: mildly successful social animals with much untapped research potential. Animal Behaviour 143:155–165.

Punttila, P., and J. Kilpeläinen. 2009. Distribution of Mound-Building Ant Species (*Formica* spp., Hymenoptera) in Finland: Preliminary Results of a National Survey. Annales Zoologici Fennici 46:1–15.

Queller, D. C., and J. E. Strassmann. 1998. Kin Selection and Social Insects. BioScience 48:165–175.

Rákóczi, A. M., and F. Samu. 2014. Coexistence Patterns Between Ants And Spiders In Grassland Habitats. Sociobiology 61:171–177.

Rasa, O. A. E. 1986. Coordinated Vigilance in Dwarf Mongoose Family Groups: The 'Watchman's Song' Hypothesis and the Costs of Guarding. Ethology 71:340–344.

Reitsma, L. 1992. Is nest predation density dependent? A test using artificial nests. Canadian Journal of Zoology 70:2498–2500.

Reyer, H.-U. 1984. Investment and relatedness: A cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). Animal Behaviour 32:1163–1178.

Robinson, E. J. 2014. Polydomy: the organisation and adaptive function of complex nest systems in ants. Current Opinion in Insect Science 5:37–43.

Rutz, C., R. G. Bijlsma, M. Marquiss, and R. Kenward. 2006. Population limitation in the Northern Goshawk in Europe: A review with case studies. Studies in Avian Biology 31:158–197.

Ruxton, G. D., S. Humphries, L. J. Morrell, and D. M. Wilkinson. 2014. Why is eusociality an almost exclusively terrestrial phenomenon? Journal of Animal Ecology 83:1248–1255.

Saitō, Y. 1986*a*. Prey kills predator: Counter-attack success of a spider mite against its specific phytoseiid predator. Experimental & Applied Acarology 2:47–62.

———. 1986*b*. Biparental defence in a spider mite (Acari: Tetranychidae) infesting Sasa bamboo. Behavioral Ecology and Sociobiology 18:377–386.

Santema, P., and T. Clutton-Brock. 2013. Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. Animal Behaviour 85:655–661.

Schmolke, A. 2009. Benefits of Dispersed Central-Place Foraging: An Individual-Based Model of a Polydomous Ant Colony. The American Naturalist 173:772–778.

Schöning, C., W. Kinuthia, and N. R. Franks. 2005. Evolution of allometries in the worker caste of *Dorylus* army ants. Oikos 110:231–240.

Scott, D. D., E. S. M. Boston, M. G. Lundy, D. J. Buckley, Y. Gager, C. J. Chaplain, E. C. Teeling, et al. 2018. Relatedness, parentage, and philopatry within a Natterer's bat (*Myotis nattereri*) maternity colony. Population Ecology 60:361–370.

Semel, B., and P. W. Sherman. 1986. Dynamics of Nest Parasitism in Wood Ducks. The Auk 103:5.

Sieving, K. E., and M. F. Willson. 1998. Nest Predation and Avian Species Diversity in Northwestern Forest Understory. Ecology 79:2391–2402.

Skelhorn, J., and C. Rowe. 2006. Prey palatability influences predator learning and memory. Animal Behaviour 71:1111–1118.

Snyder, L. E., and J. M. Herbers. 1991. Polydomy and sexual allocation ratios in the ant *Myrmica punctiventris*. Behavioral Ecology and Sociobiology 28:409–415.

Stockan, J. A., and E. J. H. Robinson. 2016. Wood Ant Ecology and Conservation. Cambridge University Press.

Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey Selection in Horned Lizards Following the Invasion of Argentine Ants in Southern California. Ecological Applications 10:711–725.

Sun, Q., K. F. Haynes, and X. Zhou. 2018. Managing the risks and rewards of death in eusocial insects. Philosophical Transactions of the Royal Society B: Biological Sciences 373.

Swenson, J. E., A. Jansson, R. Riig, and F. Sandegren. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Canadian Journal of Zoology 77:551–561.

Teppei, J., K. Yosuke, and M. Takafumi. 2019. Novel cooperative antipredator tactics of an ant specialized against a snake. Royal Society Open Science 6:190283.

Torres, J. A., R. Thomas, M. Leal, and T. Gush. 2000. Ant and termite predation by the tropical blindsnake *Typhlops platycephalus*. Insectes Sociaux 47:1–6.

Tosoni, E., M. Mei, and P. Ciucci. 2018. Ants as food for Apennine brown bears. The European Zoological Journal 85:343–349.

Turchin, P., and P. Kareiva. 1989. Aggregation in *Aphis Varians*: An Effective Strategy for Reducing Predation Risk. Ecology 70:1008–1016.

Wasserstein, R. L., and N. A. Lazar. 2016. The ASA Statement on p-Values: Context, Process, and Purpose. The American Statistician 70:129–133.

Way, M. J. 1954. Studies of the Life History and Ecology of the Ant *Oecophylla longinoda* Latreille. Bulletin of Entomological Research 45:93–112.

Weber, T. C., H. Peña, and J. M. Jech. 2009. Consecutive acoustic observations of an Atlantic herring school in the Northwest Atlantic. ICES Journal of Marine Science 66:1270–1277.

Wilgenburg, E. van, and M. A. Elgar. 2007. Colony characteristics influence the risk of nest predation of a polydomous ant by a monotreme. Biological Journal of the Linnean Society 92:1–8.

Wilgenburg, E. van, R. A. Mulder, and M. A. Elgar. 2006. Intracolony relatedness and polydomy in the Australian meat ant, *Iridomyrmex purpureus*. Australian Journal of Zoology 54:117–122.

Wilson, E. O., and B. Hölldobler. 2005. Eusociality: Origin and consequences. Proceedings of the National Academy of Sciences 102:13367–13371.

Ydenberg, R. C., and L. M. Dill. 1986. The Economics of Fleeing from Predators. (J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater, eds.) Advances in the Study of Behavior 16:229–249.