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Jeffrey Garnas

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**EUROPEAN FIRE ANTS ON MOUNT DESERT ISLAND, MAINE:
POPULATION STRUCTURE, MECHANISMS OF COMPETITION
AND COMMUNITY IMPACTS OF *MYRMICA RUBRA* L.
(HYMENOPTERA: FORMICIDAE)**

by

Jeffrey Garnas

B.A. University of Colorado, 1997

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

December 2004

Advisory Committee:

Eleanor Groden, Associate Professor of Entomology, Co-Advisor

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Thesis Co-advisors: Dr. Eleanor Groden and Dr. Francis Drummond

An Abstract of the Thesis Presented
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In the early to mid-20th century, *Myrmica rubra* Latreille established in various communities in Maine, mostly along the coast. Since its establishment, the ant has spread both locally via vegetative colony budding and regionally via human commerce to no fewer than 30 Maine communities, including one inland site. Studies were undertaken in the summer of 2002 to address questions of the ants' population structure in its introduced range by testing for intercolony aggression within and between local infestations. Using captive nests maintained in their original nest soil, *M. rubra* was tested against its close neighbors, neighbors of 10m within the same infestation, and at two locations within a distinct infestation elsewhere on the island. Aggressive behaviors were quantified, and results suggest a multicolonial population structure, with ants tolerating their close neighbors (perhaps fragments of their own colony), showing measurable aggression toward their 10m

neighbors, and significantly more aggression again toward distant neighbors from which they were separated geographically at the outset.

Pitfall and Berlese funnel sampling in four paired sites in Acadia National Park in 2002 showed little impact of *M. rubra* on the resident (non-ant) arthropod community, with the exception of a significant increase in isopod abundance. Impacts on the native ant fauna were severe, reflecting almost complete displacement and a significant reduction in species richness and diversity. Independent sampling of the homopteran community (tended by *M. rubra* and native ants for their honeydew exudates) showed an enhanced richness and abundance of several groups where *M. rubra* was present. Proportionally fewer homopterans were left untended within invaded habitat, suggesting that these insects are “ant-limited” and confirming our results that *M. rubra* may enhance such populations.

Finally, a total of 27 aggression assays against native/resident ants in Acadia National Park were performed in an attempt to quantify and characterize behavioral interactions between *M. rubra* and the native ant community. On average, *M. rubra* was able to quickly dominate the native foragers and displace them from baits, though some species were more adept at defense, generally by virtue of a well developed sting or chemical spray. A separate experiment testing discovery time and recruitment at the boundary of a local infestation showed that *M. rubra* foragers discover and recruit more quickly to a food resource. Taken together, these findings suggest that *M. rubra*, by virtue of its numerical dominance, has broken the “dominance-discovery” trade-off that serves to partition food resources, allowing native ant coexistence (Fellers, 1987).

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CHAPTER 1

Success of a new invader – Population structure and competitive displacement in *Myrmica rubra*-invaded habitat

The introduction and spread of invasive ant species in the United States and worldwide has spawned a proliferation of research addressing the impact of non-native ants on native ant communities. While as yet of limited geographical range in Maine and the Northeast, populations of the European fire ant, *Myrmica rubra*, have been exploding since the early 1990's (Grodén et al. unpublished data). Preliminary research indicates that *M. rubra* is capable of displacing native species, resulting in greatly reduced diversity in areas of local infestation. Studies of the mechanisms of displacement and of competitive interactions between *M. rubra* and native ant fauna have been undertaken; their results are forthcoming. It is the goal of this paper to provide an overview of the primary literature addressing competition between native and introduced ants, with specific focus on aspects relevant to *M. rubra* and other north temperate ants.

Competition among ant species has long been considered a major factor in shaping ant communities. While direct aggression between native ants does occur, co-evolved species are generally thought to develop strategies that minimize conflict while maximizing their own productivity and access to resources in a given habitat or environment (Hölldobler and Wilson 1990). Examples of extensive niche partitioning, regular spacing of colonies among mutually aggressive ants and the establishment of stable linear dominance hierarchies are presented throughout the

literature as evidence of past and present competition (Fellers 1987, Hölldobler and Wilson 1990, Ryti and Case 1992). Introduced ants, once established, are often able to enter and quickly dominate a habitat (Passera 1994). The mechanisms of such rapid displacement are numerous and complex, but it is clear that an outwardly radiating invasive front represents a profound disruption to the evolved strategies and trade-offs that otherwise promote diversity and co-existence among native ants (Ward 1987, Passera 1994). Native species are often outcompeted for both resources and space by exotic invaders. Their reproductives are subject to attack and predation at greatly elevated rates, and in some cases, their foragers and nest sites are attacked. A number of studies found that the majority of native species were locally or regionally extirpated in the wake of an invasion (Ward 1987, Passera 1994, Erickson 1971, Porter and Savignano 1990)

Differing environmental conditions, habitat structure and community dynamics ensure that competitive interactions on a given invasion front will take distinct forms. Considerable effort has gone into describing widely observed patterns of invasion by exotic fauna (Passera 1994, Porter and Savignano 1990, Reitz and Trumble 2002). No such description is fully capable of a predictive ecology of displacement and spread (Human and Gordon 1998, Lodge 1993), but the growing body of literature provides evidence of trends common to many ant invasions. Hölldobler and Wilson (1990) characterize “tramp ants” as polygynous, unicolonial species that often reproduce by budding, are widely dispersed by human commerce and live in close association with humankind. McGlynn (1999) makes a further distinction between tramp and invasive ants, suggesting that invasive species are also

adept at monopolizing food resources required by native ants, while tramp ants may only be capable of occupying a previously unfilled niche. *M. rubra* satisfies most, if not all, of the requirements for classification as an invasive. It is highly polygynous both in its home range and in Maine (Brain et al. 1981, Elmes and Petal 1990, Groden et al. unpublished data). Twenty-five to fifty fertile queens in a large nest are not uncommon; up to 600 have been found in a single nest (Elmes 1973, Elmes and Petal 1990). There is evidence of considerable polydomy coupled with a significant loss of intracolony aggression, potentially indicative of a level of unicoloniality and of the abandonment of the nuptial flight in favor of vegetative spread (Groden et al. unpublished data, van der Hammen et al. 2002). While *M. rubra* infestations have spread to some extent from suspected points of introduction into adjacent fields and forest, their affinity for areas of high insolation (Brian and Brian 1951) along with their tolerance for disturbed habitat have so far resulted in a distribution that appears to loosely follow patterns of human settlement in their introduced range (unpublished observation).

Competitive interaction within and among species is generally classified as either interference or exploitative in nature (Brian 1956, Schoener 1974). Interference competition refers to the direct displacement of one species by another from a limited resource. This can occur by way of encounter at the resource, where dominant ants displace competitively weaker species by employing a combination of attack, aggressive display, and/or the use of defensive chemicals. Alternatively, interference competition can result from territoriality where, by repeated chemical marking and patrol, a colony can claim an area as its own and effectively exclude

others from the resources contained within (Hölldobler and Lumson 1980, Brian 1983). Exploitation competition refers to the reduced availability of a given resource through its consumption or through the preemption of its use by another individual or species (Wilson 1971, Davidson 1998). Among ants, interference and exploitative competitive ability can be viewed as an evolutionary trade-off. Some species are adapted for rapid discovery and utilization of a food source but tend toward behavioral submissiveness and are displaced if and when a superior interference competitor arrives (Fellers 1987, Hölldobler and Wilson 1990). Baiting experiments are commonly reported in the literature and are useful in constructing linear dominance hierarchies, which rank sympatric ant species in order of competitive superiority at a contested resource. Such determinations of dominance incorporate both individual (worker size, agility and the use of chemical compounds) and colony-level attributes (worker number, recruiting ability), and tend to be stable and replicable across trials (Holway 1999, Human and Gordon 1999, Savolainen and Vepsäläinen 1988). Fellers (1987) found that the discovery rate of the food resources was independent of distance to the nest and was highly characteristic of a particular species, with the exception of baits placed very close to the nest entrance. In her experiments, the three “exploitative” competitors were consistently the first to arrive at baits, while those she called “encounter” species were almost always the last to arrive. Once the behaviorally dominant ants (the encounters) did arrive, the early-arriving submissives nearly always yielded peaceably by avoidance. Similar trends have been observed in a number of other studies (Adams and Traniello 1981,

Fowler 1990, Hölldobler and Lumsden 1980, Human and Gordon 1996, Rosengren 1986, Traniello 1989).

The invasion of an exotic can result in competitive displacement of native species through superior interference or exploitative competitive ability. More often, however, researchers have pointed to invasion by exotic ants as a disruption of the competitive trade-off between the two reciprocal forms (Holway 1999). Numerical dominance almost invariably translates into success in conflict regardless of the size, agility or defensive compounds of individual ants. As such, abundant invasive species are generally the ultimate victors of interference encounters due to overwhelming numbers and density of workers (Holway 1999, Hölldobler and Wilson 1990). High population densities translate to virtual habitat saturation, greatly increasing the probability of rapid resource discovery and facilitating efficient recruitment to and monopolization of large or stable food sources. The dominance demonstrated by invasive ants within a given habitat has been attributed in large part to the break of this trade-off. Holway (1999), in his work in communities invaded by the Argentine ant *Linepithema humile* (= *Iridomyrmex humilis*) in California, found that among native ants, species' ranks with respect to time to discovery of bait resources were inversely correlated with a rating of dominance in encounter or interference competition, in keeping with the dominance-discovery trade-off. In contrast, *L. humile* was invariably among the first to discover baits and was also ranked highest on the competitive dominance scale, able to maintain control of food resources after discovery by foragers of a competitor species. While competing theories for the proximate and ultimate causes of

unicoloniality are still being debated in the literature (Giraud et al. 2002, Tsutsui et al. 2003), this population structure (characteristic of introduced populations of *L. humile*) facilitates numerical dominance and habitat saturation, which translates into the ant's competitive superiority and break in the trade-off. Similar trends have been shown to exist in other introduced populations of *L. humile* throughout the world, as well as with the Southern Imported Fire Ant (*Solenopsis invicta*) in the Southeastern United States (Porter and Savignano 1990, Tschinkel 1993, Morrison 2000).

The question of the role of competition in structuring ant communities represents another area of debate in the literature. Many studies have cited interspecific competition as central in shaping communities of ants (Brian 1956, Elmes 1974, Fellers 1987, Rosengren 1986, Savolainen and Vepsäläinen 1988). Other research suggests that intraspecific competition may have greater influence over the observed patterns of colony distribution and overlap in the habitat (Ryti and Case 1984, Ryti and Case 1992, Bernstein and Gobbel 1979). Still others point to abiotic factors as being of paramount importance with respect to the distribution of resources, and therefore to the colonization of the habitat by ants (Connell 1983). A useful method in assessing questions of the relative importance of inter-and intraspecific competition in a given community is the study of the spatial distribution of nests or colonies (Clark and Evans 1954, Ryti and Case 1992). Nonrandom spacing of nests, when considered alongside natural fluctuations in habitat quality and the aggregation of resources, has traditionally been interpreted as an artifact of competition and mutual avoidance between colonies (Elmes 1974, Levings and Traniello 1981, Ryti and Case 1992).

Elmes (1973) found that in a limestone grassland with abundant available nesting sites, *M. rubra* nests were significantly aggregated, whereas *M. rubra* and *Lasius flavus* nests were considerably segregated. He concluded that this pattern was indicative of competition between the *M. rubra* and *L. flavus*. Competition between these two species has been supported in a number of additional studies (Brian 1972, Rosengren 1986). However, Elmes was careful to note that *M. rubra*'s tendency toward polydomous colonies (spanning more than one nest stone) could have inflated the index of aggregation. Alternatively, Ryti and Case (1984) found that in a relatively homogeneous habitat, intraspecific nearest-neighbor distances exceeded those between colonies of different species and that their model of spatial distribution functioned adequately as a predictor when only intraspecific distances were considered. They interpreted this finding to mean that intraspecific competition was the main determinant of colony assembly among the three desert ants that they studied. They also found significant aggregation across species relative to the diet overlap among them. Since food tends to be distributed patchily throughout a habitat, significant aggregation would be expected in the absence of competition. Their findings, along with subsequent work (Ryti and Case 1986, Ryti and Case 1992), have called into question the long-held belief that interspecific competition is of paramount importance in the structuring of ant communities.

Introduced ants are a special case with respect to intra- and interspecific competition. As previously mentioned, invasive species often tend toward unicoloniality, which is accompanied by a great reduction of intraspecific aggression between neighboring nests. At the same time, there is often a marked increase in

interspecific aggressiveness directed at native species that the intruder must drive off in order to establish itself. While native ants continue to be held in check by conspecifics and other ants which share a similar niche, the invasive species is free to expand its range and territory in the absence of the formidable pressures of intraspecific antagonism (Passera 1994). Several studies of *L. humile* have shown the impact of this release from intraspecific competition. Holway et al. (1998) raised colonies of *L. humile* in the laboratory in intraspecifically aggressive and non-aggressive pairs. They then measured foraging efficiency and colony growth and found that both were significantly higher for the colonies that were paired with a non-aggressive partner. They further posited that in the field, this release leads to elevated worker populations and density, giving *L. humile* along with other invasive ants the numeric edge to fully dominate a habitat. Though the exact causes of reduced aggression and facultative uniclonality are unknown for *L. humile*, studies suggest that reduced genetic variation subsequent to introduction has prompted a breakdown in nestmate discriminatory ability (Tsutsui et al. 2000, Ross and Keller 1995).

Whatever its relative contribution, competition among species clearly plays a role in shaping ant communities, and that role likely changes across habitats, species assemblages and environmental conditions. In addition, not all habitats are saturated to the level at which colonies must compete for nest sites or food. That said, there is evidence that the relatively low ant species diversity in north temperate and boreal habitats (due largely to suboptimal climatic conditions) favors the establishment of dominants in the community (Hölldobler and Wilson, 1990). Hölldobler and Wilson

(1990) refer to this trend as the “dominance-impoverishment rule,” defined as follows: “the fewer the ant species in a local community, the more likely the community is to be dominated behaviorally by one or a few indigenous species with large aggressive colonies that maintain absolute territories.” This trend has been noted in habitats in northern Europe (Vepsäläinen and Pisarski 1982, Rosengren and Pamilo 1983), where large colonies of *Formica* ants are able to outcompete colonies of lesser size and extent for sparse resources. A similar trend was noted by Ward (1987) with respect to the invasive *L. humile* dominating species-poor California riparian woodland habitats. Hölldobler and Wilson (1990) suggest that areas with physically harsh climates or geologically young habitats generally support fewer specialist species and are therefore wide open for conquest by generalists that can secure and maintain control of a larger niche. This “rule” may explain the success of *M. rubra* in dominating large tracts of land in Maine and the Northeast. *M. rubra* is a trophic and nest-site generalist with large polydomous colonies and as an exotic, appears to have been released from competition with co-evolved ant species and at least some natural enemies.

Many studies of competition among ant species and of ant community assemblages are designed to assess the role of niche partitioning (Davidson 1998, Lynch and Johnson 1988, Savolainen et al. 1989). As discussed, for many species intraspecific competition is the dominant competitive force, largely because ants of the same species necessarily share the greatest overlap of food and microhabitat needs. Co-occurring ants have partitioned habitats over the course of evolution, carving out subtle niches that satisfy each colony or species’ requirements for

production and sustainability while minimizing competition to the greatest extent possible. Ants have evolved to prefer different food types or nesting substrates, or to forage at different times of the day or season or at varying heights off the forest floor (Lynch and Johnson 1988, Savolainen et al. 1989, Savolainen and Vepsäläinen 1990). In the presence of a dominant generalist invader, the number of open available niches is greatly reduced (Passera 1994, Suarez et al. 1998). However, it appears that some small niches may continue to persist for a few species despite a high degree of infestation by an invader. Human and Gordon (1997) found that two hypogaeic ants (*Leptothorax andrei* and *Solenopsis molesta*) were able to persist in substantial numbers despite the presence of dense populations of *L. humile*. *M. rubra* colonies forage around the clock throughout the summer and are among the first ants to begin foraging in the spring (Grodén et al. unpublished data). They are capable of nesting in a number of different substrates - under stones, beneath or within fallen logs, among the roots of herbaceous or woody vegetation, in soil mounds of varying type, or in the leaf litter (Grodén et al. unpublished data). Preliminary data suggest limited coexistence with other ant species in heavily infested areas on Mt. Desert Island, ME. Yet unknown is whether this invasion will allow for the coexistence of a few cryptic species, similar to what has been seen with *L. humile*, and how the surviving communities may restructure.

Though generalized to arthropod invaders, Reitz and Trumble (2002) present a summary of eight mechanisms of competition leading to displacement, many of which incorporate the mechanisms discussed earlier in this paper and are applicable to introduced ant populations: 1) Differential resource acquisition can result in

superior exploitative ability by one species over another, leading to reduced access and availability of vital resources for native species. 2) Differential female fecundity, or the ability to create proportionately more female reproductives from the same resources, can be a strong competitive advantage. This is likely the case with *M. rubra*. Elmes and Petal (1990) reported that nearly all of *M. rubra*'s multiple queens were fertile. Polygyny appears to be common among highly successful invasive ants studied to date (Passera 1994). 3) Differential searching ability, akin to *M. rubra*'s ability to discover resources in the environment ahead of other ants. In the case of *L. humile* and *M. rubra*, superior discovery skill has an even greater advantage over native species when coupled with the ability to dominate and defend such food sources (Holway 1999, Groden et al. unpublished data). 4) Resource preemption occurs when a species utilizes a resource before another species has a chance to access it. This can also include cases where one species has an earlier seasonal phenology than others in the environment and as such has access to resources in advance of its competitors. While there is no solid evidence that resources are limiting throughout the season, *M. rubra* appears to be one of the most cold-tolerant species among Maine's ant fauna. This may confer an advantage in early-season foraging, production and nest site choice compared with species that end diapause and begin foraging later in the spring. 5) Resource degradation refers to the utilization of a limited resource that leaves it below the level of need of another species. This could apply to ant invasions if the invasive scours the habitat for scattered resources and reduces the stock of protein so that subsequent foraging efforts by native species exceeds the benefits of searching. 6) Agonistic interference

competition, such as contests over food resources, foraging or nesting sites has been clearly established as a major force in native ant displacement by exotic invaders. 7) Reproductive interference can also be a significant contributor to competitive displacement by invading organisms. This is the case for invasive ant species that prey heavily upon competitors' winged reproductives that alight on the soil in search of a suitable nest site (Hölldobler and Wilson 1990). 8) Finally, intraguild predation (i.e. predators preying on other predators or phytophages consuming plant material containing other herbivores) has been observed in invasive ants that raid the nests and consume the immatures of a competing species as part of their scavenging forays (Tschinkel 1993).

Competitive displacement can be defined as the removal of an established species from a habitat through superior use, acquisition or defense of resources (Reitz and Trumble 2001 - modified from Debach 1966). While displacement occurs regularly as part of the natural cycle of an ecosystem, it is often overshadowed by the frequency and severity of human-mediated introductions, particularly in the case of invasive ant species which may be particularly well suited to global travel, establishment and spread by virtue of their unique biology and social organization. After nearly a full century of research on invasive ant species, ecologists are just beginning to understand the mechanisms that give rise to such widespread domination by a single species. Searching for patterns across invasions as well as looking closely at the competitive interactions leading to displacement on each invasive front are essential to gaining a greater understanding of the processes involved.

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CHAPTER 2

Intercolony aggression within and between local populations of the invasive ant *Myrmica rubra* L.

INTRODUCTION

One of the major mechanisms cited in recent years to account for the widespread dominance of invasive ant species worldwide is the apparent switch to unicoloniality, a population structure characterized by a breakdown of colony boundaries and loss of intraspecific aggression (see Wilson 1971, Holway et al. 2002, Giraud et al. 2002, Tsutsui and Case 2001, Chen and Nonacs 2000). Under conditions of unicoloniality, individual colonies that would otherwise be forced to divert workers and energetic resources to the task of defending territorial borders from conspecific encroachment or attack are able to function together as a single cooperative unit over a large geographical area (Wilson 1971, Hölldobler and Lumson 1980, Hölldobler and Wilson 1990, Holway and Case 2001). Giraud et al. (2002) found that the Argentine ant (*Linepithema humile* Mayr) invasion in southern Europe comprises two enormous supercolonies, the larger of which spans an area with a maximum diameter of ca. 6000 km. Large expanses of mutually non-aggressive populations of *L. humile* have been found to exist across vast stretches of California and the Southeast, as well as in several islands in the Caribbean. Recent work, however, has revealed some spatiotemporal variability in intercolony

responses, suggesting an environmental component in the regulation of this social structure in introduced *L. humile* populations (Chen and Nonacs 2000, Suarez et al. 2002). Alternatively, the Southern Imported Fire ant (*Solenopsis invicta* Buren), also well studied in its introduced range throughout the Southern United States, exhibits two distinct social forms corresponding to the number of queens per colony. Monogynous colonies do not tolerate close neighbors and the aggression they exhibit gives rise to greater spacing between nests, whereas the polygyne form is more similar to *L. humile* and other invasive ants (e.g. *Wasmannia aurapunctata* Roger and *Pheidole megacephala* Fabricius), tending toward intercolony tolerance and effective unicoloniality (Ross et al. 2003, Ross and Keller 1995)

The genetic, social and ecological determinants of unicoloniality, perhaps key to the success of invasive ant species, are the subject of intense ongoing research and speculation (Tsutsui et al. 2000, Holway et al. 2002, Tsutsui and Suarez 2003, Giraud et al. 2002, Starks 1998, Ross et al. 2003). In the case of *S. invicta*, the monogyne (~multicolonial) and polygyne (~unicolonial) forms have been shown to differ by queen genotype at a single genetic locus (Gp-9), where the presence of a genetic switch determines queen acceptance or rejection from an established colony (in the polygyne and monogyne forms respectively), primarily through the expression of hydrocarbon cues recognized by colony workers (Ross et al. 2003, Morel et al. 1990). In *L. humile* populations, no such social polymorphism is known to exist. Rather, native populations are generally multicolonial, whereas invasive populations are unicolonial over large areas (Holway and Suarez 2004, Tsutsui and

Case 2001). Tsutsui et al. (2000) suggest that in *L. humile*, a loss of genetic diversity resulting from a population bottleneck at the time of introduction is a proximate cause of the breakdown of intercolony aggression, as fewer alleles at any/all nestmate recognition loci would lead to a reduced ability to discriminate nestmates from non-nestmates. Alternatively, Giraud et al. (2002) found that while introduced European populations of *L. humile* do exhibit lower allelic diversity at a number of neutral loci when compared with native Argentinean populations (indicating that the introduced form did in fact experience a bottleneck event), the loss of overall variation was comparatively slight and alone not sufficient to lead to the fixation of a small number of recognition alleles. They suggest that selection for common alleles at recognition loci may occur in areas of relaxed ecological constraints and may be driving the observed patterns (Giraud et al. 2002).

In addition to arising serendipitously as a consequence of lost genetic variation or other event related to invasion, unicoloniality has also been suggested as a social form that evolves under certain conditions (Seppä and Pamilo 1995, Seppä and Walin 1996, Walin et al. 2001, van der Hammen et al. 2002, DeHeer et al. 2001). Kin selection theory does not favor unicoloniality as a stable state in the long term, since under conditions of free transfer of individuals between nests, workers inevitably wind up raising unrelated individuals (Crozier and Pamilo 1996). Such a population structure may be highly advantageous as a transient state, however, particularly in the case of invasions (Tsutsui et al. 2000, Holway 1999, Holway et al. 1998). Alternatively, some researchers have suggested that in certain species,

unicoloniality may be the final stage in a progression of social forms that arises subsequent to a local invasion, though only in stable, high-quality habitats that can sustain a high ant abundance and nest density (Pederson and Boomsma 1999, van der Hammen et al. 2002). In conditions of abundant food resources and lower levels of competition, colonies no longer need to defend their territories against conspecifics and are freed to focus energy on the production of new workers and sexuals, increasing overall productivity among colonies and populations (Holway 1999, Holway and Case 2001, Holway and Suarez 2004). Also, in native areas, higher pathogen loads may attach a substantial cost to close nest proximity, worker/brood transfer and territorial overlap, as transmission rates would likely increase under a prolonged, high-density population structure. Introduced populations, likely having left a number of their pathogens behind, may not suffer such constraints (Porter et al. 1997, Holway et al. 1998, Starks et al. 1998). Given that numerical dominance in ants almost always translates to a competitive advantage in terms of both interference and exploitative competition (Hölldobler and Wilson 1990), the drastic increase in nest density and an abundant, cohesive pool of foragers could facilitate the displacement of native ant species via mechanisms of direct aggression as well as by the efficient and preemptive exploitation of available resources (Holway 1998, Davidson 1998).

Myrmica rubra (L.), an invasive Myrmicine of Holarctic origin and distribution (Collingwood 1979, Elmes 1975), has become a serious pest in certain areas in Maine and the Northeast over the past several decades. Though the full history of

the ant's introduction and spread is not known, *M. rubra* has been present in Boston since at least 1906 and in a number of Maine communities since the 1950's or earlier (Wheeler 1908, Groden et al., unpublished data). While at low densities, its variable and often ephemeral nests are scarcely noticeable to the casual observer, many of the sites of infestation in coastal Maine are characterized by an extremely high density of both colonies/nests and workers. In Maine, *M. rubra* has been found to nest in a variety of substrates, including excavated cavities in the soil, under and within rotting wood, at the base of trees and herbaceous vegetation, under stones, in moist hummocks and in and among leaf litter and debris. Populations have been shown to virtually saturate a habitat, reaching an average density of 1.1 nests per m² across sites of infestation (Groden et al., unpublished data). While highly aggressive and apparently nondiscriminating in their attacks on vertebrates and invertebrates, relatively little overt aggression is evident among *M. rubra* workers in the habitat despite the close proximity of nests and corresponding overlap in foraging ranges. Given *M. rubra*'s highly polygynous life history, apparent forfeiture of mating flights in favor of reproduction via colony budding (in Maine and in parts of their native range) (Elmes 1975, Elmes and Petal 1990, Seppä and Pamilo 1995, Seppä and Walin 1996; also see Tsuji and Tsuji 1996) and observed internest tolerance within heavily infested sites (personal observation), introduced populations superficially resemble supercolonies of *L. humile* and other invasive ants cited in the literature (Passera 1994, Tsutsui and Suarez 2003). Interestingly, similar *M. rubra* populations shown to exist in parts of northern Europe were characterized by localized patch dominance, high (while variable) levels of polygyny and polydomy,

low intercolony relatedness and high site fidelity, reproduction by budding and restricted gene flow between local patches. No direct assessments of intercolony aggression or tolerance were reported in studies of these populations (Seppä and Pamilo 1994, Seppä and Walin 1996, van der Hammen 2002). In England and other parts of Europe, local patch dominance by *M. rubra* is rarely cited, though the ant is a regular component of a more diverse ant community including *Myrmica*, *Formica* and *Lasius* species with which it coexists as a generally subordinate competitor across much of its range (Pontin 1969, Vepsäläinen and Savolainen 1990, Czechowski 1985, Brian 1952, Brian 1964). Whether the ecological conditions that give rise to patch dominance and effective unicoloniality in northern Europe have corollaries in Maine that drive the development of similar social structure, or whether such patterns have arisen as a direct or indirect consequence of the ant's introduction into a novel habitat, is unknown.

Extensive sampling and observation have shown that *M. rubra* achieves local patch dominance in infested sites in Maine; these populations appear to exhibit social dynamics similar to that reported in Scandinavia. Genetic assessments of kin structure and relatedness have not yet been performed. The goal of this research is to investigate the hypothesis that introduced populations of *M. rubra* in Maine are "unicolonial." We define unicoloniality as it is most often applied in the invasive ant literature as the abandonment of intraspecific aggression and a breakdown of colony boundaries within local patches and/or across populations (Holway et al. 1998, Human and Gordon 1996, Passera 1994). With this definition in mind, we

experimentally tested for aggression between groups of workers and colony fragments in the field.

MATERIALS AND METHODS

Mobile nest establishment:

In order to test colony-level aggression between nests both within and among discrete *M. rubra* infestations, mobile nests were established that could be easily transported between study sites. Ten nests were excavated and used in aggression assays throughout the season. Five nests were dug from an equal number of non-contiguous sites of *M. rubra* infestation on Mount Desert Island, ME in late May 2003, and five more were excavated from the same sites in late June of the same year. Care was taken to dig up each nest in its entirety, though given the highly polydomous habit of the ant (Elmes 1975, Walin et al. 2001), likely meant that each captive nest represented a fragment or satellite of the original colony. Nonetheless, each contained a representative mix of queens, brood and workers (Table 2.1). All castes were counted in the field and placed (along with several liters of original nest soil) in 9.8 liter Rubbermaid® tubs, the sides of which were coated with Fluon® to prevent climbing. Collected colonies were held for two weeks prior to being used for aggression assays, during which time they were fed a standard diet of 20% sucrose (v/v) and locally captured insects and provided with a constant source of water via a piece of saturated gauze. In addition, nest soil was misted weekly to approximate ambient soil moisture. Colonies were fed with insects collected in a

sweep net from typical *M. rubra* habitat so as to provide a varied protein source and to minimize the effects of acquired cuticular hydrocarbon composition from a single prey item, shown to influence nestmate recognition in ants (Silverman and Laing 2001).

Experimental design:

M. rubra is patchily distributed on Mt. Desert Island (as in much of Maine), and sites of dense infestation are discrete, separated from neighboring infestations by a range of hundreds of meters to kilometers. The intervening habitat is free of *M. rubra* colonies and is inhabited by no fewer than 10-20 species of a total of 40 species of native ants found on Mt. Desert Island during the course of sampling. Captive nests were assayed for intercolony aggression (generally multiple times each) at four locations relative to the original site of nest excavation. Two assay locations were chosen within each captive colony's population of origin – within 1m of the site of excavation, and approximately 10m from the site of excavation. These two treatments were chosen to represent ex-colony fragments or close neighbors and members of the same local population (and potentially of the same supercolony) respectively. In addition, captive nests were tested at two sites within a distinct, noncontiguous infestation elsewhere on the island – one site near the center of the infestation and another at the edge. Tests at the edge of a local infestation were performed based on the assumption that colonies near the boundary of a local infestation would be subject to lower nest/colony densities. However, sites were

Table 2.1 – Caste composition of captive nests used in aggression assays

Excavation site*	Date established	# workers	# larva	# pupa	# males	# queens
Wood Chip Pile	5/26/2003	5170	2200	0	0	11
Old Farm Road	5/27/2003	3585	2230	0	0	10
Sand Beach House	5/27/2003	2950	1175	0	0	15
Bear Brook Pond	5/29/2003	3400	850	0	0	27
Visitors' Center	5/29/2003	2400	1300	0	0	30
Old Farm Road	7/1/2003	1742	1600	0	0	37
Bear Brook Pond	7/2/2003	1380	335	0	0	11
Visitors' Center	7/3/2003	2300	1685	0	0	11
Sand Beach House	7/3/2003	2170	1250	0	0	16
Wood Chip Pile	7/3/2003	5100	3500	0	0	19
Average		3019.7	1612.5			18.7

* all sites are within Acadia National Park, Mt. Desert Island, Maine

generally bounded sharply by drastic changes of habitat (including roads and natural features), and data were ultimately pooled for ‘distinct infestation’ sites, leaving three treatments in the analysis. Finally, two captive colonies from Acadia National Park were assayed against colonies in an infestation approximately 75 km away in Castine, ME.

Aggression assay protocol:

Captive nests were transported among sites of *M. rubra* infestation with as little disturbance as possible. Upon arriving at each site and prior to beginning an assay, the nests were unloaded and left undisturbed in a shady spot for 20-30 minutes. The captive nest was then attached to a plastic (14 X 14 cm) foraging arena with Tygon™ tubing. Assay/foraging arenas were similar to the feeding arenas, but with a second entrance opposite the entrance for the captive foragers, allowing access to *M. rubra* foragers from the natural habitat. A removable wall of Fluon-coated plastic was tightly fitted across the center of the arena and a small (1 cm²) piece of gauze soaked in 50% sucrose solution was placed on either side as bait. This allowed both the captive and local foragers to recruit to the arena without mixing prior to the start of the timed trial.¹ Once ten foragers had arrived on each side of the central wall (approximately 2-5 minutes), the separator was gently removed and the assay begun.

¹ Early attempts to mark each captive worker by feeding the colonies a fat-soluble dye proved unsuccessful and were subsequently abandoned.

Assays were run for a total of ten minutes, and a suite of behaviors along with feeding and recruitment rates were quantified during each of five 2-minute intervals.

The number of captive and local foragers (“local” referring to those ants recruiting from the habitat as opposed to from the captive nest) were counted at the beginning of the assay, and the total number of ants entering the arena through the Tygon tube was recorded for each two-minute period by a second observer. This number minus the total number of ants in the arena (also counted per two-minute period) was used to approximate natural forager recruitment. Captive and natural recruitment was comparable (while variable) across trials. The behaviors quantified in the aggression assays included: 1) antennation, 2) threat or attack, 3) seizing/grasping, 4) carrying, 5) fighting/stinging, 6) escape/avoidance, and 7) trophallaxis (social feeding). These categories are loosely modeled after protocols defined by de Vroey (1980) and de Vroey and Pasteels (1978) for the assessment of *M. rubra*’s behavior during interspecific conflict in laboratory studies. Some behaviors were difficult to observe in the field and were dropped from the protocol (e.g. mandible opening, gaster flexion or vibration). In some surveys of aggression, prolonged antennation is considered to be indicative of the recognition of a non-nest odor and therefore is considered akin to a low level of aggression (Tsutsui et al. 2000). When exhibited by *M. rubra*, antennation was characteristically brief whether directed toward nestmates or non-nestmates and was not classed as aggressive. A threat or attack was scored when one ant lunged through space toward another forager, generally with mandibles open, whether or not contact was actually

made. Grasping behavior, highly characteristic of *M. rubra* aggression assays, was scored when one ant held on to the head, thorax or appendage of another for a few seconds or for the duration of the assay. Grasping was often perpetrated by multiple ants towards a single alien worker; several ants would surround the intruder, pulling it in several directions and effectively splaying it on the floor of the arena. Carrying behavior was scored when one ant lifted another off the floor and walked with it around the arena. Interpretation of carrying behavior is slightly complicated by the fact it is used by many ant species (including *M. rubra*) in social (such as during nest moving) and agonistic contexts (Abraham and Pasteels 1980). At the baits, however, such behavior was unambiguous enough to be safely classed as aggression.

Fighting/stinging behavior was tallied when one or both ants grappled with each other, generally rolling around the arena and flexing their gasters in an apparent attempt to sting. Whether or not a sting was actually delivered was not discernible and was therefore not measured. Escape/avoidance was counted when one or both ants retreated in an opposite direction immediately following an encounter, and trophallaxis was scored when two or more workers huddled together and appeared to share regurgitant from the buccal cavity of another ant offering a meal. Actual transfer of food could not be verified under field conditions and was identified more by the position of the ants relative to one another. In any case, the behavior was quite rare and is not treated in the analysis.

Aggression score and maximum aggression:

Aggression assays were scored in terms of the maximum level of aggression reached by any two ants at some point during the trial (Tsutsui 2000, de Vroey 1980, Obin 1986, Obin and Vander Meer 1988). Scores were assigned as follows: antennation = 0, attack/threat = 1, grasping and/or carrying = 2 and fighting/stinging = 3. We also calculated an index of whole-colony response using the following formula:

$$\text{Aggression score} = 1 * (\# \text{ attacks}) + 2 * (\# \text{ grasping}) + 2 * (\# \text{ carrying}) + 3 * (\# \text{ fights})$$

This hierarchy of behaviors is similar to those used by de Vroey (1980). Of the behaviors classed as aggressive, attack/threat was the most benign, occurring occasionally between nestmates as well as non-nestmates. Grasping and carrying behaviors were clearly aggressive acts, falling above threat behavior on the continuum. Since carrying and grasping could (and did) evolve into one another during the course of the assay trials, both were considered equivalent in terms of aggressive level. Fight behavior was the most aggressive and was weighted accordingly.

Aggression score is an aggregate function summed over all ant encounters in the assay arena and hence is influenced strongly by overall activity and level of recruitment by the foragers of each colony. As antennation occurred frequently in all trials irrespective of treatment and provided an approximate measure of overall forager activity and encounters; all treatment effects were first tested using

antennation to account for the total level of activity in the arena. However, antennation did not differ significantly between treatments (explaining little variation in the model) and was subsequently removed as a covariate in order to increase power.

Aggression by distance assays:

In 2004, a sugar bait technique was used to describe the pattern of intraspecific aggression within an infested area. This bioassay was designed to determine the aggressive response between worker ants recruited to and dominating a food source from a given foraging territory and workers from another foraging territory encountering food and “foreign” defending ants.

The bioassay was carried out on three dates: 1 July, 12 July, and 10 August 2004; in Acadia National Park at the “Woodchip Pile” site (44° 22' 38" N, 68° 15' 21" W). The method consisted of deploying a sugar bait on the ground at various flagged distances along a linear transect across the infested area. The bait was a 2-cm-square, triple-layer cotton gauze soaked in a 25% (v/v) sugar solution placed on a 6 x 10 cm glass plate. Ant recruitment to the bait was allowed until 20-25 workers settled to feed. A cardboard box top sufficient in size to cover the plate without disturbing the feeding ants was placed over the plate as it was moved to a new location along the transect, ranging from <1m (control) to 144 meters away from the point of initial recruitment. At the new location, the glass plate containing the bait was placed upon the ground and the cover was removed. The bait was observed with

a 4x magnifying glass until the first worker from the new location encountered the bait with the feeding ants from the original location. At this point a stop-watch was started and for 5 minutes the following behavioral interactions were recorded: number of antennations, threat postures/attacks, drags/carries, and abdomen flexing/stinging. After the 5-minute bioassay, the ants and bait were disposed of in soapy water and a new bait was deployed at another location along the transect. At the completion of the bioassays, the flagged transects were measured so that the distances between all bioassay locations were ascertained. On each date, a different transect was randomly selected for bioassay. The number of paired aggression bioassays conducted along a transect on each date was 25, 14, and 27 respectively. Aggression scoring was calculated in a similar manner to that previously described for captive nest assays.

Data treatment and analyses:

Analysis of variance and ANCOVA models were used in treatment and hypothesis testing, employing a square root transformation of the dependent variable (aggression scores or behavioral counts) to meet the assumptions of normality and constancy of error variance. Where appropriate, Tukey's adjustments for multiple comparisons were made (Miller 1985). A total of 51 captive nest assays were performed throughout the summer of 2003, including 49 sites on Mt. Desert Island and two in Castine, ME. Treatment sample sizes were as follows: 12 assays at the site of excavation, 13 at 10m from the site, 21 at the center and 3 at the edge of a distinct infestation. Owing to the somewhat unpredictable nature of recruitment

among foragers from the captive nests and to the difficulty in locating edge habitat, it was not always possible to execute all treatments in a single day using a given captive nest. Tests were initially run using an incomplete block design with each captive nest and site as a block, but as no significant block effects were detected, the remainder of ANOVA testing was run using only treatment as a factor in a completely randomized design.

Preliminary model exploration using a variety of temperature and weather parameters, site, captive nest, date and time of day as factors revealed no perceptible trends, suggesting that the treatments themselves were the major cause of variation. Several ANCOVA models were also explored using the number of antennation and recruitment rate as covariates, but these covariates did not show significance and were dropped. All means are reported plus or minus standard errors. Models and tests were performed using Systat for Windows, version 11.00.01 (Systat Software Inc. 2004).

Analysis of aggression score relative to distance was accomplished using a Randomization Monte Carlo Mantel test (Mantel 1967) between the paired aggression score matrix and the distance matrix (distances between locations involving aggression bioassays) to determine whether a significant ($p < 0.05$) linear correlation exists between aggression index and distance among locations. The tests were computed using PC-ORD software (PC-ORD, Multivariate Analysis of Ecological Data 1999) with 1000 permutations for each test.

RESULTS

Aggression score and behavioral tallies:

Aggression scores between captive *M. rubra* colonies and undisturbed natural colonies differed significantly with distance from the excavation site of the captive nests ($F_{3,45} = 12.09$, $p < 0.0001$, Figure 2.1). At the site of excavation, where captive colonies were tested against their former close neighbors or ex-colony fragments, there was very little aggression on average, though aggression scores did vary somewhat across trials. In seven of the 12 assays within this treatment, there was essentially no aggression, while in the other five, a small number of aggressive behaviors was tallied almost exclusively in the form of grasping and carrying. The mean aggression score of 12.75 ± 4.99 did differ significantly from zero ($F_{1,45} = 6.95$, $p = 0.011$). When captive nests were tested at 10m from the site of excavation (within the same discrete population), the mean aggression score (56.7 ± 20.6) was significantly greater than at the site of excavation (using Tukey's adjustments for multiple comparisons). This intercolony aggression within a site strongly suggests a multicolonial population structure. Substantial variation did exist within the '10m' treatment, however, raising the possibility of complex dynamics of between-colony aggression or tolerance. Aggression between nests tested at site at both the edge and the center of a distinct local patch or infestation (elsewhere on the island) showed markedly higher mean aggression than either of the within-site treatments. As comparatively few 'edge' treatments were performed ($n=3$) and results did not differ statistically from the 'center' treatment (both within the same local patch), these data

were pooled together and termed a 'distinct infestation' treatment for the remainder of the analyses.

The suite and frequency of specific aggressive behaviors varied by treatment (Figure 2.2). Escape/avoidance behavior, while viewed as low-level aggression by some researchers (Holway et al. 1998, Suarez et al. 1999, Tsutsui et al. 2000), was extremely rare (2 instances in 51 assays) and so was not depicted or treated in the analysis. Attack/threat behaviors preceded all other aggressive behaviors and represent a linear combination of grasping, carrying and fighting behaviors in addition to any attacks/threats that did not escalate to further aggression. In general, such aborted aggressive displays were rare across all treatments. Carrying behavior was nearly absent at the site of excavation ($\bar{x} = 0.6 \pm 0.3$), though it was more common at both the 10m ($\bar{x} = 5.3 \pm 1.9$) and in the pooled 'distinct infestation' treatments ($\bar{x} = 9.0 \pm 1.8$). All assay trials in which aggression was present at all were generally dominated by grasping behavior. This behavior was present in some of the 'within site' (i.e. <1m) trials, albeit at comparatively low levels ($\bar{x} = 3.58 \pm 1.42$ versus 11.62 ± 5.09 and 21.46 ± 3.21 for the '10m' and 'distinct' treatments respectively). Owing in part to the high level of variation in the '10m' treatment, the count of grasping behavior was not significantly different between this treatment and 'site,' though the behavior was significantly more common during trials in the 'distinct' versus the '10m' treatment. Overall, fight/stinging was quite rare in intraspecific trials, though the counts of this behavior differed significantly across treatments ($F_{2,46} = 4.52$, $p = 0.016$), owing to a significant difference between 'site'

and ‘distinct’ treatments. This contrasts with *M. rubra*’s behavior with respect to interspecific bouts with native ants where fighting/stinging was quite common, often appearing to be the first line of attack (see Chapter 3).

The data from the two trials conducted in August 2003 testing captive nests against an *M. rubra* population approximately 75 km to the southwest in Castine, ME (also a coastal site, referred to as ‘off-island’ in Figure 2.2) are treated separately as the small sample size makes analyzing statistical trends difficult. Results from these two assays are quite distinct from those obtained when testing captive *M. rubra* nests anywhere on Mt. Desert Island. Both were characterized by extremely high levels of aggression; when compared with the on-island treatments, counts of aggressive behavior are higher for all categories. While fighting/stinging was nearly absent on the island within a site and at low levels during assays from the ‘distinct’ treatments, the mean count of fight behaviors during the two off-island trials was 5.5 ± 0.5 , statistically distinct from all other treatment ($p < 0.001$). Grasping, carrying and attacks were also more frequent in offsite trials at varying levels of significance.

Maximum aggression by assay location:

The mean of maximum aggression was lowest in the ‘site’ trials and increased as the distance from the site of excavation increased across treatments (Figure 2.3). A significant positive correlation exists for these data, using Spearman’s rank correlation ($r_s = +0.66$, $p < 0.0001$). Given that both off-island trials were skewed toward fight behavior, the maximum aggression mean of 3 falls substantially above

any of the on-island treatments, though again the $n = 2$ sample size did not invite pairwise testing for significance with respect to this treatment.

Aggression by distance:

Significant positive correlations between aggression index and distance were observed for the three dates (1 July: $r=+0.781$, $p<0.001$; 12 July: $r=+0.727$, $p=0.007$; 10 August: $r=+0.864$, $p < 0.001$) and for pooled data ($r=+0.808$ ($p<0.001$), with an increase in aggression index over the transect distances (Figure 2.4). This supports the findings of the studies with the mobile ant colonies that at least some of the infested sites in Acadia National Park are multi-colonial, with high levels of aggression within populations. The finding of high levels of within-population aggression throughout the summer suggests that aggression may be an enduring characteristic of these populations. These results also suggest that the typical size of a functional colony at the Woodchip site is quite large and ranges between 25 and 50 m (the maximum distance at which aggression is zero) or that certain colony pairs exhibit aggression while others do not. This pattern could also indicate the importance of environmental determinants of intercolony tolerance and/or nestmate recognition, as clustered resources may influence colony odor or recognition cues, promoting local tolerance at the scale of tens of meters.

DISCUSSION

M. rubra's complex polydomous colony structure and the high nest densities it achieves within local populations suggests that each *M. rubra* infestation is a moderately sized supercolony. Foragers are observed occupying virtually every surface within an invaded habitat, from the litter layer high up into the trees, without high levels of observable conflict between colonies. However, the results of this study demonstrate that *M. rubra* populations on Mt. Desert Island are not truly unicolonial, as intercolony aggression is present both within and between local infestations. Further, aggression between colony pairs is positively correlated with the distance that separates them within a site. Whether such physical distance corresponds to genetic distance in invasive *M. rubra* populations awaits further research. Such relationships have been shown to exist in some ant species (Pirk et al. 2001, Bourke and Franks 1995). The presence of aggression within a local patch contrasts findings from other invasive ant systems, including *S. invicta* and *L. humile* (Holway et al. 1999, Porter and Savignano 1990), and supports the idea of a multicolonial structure of *M. rubra* populations in coastal Maine. Captive *M. rubra* nests were found to be tolerant of close neighbors and/or to fragments of their former colony. This pattern was maintained throughout the season despite the fact that experimental nests were reared separately for several months. This does not preclude environmental regulation of colony recognition cues but suggests the importance of endogenous factors as well. Stuart and Herbers (2000) compared colony aggression in monogynous/monodomous versus primarily

Figure 2.1 – Mean aggression scores from 10-minute tallies of behavioral assays between captive and field-recruiting *M. rubra* foragers, by treatment – 2003.

Treatments correspond the location of field assays relative to the site of excavation of the captive nest in the trial pair. SE = site of excavation, 10m = 10 meters from the site of excavation (within the same local patch), CD = center/interior of a distinct infestation, ED = edge or boundary of a distinct infestation. Sample sizes are presented within each vertical treatment bar. Error bars correspond to one standard error of the mean. Unique letters above the treatment bar signify statistical difference at the $p = 0.05$ level, using Tukey's multiple comparisons.

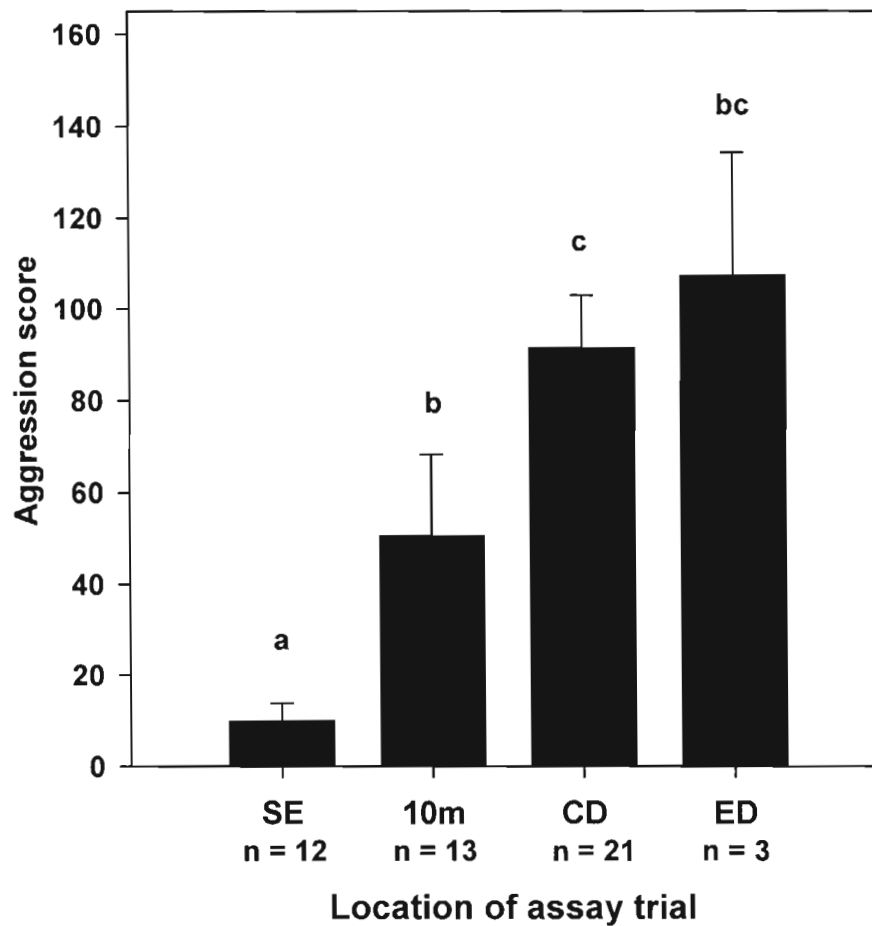


Figure 2.2 – Mean count of aggressive interactions tallied over 10-minute behavioral assays, by behavior and treatment. Treatments correspond the location of field assays relative to the site of excavation of the captive nest in the trial pair. SE = site of excavation, 10m = 10 meters from the site of excavation (within the same local patch), CD = center/interior of a distinct infestation, OI = off-island population (Castine, ME). Error bars represent one standard error of the mean.

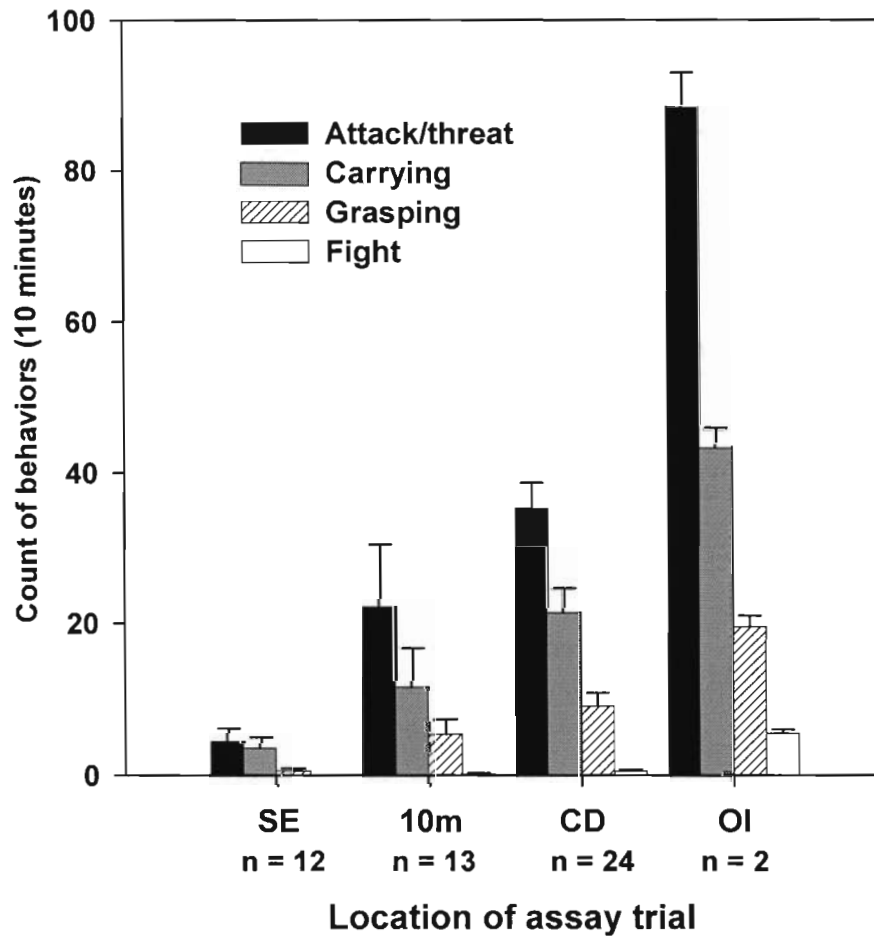


Figure 2.3 – Mean maximum aggression by treatment. Treatments correspond to the location of field assays relative to the site of excavation of the captive nest in the trial pair. SE = site of excavation, 10m = 10 meters from the site of excavation (within the same local patch), CD = center/interior of a distinct infestation, OI = off island population (Castine, ME). Maximum aggression corresponds to the following behaviors: No aggression/antennation only = 0, Attack/threat/lunge = 1, Carrying and/or grasping behavior = 2, Fighting/stinging = 3). A significant positive correlation exists for these data, using Spearman's rank correlation ($r_s = +0.66$, $p < 0.0001$). Error bars represent one standard error of the mean.

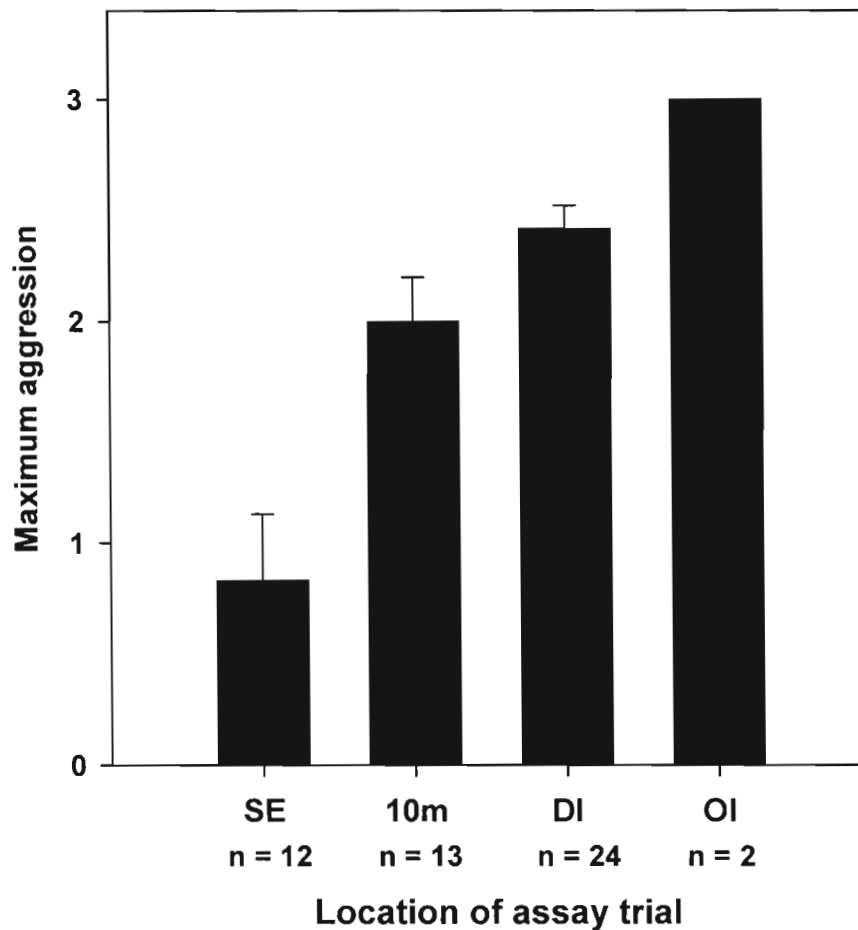
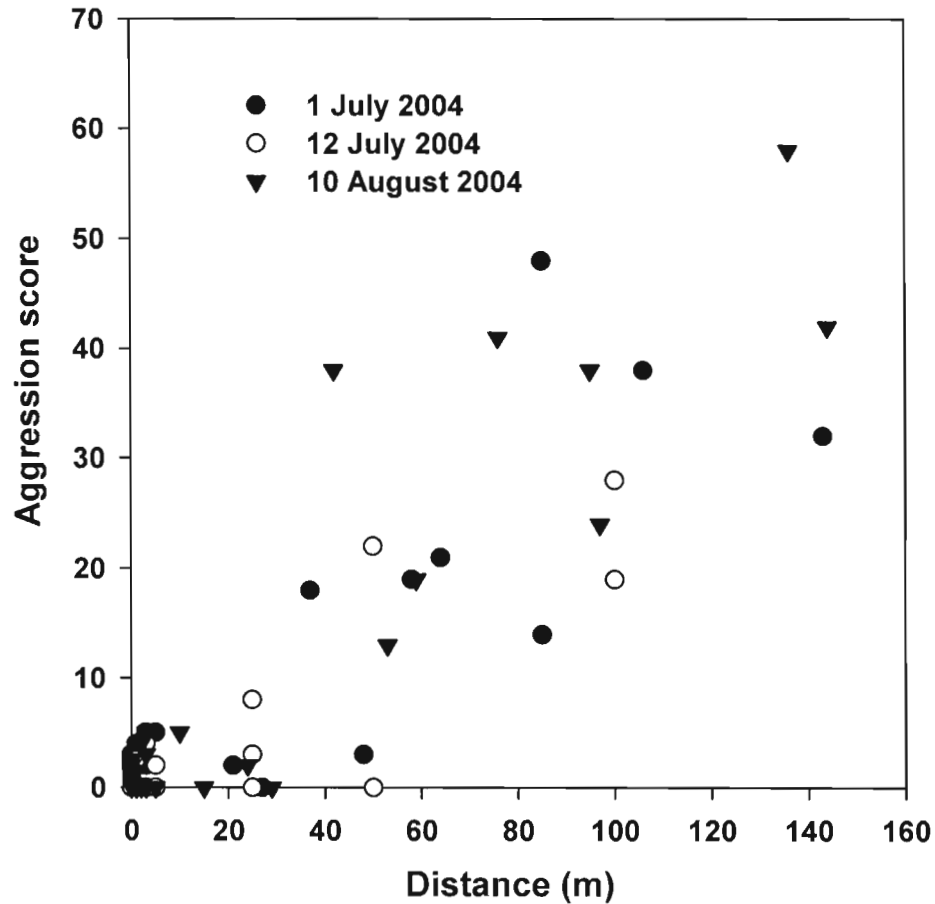


Figure 2.4 – Aggression scores at baits as a function of distance between foragers' colony of origin – 2004 Data analyzed using Mantel test; 1 July: $r=+0.781$, $p<0.001$; 12 July: $r=+0.727$, $p=0.007$; 10 August: $r=+0.0864$, $p<0.001$). When the data are pooled over the three dates, there is a significant correlation coefficient of $r=+0.808$ ($p<0.001$).



polygynous/polydomous populations of *Leptothorax longispinosus* and found that genetically controlled cues for nestmate recognition were more important where colonies occupied multiple nests. They concluded that heavy reliance on exogenous regulation of colony odor would result in a high error rate/misdirected aggression between polydomous satellite nests, as even adjacent nest sites are likely to experience subtle variations in the environment. Similarly, research on *S. invicta* and *L. humile* has confirmed that nestmate recognition cues are heritable but that exogenous factors such as diet can alter the hydrocarbon profile of a nest or colony and with it, behavior (Silverman and Laing 2000, Vander Meer et al. 1990, Obin and Vander Meer 1988, Suarez et al. 2002). Further research on kin structure and the genetics of nestmate recognition, along with the potential regulatory contribution of subtle variations in diet composition or microhabitat characteristics, is necessary in invasive *M. rubra* populations to explain these complex dynamics.

Much of the current theory surrounding the ecological and genetic preconditions for the appearance of unicoloniality has been formed in the context of ant invasions, as this social structure appears to be integral to the widespread ecological success of such species. A loss of genetic diversity at nestmate recognition loci subsequent to introduction and the selection for common alleles under relaxed ecological constraints (e.g. the shedding of pathogens and/or parasites from the native range, allowing for greater proximity of nests) have been suggested as important factors driving observed patterns in *L. humile* (Giraud et al. 2002, Tsutsui et al. 2000, Ross et al. 1996, Passera 1994, Starks et al. 1998). Unicolonial populations have been described as an alternative social form in *M. rubra*, particularly in the northern

regions of its native range, though the mechanisms leading to its expression are potentially distinct as an introduced invader (Seppä and Walin 1996, Walin et al. 2001, Seppä and Pamilo 1995, Pederson and Boomsma 1999). Van der Hammen et al. (2002) describe a linear succession in *Myrmica* ants in a stable habitat toward “low-relatedness supercolonies” that are stable in time and saturate a local habitat. The authors present a hypothetical progression from a single-queen foundation in a high-quality, novel patch to a stage characterized by excessive inbreeding and the production of sterile, diploid males. Next they predict an intermediate stage of rapid reproduction via budding, moderate relatedness and reduced inbreeding due to rare immigration of males (or gynes) from distinct populations. This is followed by effective unicoloniality, with near-zero relatedness and accompanied by high-density habitat saturation. While as yet circumstantial, indigenous *Myrmica* populations with predicted kin and colony structure have been identified and corroborate the hypothetical progression (van der Hammen et al. 2002, Seppä 1996). The authors speculate that the process of convergent selection (for similar colony odor/identifying cues) within long-lived, uniform sites could drive populations toward conditions with very low relatedness and a breakdown of colony borders within a site. While low relatedness and high nest and colony density may correspond to habitat saturation and ecological dominance and/or success, no direct assessments of intercolony aggression are provided in this body of research, and it remains untested (or unreported) whether such populations conform to the definition of unicoloniality as defined by the true loss of intraspecific aggression.

Many of the characteristics of *M. rubra* colony and kin structure in such “low-relatedness supercolonies” are clearly in evidence within invasive populations in Maine. The significantly higher aggression exhibited by colonies from distinct infestations in our study is apparently consistent with the discovery of northern European *Myrmica* populations with comparatively high levels of genetic substructure between patches (van der Hammen 2002, Seppä and Pamilo 1995). While we have no direct estimates of genetic divergence between infestations, our observation of reproduction by colony budding and the limited dispersal of reproductives between sites is consistent with such observations. Interestingly, the starting point of the creation of a unicolonial population or patch, according to van der Hammen et al. (2002), is an introduction to a novel patch, though still within the native range of the insect.

Several possibilities exist to reconcile the existence of a certain level of aggression within a site with *M. rubra*'s observed ecological dominance and habitat saturation in Maine. First of all, aggression at the ‘10m’ site was moderate and highly variable, suggesting that an infestation may comprise a few large colonies or that now distinct colonies originated as fragments of the same large colony and retain some mutual tolerance/recognition. Also, food may not be limiting in the habitat (at least during the years in which the ant has been actively studied) facilitating passive coexistence. Abundant homopterans provide food to the worker force (see Chapter 4) and may encourage vertical foraging, also reducing spatial overlap of territories, should they exist (Davidson 1998). Czechowski (1984) noted a seasonal expansion of satellite nests in the spring and a concomitant increase of overt aggression in the

habitat. In Maine, aggression was apparently temporally stable under seminatural experimental conditions, though it is likely that there are times during the year when the natural encounter rate would increase, such as during mating or during the seasonal expansion of satellite nests (Czechowski 1985; also see Appendix A). Also, as our research documented relatively low-intensity aggression on the whole (resulting in few if any casualties), it could be that moderate to low levels of aggression have little impact on colony and spatial dynamics. While still a theoretical drain on foraging efficiency, a carbohydrate surplus (from nectar or homopteran exudates) may render this loss inconsequential (Holway 1998, Davidson 1998). In summary, the benefit in the form of effective territoriality and resource domination with respect to native ant competitors may far outweigh any costs in terms of the loss of a few workers. Though not devoid of intraspecific aggression, each *M. rubra* infestation may function as a cohesive, essentially cooperating unit, potentially rendering the question of unicoloniality largely a matter of ecologists' definitions.

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CHAPTER 3

Mechanisms of competitive displacement of native ant fauna by the European Fire ant (*Myrmica rubra*) in Acadia National Park, Maine

INTRODUCTION

The success of some introduced ant species has had a devastating impact on native ant fauna in all but the most marginal habitats where these invaders occur. While a few “tramp ants” may be so closely associated with human activity and disturbance as to specialize largely on open niche habitat (Passera 1994), the superior competitive ability of most invasive species is demonstrated by their widespread ecological success and numerical dominance in habitats once occupied by rich and varied native ant communities (Porter and Savignano 1990). Studies have shown that the majority of native ant species are quickly and thoroughly displaced in the wake of an advancing invasion front, especially within optimal habitats of the invader (Holway 1998, Holway and Case 2001, Porter and Savignano 1990, Suarez et al. 1998, Cole et al. 1992, Human and Gordon 1996, Human and Gordon 1999). Many researchers have attempted to elucidate the underlying factors influencing such species’ ability to saturate the landscape with nest sites and foragers, citing an escape from natural enemies, the breakdown of nestmate recognition cues leading to the formation of large unicolonies, the absence of co-evolved competitors, and a carbohydrate surplus subsidy increasing worker activity (Holway 1998, Holway and Case 2001, Tsutsui et al. 2000, Giraud et al. 2002, Davidson 1997, Davidson 1998).

Comparatively few studies have addressed the direct or indirect mechanisms of competition and displacement along the invasion front, where natives and invasives are briefly sympatric, prior to extirpation of the native ant fauna. Human and Gordon (1996) found that Argentine ants (*Linepithema humile*) were disproportionately successful at exploiting bait resources by maintaining higher colony activity, foraging for longer periods each day and by recruiting in greater numbers to food resources when compared to their native counterparts. The more numerous *L. humile* workers also proved to be better interference competitors, displacing native species from contested baits in the majority of trials, often via direct combat or aggression. Holway (1999) went on to suggest that Argentine ants have broken the “interference-exploitation trade-off” put forward by Fellers (1987). Fellers found that in a long-established community of Eastern forest ants, there is an inverse relationship between interference and exploitative competitive ability. Large or heavily recruiting dominant ants tend to be slower to discover and initially recruit to food resources, whereas subordinate species are quick to discover and exploit such sources but are displaced when superior contest competitors arrive. Holway (1999) found a similar inverse correlation among native species in a northern California riparian woodland ($r = -0.85$; $p = 0.02$). However, introduced *L. humile* workers in Holway’s and other studies are both the first to discover and recruit to food resources and are more apt to successfully dominate such resources in direct contest with native foragers, breaking the trade-off (Holway 1999, Davidson 1998).

Myrmica rubra, a palearctic Myrmicine with a native range stretching west to east from Spain and the British Isles to Central Asia and south to north from the

Mediterranean coast through Scandinavia and central Russia, was introduced to North America around the turn of the 20th century, prior to 1908 (Collingwood 1979, Elmes 1974, Wheeler 1908, Groden et al. unpublished data). Anecdotal and distributional evidence suggests that colonies had become established in Maine by sometime in the 1930's and that distance or jump dispersal is largely human-mediated via imported or translocated nursery stock. Statewide surveys have identified significant infestations in a minimum of 30 Maine communities (Groden et al. unpublished data). *Myrmica rubra* is patchily distributed across its known range in Maine and parts of northeastern North America but form dense local infestations where its colonies occur, nearly always to the detriment of native ant fauna (Chapter 4). Occasional foragers of another species may sometimes be found within the boundaries of a local population, but the dominant pattern is one of almost total exclusion of native ants from an *M. rubra*-occupied habitat (Chapter 4).

As a generalist predator, scavenger and homopteran associate, *M. rubra* shows considerable overlap in food resources with many native ant species. Given high density of workers and its apparent competitive superiority, we hypothesized that like the Argentine ant, *M. rubra* is both the first to discover and to subsequently dominate and exploit a food resource, most often to the exclusion of native foragers. This represents a break in the interference-exploitation (or dominance-discovery) trade-off and is a likely mechanism contributing to native ant displacement along an advancing invasion front. The current study employs a variety of experimental methods using both captive *M. rubra* colonies and *in situ* competition along invasion

fronts to test this hypothesis and to parse out some of the details of *M. rubra*'s interaction with native ants, primarily in the context of competition for food resources. Patterns of displacement and of species differences with respect to native-invasive aggression/interaction are offered along with some preliminary evidence in support of other mechanisms of displacement and the likely outcomes of invasion.

MATERIALS AND METHODS

Mobile nest establishment:

In order to test the ability of *M. rubra* to displace native ant foragers from a colonized food source, ten *M. rubra* colonies were established in Rubbermaid® tubs (9.8 liters). Five nests were excavated from five non-contiguous sites of *M. rubra* infestation on Mount Desert Island, ME in late May of 2003, and five more were excavated from the same sites in late June of the same year. Care was taken to dig each nest in its entirety, though due to the highly polydomous habit of the ant, it is likely that each captive nest was a fragment or satellite of the original colony. Each however contained a representative mix of queens, brood and workers (see Table 2.1). All castes were counted in the field and placed with several liters of original nest soil in the tubs. Plastic lids equipped with 6 X 6 cm square of fine mesh were fit on top of the containers and sealed with duct tape to prevent escape. Nests were stored in ambient conditions in a shaded and protected area of Acadia National Park. A 15 X 15 cm foraging arena was attached to each nest box via 20 cm of Tygon® tubing. Sides of the foraging arena were coated with Fluon® to prevent climbing.

Newly established nests were held for two weeks prior to being used for interspecific aggression assays, during which time they were fed a standard diet of 20% sucrose solution (v/v) and captured insects. Water was provided continuously on saturated gauze and nest soil was misted weekly to approximate ambient soil moisture. Insects used for feeding were collected with a sweepnet from typical *M. rubra* habitat so as to provide a varied protein source and to minimize the effects of cuticular hydrocarbon acquired from an artificial diet (shown to impact nestmate recognition: Silverman and Laing 2001).

Assay protocols – baited arena assays:

Given that *M. rubra* so thoroughly excludes native ants from all but the most marginal habitats, *in situ* experiments can only successfully take place along the advancing front of an infestation. Five *in situ* assays were run (two against *M. fracticornis*, two against *F. glacialis* and one against *Leptothorax ambiguus*) and offer some validity to the results of assays using mobile colonies. Large sample sizes would be preferred; however, instances where infestation fronts overlap with native ant colonies (e.g. those that are not bounded by a road or other highly disturbed areas or by a sharp change in habitat type such as a wetland or dense coniferous forest) are quite rare and difficult to find.

Two variations of aggression assays were performed utilizing the mobile *M. rubra* arenas. The first (herein referred to as “baited arena assays”) tested recruitment to a protein/carbohydrate source, represented by a 5 cm³ of an equal part tuna/fruit jelly mixture placed in the center of the foraging arena on a small, flat

plate. One wall of the arena was cut away and opened to the habitat and to recruitment by native ants. Opposite the open wall was an opening equipped with a fitting that allowed the captive *M. rubra* nests to be attached via Tygon[®] tubing, which could be plugged to prevent colonization of the bait in advance of the native foragers. Baited nest/arena setups were left in proximity to a known native foraging territory for up to 14 hours, until a minimum of 10 native foragers were present at the baits. Due to lower recruitment among certain species, some assays were run when recruitment had reached 5-6 workers. This was the case with several of the *Camponotus* spp. and *Leptothorax* spp. trials. Once a sufficient number of native foragers were present, the tube to the captive colony was unplugged, allowing *M. rubra* access to the bait and arena. Behavioral interactions were logged by type and were tallied in two-minute observation intervals for as long as it took *M. rubra* to fully displace the native ants from the bait, or vice versa.

Assay protocols – aphid assays:

The second aggression assay employed a similar design, but live aphids that had already been colonized by native foragers were used as “bait” in place of the tuna/jelly mixture in the arena experiments. Most of the assays were conducted on small *Populus tremuloides* saplings (~40 cm tall), though assays against *Crematogaster cerasi* and *Formica lasioides* were conducted on isolated stems of *Spiraea alba*. In no instance did the basal area of the stem exceed 1 cm². A small hole (just larger than the base of the sapling) was cut in the bottom of the foraging arena, along with a slit that allowed it to be slipped at the base of the tree or branch.

The slit was then sealed with clear packing tape and the hole plugged with cotton around the base of the sapling. These plugs minimized the number of ants falling from the arena during the course of the assay but were loose enough to permit recruitment or escape to or from the arena. While in the case of the aphid assays it was not necessary to wait for native ants to recruit to the resource (as the aphids were already colonized), 15 minutes were allowed to pass before commencing an assay to allow time for recovery from any disruption caused by the placement of the arena. As with the arena assays, behavioral interactions were tallied in two-minute periods for between 10 and 60 minutes, depending on the time it took the activity to reach a locally stable, if temporary, equilibrium.

Behavioral tallies:

With an observer and a recorder present, it was possible to tally all of the behavioral interactions that took place throughout the duration of the assay. Behaviors were assigned to one of the following categories: antennation, attack, grasping, carrying, fighting, escape or trophallaxis. Antennation occurred when one ant tapped or passed its antenna over the cuticle of another. Attacks were tallied when one ant lunged toward another with mandibles open and preceded all other aggressive interactions such as fights or grasping. Grasping was counted when an ant held a part of another ant in its mandibles, either briefly or for an extended period of time. Grasping was often characterized by 2-6 ants surrounding a single forager of the opposing species and pulling its appendage in several directions, splaying the ant on the floor or the arena and rendering it immobile. Carrying behavior occurred

when one ant lifted another off the floor of the arena, most often marching around or leaving the arena with enemy held aloft. Since both grasping and carrying behavior occurred for variable lengths of time, each was tallied once for each two-minute interval in which it occurred. With the exception of fight behavior where both ants locked in battle attempting to sting or spray each other, behaviors were assigned to one or the other species as appropriate. Fights, in contrast, were assigned to both captive and native foragers. Escape behavior was tallied when one ant came in close contact with another and immediately ran in the other direction. This did not include ants that left the arena but were not actively escaping from an interaction with an enemy ant; these numbers were tallied separately. Finally trophallaxis, or social feeding, has been reported as an appeasement measure, often between similar species of the same genera (Hölldobler and Wilson 1990). However, this behavior was not observed in any of the interspecific aggression trials.

The number of foragers of each species present in the arena and the number of ants actively feeding at the baits were counted at the beginning of each assay and then at the end of each two-minute interval. At the end of each assay, *M. rubra* foragers were collected from the arena and from the habitat and were returned to the nest box. A representative sample of the native ant was collected for species identification.

Aggression scores and data analysis:

In order to assess total aggression for each assay and make comparisons both within and between species, an overall aggression score was calculated for *M. rubra*

and the native species for each trial. Scores were calculated by the following weighted formula:

$$\text{Aggression score} = [1 * (\# \text{ attacks}) + 2 * (\# \text{ grasp}) + 2 * (\# \text{ carrying}) + 3 * (\# \text{ fights})] / [\text{Duration of assay}] * 10$$

This score assumes a linear hierarchy of aggressive acts and averages aggression over the assay duration, smoothing any peaks or lulls. De Vroey (1980) employed a scheme based on similar categories of behavior, though her assays took place with fewer ants under laboratory conditions and she was therefore able to monitor threat as well as gaster dragging behavior. Based on considerable observation, grasping and carrying were given equivalent aggression rankings as each behavior had the potential to evolve into the other, which occurred with some regularity. From the standpoint of per capita costs and benefits, however, grasping often required that multiple ants be involved in long-term splaying of the intruder and could be lethal, whereas carrying effectively took an enemy out of the battle at the cost of a single ant. Finally, dividing by the duration of each assay and multiplying by 10 standardized the score to a 10-minute observation period to facilitate comparisons across assays of different durations.

Data from the aggression assays were analyzed by employing aggression scores, individual aggression counts by behavior and counts of overall aggressive behaviors as dependent variables in independent one-way ANOVA models, with the native ant species or genus as the independent factor. Separate models were run for ‘bait’ versus ‘aphid’ assays. Model assumptions were satisfied by square root and natural log transformations of counts and aggression respectively. Site of assay, captive

nest, time of day or season and a variety of temperature and weather patterns were included in early models, but no differences were evident and these variables were subsequently dropped from consideration. Paired t-tests were employed to look for differences between *M. rubra* and native ant aggression by species, and pairwise testing was performed where applicable when looking for species differences, adjusting for multiple comparisons using Tukey's method. All statistical models and tests were performed using SYSTAT software, version 11.00.01 (Systat 2004).

Discovery time experiment:

In order to measure the relative time to discovery and subsequent recruitment to food resources by *M. rubra* and native ant foragers, baits were monitored for the arrival of ants for a period of two hours at a single site in Acadia National Park. Beginning at 7 am on 20 August 2004, 40 petri dish lids baited with a 2 cm² of gauze soaked in 25% sucrose solution were placed along two, oppositely radiating transects 100 m south of the Bear Brook picnic area behind Jackson Laboratories (44.36° N, 68.20° W). Sugar was used as bait for convenience and has proved effective in attracting a broad cross-section of sympatric native ant species (Hölldobler and Wilson 1990). A cap from a 25-cubic centimeter (cc) scintillation vial was filled with sugar solution and inverted on each piece of gauze to ensure that the baits would not dry out or change in character over the course of the experiment. Extensive trapping in the summer of 2003 was the basis for the placement of transects. Each was situated so as to encompass the interior of the local *M. rubra* population, traverse the brief region of overlap between *M. rubra* and native ants (a

band of approximately 10 m in all directions surrounding the ~100-meter-wide infestation) and to sample the native community which had yet to come in direct contact with *M. rubra* colonies or foragers. The transects extended in opposite directions from the center of the infestation, with baits placed at approximately 5 m intervals (placed flush with the ground vegetation or soil). Habitat was essentially homogenous throughout the site, comprised largely of dense *Solidago* spp., *Rubus* spp. and *Poa/Carex* spp. understory with a mixed, open canopy comprised of *Populus tremuloides* Michx., *Betula populifolia* Marsh. and scattered *Pinus strobus* L. Once deployed, the baits were monitored every fifteen minutes for the next two hours, and the presence and number of each ant genus (species identifications were made in the field where possible) was recorded. Care was taken not to disturb feeding or foraging by maintaining as great a distance as possible from the baits during monitoring. At the end of the experiment, dishes were capped and transferred to the laboratory for species verification. Time to discovery and rate of recruitment were calculated and used as dependent variables in separate one-way ANOVA models, and species was used as the factor. Dependent variables were natural log transformed to fit assumptions of normality and homogeneity of variance.

Overnight native/invasive ant survey:

To assess potential temporal partitioning in foraging activity across ant species, 24-hour sampling using sugar-baited vials was performed in Acadia National Park in August 2004. Four sites were selected, including one site where *M. rubra* was absent (Sand Beach House North), two sites where *M. rubra* was present at low

density and limited to a small section of the sampling area (Great Meadow and Sieur du Mont Springs) and a fourth site representing a dense *M. rubra* infestation (Sand Beach House South). Twenty 25-cc scintillation vials were baited with sugar-soaked gauze and placed randomly throughout each of the four sites, beginning at 4 pm on 19 August 2004. Every three hours for 24 hours, teams of 2-3 people arrived to collect and count foragers that had recruited to the interior of the vial. The bulk of the ants were counted in the field and released at the location of capture to minimize the impact of collection on the overall foraging force of each captured species. Eight to ten native workers were collected for later identification. Each trap was replaced with clean, freshly baited vials placed on the vegetation or soil surface a meter or so away from the prior trap and located to avoid recapture of the same ants by deployment of a trap within an area of active recruitment.

Data treatment and statistical analyses:

Data from the aggression assays were analyzed in several different ways, employing aggression score, individual aggression counts by behavior and counts of overall aggressive behaviors in various ANOVA models. Model assumptions were satisfied by square root and natural log transformations of counts and aggression respectively. Site of assay, captive nest, time of day or season and a variety of temperature and weather patterns were included in early models, but no differences were evident and these variables were subsequently dropped from consideration. Paired t-tests were employed to look for differences between *M. rubra* and native ant aggression, and pairwise testing was performed where applicable when looking for

species differences, adjusting for multiple comparisons using Tukey's method. All statistical models and tests were performed using SYSTAT software, version 11.00.01 (Systat 2004).

RESULTS

Interspecific versus intraspecific aggressive behavior:

During the summer of 2003, 27 field aggression assays were performed (20 baited arena and 7 aphid assays), testing captive *M. rubra* colonies against a total of 16 species (Table 3.1). Since identification to species was not possible in the field, assays were run against whichever species happened to recruit in sufficient numbers to a baiting station; therefore, the design of the experiment is inherently unbalanced. Interaction between *M. rubra* and native foragers was characterized by fierce aggression, with a few notable exceptions discussed below. Assays against *Leptothorax* species were almost completely devoid of aggression, which is highly atypical of *M. rubra*'s interaction with the native ant community. As such, four native ant assays (n=3 and n=1; *L. longispinosus* and *L. ambiguus* respectively) are considered separately for the bulk of this paper, unless otherwise noted.

Aggression scores – bait and aphid assays:

As expected, nearly all species tested in the baited arenas displayed considerable aggression upon encountering *M. rubra* foragers at or near the food source and likewise evoked a similar response from the invading *M. rubra*. Across native ant

species, the aggression score for *M. rubra* was higher than that of the native ants ($t = 2.08$ [paired two-tailed test], $p=0.051$), owing to both the former's high level of recruitment as well as high per capita aggression by *M. rubra* foragers (Figure 3.2). Due to sample size constraints, it was not possible to compare aggression scores for all species in a pairwise fashion. Where statistical analyses were possible, *M. rubra* aggression scores did not differ significantly between assays against *M. detritinodis*, *M. americana*, and *F. glacialis*, though aggression against all three of these species was significantly higher than when the captives were pitted against *Leptothorax* species ($p < 0.006$; *L. longispinosis* and *L. ambiguus* data pooled). Similarly, native aggression scores for the arena assays did not differ for *F. glacialis* and the two *Myrmica* species but was greater than that of *Leptothorax* ($p = 0.0002$). This trend reflects the fact that neither *L. longispinosis* nor *L. ambiguus* evoked nor perpetrated measurable aggression beyond an occasional lunge by a passing *M. rubra* forager.

Aphid assays (Figure 3.2) differed from the arena assays in that recruitment by the natives was to a natural, persistent resource. As such the number of ants present can be presumed to be governed by the size and productivity of the aphid colony, and therefore to be more stable over time. Despite the structural complexity of even the smallest sapling (mean height = 32 cm), with increased surface area and hence decreased probability of encounter during the 10-minute assay, aggression scores were comparable across species for the aphid versus arena assays ($p = 0.92$ and $p = 0.76$ for *M. rubra* and native ant aggression score respectively). This was likely due in large part to the strong presence of native ants as well as to high recruitment by *M. rubra*. One main difference in the character of the battle was that when two ants

engaged in grasping or stinging/fighting behavior, they generally fell from the branch and were removed from the vicinity of the food resource. In contrast, during arena assays it was much more common for several *M. rubra* foragers to surround a native worker, splaying its legs or dragging it back and forth, effectively immobilizing (rarely killing) a single worker, though such a group effort would appear to require a greater expenditure in both energy and biomass. Species differences were slight and not statistically discernable, at least partly as a result of small sample size for the aphid trials.

Patterns of displacement during aggression trials:

Aggression assays between *M. rubra* and sympatric native ant species yielded several distinct patterns of displacement from the food resource (Figure 3.3). By design, no *M. rubra* foragers were actively feeding at the beginning of the assays, while the majority of the native foragers in the arena were present at the bait. Once *M. rubra* was given access, they had the opportunity to displace the native ants, which they did in the majority of the trials (3.3a-l). In all of these trials, native ants were displaced rapidly, most within the first 2-4 minutes, though in some cases (e.g. Fig. 3.3d-e) one or two foragers were able to move back to the bait and feed for a short time in the midst of the commotion of battle.

The aggression assays against *Leptothorax* species (Figures 3.3m-p) are treated separately, as they reveal some distinct patterns of interaction. While eventual displacement of the native did occur in all but the *L. ambiguus* trial, the process was gradual and characterized by very low levels of overt conflict. Mean paired

aggression scores were 2.25 ± 4.5 and 0.25 ± 0.5 for *M. rubra* and *Leptothorax* respectively. No instances of grasping, carrying or fighting/stinging were observed. This is likely due to the fact that *Leptothorax* foragers are only a fraction of the size of *M. rubra* workers and therefore do not represent much of a direct threat. *Leptothorax* were able to remain in the arena and feed alongside *M. rubra* virtually unmolested. Feeding was reduced by *M. rubra* when direct contact with its much larger foragers resulted in a brief display of escape or avoidance behavior. Neither *Leptothorax* species was directly driven from the bait or arena via direct aggression.

The last four plots (Fig. 3.3q-t) show two distinct patterns. *M. rubra* assays with *M. americana* (Fig 3.3q-r) were characterized by relatively high aggression and rapid, complete displacement of the native foragers from the bait. However, the battles with its congener preoccupied *M. rubra* foragers, and a few were able to feed within the duration of the trials (20 and 24 minutes respectively). The *F. aserva* assay (Fig. 3.3r) showed an enduring back and forth conflict, with *M. rubra* and *F. aserva* feeding for short bouts and in low numbers for the duration of the 60-minute assay. Aggressive and dominant (as a contest competitor), *F. aserva* workers originally battled and retreated but would steal back into the arena amidst *M. rubra* foragers, risking (and eliciting) further confrontation. Due to their greater speed and agility, they generally succeeded in retrieving bits of food or sugar solution even while *M. rubra* occupied the baits. The low recruitment by both *M. rubra* and *F. aserva* is the root of the comparatively low overall aggression scores for this trial, since per capita aggression was similar to assays with other species. In contrast to the rest of the plots, the *D. taschenbergi* trial (Fig. 3.3t) showed a pattern opposite to

what was seen for all of the other assays. *D. taschenbergi*'s chemical defenses appeared to have a powerful stunning effect on *M. rubra* workers, and their colonies were large with strong recruitment to the arena. Close contact with any of the fast-moving *D. taschenbergi* workers often caused *M. rubra* foragers to freeze in place, jerking back and forth in spastic convulsions for up to several minutes. While aggressive interaction and recruitment continued for both species throughout the assay, it was *D. taschenbergi* and not *M. rubra* that was successful in dominating the food resource.

Patterns of native ant displacement were not so easily discernible in the aphid assays (Figure 3.4). While characterized by a similar level of aggression as the arena assays, *M. rubra* was not nearly as successful in dominating the aphid resource within the time frame of the aggression assay. In fact, *M. rubra* was only successful at feeding briefly and sporadically in 4 of the 7 assays (Fig. 3.4b, c, g and e), and no clear dominance over or displacement from the resource was in evidence. Direct tending or feeding by the native workers varied widely but was shown to persist or even increase in 3 of the 7 trials (Fig. 3.4a, d, and g).

Figure 3.5 shows the relationship between the rate of recruitment to the arena by *M. rubra* foragers and the length of time that natives were able to continue feeding at the bait. The dependent variable was calculated by taking the natural log of the duration of time where the native ants maintained >1 forager at the bait that was observed to actively feed for at least a portion of the 2-minute interval. For the arena assays (Figure 3.5a), there was a negative correlation (Pearson's $r = -0.62$, $p = 0.003$)

between the rate of *M. rubra* recruitment and the amount of time that the native maintained a presence at the food source across all trials. In the aphid assays, the rate of *M. rubra* recruitment showed no significant relationship with native feeding ($r = -0.59$, $p = 0.17$, Fig. 3.5b). This is likely due at least in part to the small sample size ($n = 7$), as well as to the fact the per capita encounter frequency was lower on the structurally complex branch or sapling substrate than on the two-dimensional floor of the arena. Interestingly, there was no evident pattern or relationship between time to displacement of the native ant and aggression score ($p = 0.52$ and $p = 0.95$ for *M. rubra* and native ant aggression respectively).

Breakdown by aggressive behavior:

Figure 3.6 shows individual aggressive behaviors for both *M. rubra* and native ants. Attack/threat behaviors necessarily precede all other aggressive acts and are therefore inclusive; thus this category serves as a proxy for total aggression. Attacks that did not escalate into grasping, carrying or stinging/fight behavior were rare across all assay trials. Pooling across species, behavioral interactions were dominated by fighting/stinging behavior in both arena and aphid assays. Grasping was employed by both *M. rubra* foragers and native ants, though this behavior comprised a greater proportion of the overall tally for *M. rubra*, nearly equaling the stinging/fighting frequency in the aggregate. In contrast to *M. rubra* intraspecific assays (Chapter 2) where carrying was employed to a far greater extent, this behavior was limited to a few instances, mostly during assays with other *Myrmica* species. The high level of aggressive response by the native workers appeared to preclude

carrying behavior in the majority of cases, as any contact most often quickly led to fighting/stinging. *M. rubra* often appeared to lack the size or agility to effectively carry some of the larger, faster natives. *Camponotus* majors, for example, dwarf individual *M. rubra* workers to the degree that several of the latter would be hanging on to each leg as the native flailed about, attempting to grab *M. rubra* in its mandibles. Finally, direct escape behavior was relatively uncommon (though slightly less so for native ants). Overall, however, *M. rubra* was highly successful at driving most natives from the bait and even from the arena.

Discovery time experiment:

As predicted, *M. rubra* proved to be both the first to discover food placed in the habitat and to amass greater forager numbers when compared with native ants. Over the two hours of this experiment, 34 of 40 baits (85%) were discovered and/or colonized at one or more of the observation intervals. Aspiration and identification of all ants present at the baits upon termination of the experiment revealed the presence of a total of eight species, including *M. rubra* (Figure 3.7a). Species differences were evident with respect to discovery time (one-way ANOVA; $F_{7,27} = 3.94$; $p < 0.0001$). Since reliable identification in the field was not always possible with this suite of species, foragers that did not maintain a presence at the bait long enough to be collected were classified to genus only. Discovery time also differed by genus (one-way ANOVA; $F_{5,42} = 4.20$; $p = 0.003$; Figure 3.7b). Out of the 15 baits that *M. rubra* colonized, 13 were colonized within 15 minutes when the stations were first checked. Though not detected by the design of the experiment, it is likely

that the first foragers had arrived considerably sooner and were in fact observed crawling on the petri dish within seconds after it was placed in the habitat. The mean time to discovery for *M. rubra* foragers was 21 minutes, but the mean was skewed by a single data point where *M. rubra* arrived after 90 minutes (median time to discovery = 15 min.). This bait was located 10 or more meters outside what was considered to be the bounds of the local infestation; the few foragers that arrived likely came from a small, fringe nest. At that, on the average *M. rubra* arrived more than 10 minutes prior to the next fastest species (*M. fracticornis*; mean = 31.6 min.) and more than 21 minutes before other *Myrmica* species (mean = 42.4 min.) when the data was pooled by genus (Fig. 3.7b).

The number of *M. rubra* workers present at colonized baits rose sharply within the first observation interval and continued to increase steadily over the course of the experiment (Figure 3.8). This increase could represent either rapid and persistent post-discovery recruitment or perhaps, with so many workers in the habitat, a sustained incidental discovery by wandering foragers. In either case, recruitment by *M. rubra* was sharply higher than any of the native ants. Next to *M. rubra*, other *Myrmica* species were the most abundant at baits, and their numbers tended to increase steadily over time. Recruitment was generally low for *Camponotus*, *Formica*, and *Lasius* species, whose foragers would arrive singly or in small groups and rarely mounted any significant recruitment effort, with the exception of a few baits (Figure 3.8).

Temporal foraging patterns:

Prior research has shown that *M. rubra* forages around the clock, though foraging effort is negatively correlated with particularly hot, dry conditions or with moderate to heavy rain or excessive cold (Grodén et al. unpublished data). The summer day and nighttime temperatures in Acadia National Park are generally well within the ant's foraging optima, and there is only a slight drop in intensity during the early morning hours. Thus, the potential of temporal niche partitioning as a mechanism to facilitate coexistence with native species appears unlikely. Results of a 2004 24-hour sample of three native and one *M. rubra* sites are shown in Figure 3.9. Trap catch was somewhat sporadic with respect to most species (20 species collected in all), but the number of recruits was not linked strongly to time, as most ants were collected at various times of day and night. Other *Myrmica* species were the most consistent foragers among the native fauna and showed the highest average recruitment in all three of the native sites (even when *M. rubra* was present in low abundance). The number of foragers collected during each interval was higher for *M. rubra* in the infested site than for native species at uninfested sites.

DISCUSSION

Competition in native *M. rubra* communities:

Studies of *M. rubra* in its native range, particularly in England and Scandinavia, suggest interspecific competition as an important factor in shaping ant communities. Elmes (1974) cited the significant segregation of colonies of *M. rubra* and *Lasius*

Table 3.1 – List of resident ant species assayed for aggression against captive *M. rubra* colonies. Sample sizes for each species by assay type are given in ‘bait’ and ‘aphid’ columns.

Assay species	Assay type	
	Bait	Aphid
<i>Camponotus hurculeanus</i>	1	-
<i>Camponotus novaboracensis</i>	1	2
<i>Crematogaster cerasi</i>	-	1
<i>Dolichoderus taschenbergi</i>	1	3
<i>Formica aserva</i>	1	-
<i>Formica exsectoides</i>	1	-
<i>Formica glacialis</i>	3	-
<i>Formica lasioides</i>	-	1
<i>Formica neogagates</i>	1	-
<i>Lasius pallitarsis</i>	1	-
<i>Leptothorax ambiguus</i>	1	-
<i>Leptothorax longispinosis</i>	3	-
<i>Myrmica americana</i>	2	-
<i>Myrmica detritinodis</i>	3	-
<i>Tetramorium caespitum</i>	1	-
Total	20	7

Figure 3.1 – Mean aggression score and count of aggressive behaviors by *M. rubra* foragers toward *M. rubra* foragers from a distinct infestation versus toward native ants. Assay results were standardized to a 10-minute assay and excludes trials against *Leptothorax* spp. where aggression was uncharacteristically absent. Error bars represent one standard error of the mean. * $p < 0.05$, ** $p < 0.01$.

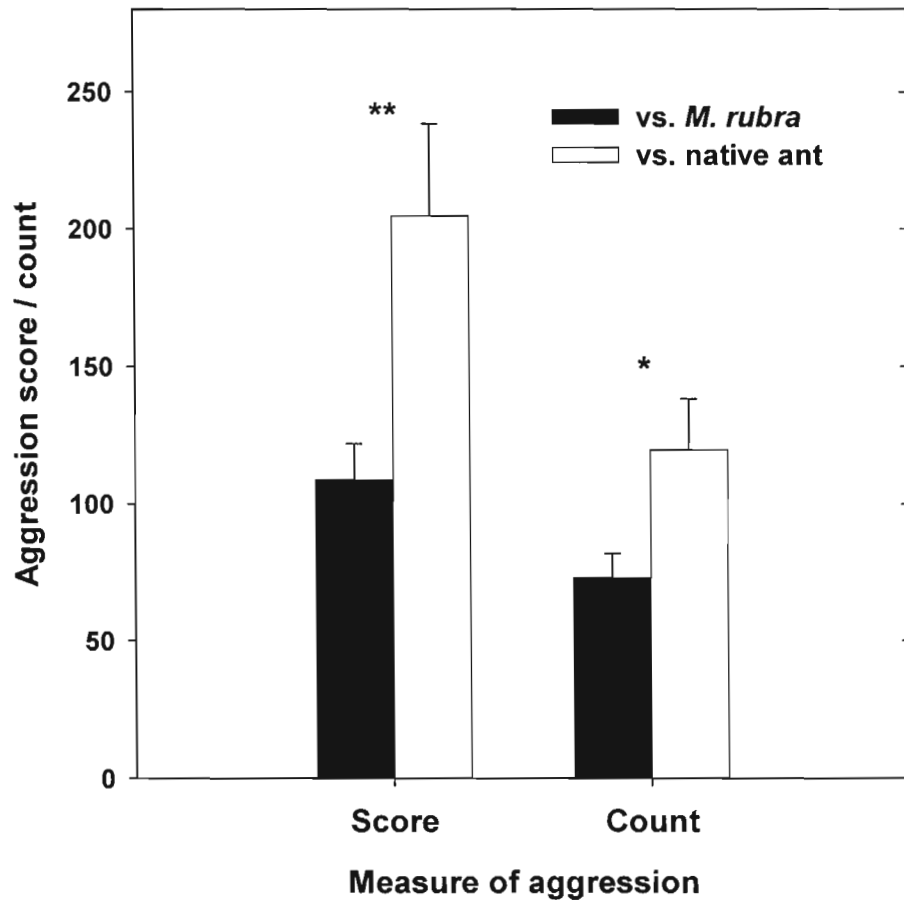


Figure 3.2 – Aggression score for *M. rubra* and native ant foragers in baited arena and aphid arena assays – 2003 Error bars are one standard error of the mean.

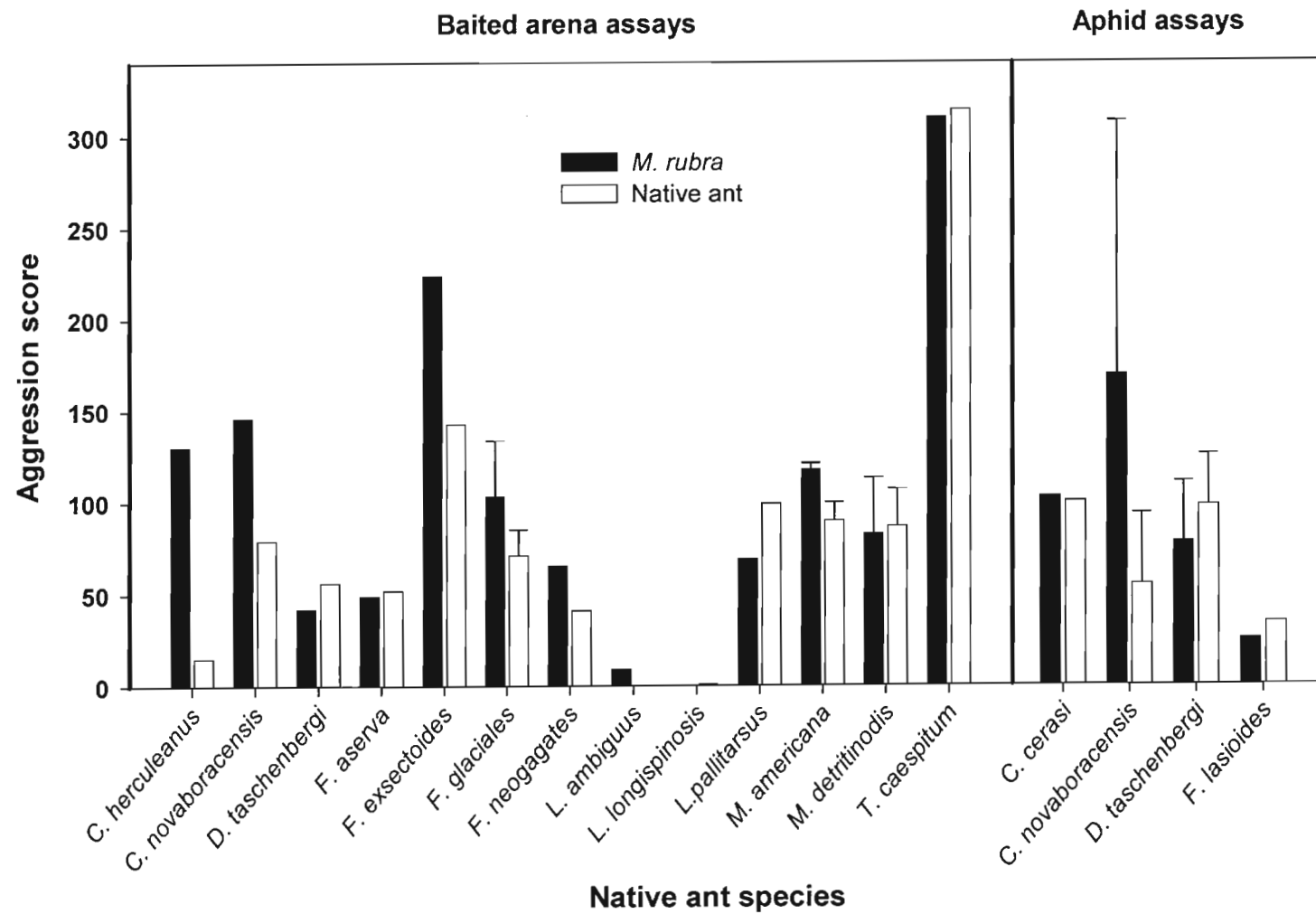


Figure 3.3 – Number of *M. rubra* and native ants actively feeding at baits over time – baited arena assays only. Solid lines correspond to *M. rubra* foragers, dotted lines to native ant foragers. Note that scale differs across subplots.

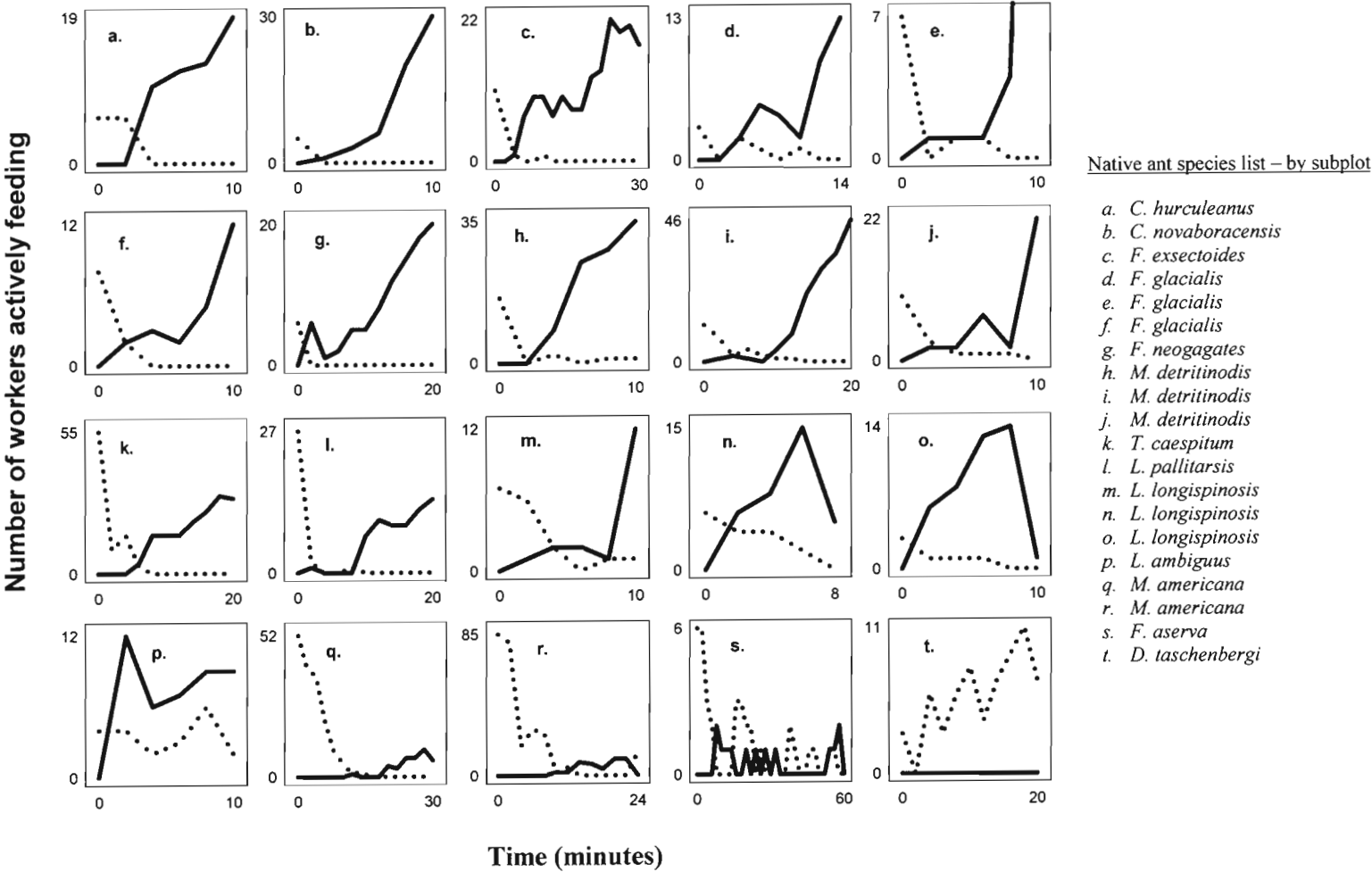


Figure 3.4 – Number of *M. rubra* and native ants actively feeding over time – aphid arena assays only. Solid lines correspond to *M. rubra* foragers, dotted lines to native ant foragers. Note that scale differs across subplots.

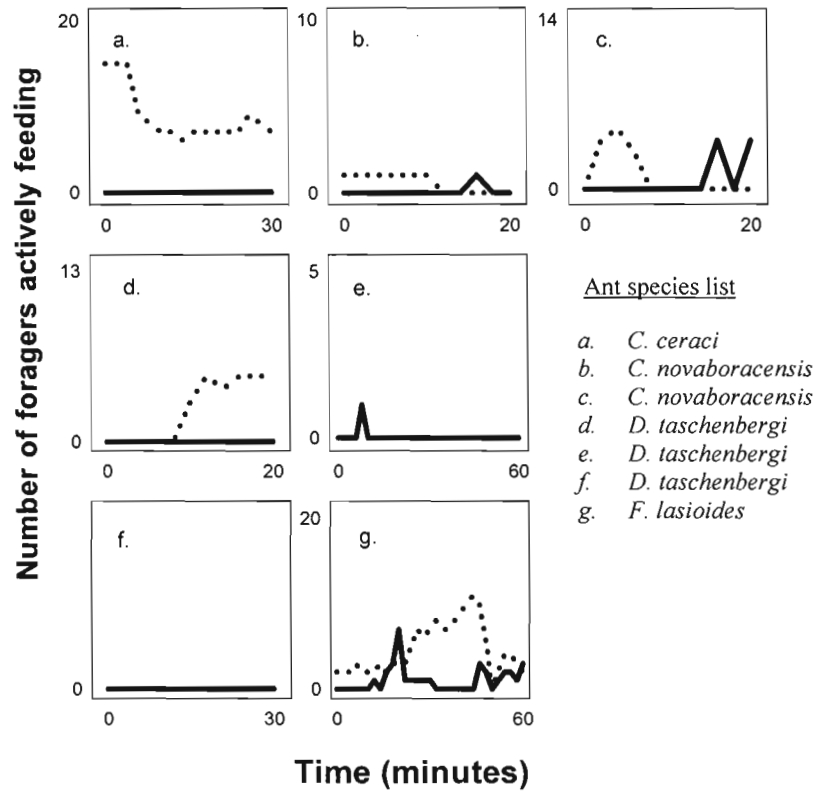


Figure 3.5 - Time native ant foragers remained at bait, as a function of *M. rubra* recruitment rate in (a) baited arena assays and (b) aphid arena assays. Y-axis shows the natural log of the last time interval where >1 native foragers remained in the arena, actively feeding at the bait resource. Pearson correlation coefficients (*r*) are given, and corresponding *p* values.

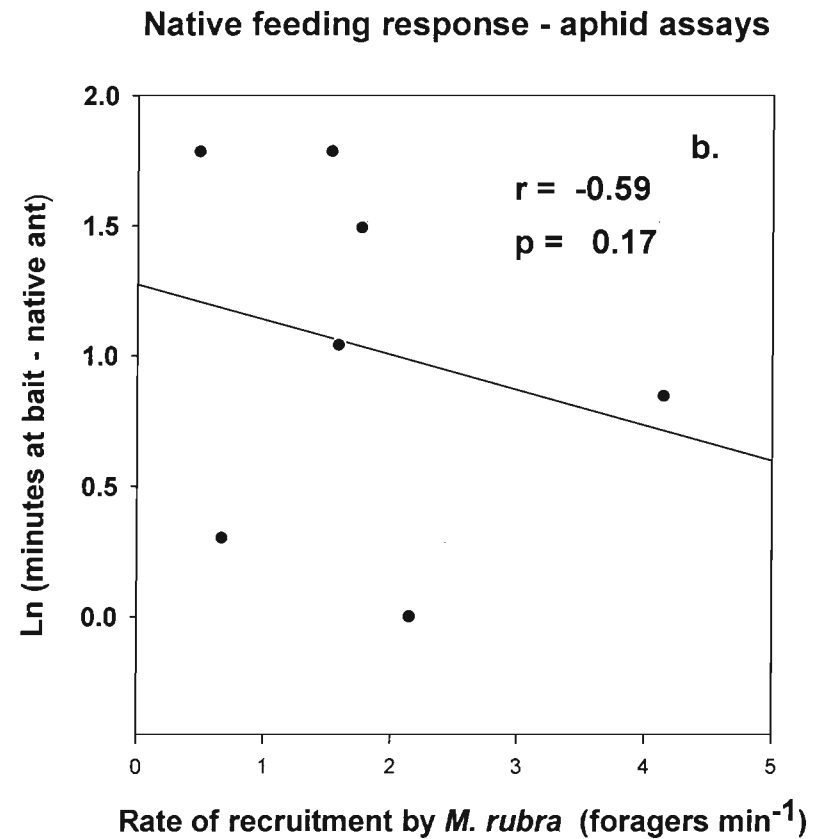
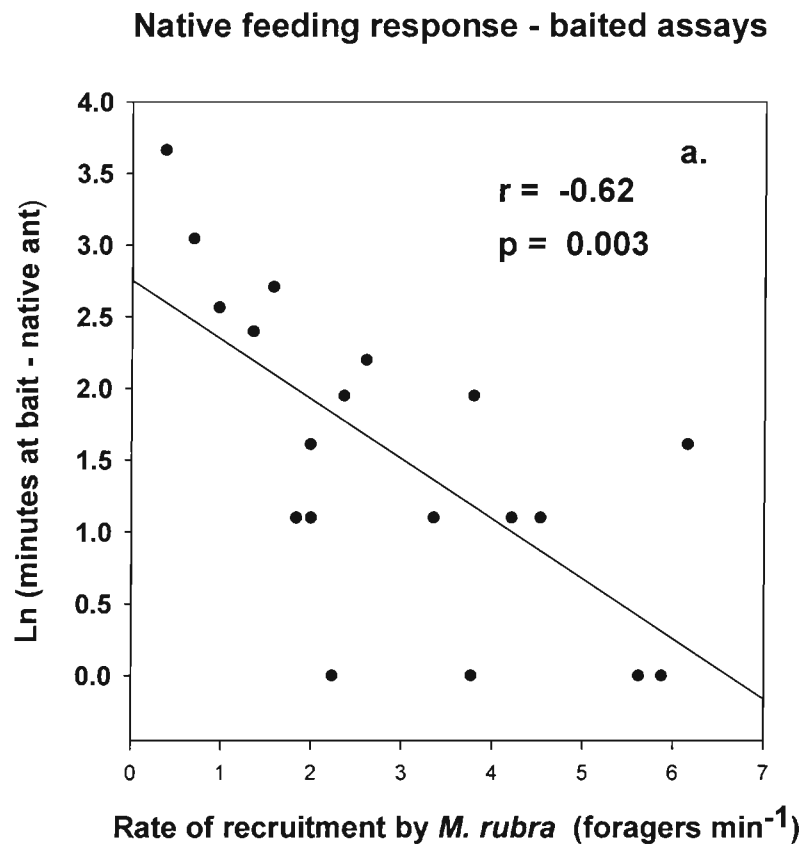


Figure 3.6 – Individual aggressive behaviors by category of aggression - *M. rubra* vs. native ant aggression. Error bars are one standard error of the mean.

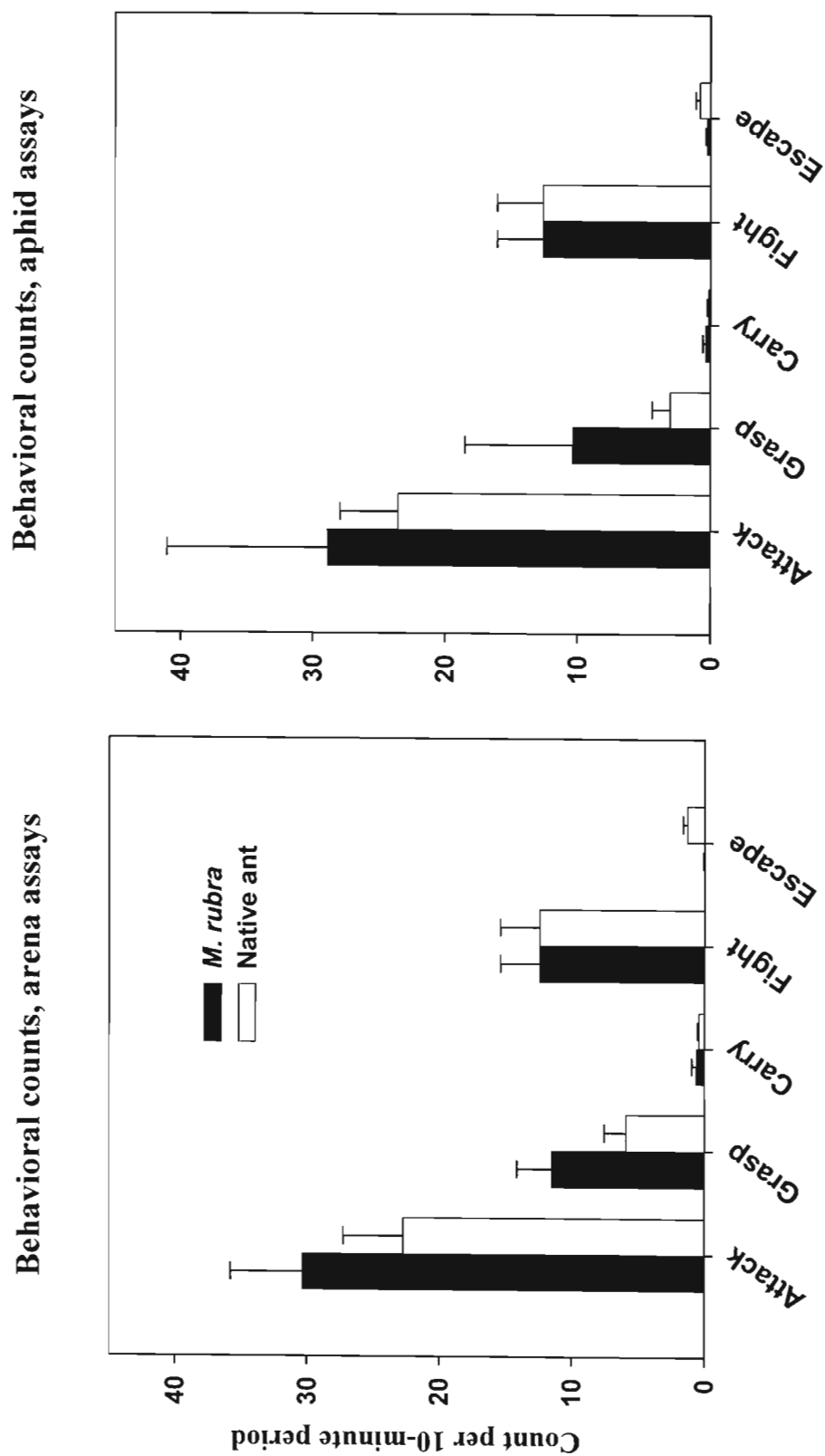


Figure 3.7 - Mean time to discovery of baits by (a) species and (b) genus. No formal tests for significant differences by species were performed (Figure 3.7a). In Figure 3.7b, we used Dunnett's test to compare *M. rubra* (control) to each native ant species independently. * $p < 0.05$, † $p < 0.10$.

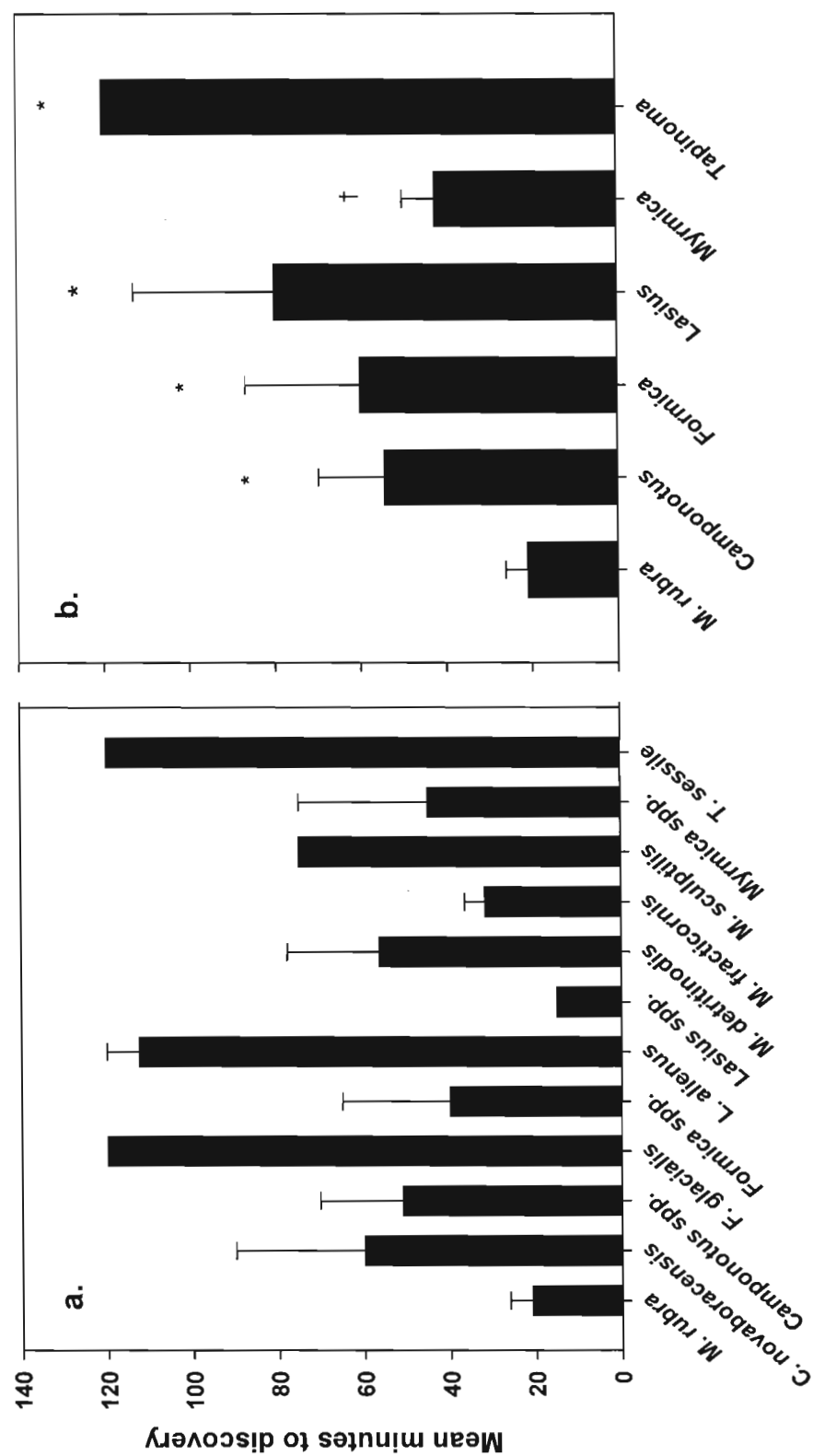


Figure 3.8 - Mean recruitment by *M. rubra* and native foragers to baits along linear transects at Bear Brook Pond site, Acadia National Park. Foragers censused at 15-minute intervals for 2 hours on the morning of 20 August 2004. Mean foragers for each species calculated as mean number of ants per bait per time interval, including only those baits to which that species ultimately recruited. Data presented by genus.

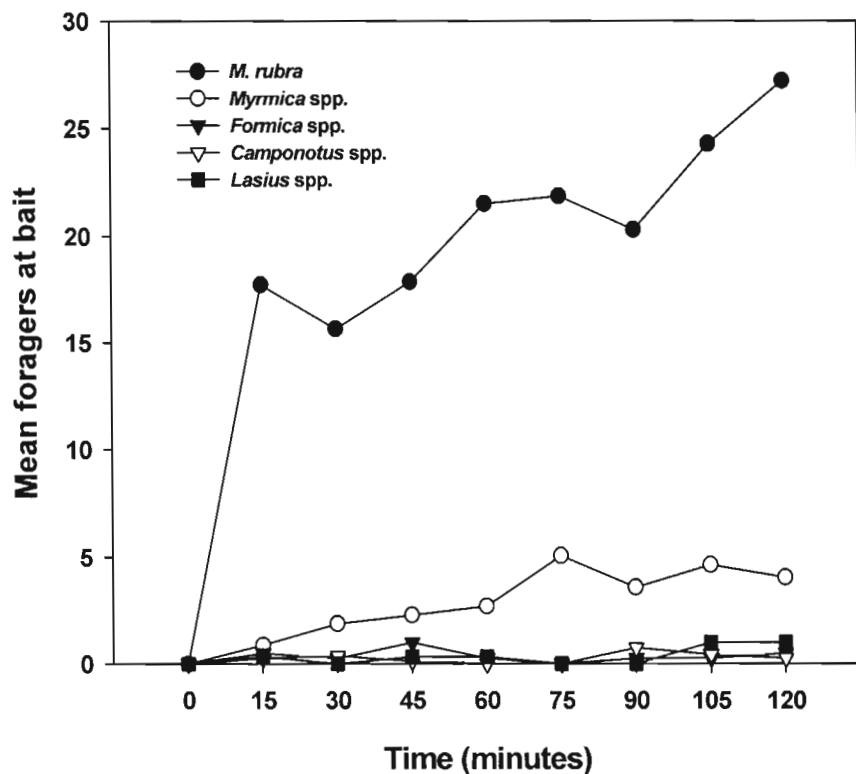
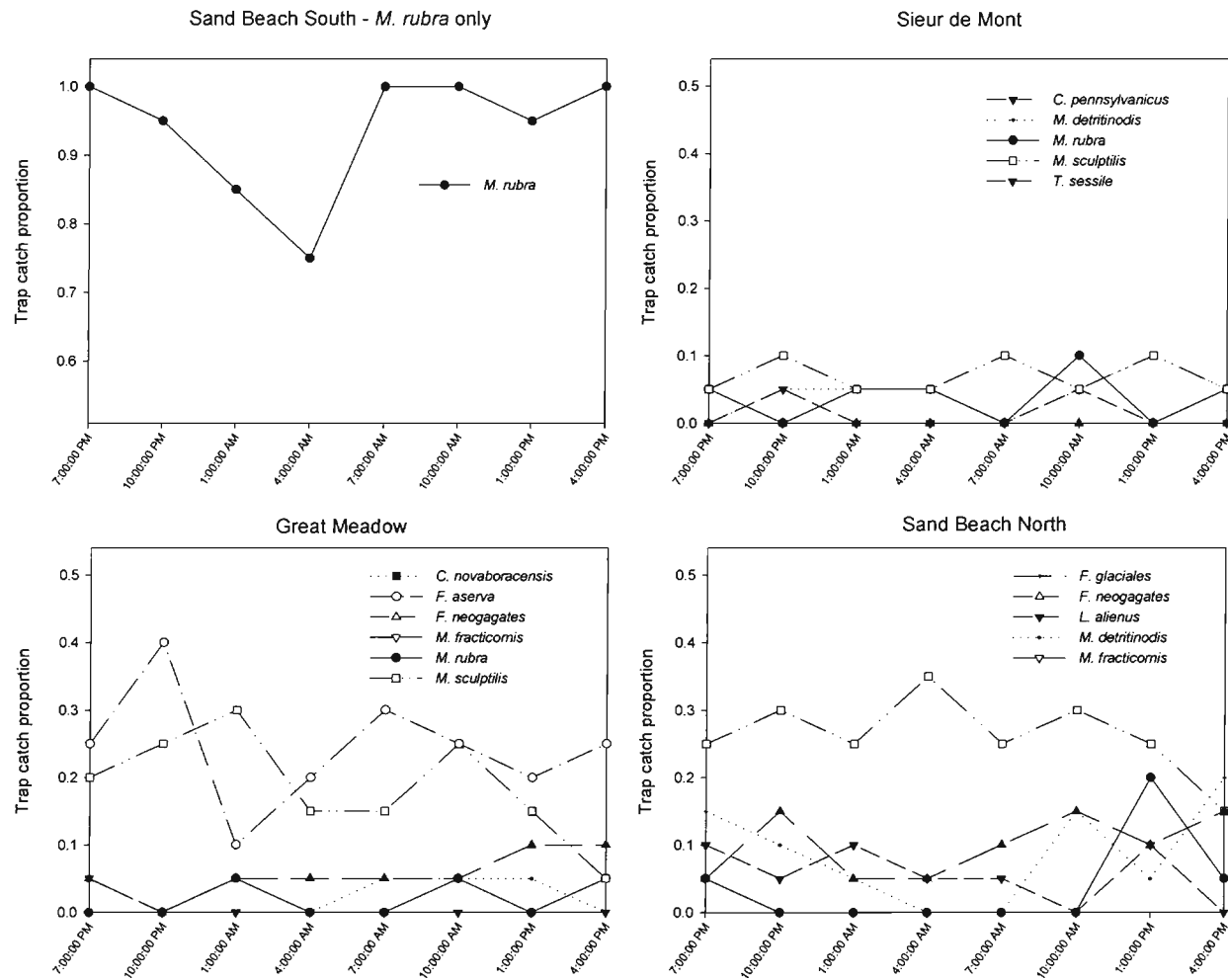


Figure 3.9 – Results from 24-hour sampling of ant foragers in four sites in Acadia National Park, 19-20 August 2004. Y-axes show the proportion of baits containing ant foragers of each species. Only the highest recruiting species per site are shown. Sand Beach South site is a dense *M. rubra* infestation. *M. rubra* is patchily distributed and at low density at Sieur de Mont and Great Meadow sites and absent from Sand Beach North.



flavus in a limestone grassland as evidence of a high degree of competition between the two species. In pairwise laboratory assays among sympatric species, *M. rubra* and *Lasius flavus* showed high levels of aggression toward each other, though aggression was common between *M. rubra* and other members of the genus *Myrmica* (Moxon 1980). Under natural conditions, native European *Myrmica* have been found to partition the habitat rather predictably along temperature/moisture gradients. *M. rubra* is capable of dominating a patch in the presence of its congeners (such as *M. scabrinodis*) in relatively cool, moist areas but may persist only at low densities under hot or dry conditions (Clarke et al. 1998). In contrast, large, polydomous colonies of *Formica* (particularly *F. rufa*, *F. exceta*, and *F. truncorum*) often dominate large areas in the northern boreal forest of Scandinavia and have been shown to significantly reduce foraging among *Myrmica* spp. (Vespalainen and Savolainen 1990). Under certain conditions, however, *M. rubra* and *M. scabrinodis* can reach high densities, competitive dominance and local patch saturation (van der Hammen et al. 2002).

Interference versus exploitation competition:

Few studies have been performed to date on interspecific competition in ant communities similar to those invaded by *M. rubra* in the Northeast. Fellers (1987) found evidence of extensive niche partitioning among woodland ants in Maryland, where species of the subfamily Formicinae (*Lasius aleinus*, *Prenolepis imparis* and *Formica subsericea*) were shown to be dominant contest competitors. Myrmicines (*Aphaenogaster rudis*, *Myrmica punctiventris*, *Myrmica emeryana* and *Leptothorax*

curvispinosis) were generally submissive upon encountering foragers of a rival species.

Like the native *Myrmica* in Fellers' (1987) work, *M. rubra* in our study was shown to encounter food resources in advance of sympatric species in our baiting experiments. Of all the species recruiting to the baits, *M. rubra* foragers were considerably more successful at rapid discovery, arriving at 13 of the 14 baits (that they ultimately colonized) within the first 15-minute observation period. Coupled with the persistent arrival of foragers (whether by active recruitment or sustained incidental discovery), *M. rubra* demonstrates a distinct advantage as an exploitative competitor, capable of feeding in large numbers before foragers of rival species arrive. Prior researchers have constructed dominance hierarchies and have ranked indigenous *Myrmica* species in the U.S. (Fellers 1987) and Europe (Savolainen and Vepsäläinen 1988, Vepsäläinen and Savolainen 1990) as intermediate to subordinate interference competitors. In contrast, aggression assays in its invasive range showed *M. rubra* to be highly effective at displacing foragers of a variety of native species from baits via direct aggression/contest competition. Thus, as with the invasive *L. humile* (Holway 1999, Human and Gordon 1996), *M. rubra* appears to have broken the trade-off between interference and exploitation competitive ability. While field trials have confirmed that *M. rubra* competes directly with native foragers at food resources along the boundaries of local infestations, it is not known how much direct or indirect competition for food contributes to the displacement of native ants. However, considerable intraguild diet overlap does exist among native species of Eastern North America (Gotelli and Ellison 2002, Fellers 1987, Hölldobler and

Wilson 1990), and *M. rubra*'s broad diet appears to overlap widely as well (Czechowski 1985). *M. rubra*'s habit of foraging around the clock from the litter layer up into the overstory canopy, and the demonstrated ability of its foragers to preempt and defend against the arrival of other species at food resources, effectively limits the potential for temporal or spatial partitioning of the habitat. Likewise, as *M. rubra* is comparatively cold-tolerant, foraging from early in the spring into late autumn (and even on warm days in the winter), seasonal fluctuations in the dominance/discovery hierarchy seem equally unlikely (Grodén et al. unpublished data). Where it has been studied in California, *Prenolepis imparis* has been found to be relatively unaffected by the presence of *L. humile* due to its higher seasonal activity during the cooler, wetter months when *L. humile* exhibits reduced foraging intensity (Sanders et al. 2001, Ward 1987, Suarez et al. 1998). *M. rubra*'s apparent season-long dominance may further limit coexistence of native ant species, though seasonal changes in food selection (e.g. protein versus homopteran honeydew) have not been assessed. Fellers (1987) found evidence for diet overlap in her Maryland study (among a suite of species similar to those in Maine), but foragers of each species preferentially selected food of differing shape and mean particle size. The current study does not address the potential for resource partitioning based on food size or type; however, it is likely that *M. rubra*'s effective territoriality allows it to dominate virtually all food resources within the boundaries of an infestation. These factors, taken together, build a strong case for the central role of food resource preemption and defense as a mechanism for the displacement of resident ant species.

Native ant defenses:

Localized interactions alone, as observed during aggression assays and within zones of overlap surrounding invaded habitat, provide little insight into the long-term impacts of *M. rubra* on the native community. It is likely that given the invader's sheer numerical dominance, it will ultimately displace all but a few native ant species (Holway and Case 2001). Pitfall and litter sampling in invaded and non-invaded territories revealed the persistence of workers of only two relatively cryptic species, *Stenamma dieki* and *Lasius subumbratus*, within areas of infestation compared with 18 species from non-infested areas (Chapter 4). These results mirror those of other studies (Porter and Savignano 1990, Cole et al. 1992, Human and Gordon 1996, Human and Gordon 1999, Holway 1998), though there is some evidence that the native community may recover over time (Morrison 2002). Alternatively, ants of the genus *Leptothorax* may be in a position to potentially withstand the invasion. Owing at least in part to their small size (2-3 mm), these ants appear to have taken the role of "insinuators" (*sensu* Wilson 1971), capable of feeding unmolested in the presence of *M. rubra* and other ants. *Leptothorax andreii* was found to persist in areas overrun by *L. humile* in California where other species have been displaced, which Human and Gordon (1997) attribute to the tiny size of *Leptothorax* individuals and colonies. Almost no overt aggression was directed toward *Leptothorax* foragers by *M. rubra* during paired aggression assays, and indeed these ants are the most abundant (and often the only) natives readily found within the boundaries of a dense infestation (personal observation; also see Chapter 4). At the other extreme, *Lasius pallitarsis*, one of the most abundant ants on Mount

Desert Island with habitat requirements overlapping (at least in part) those of *M. rubra*, was actively predated upon during aggression trials. This may translate to high vulnerability to the *M. rubra* invasion, and the ant is apparently displaced. The number of hypogaeic or otherwise cryptic species that are able to persist within an *M. rubra* infestation is unknown, though such species may be able to avoid contact with *M. rubra* by foraging underground and beneath the litter, effectively minimizing direct interaction, and may also specialize on distinct food resources, as has been shown in other invaded communities (Ward 1987).

Qualitative aspects of the interactions:

Despite clear dominance in the majority of aggression assays against native ant species, *M. rubra* was not always the obvious “victor” in the short term of the observation period. It appears from these and other data that ant species will be differentially affected by the ongoing invasion (Chapter 4). Some of the most interesting observations during aggression trials relate to the character of direct interaction with the native species. While the nature of such interaction is difficult to quantify, observational evidence may offer clues as to the relative impacts the sustained *M. rubra* invasion are likely to have in shaping future ant communities. A few species stood out during the aggression assays as better able to defend against a (short duration) attack by *M. rubra* workers. *D. taschenbergi*, for example, recruits to food in numbers that may be locally comparable to *M. rubra*, and also employed chemical defenses during aggression assays that led to convulsions and apparent disorientation in affected *M. rubra* foragers, incapacitating and sometimes killing

them. Similarly, *C. cerasi*, despite the small size of its workers, used its sting as an effective weapon, killing a number of *M. rubra* workers during the aggression trials. Like *D. taschenbergi*, *C. cerasi* was also able to ward off a short-term *M. rubra* attack in defense of their aphid resource. Interestingly, both *C. cerasi* and *D. taschenbergi* were found primarily in close association with homopterans. This fits some researchers' prediction that such a carbohydrate surplus may translate to high worker activity and/or investment in carbon-based defensive compounds (Davidson 1998). Additionally, the design of the aphid assay itself may have favored the defending native species in a short-term trial. The structural complexity of a branch as compared with the floor of an arena likely made a direct attack by the invading *M. rubra* more difficult, while offering more opportunities for the native workers to escape or hide. Nevertheless, *M. rubra* did explore a significant portion of the branch or sapling in all trials and native ants invariably defended against the attack. Many times, ants would engage in battle on the branch and then fall to the ground in fighting/stinging behavior. Ultimately, *M. rubra* experienced the most casualties in its battles against *C. cerasi* and *D. taschenbergi*, while *Camponotus* spp. majors were occasionally able to grab hold of a worker and cut it in two with its powerful mandibles.

Alternative modes of displacement:

A number of other mechanisms could contribute to the displacement of native ant species from an invaded habitat beyond direct or indirect competition for food resources. Competition for territory or nest sites, direct predation on reproductive

propagules/incipient colonies, or subtle alteration of the habitat (mediated by altered patterns of seed dispersal/vegetation dynamics or the exclusion or facilitation of non-ant organisms) could also contribute to the observed declines and community restructuring. Data from artificial nest substrates placed in invaded and uninvaded habitats and monitored biweekly for the past three seasons suggests that ant populations in Acadia National Park are not nest site limited, as the vacancy rate of apparently suitable nest sites hovers around 50% throughout the season (Appendix A). While nest sites do not appear to be particularly scarce or limiting in either the presence or absence of *M. rubra*, the lack of foraging territory in a dense *M. rubra* infestation may essentially make the sites unsuitable. *M. rubra* workers do on occasion lay siege to mounds of native ants. In one instance, a moderately large *Formica glacialis* colony was ultimately displaced after several months of siege and direct attack. *M. rubra* was also observed to opportunistically raid the brood of native nests (personal observation). Lastly, as *M. rubra* has been observed preying upon male and female reproductives of sympatric species during their mating swarms, many of these potential propagules are thus unable to found new colonies in the presence of *M. rubra* foragers (personal observation, see Appendix C). By these mechanisms, reproduction of competitor species may be limited, and new colonies are excluded from the boundaries of an infestation. While the relative contribution of direct predation of workers and reproductives is unknown, such behavior has been witnessed to occur against *C. noveboracensis* as well as *Lasius pallitarsis* (personal observation, Appendix C). Finally, there exists the possibility of apparent competition between introduced and native ants based on shared predators, parasites

or pathogens, though its relative contribution to community dynamics in invaded ecosystems is unknown (Holway 1999).

The role of population structure in determining competitive ability:

Davidson (1998) outlines a number of potential requirements for the ecological success of an invasive ant species that appear to relate to *M. rubra* and its role as a superior competitor. Numerical dominance in ants correlates strongly with behavioral dominance (Vepsäläinen 1982, Savolainen and Vepsäläinen 1990). Under certain circumstances, where changes in the population structure of an invasive ant lead to high nest densities and a superabundance of foragers, an invasive ant may exhibit *de facto* territoriality, even if individual colonies do not defend an absolute area beyond their immediate nest site.

Numerical dominance may be key to the ecological success of ant species (Davidson 1998, Holway 1998, 1999). This may be especially true in invasive ants that, having left their natural enemies behind, no longer experience the costs associated with living in high density populations (Giraud et al. 2002). In their native range, predators, parasitoids and pathogens may exert selection pressure in favor of nestmate discrimination cues and colony autonomy regulated by intraspecific aggression, as high nest or worker densities may facilitate pathogen transmission and allow predators/parasitoids to easily locate colonies or foragers as prey. Phorid fly parasitoids have also been shown to directly dampen foraging behavior in *S. invicta*, and their absence may lead to enhanced activity and competitive ability (Orr et al. 1995). Dense and enduring populations of ants could

also support increased population levels of such natural enemies where they occur. Hence, the presence of natural enemies may ultimately select for greater intercolony spacing and a multicolonial population structure (Giraud et al. 2002, Davidson 1998). Alternatively, there may be a considerable advantage to living in a highly polygynous/polydomous society with little overt aggression between neighboring colonies in invaded habitats where natural enemies are absent.

High nest and colony density itself confers numerical dominance, which in turn favors the larger group in both interference and exploitative competition with native competitors (Human and Gordon 1996, Human and Gordon 1999, Holway 1999, Davidson 1998, Hölldobler and Lumson 1980). *M. rubra*'s polydomous habit, coupled with its flexibility to nest in a variety of substrates (leaf litter, downed woody debris, excavated soil nests, under stones, etc. -- Groden et al. unpublished data) give colonies the ability to situate satellite nests in close proximity to enduring resources (i.e. homopterans), further facilitating dominance over and rapid discovery and recruitment to resources. It is common in invaded habitats to find *M. rubra* nesting at the base of vegetation that supports one or more homopteran colonies (personal observation 2004). In conjunction with its flexible nesting requirements, *M. rubra*'s polydomous colony structure also confers the potential for colonies to situate queens, larvae and nursery workers where conditions are optimal for brood production/development without sacrificing proximity to homopteran or other resources. Davidson (1998) suggests that reliance on homopteran honeydew may be "necessary but not sufficient" to ecological dominance among ant species. She and others (Holway et al. 2002, Sanders et al. 2001) theorize that an abundant high-

energy, low-nitrogen food source may subsidize a high level of worker activity and/or investment in carbon-based defensive compounds. Energy surplus may thus be translated into enhanced foraging intensity and increased potential for colony or territorial defense. This model appears to fit well with observations as well as our experimental results for this invader.

CONCLUSION

Our studies demonstrate that invasive populations of *M. rubra* outcompete native ants in the acquisition of food, implicating the ant's dominance in both interference and exploitation competition as key to native ant exclusion from bait resources. This dominance, typically found to be inversely related in native species, results in effective (if not behavioral) territoriality over relatively large areas (10's to 100's of meters). This pattern appears to be common to invasive ant species studied to date and both stems from and contributes to their numerical dominance. While other forms of intraguild competition undoubtedly occur, competition for food appears to be a central element in modeling and understanding native ant displacement in invaded ecosystems.

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CHAPTER 4

Native ant displacement and community restructuring by the invasive

European Fire ant, *Myrmica rubra* L.

INTRODUCTION

Changes to communities in response to the invasion of one or more non-indigenous organisms have been the subject of considerable discussion and research over the past half-century (Elton 1958, Simberloff 1981, Lodge 1993, Pimm 1986). In many cases, widespread negative impacts on native fauna are clearly in evidence (Erickson 1971, Ward 1987, Porter and Savignano 1990, Cole et al. 1992, Human and Gordon 1997, Bolger et al. 2000, Holway 1998, Suarez et al. 1998, Morrison 2002). However, finer scale analyses of which species or segments of a given population will be most impacted (positively or negatively) by an invasion have yet to demonstrate unambiguous patterns of displacement and coexistence across ecological systems. Island biogeography theory posits that there is a finite number of species with overlapping resource requirements that can exist in any given habitat. The addition of a non-indigenous organism thereby increases the extinction probability of native taxa (reviewed in Simberloff 1997, Simberloff and Von Holle 1999). The numerical abundance of many introduced animals, including ants, has been shown to afford invaders a significant competitive edge and also increases the breadth of the niche that they occupy, elevating the probability of widespread displacement of native fauna and restructuring communities and ecosystems

(Chapter 3, Human and Gordon 1997, Human and Gordon 1999, Gotelli and Arnett 2000, Holway 1999, Petren and Case 1996, Williams 1994, Morrison 2000).

The generally slow, steady spread of invasive ants from invaded to non-invaded habitats and incidents of jump dispersal (generally as stowaways of human commerce) (Passera 1994, Suarez et al. 2001) has been identified by a number of researchers as presenting an ideal natural experiment for the study of community change and competitive displacement by invading organisms (Porter and Savignano 1990, Bolger et al. 1997, Holway 1998, Human and Gordon 1997, Morrison 2002). As a result, many have characterized changes in community structure and composition of native ants, arthropods, birds (Wilson and Silvy 1988, Lockley 1995), small mammals (Holtcamp 1997, Ferris et al. 1998, Allen et al. 2004), lizards (Suarez et al. 2000, Suarez and Case 2002), and even large vertebrates (Allen et al. 1993, Allen and Lutz 1997, Allen et al. 1997) following invasions, and have uncovered a variety of patterns and responses. In the short term, ant invasions appear to be almost universally accompanied by a commensurate decrease in native ant species richness, diversity and abundance, though recent work suggests that some communities may rebound once the initial front has passed (Morrison 2000). Impacts on other taxonomic communities have been mixed. A number of studies have shown a decline in native arthropod richness, diversity and abundance (Human and Gordon 1997, Bolger et al. 2000, Porter and Savignano 1990) while others have detected little change (Holway 1998). One drawback frequently cited by authors of such studies is the difficulty in finding matched habitat that differs only in the presence or absence of a particular invader. For example, as the Argentine ant

(*Linepithema humile*) is strongly associated with edge habitat, it is difficult to separate edge effects from changes in the community structure resulting from the ant invasion (Bolger et al. 2000, Morrison 2002, Human and Gordon 1997).

M. rubra, a common Myrmicine of Europe and Western Asia, has established and spread in a number of communities in Maine and northeastern North America (Grodén et al. unpublished data). *M. rubra* shares many characteristics with other well studied invasive ant fauna that make them especially detrimental to invaded ecosystems (Chapter 2, Chapter 3, Grodén et al. unpublished data). They are highly polygynous and occupy colonies that span multiple, often ephemeral, polydomous nest sites (Brian 1952, Walin et al. 2001, Elmes and Petal 1990). Reproduction takes place largely (if not entirely) via colony budding, contributing to the establishment of large networks of interconnected nests that are not regulated by traditional mechanisms of intraspecific competition or territorial aggression (Walin et al. 2001, Seppä 1996). Given the high density of nests within an invaded habitat, it superficially appears that neighboring colonies are mutually tolerant of one another, although nestmate discrimination and moderate levels of intercolony aggression within local sites are observed (Chapter 3). In Maine, *M. rubra* foragers outcompete native foragers by direct interference and rapid discovery/exploitation of food resources (Chapter 3). Such factors, coupled with our observations of a depauperate native ant fauna within the boundaries of infestations, suggest the widespread displacement of native ants. The plausible disruption by *M. rubra* of aspects of ecosystem function, along with the implications of the manyfold increase in nest and worker density within invaded sites, suggest the potential for decreased richness and

diversity within certain subsets of the native arthropod fauna, most likely via mechanisms of direct predation and competition for limiting resources (Elton 1958, Holway et al. 2002, Lodge 1993, Erickson 1971). A concomitant increase might be expected among arthropod taxa that possess or acquire some form of association with the ant, such as small scavengers resistant to predation but able to subsist on dead workers or colony refuse (Human and Gordon 1999, Wilson 1971) or among those groups whose predators or competitors have been suppressed or displaced by the invasion (Gotelli and Arnett 2000). We also hypothesize that populations of honeydew-producing insects of the order Homoptera will be enhanced where *M. rubra* is present, as these insects are often direct beneficiaries of protection by a great abundance of ant attendants (Helms and Vinson 2003, Vinson and Scarborough 1991). Finally, by virtue of their aggressive demeanor and painful sting, *M. rubra* may adversely affect or even displace a number of vertebrate species that would otherwise forage or nest in infested habitats (Allen et al. 1995, Allen and Lutz 1997, Allen et al. 2004, Holtcamp et al. 1997, Killion et al. 1995).

The current study uses a variety of sampling methods to assess the impact of the European Fire ant, *M. rubra*, on native ant, arthropod, homopteran and small mammal communities. The patchy distribution of this invader allowed us to match sites of high ant density with adjacent sites of similar character and composition (but lacking *M. rubra*), thereby facilitating the quantification of local impacts of this invasion in Maine.

MATERIALS AND METHODS

Pitfall trapping of ants and invertebrates:

In the Summer of 2002 pitfall trap transects were deployed at eight sites in Acadia National Park, Mount Desert Island, ME. Four sites were located in areas of significant *M. rubra* infestation, and each was paired with a site of similar habitat where *M. rubra* was either absent or in very low abundance. Care was taken to match the dominant under- and overstory, major soil type, and average soil insolation/canopy density. All sites and traps were within 100 m of a road, so while edge effects may have influenced community structure and composition, impacts were likely uniform across paired sites, used as statistical blocks in the analysis. Six traps per site were deployed in a 30 m linear transect at 6 m intervals. Traps were 100 mL plastic cups, 20 cm deep and 7.5 cm across at widest diameter, buried flush with the soil/litter surface and filled halfway with a 50% mixture of propylene glycol and water. All sites were sampled for a period of five days, from 25-30 June, 9-16 July, 22-29 July, and 17-22 August 2002 at the Wood Chip Pile, Old Farm Road/Sieur du Mont, Bear Brook Pond, and Sand Beach House site pairs respectively. Any seasonal changes in the community over the course of the study were accommodated in the design by sampling both sites per block simultaneously. Given the reasonable threat of rain sometime during the five-day intervals when each of the trap sets was deployed, 16 X 16 cm roofs of sheet metal were erected over the mouth of each cup (held in place with three 12 cm nails inserted into the soil layer). Though the roofs may have reduced trap catch of adult flying insects (many were

still collected), it is unlikely that sampling of the mobile soil arthropod community was altered. After five days, traps were collected and the insects sorted and preserved in 70% ethanol.

Berlese funnel trapping of ants and invertebrates:

In order to sample a different aspect of the invertebrate litter and soil fauna that may potentially be impacted by invasion of *M. rubra*, litter samples were also collected from each site. Litter was collected by pushing a sheet metal ring (a 20 cm-diameter heating duct coupling) partly into the soil surface and collecting all litter within its boundaries, along with the top few centimeters of soil. Three rings worth of material (corresponding to an area of 0.37 m² per sample) were collected from three randomly located quadrats within each site. Three such samples were collected from each site and transported to the lab in plastic trash bags. Soil and litter fauna were collected and preserved in 70% ethanol using a Berlese funnel extraction method (Southwood 1978) for six days.

Survey of homopteran families:

In the Summer of 2003, six sites were surveyed using three different sampling methods intended to characterize the homopteran community in the presence and absence of *M. rubra*. Three pairs of sites were chosen, again attempting to match infested and non-infested habitats. At each site, 10 sweepnet samples, 15 quadrat samples and 50 visually searched branch samples were taken. Representatives of all ant species and piercing/sucking insects from each sample were collected in alcohol

for species identification. For the sweepnet samples, 10 points were randomly chosen within each site, and 10 standardized sweeps with a canvas net (36 cm diameter) were taken at each site through the herbaceous understory as the experimenter maintained a slow gait (one sweep corresponding to each large step). Captured insects were carefully emptied into vials and killed with 70% ethanol for later identification. For the quadrat samples, a transect of ~150 m was established at each site. Every 10 m along the transects, a 1 m² quadrat made of PVC piping was placed on the ground and staked into place. All grasses and herbaceous vegetation within the designated area were thoroughly searched for homopterans and/or ants, as were any trees or saplings that fell within an imaginary vertical column delimited by the square frame. Only the portion of any trees that fell within that column was searched, and only up to a height of 2 meters. Finally, traveling along the same transect extended visually 5 m in each direction (forming a 10m strip), 50 trees were randomly selected and a single branch at roughly eye level (on the side of the tree corresponding to an alternating compass direction) chosen. One meter at the terminal end of the branch was thoroughly searched for homopterans and for potential ant associates. Trees were identified in the field and all insects were collected and returned to the laboratory for classification.

Survey of small mammal foraging:

On the nights of 16 July and 6 August 2003, surveys were conducted to assess small mammal foraging at four paired sites with and without *M. rubra*. Twenty Sherman[®] live traps, baited with balls of peanut butter (diameter ~ 2.5 cm) rolled in

sugar and dry oatmeal, were set out every 10 m along two roughly parallel transects within each site. Traps were set at 6 pm and checked every two hours until 10 am the next morning for the presence or absence of small mammals. At least one person per sampling team was prepared to identify all captured animals to species, though only white-footed deer mice (*Peromyscus maniculatus*) were captured. Once a trap was found to contain a catch, it was removed from the site and therefore was considered only once in the analysis. Traps were checked at frequent intervals to minimize the risk that trapped animals be attacked and/or killed by *M. rubra*'s aggressive foragers, and also to rebait and reset traps that had sprung but did not contain a catch.

Identification of arthropod fauna and data analysis:

All arthropods from pitfall and funnel samples were sorted to the lowest taxonomic grouping (morphospecies) possible. Most were identified to the family level, though some were assigned to genus or species and still others, to morphospecies (Oliver and Beattie 1993, Oliver and Beattie 1996). Some non-insect groups (collembolans, isopods, millipedes, some arachnids, etc.) were sorted and identified to class or order only. All ants were sorted to species, with the exception of a few males that could only be successfully identified to genus. Representative ant specimens were confirmed by Dr. André Francoeur (Université du Québec à Chicoutimi) and Mr. Stefan Cover (Harvard Museum of Comparative Zoology); voucher specimens are held in the Department of Biological Sciences, University of Maine.

Analyses were similar across surveys as each employed a randomized block design in which each site pair represented a statistical block. For pitfall and funnel data, species richness, Shannon-Weiner's index of diversity and overall arthropod abundance were calculated for each taxonomic group and trap method, square root transformed and analyzed in separate MANOVA's using pitfall and funnel values as dependent variables and block and *M. rubra* presence/absence as factors. *M. rubra* individuals were excluded from the calculation of the above indices as their great abundance in areas of infestation would have skewed results. Identical indices were calculated for the homopteran data (abundance being derived from sweepnet samples only) and used in a randomized block MANOVA model, using each sample as a random factor nested within site (nested subsampling model). Sweepnet abundance was looked at separately in a nested, blocked MANOVA, using the abundance of each of the five homopteran families collected as dependent variables, *M. rubra* presence/absence as a factor, and each paired site as a statistical block, with sweepnet samples nested within the block. Small mammal abundance was analyzed in a repeated measures ANOVA. Small mammal richness and diversity could not be assessed, as we trapped only white-footed deer mice. All statistical models and tests were performed using Systat for Windows, version 11.00.01 (Systat Software Inc. 2004).

RESULTS

Ant impacts:

The strongest impacts of *M. rubra*'s invasion on native organisms were revealed in our measurements of the native ant community. Across all sites containing *M. rubra*, a total of five groups of native ants were encountered, compared to 20 total groups in uninvaded territory (Table 4.1). In this case taxonomic "group" differs from species in that it includes *Formica* spp. and *Myrmica* spp. as taxonomic classes for the cases where accurate determinations could not be made (e.g. males and some gynes). Of the handful of the individuals that were collected (six in all, not including *M. rubra*), two were gynes of the genus *Formica* (one *F. aserva* and the other unidentified) and one was a male of the genus *Myrmica*. As winged individuals could have arrived by chance in samples regardless of whether their colonies were present locally, their appearance in no way represents local spatial overlap or coexistence. Overall, 19 species were collected in pitfall and funnel traps, a representative subset of the species found in the course of our research over two years (36 species in all). When these data were assessed by trap type (Figure 4.1a), significantly reduced species richness was evident in the presence of *M. rubra* (MANOVA, $F_{2,2} = 39.70$, Wilks' lambda p-value = 0.025), with significant patterns in both pitfall and litter samples. A similar trend was observed for species diversity ($H' =$ Shannon-Weiner's index; Figure 4.1b). However, due to the small numbers of species in litter samples in both the presence and absence of *M. rubra*, a MANOVA using diversity by sampling method as dependent variables did not show significance

at the 0.05 or 0.10 level ($F_{2,2} = 7.24$, $p = 0.12$). A univariate assessment of pitfall traps alone, however, did reveal higher diversity in uninvaded sites ($F_{1,3} = 21.6$, $p = 0.019$). Native mean ant abundance per trap revealed the most drastic differences, showing a strong negative impact of *M. rubra* on native foragers ($F_{2,2} = 211.7$, $p = 0.004$; Figure 4.1c).

Impacts on resident arthropods:

The comparison of invaded with non-invaded sites revealed few measurable effects of *M. rubra*'s presence or absence on species richness, diversity or abundance of non-ant resident arthropods. Table 4.2 presents a list of all taxa collected and considered in the analysis along with the distribution and abundance of each in our samples, pooled across sites. Abundance and distribution of taxonomic groups was variable within and between sites, but no discernible trends were evident across sampling method and treatment. One notable exception are the isopods, which were considerably more abundant in pitfall traps within areas of *M. rubra* infestation. No significant differences were detected for richness, diversity and abundance of arthropod groups using multivariate analyses ($F_{2,2} = 1.01$, Wilks' lambda-derived p -value = 0.49 for richness; $F_{2,2} = 2.49$, $p = 0.29$ for diversity; $F_{2,2} = 1.57$, $p = 0.39$ for abundance; Figure 4.2a-c). The greater relative abundance of arthropods per trap in pitfall samples from *M. rubra* infestation was entirely driven by greater isopod catch (Figure 4.2d and Figure 4.3). Though not statistically significant in a univariate analysis of isopod abundance in pitfall traps ($F_{1,3} = 72.14$, $p = 0.12$), this trend seems to suggest some association between isopods and *M. rubra*, especially as groups of

isopods are often found in close proximity with *M. rubra* when nesting under flat stones or under downed woody debris (unpublished observation). Whether this link is explained by overlapping microhabitat preference or by a more direct association is yet unknown. Interestingly, between 50-100% of the terrestrial isopods (depending on the source) are not endemic but rather were introduced from Europe sometime in the last few centuries (Jass and Klausmeier 2000), which could have implications concerning changes to native communities due to prior or concurrent invasions by a variety of taxa.

Homopteran survey results:

Family-level richness is higher on average across sampling methods where *M. rubra* occurs (Figure 4.4). Variance in the sweepnet samples is high and, coupled with a small sample size, the means do not differ statistically in a univariate ANOVA ($F_{1,2} = 0.42$, $p = 0.58$). Using site richness from branch and quadrat samples as dependent variables in a randomized block MANOVA, richness was significantly higher where *M. rubra* was present than in non-invaded sites ($F_{2,1} = 6110.29$, Wilks' lambda-derived p -value = 0.009). Sweepnet samples provided a measure of abundance and were analyzed separately for the mean number of individuals per sample of each homopteran family collected. Across all five families identified, each tended toward higher abundance in the presence of *M. rubra* (Figure 4.5). There was a significant block**M. rubra* presence/absence interaction term ($F_{8,102} = 2.98$; $p = 0.003$) in the original MANOVA model, suggesting a variable response to the presence of the invader across sites. No significant effects specific to the

presence or absence of *M. rubra* alone could be demonstrated statistically across sites. Hence, we chose to look at the trends at each site (Figure 4.6). Only at the Miller Greenhouse site was the increase in homopteran abundance with *M. rubra* shown to be statistically significant ($F_{4,15} = 10.51$, Wilks' $p = 0.0003$).

In both branch and quadrat samples, a greater proportion of samples contained homopterans in *M. rubra*-infested versus noninfested sites ($F_{2,1} = 6088.2$, Wilks' lambda-derived $p = 0.009$; Figure 4.7). The proportion of homopterans actively tended by ants was also greater in *M. rubra* sites ($30.0 \pm 5.3\%$ vs. $2.7 \pm 0.6\%$ and $100 \pm 15.5\%$ vs. $8.9 \pm 5.8\%$ for branch and quadrat samples respectively). *M. rubra* comprised 100% of the ant attendants within sites of infestation, whereas tending ants were divided nearly evenly among *Formica glacialis*, *Lasius alienus*, *Formica neogagates* and *Camponotus hursculeanus* in uninvaded sites. Sampling took place in the afternoon on relatively sunny days so direct comparison is possible, though the time of optimal tending could vary by ant species. Comparing the proportion of homopterans sampled that were actually tended by ants yielded only marginal significance ($F_{2,1} = 115.4$, $p = 0.066$), probably due to low power associated with limited sample size.

Small mammal survey results:

A total of 50 small mammals were caught in live traps over eight sites and two sampling dates, 20 in infested sites and 30 in non-infested sites. All were identified as white-footed deer mice (*Peromyscus maniculatus*). During nights when sampling took place, more mice were captured in sites without *M. rubra* (Figure 4.8). When

analyzed by site pair and sampling date, no statistical differences were found based on the presence or absence of *M. rubra* ($F_{1,3} = 0.53$, $p = 0.52$). Despite this lack of significance in our tests, the trends of reduced trap catch within sites of infestation were consistent enough to warrant further study.

DISCUSSION

Effects on resident ants:

Data from pitfall and litter samples clearly demonstrate that resident ant species have declined precipitously in habitats invaded by *M. rubra*. Of the two species whose workers were collected in infested sites (*Lasius subumbratus* and *Stenamma dieki*), both have small, cryptic colonies with foragers that remain largely beneath the litter or soil layer (Creighton 1950). No ants of the genus *Leptothorax* were collected in *M. rubra* areas, and only two were found in non-infested sites, though these ants are relatively common within sites of infestation (unpublished data). This could represent sampling bias, as foragers are tiny and likely travel relatively short distances from the nest. Their absence from litter extractions could signify that the area sampled was insufficient relative to colony density to adequately assess these ants' distribution. Several species of *Leptothorax* (*L. ambiguus*, *L. longispinosis*, *L. curvispinosis*, *L. muscorum* complex) were routinely collected in sugar-baited vials both in and outside of areas of infestation in Maine. In addition, possibly due to their small size and ability to remain "below the radar," *L. ambiguus* and *L. longispinosis*

Table 4.1 - Resident ant species catch by sampling method – Mt. Desert Island, ME - 2002 Data pooled across sites and date.

		<i>M. rubra</i>			
		present		absent	
		Pitfall	Funnel	Pitfall	Funnel
Hymenoptera - native ant					
Formicidae					
Formicinae					
	<i>Camponotus novaboracensis</i>	-	-	4	-
	<i>Camponotus pennsylvanica</i>	-	-	30	1
	<i>Formica aserva</i>	1	-	1	-
	<i>Formica fusca</i>	-	-	2	-
	<i>Formica glacialis</i>	-	-	13	-
	<i>Formica neogagates</i>	-	-	5	-
	<i>Formica</i> spp.	1	-	1	-
	<i>Formica subsericea</i>	-	-	3	-
	<i>Lasius alienus</i>	-	-	1	1
	<i>Lasius pallitarsis</i>	-	-	6	-
	<i>Lasius subumbratus</i>	-	1	-	-
Myrmicinae					
	<i>Aphaenogaster fulva</i>	-	-	1	-
	<i>Aphaenogaster rudis</i>	-	-	2	-
	<i>Leptothorax muscorum</i> cplx.	-	-	-	2
	<i>Myrmecina americana</i>	-	-	-	1
	<i>Myrmica</i> spp.	1	-	1	1
	<i>Myrmica detritinodis</i>	-	-	25	-
	<i>Myrmica fracticornis</i>	-	-	14	1
	<i>Stenamma diecki</i>	-	2	2	1
Ponerinae					
	<i>Amblyopone pallipes</i>	-	-	1	1
Hymenoptera - nonnative ant					
Formicidae					
Myrmicinae					
	<i>Myrmica rubra</i>	27083	252	27	1
	<i>Tetramorium caespitum</i>	-	-	1	-
<i>M. rubra</i> excluded					
	Richness	3	2	18	8
	Abundance	3	3	140	9
	Diversity index*	1.10	0.64	2.21	2.04

*Shannon-Weiner index of diversity

$$H' = -\sum_{i=1}^s p_i \ln p_i \quad (H')$$

Table 4.2 - Arthropod catch by sampling method – 2002 Data pooled across sites and date.

	<i>M. rubra</i> present			<i>M. rubra</i> absent		
	Pitfall	Funnel	Total	Pitfall	Funnel	Total
Insecta						
Blattaria	29	4	33	16	7	23
Coleoptera						
Anobiidae	-	1	1	-	-	-
Buprestidae	1	-	1	-	-	-
Cantharidae	-	1	1	-	2	2
Carabidae	4	-	4	9	1	10
Carabid larva	-	3	3	1	5	6
Cerambycidae	-	1	1	-	1	1
Chrysomelid larva	-	1	1	-	1	1
Coleopteran larvae	-	2	2	-	14	14
Curculionidae	34	12	46	22	12	34
Curculionid larvae	-	4	4	4	44	48
Elateridae	1	-	1	1	-	1
Lathridiidae	-	-	-	1	-	1
Mycetophagidae	-	-	-	-	1	1
Nitidulidae	13	-	13	1	3	4
Scarabidae larvae	-	1	1	3	-	3
Scolytidae	-	1	1	-	-	-
Staphylinidae	18	1	19	21	2	23
Staphylinid larvae	-	-	-	1	-	1
Coleoptera - other	1	1	2	-	-	-
Collembola	74	9	83	54	9	63
Diptera						
Chironomidae	11	3	14	43	4	47
Dipteran larvae	-	49	49	-	3	3
Muscoid flies	3	-	3	-	-	-
Simuliidae	1	-	1	2	-	2
Syrphid larvae	-	1	1	-	4	4
Tipulidae	-	1	1	-	1	1
Diptera - unknown	11	3	14	43	4	47
Hemiptera						
Lygaeidae	1	-	1	1	3	4
Miridae	2	1	3	-	7	7
Pentatomidae	-	-	-	-	1	1
Homoptera						
Aphidae	1	6	7	-	2	2
Cercopidae	-	-	-	2	-	2
Cicadellidae	12	-	12	12	2	14
Hymenoptera						
Ichneumonidae	-	-	-	1	-	1
Parasitica	33	-	33	7	-	7
Pompilidae	-	-	-	1	-	1
Vespidae	1	-	1	-	-	-
Formicidae	3	3	6	113	9	122
Lepidoptera						
Lepidoptera adult	1	-	1	1	-	1
Lepidoptera larva	-	-	-	1	1	2
Geometridae	-	-	-	1	3	4
Orthoptera - Rhaphidophoridae	-	-	-	2	-	2
Psocoptera - Psocidae	1	-	1	-	1	1
Siphonaptera	-	1	1	-	-	-
Symphyla	-	1	1	-	-	-
Thysanoptera	7	3	10	-	1	1
Chilopoda	2	25	27	9	54	63
Diplopoda	25	23	48	8	82	90
Isopoda	587	39	626	115	33	148
Arachnida						
Acari	1	6	7	15	62	77
Trombiculidae	0	12	12	18	0	18
Opiliones - Phalangidae	14	1	15	20	1	21
Pseudoscorpionida	-	-	-	-	1	1
Araneae						
Gnaphosidae	27	4	31	42	18	60
Araneidae	1	-	1	-	2	2
Linyphiidae	2	-	1	1	-	1
Richness	31	32	46	33	36	49
Abundance	922	224	1145	591	401	993
Diversity (H')	1.62	2.64	2.04	2.63	0.44	2.94

Figure 4.1 – Mean (a) richness, (b) diversity and (c) abundance of resident ants per site in pitfall and litter samples in the presence and absence of *M. rubra* – Mt. Desert Island, Maine – 2002 Error bars are one standard error of the mean.

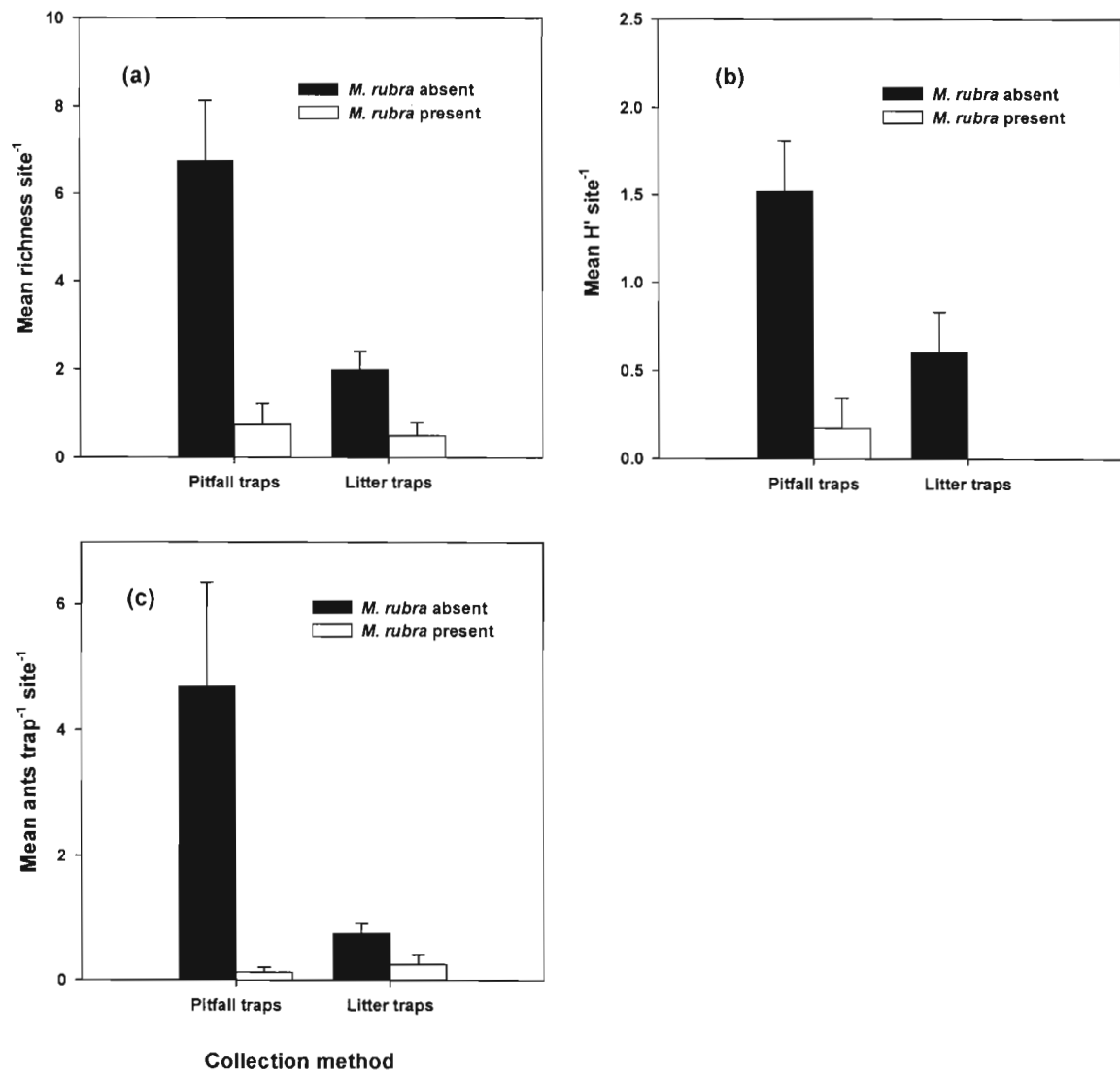


Figure 4.2 – Mean (a) richness, (b) diversity, (c) abundance and (d) abundance with isopods removed of resident arthropod groups in the presence and absence of *M. rubra*, by site and sampling method – Mt. Desert Island, Maine – 2002
 Error bars represent one standard of the mean

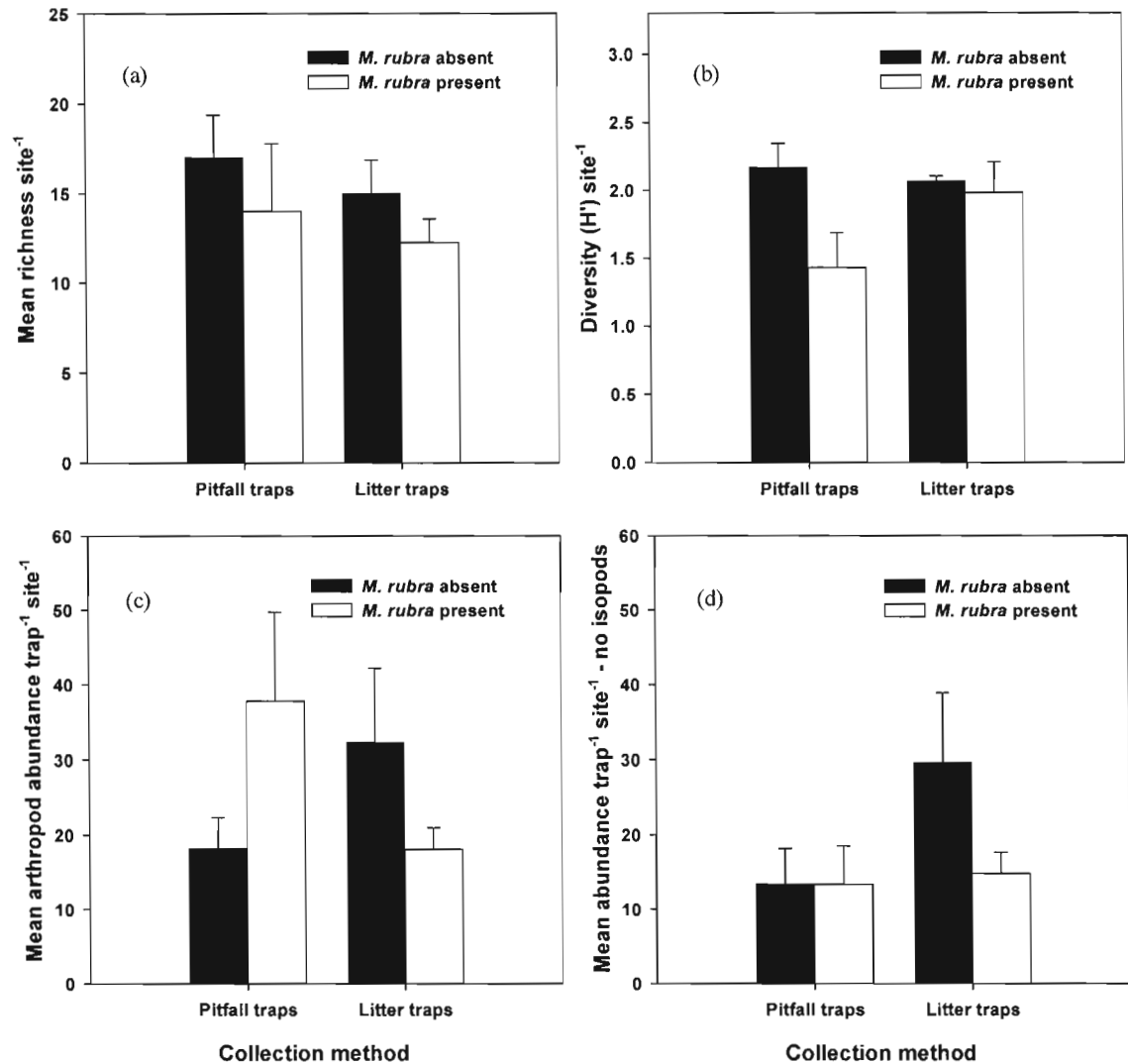


Figure 4.3 - Mean isopod abundance per sample in four sites in Mt. Desert Island, Maine, by presence/absence of *M. rubra* and sampling method – 2002
Error bars are one standard error of the mean.

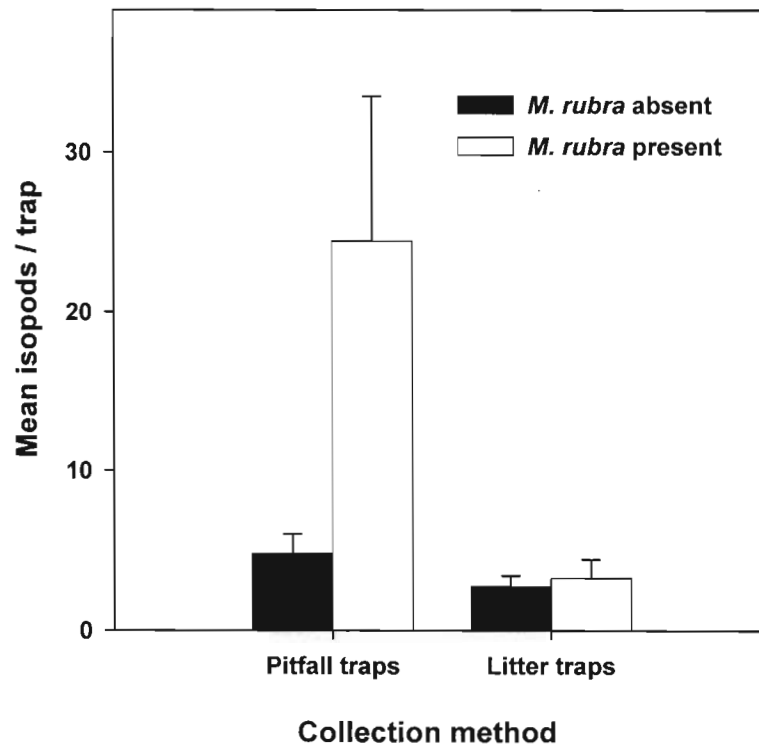


Figure 4.4 - Homopteran family richness at three site pairs in Mt. Desert Island, Maine, by presence/absence of *M. rubra* across three sampling methods – 2003
Error bars are one standard error of the mean.

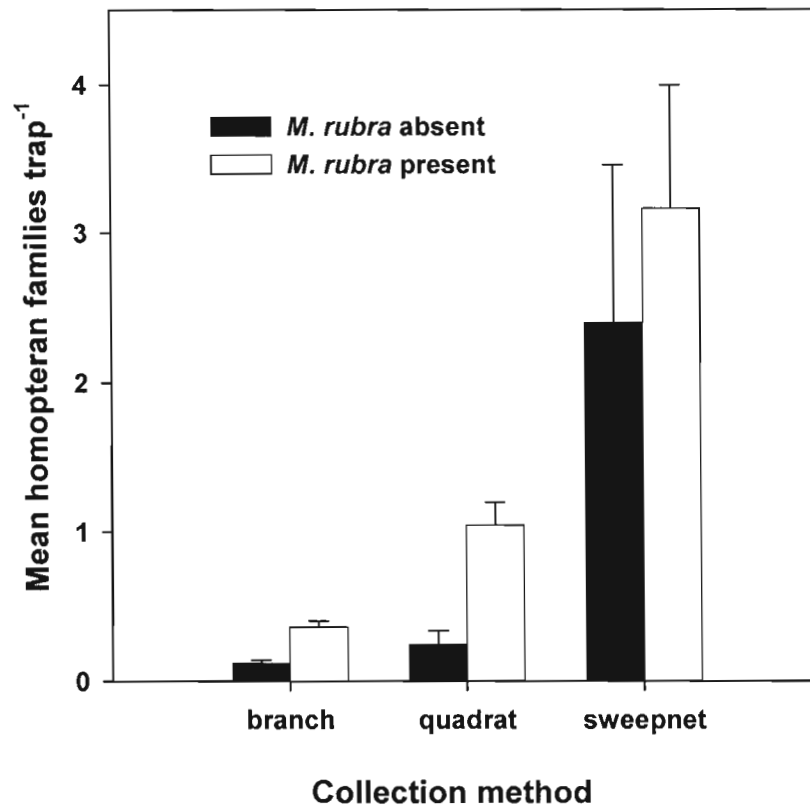


Figure 4.5 – Mean abundance of homopterans collected in sweepnet samples across three sites in Mt. Desert Island, Maine by the presence and absence of *M. rubra* - 2003. Data presented from the five most abundant homopteran families only. Error bars are standard errors of the mean.

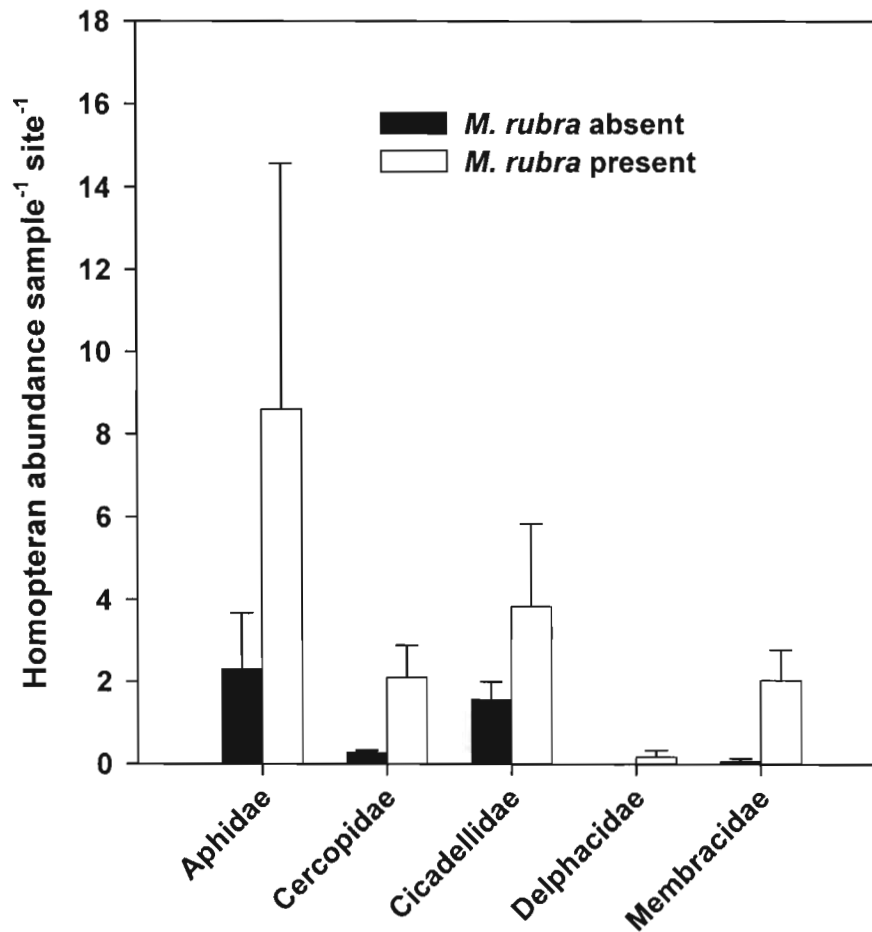


Figure 4.6 - Mean abundance by site of homopterans collected in sweepnet samples, by presence and absence of *M. rubra* (a) Bear Brook Pond, (b) Miller Greenhouse and (c) the Visitors' Center, Acadia National Park / Mt. Desert Island, Maine – 2003 Data presented from the five most abundant homopteran families only. Error bars are standard errors of the mean.

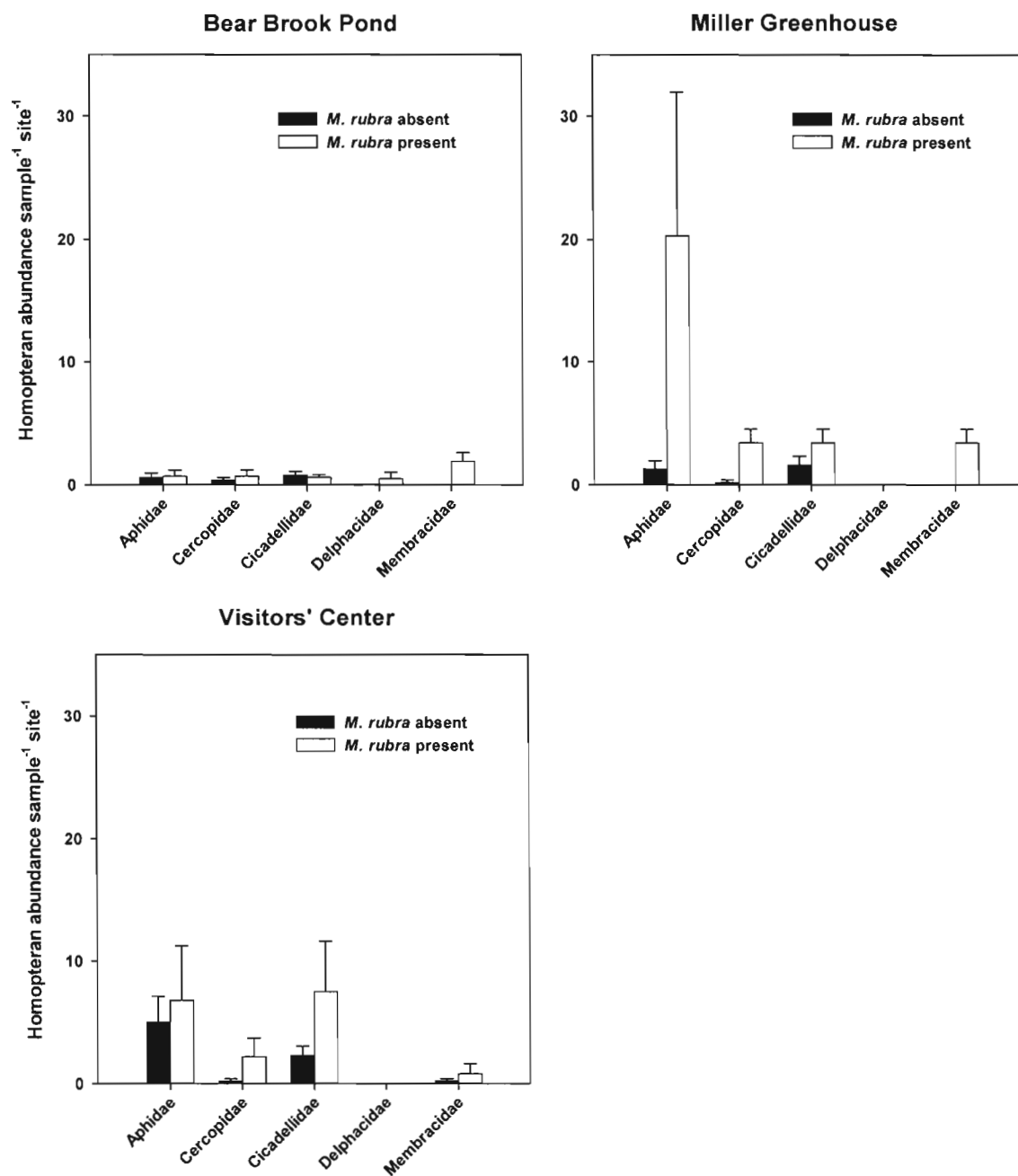


Figure 4.7 – Proportion of branch and quadrat samples containing homopterans by presence and absence of *M. rubra*, and the proportion of homopterans actively tended by ants. Full bars depict proportion of samples containing homopterans (pooled across family); black portions of bars depict proportion of homopterans sampled that were actively tended by ants. All homopterans tended by *M. rubra* in invaded sites. In non-*M. rubra* sites, active tending by 4 species was observed: *F. glaciales*, *L. aleinus*, *F. neogagates*, and *C. hurculeanus*. Error bars are one standard of the mean.

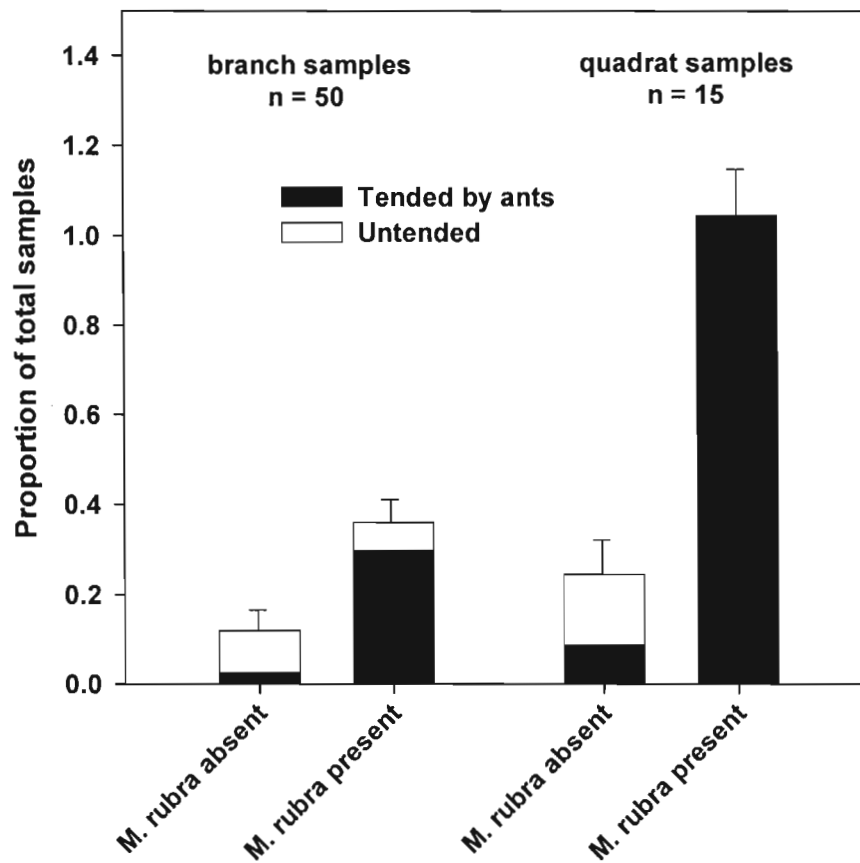
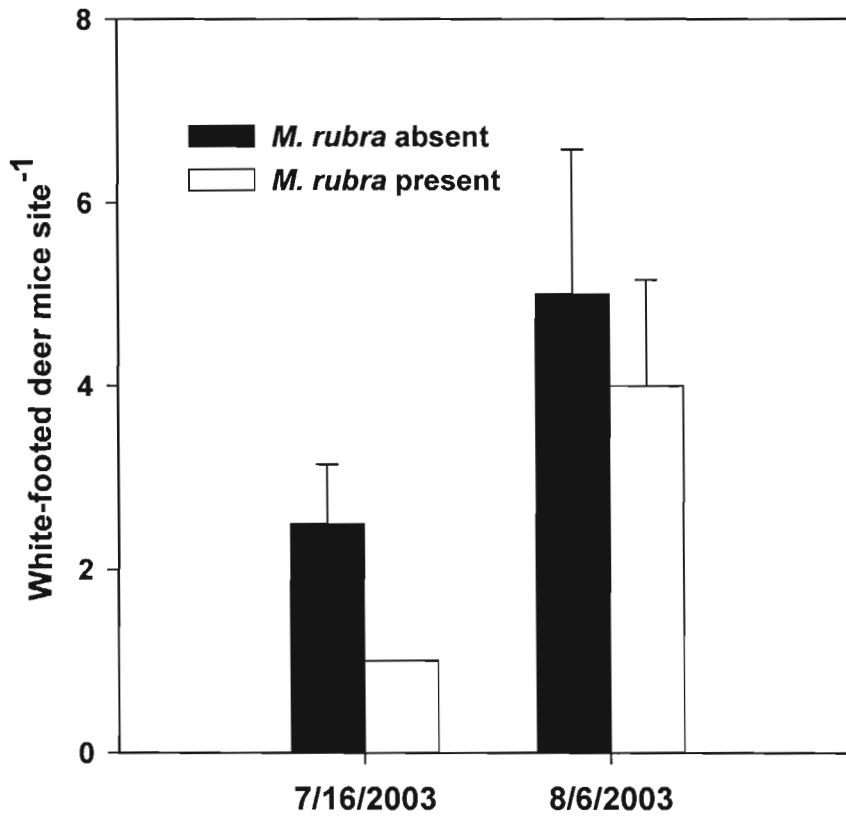


Figure 4.8 – Mean number of white-footed deer mice captured in Sherman[®] live traps on 16 July and 6 August 2003 in four sites on Mt. Desert Island, Maine
Error bars are one standard error of the mean.



have also been shown to be relatively immune to direct interference competition by *M. rubra* foragers, based on aggression assays at a food resource (Chapter 3). All other ant species that appeared in non-invaded sites were entirely absent from *M. rubra* areas.

While native ant richness, diversity and abundance were strongly suppressed in the presence of *M. rubra*, more than 27,000 individual ants (up to a 100-fold increase over resident-only areas depending on trap method) were collected in invaded sites, due almost entirely (>99.9%) to a superabundance of *M. rubra* nests and workers. Such vast numerical dominance coupled with a high worker and nest density would seem to make competition with native colonies inevitable, and *M. rubra* foragers have an advantage with respect to the discovery and exploitation of food resources, as well as in direct contest competition with native foragers (Chapter 3). Thus, as has been found in a number of ant-invaded ecosystems, competition is the most likely driver of native ant displacement (Porter and Savignano 1990, Holway 1998, Suarez et al. 1998), though other forces contributing to the creation or maintenance of the observed changes to the community (e.g. prior habitat disturbance or invasions by other organisms) cannot be entirely ruled out. The role of intraguild predation in structuring the community or displacing native ants is yet unknown, though *M. rubra* workers have occasionally been observed carrying smaller, soft-bodied *Lasius pallitarsis* workers into the nest, as well as fiercely attacking other species' male and female alates (Chapter 3, and personal observation).

The above trends conform closely to findings by a number of researchers for invasive ant species worldwide (Suarez et al. 1998, Porter and Savignano 1990, Human and Gordon 1997, Holway 1998, Cole et al. 1992, Ward 1987, Wojcik 1994). Several studies have also documented differential impacts on the native ant fauna. Wojcik et al. (2001) found that while richness and diversity generally declined in the wake of invasion by the polygyne form of *Solenopsis invicta*, some species were significantly positively correlated with the ranked percent occurrence of Southern imported fire ants, including two introduced forms (*Paratrechina longicornis* and *Tetramorium simillimum*) and one native (*Odontomachus brunneus*). Ant species in the current study were not collected in sufficient abundance in invaded sites to assess patterns of coexistence, though as stated, the few ants collected were among the most cryptic in the landscape. Other than *M. rubra*, the only introduced species we sampled was a single individual of *Tetramorium caespitum* in an uninvaded area pitfall trap. During aggression assays, however, *T. caespitum* was shown to recruit heavily in the context of colony defense and on a small experimental scale, was capable of sustaining a roughly even battle with *M. rubra* workers (Chapter 3). However, *T. caespitum* was relatively rare in our study sites and appeared to overlap only marginally in microhabitat preference. Whether or not individual species will emerge as long-term survivors in invaded areas, or whether there will be a more general recovery of the ant community over time remains uncertain, though our data do suggest species-specific impacts on community structure and composition.

Effects on resident arthropods:

Studies of invasive ant impacts on resident non-ant arthropod communities have produced far less consistent results than assessments of the native ant fauna alone. Some have cited a significant decrease in the diversity and richness of arthropod groups, along with an overall reduction in abundance (Human and Gordon 1997, Porter and Savignano 1990, Morrison 2002, Bolger et al. 2000, Erikson 1971). Our results, however, are similar to Holway's (1998) findings with the Argentine ant in Northern California, in showing no significant change in richness or diversity of taxonomic groups or overall non-ant arthropod abundance. While distribution varied by site, there was no relationship between community indices and *M. rubra* density as measured by pitfall samples. Likewise, the selective inclusion or removal of particular taxonomic groups did little to change the results of the analysis. The only consistent pattern we were able to detect was an increase in isopod abundance in invaded sites. Interestingly, significant positive and negative responses by isopods have been measured in a number of studies on invasive ant effects (Cole et al. 1992, Human and Gordon 1999, Porter and Savignano 1990), while other studies show no measurable effect (Holway 1998, Bolger et al. 2000). Two complications arise in the interpretation of this finding in our study system. First, some isopod species are known to be myrmecophilous associates of a variety of ant species, including members of the genus *Platyarthrus*, shown to be a nest site associate of a number of ant species, including *M. rubra* (Brooks 1942, Hölldobler and Wilson 1990). Second, various sources have estimated that in North America, up to 100% of terrestrial isopods (outside of cave-dwelling forms) are themselves introduced

species (Garthwaite et al. 1995, Jass and Klausmeier 2000). This raises the question of whether or not there are some subtle attributes in the habitat or community that make it susceptible to arthropod invasion, or whether prior arthropod invasions can facilitate future ones (Simberloff and Von Holle 1999). Many isopods are scavengers and may be able to survive and thrive on larval exuviae within *M. rubra* nests or by consuming dead workers or other colony waste. In any case, where *M. rubra* nests under stones or downed woody debris, it is common to see isopods living in close proximity, often within the same nest (unpublished data). No evidence of natural predation by ants on isopods has been observed, though the possibility cannot be discounted.

Unlike some studies of *L. humile* that found a reduction of Collembola (springtails) in the presence of invading ants, potentially due to their apparent sensitivity to habitat disturbance (Cole et al. 1992, Human and Gordon 1997, Bolger et al. 2000), we found roughly equivalent numbers in samples from infested versus non-infested areas. In fact, there was a slight (though nonsignificant) increase in collembolan abundance where *M. rubra* was present, and they seem to co-occur with some frequency within nest sites (personal observation). We have no evidence from Maine as to whether collembolans are taken as prey in invaded habitats, or whether any association exists between the two groups. It has recently been shown, however, that under controlled field conditions, *M. rubra* foragers will hunt and capture individual springtails, and the proportion taken as prey (from an experimental arena) is related to the natural springtail density in the habitat where the colony is located

(Reznikova and Panteleeva 2001). This suggests the possibility that *M. rubra* may be capable of switching to springtails as a mass prey.

Effects on homopterans:

Despite the widespread utilization of homopteran honeydew as a carbohydrate resource by invasive ants (Davidson 1998, Passera 1994) and the frequently cited assertion that such invaders may indirectly harm vegetation by augmenting homopteran populations and increasing sap herbivory, few studies have directly addressed actual changes in the prevalence, abundance or community composition of homopteran associates in an ant-invaded habitat (Helms and Vinson 2003). *L. humile* and *S. invicta* have both been shown to reduce aphid predator effectiveness (Vinson and Scarborough 1991, El-Zaidy and Kennedy 1956) as well as to interfere with the attack by parasitoids (Flanders 1958, Vinson and Scarborough 1991), suggesting the potential for ant associates to foster greater homopteran populations. Helms and Vinson (2003) estimated that approximately 50% of a *S. invicta* colony's daily energy requirements may derive from various species of Homoptera, and that these ants are widely associated with an invasive mealybug whose colonies comprise nearly 70% of insects tended by this ant. In our study system, a foliar-directed effort at such sampling revealed that diversity, richness and abundance of homopteran families and individuals are indeed enhanced by the presence of *M. rubra*. No such trends were evident in our litter or pitfall sampling (despite the fact that some homopterans were captured), suggesting that a directed effort is necessary to adequately assess this population. Abundance from sweepnet samples showed a

more or less even distribution among cercropids, cidadellids, and membracids, though there were slightly more aphids per sample on average. Though not identified to the species level, each family appeared to comprise a variety of species, suggesting that *M. rubra* is a generalist associate of homopteran families and species (Brian and Brian 1951, Brian and Abbott 1977). It is also interesting to note that the proportion of Homoptera that were actively tended by ants at the time of sampling was significantly higher in infested versus non-infested areas. In a study of New York Ironweed (*Vernonia noveboracensis*), aphid and membracid colonies were shown to survive longer and produce more adults when tended by either *Tapinoma* or *Myrmica* ants. Further, survivorship was significantly enhanced in aphid colonies when tended specifically by *Myrmica* (Bristow 1984). Similar findings by Morales (2000) suggest enhanced survivorship of membracids when tended by *Formic* and other ant species. The details of differential benefits to homopterans of attendance by *M. rubra* have yet to be investigated, though the large proportion of untended colonies (72.4% in non-invaded versus 8.9% in invaded areas across sites and sampling method) suggests a dearth of native ant attendants, even under natural (non-invaded) conditions.

Small mammal survey:

M. rubra foragers have a painful sting and employ it liberally. While adult rodents may be quick (or resistant) enough to tolerate this nuisance, the costs of being stung and of moving in response to or avoidance of ant attacks may outweigh the benefits of a rich food source in the form of seeds or insects. Vertebrates unable

to rapidly escape may even be vulnerable to ant predation. During an unrelated small mammal foraging study in 2001, several chipmunks were found dead inside live traps, presumably killed by the *M. rubra* workers that swarmed their remains, suggesting that when flight from an area is precluded, ants are capable of killing small mammals (Bruce Connery, personal communication). Ants may prove considerably more menacing to less mobile, hairless young. Studies of *S. invicta* have shown direct mortality and decreases in growth rate for small mammals, as well as a negative correlation between the two with respect to nest densities (Allen et al. 2004, Killion et al. 1995). There is also the potential for competition between small mammals and ants (at least for insects), though our studies did not reveal a reduction in insect prey.

White-footed deer mice were captured in slightly greater abundance in the absence of *M. rubra* in our study, though the differences were not statistically significant. However, the observations suggest that more intensive surveys may reveal discernible trends. Though certainly more difficult to carry out, studies of nest/burrow densities in infested and uninfested areas may reveal stronger trends. In terms of foraging, studies that include a behavioral component in their models have proved more fruitful. Holtcamp et al. (1997) found that deer mice foraged selectively in “rich” patches where *S. invicta* were present, whereas they showed no preference in its absence. Mice also made three times as many foraging trips in ant patches, reflecting their tendency to flee areas of high ant density to consume seeds elsewhere. This study shows the potential for behavioral change that could be

associated with greater energetic costs and increased predation risk (Holtcamp et al. 1997, Allen et al. 2004).

Limitations of the current research:

The studies reported herein represent a preliminary assessment of various communities deemed particularly susceptible to change in the face of an ongoing *M. rubra* infestation. The design used attempts to control for habitat variation by employing this invader's highly patchy distribution. There are a number of factors that limit our ability to interpret the results we gathered, however. First of all, without accurate records concerning the timing of *M. rubra*'s establishment and advance on Mt. Desert Island, Maine, we can as yet only speculate as to the approximate age of each of the sites currently being lumped together under the term "infested." Morrison (2002) showed that communities can recover to some extent, or at least rebound from the initial widespread displacement of native ant fauna created by the advancing front of *S. invicta*, when he replicated experiments performed by Porter and Savignano (1990). Together, the researchers had the advantage of being able to track the invasion from its establishment, suggesting that after 11 years, measurable recovery was apparent. While if recovery in ecological time is a phenomenon common to invasive ants, the time to recovery would doubtless vary considerably geographically and would depend greatly on the characteristics of the original community as well as the invader.

CONCLUSION

Areas infested with colonies of *Myrmica rubra* appear distinct from a human standpoint, if only because they support a high density of stinging ants. Prior research on the population or behavioral responses of organisms potentially impacted by invasive ant species has shown a variety of trends, some of which are mirrored in the current study. *M. rubra* clearly displaces native ant species and there is evidence of a restructuring of the native ant community in favor of more cryptic species. The trend toward an enhanced homopteran community that is tended by more ants was also evident in our sampling and merits further study. While drastic changes in the ground-dwelling arthropod community were not detected (outside of a possible increase in isopod abundance), finer-scale or more detailed analyses may yet reveal differences between invaded and non-invaded community structure and dynamics. Finally, small mammal foraging, though reduced in the presence of *M. rubra*, showed no significant differences when compared with non-infested areas. Whether or not these and other patterns will persist, subside or increase in coming years as the invasion ages and advances is a question worthy of continued research, both in service of potential conservation efforts and the theoretical advancement in the field of invasion biology.

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APPENDIX A

Patterns of artificial nest site colonization and colony movement by the invasive European fire ant (*Myrmica rubra*) in Acadia National Park

METHODS

In order to assess seasonal patterns of colonization, colony movement and local spread in the invasive ant *M. rubra*, artificial nesting substrates were set out in three areas of infestation in Acadia National Park (Sand Beach House, Visitors' Center, and Old Farm Road) during the first week of June, 2002. These substrates were monitored every two weeks during seasonal ant activity through 2004. One similar site (Sieur du Mont) without *M. rubra* was selected for comparison with the native ant community. Ten patio stones (five 20 X 40 X 2.6 cm and five 30 X 30 X 2.6 cm) were paired with 40 X 40 X 1.5 cm plywood boards and placed randomly in each site, encompassing a variety of microhabitat conditions (soil type and moisture, average insolation, surrounding vegetation, etc.). Boards and slates were placed as flush with the soil surface as possible, and boards were weighted with a large stone. Biweekly monitoring included briefly lifting the stone or board to check for the presence/absence of a nest. Queens, males and gynes were counted when present, and the number of workers, larvae and pupae were estimated to the nearest fifty. Several workers were collected and identified in the laboratory when positive species identification in the field was not possible.

Figure A.1 – Artificial nest site colonization, 2002 and 2003 Stones and boards sampled for nest presence/absence in three sites of *M. rubra* infestation from 7 June through 25 October 2002, and from 27 April through 25 October 2003. Standard errors represent one standard error of the mean.

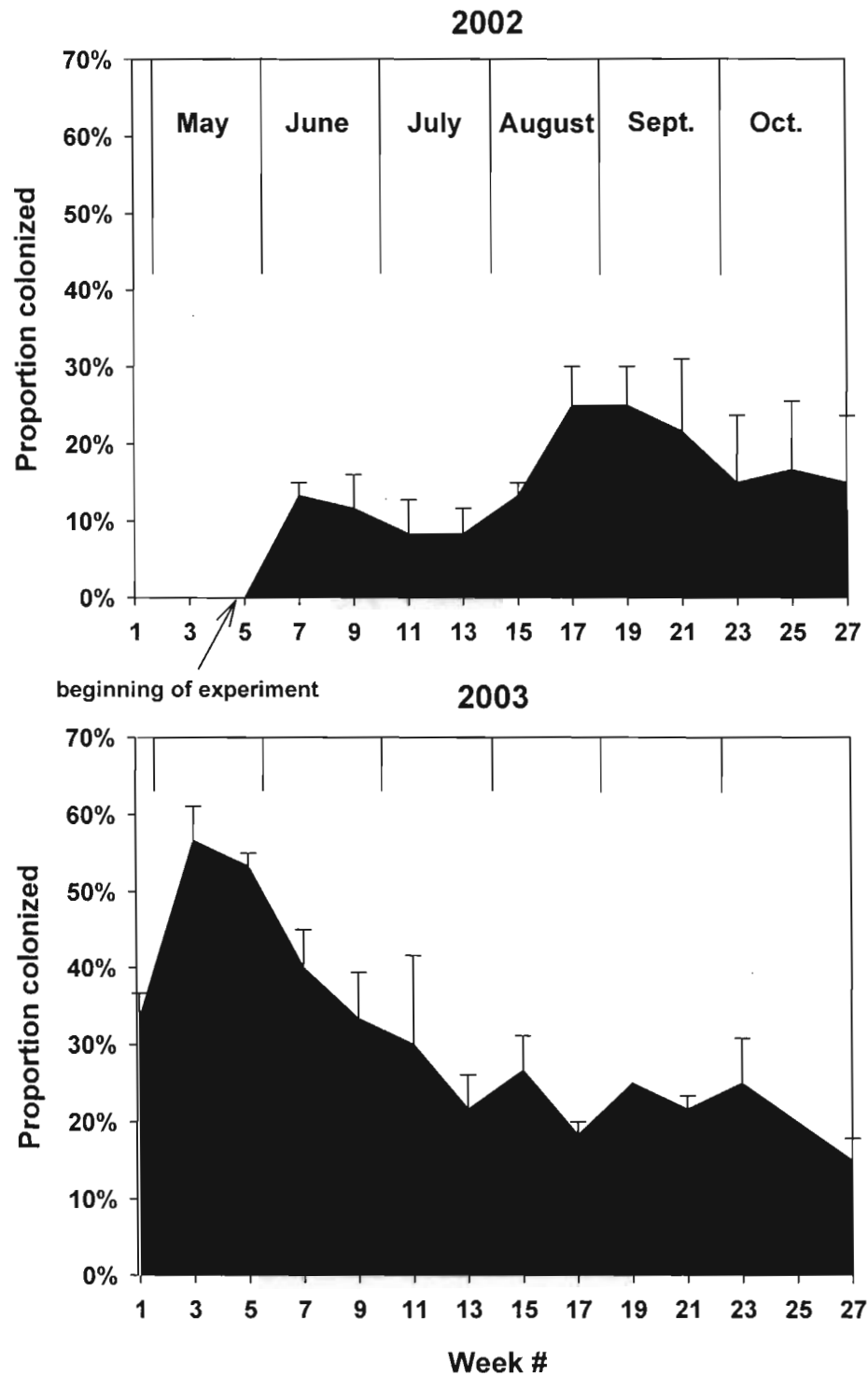


Figure A.2 – Frequency distribution of the number of times artificial nesting substrates were occupied by *M. rubra* colonies – 2002 and 2003. *M. rubra* colonies moved often, and substrates were often recolonized within the same season. “Times occupied” refers to the number of uninterrupted periods of occupation by an *M. rubra* colonization in a single season. Error bars are one standard error of the mean.

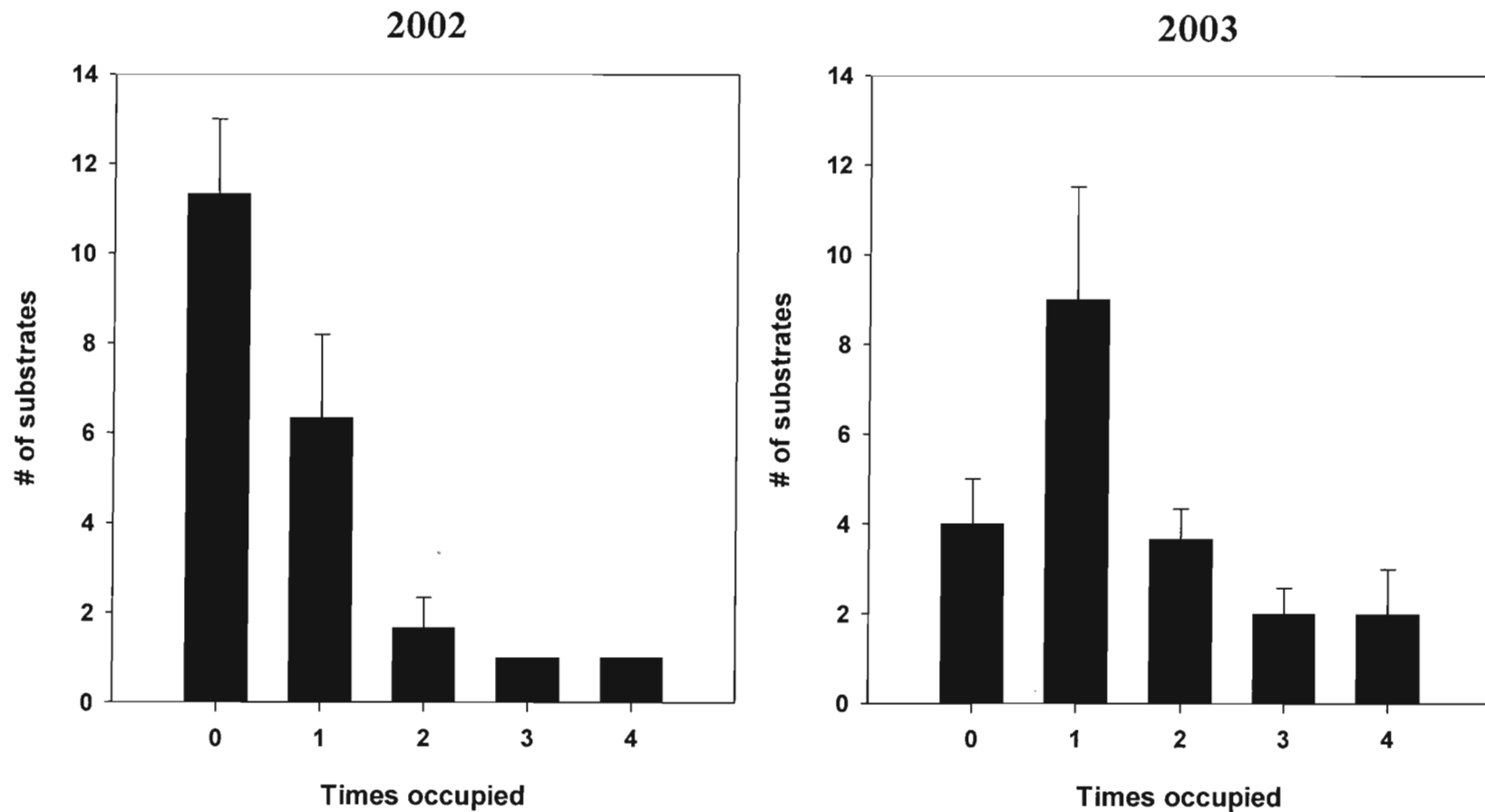


Figure A.3 Artificial nest site vacancies and new colonizations by week – 2002 Week 1 = June 7, Week 21 = 25 October 2003. Error bars are one standard error of the mean.

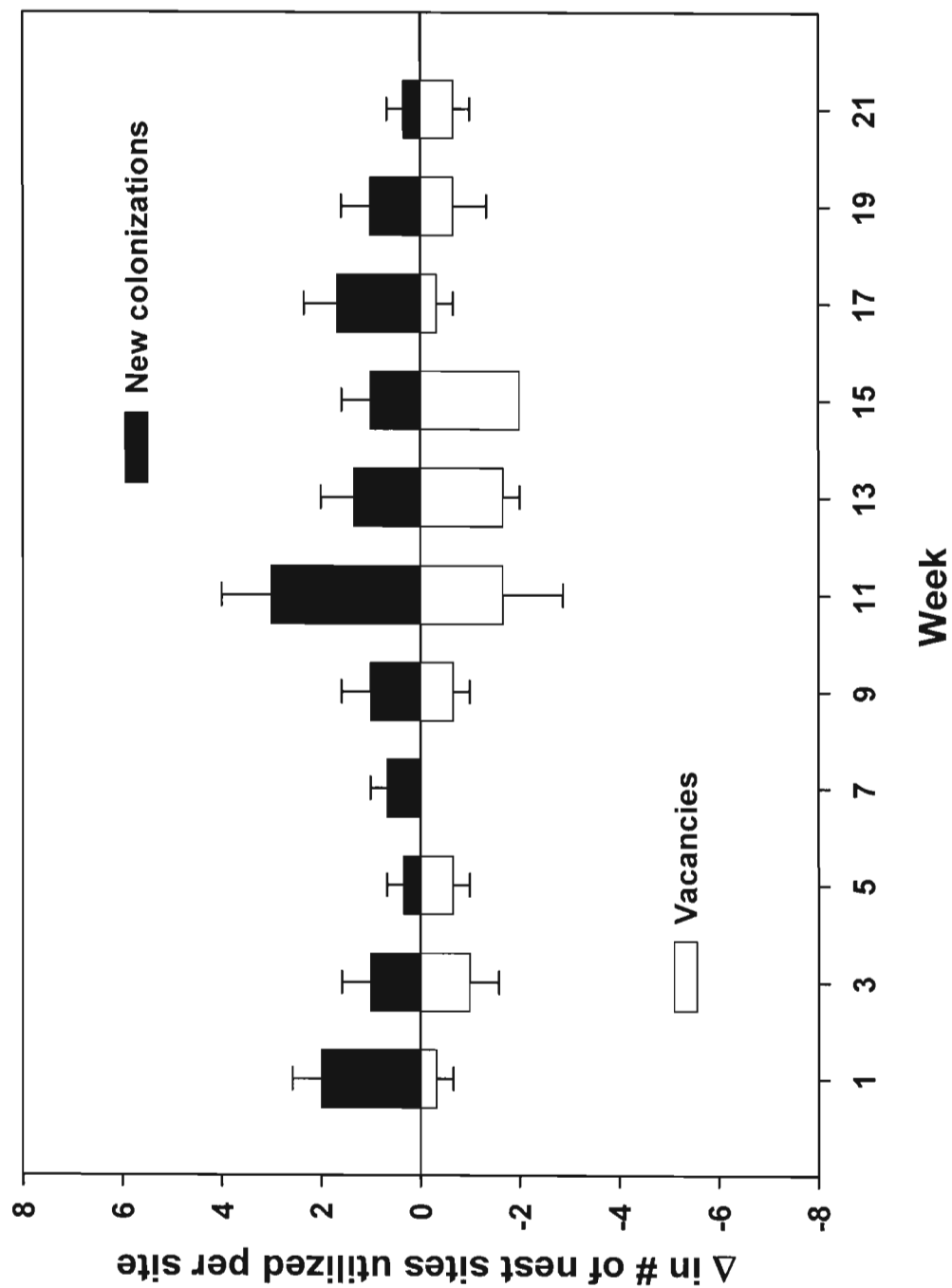
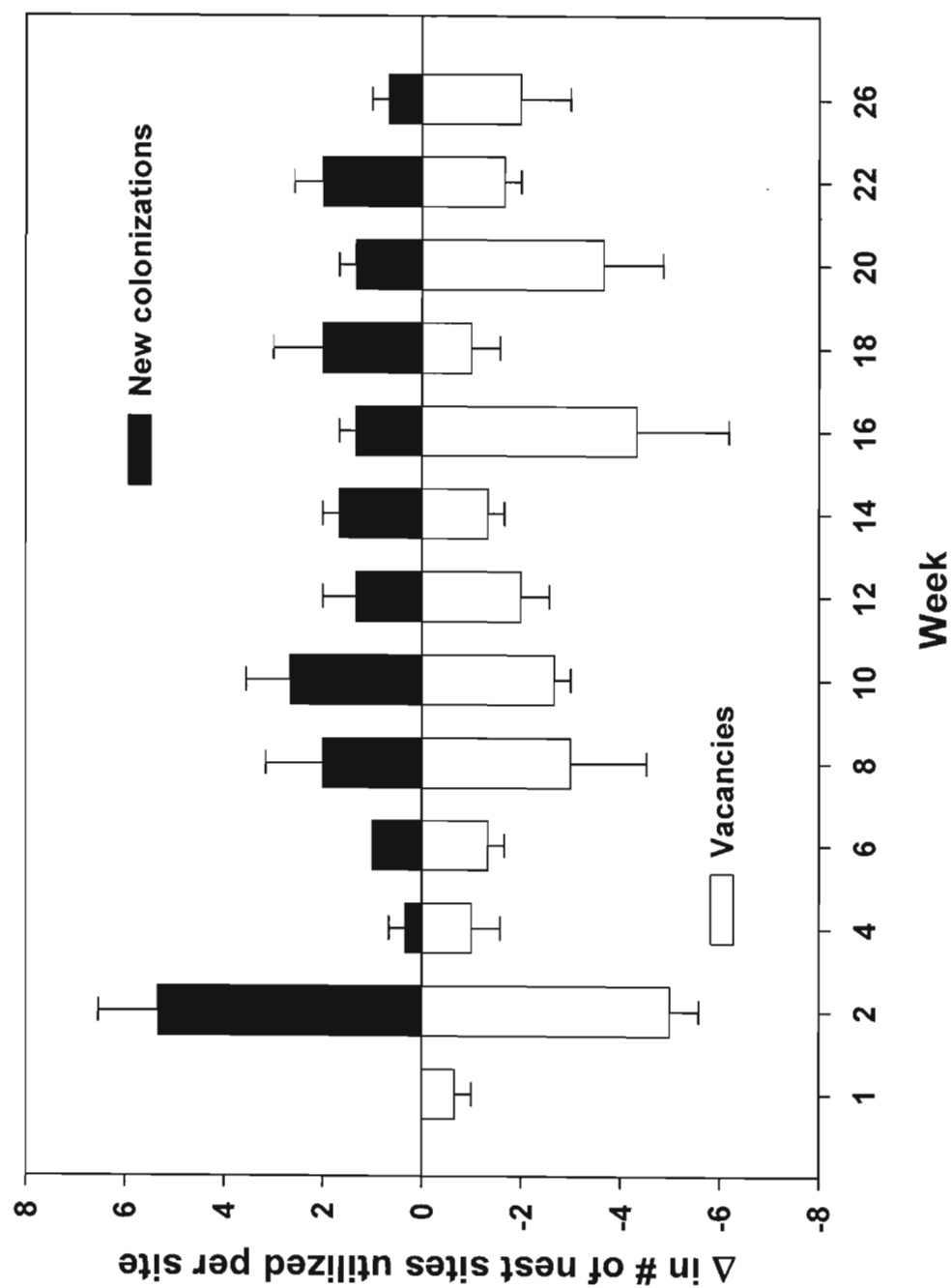


Figure A.4 Artificial nest site vacancies and new colonizations by week – 2003 Week 1 = 26 April, Week 26 = 25 October 2003. Error bars are one standard error of the mean.



APPENDIX B

Mapping the boundaries of a local infestation / estimates of site expansion – 2002 to 2003

METHODS

The boundaries of local *M. rubra* infestations in Maine are often well defined, and overlap with the native ant community is minimal. To assess the level of this overlap and to map the full boundaries of a local patch, extensive trapping within a single site in Acadia National Park (Bear Brook Pond) over six days was performed. Several different baits inside of 25 cc polypropylene vials including 50% (v/v) sugar syrup, tuna fish, tuna fish with grape jelly, and Pecan Sandies™ were employed to attract the greatest possible diversity of foraging ants, and sampling times were varied throughout the day from dawn until dusk. Figure B.1 shows a schematic of the boundaries of the infestation as determined by this sampling. Painted stakes were set out to physically mark the approximate line corresponding to the outermost edge of *M. rubra* recruitment. In addition, an exhaustive survey of nest sites within a 2 X 15 m swath of the forest floor along the southern edge of the Bear Brook Pond infestation revealed very low overlap with the native ant community (Figure B.2). Five additional 2 X 15 m plots were situated so as to encompass the boundary area between *M. rubra* and the native ant community and were sampled by placing sugar-baited vials at 1m intervals on both 20 and 28 August 2002, and then sampling for all ants after two hours. Native ants were collected and identified to genus. On 19

and 23 August 2003, all six blocks were sampled again (using the same protocol), extending the transects where necessary. The relative change in position of the last trap containing ≥ 1 *M. rubra* forager over the two years was then calculated. Over the six transects, there was a mean increase of 2.1 ± 1.1 meters by *M. rubra*, and though there was some variation across transects, 5 of the 6 reflected a gain of territory. Such a slight change over the course of a year is difficult to interpret given annual variability in site quality and daily changes in foraging force and the direction of foraging. Further sampling over multiple sites and seasons is needed in order to better estimate local spread.

Figure B.1 - Map of a single *M. rubra* infestation – Bear Brook Pond, Acadia National Park - 2002-03 Blocks represent areas of repeated sampling to test for expansion or contraction of the local infestation or patch

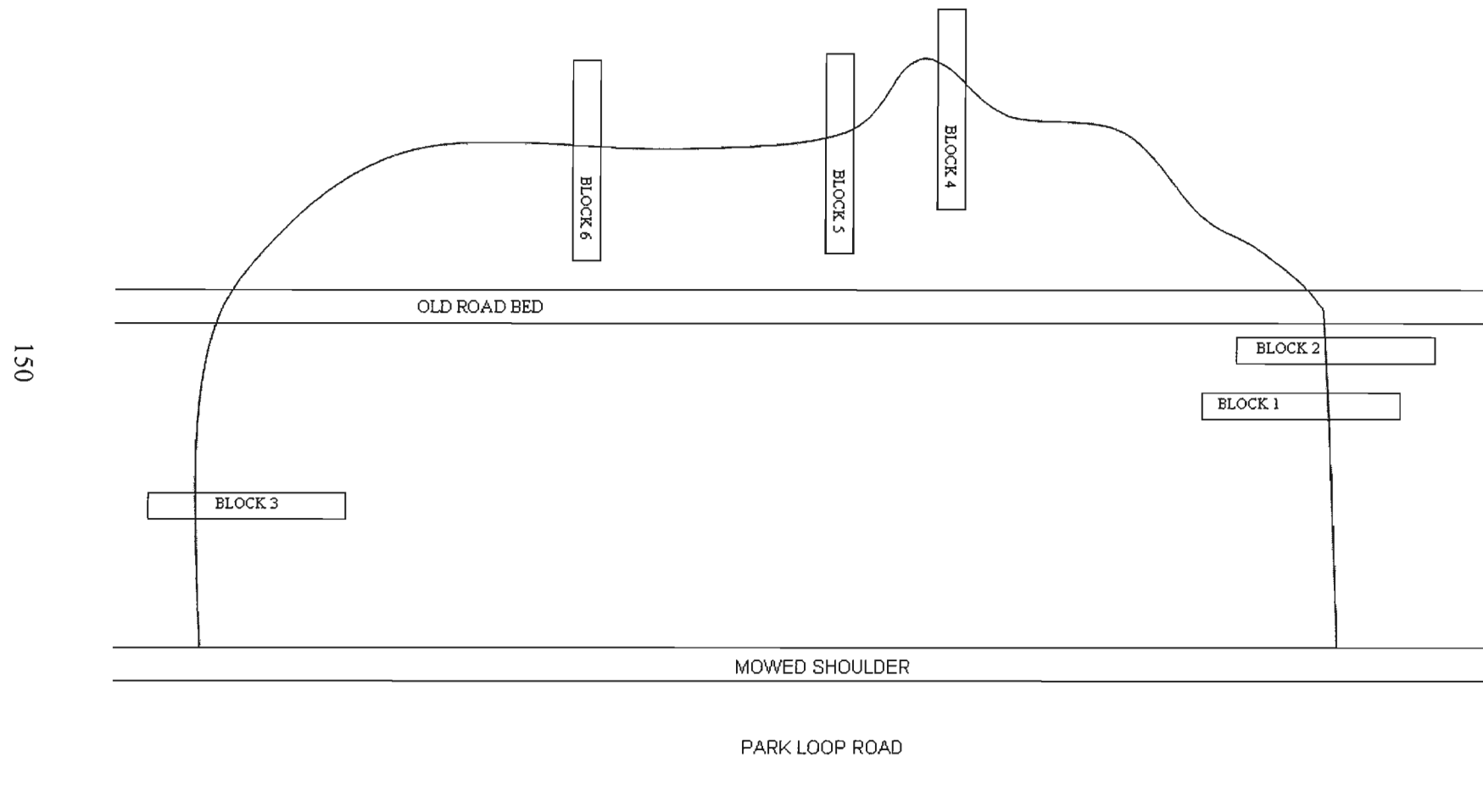
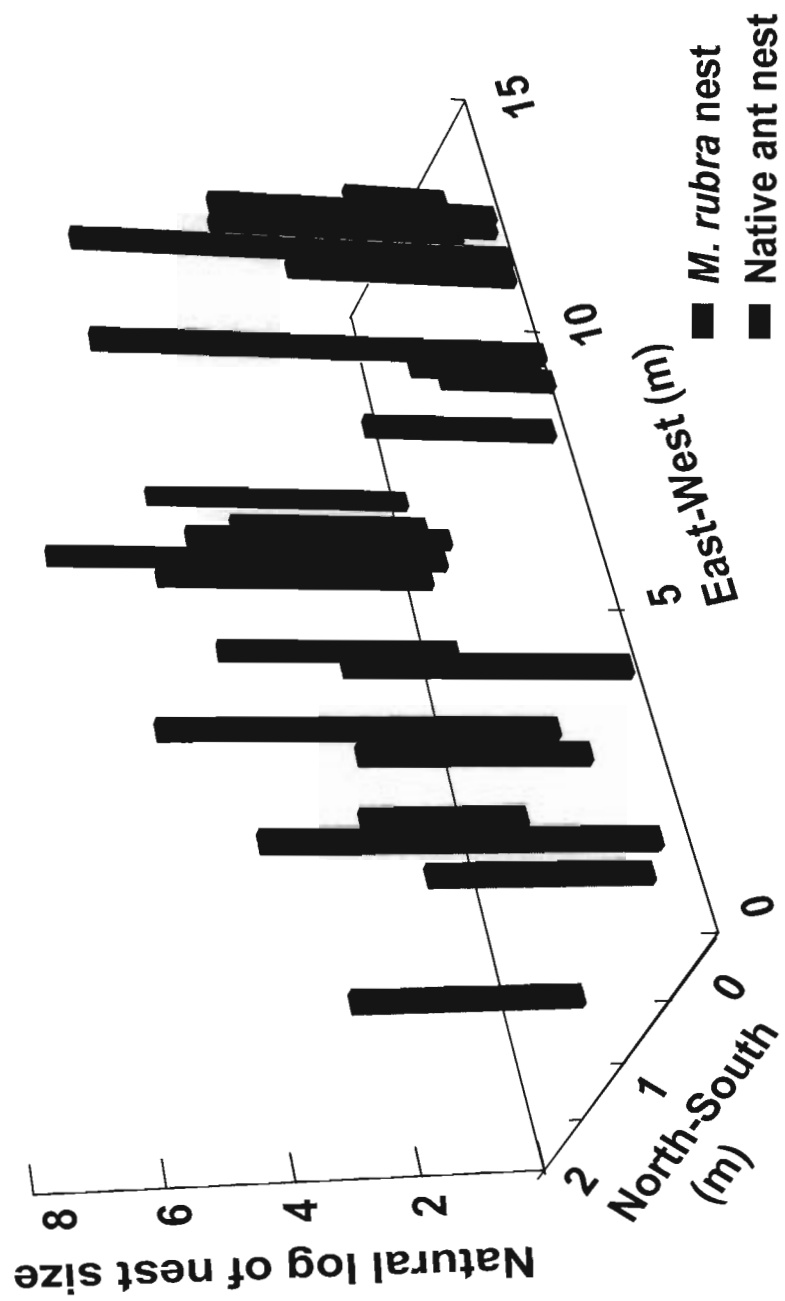


Figure B.2– Map of all nest sites within a 2 X 15 m plot – Bear Brook Pond (Block 1) – 2002



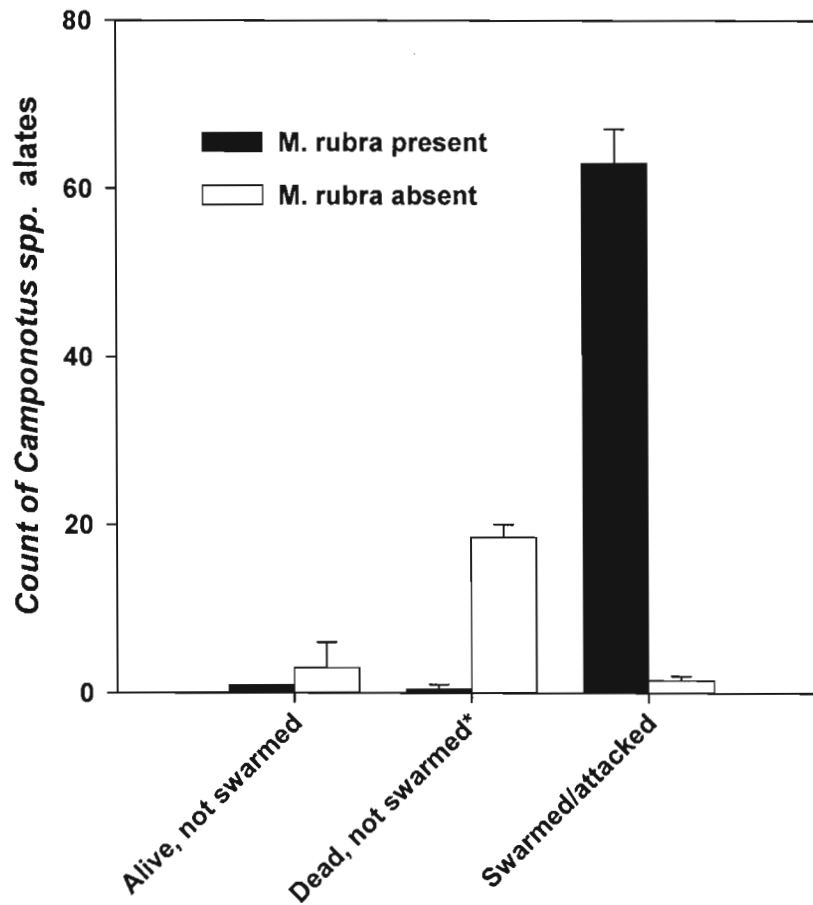
APPENDIX C

Potential impact of *M. rubra* on nest foundation and dispersal of a common native ant

METHODS

At 7:30 pm on 22 June 2002, I happened upon the tail end of a mating flight of the large carpenter ant, *Camponotus noveboracensis*. Prior sampling had shown that on the south side of the busy roadside where many of the queens were alighting (Rt. 233 in Acadia National Park), *M. rubra* was at high density, while on the other side of the street, they were virtually absent. To capture relative ant aggression towards the potential foundress queens, I ran a paired 200-meter transect on the side of the road and exhaustively counted all of the *C. novaboracensis* individuals that were either traveling on the ground unmolested or were attacked and swarmed by ants (by natives on north side transects, *M. rubra* the south). A proportion of the dead foundress queens may have been hit by passing traffic, but *M. rubra* was also seen actively preying on otherwise healthy individuals, attacking them in large numbers. Though the mating flight was tapering off and many queens had already found a place to hide, Figure B.1 shows the potential relative impact of *M. rubra* on such a localized event relative to predation by native ants.

Figure C.1 – Attack frequency by *M. rubra* and native ants on gynes of *Camponotus* spp. during its mating and dispersal flight "Swarmed" refers to the condition of direct attack or feeding by 10 to more than 200 *M. rubra* foragers



APPENDIX D

Distribution and abundance of *M. rubra* in Acadia National Park, 2002

METHODS

During the summer of 2002, extensive sampling was performed in 29 sites in Acadia National Park. Sites were selected in advance on a map with the intent of varying the habitat type to be sampled, within the range of what is present on Mt. Desert Island. Each site was sampled with twenty 25 cc polypropylene vials, baited with a 2 X 2 cm square of 3-ply sterile gauze dipped in a 50% (v/v) sugar solution. Sampling was performed at three sites between the hours of 3 pm and 5 pm roughly every two weeks from 21 May 2002 to 13 September 2002. Traps were deployed by laying them out randomly in various microhabitats, taking care to set the vials flush with the soil or vegetation surface. After two hours, all *M. rubra* foragers were counted and released and native foragers were collected for later identification. The overall habitat of the site was noted and temperature and humidity data logged. For each trap, the three nearest, dominant understory and overstory plants were also noted and identified in the field to the level of genus or family.

The level of the *M. rubra* infestation was determined by the number of traps containing *M. rubra* (0 traps = No *M. rubra*; 1-5 traps = low density; 6-20 traps = high density).

Figure D.1 – Mean abundance of native and *M. rubra* foragers by level of infestation in 29 locations in Acadia National Park, Maine – 2002 Standard errors are one standard error of the mean.

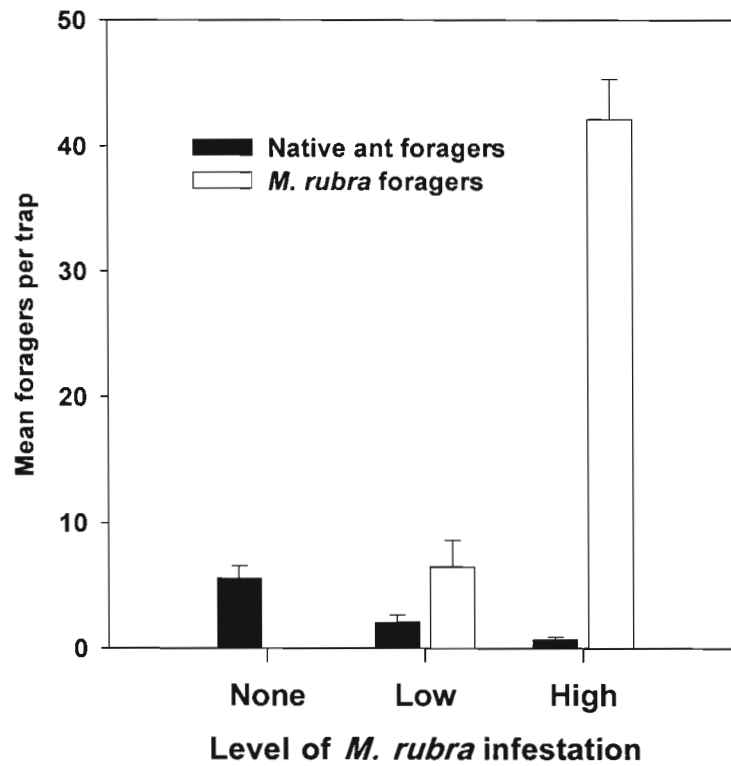
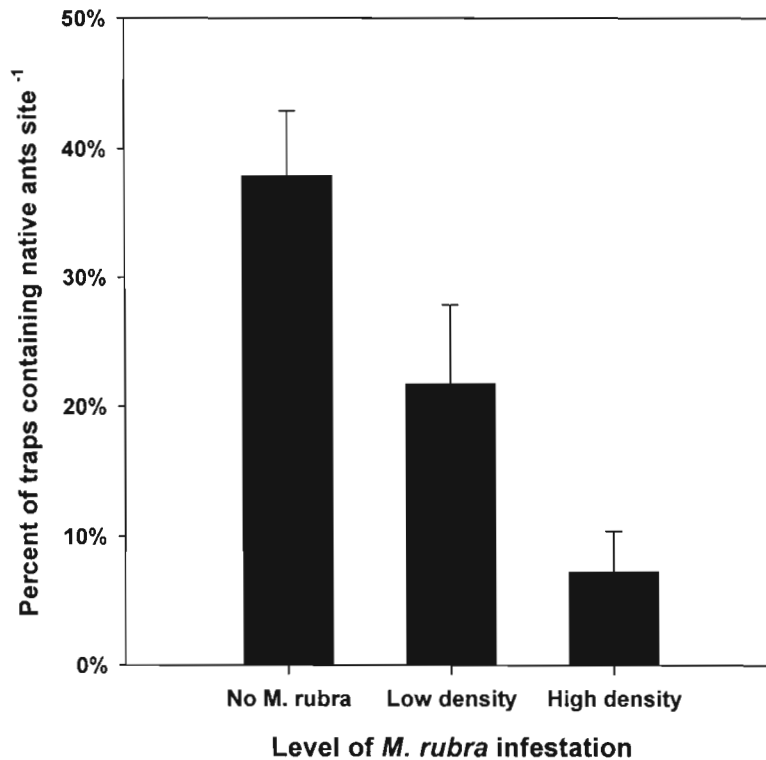


Figure D.2 - Percent of sugar traps containing native ants by level of *M. rubra* infestation Twenty-nine sites were sampled. Sites where *M. rubra* foragers were found in <5 (of 20) traps were considered low density, those where *M. rubra* was contained in 5 or more traps were considered as high density sites. Error bars are one standard error of the mean.



BIOGRAPHY OF THE AUTHOR

Jeffrey Garnas was born on April 15, 1974 and lived most of his early life in the township of West Milford, in northern New Jersey. He attended Northwestern University from 1992-1994, and graduated from the University of Colorado in 1997 with a B.A. in Psychology. Before and after graduation, Jeff traveled extensively in North and South America, Europe, and eastern Africa (Kenya). He has worked for various nonprofit organizations and as a tech support analyst/database programmer for a California law firm. Jeff entered the University of Maine Master's program in May of 2002 and will receive a degree in Ecology and Environmental Sciences from The University of Maine in December 2004.