

Distribution of an Invasive Ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine

ELEANOR GRODEN, FRANCIS A. DRUMMOND, JEFFREY GARNAS,¹ AND ANDRÉ FRANCEOUR²

Department of Biological Sciences, University of Maine, Orono, ME 04469

J. Econ. Entomol. 98(6): 1774–1784 (2005)

ABSTRACT Introduced populations of the north temperate ant species, *Myrmica rubra* (L.), have become pestiferous in various locations in the northeastern United States, particularly in coastal communities in Maine. Native populations of this ant are widely distributed throughout northern Europe and western Asia; however, nest densities in its native range do not usually reach the high levels observed for many introduced populations. This aggressive ant readily stings, and because of its high densities, homeowners continually encounter nests at a frequency that interferes with use of their properties. Surveys were conducted in Maine from 2001 through 2004 to determine the statewide extent of current infestations. Nests in established populations in coastal Maine were sampled from April through September to assess seasonal changes in the density and composition of colonies. Similarities and differences between introduced populations of *M. rubra* in Maine and published reports of this species in Europe are discussed. Museum records of this species in North America were also researched and are presented.

KEY WORDS *Myrmica rubra*, invasive species, Formicidae, distribution

EXOTIC SPECIES CAN HAVE substantial impacts upon the ecology of their introduced ranges. There are many dramatic documented cases involving plants, animals, fungi, and microbes (Elton 1958, Simberloff 1981, Lodge 1993, Holway et al. 2002b). The introduction of exotic species has been reported to be second only to habitat destruction in its contribution to declines in native species abundance (Wilson 1992). It is estimated that up to 46% of the population declines of plants and animals on the endangered species list can be attributed, at least in part, to exotic species (OTA 1993, Wilcove et al. 1998).

Social insects have been among the most successful animal invaders (Holway et al. 2002b). *Apis mellifera scutellata* Lepeletier; Formosan termite, *Coptotermes formosanus* (Shiraki); *Paravespula germanica* (L.); and several ant species have become established over broad geographic areas reaching high population densities. The more problematic ant species include *Solenopsis invicta* Buren and the Argentine ant, *Linepithema humile* (Mayr), both natives to Central and South America and both introduced into the United States, South Africa, Europe, and Australia; and *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, a native to Asia Minor that is currently invading southern and central Europe (Holway et al. 2002b). These

introduced ants have had detrimental impacts on native biodiversity in their introduced range through direct competition with and predation on native species (Erickson 1971, Ward 1987, Porter and Savignano 1990; Cole et al. 1992; Human and Gordon 1997, Holway et al. 1998, Bolger et al. 2000, Morrison 2000, Suarez et al. 2000) and indirectly by disrupting ecological processes such as ant-plant mutualisms (Bond and Slingsby 1984). A number of less studied species of ants also have become successful invaders (Holway et al. 2002b), and documenting the progression of the invasions and characteristics of the species that lead to their success is important for managing their impacts. The ant *Myrmica rubra* (L.) is exhibiting characteristics of an invasive ant species in parts of the northeast United States and eastern Canada (Garnas 2005). Although populations are still fragmented, documentation of the current state of the invasion will provide a baseline from which to assess further spread.

M. rubra is a Palearctic north temperate ant species with a native range that extends from Ireland and Great Britain, through northern Europe to western Siberia (Czechowski et al. 2000). Populations can be found from as far north as the Arctic Circle and south to the Black Sea (Agosti and Collingwood 1987, Elmes et al. 1999). An occurrence of *M. rubra* also has been reported from Japan (Onoyama 1989), but this report is thought to be a misidentification (Czechowski et al. 2000). The first report of *M. rubra* in the United States, published by Wheeler (1908) in the early part of the 20th century, described an established population

¹ Current address: Department of Biology, Dartmouth College, Hanover, NH 03755.

² University of Quebec at Chicoutimi, Chicoutimi, Quebec, Canada G7H 2B1.

at the Arnold Arboretum in Forest Hills, MA. Subsequent catalogues of Formicidae in North America (Weber 1947, Creighton 1950) have listed *M. rubra* as an introduced species in the northeastern United States. However, the geographic distribution of introduced populations in North America has not been previously reported.

There has been some confusion in the literature regarding the species name of *M. rubra*. This has resulted in an unclear picture of its geographic distribution. The species was first described as *Formica rubra* Linnaeus in 1758, although Santschi (1931) suggests that Linnaeus was actually describing *M. ruginodis* Nylander. *M. rubra* has subsequently acquired a list of synonyms: *M. laevinodis* Nylander, *M. laevinodis* variety *bruesi* Weber, *M. longiscapus* Curtis, *M. rubra laevinodis* Nylander, and *M. rubra r. champlaini* Forel (Brian and Brian 1949, Bolton 1995). The examination of the museum types of *champlaini* by Francoeur reveals a straight synonymy with *M. brevispinosa* Wheeler. In addition, it is still debated whether the occurrence of a microgyne form associated with *M. rubra* is a current or evolving social parasite species or an alternative gyne form of *M. rubra* (Czechowski et al. 2000).

M. rubra colonies are both polygynous and polydomous (Elmes 1973). Elmes (1974a) reports an average of 15 queens per nest in England, with up to 670 queens observed in a single nest (G. W. Elmes, personal communication). Queen number per nest is highly dynamic within and between seasons and seems to regulate the population dynamics of *M. rubra* (Brian et al. 1981, Elmes and Keller 1993). Within its native range, nuptial flights generally occur in August or September (Boomsma and Leusink. 1981, Woyciechowski 1990), at which time claustral queens disperse to establish new colonies, or newly mated gynes are recruited into existing nests (Elmes 1980). Colonies also are known to reproduce and spread by budding (Elmes 1980), where a group of queen(s), workers, and brood leave an existing nest and colonize a new nesting habitat. Budding can occur throughout the active foraging season. *M. rubra* is an omnivorous species, acquiring protein from a variety of prey (primarily invertebrate), and carbohydrates from homopterans and plant exudates (McGlynn 1994, Reznikova and Panteleeva 2001, Cogni et al. 2003). Although *M. rubra* is frequently observed tending homopterans, its distribution has not been associated with a particular species, as has been suggested for invasive populations of *S. invicta* (Helms and Vinson 2003).

M. rubra is a stinging species and has been suggested to be the most aggressive of the *Myrmica* species in Europe (G. W. Elmes, personal communication). State entomologists in Maine first received reports of problems with a stinging red ant in the Town Hill area on Mt. Desert Island (Hancock County) some time between the late 1960s and mid 1970s (R. G. Dearborn, personal communication). A problem with stinging red ants was reported in Boothbay Harbor, Lincoln County, ME, in 1986 and the species was confirmed as *M. rubra*. Anecdotal reports of pestiferous populations

in Eastport, ME, and other Maine coastal communities had been received by state and University of Maine Cooperative Extension entomologists by the early 1990s. However from 1993 through 2003, the number of complaints increased dramatically, particularly on Mt. Desert Island and in the mid-coast area of the state (Camden–Rockport region). This study describes the current known distribution of *M. rubra* in Maine and reports on historic records and other documented occurrences of this species in the northeastern United States and Canada.

Materials and Methods

In 2001, locations of pestiferous stinging ant populations reported previously to Maine State and University of Maine Cooperative Extension entomologists were identified using the key from Creighton (1950). Identifications were verified by S. Cover (Museum of Comparative Zoology, Harvard University, Cambridge, MA). Each site was visited between 1 July and 28 August 2001. At each site, 20 baited traps were deployed along a linear transect across a variety of habitats throughout the site. Each trap consisted of an open 25-cc polyethylene vial laid on its side and baited with a 2 by 2-cm² piece of cotton gauze saturated with a 25% aqueous sucrose solution. Traps were left for 2 h, after which they were capped and returned to the laboratory for identification of ants that recruited to the inside of each vial. Determinations of whether individuals belonged to the species *M. rubra* were based upon the morphological characteristics described by Creighton (1950), Bolton and Collingwood (1975), and Seifert (1988).

During July and August 2002, ≈100 telephone contacts were made with town offices and selectmen, county extension agents, professional exterminators, public parks and recreation managers, and greenhouse, nursery, and landscaping business operators in 46 communities throughout all eight coastal counties within the state. In addition, articles about *M. rubra* that requested information on the location of infestations were published in both major daily newspapers in the state and a number of local weekly papers. Media coverage of this invasive ant problem also was carried on three statewide television news stations and two statewide radio stations. Reports of complaints of stinging ants fitting the size and color description of *M. rubra* were investigated with visits to the sites for sampling or via samples submitted to us by homeowners.

In 2003 sampling efforts were focused on determining the extent of the infestation in Acadia National Park and surrounding communities on Mt. Desert Island. Requests for information on infestations were published in the local newspaper in the spring and reports received were followed up with a visit to the site for sampling. Additional statewide infestations were confirmed via samples submitted by homeowners and site visits in 2003 and 2004.

The abundance of *M. rubra* nests within two infested sites in Acadia National Park on Mt. Desert Island were sampled monthly between July and August 2002. On three dates (in mid-June, July, and August 2002), 10 1-m² square sampling frames were placed randomly along two parallel transects in each of two sites of known *M. rubra* infestation. Transects were situated to encompass a range of microhabitat conditions within each site, minimizing biased sampling of a particular habitat. Sampling frames were staked to the ground to prevent movement and the area was searched exhaustively for ant nests, including under logs and stones, in downed woody debris, at the base of trees, among the roots of vegetation, in the soil and throughout the leaf litter. The nesting type or substrate was recorded along with apparent microhabitat conditions. An aggregation of workers in the presence of brood and/or sexuals (queens, gynes, or males) was considered to be a nest and, whereas a single colony may often span multiple nest sites (polydomy), each aggregation was counted separately if aggregations of workers and brood were separated by at least 20–25 cm. To determine caste composition over time, nests were excavated with a shovel, and all contents were placed in a 1 by 0.5-m² plastic food-grade container. All workers, larvae, pupae, queens, and males were either counted in the field or the container was sealed and transported back to the laboratory. In the laboratory, ants were either counted immediately or stored at 8°C for up to 1 mo before counting. An additional one to three nests were sampled monthly from May through September in 2002 and May through August in 2003 and 2004. In 2004, 10–12 nests were sampled at each of four field sites on Mt. Desert Island every 2 wk from April through September and assessed in the field for the presence of each *M. rubra* life stage. Nests were located and colonies were temporarily excavated to determine the presence/absence of eggs, larvae, pupae, males, and alate and dealated gynes.

An overwintering study was conducted during winter 2002–2003. Thirty nests were located and marked with flags in Acadia National Park on 7 September 2002. The nest sites were sampled again in early May 2003 (at the time when most of the ice was starting to thaw from the interior of the nest sites) to determine whether *M. rubra* colonies were still present and alive.

Specimens of *Myrmica* deposited in the following museum collections were examined for the presence of *M. rubra*: the Harvard Museum of Comparative Zoology in Cambridge, MA; the University of Massachusetts in Amherst, MA; the American Museum of Natural History in New York, NY; the U.S. National Museum (Smithsonian) in Washington, DC.; the Natural History Museum of Los Angeles County, Los Angeles, CA; the University of Maine in Orono, ME; the Proctor Insect Collection in Acadia National Park, Bar Harbor, ME; and Dr. André Francoeur's private collection (Chicoutimi, Quebec, Canada). The collection date and location of all *M. rubra* specimens were recorded.

Results and Discussion

M. rubra infestations were confirmed in nine towns or cities within Maine in 2001. These included communities within six of the eight coastal counties and one infestation in the inland county of Kennebec. The Kennebec County infestation is located ≈70 km from the coast; however, the property owners reported purchasing potted plant material from a nursery in an infested coastal area. In 2002, *M. rubra* infestations were confirmed in a community within the previously unreported, coastal Cumberland County and nine additional towns within counties known to have infestations of the ant. Infestations were confirmed in an additional four towns in these same counties in 2003, and an additional seven communities in 2004, bringing the total with *M. rubra* infestations to 29 Maine communities (Fig. 1). Currently, most infestations seem to be situated within 10 km of the coast, and although still patchily distributed, extend from the southern border of the state in Kittery to the northeastern coastal town of Eastport and the interior northeastern town of Calais, both of which border New Brunswick, Canada. New Brunswick also is infested. We found an infestation on Campobello Island, and a report exists of an infestation in the Bay of Fundy area (J. O. Schmidt, personal communication). At some sites, infestations occupy no more than a 50-m² patch, whereas at others, local populations can span adjacent properties along a continuous 5- to 6-km stretch of road, as in Eastport, ME. The largest and most dense infestations are concentrated in Eastport, Boothbay Harbor, and in the communities on Mt. Desert Island and coastal Knox County.

Intensive sampling on Mt. Desert Island has shown that there are multiple patches of infestation, including a large infested area that extends along Rte 3 from ≈2 km north of the Bar Harbor town center to ≈1.5 km south, including most of the town (Fig. 2). It is uncertain whether this infestation is contiguous with the infested areas along the northern coast of the island from Hadley Point to Salisbury Cove, and infested areas south to Sand Beach within Acadia National Park, or whether these areas represent discrete populations with limited gene flow. Of note is the fact that at several locations, infested patches seem to be limited by human or natural barriers, such as roads or streams or mature spruce–fir forest.

Within most of the *M. rubra* infested areas in Maine, populations have achieved unusually high densities compared with that observed within their native range (Brian 1956, Elmes 1974b, Elmes 1975, Boomsma and De Vries 1980). Nest densities within the sampled infested sites in Acadia National Park reach an average of 1.24 nests/m² in July (Fig. 3), with localized densities within each 1-m² sampled area ranging from 0 to 4 nests/m². In comparison, a preliminary survey of nest densities in its native range in the United Kingdom revealed a range of densities from 0.02 to 0.13 nests/m², $n = 12$ geographic populations (F.A.D. and E.G., unpublished data). A number of factors including habitat, latitude, and season may influence



Fig. 1. Current known towns in Maine with *M. rubra* infestations.

differences in invasive ant nest density (Porter et al. 1977). However, in 2003, G. W. Elmes (personal communication) stated that during his extensive collection of *M. rubra* throughout its native range in Europe, he did not observe nest densities comparable with those currently common in its introduced range in Maine. Garnas (2005) found that although *M. rubra* is polydomous, these high-density populations within infested sites do consist of discrete colonies and do not exhibit unicolonial population structure as described for *L. humile* in its invaded range (Tsutsui and Case 2001).

M. rubra uses a variety of microhabitats for nesting; most frequently nests were found under or within downed woody debris or in the leaf litter where they

place their brood in a curled leaf (Fig. 4). Within their native range, *M. rubra* has been reported to exploit different habitats and to use different nesting substrates in different parts of its range. They are found more commonly under stones along pasture edges in England (Elmes 1975, 1981), but primarily nest in rotten wood in wet, shady woodlands along the Black Sea (G. W. Elmes, personal communication), and moss tussocks in open pine forests in Russia (E.G. and F.A.D., unpublished data). In Maine, *M. rubra* seems to not only exploit multiple nesting microhabitats but also multiple ecosystems. *M. rubra* infestations were found in lawns and gardens, old field habitats, scrubshrub, wetlands, and deciduous forests. *M. rubra* has not been observed within the dense spruce-fir conif-

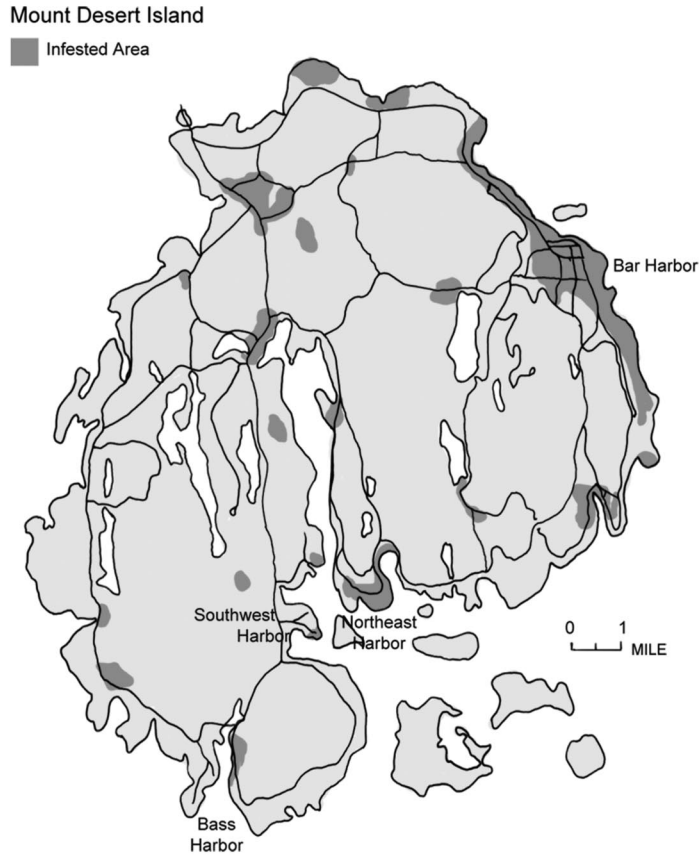


Fig. 2. Current known distribution of *M. rubra* infestations on Mt. Desert Island in Maine, 2004.

erous forest habitat along the Maine coast, although we have observed them nesting and foraging within the coastal zone at the edge of the spruce-fir forest down into the intertidal zone.

The size of *M. rubra* nests sampled in 2002–2004 varied considerably (Tables 1 and 2), but they do not differ in size (number of workers) from nests reported

throughout their native range (Brian 1952b, Elmes 1973, Elmes and Wardlaw 1981, Wardlaw and Elmes 1996, Seppa and Walin 1996). Worker densities ranged from 297 to >10,000 per nest, and queen number ranged from 0 to 194 per nest. The ratio of queens: workers within a nest also seems to be similar to *M. rubra* colonies in their native range (Elmes 1973). However, Elmes and Petal (1990) suggested that queen number in the genus *Myrmica* seems to be an adaptive trait, and so it would not be surprising if the

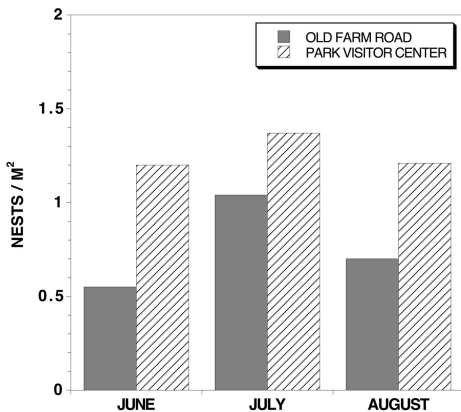


Fig. 3. Density of *M. rubra* nests sampled at two locations in Acadia National Park in Maine, 2002.

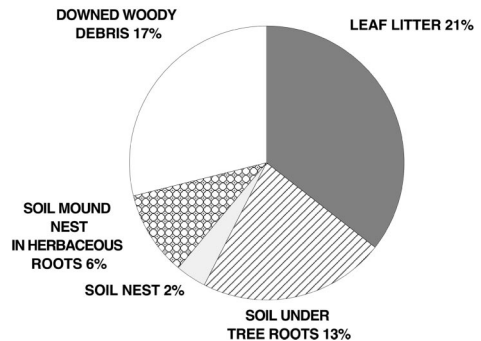


Fig. 4. Micro-habitats used by *M. rubra* for nesting in Acadia National Park in Maine, 2002.

Table 1. Age structure of *M. rubra* nests sampled 2002–2003

Date	Workers	Queens	Larvae	Pupae	Alate males	Alate queens	<i>n</i>
14 April	2,406 ± 1,170	2.0 ± 1.2	105 ± 40.8	0	0	0	3
23 May–1 June	1,268 ± 259	4.0 ± 1.0	93 ± 71	0	0	0	2
24–30 June	5,578 ± 2,176	27.0 ± 14.0	1,599 ± 614	0	0	0	4
18–20 July	1,268 ± 505	5.5 ± 2.2	521 ± 266	593 ± 289	1.3 ± 1.3	0	3
7–9 Aug.	4,484 ± 1,068	64.0 ± 33.5	1,322 ± 281	1,392 ± 232	41.4 ± 12.3	0	5
2 Sept.	693	16	98	0.0	44	0	1

Table 2. Age structure of *M. rubra* nests sampled, 2004

Date	Workers	Queens	Eggs	First instars	Second instars	Third instars	Pupae	Alate males	Alate queens
13 June	1,725 ± 356	17.5 ± 6.6	236 ± 56	9 ± 8	0	470 ± 222	0	0	0
23 June	3,006 ± 988	25.8 ± 7.7	445 ± 73	26.8 ± 11.9	23.0 ± 6.3	410 ± 180	2.8 ± 2.4	0	0
7 July	5,038 ± 2,702	22.8 ± 15.8	1,593 ± 494	131 ± 58	321 ± 183	2,669 ± 1,000	983 ± 809	0	0
21 July	2,217 ± 957	14.8 ± 1.8	926 ± 261	66.5 ± 16.6	206 ± 67	821 ± 315	889 ± 387	4.3 ± 1.7	0
4 Aug.	1,726 ± 338	18.3 ± 6.7	745 ± 272	100 ± 43	286 ± 140	973 ± 559	1,513 ± 301	51.8 ± 49.4	0
18 Aug.	2,714 ± 1,599	30.5 ± 13.7	682 ± 436	123 ± 93	171 ± 105	145 ± 56	298 ± 103	128 ± 102	0
5 Sept.	2,802 ± 853	16.5 ± 10.4	10.3 ± 9.6	4.5 ± 4.5	46.8 ± 25.4	275 ± 171	21.0 ± 5.7	20.0 ± 5.7	0

Data are mean ± SE of four nests collected on each date.

ratio of queens to workers varied geographically. *M. rubra* queens produce both rapid brood that matures during the summer season to produce workers during the same season, and diapause brood that overwinters and produces both workers, gynes, and males the following summer (Elmes and Wardlaw 1981, Elmes and Wardlaw 1983, Kipyatkov and Lopatina 1997a). Larvae were present in the nests in Maine at all times of the year (Fig. 5), and those present in nests in April and September were third instars, likely in diapause (Kipyatkov and Lopatina 1997b, Kipyatkov 2001). Eggs were not present in overwintered nests, but early season oviposition activity was first detected in 14% of sampled nests by 15 May 2004, and in 75% of nests by 29 May 2004 (Fig. 5). The number of eggs per nest was greatest in July (Table 2), but some eggs were observed through September. The increasing number of larvae in nests in late June likely represent the combined density of larger diapausing third instar larvae that will mature to gynes or males and new production of both rapid and diapausing early instar larvae from the current year's egg hatch (Elmes 1982, Elmes et al. 1999). Pupae were observed in nests from late July through mid-August in 2002 and 2003 and from early July through September in 2004. Alate males were observed in nests from mid-July through September in all years. However, no alate queens were observed in any nests from 2001 to 2003. During these 3 yr of study, we observed only two alate queens in the many infested areas in which we worked almost daily. An increase in average queen numbers in nests in early August suggests that gynes were produced. However, they may be present in the nest as virgin alates only briefly, mating in the nests soon after eclosion and not participating in nuptial flights and dispersal. It is possible that nuptial flights occur later in September when our sampling frequency was less regular. However, we also monitored five sticky traps weekly at one infested site on Mount Desert Island in August and September in 2001 and three water pan traps weekly

at each of three infested sites from May through September in 2002 and 2003. No alate males or queens were captured. We did observe some alate queens in 30% of the nests observed in the field on 18 August 2004 (Fig. 5). However, again, we saw no evidence of a nuptial flight by the end of August, at which time

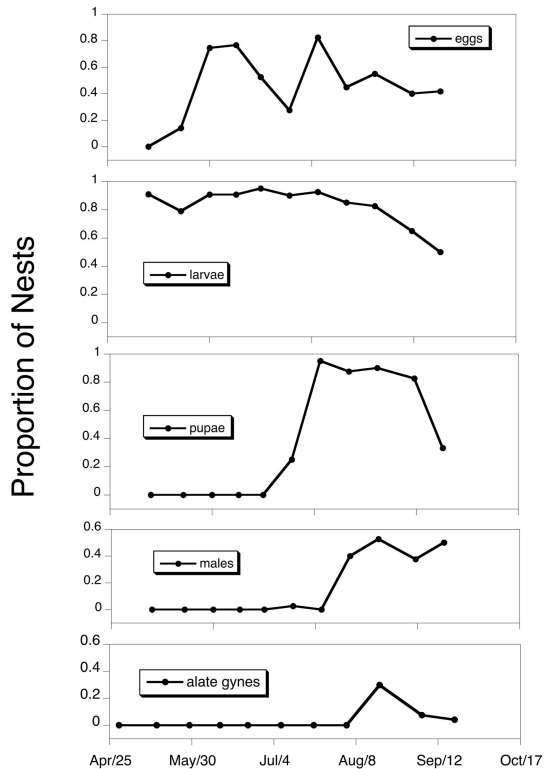


Fig. 5. Proportion of nests on Mt. Desert Island, ME in 2004, containing life stages of *M. rubra* (*n* = 24–44 nests per sample date).

alate gynes were present in <8% of nests. This evidence suggests that if nuptial flights do occur, they are likely infrequent and/or small relative to the size of the populations (Boomsma and Leusink 1981). A similar phenomenon has been observed for the Argentine ant in citrus groves in California. Markin (1970) suggests that nuptial flights for this invasive species are also rare and heavily male biased when they do occur, and new gynes more frequently mate and remain within their nest. The characteristics of reduced nuptial flights and a greater dependence on colony budding for dispersal may contribute to the successful attainment of locally high densities, which overwhelm native species and favors spread of the introduced species (Holldobler and Wilson 1990, Passera 1994, Hiebeler 2004). The pattern of local infestations observed for *M. rubra* also suggests that if nuptial flights occur, they are likely very rare. Numerous sites exist where dense infestations end abruptly at a natural or synthetic barrier, such as a stream or a road, although identical habitat is available on the opposite side of the barrier.

Records of *M. rubra* specimens in museums (Table 3) suggest that this species has been introduced on multiple occasions and that established populations have likely existed in Newport, RI, several locations in Massachusetts, coastal New Hampshire and Maine; Buffalo, New York; and Quebec and Ontario, Canada. We are aware that infestations still exist in the Tiff Nature Preserve in Buffalo and several locations in Massachusetts, including the Fresh Pond site in Cambridge and Arnold Arboretum in Forest Hills. In addition, we have received samples of *M. rubra* from Williamstown and Lennox in western Massachusetts and confirmed infestations in Wakefield and Gloucester in the eastern part of the state. We also have received reports of *M. rubra* populations in southern New Hampshire and southern Vermont (E. Adams, personal communication), in Ithaca and Geneva, NY, and in Toronto, Canada. Of note is that the infestations inland from the coast in Maine, New York and the other New England states are associated with very moist habitats, including the edges of lakes or ponds, moist forests, or wetlands (our observations and E. Adams, personal communication).

The interregional transport of plant material for the nursery industries has been responsible for the movement of pest species to new regions, as is the case for some of the introductions of *S. invicta* (McGlynn 1999, Holway and Suarez 1999, Morrison et al. 2004) and *L. humile* (Holway 1995, Suarez et al. 2001). Similarly, it is highly probable that current *M. rubra* populations were introduced to North America in imported plant material, given that the ants were intercepted several times in shipments on different vegetation shipped from Europe (Table 3). Of interest is that populations in coastal communities in Maine, in some locations in Massachusetts (Worcester, Williamstown, Lennox, Gloucester, and Wakefield), and in Buffalo have become particularly dense and pestiferous, whereas this is not the case with the Arnold Arboretum population. The director of the Arboretum and the grounds crew

were not aware that the ant still existed there, yet sampling at the original site of the established colonies (Wheeler 1908) on 28 August 2001, revealed the persistence of a low-density population. This difference in local densities between populations may be due to differences in their source population, adaptations or changes in population structure acquired by the ant subsequent to its introduction, or variation in local environmental factors and native ant competitors that contribute to the regulation of populations in Europe.

Although established *M. rubra* populations seem to be associated with human activities, this may be because people have been responsible for moving them around rather than that the ants are more successful in disturbed habitats. *M. rubra* has successfully invaded natural landscapes in Acadia National Park on Mt. Desert Island and in Eastport, ME, where it is having negative impacts on native ant species (Garnas 2005), suggesting that these ants are invasive rather than solely tramp species (i.e., reliant on human-mediated dispersal and live in association with humans) (Holway et al. 2002a). Abiotic factors such as seasonal heat accumulation (Mallis 1941, Porter 1988, Korzukhin et al. 2001), lethal temperatures (Cokendolpher and Phillips 1990, Vinson 1997, Walters and MacKay 2004), soil type (Way et al. 1997, Rosson 2000), soil moisture (Korzukhin et al. 2001), and elevation (Human et al. 1998) have been shown to be influential in defining the distribution of the *S. invicta* and the Argentine ant within its invaded range.

The extensive range of *M. rubra* in Europe suggests that it may not be climatically limited by cold temperatures in its distribution throughout the northeastern United States and eastern Canada. We found 100% survival of the 30 monitored nests over the 2002–2003 winter on Mount Desert Island. However, Elmes et al. (1999) found variation in the physiological development of *M. rubra* that correlates with latitude, demonstrating local adaptation of populations to local climatic conditions. Hence, North America's invasive populations may originate from populations preselected for survival in similarly cold winters. The range of conditions tolerated by the source population and the adaptability of the invasive population may determine the success of establishment within climatic zones in North America, especially in regards to extreme high summer temperatures (Brian 1973).

The distribution of invasive ant species also has been shown to be dependent upon many biotic ecological factors, most importantly, competition from other ant fauna (Holldobler and Wilson 1990, Way et al. 1997, Holway 1999), and availability of food resources (Morrill et al. 1978, Vinson 1997). Interspecific competition has been hypothesized to determine the distribution of *M. rubra* within the United Kingdom (Brian 1952a, Elmes 1978), and the availability of food resources has been suggested to limit its populations in central Europe (Uchmanski and Petal 1982). Other biotic factors also have been suggested to affect invasive ant distributions, including the surrounding plant community (Kennedy 1998), human

Table 3. Museum records of *M. rubra* specimens collected in North America

Yr	Day	Location	Collector	W	Q	M	Collections	Note
1902	Aug. 15	Woods Hole, MA	Wheeler	0, series	1,1	0,2	MCZ, AMNH	
1902	Oct. 17	Forest Hills, MA	Wheeler	1			MCZ	
1910	Oct. 12	Forest Hills, MA	Wheeler				MCZ	
1912	May 5	Forest Hills, MA	W.M. Mann	6	2		USNM	
1915	April 5	Montreal, Quebec	J.I. Beauline	3			CAFR	
1916	April 29	Forest Hills, MA	Wheeler	2			MCZ	
1919	April 23			3			USNM	From Belgium, on box wood
1924	Aug. 20	New York, NY	R.L. Trigg	6			USNM	From Germany, on Dahlias
1925	Mar. 12	Cambridge, MA	White	2			MCZ	
1926	July 27	Woods Hole, MA		2			MCZ	Var. bruesi Wheeler
1927	June 29	Woods Hole, MA		6	1	2	USNM	
1927	Nov. 17	Arnold Arboretum, Forest Hills, MA	A.C. Burrill	3			MCZ	Foot of old Salix alba
1928	Nov. 21	Philadelphia, PA	Howley & Einger	1			MCZ	From Ireland, on packing moss
1931	Jan. 25	Philadelphia, PA	A.B. Wells	1			MCZ	From Germany, in soil about horseradishes
1933	April 14	Forest Hills	Weber	4, series			MCZ, AMNH	
1933	Sept. 24	Forest Hills	Weber	5	1		MCZ	
1945	May 26	Hoboken, NJ		3			MCZ	From England, Prunus-Poeny moss package
1946	May 2	Washington D.C.		12			USNM	From Frankfurt, Germany, with Narcissus bulbs
1952	May 4	Arlington, MA	W.L. Brown	8	2		MCZ	
1952	July 12	Eastport, ME	I.M. Shaw	6,6			USNM, MCZ	
1954	May 3	Shafer Glen, Woburn, MA	W.L. Brown				MCZ	
1957	May 18	Quebec, Quebec	J.P. Laplante	14			CAFR	In soil
1966	June 6	Newport, RI		1			USNM	In garden
1967	Aug. 5	Cambridge, MA	R.J. Hampton	13		2	CAFR	
1967	Aug. 5-8	Fresh Pond, Cambridge, MA	R.J. Hampton	3	2		MCZ	
1973	Mar. 16	Newark, NJ	W.B. Wood	5	1		USNM	From Holland, on roots of Astible
1975	Mar. 12	Harvard University, Cambridge, MA					MCZ	
1975	April 26	Boston, MA	Harrison	3			MCZ	
1975	Oct. 13	Meaford, Ontario	J.T. Huber	1			CAFR	Very abundant
1977	May 28	Portsmouth, NH	B. Johnson	1			MCZ	
1977	May 28	Isles of Shoals, ME	B.M. O'Connor	14			CAFR	
1979	Aug. 5	Brossard, Quebec	R.J. Harrison	6			CAFR	
1981	Nov. 30	Appledore Island, Isles of Shoals, ME	A.C. Borrer	3			MCZ	
1982	May 17	Rock Meadow, Belmont, MA	Carlin	4	3	1	MCZ	
1982	April 16	Harvard University, Cambridge, MA	Thayer/Courver	2/2	1		MCZ	
1982	Aug. 29	Arnold Arboretum, Forest Hills, MA	G. Helmes	5		1	CAFR	
1988	July 9	Buffalo, NY	Gall	16				Tiff Nature Preserve
1994	May 14	Buffalo, NY	Williams	8			MCZ	Tiff Nature Preserve
1990	May 2	Bedford, MA	Couver		1		MCZ	
1997		Bar Harbor, ME	G. Ouellette				MCZ	
1997		Guelph, Ontario	J. Huber	Series			CAFR	
1998	May 5	Halifax Co., York, Nova Scotia	Ward	2	1		MCZ	Ground nest in mixed conifers
2003	Aug. 27	Williamstown, MA	M. Morales	7	1		MCZ	Eph's Pond, Williams College
2003	May 17	Toronto, Ontario	P.K. Chan		1		CAFR	Dealate in pitfall trap
?		Forest Hills, MA		1			LACM	
?		Boston, MA	C.A. Davis	3			MCZ	From Poland on Dahlia roots
?		New York, NY	E. Kostal	11			USNM	From Germany, in soil

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; AMNH, American Museum of Natural History, New York, NY; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA; CAFR, Dr. André Francoeur's collection, University of Quebec at Chicotimi; USNM, U.S. National Museum at Smithsonian Institute, Washington, DC).

disturbance (Passera 1994, Suarez et al. 1998, Williams 2003), and initial colony size (Hee et al. 2000). The potential role of these factors on *M. rubra* populations in its introduced range is unknown. The interaction of these biotic and abiotic factors can make the prediction of potential invasive range complex and uncertain (Bestelmeyer 2000, Holway et al. 2002a).

The 100-yr-old report of an established *M. rubra* population demonstrates that the introduction of this species is not a new phenomenon. However, the spread of very dense pestiferous populations, particularly in coastal areas of Maine, is more recent. The Proctor Collection (Proctor 1946), a fairly comprehensive effort to catalog the insects on Mt. Desert

Island between 1938 and 1945, does not contain any *M. rubra* specimens. This suggests that either the ant was introduced after this time or the densities were low enough to avoid detection. Whether the more recent apparent spread of *M. rubra* populations represent a geometric increase after a long period of establishment, a postintroduction adaptation in the population that favors its success, or a response to the record warm annual temperatures experienced in the northeastern United States over the past decade, is unclear. It is certain, however, that *M. rubra* populations are becoming a more serious problem for residents in coastal Maine communities.

Acknowledgments

We are indebted to Graham Elmes for sharing a wealth of knowledge on *Myrmica* ants and for critically reviewing this manuscript. We also thank Stefan Cover (Harvard Museum of Comparative Zoology) for assistance with museum specimens and records and for identification of local *M. rubra* populations in Massachusetts. Several students assisted with surveys, including Joseph Fisher, Shicai Yan, Nathan Drummond, Gabrielle Gosselin, Anthony O'Neal, Carrie Graham, and Seth Carboneau. This project as supported by the USDA-APHIS Cooperative Agricultural Pest Survey (CAPS) Program, the National Park Service at Acadia National Park, and the Maine Agricultural and Forestry Experiment Station (Publication no. 2826).

References Cited

- Agosti, D., and C. A. Collingwood. 1987. A provisional list of the Balkan ants (Hymenoptera, Formicidae) and a key to the worker caste. I. Synonymic list. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 60: 51–62.
- Bestelmeyer, B. T. 2000. The trade-off between thermal tolerance and behavioral dominance in a South American ant community. *J. Anim. Ecol.* 69: 998–1009.
- Bolger, D. T., A. Suarez, K. R. Crooks, S. A. Morrison, and T. Case. 2000. Arthropods in urban habitat fragments in Southern California: area, age, and edge effects. *Ecol. Appl.* 10: 1230–1248.
- Bolton, B., and C. A. Collingwood. 1975. Hymenoptera, family Formicidae. Handbooks for the Identification of British Insects 6: 1–34.
- Bolton, B. 1995. A new general catalogue of the ants of the World. Harvard University Press, Cambridge, MA.
- Bond, W., and P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65: 1031–1037.
- Boomsma, J. J., and A. De Vries. 1980. Ant species distribution in a sandy coastal plain. *Ecol. Entomol.* 5: 189–204.
- Boomsma, J. J., and A. Leusink. 1981. Weather conditions during nuptial flights of four European ant species. *Oecologia (Berl.)* 50: 236–241.
- Brian, M. V., and A. D. Brian. 1949. Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander (Hymenoptera: Formicidae). *Trans. R. Entomol. Soc. Lond.* 100: 393–409.
- Brian, M. V. 1952a. Interaction between ant colonies at an artificial nest-site. *Entomol. Mon. Mag.* 88: 84–88.
- Brian, M. V. 1952b. The structure of a dense natural ant population. *J. Anim. Ecol.* 21: 12–24.
- Brian, M. V. 1956. The natural density of *M. rubra* and associated ants in Scotland. *Insectes Soc.* 3: 473–487.
- Brian, M. V. 1973. Temperature choice and its relevance to brood survival and caste determination in the ant *Myrmica rubra* L. *Physiol. Zool.* 46: 245–252.
- Brian, M. V., R. M. Jones, and J. C. Wardlaw. 1981. Quantitative aspects of queen control over reproduction in the ant *Myrmica*. *Insectes Soc.* 28: 191–207.
- Cogni, R., A.V.L. Freitas, and P. S. Oliveira. 2003. Inter-habitat differences in ant activity on plant foliage: ants at extrafloral nectaries of *Hibiscus pernambucensis* in sandy and mangrove forests. *Entomol. Exp. Appl.* 107: 125.
- Cokendolpher, J. C., and S. A. Phillips, Jr. 1990. Critical thermal limits and locomotor activity of the red imported fire ant (Hymenoptera: Formicidae). *Environ. Entomol.* 19: 877–881.
- Cole, F. R., A. C. Medeiros, L. L. Loope, and W. W. Zuehlke. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73: 1313–1322.
- Creighton, W. S. 1950. The ants of North America. *Bull. Mus. Comp. Zool.* 104.
- Czechowski, W., A. Radchenko, and W. Czechowska. 2000. The ants (Hymenoptera, Formicidae) of Poland. Warszawa, Poland.
- Elmes, G. W. 1973. Observations of the density of queens in natural colonies of *Myrmica rubra* L. (Hymenoptera, Formicidae). *J. Anim. Ecol.* 42: 761–771.
- Elmes, G. W. 1974a. The effect of colony population on caste size in three species of *Myrmica* (Hymenoptera Formicidae). *Insectes Soc.* 21: 213–229.
- Elmes, G. W. 1974b. The spatial distribution of a population of two ants species living in limestone grassland. *Pedobiologia* 14: 412–418.
- Elmes, G. W. 1975. Population studies on the genus *Myrmica* (Hymenoptera, Formicidae), with special reference to Southern England. Ph.D. dissertation. University of London, London, United Kingdom.
- Elmes, G. W. 1978. Populations of *Myrmica* (Formicidae) living on different types of *Calluna* moorland—a semi-natural habitat of southern England. *Memorabilia Zool.* 29: 41–60.
- Elmes, G. W. 1980. Queen numbers in colonies of ants of the genus *Myrmica*. *Insectes Soc.* 27: 43–60.
- Elmes, G. W. 1982. The phenology of five species of *Myrmica* (Hym. Formicidae) from South Dorset, England. *Insectes Soc.* 29: 548–559.
- Elmes, G. W., and J. C. Wardlaw. 1981. The quantity and quality of overwintered larvae in five species of *Myrmica* (Hymenoptera: Formicidae). *J. Zool.* 193: 429–446.
- Elmes, G. W., and J. C. Wardlaw. 1983. A comparison of the effect of temperature on the development of large hibernated larvae of four species of *Myrmica* (Hym. Formicidae). *Insectes Soc.* 30: 106–118.
- Elmes, G. W., and J. Petal. 1990. Queen number as an adaptable trait: evidence from wild populations of two red ant species (genus *Myrmica*). *J. Anim. Ecol.* 59: 675–690.
- Elmes, G. W., and L. Keller. 1993. Distribution and ecology of queen number in ants of the genus *Myrmica*, pp. 294–307. *In* L. Keller [ed.], *Queen number and sociality in insects*. Oxford University Press, Oxford, England.
- Elmes, G. W., J. C. Wardlaw, M. G. Nielsen, V. E. Kipyatkov, E. B. Lopatina, A. D. Radchenko, and B. Barr. 1999. Site latitude influences on respiration rate, fat content, and the ability of worker ants to rear larvae: a comparison of *Myrmica rubra* (Hymenoptera: Formicidae) populations over their European range. *Eur. J. Entomol.* 96: 117–124.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, United Kingdom.
- Erickson, J. M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. *Psyche* 78: 257–266.

- Garnas, J. 2005. European fire ants on Mount Desert Island, Maine: population structure, mechanisms of competition and community impacts of *Myrmica rubra* L. (Hymenoptera: Formicidae). M.S. thesis, University of Maine, Orono, ME.
- Hee, J. J., D. A. Holway, A. V. Suarez, and T. J. Case. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. *Conserv. Biol.* 14: 559–563.
- Hiebeler, D. E. 2004. Competition between near and far dispersers in spatially structured habitats. *Theor. Pop. Biol.* 66: 2050–218.
- Helms, K. R., and S. B. Vinson. 2003. Apparent facilitation of an invasive mealybug by an invasive ant. *Insectes Soc.* 50: 403–404.
- Holldobler, B., and E. O. Wilson. 1990. *The ants*. Belknap, Cambridge, MA.
- Holway, D. A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in northern California. *Conserv. Biol.* 9: 1634–1637.
- Holway, D., A. Suarez, and T. Case. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* (Wash. DC) 282: 949–953.
- Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology* 80: 238–251.
- Holway, D. A., and A. V. Suarez. 1999. Animal behavior: an essential component of invasion biology. *Trends Ecol. Evol.* 14: 328–330.
- Holway, D. A., A. V. Suarez, and T. J. Case. 2002a. Role of abiotic factors in governing the susceptibility to invasion: a test with Argentine ants. *Ecology* 83: 1610–1619.
- Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002b. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33: 181–233.
- Human, K., and D. Gordon. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. *Conserv. Biol.* 11: 1242–1248.
- Human, K. G., S. Weiss, A. Weiss, B. Sandler, and D. M. Gordon. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environ. Entomol.* 27: 822–833.
- Kennedy, T. A. 1998. Patterns of an invasion by Argentine ants (*Linepithema humile*) in a riparian corridor and its effects on ant diversity. *Am. Midl. Nat.* 140: 343–350.
- Kipyatkov, V. E. 2001. Seasonal cycles and the forms of dormancy in ants (Hymenoptera: Formicoidea). *Acta Soc. Zool. Bohem.* 65: 211–238.
- Kipyatkov, V. E., and E. B. Lopatina. 1997a. Experimental study of seasonal cycle of rapid brood production in the ants *Myrmica rubra* L. and *Myrmica ruginodis* Nyl. from two different latitudes. *Proc. Int. Coll. Soc. Insects* 3–4: 195–206.
- Kipyatkov, V. E., and E. B. Lopatina. 1997b. Seasonal cycle and winter diapause induction in ants of the genus *Myrmica* in the Polar Circle region. *Proc. Int. Coll. Soc. Insects* 3–4: 277–286.
- Korzukhin, M. D., S. D. Porter, L. C. Thompson, and S. Wiley. 2001. Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. *Environ. Entomol.* 30: 645–655.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8: 133–137.
- Mallis, A. 1941. A list of the ants of California with notes on their habitats and distribution. *Bull. S. Calif. Acad. Sci.* 40: 61–100.
- Markin, G. P. 1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in southern California. *Ann. Entomol. Soc.* 63: 1238–1242.
- McGlynn, K. 1994. The foraging behavior of the common ant, *Myrmica rubra* (L.). Ph.D. dissertation, Goldsmiths College, University of London, London, United Kingdom.
- McGlynn, T. P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *J. Biogeogr.* 26: 535–548.
- Morrill, W. L., P. B. Martin, and D. C. Sheppard. 1978. Overwinter survival of the red imported fire ant effects of various habitats and food supply. *Environ. Entomol.* 7: 262–264.
- Morrison, L. 2000. Mechanisms of interspecific competition among invasive and two native fire ants. *Oikos* 90: 238–252.
- Morrison, L. W., S. D. Porter, E. Daniels, and M. D. Korzukhin. 2004. Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biol. Invasions* 6: 183–191.
- Onoyama, K. 1989. Confirmation of the occurrence of *Myrmica rubra* (Hymenoptera, Formicidae) in Japan, with taxonomic and ecological notes. *Jpn. J. Entomol.* 57: 131–135.
- [OTA] Office of Technology Assessment. 1993. Harmful non-indigenous species in the United States. United States Congress, Office of Technology Assessment, Washington, DC.
- Passera, L. 1994. Characteristics of tramp species, pp. 23–43. *In* D. F. Williams [ed.], *Exotic ants: biology, impact, and control of introduced species*. Westview Press, Boulder, CO.
- Porter, S. D. 1988. Impact of temperature on colony growth and development rates of the ant, *Solenopsis invicta*. *J. Insect Physiol.* 34: 1127–1133.
- Porter, S. D., and D. A. Savignano. 1990. Invasion of polygynous fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106.
- Porter, S. D., D. F. Williams, R. S. Patterson, and H. G. Fowler. 1977. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies. *Environ. Entomol.* 26: 373–384.
- Proctor, W. 1946. Biological survey of the Mount Desert Region; Part VII. The Insect Fauna. Winstar Press, Philadelphia, PA.
- Reznikova, Zh. I., and S. N. Panteleeva. 2001. Interaction of the ant *Myrmica rubra* L. as a predator with springtails (Collembola) as a mass prey. *Doklady Biol. Sci.* 380: 475–477.
- Rosson, J. 2000. Abiotic and biotic factors affecting the distribution of *Solenopsis invicta* Buren, *Brachymyrmex* sp., and *Linepithema humile* (Mayr) in east Baton Rouge Parish, Louisiana. M.S. thesis, Louisiana State University, Baton Rouge, LA.
- Santschi, F. 1931. Note sur le genre *Myrmica* Latr. *Rev. Suisse Zool.* 38: 335–355.
- Seifert, B. 1988. A taxonomic revision of the *Myrmica* species of Europe, Asia Minor, and Caucasus (Hymenoptera, Formicidae). *Abhandlungen Berichte des Naturkundemuseums Gorlitz.* 62: 1–75.
- Seppa, P., and L. Walin. 1996. Sociogenetic organization of the red ant *Myrmica rubra*. *Behav. Ecol. Sociobiol.* 38: 207–217.
- Simberloff, D. 1981. Community effects of introduced species. Pages 53–81. *In* Anonymous, *Biotic crises in ecological and evolutionary time*. Academic, New York.

- Suarez, A. V., D. T. Bolger, and T. J. Case-Williams. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79: 2041–2056.
- Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. *Ecol. Appl.* 10: 711–725.
- Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proc. Natl. Acad. Sci. U.S.A.* 98: 1095–1100.
- Tsutsui, N. D., and T. J. Case. 2001. Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. *Evolution* 55: 976–985.
- Uchmanski, J., and J. Petal. 1982. Long term stability of ant colonies: a simulation model. *J. Anim. Ecol.* 51: 832–856.
- Vinson, S. B. 1997. Invasion of the red imported fire ant (Hymenoptera: Formicidae): spread, biology, and impact. *Am. Entomol.* 43: 23–39.
- Walters, A. C., and D. A. MacKay. 2004. Comparisons of upper thermal tolerances between the invasive fire ant (Hymenoptera: Formicidae) and two native Australian ant species. *Ann. Entomol. Soc. Am.* 97: 971–975.
- Ward, P. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* 55: 1–16.
- Wardlaw, J. C., and G. W. Elmes. 1996. Exceptional colony size in *Myrmica* species (Hymenoptera, Formicidae). *Entomologist*. 115: 191–196.
- Way, M. J., M. E. Cammell, M. R. Paiva, and C. A. Collingwood. 1997. Distribution and dynamics of the Argentine ant, *Linepithema (Iridomyrmex) humile* (Mayr) in relation to vegetation, soil conditions, topography and native competitor ants in Portugal. *Insectes Soc.* 44: 415–433.
- Weber, N. A. 1947. A revision of the North American ants of the genus *Myrmica* Latreille with a synopsis of the Palearctic species. I. *Ann. Entomol. Soc. Am.* 41: 267–308.
- Wheeler, W. M. 1908. A European ant (*Myrmica laevinodis*) introduced into Massachusetts. *J. Econ. Entomol.* 1: 336–339.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Williams, G. Y. 2003. Disturbance of Argentine ants: effects of abiotic factors and human disturbance on the Palos Verdes Peninsula. *Calif. State Sci. Fair Summary*.
- Wilson, E. O. 1992. *The diversity of life*. W.W. Norton & Co., New York.
- Woyciechowski, M. 1990. Mating behavior in the ant *Myrmica rubra* (Hymenoptera, Formicidae). *Acta Zool. Cracov.* 33: 565–574.

Received 25 February 2005; accepted 14 July 2005.
