INVITED REVIEW

The Ecology, Policy, and Management of Ants in Hawaii

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Abstract. Ants represent a wholly introduced component of Hawaiian ecosystems. The establishment of roughly 45 ant species over the past two centuries has wide ranging implications for agriculture, other sectors of the economy, and the conservation of native biodiversity. Although ants have received considerable attention in Hawaii, many questions regarding the factors that determine their distributions and influence patterns of species co-occurrence remain largely unexplored. More focus has been directed at their ecological effects, both in agriculture, where they tend pestiferous homopteran insects, and in natural areas, where they can directly threaten native invertebrates and vertebrates and indirectly impact native plants. Increased awareness of the negative repercussions of ant introductions in Hawaii has led to improvements in preventative quarantine policy in the last decade, however agencies responsible for ant and other invasive species interdiction remain severely understaffed. Efforts to control or eradicate ant infestations for conservation purposes in Hawaii represent a recent development, and have so far met with variable success. Such efforts may also require a greater investment to improve results. The threat of other destructive ant species, such as the red imported fire ant, arriving in Hawaii underscores the importance of an early detection network and an established infrastructure ready for rapid response.

Introduction

The challenges facing pre-historic plant and animal colonizers of the remote Hawaiian Islands were undoubtedly among the most difficult anywhere, and resulted in a fauna and flora that evolved from just a relative few successful arrivals. For example, it is estimated that only 350–400 insect species colonized the islands, however these subsequently diversified to form a native insect fauna that likely exceeds 10,000 species (Howarth 1990). As might be expected of the world's most isolated archipelago, the colonizers that did arrive formed an extremely idiosyncratic fauna, with only approximately 15% of the world's insect families represented among its native members (Howarth 1990).

Perhaps the most significant peculiarity of the Hawaiian invertebrate fauna is the complete absence of social insects, including the ants (Wilson and Taylor 1967b, Howarth 1985). In most areas of the world, ants are recognized to be highly important components of biotic communities, strongly influencing nutrient and energy flow through predation, scavenging, soil turning, mutualisms and other means (Hölldobler and Wilson 1990). Hawaii's lack of ants therefore gives rise to fascinating questions in ecology and evolution, such as how ecological roles traditionally dominated by ants might be filled by descendants of the few taxa that did arrive (Wilson 1996), or how patterns of assembly and interspecific interactions among the recently introduced ant fauna compare to those of more coevolved commu-

nities (as in Wilson and Taylor 1967a, Morrison 1996a). More urgently, the recent arrival of ants has profound implications for conservation: invasive ants appear to be among the most potent forces threatening native arthropod species, and in certain situations may result in wider impacts. As in many other locales, introduced ants can also become pests of Hawaiian agriculture and urban settings.

Reimer and colleagues have provided comprehensive reviews that address the role of ants as pests (Reimer et al. 1990) as well as their threats to native biodiversity in Hawaii (Reimer 1994). Not surprisingly, ants continue to attract the attention of researchers, resource managers and policymakers, and our goal in this paper is to review the findings and developments that have taken place primarily during the last decade. We focus on more recent work studying the ecology of several invasive ant species, efforts at eradication and control, and advances in the areas of prevention, quarantine and policy. We devote the bulk of our attention to work relevant to the conservation of natural areas and native biodiversity, but in the case of invasive ants, there is considerable overlap between the concerns of conservationists, agricultural producers, and even the general public and tourist industry.

I. Hawaiian Ants and Their Ecological Effects

Biogeography of Hawaiian ants

Approximately 45 species of ants have established in Hawaii, although a few of these species have not been collected in many decades and possibly no longer occur (see Appendix). This total equals or surpasses the known number of ant species introduced to nearly every other biogeographic region of the world (McGlynn 1999). Hawaii's extreme diversity of biomes (Gagne and Cuddihy 1990) and lack of native ants undoubtedly contribute to this condition. Because all of the current species have arrived in association with human activity, they hail from all corners of the globe: six continents as well as oceanic islands are represented among the sources of the modern Hawaiian fauna (McGlynn 1999, Appendix). The rate at which these species accrue, the ultimate species richness at equilibrium in the islands, species distribution patterns, and the assemblages that are formed are all topics of interest. Each of these topics has as yet received relatively little attention.

The formation of the ant fauna. We do not know how long the first recorded species had already been present when naturalists began collecting ants in the 1880s. In addition, the date of first record for several species in taxonomically confusing groups is difficult to determine with confidence. In general, however, if we assume that the lag period between establishment and first record has, on average, remained fairly constant over time, then the pattern of ant species detection should approximate the pattern of species accumulation. While the rate of new species detection over short time intervals has fluctuated considerably, the overall pattern is best described by a decelerating curve and suggests that the rate of species accumulation over the past several decades has begun to slow (Fig. 1). This has occurred at the same time that the pace of commerce and importation of goods into Hawaii has greatly increased (HDOT 2002).

A decreasing rate of species accumulation might be explained in several ways. First, it is possible that the Hawaiian Islands are approaching an equilibrium number of ant species and that new arrivals fail to establish because of competition from pre-existing ants. Almost 40 years ago, Wilson and Taylor (1967a) hypothesized that Polynesian islands had reached a quasi-equilibrium with respect to ant species that was maintained by competitive exclusion among the introduced tramp fauna. Morrison (1996b) subsequently found that substantially more species actually exist in Polynesia than previously realized, and argued that, with the exception of several dominant species, there was little evidence for competitive
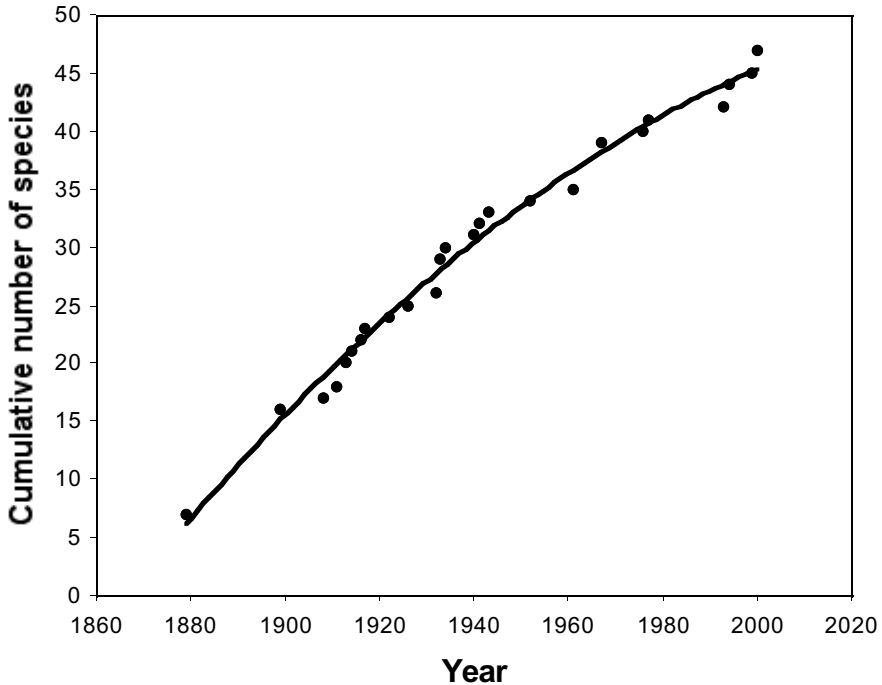
Figure 1. The approximate rate of ant species accumulation in Hawaii. This figure graphs the cumulative number of species documented as established over time, based on the year of first record. Several of these species may no longer occur; see Appendix for information on individual species. The overall trend is fit significantly better by a curve than a line ($F_{1, 23} = 45.628$, $P < 0.001$, for comparison of one-term linear model versus two-term quadratic model; $R^2 = 0.988$ for the fitted curve).

exclusion among these ants. Although it is possible that the higher current total number of species in Hawaii is approaching equilibrium, nearly all of the species that have established over the past 100 years still occur in the islands. If the influx of new ant species propagules is indeed constant (or increasing with commerce) and total species richness is near equilibrium level, it is unlikely that only new arrivals would fail to persist (as would be implied by Figure 1). Despite priority effects, it might be more reasonable to expect some turnover in species composition within the island chain.

An alternative explanation for the apparent decreasing rate of ant species accumulation in Hawaii is that better quarantine efforts in recent decades have stemmed the tide of introductions. As the number of state agricultural inspectors has actually fallen over the past 20 years (N. Reimer unpubl. data), while the volume of trade has steadily climbed, this explanation seems unlikely.

A third hypothesis posits that there is a limited pool of ant species that are easily dispersed through human activities, and Hawaii has already received most of them. For example, Hawaii already has five of the six or so species recognized as the most highly invasive worldwide (Holway et al. 2002). While McGlynn (1999) lists approximately 100 species in addition to those already established in Hawaii as species that have been transferred throughout the world, it is unclear how many of these have only been intercepted in quarantine rather than truly becoming established outside their native ranges (e.g., he lists 48 species as transferred to Hawaii that are not actually established). Hawaii has in fact intercepted at least 50 species in addition to those established (N. Reimer unpubl. data). However, Hawaii Department of Agriculture records from 1995 to 2003 indicate that of 451 total ant interceptions originating from outside the state, only 18.2% represented new species (N. Reimer unpubl. data). In contrast, 8 species already widespread in Hawaii represented 73.4% of all ant interceptions (with the Argentine ant, *Linepithema humile* [Mayr], alone making up 43.7% of interceptions). The vast majority (ca. 97%) of all arrivals included only non-reproductive adult castes, and it seems likely that the much higher rate of transport among a relatively small number of species predisposes them to eventual colony establishment.

Distributional patterns. As a group, ants occupy most Hawaiian habitat types, from coastal strand to subalpine shrubland over 2700 m elevation. Most ant species, however, are limited to elevations below approximately 900 m (Reimer 1994). This is likely due in part to the fact that ports of entry are located in the lowlands, and incoming species must therefore survive at least temporarily in lowland climates in order to persist (Reimer 1994). In addition, a bias towards tropical and subtropical climatic regimes among source areas of tramp ant species could contribute to this pattern.

In Hawaii, as elsewhere, species distributions will be a product of both biotic and abiotic forces, although the relative strengths of these forces are likely to vary across habitat type. In lowland to dry and mesic middle-elevation habitats, interspecific competition between ant species (e.g. Fluker and Beardsley 1970) likely plays a substantial role in determining species ranges, along with abiotic conditions that undoubtedly help determine competitive advantages among sites. For example, the dominant invasive Argentine ant once occurred at multiple, subtropical lowland sites on Oahu (Wilson and Taylor 1967b, Huddleston and Fluker 1968) and was even observed displacing the big-headed ant at some of these sites (Fluker and Beardsley 1970). Over time, however, it appears that the Argentine ant, which is most prevalent in Mediterranean and temperate (i.e. higher elevation in Hawaii) climates worldwide (Suarez et al. 2001), was out-competed by other species throughout Oahu's lowlands, and it may no longer occur anywhere on the island. In general, it is often possible to observe shifting patterns of ant species abundances and distributions in lowland areas, and the specific causes underlying these dynamics remain relatively unstudied.

In and adjacent to wet upland habitats, it appears that abiotic conditions are the primary factors determining ant species distributions. Few species have been able to colonize undisturbed wet montane forest (Reimer 1994), and those that can occasionally be found there (e.g. *Hypoponera opaciceps* [Mayr], *Cardiocondyla kagutsuchi* [Terayama]) occur sporadically and in small numbers. This exception is an important one, as much of Hawaii's remaining intact natural areas consists of montane rainforest and cloudforest. High levels of moisture and cold soil temperatures in these areas are probably among the most important factors that exclude nearly all of the species in Hawaii's current ant assemblage. Yet other than general observations of distributional patterns in relation to elevation and habitat type, almost no work has attempted to determine particular abiotic tolerances of ant species. Recent analysis of Argentine ant spread in Haleakala National Park has begun to address this topic (Krushelnycky et al. in press b). At this site, records of invasion over a period of thirty years indicate that increasing rainfall can prevent spread from mesic shrubland into

wetter shrubland and forest, probably due in large part to its effects on vegetative cover and soil temperature. At the same time, elevation, most likely as a surrogate for temperature, can exert a strong influence on rate of spread within suitable habitat.

Much work remains to understand the specific factors, and their interactions, that dictate both the distributional patterns of particular species and the patterns of species co-occurrence throughout the Hawaiian Islands. In addition to the measurement of limiting thresholds of abiotic variables for individual ant species, distributional surveys (e.g. Huddleston and Fluker 1968, Fellers and Fellers 1982, Medeiros et al. 1986, Reimer et al. 1992, Wetterer 1998, Wetterer et al. 1998) represent a critical step towards attaining this goal. Besides providing essential information relevant to various research questions and conservation decisions, ant distributional surveys can serve as one avenue for studying the dynamics of interspecific interactions. Analysis of ant distributional patterns on some of the Society Islands, for instance, revealed that patterns of species co-occurrence are highly non-random and that groups of dominant and subordinate species commonly assemble within the introduced fauna (Morrison 1996a).

Ecological effects of ants in Hawaii

While most of Hawaii's ant species have in common the ability to be easily transported in cargo, the current assemblage represents a range of behavioral repertoires and colony arrangements, and includes genera that can be classified in several different ecological functional groups (Andersen 1997). Hawaiian ants forage primarily below ground (e.g. *Hypoponera spp*.), or primarily above ground, including arboreally; nest under rocks, in the soil, within logs, under bark, in hollow branches and twigs (*Pseudomyrmex gracilis* [Fab.]), or in other vegetative matter; form small, discrete colonies or expansive unicolonial populations; and range from inconspicuous, specialist predators (*Strumigenys spp*.) to community dominant generalists. (Most of the more specialized ecological strategies evolved among the ants, however, are absent, such as obligate plant mutualists, fungus growers and nomadic mass raiders of the army ant model).

Among these, a small subset of species stand apart as the most dominant invasive ants in Hawaii and around the world (see Holway et al. 2002 for a thorough review). These include the big-headed ant (*Pheidole megacephala* [Fab.]), the Argentine ant (*L. humile*), the long-legged or yellow crazy ant (*Anoplolepis gracilipes* [F. Smith]), the little fire ant (*Wasmannia auropunctata* [Roger]) and the tropical fire ant (*Solenopsis geminata* [Fab.]); a sixth, and perhaps the most destructive, the red imported fire ant (*Solenopsis invicta* Buren), has yet to establish in Hawaii. In their introduced ranges, these species share key biological features, including multiple queens per nest (polygyny), multiple nests per colony (polydomy), and greatly reduced intraspecific aggression, that lead to the formation of large, continuous unicolonial populations (although *S. invicta* and *S. geminata* can have both polygyne and monogyne forms) (Holway et al. 2002). At least one other species in Hawaii, *Paratrechina longicornis* (Latreille), is sometimes included in this list because of its polygynous social structure and ability to reach high densities (McGlynn 1999, Wetterer et al. 1999). Each of these species tends to dominate invaded areas through a combination of aggressive behavior, generalist diet and numerical advantages over other arthropods (Holway et al. 2002). Although other ant species may also pose problems in Hawaii and should not be ignored (Reimer 1994, Wetterer 1998, Banko et al. 2002), the above-mentioned species are likeliest to exert the greatest impacts in both agriculture and natural areas.

The role of ants in agriculture. Early in the 20th century, species such as the big-headed ant were briefly considered to be beneficial predators in agriculture (Illingworth 1917). Before long it became clear that the negative effects of ants on Hawaii's main agricultural crops outweighed any benefits (e.g. Illingworth 1931). The most consistent and detrimental

effect of ants in agriculture is an indirect one. By tending and protecting honey-dew producing Homoptera such as aphids, scales and mealybugs, ants cause great increases in the abundances of these pest insects. In pineapple, this leads to the transmission of wilt disease by a pair of mealybug species (Beardsley et al. 1982, see Jahn et al. 2003 for a review of this topic). In coffee, the presence of *P. megacephala, A. gracilipes* or occasionally *L. humile* often results in outbreaks of green scale (*Coccus viridis* [Green]). The large amounts of honeydew excreted by this scale promotes the growth of sooty mold, which reduces fruit production and may sometimes cause tree death (Reimer et al. 1990). Ants also tend mealybugs in sugar cane (Reimer et al. 1990), but the principal damage caused by ants in this crop has been their destruction of drip irrigation equipment (Chang and Ota 1990). Other, more minor crops are also affected by ants, including cut flowers, dryland taro, and beans (Reimer et al. 1990). In all of the cases where ants tend pestiferous insects, the primary control method involves control of the ants, not the pest homopteran; in the absence of ants, homopterans rarely reach pest proportions. Experimental studies in both agricultural (Reimer et al. 1993, Gonzalez-Hernandez et al. 1999) and non-crop systems (Bach 1991) have demonstrated that ants boost homopteran numbers by removing predators and often by interfering with parasitoids, and that in the absence of ants homopteran densities decrease.

Impacts of ants on native arthropods. Many of Hawaii's ant species range to some degree outside of urban and agricultural landscapes, and the potential for severe consequences resulting from ant invasions into natural areas is high. For instance, ants can prey directly upon native arthropods, exclude them through interference or exploitation competition for food resources, or displace them by monopolizing nesting or shelter sites. Numerous authors have in fact cited ants as significant factors that have likely contributed to the decline of a wide variety of native arthropods (e.g. Perkins 1913, Zimmerman 1970, Howarth 1985, Loope et al. 1988, Leibherr and Polhemus 1997, Gillespie 1999, Daly and Magnacca 2003), often arguing that evolutionary naiveté and ill-suited adaptations with respect to ants predispose many native arthropods to suffer disproportionately. While these contentions seem reasonable, demonstrating and quantifying the impacts caused by ants is a difficult proposition in many situations. Most ant species are limited to habitats below approximately 900 m elevation (Reimer 1994). With some exceptions, lowland areas have been highly altered, are usually dominated by introduced vegetation, and in general, support relatively few native arthropods. Teasing apart the effects of ant invasion from all the confounding sources of prior and subsequent impact is in most cases impossible, not least because there are typically no ant-free sites with which to draw comparisons.

Occasionally, however, a new invasion by a dominant ant causes dramatic effects that are detectable above and beyond those caused by prior ant species or other sources of native habitat degradation. The striking pattern of presence and absence of a range of endemic arthropod groups, and in particular beetles, within and without habitat invaded by *P. megacephala* led Perkins (1913) to draw some of the earliest conclusions about the devastating effects of this ant in Hawaii. Although already widespread, he reported that *P. megacephala* was still invading new areas and concurrently eliminating native arthropods around the turn of the 19th century. Similarly, at Puaaluu and Oheo streams on Maui, the invasion of *A. gracilipes* into low elevation riparian corridors in the 1970's is the most likely explanation for an apparently synchronized decrease of native aquatic insects (Hardy 1979). More recently, invasion of *P. megacephala* into some forested areas of eastern Kauai appears to have heavily impacted endemic ground crickets in the genus *Laupala* (LaPolla et al. 2000). The dramatic increase in ant numbers observed at these Kauai sites undoubtedly affected other ground active arthropods as well, however the degree to which this effect has penetrated forest distant from roadsides and trailsides is unclear.

Even in more pristine upland habitat, accurately assessing the impacts of ant invasions

can be difficult. The rapid turnover of habitat type over relatively short distances that characterizes the Hawaiian islands presents a major challenge to drawing conclusions about large-scale exclusionary patterns between ants and native arthropods. Changes in habitat necessarily lead to changes in arthropod community composition (Gagne 1979), irrespective of ant presence. Patterns of repeated absence of particular taxonomic groups in the presence of ants across many sites and habitat types, however, can make a compelling case. In one such example, Gillespie and Reimer (1993) found endemic *Tetragnatha* spiders to coexist with many ant species, yet these spiders were conspicuously absent at sites invaded by *P. megacephala* and *A. gracilipes*. This pattern was derived from observations at over 60 sites on 5 islands, and was supported by laboratory trials in which *Tetragnatha* spiders were found to be much more susceptible to ant predation than were several non-native spiders due to an absence of appropriate behavioral and morphological defense mechanisms. In another case, Gagne (1979) found that most endemic arthropod groups were absent below approximately 750 m elevation along an elevational transect situated within mostly native vegetation in Hawaii Volcanoes National Park, correlating with an increasing abundance of *P. megacephala* and other ants.

The clearest opportunities for measuring the ecological effects of ant invasions in Hawaii exist at smaller-scale individual sites at middle to high elevations, where ants are often still in the process of invading mostly ant-free habitat. In these situations, arthropods can be sampled in adjacent plots located in the same habitat type but situated inside and outside invading ant populations. To date, the only comprehensive, quantitative study that has taken advantage of these conditions investigated the impacts of two invading Argentine ant populations at Haleakala National Park (Cole et al. 1992). Pitfall sampling and under-rock surveying revealed that a wide range of endemic arthropods was significantly reduced in abundance within ant-invaded areas. The affected groups included, among others, herbivores (*Agrotis spp.* [Lepidoptera: Noctuidae]), predators and scavengers (*Mecyclothorax* and *Blackburnia spp.* [Coleoptera: Carabidae], *Lycosa Hawaiiensis* Simon [Araneae: Lycosidae]), and pollinators (*Hylaeus spp.* [Hymenoptera: Colletidae]). Another study currently under way is using a similar approach to assess the effects of ant invasion on both ground and shrub faunas at five high elevation (1900 - 2800 m) sites of invasion on Maui and Hawaii Island (P. Krushelnycky and R. Gillespie unpubl. data). The goal of this study is to determine the generality of the effects of ants on arthropod community structure between different sites and habitat types, and to identify which native taxa are most consistently placed at risk.

Perhaps the greatest concern stemming from ant invasions in natural areas is the potential for endemic species extinction. Many Hawaiian arthropod species have very limited distributions (Howarth 1990), and the expansive unicolonial populations of the most dominant invasive ants can sometimes occupy an endemic species' entire natural range. It is exceedingly difficult to conclusively demonstrate the extinction of a native species as a result of an invasion. Nevertheless, Perkins (1913) and Zimmerman (1948) felt that *P. megacephala* was likely responsible for extinctions of numerous lowland arthropods. Zimmerman (1970) even provided a specific example of a flightless dolichopodid fly that could no longer be found after its only known locality was overrun by *P. megacephala*, although other factors may have also played a role (Evenhuis 1997). Recently, three species of carabid beetles have been rediscovered adjacent to Argentine ant populations in Haleakala National Park after going undetected for over 100 years (Krushelnycky et al. in press a). None of these species have been found within ant-invaded areas, and all appear to have extremely localized distributions: all have been collected only above 2400 m in the west slope and summit area of Haleakala volcano. If the ongoing spread of the two ant populations cannot be halted or reversed, we may be placed in the unfortunate position of watching these beetle species

go extinct. Moreover, the invasion by Argentine ants of the majority of the subalpine shrubland and aeolian zone habitats at the top of Haleakala, as predicted (Krushelnycky et al. in press b), has the potential to eliminate other spectacular examples of Hawaiian evolution. For instance, a flightless moth that hops around the cinders (*Thyrocopa apatela* [Walsingham]), a flightless lacewing with spiked, beetle-like forewings (*Micromus cookeorum* [Zimmerman]), and a silversword-feeding long-horned beetle (*Plagithmysus terryi* [Perkins]) are only found there.

Although many native arthropod groups appear to suffer from ant invasion, some are able to persist and a few probably benefit from ant presence. A number of native flies coexist with ants in greatly altered lowland habitats (Montgomery 1975, Asquith and Messing 1993, Asquith 1995). At more intact, higher elevation sites, some mirid bugs and spiders persist in the presence of Argentine ants (while other species in both groups are eliminated), and contrary to previous reports from other localities (Muir 1916), native delphacid planthoppers appear to tolerate ants (P. Krushelnycky and R. Gillespie unpubl. data). In addition, some *Nysius* seed bugs can withstand ant invasion, and some endemic mealybugs may benefit from ant tending (Reimer et al. 1990). The long-term effects of ant presence in Hawaii's natural areas represent a highly important topic that deserves more research attention.

Effects on vertebrates and plants. The greatest loss in biodiversity resulting from ant invasion will necessarily occur among the arthropods, but introduced ants can also impact other native species, both directly and indirectly. As in other locations (Holway et al. 2002), ants can potentially reduce hatching success, growth rates and overall reproductive success of ground-nesting birds in Hawaii. Injuries from the aggressive, stinging tropical fire ant (*S. geminata*) are observed on the feet and undersides of wedge-tailed shearwater (*Puffinus pacificus*) chicks on some of Hawaii's offshore islands (S. Plentovich pers. comm.). Some injuries to the feet of chicks are severe and can result in the loss of more than 20% of the affected tissue. *P. megacephala* also attacks the feet of shearwater chicks, although observations are limited to Kure Atoll (C. Vanderlip pers. comm.). The Argentine ant can recruit heavily to pipped Nene (*Branta sandvicensis*) eggs, attacking the emerging chicks (F. Duvall pers. comm.), and this ant may reduce suitable habitat for the tree-nesting Palila (*Loxioides bailleui*) on Mauna Kea (Banko et al. 2002). As an exception, the Uau (or Hawaiian petrel, *Pterodroma sandwichensis*) appears to be unaffected by Argentine ant invasion of its nesting habitat in the cliffs high in Haleakala crater (Krushelnycky et al. 2001). In this case, cold temperatures within the petrel burrows likely discourage heavy ant foraging to the nest chambers.

As in agriculture, Hawaii's native plants can be damaged by elevated populations of homopterans in the presence of ants. In comparison to agricultural systems, however, this facultative relationship between ants and honeydew-producing insects typically appears less dominant in natural areas, particularly in higher elevation habitats. The reason for this is unclear, because ants can occasionally be found heavily tending scales on native plants in natural areas, and on some plant species, aphid densities are higher on individuals located within ant populations as compared to those outside ant populations (P. Krushelnycky unpubl. data). Moreover, native forests dominated by *Pisonia grandis* on several low coral islands in the Indian and southern Pacific Oceans have suffered dramatic tree mortality due to outbreaks of a scale, *Pulvinaria urbicola* Cockerell, tended by incredible densities of *A. gracilipes*, *P. megacephala* or other ants (Smith and Papacek 2001, Hill et al. 2003). This same indirect effect was also recently detected in the north Pacific at Palmyra Atoll, located approximately 1500 km south of Hawaii, when the spectacular *P. grandis* forests began rapidly dying. Such ant-scale mutualisms in native forest have sometimes developed decades after the ants are already established (O'Dowd et al. 2003), possibly indicating that a key feature is the arrival of the right homopteran mutualist.

Another mechanism by which ants can indirectly affect native plants is through their impacts on pollinators. The severe reduction in larval numbers of both *Hylaeus* bees and *Agrotis* moths resulting from Argentine ant invasion at Haleakala National Park was proposed by Cole et al. (1992) as a potential threat to the Haleakala silversword (*Argyroxyphium sandwicense macrocephalum*) and other obligate outcrossing species. More recent work modeling silversword demography suggests that seemingly moderate reductions in rates of seed set (e.g. from 30% to 20%) can lead to dramatic population declines over the long term (Forsyth 2002). If Argentine ants eventually invade large parts of Haleakala crater and concurrently reduce pollinator numbers throughout their range, silversword seed set could be reduced enough to place this iconic plant in jeopardy. In addition to preying upon pollinators, ants may exclude pollinators from flowers or exploit their resources through nectar thieving, both of which could also reduce seed set. Lach (in press) found that *A. gracilipes*, *P. megacephala* and *L. humile* all recruit to a high proportion of ohia (*Metrosideros polymorpha*) flowers, with *A. gracilipes* and *L. humile* actively defending these nectar sources. Native *Hylaeus* bees were less likely to land on flowers occupied by *P. megacephala*, and seed set was slightly lower in flowers visited by *L. humile* relative to those in which ants were excluded (Lach, in press). While these effects were moderate in ohia, it is possible that suppressed pollinator visitation due to ant presence may be more detrimental in rare, or less fecund, native plant species.

Finally, ants may in some cases impact native plants, as well as the animals that depend on them, by interfering with biological control of invasive plants. Reimer (1988), for example, found that *P. megacephala* can reduce the number of thrips biocontrol agents on *Clidemia hirta*, and may thereby increase the plant's vigor.

II. Prevention, Quarantine and Rapid Response

Although the rate of establishment of new ant species in Hawaii appears to have slowed in recent decades (Fig. 1), we cannot predict with certainty that the future colonization pattern will follow the same trend. Moreover, the number of additional species arriving is probably less important than their identities: several dozen new cryptobiotic species would be less worrisome than the arrival of *S. invicta* alone. The intentional or accidental introduction of weaver ants (*Oecophylla smaragdina* [Fab.] and *O. longinoda* [Latreille]) would also likely inflict tremendous impacts in natural areas (Loope et al. 2001). The fact that Hawaii has already been invaded by many damaging ant species does not negate the need to keep out others. Improved border protection and an established infrastructure for rapid response are essential if we hope to minimize the losses to our state's native biodiversity and economy that could result from such unwanted newcomers. The following summaries present some of the recent efforts and developments concerning these issues.

Prevention overview for Hawaii

Hawaii has some of the strongest state laws in the U.S. involving agricultural quarantine (NRDC/TNCH 1992, OTA 1993). The Hawaii Department of Agriculture (HDOA) is mandated to regulate importation of all plants and animals into the state. Mainly as a result of low staffing levels, however, HDOA is not currently able to monitor pathways into Hawaii from the continental U.S. to desirable levels. Blitz inspection sampling by HDOA of air cargo at Kahului Airport, Maui, during 20 weeks of 2000-2001, provided a means of evaluating unaddressed risk. Interceptions during this period of heightened inspection included 279 insect species, 125 of which were not known to be established in Hawaii, and 47 plant pathogen species, 16 of which were not known to occur in Hawaii (HDOA 2002).

For protection from organisms entering Hawaii from other countries, HDOA must pri-

marily rely on federal agencies—the Department of Homeland Security (DHS) and the United States Department of Agriculture (USDA). Federal quarantine officers have the option of referring for state inspection items from international arrivals that they suspect are subject to Hawaii agricultural quarantine, depending in practice on knowledge and commitment of the individual federal officer to intervene on behalf of state regulations. For ant species not yet established in Hawaii, however, this situation changed in 2002; federal quarantine officers are now charged with taking action themselves (USDA, APHIS, PPQ 2002—see below). This USDA policy change was supported by a risk assessment submitted by the Hawaii Ant Group, an informal, interagency collaboration established in September 1999, primarily to provide technical support to HDOA for addressing containment and possible eradication of the little fire ant (*W. auropunctata*) and prevention of establishment of the red imported fire ant (*S. invicta*).

Efforts to address the red imported fire ant

The South American red imported fire ant, *S. invicta*, had been intercepted by HDOA inspectors in 1991. Identified as among Hawaii's "Ten Least Wanted" pests in a 1996 educational brochure (CGAPS 1996), this notorious species has invaded more than 125 million ha in the southern U.S. since the 1930's despite a USDA federal quarantine. In 1998, *S. invicta* reached California, where it is still sparse (and still subject to an eradication campaign) but likely to invade most of the state within the next few years—a situation that poses an immense threat to Hawaii because of its high volume of trade with California. The red imported fire ant has invaded numerous Caribbean islands (Davis et al. 2001) from Florida in the last 20 years, and it is capable of doing the same in the Pacific unless concerted action is taken. Already it has reached Australia and New Zealand, where eradication campaigns are underway (Queensland Department of Primary Industries and Fisheries 2003; New Zealand Ministry of Agriculture and Forestry 2004), as well as Malaysia (Na and Lee 2001) and Taiwan (Chiu Yu-Tzu 2004).

In the continental U.S., *S. invicta* threatens public health and safety, industry, biodiversity and quality of life. Its aggressive nature and powerful sting have occasionally caused the deaths of people, injury to many people annually, and injury and death of wildlife, livestock, and pets (Vinson 1997). If *S. invicta* establishes in Hawaii, it is likely to invade most non-rainforest areas, except for the highest-elevation areas on Hawaii's volcanoes (VanGelder and Korzhukin 2001, Morrison et al. 2004). Consequently, it has the strong potential to negatively affect agricultural lands, parks, residential and other private properties, tourist destinations and native biodiversity in natural areas. *Solenopsis invicta* colonies grow rapidly and reach exceptional sizes; individual mature nest mounds may contain up to 200,000 workers, and there can be more than 500 mounds per hectare (Vinson 1997). Large numbers rapidly swarm onto anything that is unfortunate enough to disturb the colony, and each individual ant can deliver multiple painful stings. Naïve people, i.e. tourists and children, are most are risk for being stung. Attracted to electric equipment, the red imported fire ant commonly infests and damages electrical distribution systems, communication systems, air conditioners, well pumps, traffic boxes, and airport runway lights (Vinson 1997). If *S. invicta* becomes established in Hawaii, extensive use of pesticides to protect the state's residents, wildlife, tourist industry, agriculture, and other industries would almost certainly be employed, as it has in the continental U.S.

The stakes are clearly high for Hawaii to prevent establishment of this species, and HDOA reacted quickly to the news of its establishment in California by implementing stringent measures for importation into Hawaii of certain high-risk items in early 1999. This emergency measure required pre-treatment, at point of origin, of all potted plants and baled hay and straw from infested states (not only localities officially documented to be infested, as

the federal quarantine requires). Two states with *S. invicta* complained that, as a result of a revised federal quarantine rule for *S. invicta*, Hawaii was not legally entitled to require stronger measures than the federal quarantine already in place. (In the following year, federal "preemption" was codified by the Plant Protection Act of 2000, making it illegal for a state to impose more stringent restrictions if USDA has a federal quarantine program to prevent spread of a pest.). As a result of preemption, HDOA does not require treatment but recommends that USDA-approved treatments be used. If such treatments are used, HDOA relies on certification and does not inspect the commodity. If not treated, the material is held in quarantine upon arrival in Hawaii until fully inspected. Since this policy has been in place, approximately 97% of commodities have arrived treated (N. Reimer unpubl. data).

In early 2001, USDA provided assistance to the Hawaii Ant Group and HDOA in developing an affective strategy for the *S. invicta* prevention issue. The resultant approach avoided focus just on *S. invicta*, and instead addressed all non-native ants not already widespread in Hawaii. This strategy made it possible to avoid clashing with the preemption policy promulgated by the Plant Protection Act, but also provided hope of additional protection for Hawaii from all new ant species. The Hawaii Ant Group requested a change in the USDA policy so that standard operating procedure would require taking action whenever ants are detected in shipments to Hawaii (Hawaii Ant Group 2001b). At the time, existing USDA policy mandated that all ants intercepted from commodities bound for Hawaii (or any other U.S. port of entry) were non-reportable and did not require quarantine action except for non-native (to the U.S.) species in eight genera (*Acromyrmex*, *Atta*, *Crematogaster*, *Messor*, *Pheidole*, *Pogonomyrmex*, *Solenopsis* (subgenus *Solenopsis* only) and *Tetramorium*). Additionally, regulatory action would not have been taken on shipments infested with established, non-native continental ant species even within these eight genera unless they were under domestic quarantine control (Hawaii Ant Group 2001b). The request was accompanied by a risk assessment documenting the potential destructive effect upon Hawaii of establishment of any new ant species.

Within six months, USDA accepted the Hawaii Ant Group's request and communicated the change in policy to inspectors at all U.S. ports of entry (USDA, APHIS, PPQ 2002). According to the new policy, all "species of ants intercepted at all U.S. ports of entry and destined to, or through, the State of Hawaii would require quarantine action and would be considered reportable if 1) they are not already established and widespread in Hawaii, and 2) the life stages found in a given shipment indicate the ability to reproduce." The order listed the 40+ non-reportable ant species already widespread in Hawaii.

To complement and bolster these policy changes, the Hawaii Ant Group drafted a Red Imported Fire Ant Prevention Plan (Hawaii Ant Group 2001a). Actions identified as necessary for preventing establishment of *S. invicta* in Hawaii fell within four major groups: 1) determination of pathways through which *S. invicta* is transported and development of strategies for preventing it from reaching Hawaii; 2) development of strategies for detecting *S. invicta* quickly if it reaches the state; 3) establishment of methods with which to deal with incipient populations before they become firmly established; and 4) outreach to all red imported fire ant-affected sectors and the public. To fully implement the measures formulated would require immense cooperation among many sectors, both public and private. The plan was essentially complete by October 2001, but as of mid-2004 it remains largely a conceptual plan. Some important facets, however, have been addressed by HDOA and others (e.g. Gruner n.d., VanGelder and Korzhukin 2001, Gutrich et al. 2004).

Efforts to address the little fire ant

Whereas the threat of red imported fire ant introduction to Hawaii has been clear for several decades, the little fire ant, *W. auropunctata,* was a relatively unanticipated introduc-

tion, for example, not raised as an imminent invasive species threat by Loope et al. (2001). The little fire ant is nevertheless a very serious pest that can attain very high densities, and like *S. invicta*, its powerful sting poses problems for domestic animals, wildlife, agricultural workers and others who come in contact with it (reviewed in Wetterer and Porter 2003). Not surprisingly, it has also had tremendous impacts on native invertebrate communities in natural areas (Wetterer and Porter 2003).

The little fire ant was first detected in Hawaii in March of 1999 near Pahoa, Puna district, Hawaii Island (Conant and Hirayama 2000). It could have reached Hawaii Island from Florida, but a foreign source is also likely. This species is native to portions, if not most, of South and Central America and occurs in nearly all Neotropical countries and Caribbean islands (Wetterer and Porter 2003). It is invasive in the Galapagos, several locations in West Africa, in Florida, and in several Pacific island nations (New Caledonia, Wallis and Futuna, Solomon Islands, Vanuatu and most recently Tahiti) (Wetterer and Porter 2003, J-Y Meyer pers. comm.).

As soon as the little fire ant was detected on Hawaii Island, HDOA developed a pest advisory (Conant et al. 1999), and assigned entomologist Patrick Conant to lead efforts to address this new invasion. The interagency Hawaii Ant Group advocated the view in September 1999 that combating the little fire ant is exceptionally important since it makes an excellent surrogate for combating the red imported fire ant. HDOA efforts have involved detection, experimental efforts at eradication of local populations, and inter-island quarantine. They have been hindered by low staffing levels; lack of public and commercial awareness; lack of access to nursery sales records; the difficulty of detecting this ant; lack of a registered ant control product for use in orchard fruit and vegetable crops; the failure of most people to take the threat of its invasion seriously; and the likelihood that the ant had been present for as long as a decade before being discovered. HDOA demurred from an all-out eradication effort and enactment of an intra-island quarantine to prevent infected nurseries from selling plants. Whereas three populations totaling 12 ha in size were known on Hawaii Island in September 1999, this number has escalated to 31 populations totaling over 76 ha by January of 2004. Eight populations in January 2004 involved nursery infestations, and the nurseries were still selling plants (P. Conant unpubl. data).

Still, as of mid-2004 other Hawaiian islands were unknown to have *W. auropunctata* except for a single Kauai population. The current quarantine of Hawaii Island involves peanut butter baiting of any plants growing in media or soil before shipping; if *W. auropunctata* is detected, plants must be treated before leaving the island. However, a communication from experts at USDA, Agricultural Research Service in Florida to the Hawaii Ant Group (E. VanGelder pers. comm.) suggests that a quarantine at least as rigorous as the federal quarantine for *S. invicta* is needed to be successful—i.e., requiring that all risk goods shipped out of the high-risk area be treated. Because of the difficulty of detection and control, as well as the large and growing number of known Hawaii Island populations, the current prognosis is that eradication of the little fire ant is unlikely without a very large injection of funds and intra-island quarantine, but that confinement to Hawaii Island through improved inter-island quarantine may be possible. Surveys for *W. auropunctata* in high-risk areas (i.e. in the vicinity of recent plantings, especially of palms) of all islands are also necessary, and have recently begun on Maui and Kauai.

The limited success to date against this species underscores the importance of early detection and a pre-existing infrastructure ready for rapid response (Wetterer and Porter 2003). These factors have been key to New Zealand's effectiveness in dealing with recent *S. invicta* incursions in Auckland and Napier (New Zealand Ministry of Agriculture and Forestry 2004), and will become critical should *S. invicta* arrive in Hawaii.

The Pacific Ant Prevention Plan

Pacific island countries and territories (PICT) comprise over 25 countries, most of which are served by two important regional international organizations, the Secretariat of the Pacific Community (or SPC, which addresses agricultural issues) and the South Pacific Regional Environment Programme (or SPREP, which addresses biodiversity issues). Biodiversity of PICT is particularly vulnerable to effects of invasive species (SPREP 2000). Special concern regarding ant invasions has arisen now that the red imported fire ant occurs at or near the coast on both sides of the Pacific, and the little fire ant has arrived in Hawaii and is spreading in the western Pacific. These and other species threaten all Pacific islands, including Hawaii and the U.S. affiliated islands of Guam, Commonwealth of the Northern Marianas, Federated States of Micronesia, American Samoa, and Palau. What is the prognosis for a successful Pacific regional prevention program for invasive ants?

The SPC-Plant Protection Service (PPS), based in Suva, Fiji, works in partnership with 22 PICT members to maintain effective quarantine systems and to assist with regionally coordinated eradication/containment efforts. Priorities for emphasis are determined by member countries, which meet periodically as the Pacific Plant Protection Organization (PPPO). The most concerted and successful effort of PPPO and SPC-PPS to date has been with a regional program to address the many species of invasive host-specific fruit flies (Diptera: Tephritidae), which damage crops and reduce the ability of the countries to export much of their agricultural produce. A major Pacific island conservation meeting in Rarotonga in July, 2002, sponsored by SPREP and others, recommended prevention of new terrestrial and marine species introductions through implementation of improved quarantine legislation and practices (SPREP 2002). Subsequently, a workshop sponsored by the Invasive Species Specialist Group (ISSG) of IUCN was held in Auckland, New Zealand, in September 2003, and resulted in the compilation of a draft Pacific Ant Prevention Plan (Pacific Invasive Ant Group 2004).

The Pacific Ant Prevention Plan was presented to and embraced by 21 Pacific island countries and territories present at a PPPO meeting, the "Regional Biosecurity, Plant Protection and Animal Health" meeting held by SPC in Suva, Fiji, in March 2004 (Pacific Plant Protection Organization 2004). Like Hawaii's Red Imported Fire Ant Prevention Plan, the Pacific Ant Prevention Plan is still a conceptual work, but ISSG and others are working toward obtaining the international funding needed to implement the plan with the assistance of SPC. The project presents an exceptional opportunity for agriculture and conservation interests to work together with international and bilateral aid entities at regional and country levels to build much needed quarantine capacity. Increased quarantine protection is desperately needed by PICT in order to address invasions that jeopardize both agriculture and biodiversity.

III. Mitigating the Consequences of Ant Introductions

It is obviously too late to prevent the arrival of the many destructive ant species already in Hawaii. It is sometimes possible, however, to use control techniques to reduce the impacts of species already established. The control of ants in agriculture and suburban/urban situations, in particular, is well developed and has a long history. In recent years, ant control for the purpose of protecting biodiversity has gained momentum as well. As with the control of any pest, however, control techniques directed against ants will usually come with a cost. In agriculture, the use of pesticides can result in runoff or drift outside the intended area, and may adversely affect beneficial insects. In natural areas, such non-target impacts have the potential to involve native species. Non-target impacts must therefore be carefully evaluated whenever chemical control is being considered.

Ant control in agriculture

Ant control efforts in agriculture have relied almost exclusively on pesticides to reduce numbers of ants in target areas. In recent decades, chemical control techniques have used delayed-action toxicants formulated in bait carriers as a more effective means of targeting pest ants (McEwen et al. 1979). Because of the social behavior and efficient foraging abilities of ants, these baits permit the use of much lower doses of active ingredient and generally have higher specificity than blanket applications of contact pesticides. Subsequent to the de-registration of chemicals such as mirex and heptaclor in the late 1970's and early 1980's, hydramethylnon became a commonly used replacement because of its less persistent nature, and has been incorporated in numerous baits designed for structural and turf applications. Currently, however, it cannot be broadcast in most agricultural crops.

One exception is Hawaiian pineapple; hydramethylnon (formulated in the product Amdro) is used by the pineapple industry to control ants as an integral part of the strategy for preventing wilt disease. When ant numbers are reduced, natural enemies are usually able to bring about effective biological control of the mealybug disease vectors (Jahn et al. 2003). Other Hawaiian crops, however, have had no registered chemical products with which to control ant pests in recent years (G. Taniguchi pers. comm.). In response to this need, containerized bait stations were investigated in agricultural settings as an alternative to broadcast application of pesticides (Taniguchi et al. 2003). Bait stations provide the advantage of lower non-target risks and pesticide residues while prolonging the activity of light-sensitive toxicants. Supported by this work, a Special Local Need registration has recently been authorized by the EPA for the bait station use of Amdro ant bait (hydramethylnon) in over 50 Hawaiian tropical fruit and nut orchard crops. Insect growth regulators have also been researched for ant control in Hawaii (Reimer and Beardsley 1990, Reimer et al. 1991, Taniguchi et al. 2003), but so far have only been used sparingly in agriculture. In some situations, cultural practices or technological advances, such as the development of drip irrigation tubes resistant to ant chewing in sugar cane (Chang and Ota 1990), may be effective in reducing the impact of ants in agriculture.

An alternative to chemical control is biological control. In the case of invasive ants, this option is still in relatively early stages of development. Research to date has focused on developing parasitic phorid flies (Morrison et al. 1997), a fungus (Oi et al. 1994, Thorvilson et al. 2002) and a microsporidium (Oi and Williams 2002) for control of *S. invicta*, and similar biocontrol agents may eventually be developed for other invasive ants. Biological control may thus become a long-term technique for reducing some of the problems associated with invasive ants in Hawaii, but when used alone it holds little potential as a means for eradicating target ant populations.

Ant control for conservation purposes

Eradication of ant populations has recently become a goal in the conservation of certain natural areas. It is often the case that little can be done to ameliorate the impacts caused by introduced arthropods once they become firmly established in natural areas, but some of the most destructive introduced ants may represent an important exception. Because of their unicolonial structure, populations of some of these species can occur as discrete entities even when their overall distributions are much wider. This is a direct result of their budding mode of dispersal, in which mated queens found new nests by walking to nearby locations with retinues of workers (Holway et al. 2002). The lack of nuptial flights means that eradication of incipient populations could result in the permanent removal of these species from particular areas of concern, as long as re-introduction by humans can be prevented or quickly detected.

Eradication of invasive ant populations is by no means an easy task. Nevertheless, a growing number of successes around the Pacific provide evidence that under the right cir-

cumstances, eradication is possible. In the Galapagos, a 3 ha population of *W. auropunctata* was eradicated from Santa Fe Island in the 1980's and 1990's (Abedrabbo 1994), and a current effort is on the path to successfully eradicating a 21 ha population from the island of Marchena (Causton et al., in press). In New Zealand, a 13 ha population of *L. humile* is nearly eradicated on Tiritiri Matangi Island (C. Green pers. comm.), an incipient *S. invicta* infestation has been eradicated from the vicinity of Auckland airport, and a newly detected *S. invicta* population in Napier is currently being targeted (New Zealand Ministry of Agriculture and Forestry 2004). Eradication efforts in Australia have been the most ambitious to date: *P. megacephala* and *S. geminata* have been eradicated from a combined area of about 33 ha in Kakadu National Park (Hoffmann and O'Connor 2004), *L. humile* was eradicated from parts of Bunbury, Western Australia (Davis et al. 1998), and a massive effort is underway to eradicate *S. invicta* from over 50,000 ha of Brisbane (Queensland Department of Primary Industries and Fisheries 2003). In addition, Australian workers have targeted *A. gracilipes* for control on Christmas Island in the Indian Ocean.

These efforts have all employed the use of baits and toxicants, many of which were developed for agricultural or urban settings. We do not advocate the indiscriminate use of pesticide in Hawaii's natural areas; even though some toxicants, such as hydramethylnon, break down quickly, their use will likely be accompanied by at least some undesirable nontarget effects. Non-target impacts need to be considered especially carefully in situations where whole islands or the majority of a given habitat is treated, as entire populations of rare species could be eliminated. When the benefits of ant control have been judged to greatly outweigh non-target risks, however, and the target infestation occurs as a discrete and tractable entity, bait and toxicants may be an effective means of protecting native biodiversity.

Attempts to eradicate or control ants for conservation purposes in Hawaii have only begun in earnest within the last decade. These attempts have so far met with variable success, and we summarize the major initiatives below.

The Argentine ant at Haleakala National Park. The Argentine ant was first recorded in Haleakala National Park in 1967 (Huddleston and Fluker 1968), and over the next 30 years this species invaded over 500 ha of parkland and adjacent ranchland. In the process, a second unicolonial population became established higher up on the volcano's crater rim, and this upper population proceeded to spread down the steep crater walls to the crater floor. Analysis of the patterns of spread of the two populations suggests that the Argentine ant has the potential to invade nearly 50% of the park and 75% of the park's subalpine shrublands and aeolian zones (Krushelnycky et al. in press b), lending considerable support to its status as one of the most significant threats to the park's unique biodiversity.

In 1994 a concerted effort was initiated to investigate control techniques. The two populations in the park are well isolated from other Argentine ant invaded sites on the island, and despite the size of the infestations, it was hoped that eradication might still be possible with an effective bait and toxicant combination. A year-long bait preference test determined that among solid, granular baits (which can be aerially broadcast), the commercially available product Maxforce Granular Insect Bait (a.i. hydramethylnon) was the most attractive to this species (Krushelnycky and Reimer 1998a). However subsequent experiments in which small, 625 m^2 plots were treated with Maxforce, including several treatment variations, resulted in an unacceptable level of nest survival (Krushelnycky and Reimer 1998b). Similar results were obtained in subsequent trials conducted in 1 ha plots. It was judged that in order to eradicate Argentine ants from the park, complete mortality in experimental plots was a prerequisite; challenges and difficulties would only increase on a larger scale.

A secondary goal with respect to Argentine control at Haleakala National Park, that of containment, arose from the results of initial experiments with Maxforce bait. While eradi-

cation in treated areas did not occur, a massive reduction in foraging worker numbers was evident soon after treatment (Krushelnycky and Reimer 1998b). In 1996, an experimental plot situated along a rapidly expanding section of the lower Argentine ant population margin demonstrated that the substantial mortality resulting from Maxforce treatment could halt population expansion for at least one year (Krushelnycky et al. 2004). As a result, the entire expanding margins of both populations in the park have been treated once annually since 1997. While this experimental strategy has not completely stopped all outward spread, it has significantly slowed the invasion process (W. Haines unpubl. data) and is viewed as an important technique for maintaining the possibility of eradication. A non-target study conducted at this site suggested that relatively few non-ant arthropod groups are impacted from Maxforce treatments (W. Haines unpubl. data). The short duration of hydramethylnon activity in field conditions, combined with efficient retrieval of bait by ants, are likely responsible for this outcome.

Subsequent research into alternative bait and toxicant combinations for the purpose of Argentine ant eradication has employed the toxicants fipronil, abamectin and the insect growth regulator methoprene in various bait carriers (W. Haines, P. Krushelnycky and E. Van Gelder unpubl. data). None of these formulations has achieved eradication within experimental plots. The challenges facing the eradication of Argentine ants from Haleakala are formidable: the large size of the infestation, very high density of nests in some areas and extreme topography all necessitate a highly effective treatment technique in order to have a reasonable hope of success. The increasing number of apparent successes outside Hawaii, however, suggests that eradication may still be a possibility at Haleakala.

The little fire ant in Hawaii. Control of the little fire ant would benefit many interests in Hawaii, including conservation, tourism, public health and agriculture. Current efforts differ from traditional agricultural or urban control, however, in that indefinite suppression in target areas is not yet the goal. Although the rapidly growing number of known infestations suggested the difficulty of statewide eradication, several HDOA workers were allocated to attempt control or eradication of localized source populations on Hawaii Island.

As in the Galapagos eradication campaigns, HDOA employees have primarily used Amdro granular ant bait to target the little fire ant. This product is quite effective against *W. auropunctata* when it can be evenly broadcast throughout a population and when excessive humidity or rainfall does not disrupt application operations. Many of the infested sites in Puna support thick vegetation, however, making it difficult to achieve the thorough coverage necessitated by the little fire ant's short foraging distance. In addition, frequent rainfall has hampered the effectiveness of Amdro applications. Even more problematic, several infestations occur in fruit orchards, where no satisfactory technique for eradication is available. Probably the greatest challenge in controlling this species results from its small size and inconspicuous behavior at low densities. These traits make it difficult to detect until it is already well established, and combine with the high volume of intra-state trade in ornamental plants to greatly increase the likelihood of undetected, long-distance dispersal.

The little fire ant's inconspicuous behavior at low densities also makes intensive post-treatment monitoring obligatory (Causton et al., in press). For example, HDOA had found, treated twice, and attained apparent eradication of a small, residential Kauai *W. auropunctata* population in November 1999 based on monitoring for a year after treatment. A population was rediscovered at the same site in late 2003, however, and is now being targeted in a renewed cooperative effort by HDOA and the Kauai Invasive Species Committee. Despite the potential eradication of several of the smaller Hawaii Island infestations, and despite the temporary assistance of several state Emergency Environmental Workforce employees, the list of known infested sites continues to grow. HDOA can no longer treat all known populations, and relies on suburban property owners to address their own infestations (P. Conant

pers. comm.). By all accounts, *W. auropunctata* is a very difficult species to eradicate or control. Without a substantial increase in effort, it seems likely that Hawaii will quickly reach the point where the only recourse for little fire ant control will involve repeated, indefinite applications of pesticide in affected areas, perhaps combined with a far-term program to pursue biological control.

Control efforts on small islands. Many of Hawaii's offshore islets and remote coral atolls support seabird colonies, primarily because of the absence of people and introduced mammals. Ants inhabiting these important wildlife refuges potentially impact ground nesting seabirds and native arthropods. Experimental eradication of ants has therefore been attempted at several of these sites. At Midway Atoll in the Northwest Hawaiian Islands, Maxforce granular ant bait was broadcast twice in August 2001 on Spit Island (ca. 4 ha). Prior studies had determined this to be the best bait and method of application for the ant species and prevalent conditions (N. Reimer and C. Swenson unpubl. data). *S. geminata*, the dominant ant on Spit before treatment, was not detected again until one year later in August 2002. Because this species conducts mating flights, it is unclear whether these ants represented surviving nests or new colonizers from nearby islands in the atoll (C. Swenson pers. comm.).

In 2002, Mokuauia and Moku Nui Islets, both off the windward coast of Oahu, were treated with Amdro granular ant bait. One treatment with Amdro appears to have eradicated the dominant ant species, *P. megacephala*, from Mokuauia (ca. 3.9 ha) (S. Plentovich pers. comm.). Unfortunately, *S. geminata* subsequently colonized the islet. On Moku Nui (ca. 4.8 ha), both *S. geminata* and *P. longicornis* were abundant prior to treatment. Two broadcast applications of Amdro caused significant declines in both species. The substantial reduction of the aggressive *S. geminata* has in turn resulted in significantly fewer observations of sting-related injuries among wedge-tailed shearwater chicks relative to those nesting on the adjacent, untreated Moku Iki (S. Plentovich pers. comm.). The results of these small-island experiments are still being assessed for efficacy, feasibility and non-target effects, and as yet have not led to standard management practices.

Conclusions

The advent of new bait and toxicant combinations designed specifically for ants has expanded the range of possible management actions that can be considered in agricultural, urban and even natural settings. While attempts at eradication of the most destructive species have so far met with only limited success in Hawaii, eradication campaigns elsewhere suggest that with a more serious investment of effort and money, these results can be improved upon. As with most other invasive species, smaller ant populations will be easier to eradicate than larger ones. Consequently, prevention, early detection and rapid response remain the most practical strategies for dealing with invasive ants.

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Appendix

Ant species reported as established in Hawaii. We do not include a handful of non-cryptobiotic species that were only collected once or twice many decades ago, and which probably never truly established. Many of the species listed here were first recorded under synonyms, and in some instances were initially misidentified. We provide only currently recognized names; see notes below and original literature for details. Unless otherwise noted, all determinations of native locality were taken directly from McGlynn (1999).

Species	Year of first record	Citation	Native locality
1. Amblyopone zwaluwenburgi (Williams)	1941[1]	Williams 1946	unknown
2. Anoplolepis gracilipes (F. Smith)	1952[2]	Zimmerman 1953	Africa or tropical Asia
3. Brachymyrmex obscurior Forel	1914[3]	Timberlake 1925b	Neotropics
4. Camponotus variegatus (F. Smith)	1879	Smith 1879	Indo-Pacific area
5. Cardiocondyla emeryi Forel	1943	Swezey 1944	Africa and Near East[4]
6. Cardiocondyla kagutsuchi Terayama	1967[5]	Huddleston and Fluker 1968	India to SE Asia?[4]
7. Cardiocondyla minutior Forel	1893	Seifert 2003	Indomalayan region[4]
8. Cardiocondyla obscurior Wheeler	1994	Seifert 2003	unknown[4]
9. Cardiocondyla venustula Wheeler	1967[5]	Huddleston and Fluker 1968	Africa[4]
10. Cardiocondyla wroughtonii (Forel)	1893	Seifert 2003	Indomalayan region?[4]
11. Cerapachys biroi Forel	1908	Swezey 1916	SE Asia
12. Hypoponera opaciceps (Mayr)	1899	Forel 1899	Brazil
13. Hypoponera punctatissima (Roger)	1879[6]	Smith 1879	Europe?
14. Hypoponera zwaluwenburgi (Wheeler)	1933[7]	Wheeler 1934	unknown
15. Lepisiota sp.	1994	Kumashiro et al. 2001a	unknown
16. Leptogenys falcigera Roger	1879	Smith 1879	Africa
17. Linepithema humile (Mayr)	1940	Zimmerman 1941	South America
18. Monomorium destructor (Jerdon)	1899	Forel 1899	Africa or India
19. Monomorium floricola (Jerdon)	1899	Forel 1899	India and SE Asia
20. Monomorium liliuokalanii Forel	1899	Forel 1899	Europe
21. Monomorium pharaonis (Linnaeus)	1913	Gulick 1913	Africa?

Species	Year of first record	Citation	Native locality
22. *Monomorium sechellense* Emery	1916	Timberlake 1925a	Asia?
23. *Ochetellus glaber* (Mayr)	1977	Beardsley 1980	Australia and New Caledonia
24. *Paratrechina bourbonica* (Forel)	1879	Smith 1879	unknown
25. *Paratrechina longicornis* (Latreille)	1899	Forel 1899	Africa?
26. *Paratrechina vaga* (Forel)	1899	Forel 1899	Australia and SE Asia
27. *Pheidole fervens* F. Smith	1967	Huddleston and Fluker 1968	Asia
28. *Pheidole megacephala* (Fabricius)	1879	Smith 1879	Africa?
29. *Pheidole moerens* Wheeler	2000	Gruner et al. 2003	Puerto Rico?
30. *Plagiolepis alluaudi* Emery	1913	Gulick 1913	India?
31. *Ponera sweyezi* (Wheeler)	1933	Wheeler 1934	unknown
32. *Pseudomyrmex gracilis* (Fabricius)	1976	Beardsley 1979	Neotropics
33. *Pyramica membranifera* (Emery)	1932[8]	Wheeler 1933	Europe?
34. *Solenopsis geminata* (Fabricius)	1879	Smith 1879	Neotropics
35. *Solenopsis papuana* Emery	1967	Huddleston and Fluker 1968	Papuanal region
36. *Solenopsis* sp.	2000	Gruner et al. 2003	unknown
37. *Strumigenys emmae* (Emery)	1922	Timberlake 1925a	Papuanal region
38. *Strumigenys godeffroyi* Mayr	1961	Wilson and Taylor 1967	Polynesia
39. *Strumigenys lewisi* Cameron	1917[9]	Williams 1921	Asia
40. *Strumigenys rogeri* Emery	1933	Wilson and Taylor 1967	Neotropics
41. *Tapinoma melanocephalum* (Fabricius)	1899	Forel 1899	Unknown
42. *Technomyrmex albipes* (F. Smith)	1911	Swezey 1914	Indo-Pacific area
43. *Tetramorium bicarinatum* (Nylander)	1879	Smith 1879	SE Asia
44. *Tetramorium insolens* F. Smith	1993	Kumashiro et al. 2001b	Indo-Pacific area[10]
45. *Tetramorium simillimum* (F. Smith)	1934	Wheeler 1934	Europe
46. *Tetramorium tonganum* Mayr	1926	Swezey 1927	Pacific region
47. *Wasmannia auropunctata* (Roger)	1999	Conant and Hirayama 2000	Neotropics

[1]A total of five workers were collected in 1941 and 1945. This cryptobiotic species may still be present.

[2]Although the first published collection of this species was in 1952, specimens dated 1942 are deposited in the B.P. Bishop Museum.

[3]This species was reported only once from an orchid basket in Honolulu in 1914, until it was found to be established on Maui in 1997. The Maui population probably represents a separate introduction.

[4]Native localities for *Cardiocondyla* spp. were inferred, where possible, from Seifert (2003).

[5]Huddleston and Fluker's (1968) "*Cardiocondyla* sp. *c*" was later identified as *C. venustula*. More recent work indicates that both *C. venustula* and *C. kagutsuchi* are present in Hawaii, although *C. venustula* may currently be limited to Kauai (B. Seifert pers. comm. and P. Krushelnycky unpubl data). As Huddleston and Fluker (1968) reported "*C.* sp. *c*" from multiple islands, including Kauai, and *C. kagutsuchi* is very difficult to distinguish from *C. venustula*, we have decided to attribute both species to "*C.* sp. *c*", and have assigned 1967 as the year of first record for both species.

[6]Smith (1879) reported one ponerine present – *Ponera contracta* (= *P. coarctata*). Gulick (1913) related that Perkins believed this to be a misidentification of either *P. perkinsi* (= *Hypoponera opaciceps*) or *P. kalakauae* (= *H. punctatissima*). Because *H. punctatissima* was considered to be similar to *P. coarctata* (according to Forel 1899), we have decided to attribute the earlier record to *H. punctatissima*.

[7]This cryptobiotic species was last recorded in 1967.

[8]Last captured in 1945. This cryptobiotic species may still be present.

[9]Last captured in 1920. This cryptobiotic species may still be present.

[10]Native locality inferred from Bolton (1979).