

## **Technical Report HCSU-027**

# SURVEY OF INVASIVE ANTS AT HAKALAU FOREST NATIONAL WILDLIFE REFUGE

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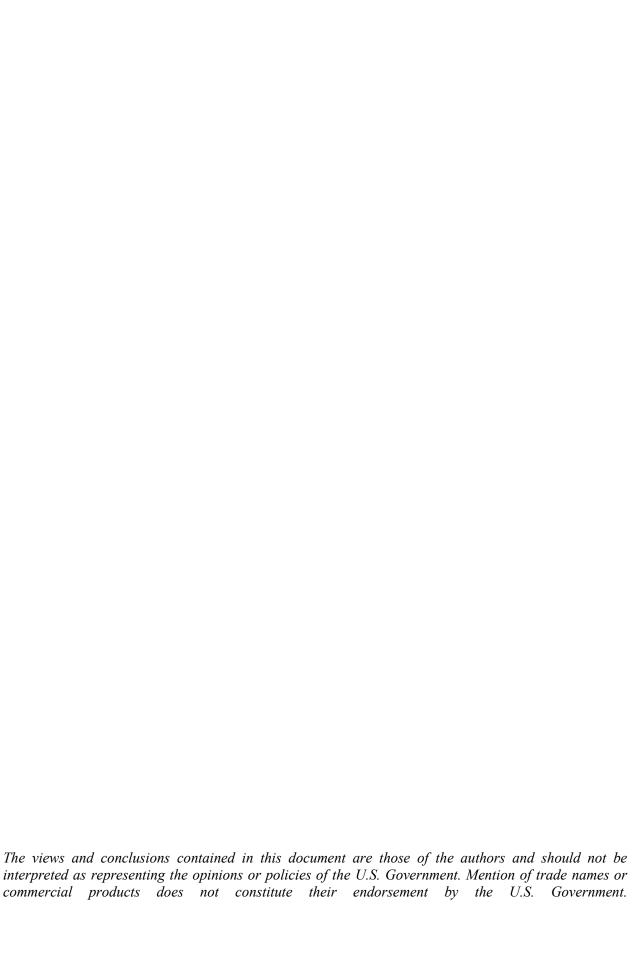
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## Citation

Peck, R. W., and P. C. Banko. 2011. Survey of invasive ants at Hakalau Forest National Wildlife Refuge. Hawai'i Cooperative Studies Unit Technical Report HCSU-027. University of Hawai'i at Hilo. 25 pp., incl. 12 figures, 1 table.

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This product was prepared under Cooperative Agreement G09AC00220 for the Pacific Island Ecosystems Research Center of the U.S. Geological Survey.



## **Table of Contents**

| Table of Contents  |    |
|--|----|
| List of Figures  |    |
| List of Tables   |    |
| Introduction   |    |
| Methods  |    |
| Areas surveyed   | 2  |
| Sampling protocols   | 2  |
| Location of sample points along roads and fences   |    |
| Location of sample points within koa corridors   |    |
| Focused sampling within closed-canopy forest adjacent to road populations  |    |
| Grass plots  |    |
| Survey of building compound on the Hakalau Forest Unit   |    |
| Survey of roads adjacent to Hakalau Forest Unit  |    |
| Results  |    |
| Hakalau Forest Unit  |    |
| Kona Forest Unit   | 1  |
| Discussion   | 12 |
| Acknowledgements   |    |
| Literature Cited   | 20 |
| List of Figures  |    |
| Figure 1. Locations of areas surveyed for ants on and adjacent to Hakalau Forest NWR                                   | 3  |
| Figure 2. Map of the upper portion of Hakalau Forest Unit showing areas sampled during the surv                        | ey |
| Figure 2. Pait and and nitfall tran  |    |
| Figure 3. Bait card and pitfall trap   |    |
| Figure 5. Cardiocondyla kagutsuchi feeding on bait and view of a worker ant  |    |
| Figure 6. Map of ant detections within the Naūhi, Hakalau, and Puaʻākala sections of Hakalau For NWR                   |    |
| Figure 7. Map of ant detections within the Maulua Section of the Hakalau Forest Unit of Hakalau                        |    |
| NWR  |    |
| Figure 8. Map of ant detections in the Hakalau Forest Unit and along Keanakolu-Mana and Blair I                        |    |
| Figure 9. Solenopsis papuana and Nylanderia bourbonica workers   |    |
| Figure 10. Map of ant detections in the Kona Forest Unit   | 13 |
| Figure 11. Typical closed-canopy habitat surveyed in Hakalau Forest NWR  |    |
| Figure 12. Typical Cardiocondyla kagutsuchi habitat in Hakalau Forest NWR  | 16 |
|  |    |
| List of Tables   |    |
| Table 1. Survey effort (number of stations and kilometers of transects) in different habitats potenti occupied by ants | •  |

## **Executive Summary**

We conducted a survey for invasive ants at Hakalau Forest National Wildlife Refuge, Hawai'i Island, during 2009–2010 to evaluate potential threats to native arthropod communities and food webs. The focal area of the survey was the upper portion of the Hakalau Unit of the refuge, where native forest was being restored in abandoned cattle pastures. This area, between 1575 and 1940 m elevations, contained much alien kikuyu grass (*Pennisetum clandestinum*), but koa (*Acacia koa*) trees and other native species that were planted in the past 20 years were rapidly filling in the pasture. We surveyed for ants at predetermined points along roads, fences, and corridors of planted koa. Sampling methods primarily consisted of hand searching and pitfall traps, but bait cards were used additionally in some instances. Our results indicated that a single species, Cardiocondyla kagutsuchi, was widespread across the upper portion of the refuge. Cardiocondyla kagutsuchi seemed absent, or at least rare, in areas of tall, dense grass. Due to the undulating topography of the area, however, the dense grass cover was interspersed with outcroppings of exposed, gravelly soil. Presumably due to warming by the sun, many of the outcropped habitats supported colonies of C. kagutsuchi. We did not detect ants in the old-growth forest below the abandoned pastures, presumably because microhabitat conditions under the forest canopy were unsuitable. Although ecological impacts of C. kagutsuchi have not been reported, they may be limited by the small size of the ant, the relatively small size of colonies, and the apparent preference of the ant for disturbed areas that are dominated by alien species. Notably, our survey of Keanakolu-Mana Road between the Observatory Road (John A. Burns Way) and the town of Waimea detected a population of Argentine ants (*Linepithema humile*) approximately 5.1 km north of the Maulua Section of the refuge.

We also surveyed for ants on the Kona Forest Unit of the refuge. This small survey focused on approximately 14 km of roads located below about 1600 m elevation. We found two species, *Solenopsis papuana* and *Nylanderia bourbonica*. *Solenopsis papuana* was more widespread, being found along the southern, northern, and western boundaries, while *N. bourbonica* was detected only at 790 m elevation on the southern boundary. Of the two species, *S. papuana* seemed more likely to affect native arthropod communities due to its tendency to form relatively large, aggressive colonies and its ability to inhabit intact mesic and wet forests below 1100 m elevation. In contrast, the restriction of *N. bourbonica* to disturbed habitats indicated a reduced threat to native arthropod communities. Our results on the Kona Forest Unit corroborated those of a study conducted during 1999–2000, although the earlier study was more intensive over time and yielded small numbers of two additional species, *Cardiocondyla wroughtonii* and *Tetramorium bicarinatum*, both of which were detected below 792 m elevation along the southern boundary.

#### Introduction

Extreme isolation of the Hawaiian archipelago has resulted in an insect fauna likely devoid of native ants. Nevertheless, transported by the shipping trade throughout the Pacific Ocean, ants were quick to colonize Hawai'i. Their impacts were soon recognized, as Andrew Bloxom (1925) noted in his diary in 1825 that ants made "sad ravages" of bird specimens he had collected in his capacity as naturalist aboard the H.M.S. *Blonde*. R.C.L Perkins (1913) made similar comments about the sweeping impacts of ants on native insects, and based on his collections, 20 species had been reported in the islands by the end of the 19<sup>th</sup> century (Forel 1899). The number of ant species in Hawai'i continues to grow. The notorious little fire ant (*Wasmannia auropunctata*), first found in Hawai'i in 1999, is among the most recent invaders. To date, as many as 47 species have inadvertently been introduced to the Hawaiian Islands (Krushelnycky *et al.* 2005b). Most ants found in Hawai'i are among a suite of tramp species that are widely distributed among many islands in the Pacific Basin.

Ecological impacts of most invasive ant species are unknown, but some species can profoundly alter native arthropod communities and ecosystems. For example, Perkins (1913) reported that it was nearly

impossible to collect native insects within the range of big-headed ants (*Pheidole megacephala*), which by the 1890s were widespread in lowland habitats. *Pheidole megacephala* also significantly reduced abundances of native ants as well as several other orders of insects after invading pockets of wet forest in the Northern Territories of Australia (Hoffmann *et al.* 1999, Hoffmann and Parr 2008). Similarly, invasive Argentine ants (*Linepithema humile*) reduced the diversity and abundance of several groups of non-ant arthropods in Hawai'i (Cole *et al.* 1992, Krushelnycky and Gillespie 2008) and northern California (Human and Gordon 1997), although non-ant arthropod communities seemed little affected elsewhere (Holway 1998, Rowles and O'Dowd 2009). Significantly, the Argentine ant invasion on Haleakalā Volcano, Maui, affected native species more than non-native species (Krushelnycky and Gillespie 2010). Yellow crazy ants (*Anoplolepis gracilipes*) reduced numbers of native arthropods in the Seychelles (Haines and Haines 1978) and in Tokelau (Lester and Tavite 2004), and altered the composition and structure of forest vegetation on Christmas Island in the Indian Ocean by decimating populations of land crabs, the dominant grazer of understory seedlings (O'Dowd *et al.* 2003).

The vast majority of invasive ant research conducted worldwide has focused on a relatively small number of species with widespread distributions and highly aggressive behavior. For the majority of the other invasive ants, little is known about their distribution, habitat requirements, and ecological impacts. Our survey developed as a result of *Cardiocondyla katgutsuchi* being detected on the Hakalau Unit of Hakalau Forest National Wildlife Refuge during 2008. This small, somewhat cryptic species was found within a stand of young koa (*Acacia koa*) trees that had been planted in former pasture land above the mature, closed canopy, native forest. The ant was subsequently found in the greenhouse area, where plants are propagated and prepared for planting on the refuge. Due to the high ecological value of the refuge for forest birds and their arthropod prey, surveys were developed to understand the extent to which this or other ant species had invaded the refuge.

The primary objective of our study was to survey areas of the Hakalau Forest Unit of the refuge where ants were most likely to occur due to planting and other disturbance. We predicted that ants would only be detected in disturbed areas above the main forest because initial detections were associated with human activity and because other ant species in Hawai'i generally avoid closed-canopy, mesic or wet, montane forests. Therefore, we focused the survey to roadsides, fence lines, and strips of koa and other species that were planted in the former pasture lands above the mature forest. To better understand threats to this unit of the refuge, we also sampled roads traveling through habitat adjacent to the refuge.

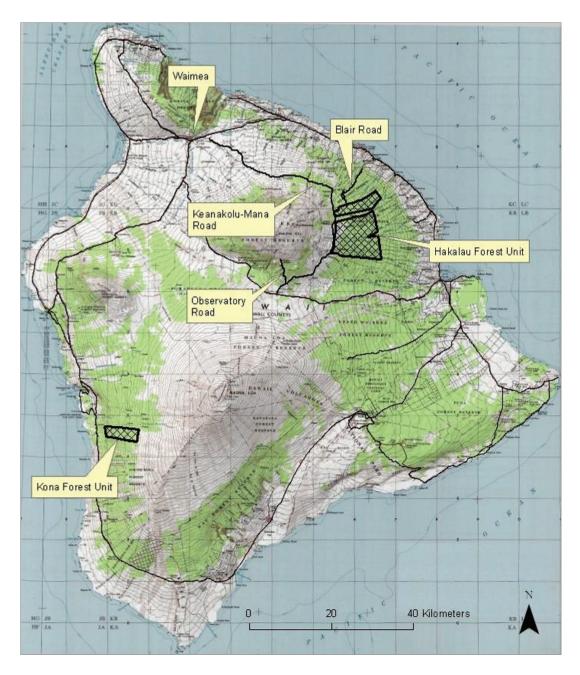
Our secondary objective was to survey ants within the Kona Forest Unit of the refuge. A survey of the Kona Forest Unit conducted by Haines and Foote (2005) found several species of ants along the lower portion of the southern boundary. We resurveyed that area as well as several newer roads not examined during that study.

#### Methods

#### Areas surveyed

We surveyed for ants on windward Hawai'i Island at the Hakalau Forest Unit of Hakalau Forest National Wildlife Refuge (NWR), on adjacent lands to the north of the refuge, and along the main road running along the western border of the refuge. On leeward Hawai'i, we conducted surveys at the Kona Forest Unit of Hakalau Forest NWR. Survey locations are shown in Figure 1 and discussed in detail below. In total, we surveyed nearly 150 km of transects through a variety of habitats (Table 1).

In the Hakalau Forest Unit, we focused our surveys on former pastures where koa and a few other native species had been planted in long strips extending down to the mature forest of 'ōhi'a (*Metrosideros polymorpha*) and koa to provide habitat corridors for the re-colonization of native plants, birds, and



**Figure 1.** Locations of areas surveyed for ants. The Hakalau Forest and Kona Forest units comprise Hakalau Forest National Wildlife Refuge (NWR). Blair Road lies within Hilo Forest Reserve and Laupāhoehoe Natural Area Reserve. Keanakolu-Mana Road extends from Observatory Road to the town of Waimea.

arthropods. The forest restoration area lies primarily above 1575 m elevation and represents habitat favorable to ants due to the relatively open canopy of the newly-emerging forest. Within this area, roads (both gravel-based and those tracked through grass), fence lines, and planted corridors of koa were surveyed. Fence lines within several areas of closed-canopy forest were surveyed to assess the prediction that heavily-shaded environments were unsuitable habitats for ants. Fence lines running through closed-canopy forest that we surveyed included: 1) the contour fence running at approximately 1575 m elevation

**Table 1.** Survey effort (number of stations and kilometers of transects) in different habitats potentially occupied by ants.

|                        |          |          |            |          |              |          | Closed              | -canopy  |
|------------------------|----------|----------|------------|----------|--------------|----------|---------------------|----------|
|                        | Road     |          | Fence line |          | Koa corridor |          | forest <sup>1</sup> |          |
|                        | Stations | Transect | Stations   | Transect | Stations     | Transect | Stations            | Transect |
|                        |          | (km)     |            | (km)     |              | (km)     |                     | (km)     |
| Hakalau Unit           | 164      | 37       | 151        | 32       | 37           | 3.7      | 20                  | 0.8      |
| Blair Road             | 20       | 9        | ns         | ns       | ns           | ns       | ns                  | ns       |
| Keanakolu-Mana<br>Road | 35       | 50       | ns         | ns       | ns           | ns       | ns                  | ns       |
| Kona Unit              | 68       | 14       | ns         | ns       | ns           | ns       | ns                  | ns       |

Focused sampling where stations were near roads and along a transect following an adjacent fence line ns = not sampled

adjacent to the end of the road at Pua'ākala (800 m of fence surveyed); 2) the fence running downslope along the southern boundary of the refuge (along Nukupahu Gulch) for approximately 500 m below the 1575 m fence; 3) the fence along the boundary shared between the Nāuhi Section of the refuge and the Piha Section of Hilo Forest Reserve (state land) for approximately 400 m below Nāuhi Camp; and 4) in forest habitat adjacent to two sites on roads where ants had been detected. We also surveyed for ants around refuge buildings (Hakalau Forest Unit), including the greenhouse, where *C. kagutsuchi* was found in October 2008.

We were unable to access remote, lower-elevation areas of the Hakalau Forest Unit, but we were able to sample adjacent habitats along Blair Road within Hilo Forest Reserve and Laupāhoehoe Natural Area Reserve, located directly north of the Maulua Section of the refuge (Figure 1). This area is generally similar to the refuge in rainfall, forest canopy structure and closure, and degree of disturbance. We surveyed 9 km between 700 and 1600 m elevation along Blair Road, a rock- and gravel-based track that seemed to represent suitable habitat for ants except for the generally closed forest canopy. We also surveyed approximately 50 km along Keanakolu-Mana Road between Observatory Road (John A. Burns Way) and the town of Waimea to identify distributions of ants along the route by which they were most likely to be dispersed to the refuge (Figure 1).

In the Kona Forest Unit (Figure 1), the survey took place on the three roads that run along contour at approximately 600, 1050 and 1450 m elevation, and along major portions of the southern and northern boundary roads west of (below in elevation) the intersecting road at 1450 m elevation. In total, we surveyed along 14 km of road in this unit.

## Sampling protocols

We conducted ant surveys in the Hakalau Forest Unit during October–December 2009 and in the Kona Forest Unit during 11 March, 29 April, and 6 May 2010. Drier than normal conditions prevailed during the surveys, although ground cover and other vegetation were generally green, especially in the Hakalau Forest Unit.

Following a preliminary survey of the Hakalau Forest Unit in October 2008, during which scattered populations of *C. kagutsuchi* were found along Pedro Road and nearby fence lines, we surveyed for ants at pre-established points using one or more standard techniques, including: 1) hand-searching the ground for a minimum of five person-minutes; 2) pitfall-trapping; and 3) baiting.

Pitfall traps consisted of 150-ml plastic specimen cups buried with their open tops flush with the ground. Each trap was filled with approximately 30 ml of preservative (propylene glycol mixed with water to

form a 50% solution) and was covered with an 18-cm diameter plastic picnic bowl elevated slightly above the ground by rocks to prevent flooding during rain. Roads were generally too rocky to install pitfall traps, so we placed traps within 2 m of the roadway. Bait consisted of canned tuna drained of oil and mixed with corn syrup (50/50 mix). Approximately 1 cc of bait was placed on a 7 x 5 cm card, which was placed on the ground. Where necessary, tall or thick grass was spread to allow the bait card to be in contact with the ground.

Because *C. kagutsuchi* generally do not recruit aggressively to baits, survey methods in the Hakalau Forest Unit focused on hand-searching and pitfall-trapping, although baiting was used to supplement the survey in some instances. In the Kona Forest Unit, however, where several ant species had previously been identified, we surveyed primarily by baiting but with supplemental hand-searching. The survey along Blair Road was conducted by baiting and hand-searching while stations along Keanakolu-Mana Road were surveyed by hand-searching.

## Location of sample points along roads and fences

A sampling protocol establishing survey points at 100-m intervals along roads and fences was developed using Hawth's Analysis Tools (Spatial Ecology.com) for ArcGIS prior to onset of the surveys. Hawth's Analysis Tools allows points to be generated at fixed distances along pre-determined lines identified within GIS layers. Sample points were then loaded onto GPS units (Garmin GPSmap 60CSx) for location in the field. In areas where fences were immediately adjacent to roads, we searched primarily along the roadway where gravel or exposed soil was most likely to harbor ants.

## Location of sample points within koa corridors

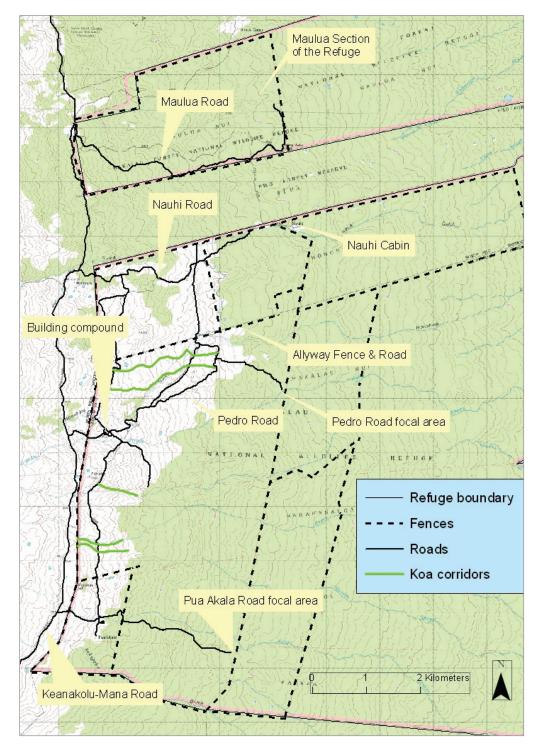
We surveyed for ants within five planted corridors of young (10–20 years) koa, located between Puaʻākala Road and the Alleyway fence line (Figure 2), using the same sampling methods as used along roads and fences. Stations were placed at 100-m intervals within the approximate center of each corridor (corridors were generally two to three trees wide). The number of stations within each corridor ranged between 6 and 13, depending upon corridor length. Pitfall traps were placed at each station and we searched by hand for ants within about a three-meter radius of the station for five minutes. We also spent up to five minutes opportunistically searching micro-sites within corridors where exposed, rocky substrates or other conditions seemed especially suitable for ants.

#### Focused sampling within closed-canopy forest adjacent to road populations

We conducted focused surveys adjacent to known populations of ants at the bottom of Puaʿākala and Pedro Roads to determine whether ants had penetrated mature forest habitat. In both areas, we surveyed 10 sites located 8–61 m of the road within habitats that seemed most likely to harbor ants, such as leaf litter at the base of trees and shrubs or exposed moss or soil where the grass cover was relatively thin (Figure 3). We sampled the forest floor at each site by hand-searching (for five minutes), pitfall trapping (n = one trap), and baiting (n = two bait cards). Bait cards were checked at approximately 10-min intervals for one hour, and pitfall traps were retrieved after about one week. Additionally, we surveyed for ants by baiting and hand-searching at 100-m intervals for 800 m (400 m in each direction) along the fence extending perpendicularly through the forest at the bottom of Puaʿākala Road.

## Grass plots

We conducted a small-plot experiment in which grass was mowed and ants surveyed by baiting and hand-searching to test whether thick grass cover was unsuitable habitat for ants or whether our survey methods were ineffective in thick grass. Four study areas were established adjacent to roads where ants were detected. At each study area, four 1 x 1 m plots were established in grass approximately 2–5 m from the road. Within each of the 16 plots, we clipped the grass to a height of 2–3 cm and immediately hand-



**Figure 2.** Locations of sampling routes in the upper portion of Hakalau Forest Unit of Hakalau Forest NWR. The lower part of the refuge, not sampled for ants, has been cropped from view.



**Figure 3.** Bait card (small square slightly left of center) and pitfall trap (covered by yellow bowl) located in forest adjacent to the location at the bottom of Pedro Road where *C. kagutsuchi* was found.

searched for ants. Following about five minutes of hand-searching, one bait card was placed at the center of each plot and monitored for ants for one hour (Figure 4).

Survey of building compound on the Hakalau Forest Unit

We spent 1.5 person-hours surveying for ants by hand-searching around the greenhouse and other buildings within the Hakalau Forest Unit compound.

Survey of roads adjacent to Hakalau Forest Unit

Blair Road, located directly north of the Maulua Section of the refuge, was surveyed by baiting and hand-searching at 20 stations spaced at 500-m intervals.

We also surveyed for ants along Keanakolu-Mana Road, running above the Hakalau Forest Unit. We hand-searched for 10 person-minutes at each of 35 stations spaced at 1–2 km intervals. We sampled at 15 stations between the Puaʻākala section of the refuge and the Observatory Road and 20 stations between the Maulua section of the refuge and the town of Waimea.



**Figure 4.** Sampling plot (1 m<sup>2</sup>) with thick grass trimmed to 2–3 cm height. Immediately after trimming the grass, ant surveys were conducted by hand-searching and baiting (see white bait cards at center-left).

## **Results**

We detected four species of ants during our surveys. *Cardiocondyla kagutsuchi* and *L. humile* were found during the windward surveys, and *Solenopsis papuana* and *Nylanderia bourbonica* (until recently known as *Paratrechina bourbonica*) were found during the leeward surveys. Ants were found above 1500 m elevation during the windward surveys and below 600 m elevation during the leeward surveys. We detected ants only in relatively disturbed areas, especially along roads. We saw no evidence of ant penetration into closed-canopy forest away from roads or fence lines.

#### Hakalau Forest Unit

#### Roads and fences

Ants were found at 96 of 315 stations at the Hakalau Forest Unit. All ants detected were *C. kagutsuchi* (Figure 5). Ants were found intermittently along Maulua, Pedro, and Puaʻākala roads, and as low as 1600 m elevation on Nāuhi Road (Figures 6 and 7). No ants were found at Nāuhi Camp (approximately 1575 m elevation) or along the widened portion of road directly above the cabin. Neither were ants found along fence lines passing through closed-canopy forest on the refuge, including the fence at the bottom of Puaʻākala Road.



**Figure 5.** Cardiocondyla kagutsuchi feeding on bait mixture of tuna and corn syrup (left), and a close-up view of a worker ant (right).

#### Koa corridors

Overall, ants were found in four of the five koa corridor transects, where grass was densely distributed. Although they were recorded at only 2 of 37 pre-established stations distributed over all corridors surveyed (Figure 6), ants were patchily distributed within the corridors, being found at six additional locations between stations where there was exposed, gravelly substrates.

#### Focused sampling within closed-canopy forest adjacent to ant populations

Of the 20 stations sampled within forest habitat adjacent to the bottoms of Puaʻākala and Pedro Roads, *C. kagutsuchi* was detected once on a bait card placed 22 m from Puaʻākala Road on a gravelly patch of ground within an area otherwise dominated by grass. Ants were not captured in a nearby pitfall trap placed in dense grass. No ants were found at any of the eight stations running along the "1600-m fence" adjacent to this site.

#### **Grass plots**

No ants were found by hand-searching in any of the 16 plots in which grass had been clipped, but *C. kagutsuchi* was subsequently found at a bait card in one plot.

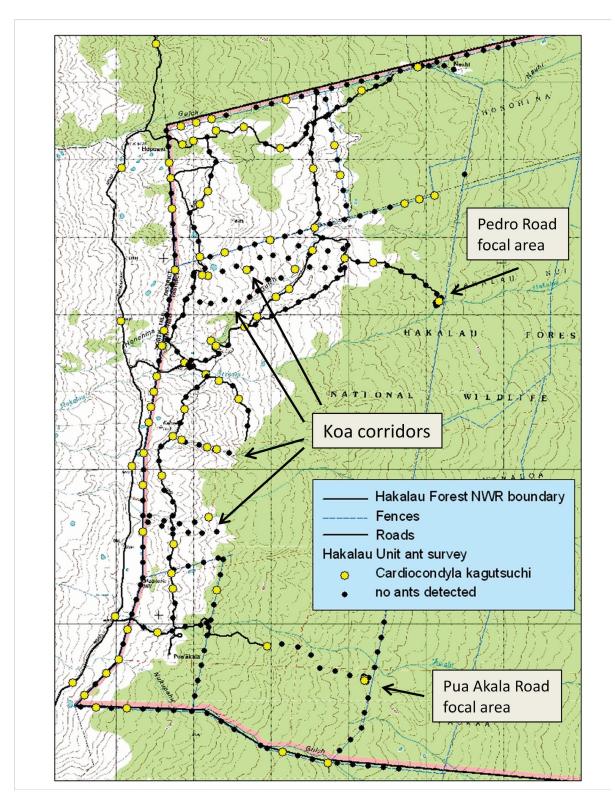
#### Refuge building compound

Our survey of the building compound found *C. kagutsuchi* at several places between the volunteer cabin and the University of Hawai'i facility. We did not find ants near the greenhouse, despite having found *C. kagutsuchi* there in October 2008.

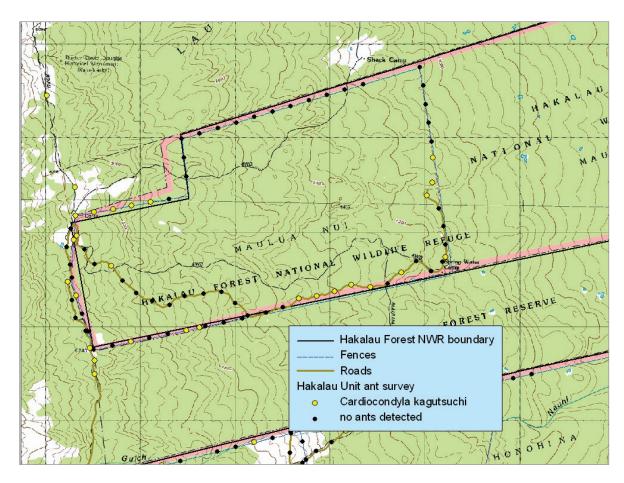
#### Surveys of roads adjacent to Hakalau unit

Cardiocondyla kagutshuchi was found at 3 of 20 stations located along Blair Road (Figure 8). Ants were detected at the first and second stations (700 and 770 m elevation, respectively) and at the top gate bordering open-canopy ranch land (1650 m elevation). Ants were not detected at stations between those points, where the canopy was more complete and understory vegetation less disturbed.

Cardiocondyla kagutsuchi was found at 6 of 15 stations along Keanakolu-Mana Road between the refuge and the Observatory Road, with ants detected as far as 12 km east of the Puaʻākala section of the refuge (Figure 8). Although rain reduced survey effort to four stations over the westernmost 14 km of Keanakolu-Mana Road, *C. kagutsuchi* was detected at stations located 1, 2, 3, and 17 km from the refuge. Additionally, *L. humile* was found at all stations between 6 and 15 km from the Maulua section of the



**Figure 6.** *Cardiocondyla kagutsuchi* (yellow circles) was detected intermittently along roads, fence lines, and planted koa corridors but not in dense forest or undisturbed sites during surveys within the Naūhi, Hakalau, and Puaʻākala sections of Hakalau Forest NWR.

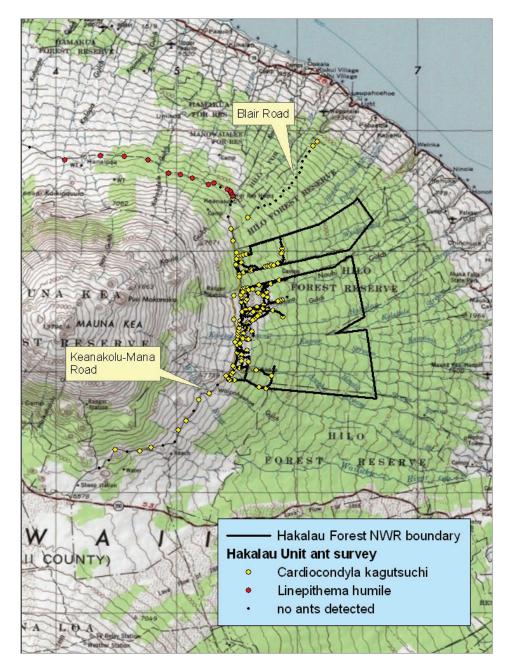


**Figure 7.** Cardiocondyla kagutsuchi (yellow circles) was detected frequently along roads and fence lines, except the fence line along most of the northern boundary during surveys within the Maulua section of the Hakalau Forest Unit of Hakalau Forest NWR.

refuge (Figure 8). A more intensive, follow-up survey, consisting of baiting and hand-searching, located the population front of Argentine ants at the gate just north of Keanakolu Ranger Station, a linear distance of 5.1 km from the refuge boundary, or 5.8 km along the road. *Cardiocondyla kagutsuchi* was found less than 100 m south (towards the refuge) of the Argentine ant population front. Only one ant species was found at any given station along the entire road.

## Kona Forest Unit

Two species of ants were found in the Kona Forest Unit of the refuge (Figures 9 and 10). *Solenopsis papuana* was found between 550 and 750 m elevation at two stations along the northern boundary, four stations along the bottom road, and three stations along the southern boundary. *Nylanderia bourbonica* was found at a single station at 790 m elevation on the southern boundary. No ants were detected along the middle contour road (1050 m elevation), along a short section of the northern boundary (four stations) between 1485 and 1590 m elevation, or along the southern boundary between 850 and 1667 m (where the "5400-ft Road" intersects the southern boundary road).



**Figure 8.** Results of ant surveys in the Hakalau Forest Unit of Hakalau Forest NWR and Keanakolu-Mana and Blair Roads. Populations of *Cardiocondyla kagutsuchi* (yellow circles) and *Linepithema humile* (Argentine ant; red circles) were not intermingled, and only *C. kagutsuchi* was detected on the refuge.

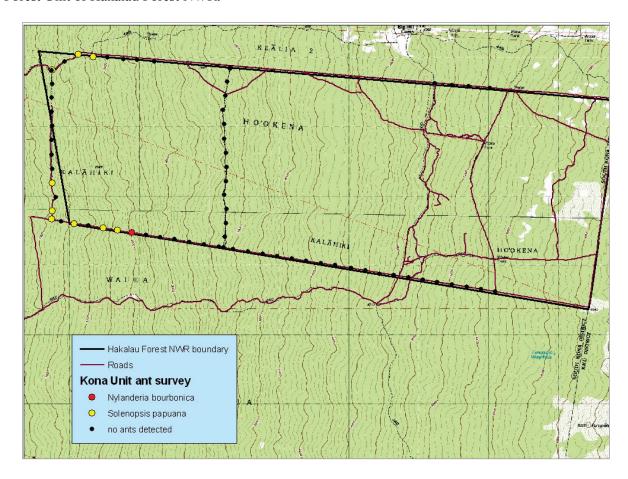
#### **Discussion**

The methods we used to survey ants were likely adequate to have detected most surface-dwelling ant species found in Hawai'i, especially the more aggressive invasive species having the greatest potential to affect native species and disrupt communities. Nevertheless, hand-searching was the most effective method of detecting *C. kagutsuchi*. Of 66 stations where ants were detected and both pitfall-trapping and



Photos: April Nobile, www.antweb.org

**Figure 9.** *Solenopsis papuana* (left) and *Nylanderia bourbonica* (right) were collected on the Kona Forest Unit of Hakalau Forest NWR.



**Figure 10.** *Solenopsis papuana* (yellow circles) was distributed along roads on the lower (western) portion of the Kona Forest Unit of Hakalau Forest NWR, whereas *Nylanderia bourbonica* (red circle) was found at only one station along the southern boundary road.

hand-searching took place, ants were detected only by hand-searching on 59 occasions and only by pitfall-trapping on 3 occasions. This comparison should be viewed with caution, though, because pitfall traps were often placed in areas with more grass than where hand-searching was conducted. The likelihood of detecting *C. kagutsuchi* either by hand-searching or by baiting was similar, with ants found seven times only by hand-searching and two times only by baiting. That we detected only four ant species was not surprising, given the preponderance of relatively cool, wet, montane forest or areas of dense grass cover included in the survey. These conditions are not generally favorable to ants in Hawai'i (Reimer 1994, Krushelnycky 2005a), and explain why we found ants almost entirely in disturbed habitats along roads, fence lines, and exposed, rocky substrates. Only one highly invasive species, the Argentine ant (*L. humile*), was found during the survey, and occurred only along a road passing through pasture lands and heavily grazed woodland outside the refuge.

#### Hakalau Forest Unit

Cardiocondyla kagutsuchi was frequently recorded across the entire upper portion of the refuge and along Keanakolu-Mana Road, suggesting that most patches of suitable habitat had been colonized, especially along roads, fences, planted koa corridors within former pasture lands, and exposed, rocky substrates. The infrequency and low numbers in which *C. kagutsuchi* was detected in dense grass underscored its preference for substrates exposed to sunlight. Furthermore, the near-absence of ants in forests near the bottoms of Puaʻākala and Pedro roads and along fence lines in densely-shaded habitats (Figure 11) suggested that *C. kagutsuchi* was not likely to establish colonies below the former pasture lands, except in disturbed areas.

Cardiocondyla kagutsuchi was found at the bottom of Pedro Road in 2008 during reconnaissance surveys, but not in 2009, suggesting that populations may be dynamic and their existence transient at some locations, particularly at the margins of their distribution. Heinze *et al.* (2006) noted that locations of Cardiocondyla nests were frequently ephemeral and that colonies often migrated among nest sites as food resources were depleted. Therefore, at potentially marginal sites, colonies of *C. kagutsuchi* may appear and disappear when environmental conditions change.

Microclimatic conditions near the soil surface were likely the most important factor determining the distribution of *C. kagutsuchi* on the refuge. For many species of ants, temperature influences foraging activity as well as the rate at which eggs, larvae, and pupae develop. When temperatures are too low for too long, development cannot be completed. Temperature requirements for most species of *Cardiocondyla* are unknown, but Creighton and Snelling (1974) reported that *C. emeryi* workers did not begin to forage until ground surface temperatures reached 21°C (70°F). In areas we surveyed and in Hawai'i generally, factors most likely to affect ground surface temperatures include elevation, rainfall, topography, and vegetation cover. Habitats featuring relatively warm and dry conditions (see Figure 12) were more likely to support *C. kagutsuchi*.

#### Cardiocondyla life-history and distribution in Hawai'i

The genus *Cardiocondyla* includes at least 40 species, most of which are native to the Old World tropics and subtropics (Bolton 1995). Six species of *Cardiocondyla* have become established in Hawai'i (Krushelnycky *et al.* 2005b). Most *Cardiocondyla* are considered tramp species, having been widely distributed among islands of the Pacific Basin by humans. The native distribution of *C. kagutsuchi* includes Ishigaki Islands, within the Okinawan Archipelago of Japan (Terayama 1999). The source of *C. kagutsuchi* in Hawai'i is unclear, but it may have arrived relatively early, given its distribution on O'ahu, Maui, and Hawai'i, where it is found at numerous locations on Mauna Kea and Mauna Loa volcanoes. *Cardiocondyla kagutsuchi* was described as a new species only in 1999 (Terayama 1999), which means that specimens collected earlier than that date were identified as a different species. Taxonomic differentiation between *C. kagutsuchi* and *C. venustula* is problematic due to similar morphologies, so previous records of *C. venustula* in Hawai'i may have been *C. kagutsuchi*. Populations of *C. venustula* 



**Figure 11.** Closed-canopy habitat about 300 m north of Naūhi Cabin where ants were not detected. In closed-canopy habitats, the soil rarely dried out and temperatures remained relatively cool during the survey.

have thus far only been confirmed on Kaua'i (Paul Krushelnycky, University of Hawai'i, personal communication).

Unlike highly aggressive species, such as Argentine ants, big-headed ants and red imported fire ants (*Solenopsis invicta*), little is known about the life-history of *C. kagutsuchi* or its congeners. Nest size varies greatly among ant species, and in general, nests of *Cardiocondyla* are relatively small, ranging from one to several queens and from tens to hundreds of workers (Seifert 2003, Heinze *et al.* 2006). Nests of *C. kagutsuchi* may be restricted to underground locations, although nests are difficult to locate



**Figure 12.** Exposed, rocky outcrops along the margin of this ravine were typical habitats in which *C. kagutsuchi* was found on Hakalau Forest National Wildlife Refuge. Here, the ground is often relatively warm and dry compared to areas shaded by dense grass, shrubs or trees.

due to the small size (1–2 mm) of their openings and the absence of well-defined worker trails leading to nests. Yamouchi (in Seifert 2003) found that *C. kagutsuchi* nested in open, disturbed habitats with bare or thinly-vegetated ground. Nevertheless, other species of *Cardiocondyla*, including species found in Hawai'i (*C. wroughtonii* and *C. obscurior*), have been reported to nest in plants above ground (Seifert 2003), so *C. kagutsuchi* may nest above-ground as well. *Cardiocondyla* workers forage solitarily, although they occasionally use tandem-running behaviors to lead nest mates to food (Wilson 1959, RWP personal observation). Tandem-running involves continuous physical contact between two ants and differs greatly from the pheromone-based trail-following behavior of many other ant species. The small number of individuals within nests combined with their relatively inefficient mode of recruitment to food resources helps explain why baiting is a relatively ineffective method of surveying for these ants.

Cardiocondyla ants are thought to expand their range primarily by population budding (Heinze et al. 2006). Budding generally involves short-range emigration of a subset of ants from a nest (generally one or two queens and 20 or more workers) into adjacent, unoccupied habitat. New colonies can also be established without emigrating queens, as Cardiocondyla workers can release pheromones that will cause undifferentiated eggs to develop into reproductively viable queens (Heinze et al. 2006). Queens of Cardiocondyla develop wings, but it is unclear to what extent they disperse by flying, as wings are often dropped within the nest (Creighton and Snelling 1974). Cardiocondyla males are dimorphic, with one

type winged and capable of flight. The other male form ("ergatoids") does not develop wings, but it has more robust mandibles, suggesting that it competes aggressively for access to virgin queens within the nest (Heinze *et al.* 2006). Flight dispersal may explain how *C. kagutsuchi* is able to colonize "islands" of exposed soil within the "sea" of apparently inhospitable grass in former pasture land on the Hakalau Forest Unit of the refuge. Small body size and the ability of a few individuals to form viable nests facilitate colonization of potting soil and other cargo that may be widely distributed by people.

#### **Potential impacts of** Cardiocondyla

Cardiocondyla are considered to be generalist foragers of arthropod prey, but their impacts on native species are unknown. In one of the few studies on individual species of Cardiocondyla, C. emeryi was thought to prey on small, soft-bodied insects and to scavenge for larger arthropods (Creighton and Snelling 1974). In areas where C. kagutsuchi overlaps with more aggressive species, such as Argentine and big-headed ants, they may reduce competition by occupying a feeding niche unfilled by the more dominant species (Heinze et al. 2006).

To our knowledge, *C. kagutsuchi* has not been observed foraging in trees, and was not obtained in samples of foliage we collected when surveying arthropods in the young koa corridors on the refuge during 2007 and 2008 (U.S. Geological Survey unpublished data). *Cardiocondyla kagutsuchi* appears to be exclusively ground-dwelling and seems unlikely to appreciably affect native arboreal invertebrates or the native birds that eat them unless they intercept caterpillars and other insects that pupate on the ground or migrate between the litter layer and foliage or bark substrates.

## **Argentine ants**

Although *C. kagutsuchi* may pose a relatively minor threat to upper-elevation habitats of the Hakalau Forest Unit, invasion of the refuge by the highly aggressive Argentine ant (*L. humile*) could have much greater consequences for native communities. The large population of Argentine ants found along Keanakolu-Mana Road less than 6 km north of the Maulua Section of the refuge may be advancing southward toward the refuge. We did not survey habitat adjacent to this road, but the region is largely open grassland that seems suitable for Argentine ants. The population we found may be part of a larger population that extends into subalpine habitats on Mauna Kea, including lands near Pu'u Mali to about 1900 m elevation and above the Hanaipoe area of Keanakolu-Mana Road (U.S. Geological Survey unpublished data). Argentine ants have also invaded Pōhakuloa Training Area as well as the mixed naio (*Myoporum sandwicense*) and māmane (*Sophora chrysophylla*) woodlands on the western slope of Mauna Kea (Wetterer *et al.* 1998).

Argentine ants can profoundly impact ecosystems that they invade, and they have altered arthropod abundances and community structure in Hawai'i (Cole *et al.* 1992, Liebherr and Krushelnycky 2007, Krushelnycky and Gillespie 2008) as well as elsewhere (Human and Gordon 1997, Holway 1998, Suarez *et al.* 1998). Like *C. kagutsuchi*, Argentine ants are one of the few ant species in Hawai'i that can tolerate cold temperatures that are found at higher elevations. The Argentine ant is also similar to *C. kagutsuchi* in avoiding sites that are cold and wet, so it would probably not thrive on the refuge under closed-canopy or thick grass. In Haleakalā National Park, a population of Argentine ants, radiating from Hosmer Grove campground (2065 m elevation) since at least 1967 (Huddleston and Fluker 1968), had spread 2.5 km leeward into relatively dry subalpine shrubland by 1997, while it had not spread windward into a slightly wetter area of dense vegetation (Krushelnycky *et al.* 2005a).

#### Ants detected within Hilo Forest Reserve and Laupāhoehoe Natural Area Reserve

Survey results from Blair Road within the Hilo Forest Reserve and Laupāhoehoe Natural Area Reserve adjacent to the refuge indicated that ants had not moved into closed-canopy habitat below elevations where they were found on the refuge. *Cardiocondyla kagutsuchi* detected along Blair Road occurred at the highest station (1640 m) and the two lowest stations (approximately 680 and 740 m elevation,

respectively). Habitat encompassing the high-elevation station consisted of relatively open forest supporting an understory dominated by grass and numerous patches of exposed soil, which was generally similar to habitats at comparable elevation on the refuge. At the lowest sites, the forest canopy was moderately closed but relatively short, and common guava (*Psidium guajava*) and other alien species were common elements of the vegetation. Because ants were not found at disturbed sites along Blair Road at elevations matching the lower regions of the refuge (850–1100 m), we doubt that ants would have been detected had our surveys in the Hakalau Forest Unit extended further downslope.

#### **Kona Forest Unit**

Our finding of *S. papuana* and *N. bourbonica* on the Kona Forest Unit of the refuge was consistent with that of Haines and Foote (2005), who found both species at several stations along the southern boundary road during four surveys for ants during November 1999 and June 2000. *Solenopsis papuana* was relatively widespread in our survey, being detected along the southern and northern boundary roads as well as at a point on the lower (western) boundary road. Much of the lower boundary road was recently cut through the forest, but it runs adjacent to a decades-old road in some places. The uppermost elevation (750 m) at which *S. papuana* was collected was nearly identical during the two studies. In contrast, we found *N. bourbonica* only at 790 m elevation, whereas Haines and Foote (2005) found *N. bourbonica* as high as 930 m elevation. Nevertheless, they detected the vast majority of *N. bourbonica* at or below 777 m elevation, suggesting that colony size decreased with elevation.

Haines and Foote (2005) collected two species that we did not find: *Cardiocondyla wroughtonii* and *Tetramorium bicarinatum*. They collected only a few specimens of each species, and each was collected at a single location along the southern boundary road (*C. wroughtonii* at 777 m elevation and *T. bicarinatum* at 625 m elevation). Additional sampling might yet detect these ant species. Little is known about the ecological impacts of *C. wroughtonii* and *T. bicarinatum*, but both species are probably restricted to disturbed habitats.

Surveys have not been conducted to determine whether ants have penetrated forests adjacent to the roads where they have been found, but *S. papuana* is one of only a few species found in Hawai'i that persists in wet forests, primarily at elevations below 1100 m (Reimer 1994). *Solenopsis papuana* forms large, multiqueen (polygyne) colonies and is considered likely to have "a severe impact on native biota" due to highly-effective predation on arthropods (Reimer 1994). Although few studies have quantified the impact of this ant, Gillespie and Reimer (1993) found a significant inverse relationship between the abundance of *S. papuana* and the diversity of native *Tetragnatha* spiders. Gillespie and Reimer (1993) considered *S. papuana* to be the ant posing the most serious threat to Hawaiian forest arthropods, and they believed that its distribution was expanding. This ant was first detected in Hawaii in 1967 (Huddleston and Fluker 1968), and it is now found on all the main Hawaiian Islands (Nishida 2002).

Nylanderia bourbonica seems less likely to penetrate intact forest and affect native arthropod communities. Working at Kalōpā State Recreational Area on Hawai'i Island (600 m elevation), LaPolla et al. (2000) found N. bourbonica "at the edge of the woods, but none inside the woods," and did not consider it or S. papuana to be threats to native Laupala crickets, even though they sometimes occupied the same habitat. Similarly, Reimer (1994) found N. bourbonica in "disturbed montane habitats such as roadsides and urban developments, never in undisturbed sites," and Gillespie and Reimer (1993) detected no negative effects of this ant on spider communities in native forest.

Considering that neither our survey nor that of Haines and Foote (2005) detected ants above 930 m, it is likely that ants were rare or absent there. Nevertheless, the higher-elevation habitats of the refuge may be suitable for Argentine ants, and precautions to prevent their spread would seem warranted.

#### Controlling ants and preventing their spread

While eliminating *C. kagutsuchi* on the Hakalau Forest Unit of the refuge could help protect some native species, eradication probably would be difficult for two reasons. First, to our knowledge, no insecticidal bait has been proven successful at eradicating *Cardiocondyla* ants in a natural setting. Although commercially available baits targeting other ant species may be effective at destroying nests of *C. kagutsuchi*, efficacy testing to determine palatability, dosages and application frequencies would be required. Second, the ants are widespread throughout disturbed habitats on the refuge, and repeatedly applying baits and monitoring results along kilometers of roadways, fence lines, and restoration sites could be expensive. Even relatively small, plot-based studies generally demonstrate the difficulty of destroying all nests (Krushelnycky and Reimer 1998, U.S. Geological Survey unpublished data). Nevertheless, small-scale eradication of invasive ants in natural areas has been achieved (Hoffmann and O'Connor 2004, Plentovich *et al.* 2009, Vanderwoude *et al.* 2010, Hoffmann 2011).

Preventing the introduction of Argentine ants onto the refuge is clearly important. Although Argentine ants may eventually invade the refuge, their natural rate of spread from population budding (Krushelnycky *et al.* 2005a) suggests that their arrival would be decades from now. On the other hand, Argentine ants may colonize the refuge earlier via accidental transport in vehicles carrying a variety of cargo, including field gear and supplies, building supplies, gravel or fill for road construction, and soil for potted plants. Therefore, ensuring that vehicles are free of ants before being driven onto the refuge is critical to preventing new invasions. Furthermore, regular monitoring of parking areas and sites of human activity, such as the greenhouse and the main building compound, would be an effective method for early detection of new ant invasions.

The most aggressive species, such as the Argentine ant, big-headed ant, yellow crazy ant, and so-called "fire ants" (*S. geminata* and *W. auropunctata*), recruit quickly and in large numbers to baits, making their detection relatively easy. Although using available methods to control ants at the landscape scale may be infeasible, if not impossible, efforts to eradicate small, localized populations are much more likely to succeed. Thus, early detection of ant invasions and their prompt eradication are important, cost-effective actions that can help protect the biological resources of the refuge.

## Acknowledgements

This work was funded in part by the U.S. Geological Survey's Science Support Partnership and Invasive Species Programs. We thank Matt Stelmach, Meghan Cooling, and Mark McGregor for help in the field and in the lab. We also thank Jack Jeffrey, Dick Wass, Jim Kraus, Jim Glynn, and Lance Koch for encouraging and facilitating our work on Hakalau Forest National Wildlife Refuge. We also thank Paul Krushelnycky and Cas Vanderwoude for their insightful comments on the manuscript. Administrative support from Hawai'i Cooperative Studies Unit (Pacific Aquaculture and Coastal Resources Center, University of Hawai'i at Hilo) and Pacific Island Ecosystems Research Center (U.S. Geological Survey) is appreciated.

#### Literature Cited

Bloxam, A. 1925. Diary of Andrew Bloxam. Bernice P. Bishop Museum Special Publication No. 10, Honolulu, HI.

Bolton, B. 1995. A taxonomic and zoogeographical census of the extant ant taxa (Hymenoptera: Formicidae). Journal of Natural History 29:1037–1056.

Cole, F. R., Medeiros, A. C., Loope, L. L., 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., and R. R. Snelling. 1974. Notes on the behavior of three species of *Cardiocondyla* in the United States (Hymenoptera: Foricidae). New York Entomological Society 82:82–92.

Forel, A. 1899. Heterogyna (Formicidae), Vol. 1, pp. 116–122. *In* D. Sharp (ed.). Fauna Hawaiiensis. Cambridge University Press, Cambridge, England.

Gillespie, R. G., and N. J. Reimer. 1993. The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). Pacific Science 47:21–33.

Haines, L. H., and J. B. Haines. 1978. Colony structure, seasonality and food requirements of the crazy ant, *Anoplolepis longipes* (Jerd.) in the Seychelles. Ecological Entomology 3:109–118.

Haines, W., and D. Foote. 2005. Rapid assessment of invertebrate fauna of the Kona Forest unit of Hakalau National Wildlife Refuge. Hawai'i Cooperative Studies Unit Technical Report HCSU-001, University of Hawai'i at Hilo.

Heinze, J., Cremer, S., Eckl, N., and A. Schrempf. 2006. Stealthy invaders: the biology of *Cardiocondyla* tramp ants. Insectes Sociaux 53:1–7.

Hoffmann, B. D. 2011. Eradication of populations of an invasive ant in northern Australia: successes, failures and lessons for management. Biodiversity and Conservation 20:3267–3278.

Hoffmann, B. D., Anderson, A. N., and G. J. E. Hill. 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. Oecologia 120:595–604.

Hoffmann, B. D., and S. O'Connor. 2004. Eradication of two exotic ants from Kakadu National Park. Ecological Management and Restoration 5:98–105.

Hoffmann, B. D., and C. L. Parr. 2008. An invasion revisited: the African big-headed ant (Pheidole megacephala) in northern Australia. Biological Invasions 10:1171–1181.

Holway, D. A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia 16:252–258.

Huddleston, E. W., and S. S. Fluker. 1968. Distribution of ant species in Hawai'i. Proceedings of the Hawaiian Entomological Society 20:45–60.

Human, K. G., and D. M. Gordon. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. Conservation Biology 11:1242–1248.

Krushelnycky, P. D., and R. G. Gillespie. 2008. Compositional and functional stability of arthropod communities in the face of ant invasions. Ecological Applications 18:547–1562.

Krushelnycky, P. D., and R. G. Gillespie. 2010. Correlates of vulnerability among arthropod species threatened by invasive ants. Biodiversity and Conservation 19:1971–1988.

Krushelnycky, P. D., and N. J. Reimer. 1998. Efficacy of Maxforce bait for control of the Argentine ant (Hymenoptera: Formicidae) in Haleakalā National Park, Maui, Hawai'i. Environmental Entomology 27: 1473–1481.

Krushelnycky, P. D., Joe, S. M., Medeiros, A. C., Daehler, C. C., and L. L. Loope. 2005a. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. Diversity and Distributions 11:319–331.

Krushelnycky, P. D., Loope, L. L., and N. J. Reimer. 2005b. The ecology, policy and management of ants in Hawai'i. Proceedings of the Hawaiian Entomological Society 37:1–25.

LaPolla, J. S., Otte, D., and L. A. Spearman. 2000. Assessment of the effects of ants on Hawaiian crickets. Journal of Orthoptera Research 9:139–148.

Lester, P. J., and A. Tavite. 2004. Long-legged ants, *Anoplolepis gracilipes* (Hymenoptera: Formicidae), have invaded Tokelau, changing composition and dynamics of ant and invertebrate communities. Pacific Science 58:391–401.

Liebherr, J. K., and P. D. Krushelnycky. 2007. Unfortunate encounters? Novel interactions of native *Mecyclothorax*, alien *Trechus obtusus* (Coleoptera: Carabidae), and Argentine ant (*Linepithema humile*, Hymenoptera: Formicidae) across a Hawaiian landscape. Beetle Conservation 11:61–73.

Nishida, G. M. 2002. Hawaiian terrestrial arthropod checklist. Fourth edition, Bishop Museum Technical Report No. 22, Honolulu, HI.

O'Dowd, D. J., Green, P. T., and P. S. Lake. 2003. Invasional 'meltdown' on an oceanic island. Ecology Letters 6:812–817.

Perkins, R. C. L. 1913. Introductory essay on the fauna. Pp. xv–ccxxviii. *In* D. Sharpe (ed.). Fauna Hawaiiensis. Vol. 1, Part VI. Cambridge University Press, Cambridge, United Kingdom.

Plentovich, S., Hebshi, A., and S. Conant. 2009. Detrimental effects of two widespread invasive ant species on weight and survival of colonial nesting seabirds in the Hawaiian Islands. Biological Invasions 11:289–298.

Reimer, N. J. 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. Pp. 11–22. *In* D. Williams (ed.). Exotic Ants. Westview Press, Boulder, CO.

Rowles, A. D., and D. J. O'Dowd. 2009. Impacts of the invasive Argentine ant on native ants and other invertebrates in coastal scrub in south-eastern Australia. Austral Ecology 34:239–248.

Seifert, B. 2003. The ant genus Cardiocondyla (Insects: Hymenoptera: Formicidae)—a taxonomic revision of the *C. elegans*, *C. bulgarica*, *C. batesii*, *C. nuda*, *C. shuckardi*, *C. stambuloffii*, *C. wroughtonii*, *C. emeryi* and *C. minutior* species groups. Annalen des Naturhistorischen Museums in Wien 104 B:203–338.

Suarez, A. V., Bolger, D. T., and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. Ecology 79:2041–2056.

Terayama, M. 1999. Taxonomic studies of the Japanese Formicidae, Part 6. Genus *Cardiocondyla* Emery. Memoirs of the Myrmecological Society of Japan 1:99–107.

Vanderwoude, C., Onuma, K., and N. Reimer. 2010. Eradicating *Wasmannia auropunctata* (Hymenoptera: Formicidae) from Maui, Hawaii: The use of combination treatments to control an arboreal invasive ant. Proceedings of the Hawaiian Entomological Society 42:23–31.

Wetterer, J. K., Banko, P. C., Laniawe, L. P., Slotterback, J. W., and G. J. Brenner. 1998. Nonindigenous ants at high elevations on Mauna Kea, Hawai'i. Pacific Science 52:228–236.

Wilson, E. O. 1959. Communication by tandem running in the ant genus *Cardiocondyla*. Psyche 66:29–34.