Pacific Science (1998), vol. 52, no. 3: 228–236

Nonindigenous Ants at High Elevations on Mauna Kea, Hawai'i[1]

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ABSTRACT: Ant surveys were conducted at high elevations (1680–3140 m) on the western slope of Mauna Kea Volcano on the island of Hawai'i to determine the extent of ant infestation in those highland communities and particularly to evaluate the potential threat of ants in the highlands to native Hawaiian species. Ants were surveyed at 10 long-term sampling sites. Ants were common on Mauna Kea up to 2000 m elevation, but densities quickly dropped off above that. Five species of ants were collected: *Linepithema humile* (Mayr), *Cardiocondyla venustula* Wheeler, *Pheidole megacephala* (Fabricius), *Tetramorium bicarinatum* (Nylander), and *Monomorium pharaonis* (Linnaeus). Other than *L. humile,* these collections on Mauna Kea are the highest recorded locales in the Hawaiian Islands.

ANTS ARE AN EXTREMELY important component of most terrestrial ecosystems. Many remote Polynesian islands, however, lack native ants (Wilson and Taylor 1967). When ants invade such islands, they can have dramatic effects, preying on the relatively defenseless endemic fauna (Hölldobler and Wilson 1990, Gillespie and Reimer 1993). Loss of species that serve key functions in the natural community (e.g., important prey species, pollinators, seed dispersers) may have cascading effects leading to the loss of many additional native species (Howarth 1985).

Although the Hawaiian Islands have no indigenous ants, more than 40 species of introduced ants have become established there, primarily at low elevations, where they have been implicated in the extermination of much of the native fauna. Until recently, most ant species in Hawai'i probably arrived by sea accompanying human commerce, and they had to survive under lowland tropical conditions before spreading to other locales. This may explain why relatively few ant species have invaded the cooler highland areas of Hawai'i (Reimer 1994, Wetterer 1998). In this study, we conducted ant surveys at high elevations on the slopes of Mauna Kea Volcano on the island of Hawai'i to determine the extent of ant infestation in those highland communities.

Currently, three ant species are considered major pests in Hawai'i: *Pheidole megacephala* (Fabricius) (the bigheaded ant) and *Anoplolepis longipes* (Jerdon) (the longlegged ant), which dominate the lowlands, and *Linepithema humile* (Mayr) (the Argentine ant, formerly *Iridomyrmex humilis*), which dominates the highlands (Reimer 1994). All three of these ant species are highly aggressive and territorial, resulting in mutually exclusive distributions (Fluker and Beardsley 1970).

Pheidole megacephala and *A. longipes* can have large direct impacts on populations of both invertebrates and vertebrates in lowland tropical island communities (Zimmerman 1948, Hardy 1979, Haines et al. 1994, Swaney 1994), as well as indirect impacts on native vertebrate populations by eliminating

[1] Financial support was provided by the U.S. Government, Harvard University, Wheaton College, and Columbia University. Manuscript accepted 27 October 1997.

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key invertebrate prey species (Banko and Banko 1976). In particular, breeding passerine birds often depend heavily on feeding captured insects to their nestlings. Such competitive exclusion may be responsible, in part, for the disappearance of most native Hawaiian forest birds from the lowlands, even in areas where the forest has remained relatively intact (Banko and Banko 1976, Scott et al. 1986).

At higher elevations (above 900 m) in Hawai'i, *L. humile* is considered the primary pest ant (Cole et al. 1992, Reimer 1994). This species was first found in Hawai'i at an army post near Honolulu in 1940 (Zimmerman 1941), but quickly spread to other locales (Wilson and Taylor 1967). Wilson and Taylor (1967) noted that populations of *L. humile* in Hawai'i were often associated with army camps and bivouacs, and concluded that colonies probably were being transported inadvertently with army supplies and equipment. Cole et al. (1992) documented the extreme destructive power of *L. humile* in the highlands of Maui. They found drastic reductions in the populations of native invertebrate species attributable to the presence of *L. humile.* In addition, *L. humile* is a threat to vertebrate populations. Newell and Barber (1913) reported that *L. humile* workers attack and kill hatching birds. "The nests of many birds are frequented by ants in the same way, and the number of young birds destroyed in this manner must be considerable" (Newell and Barber 1913:24–25).

In our study, we wished to evaluate the potential threat of ants in the highlands to native Hawaiian species such as the Palila (*Loxioides bailleui* [Oustalet]), an endangered bird now found only at high elevations on Mauna Kea. The Palila once occurred over wide areas of the island of Hawai'i, ranging up the slopes of three of the volcanoes, Mauna Kea, Mauna Loa, and Hualālai, and down to sea level (Scott et al. 1986, Fancy et al. 1993, Jacobi et al. 1996). Now, however, the Palila is found only in the dry and mesic forests of māmane (*Sophora chrysophylla* [Salisbury] Seem.) and naio (*Myoporum sandwicense* A. Gray) trees on the slopes of Mauna Kea, at elevations between 2000 and 2850 m, with highest densities between 2100 and 2300 m (Scott et al. 1984, Fancy et al. 1993, Jacobi et al. 1996). Other māmane-naio forests on Mauna Kea, Mauna Loa, and Hualālai appear to be suitable Palila habitat, yet the birds are absent (Fancy et al. 1993). Although avian malaria has been implicated in the disappearance of native birds in Hawai'i below 600 m elevation (Warner 1968), this disease is almost nonexistent above 1500 m elevation (van Riper et al. 1986). Instead, we suggest that it is possible that ants are at least partly responsible for excluding the Palila from highland areas. It is particularly worrisome that *L. humile* is found in areas up to 2880 m elevation on the nearby island of Maui (Cole et al. 1992). Thus, it seems that *L. humile* has the potential of spreading throughout all of the Palila's current range. We were therefore particularly interested in establishing the current range of *L. humile* to evaluate its threat to the remaining populations of the Palila. The potential impact of introduced ants on whole populations of native birds has been well documented in the case of the red imported fire ant (*Solenopsis invicta* Buren) in North America (e.g., see Allen et al. 1995).

MATERIALS AND METHODS

We conducted this study at high elevations (1680–3140 m) on Mauna Kea Volcano in Hawai'i. We surveyed ants using four different methods: pitfall traps, Malaise traps, foliage beating, and baited transects. We deposited voucher ant specimens from this study in the Museum of Comparative Zoology, Harvard University.

Pitfall Traps, Malaise Traps, and Foliage Beating

In 1992, we established pitfall traps at seven "3-yr" study sites (sites 1–7) in the māmane and naio forests on the dry western slope of Mauna Kea and at three "1-yr" study sites (sites 8–10) on the northern, eastern, and southern slopes (Table 1, Figure 1; for detailed descriptions of the sites and maps see

TABLE 1

NAME, ELEVATION, AND SAMPLING DATES AT 10 LONG-TERM SAMPLING SITES, 10 WITH PITFALL TRAPS AND EIGHT WITH MALAISE TRAPS

SITE		ELEVATION (m)	PITFALL DATES	MALAISE DATES
1	Ahumoa	2010	Apr. 1992–Jan. 1995	June 1995–Sept. 1995
2	Palila Camp	2320	Apr. 1992–Jan. 1995	June 1992–Sept. 1995
3	Mauka	2590	Apr. 1992–Jan. 1995	June 1992–Sept. 1995
4	Skyline	2880	Mar. 1992–Jan. 1995	—
5	Kemole	2400	Apr. 1992–Jan. 1995	—
6	Mana'o	2430	Mar. 1992–Jan. 1995	June 1993–Sept. 1995
7	Pōhakuloa	1990	Mar. 1992–Jan. 1995	Dec. 1992–Sept. 1995
8	Kalepeamoa	2620	Nov. 1992–Nov. 1993	Oct. 1992–Nov. 1993
9	Kaluamakani	2560	Nov. 1992–Nov. 1993	Oct. 1992–Nov. 1993
10	Kanakaleonui	2550	Nov. 1992–Nov. 1993	Oct. 1992–Nov. 1993

Scott et al. [1986]). At each site, we set up the 10 pitfall traps spaced at least 10 m apart. Eight of the traps were placed near the base of trees or shrubs and two were placed in open areas. Each trap consisted of a 250-ml plastic cup buried up to its lip and filled about halfway with ethylene glycol. A wooden board suspended a few centimeters above the trap shielded it from falling debris and rain. At eight of the sites, we also established single Malaise traps (Table 1). We collected the accumulated invertebrate samples from each pitfall and Malaise trap once or twice per month.

We also sampled ants by beating the foliage of trees once per month. In the area bounded by sites 1, 4, 5, and 6, we sampled 186 marked māmane trees and 80 marked naio trees at 150-m intervals along transects. At sites 7, 8, 9, and 10, we sampled māmane trees spaced at least 20 m apart. At each site we sampled 30 to 55 marked trees, once per month. We sampled foliage by shaking or beating branches in up to 10 sections of each tree, holding a 30 by 35 cm collecting pan beneath.

Bait Transects

From June to August 1994, we surveyed ants at 224 bait stations along nine transects: five "horizontal" transects along roads on the western flank of Mauna Kea and four "vertical" transects up the slope of Mauna Kea (Figure 1). The horizontal transects were next to four roads that ran along the contour of the mountain. Horizontal transect A (Saddle Road) was next to a highway; transects B, C, D, and E (Mauna Kea Trail, Infantry Road, Kemole Road, and Skyline Road) were next to dirt roads. Three of the four vertical transects (F, G, and H) were the same as those established for the Hawai'i Forest Bird Survey (transects 102, 106, and 107 in Scott et al. [1986]) and also used for the annual census of Palila (Scott et al. 1984). Permanent stations along each transect were marked at 150-m intervals. The fourth vertical transect (I) ran next to Observatory Road on the south face of the mountain. We sampled along each transect at 150-m intervals, except on transect A, where we sampled at 800-m intervals, to avoid interruption of highway traffic through this military training area.

At each bait station, we laid out approximately 2 g of tuna on the ground near the base of the three trees or bushes closest to the station marker, clearing away any surface vegetation and marking each spot with flagging tape. We then revisited each station after 1 to 4 hr and collected ants at each bait. Fellers and Fellers (1982) used a similar baiting technique in their survey of *L. humile* at high-elevation sites on Maui.

As a measure of the density of ants at bait

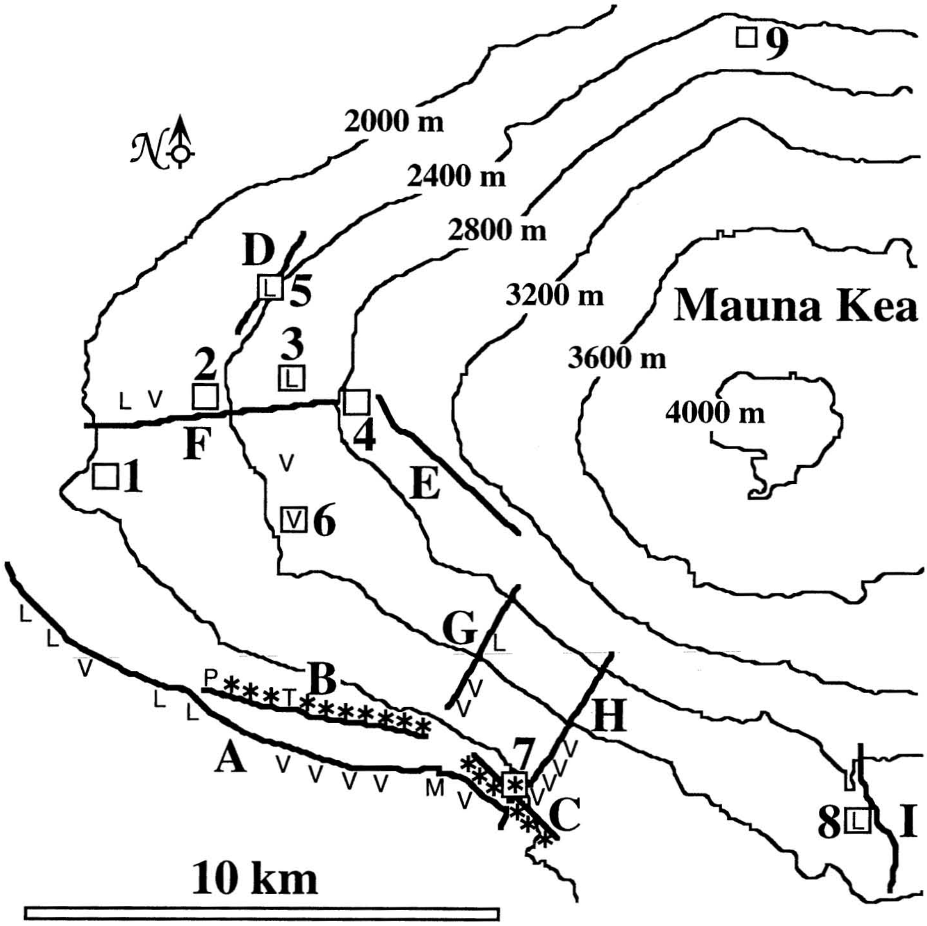

FIGURE 1. Location of study sites on the western slope of Mauna Kea Volcano. Squares mark nine long-term sampling sites (sites 1–9; see Table 1; a tenth site, Kanakaleonui, was located on the eastern slope of Mauna Kea). Lines mark the nine bait transects (transects A–I; see Table 2). Collection locales for different ants species: L, *Linepithema humile;* V, *Cardiocondyla venustula;* P, *Pheidole megacephala;* T, *Tetramorium bicarinatum;* M, *Monomorium pharaonis.* *, areas below 2020 m elevation where *Linepithema humile* or *Cardiocondyla venustula* occurred (locales were too numerous to label individually [transect B, 20 sites; transect C, 14 sites; and the lower part of transect H, four sites]). Palila populations occur between 2000 and 2850 m elevation around the western and southern slopes of Mauna Kea. A small population also occurs on the eastern slope of Mauna Kea.

stations, we estimated the number of ants visiting a station in a 5-min interval. We defined "low" as 10 or fewer ants, "medium" as 11 to 100 ants, and "high" as more than 100 ants. At low-density sites, ants often located only one of the three baits. At the high-density sites, ants generally located all baits within 5 min, and all baits were covered with several hundred ants within 15 min.

RESULTS

Pitfall Traps, Malaise Traps, and Foliage Grids

Of the 10 pitfall trap sites, we consistently found ants only at site 7 (Pōhakuloa, 1990 m elevation). At all 10 site 7 pitfall traps we collected large numbers of *Linepithema*

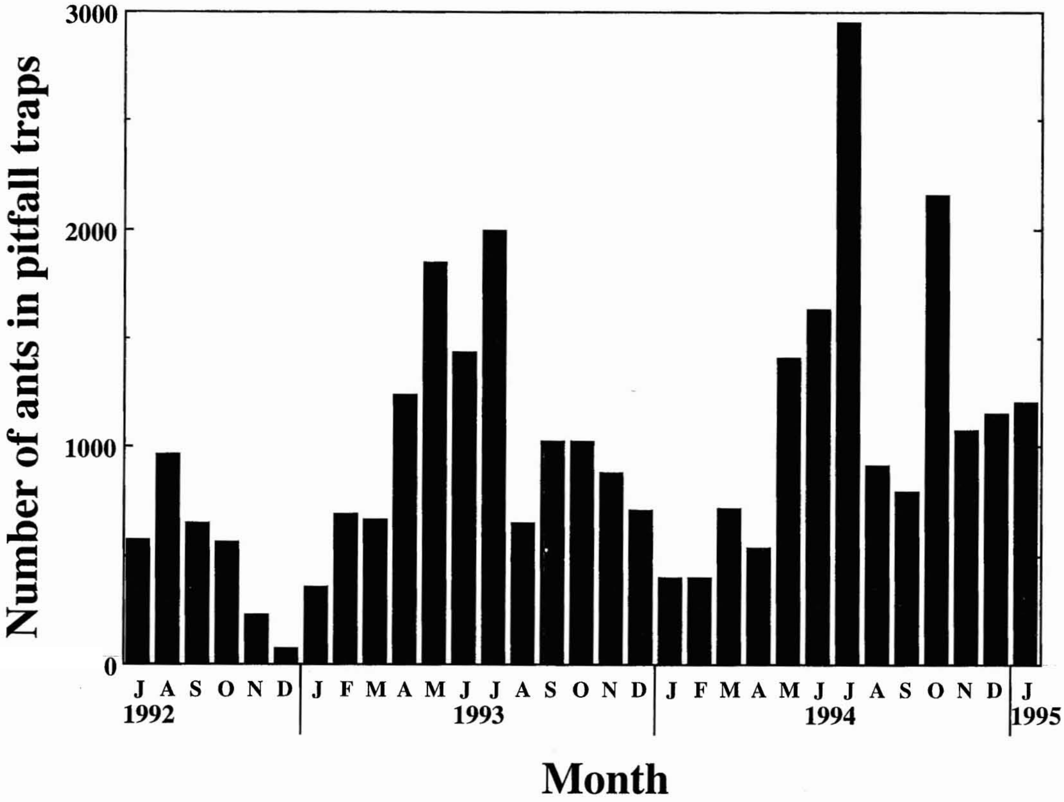

FIGURE 2. Combined monthly totals for ants in 10 pitfall traps at site 7 (Pōhakuloa) for July 1992 to January 1995.

humile workers every month. The overall monthly average for the 10 site 7 traps combined was 992 ± 623 ants per month for July 1992 to January 1995. Numbers were higher in summer months and appeared to increase over the 31 months of collection (Figure 2).

We found a total of six individual ants in pitfall traps at four other sites from April 1992 to September 1995. At site 3 (Mauka, 2590 m elevation): two *L. humile* workers in August 1994; at site 5 (Kemole, 2400 m elevation): one *L. humile* worker in May 1994; at site 6 (Mana'o, 2430 m elevation): two *Cardiocondyla venustula* Wheeler workers (=*Cardiocondyla "a"* in Huddleston and Fluker [1968] and Huddleston et al. [1968] [S. Cover, pers. comm.]), one in November 1993 and one in November 1994; at site 8 (Kalepeamoa, 2590 m elevation): one *L. humile* in May 1993.

From the eight Malaise traps, we found *L. humile* workers only at site 7 (Pōhakuloa, 1990 m elevation). From December 1992 to June 1994, we collected a mean of 334.1 *L. humile* per month at this one trap.

In the foliage beatings, all trees at site 7 (Pōhakuloa, 1990 m elevation) yielded *L. humile* workers, often in very high numbers (>100 ants per tree). Two additional sites yielded ants. Between sites 1 and 2 (see Figure 1), on four separate occasions between 14 May 1992 and 11 December 1992, the same māmane tree yielded one to three *L. humile* workers; then on 23 August 1995, we collected 11 *C. venustula* workers from one tree and several hundred *C. venustula* work-

TABLE 2

ANTS COLLECTED AT BAIT STATIONS ALONG FIVE HORIZONTAL AND FOUR VERTICAL BAIT TRANSECTS ON MAUNA KEA

SITE	ELEVATIONAL RANGE	NO. OF STATIONS	NO. WITH ANTS
Horizontal transects			
A. Saddle Road	1680–1980	19	11
B. Mauna Kea Trail	1770–1930	37	22
C. Infantry Road	1970–2040	18	14
D. Kemole Road	2350–2400	16	0
E. Skyline Road	2950–3140	27	0
Vertical transects			
F. Transect 102	1900–2820	37	0
G. Transect 106	2180–2930	20	3
H. Transect 107	1990–3010	27	8
I. Observatory Road	2440–2820	23	0
Total	1680–3140	224	58

TABLE 3

DENSITY OF ANTS COLLECTED AT BAIT STATIONS AT DIFFERENT ELEVATIONS ON MAUNA KEA

ELEVATION	ANT DENSITY[a] H	M	L	0	TOTAL SITES	% WITH ANTS
2400–	0	0	1	88	89	1.1
2200–2400	0	0	2	36	38	5.3
2020–2200	0	0	4	16	20	20.0
–2020	28	9	14	24	77	66.2
Total	28	9	21	165	224	25.4

[a] H, high; M, medium; L, low; 0, no ants collected.

ers from another tree. At the latter tree, the ants were carrying conspecific pupae and were apparently moving to a new nest site. Finally, between sites 3 and 6 (see Figure 1), on two occasions (20 October 1994 and 15 September 1995) we collected a single *C. venustula* worker.

Bait Transects

We observed ants at 58 of the 224 bait stations (Table 2), representing five different species: *Linepithema humile, Cardiocondyla venustula, Pheidole megacephala, Tetramorium bicarinatum* (Nylander), and *Monomorium pharaonis* (Linnaeus). Ants were less common at higher elevations (Table 3). We observed ants at seven of the 147 bait stations above 2020 m elevation (5%), always in low densities (Table 3, Figure 1). At the highest of these seven sites (2520 m), the ants were *L. humile;* at the other six, *C. venustula* (maximum elevation 2320 m). We observed ants at 51 of the 77 bait stations below 2020 m elevation (66%). In addition to *L. humile* and *C. venustula,* we found three additional ant species at bait stations, each at high densities at a single bait station: *Ph. megacephala* (1770 m elevation), *T. bicarinatum* (1820 m elevation), and *M. pharaonis* (1930 m elevation). The remaining 48 bait stations with ants below 2020 m elevation all attracted either *L. humile* or *C. venustula.* Unfortunately, we kept samples from only 12 of these sites, because we did not, at the time, recognize the difference between *L. humile* and *C. venustula* by eye and assumed that they were all *L. humile.* Of these 12 samples, four were *L. humile* and eight were *C. venustula.*

All high-density populations of ants on Mauna Kea were found on or adjacent to Pōhakuloa Military Camp, suggesting that the ants may have been introduced to the area by the military.

DISCUSSION

Ants were common on Mauna Kea up to 2020 m elevation and occurred at low densities at scattered sites above 2020 m. We found a total of five species of ants, all common "tramp" species with worldwide distributions. *Linepithema humile* and *Cardiocondyla venustula* were by far the most common and widespread species; *Pheidole megacephala, Tetramorium bicarinatum,* and *Monomorium pharaonis* occurred at only one site each. For these five species, elevational limits listed by Reimer (1994) versus the maxima in our study were as follows: *L. humile:* 2800 m versus 2640 m, *C. venustula:* 1900 m versus 2430 m, *Ph. megacephala:* 1200 m versus 1770 m, *T. bicarinatum:* <900 m versus 1820 m, and *M. pharaonis:* <900 m versus

1930 m. Thus, our highest collection sites were at elevations 500 to 1000 m higher than previously reported for four of the five ant species.

Although the destructive capacity of *L. humile* is well documented, the impact of *C. venustula* is unstudied and deserves further attention. Huddleston and Fluker (1968) stated that in Hawai'i, *C. venustula* appears to be the dominant ant species where neither *Ph. megacephala* nor *L. humile* is present. *Pheidole megacephala, T. bicarinatum,* and *M. pharaonis* are all considered typically lowland species (Reimer 1994) and may have little probability of becoming major pests at high elevations.

In Haleakalā National Park on Maui, Cole et al. (1992) estimated that *L. humile* occupies about 1.5% of the park, reaching elevations up to 2880 m, and has a severe impact on the invertebrate fauna. Cole et al. (1992) concluded that the *L. humile* population in Haleakalā is still expanding. Similarly, the apparent increase in the number of *L. humile* we collected in pitfall traps at Pōhakuloa (site 7; Figure 2) suggests that ant populations at high elevations on Mauna Kea may be still growing and have not yet reached their full potential.

Many factors may be influencing the distribution of the Palila in Hawai'i, including food availability and the abundance of alien predators, such as rats and cats. Our results support the proposal that high densities of ants on Mauna Kea may have contributed to the exclusion of Palila from elevations below 2000 m, although the evidence for this is only circumstantial. We found high densities of ants only in areas below 2000 m where the Palila is now absent. Any expansion of the ants' range to higher elevations may have an impact on the Palila and other native Hawaiian species. Continued monitoring is needed to determine whether ants are still spreading up Mauna Kea and whether Palila populations are showing a parallel retreat.

Fancy et al. (1993) proposed that some Palila should be translocated from their current range to apparently suitable areas of their former range on Mauna Kea, such as the Pōhakuloa area (site 7) and to similar habitats on Mauna Loa and Hualālai. However, if ants heavily infest these areas, as they do in the Pōhakuloa area, reintroductions of Palila may prove difficult, if not impossible. Gagné (1979) found *L. humile* on Mauna Loa at elevations up to 2400 m. Surveys are needed to evaluate the level of ant infestation on Mauna Loa and Hualālai before any attempt is made to reestablish Palila there.

Efforts are now under way to prevent the spread of *L. humile* in Haleakalā National Park on Maui using pesticides (Krushelnycky and Reimer 1996). Similar measures may be desirable on Mauna Kea, particularly if ants continue to expand their distributions on the mountain. Because there are no native Hawaiian ants, biological control using ant-specific parasites, such as many species of phorid flies (Disney 1994), could be particularly successful (Reimer et al. 1990). The highland forests of Mauna Kea must be protected against the introduction of additional cold-tolerant ant species that may thrive in highland forests.

ACKNOWLEDGMENTS

We thank M. Wetterer, L. Morrison, and D. Gruner for comments on the manuscript, and S. Cover and M. Bennett for identifying the ants.

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