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Nonindigenous Ants Associated with Geothermal and Human Disturbance in Hawai'i Volcanoes National Park[1]

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ABSTRACT: Although the Hawaiian Islands lack indigenous ants, more than 40 exotic species have become established there, primarily in lowland areas, where they have been implicated in the extermination of much of the endemic Hawaiian fauna. In June to August 1994, I surveyed ants in the Kīlauea Caldera region (elevation 1090–1240 m) of Hawai'i Volcanoes National Park to evaluate the current range and potential impact of ants in this protected montane ecosystem. Ants were common in areas disturbed by geothermal or human activity, but rare in undisturbed forest. A total of 15 ant species was collected, including 10 "lowland" ant species that are generally restricted to elevations below 900 m in Hawai'i. *Pheidole megacephala* and *Anoplolepis longipes,* major pest species in lowland Hawai'i, occurred in very high densities in and around the geothermal area near the park headquarters. *Paratrechina bourbonica* and *Cardiocondyla venustula,* two cold-tolerant species, were the most common ants in a second geothermal area, the Puhimau hot spot, and in areas disturbed by human activity, including roadsides. *Linepithema humile,* a major pest species in drier highland areas, occurred only in and around park buildings. The geothermal areas and park buildings appear to serve as warm "habitat islands" that allow *Ph. megacephala, A. longipes,* and other lowland ants to extend their ranges to higher elevations. Colonization of geothermal areas by lowland ant species, such as *Ph. megacephala* and *A. longipes,* poses a threat to endemic Hawaiian species in those areas. Colonization of roadsides and other disturbed areas by more cold-tolerant ants, such as *P. bourbonica, C. venustula,* and *L. humile,* poses a more general threat to endemic Hawaiian species found at higher elevations.

THE HAWAIIAN ISLANDS have perhaps 10,000 endemic species of insects, including such unique forms as predaceous inchworms, intertidal crickets, and damselflies with terrestrial larvae (Howarth et al. 1988, Wilson 1992). Like many other remote Polynesian islands, however, the Hawaiian Islands lack an indigenous ant fauna (Wilson and Taylor 1967). When ants invade such islands, they can have devastating effects on the native ecosystems, 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, scavengers, decomposers) may have cascading effects leading to severe disruptions of natural nutrient cycling and the subsequent loss of additional native plant and animal species (Howarth 1985).

More than 40 species of exotic ants have become established in the Hawaiian Islands, primarily in lowland areas (Reimer 1994). Most of these species probably arrived accompanying human traffic to Honolulu, a lowland port of entry on the island of O'ahu (Reimer 1994), where they had to survive under lowland tropical conditions before spreading to other locales. This may explain

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why relatively few ant species have invaded the cooler highland areas of the Hawaiian Islands (Reimer 1994). In the study reported here, I surveyed the Kīlauea Caldera region of Hawai'i Volcanoes National Park on the island of Hawai'i to evaluate the current range and potential impact of exotic ants in that protected highland habitat.

Three ant species are currently recognized as major pests in the Hawaiian Islands: *Pheidole megacephala* (Fabricius) (the bigheaded ant) and *Anoplolepis longipes* (Jerdon) (the longlegged ant) in lowland areas, and *Linepithema humile* (Mayr) (the Argentine ant, formerly *Iridomyrmex humilis*) in highland areas (Reimer 1994). *Pheidole megacephala* was the first of these three to become established in Hawai'i. By 1880, it was one of the most common insects in the Hawaiian Islands (Wilson and Taylor 1967). *Anoplolepis longipes* and *Linepithema humile* arrived later; they were first collected in Hawai'i in 1952 and 1940, respectively (Wilson and Taylor 1967). All three major pest species are highly aggressive and territorial, resulting in mutually exclusive territories (Fluker and Beardsley 1970).

Pest ants in the lowlands of Hawaiian islands have been implicated in the extermination of much endemic fauna (Reimer et al. 1990, Reimer 1994). Zimmerman (1948) reported that the "voracious immigrant ant," *Ph. megacephala,* eliminates most endemic insects throughout its range. Similarly, Hardy (1979) implicated *A. longipes* in the loss of most of the insect fauna at a lowland site on the island of Maui. Native Hawaiian spiders have been exterminated in areas invaded by *Ph. megacephala* and *A. longipes*, replaced by nonindigenous spiders (Gillespie and Reimer 1993). On the island of Niuafo'ou in Tonga, *A. longipes* kills the hatchlings of the endemic incubator bird (*Megapodius pritchardii*), first attacking the birds' eyes (Swaney 1994). *Anoplolepis longipes* is also known to prey upon newborn pigs, dogs, cats, rabbits, rats, and chickens (Haines et al. 1994). Ants also may have an important indirect impact on native vertebrate populations by eliminating key invertebrate prey species (Banko and Banko 1976). In particular, breeding passerine birds often depend heavily on feeding insects to their nestlings. Such competitive exclusion may be, in part, responsible 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).

Linepithema humile, an important pest ant of subtropical and temperate regions (Holway 1995) was first found in Hawai'i at an army base near Honolulu (Zimmerman 1941), but quickly spread to other locales (Wilson and Taylor 1967). This species is now considered the primary ant pest of higher elevations (above 900 m) in the Hawaiian Islands (Cole et al. 1992, Reimer 1994). 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 directly attributable to the presence of *L. humile. Linepithema humile* is also a threat to native vertebrate populations. Newell and Barber (1913) described how *L. humile* attacks birds: "the workers swarm over young chicks in such numbers as to cause their death.... nests of many birds are frequented by the ants in the same way, and the number of young birds destroyed in this manner must be considerable."

Several previous studies surveyed ants in Hawai'i Volcanoes National Park (HVNP). Huddleston and Fluker (1968) surveyed four sites in HVNP and found four species of ants, including none of the three major pest species mentioned above (see Table 1). Later, Gagné (1979) sampled the canopies of trees at nine sites along an elevational transect in HVNP from 15 to 2400 m elevation and found three ant species: two species at low elevations (*Plagiolepis alluaudi* Forel and *Ph. megacephala*) and one species at higher elevations (*L. humile*). Medeiros et al. (1986) sampled 15 sites in HVNP from sea level to 2000 m elevation, including four building sites in the Kīlauea Caldera area. They found a total of six species, including all three major pest species (see Table 1). In addition, Medeiros et al. (1986) reported two other species collected by C. Davis (see Table 1). Finally, from 1988 to 1991, Clive Jorgensen and his associates surveyed for ants at 144 sites within HVNP, from sea level to 3000 m elevation (Jorgensen et al., unpubl. data). They found a total of 19 species of ants, bringing to 20 the total number of ant species reported from HVNP (see Table 1).

This study was motivated by my observations of extremely high densities of *Ph. megacephala* and *A. longipes* throughout the geothermal area at the northern edge of Kīlauea Caldera (1200–1220 m elevation), near park headquarters. The only previously published records of these lowland ant species at such high elevation were made by Medeiros et al. (1986) at two sites located a short distance west of the geothermal area: one collection of *Ph. megacephala* at Kīlauea Military Camp (1220 m elevation) and one collection of a single specimen of *A. longipes* at a nearby campground (1190 m elevation). My observations suggested a recent large-scale invasion of lowland ants into this region.

MATERIALS AND METHODS

Between 21 June and 20 August 1994, I surveyed ants in the Kīlauea Caldera region (19° 25′ N, 155° 15′ W; elevation 1090–1240 m, annual rainfall ~2.3 m) of Hawai‘i Volcanoes National Park (HVNP). Kīlauea Caldera, at the summit of Kīlauea Volcano, is located on the southeastern flank of the much larger Mauna Loa Volcano (summit elevation 4169 m).

I surveyed along marked transects, trails, and roads and around park buildings, concentrating efforts in two geothermal areas: the Steaming Bluff–Sulfur Banks area near the park headquarters at the northern edge of Kīlauea Caldera, and the Puhimau hot spot, 5 km to the south, near Puhimau Crater. The hot soil conditions in these areas prevent the growth of trees and other plants with deep root systems (see Glime and Iwatsuki 1994). I also surveyed the areas surrounding the Steaming Bluff–Sulfur Banks area, as well as along the trails and roads through primarily forested areas between the two geothermal areas.

I set out a total of 211 bait stations at 100-m intervals along transects, usually by the side of a trail or road. At each station I laid out approximately 2 g of tuna near the base of each of three trees or plants, spaced 1.5–2.5 m apart along the transect. I then revisited each station after 1–3 hr and collected ants attracted to the baits. Fellers and Fellers (1982) used a similar baiting technique in their survey of *L. humile* at high-elevation sites on Maui. All surveys were conducted during daylight hours.

As a measure of the density of ants at bait stations, I estimated the number of ants visiting a station in a 5-min interval. “Low” was defined as 10 or fewer ants, “medium” as 10 to 100 ants, and “high” as more than 100 ants. At low-density sites, ants often located only one of the three baits. At high-density sites, ants generally located all baits within 5 min, and all baits were covered with several hundred ants within 15 min.

Bait station sites were divided into five categories defined as follows.

(1) “HQ geothermal” ($n = 45$, 1200–1220 m elevation): trails and roads through the geothermal area near the park headquarters, from the eastern edge of Sulfur Banks to the western edge of Steaming Bluff. The vegetation in this area is primarily grass, herbs, ferns, and stunted ‘ōhi‘a trees (*Metrosideros polymorpha*). Hundreds of tourists visit this area daily.

(2) “Puhimau hot spot” ($n = 35$, 1090–1100 m elevation): permanent transects marked with metal stakes through the Puhimau hot spot area, extended west to the 1974 lava flow and east to Chain of Craters Road. I also included the 300-m dirt road into the hot spot area and 400 m along Chain of Craters Road adjacent to the hot spot area (between the road into the hot spot area and the turnoff to Puhimau Crater). There is little vegetation through most of this area because of the high temperature of the soil. Few tourists visit this area.

(3) “Roadside” ($n = 12$, 1100–1120 m elevation; $n = 1$, 1190 m elevation): Chain of Craters Road between Crater Rim Trail and the turnoff for Puhimau Crater (10 in forest and two in lava fields from the 1974 lava flow), plus one site described below under “Forest.”

(4) "HQ periphery" ($n = 63$, 1160–1230 m elevation): trails and roads through the area immediately surrounding the Steaming Bluff–Sulfur Banks geothermal areas, from the center of the Kīlauea Military Camp to the west, Crater Rim Drive to the north, to the closed part of Crater Rim Drive between Volcano House and the start of Crater Rim Trail to the east. (The drop-off into Kīlauea Caldera borders to the south.) Vegetation in these areas ranges from mowed lawns of Kīlauea Military Camp and the park headquarters to closed-canopy forest on the trails between Steaming Bluff and the park headquarters. These areas are disturbed by human activity to differing degrees.

(5) "Forest" ($n = 55$, 1120–1200 m elevation): "undisturbed" closed-canopy forest, along Crater Rim Trail, between the end of the closed section of Crater Rim Drive and Chain of Craters Road. The site where the trail crosses Crater Rim Drive at the Thurston Lava Tube, I classified as "Roadside." Numerous tourists walk these trails each day.

In addition, I surveyed six building sites in the Kīlauea Caldera area, using baits and asking park employees the location of any ants they had seen. The six main areas I surveyed in this way were as follows: (1) Research Center buildings (1180 m elevation); (2) Nāmakani Paio campground cabins and cooking shelter (1190 m elevation); (3) Kīlauea Military Camp buildings (1220 m elevation); (4) Jagger Museum and Hawaiian Volcano Observatory (1240 m elevation); (5) Park headquarters buildings: Kīlauea Visitor's Center, Volcano House Hotel, and Volcano Art Center (1210 m elevation); (6) Volcano Golf Course restaurant and clubhouse (1240 m elevation).

Voucher ant specimens from this study have been deposited in the Museum of Comparative Zoology, Harvard University.

RESULTS

Summary of Ant Species

I collected a total of 15 different ant species in the Kīlauea Caldera region of HVNP (Table 1). All 15 species have been previously reported from other parts of Hawai'i (Huddleston and Fluker 1968) and have wide distributions in the Pacific and elsewhere (Wilson and Taylor 1967).

Ten of these species are considered to be "lowland" species in Hawai'i, usually restricted to elevations below 900 m (Reimer 1994). The other five species appear to be more "cold-tolerant" species and commonly extend their ranges above 900 m elevation. I included *Pheidole megacephala* and *Anoplolepis longipes* as lowland species, because the only previously published records of these ants above 900 m are from the same area as this study.

Ants at Bait Stations

I found ants at 123 of the 211 (58%) bait station sites (Table 2). The density and species diversity of ants varied dramatically among different parts of the study area (Table 2). Ants were common only in areas disturbed by human or geothermal activity. Ants occurred at 87 of 93 (94%) highly disturbed geothermal and roadside sites. Ants were at highest densities in the HQ geothermal area, where I found several hundred ants at all 45 bait sites. Ants were more diverse, but generally at lower densities, in the Puhimau hot spot. Ants were common along roads, but not diverse (three species). In the HQ periphery area ants occurred at 33 of 63 (52%) sites. In closed-canopy forest within the HQ periphery (about half the sites), ants were generally absent. In other "undisturbed" closed-canopy forest away from the disturbed areas, ants occurred at only 3 of 55 (5%) sites.

Pheidole megacephala and *Anoplolepis longipes,* major pest species otherwise largely confined to lowland areas in Hawai'i, occurred only in the HQ geothermal area and the nearby HQ peripheral area. These two species were present in extremely high densities in the HQ geothermal area and occupied mutually exclusive territories. *Pheidole megacephala* occupied the eastern part of the geothermal area (e.g., Sulfur Banks), whereas *A. longipes* occupied the western part (e.g., Steaming Bluff). I found lower densities of

TABLE 1

ANT SPECIES COLLECTED IN HAWAIʻI VOLCANOES NATIONAL PARK IN DIFFERENT STUDIES

SPECIES	STUDIES[a]						"ELEVATION LIMIT" (m)
	H&F	G	M+	D	J+	W	
"Lowland" species							
Anoplolepis longipes			X		31	28	1,200
Pheidole megacephala	X	X			37	26	1,200
Cardiocondyla nuda					6	10	<900
Tapinoma melanocephalum					12	9	<900
Tetramorium bicarinatum	X				3	5	<900
Monomorium monomorium					5	3	<900
Paratrechina longicornis					3	1	<900
Cardiocondyla emeryi		X			4	1	<900
Monomorium pharaonis				X		1	<900
Pheidole fervens					1	1	<900
Technomyrmex albipes				X	3		<900
Plagiolepis alluaudi	X	X			11		1,000
Hypoponera sinensis					1*		<900
Camponotus variegatus					2		500
"Cold-tolerant" species							
Paratrechina bourbonica	X		X		37	44	1,200
Cardiocondyla venustula					46	29	1,900
Linepithema humile		X	X		7	9	2,800
Hypoponera punctatissima					1	7	1,200
Hypoponera opaciceps	X		X		2	1	2,700
Paratrechina vaga					64*	*	1,200

[a]H&F, Huddleston and Fluker (1968); G, Gagné (1979); M+, Medeiros et al. (1986); D, C. Davis (in Medeiros et al. 1986; J+, Jorgensen et al. (unpubl. data); W, this study. "Lowland" and "cold-tolerant" defined in text; "elevation limit" from Reimer (1994). For Jorgensen et al. (unpubl. data) and this study, I list the total number of separate collection sites for each species. In this study, this includes bait stations along transects, surveys of building sites, and three observed introductions.

* See text.

TABLE 2

COLLECTION FREQUENCY OF ANT SPECIES AT THE 211 BAIT STATIONS AROUND KĪLAUEA CALDERA (SEE TEXT FOR DESCRIPTIONS) (TOTAL NUMBER OF COLLECTIONS ADD UP TO MORE THAN THE NUMBER OF SITES WITH ANTS BECAUSE MORE THAN ONE ANT SPECIES OCCURRED AT MANY SITES)

SPECIES	HQ GEOTHERMAL	PUHIMAU HOT SPOT	ROADSIDE	HQ PERIPHERY	FOREST
"Lowland" species					
Anoplolepis longipes	24			1	
Pheidole megacephala	20			5	
Cardiocondyla nuda		7	1	2	
Tapinoma melanocephalum		8		1	
Tetramorium bicarinatum		1		4	
Monomorium monomorium	1	1		1	
Cardiocondyla emeryi		1			
"Cold-tolerant" species					
Paratrechina bourbonica	2	10	10	19	2
Cardiocondyla venustula		15	1	13	
Linepithema humile				3	
Hypoponera punctatissima		1		4	2
Hypoponera opaciceps		1			
Sites with ants	45/45	31/35	11/13	33/63	3/55

Ph. megacephala at five bait sites in the HQ periphery, all within 150 m of the HQ geothermal area: one on Crater Rim Drive north of the thermal area and four on the service road east of Sulfur Banks. I found *A. longipes* at one bait site in the HQ periphery, at the start of the closed section of Crater Rim Drive east of Volcano House.

Paratrechina bourbonica (Forel), a cold-tolerant species, was the most widespread ant species in this study (Tables 1 and 2). Within the HQ geothermal area, *P. bourbonica* at high density cooccupied one site with *A. longipes* at low density and was sole occupant of another site. *Paratrechina bourbonica* was common in the HQ periphery and around the Puhimau hot spot. Along roadsides, *P. bourbonica* was the only common species, and it occurred at two sites in "undisturbed forest," both within 200 m of a road.

Cardiocondyla venustula Wheeler (= *Cardiocondyla "a"* in Huddleston and Fluker [1968] and Huddleston et al. [1968]: S. Cover and N. Reimer, pers. comm.), another cold-tolerant species, was also common, but with a more limited distribution than *P. bourbonica* (Table 2). Although *C. venustula* was common in the HQ periphery and the Puhimau hot spot, this species was absent from the HQ geothermal area and forest sites, and was collected only once at a roadside site.

I collected *Linepithema humile* (formerly *Iridomyrmex humilis*), a major pest species in drier highland areas, at only three bait station sites. These three sites were all within 150 m of park buildings: two on the Kīlauea Military Camp and one near the park residential area.

I also collected seven other ant species at the bait stations, five lowland species [*Cardiocondyla nuda* (Mayr), *Tapinoma melanocephalum* (Fabricius), *Tetramorium bicarinatum* (Nylander) (= *T. guineese* [Bolton 1977]), *Monomorium monomorium* Bolton (= *M. minutum* Mayr [Bolton 1987]), and *Cardiocondyla emeryi* Forel] and two cold-tolerant species [*Hypoponera punctatissima* (Roger) and *Hypoponera opaciceps* (Mayr)]. The five lowland species and *H. opaciceps* were restricted almost entirely to the HQ periphery and the Puhimau hot spot. *H. punctatissima*, however, also occurred in low densities at two "undisturbed forest" sites, one of which was more than 600 m from any disturbed area.

Ants at Building Sites

I found ants, representing a total of seven different species, in and around five of the six building sites that I surveyed in the Kīlauea Caldera area (Table 3). The buildings around the Volcano Golf Course were completely free of ants, possibly due to the use of pesticides.

The most widespread species at the building sites were *L. humile* and *A. longipes*. I collected *L. humile* in or around five buildings at three building sites and *A. longipes* in or around three buildings at two building sites. I collected five other species at one building site each. Two species, *P. bourbonica* and *Ph. megacephala*, were also common at bait stations. The other three species, however, I collected only at building sites. I found large numbers of *Pheidole fervens* Smith by the back door of the Volcano Art Center and *Paratrechina longicornis* (Latreille) in the cooking shelter at the Nāmakani Paio campground. Finally, I collected *Monomorium pharaonis* (L.) (as well as *Ph.*

TABLE 3

SUMMARY OF ANT SPECIES FOUND AT EACH BUILDING SITE, INCLUDING NUMBER OF DIFFERENT BUILDINGS WHERE I COLLECTED A SPECIES

	SITES[a]				
SPECIES	RC	NP	KMC	JM	HQ
"Lowland" species					
Anoplolepis longipes	1	*			2
Pheidole megacephala	1		*		
Paratrechina longicornis		1			
Pheidole fervens					1
Monomorium pharaonis	1				
Cardiocondyla emeryi				*	
"Cold-tolerant" species					
Paratrechina bourbonica	1		*	*	
Linepithema humile	2*	*	2*	2	

[a]RC, Research Center; NP, Nāmakani Paio campground; KMC, Kīlauea Military Camp; JM, Jagger Museum and Hawaiian Volcano Observatory; and HQ, Volcano House Hotel, Kīlauea Visitor's Center, and Volcano Art Center. I found no ants in the buildings around Volcano Golf Course. The first four sites were also surveyed by Medeiros et al. (1986). *, collected by Medeiros et al. (1986).

megacephala) from material delivered to the Research Center as described below.

New Introductions of Ants to Hawai'i Volcanoes National Park

On three occasions during the course of this study, I witnessed ants being imported into HVNP through human activity. On 22 June, a computer monitor was delivered to the Research Center from Texas by express mail. Inside the cardboard walls of the box were several hundred *M. pharaonis.* On 13 August, I found a few dozen *L. humile* living inside a car belonging to a researcher who commuted to the Research Center from her home outside the park. On 17 August, a park visitor found several hundred *Ph. megacephala* inside a bag of bagels purchased from a supermarket in Hilo, near sea level. All three of these ant species are common "tramps" that typically spread through colony budding (groups of workers accompanying inseminated queens), increasing the possibility of successful colonization (Hölldobler and Wilson 1990).

Ants Not Found in This Study

There are several ant species previously collected in HVNP that I did not find in this study: *Plagiolepis alluaudi, Technomyrmex albipes* (Smith), *Camponotus variegatus* (F. Smith), *Hypoponera* cf. *sinensis,* and *Paratrechina vaga* (Forel). All, except *P. vaga,* are "lowland" species that may be currently restricted to lower-elevation regions of HVNP. Alternatively, it is possible that these species do occur in the area surveyed in this study, but eluded collection because of their habits. For example, *P. alluaudi* and *T. albipes* tend to be arboreal (David 1961, Wetterer 1997) and *C. variegatus* is nocturnal (Reimer 1994). *Hypoponera sinensis* appears to be rare; Jorgensen et al. (unpubl. data) collected it only once in HVNP. Whether this one specimen is actually *H. sinensis* is questionable (L. Morrison, pers. comm.). Additional arboreal, nocturnal, or rare ant species may also have been missed in my study, along with species not attracted to tuna bait. Also, in some cases more aggressive ants may have excluded other species from the tuna bait.

It is possible that some of the specimens identified as *P. bourbonica* are actually *P. vaga,* because there are no satisfactory traits for distinguishing the workers of these two species (Wilson and Taylor 1967). In fact, Trager (1984) examined some of Wilson and Taylor's (1967) Polynesian and Melanesian "*vaga*" material and found that it contained "some workers of *bourbonica* as well as those of at least two other distinct species, differing in vestiture and proportions, and only one (or perhaps none) of which can be true *vaga.*"

DISCUSSION

Distribution and Spread of Ants in Hawai'i Volcanoes National Park

Although a diversity of ants occur in the Kīlauea Caldera region of Hawai'i Volcanoes National Park, they are common only in areas disturbed by human and geothermal activity. This supports the observation that exotic species in general tend to be more successful at invading disturbed habitats (Elton 1958, Orians 1986). Despite high densities of ants in disturbed areas and along roadsides, ants show little penetration into nearby undisturbed forest. The ant species present in the park may have little ability to invade intact montane forest. Alternatively, ants may simply have not yet spread to suitable habitat in the forest.

The two most recent surveys in Hawai'i Volcanoes National Park (Jorgensen et al. [unpubl. data] and this study) found many more ant species than previous studies. Several of the previously uncollected ant species are surprisingly widespread. For example, in this study, *Cardiocondyla venustula, Cardiocondyla nuda,* and *Tapinoma melanocephalum* occurred at 29, 10, and 9 sites, respectively. The two most recent ant surveys were more thorough than previous studies, and this alone may explain the increase in the number of species collected. There is strong evidence, however, that ants are spreading rapidly in the park. For example, neither

Huddleston and Fluker (1968) nor Gagné (1979) found *A. longipes* in HVNP, even in their low-elevation collections. Medeiros et al. (1986) collected *A. longipes* at three sites: at sea level, at 365 m elevation, and a single individual worker under a garbage can at Nāmakani Paio campground (1190 m elevation). Currently in HVNP, both along the coast and in the HQ geothermal area, *A. longipes* occurs at such remarkably high densities that hundreds of ants covered the tuna bait in a matter of minutes. In addition, the back porch of Volcano House is swarming with these ants. It seems unlikely that such populations were simply overlooked by the earlier studies. Rather, it seems more probable that *A. longipes* has invaded these areas within the past decade and is multiplying rapidly.

Haines et al. (1994) stated that the spread of *A. longipes* to new areas in the Seychelles "is almost certainly due to the accidental transfer of colonies in vehicles and in produce, such as coconut husks, vegetables, and building material." Similarly, Cole et al. (1992) believed that human activity was responsible for the spread of *L. humile* in the highlands of Maui. My observations of three introductions of ants into HVNP support the proposal that human activity is at least partly responsible for the spread of ants through Hawai'i Volcanoes National Park. The express mail delivery of ants into the park is particularly worrisome. Using this route, temperate ant species may now bypass the tropical conditions of Honolulu and arrive directly in the highlands of Hawai'i.

Geothermal Areas and Buildings as "Habitat Islands"

The geothermal areas and park buildings appear to serve as "habitat islands" of warmer climate that allow these ant species to extend their ranges to higher elevations. The Kīlauea Caldera region is the highest elevation recorded for *A. longipes* in Hawai'i (also see Medeiros et al. 1986). The only higher-elevation collection site in Hawai'i for *Ph. megacephala* is a single isolated collection site on the western slope of Mauna Kea, Hawai'i (1770 m elevation [Wetterer et al. 1998]). Eight other ant species I collected in the geothermal areas and building sites are also usually restricted to elevations below 900 m (Table 1).

Anoplolepis longipes and *Ph. megacephala* appear to have displaced most other ant species from the HQ geothermal area, but do not occur at the Puhimau hot spot. It appears that *Ph. megacephala* and *A. longipes* have not colonized this isolated habitat island. Although the Puhimau hot spot is at a lower elevation than the HQ geothermal area and closer to a possible source of colonization by lowland ants, there is little human traffic to the Puhimau area.

Thermal habitat islands occur around geothermal areas worldwide (e.g., see Glime and Iwatsuki 1994). Often these areas are highly alkaline, enriched with sulfur and other chemicals, and are inhabited only by tolerant species. Geothermal vents, in such areas as Yellowstone National Park, USA, are the sources of numerous unique thermophilic microorganisms (Brock 1978, Pool 1990). The ecological significance of geothermal habitat islands for native Hawaiian species in HVNP deserves further study. Geothermal areas may serve as refuges for less cold-tolerant native species, particularly in the winter months. Some of these species may in turn serve as food resources for other native species. Whether any endemic Hawaiian species are found only in geothermal areas is unknown.

Possible Impact of Ants in Hawai'i Volcanoes National Park

The spread of exotic ants through Hawai'i Volcanoes National Park poses a serious threat to endemic Hawaiian species. High densities of *Ph. megacephala* and *A. longipes* threaten endemic Hawaiian invertebrate and plant species found around high-elevation geothermal areas and nearby disturbed areas. In addition, these ant populations may serve as a source for the spread of ants to other high-elevation sites. The potential impact of *Ph. megacephala* and *A. longipes* at high elevations in Hawai'i, however, depends on the ability of these ants to survive at high elevations away from geothermal areas and buildings. Recent surveys have found *Ph. megacephala* at high elevations on the saddle between Mauna Loa and Mauna Kea (Wetterer et al. 1998 and P. Oboyski, unpubl. data).

The potential impact of more cold-tolerant ants may be even more profound. The great impact of *L. humile* on native fauna in drier highland regions of Hawai'i has been documented, but the importance of *L. humile* in wetter highlands appears to be much more limited. The rare occurrence and low density of *H. punctatissima* supports Reimer's (1994) conclusion that the ecological importance of this species is "probably minimal." The ecological importance of more common cold-tolerant ant species, such as *P. bourbonica* and *C. venustula,* remains unknown. *Paratrechina bourbonica* has the potential for serious impact in montane regions of Hawai'i Volcanoes National Park because it appears to be able to colonize all habitats, including intact forest. A congener of this species, *Paratrechina fulva* (Mayr), is an important pest where it has been introduced (Zenner-Polania 1994). *Cardiocondyla venustula* is common at elevations up to 2000 m on nearby Mauna Kea (unpubl. data). The highland forests of Hawai'i Volcanoes National Park must be protected against human disturbance and the introduction of additional ant species that may thrive in highland forests.

Decisions on future conservation of natural areas in Hawai'i may depend critically on the current distribution of pest ants as well as their potential future distributions. A data base on the distribution of ants in the Hawaiian Islands should be useful, not only to other researchers interested in examining the impact of ants, but also to researchers examining other ecological questions where the presence or absence of ants should be controlled. Establishing a baseline for the distribution of pest ant species in Hawai'i is essential for any large-scale studies of ant management and control. The effectiveness of control methods must be gauged against known distributions. 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).

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