Impact of the Argentine Ant, *Linepithema humile* on the Native Ants of Santa Cruz Island, California

by

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ABSTRACT

We examined the impact of the non-indigenous Argentine ant, *Linepithema humile* (Mayr), on the native ants of Santa Cruz Island (SCI), the largest of the California Channel Islands. *Linepithema humile*, a South American native, was first found on SCI in 1996 and now occupies two areas comprising less than 1% of the island. We surveyed ants using four methods: visual surveys, bait stations, tree surveys, and soil/litter samples. We found a total of 23 ant species, including two species not native to SCI: *Cardiocondyla ectopia* Snelling and *Linepithema humile*. Numerous native ants occurred at sites uninfested by *L. humile* and co-occurred with *L. humile* at the outer boundaries of *L. humile*-infested territory, but at sites more than 10 m within *L. humile*-infested territory, all but two of these species disappeared, probably due to exclusion by *L. humile*. Only two tiny ant species, *Solenopsis molesta* Say and *Monomorium ergatogyna* Wheeler, were found to coexist deep within the *L. humile*-occupied areas.

Key Words: Ants, California, Channel Islands, exotics, invasive species, *Linepithema*, tramp ants

INTRODUCTION

Tramp ants associate with humans and are spread by human commerce (Williams 1994). They travel the world hidden in our plant products, packaging material, building supplies, and heavy machinery such as logging and military equipment (e.g., Haines *et al.* 1994; Wetterer 1998). Although the ecological importance of most tramp ant species remains undocumented, several are known to have dramatic impacts (Williams 1994). Here, we examine the impact of a highly-destructive tramp species, the Argentine ant, *Linepithema humile* **(Ma,**

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on the ant fauna of Santa Cruz Island, off the coast of southern California.

Linepithema humile, native to South America, is now a pest in subtropical and warm temperate regions around the world, including Madeira (Schmitz 1896), southern Europe (Way *et al.* 1997), southern United States (Barber 1916), Bermuda (Haskins & Haskins 1965, 1988), United Arab Emirates (Collingwood *et al.* 1997), South Africa (Hattingh 1945), Australia (Majer 1994), New Zealand (Green 1990), Hawaii (Cole *et al.* 1992; Wetterer *et al.* 1998), and Japan (Sugiyama 2000). This species appears to thrive particularly well in areas with "Mediterranean climates" (Vega & Rust 2001). Skaife (1961) described *L. humile* as "by far the most harmful of all the species of ants found in the world." The invasion of *L. humile* is of particular concern on oceanic islands, due to the vulnerability and endemism typical of island ecosystems (e.g., see Cole *et al.* 1992).

Linepithema humile was first introduced to California early in the 1900's (Woodward 1908) and has spread across the state, exterminating numerous native ants and other invertebrates (Ward 1987; Holway 1995; Human & Gordon 1997; Holway *et al.* 1998; Kennedy 1998; Holway 1999). The impact of *L. humile* on native ants is so dramatic that Holway (1995) considered the finding of any native epigeic (above-ground foraging) ants in an area as sufficient indication that *L. humile* was not present. Several small subterranean ants, however, appear to be able to coexist with *L. humile*. For example, Wilson & Taylor (1967) noted that *L. humile* "excludes other larger ant species, including the formidable *Pheidole megacephala*. One species found to be compatible with it on Hawaii is the diminutive *Cardiocondyla nuda*."

In 1996, Adrian Wenner first discovered *L. humile* on Santa Cruz Island (SCI) (Calderwood *et al.* 1999). In July 1997, surveys found that *L. humile* occurred at two small, non-contiguous areas of SCI, both surrounding dismantled Navy support facilities (Calderwood *et al.* 1999). The area occupied by the two *L. humile* populations were approximately 1.5 km^2 and 0.05 km^2, less than 1% of the island (Calderwood *et al.* 1999). In the present study, we surveyed ants outside and inside the two known *L. humile*-infested areas to evaluate the impact of *L. humile* on other ant species on SCI.

Study site

Santa Cruz Island (34°00'N; 119°44'W) is the largest (245 km^2) and most ecologically diverse of the California Channel Islands (Junak *et al.* 1995). Santa Cruz Island has more than 140 species of land birds (Power 1976; Diamond & Jones 1980) and numerous terrestrial and marine mammals (Wenner & Johnson 1980). Many plants and animals are endemic to the Channel Islands, including more than 100 endemic species of insects (Miller 1985). In the past, SCI was used for ranching and some agriculture and tourism (Junak *et al.* 1995). There were also several military installations. SCI is now entirely a nature reserve, with a permanent human population of fewer than twenty people. One largely unmanned Navy radar installation also remains. The island is far from pristine, with large populations of exotic plants (e.g., fennel, *Foeniculum vulgare*) and animals (e.g., pigs, *Sus scrofa*) (Junak *et al.* 1995).

METHODS

In March 1998, we surveyed the ants of Santa Cruz Island with the help of A. Calderwood (Santa Barbara Natural History Museum), A. Wenner (UC Santa Barbara), C. Dunning (UC Riverside), M. Patten (UC Riverside), J. Burger (UC Riverside), L. Patterson (Biosphere 2 Center), and eight undergraduate students from Columbia University's Biosphere 2 Center. In April 1998, E. Hebard surveyed with the help of J. Howarth. In May 1998, we surveyed with the help of R. Lee (The Clorox Company), A. Southern (Biosphere 2 Center), and seven undergraduate students from Biosphere 2 Center.

We surveyed ants in six areas of SCI with substantial human traffic, the most likely places to find *L. humile*, as well as along routes connecting these sites. The first two of these sites were the areas previously identified as occupied by *L. humile*. 1) The "Lower MariPro" site surrounds a former U.S. Navy / MariPro installation above Valley Anchorage. The installation was dismantled in 1995 and all that remains is a concrete foundation and fuel tank. 2) The "Upper MariPro" site centers on a clearing that was formerly the location of another Navy /MariPro installation, dismantled in 1995. 3) The "Navy Radar" site surrounds an active U.S. Navy radar installation on the hill top directly adjacent to the Upper MariPro site. 4) The "Prisoner's Harbor" site includes the pier where all shipments enter and leave the island as well as numerous storage buildings. Building material removed from the Lower and Upper MariPro sites has been stored here. 5) The "Stanton Ranch" site surrounds the buildings now used as the island headquarters of The Nature Conservancy (TNC). Currently, five people live permanently at this site. Numerous volunteers and TNC donors visit this site throughout the year. 6) The "Field Station" site surrounds the University of California Santa Cruz Island Reserve Field Station which is used as a base for research on the island. Currently, three people live permanently at this site. Numerous researchers and university classes visit this site throughout the year. Some building material salvaged from the MariPro sites was brought to the field station.

Visual surveys

March - May 1998, we conducted visual surveys, searching for ants on surfaces and under movable objects in the six areas described above.

Bait station survey

March - April 1998, we collected ants at 384 bait stations placed at 20 m intervals along transects through the six areas described above and at 100 m intervals next to the roads connecting these six areas.

We used two types of bait, tuna and Keebler's Pecan Sandies™ cookies. A bait card consisted of approximately 2 g of bait at the center of a 7.6 x 12.7 cm index card. We folded each card in half and placed it flush with the ground about one meter from the road, trail, transect, or building, using a small rock or branch to weight the top half of the card. Each bait station had two bait cards, one with tuna and one with cookie. We returned to each station 2-3 hours later, quickly and carefully placing the bait station cards, along with all ants at the bait, in zip-lock plastic bags. We then placed the bags in a freezer to kill the ants.

Tree and soil/litter surveys

On 22 May 1998, we surveyed ants on 18 Santa Cruz Island Manzanita trees (*Arctostaphylos insularis*) within and around Upper MariPro. We selected six trees immediately outside the area of occupation ("uninfested" trees), six trees on the outermost boundary of the occupation ("border" trees), and six trees that were more than 10 m within the area of *L. humile* occupation ("infested" trees). At each tree, two of us (JKW & ALW) using aspirators collected all the ants observed in a 5 min period.

On 22 May 1998, we also collected six soil/litter samples at Upper MariPro, three immediately outside *L. humile*-infested area and three located more than 10 m inside the *L. humile*-infested area. We placed approximately 1 liter of each sample in Berlese funnels for five days to extract soil invertebrates.

RESULTS

Visual surveys

In our visual surveys, we found 23 ants species (Table 1; see Wetterer *et al.*, 2000 for more taxonomic details and a full list of the 34 ant species known from SCI). Only two species were non-native: *Cardiocondyla ectopia* and *Linepithema humile*. *Cardiocondyla ectopia*, an Old World

Table 1. Ant species found on Santa Cruz Island in the present study. We indicate the total number of sample sites where we collected each species using visual surveys, bait stations, tree, and Berlese samples.

Species	Sites
Linepithema humile (Mayr)	83
Monomorium ergatogyna Wheeler	152
Formica moki Wheeler	80
Tapinoma sessile (Say)	53
Pheidole hyatti Emery	33
Prenolepis imparis (Say)	29
Solenopsis molesta Say (s.l)	29
Camponotus hyatti Emery	26
Camponotus semitestaceus Emery	26
Camponotus sp. near *vicinus*	18
Crematogaster marioni Buren	15
Dorymyrmex insanus (Buckley) (s.l)	14
Cardiocondyla ectopia Snelling	3
Hypoponera opacior (Forel)	3
Messor chamberlini Wheeler	3
Pheidole californica Mayr	3
Brachymyrmex cf. *depilis*	2
Camponotus clarithorax Emery	2
Dorymyrmex bicolori Wheeler	2
Leptothorax andrei Emery	2
Polyergus sp.	2
Pseudomyrmex apache Creighton	2
Pogonomyrmex subdentatus Mayr	1

species (Snelling 1974), was found only in the visual surveys at three sites around the cafeteria building of the Stanton Ranch, and appears to be a very recent invader. We found *L. humile* only in the Lower MariPro and Upper MariPro sites. The outer boundaries of the *L. humile*-infested areas were generally distinct, with dense populations of *L. humile* disappearing and substantial populations of native ants appearing over a transition zone of 10 m or less.

Bait station survey

At all 384 bait stations combined, we collected a total of 18 ant species (17 native ant species plus *L. humile*; Table 2). At the 303 stations outside the areas occupied by *L. humile*, we made 309 native species records (mean = 1.0 records / station) representing 17 ant species. At 11 "border" stations located at the outer edges of the *L. humile* populations, we made 11 native species records (mean = 1.0 records/station) representing six species of ants found at the same bait stations as *L. humile*. However, at the 70 bait stations more than 10 m inside the two areas occupied by *L. humile*, we made only 24 native species records

Table 2. Number of bait stations on Santa Cruz island where different ant species were collected, outside, on the border, and more than 10 m inside the two areas occupied by *L. humile*. * = species found at a significantly higher proportion of stations outside the *L. humile*-occupied areas than at stations inside the areas (Chi-squared test, df = 1, p <0.05).

Ant species	Outside n = 303	Border n = 11	Inside n = 70	X^2
Linepithema humile		11	55	—
Monomorium ergatogyna	116	4	21	1.7
Formica moki	53	2		16.5*
Tapinoma sessile	50	1		13.4*
Prenolepis imparis	22	2		5.4*
Solenopsis molesta	17		3	0.2
Pheidole hyatti	17	1		4.1*
Camponotus semitestaceus	13			3.1
Dorymyrmex insanus	9	1		1.8
Crematogaster marioni	2			0.5
Pheidole californica	2			0.5
Leptothorax andrei	2			0.5
Brachymyrmex cf. *depilis*	1			0.2
Camponotus cf. *vicinus*	1			0.2
Camponotus hyatti	1			0.2
Dorymyrmex bicolori	1			0.2
Hypoponera opacior	1			0.2
Messor chamberlini	1			0.2

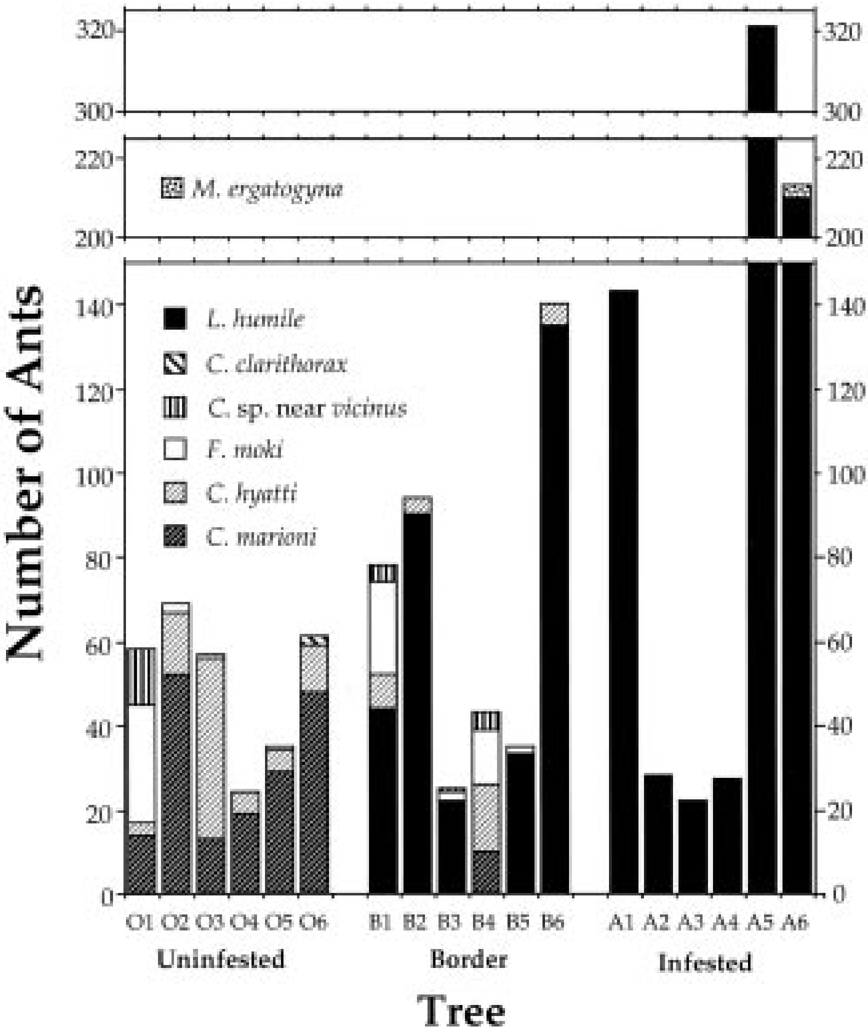
(mean = 0.3 records/station) representing just two ant species, *S. molesta* and *M. ergatogyna*. [Thus, whereas there was no decrease in native ant species recorded at baits with *L. humile* present at the outer edge of the *L. humile*-infested areas, there was a significant drop off in native ants more than 10 m inside the two infested areas.

All 17 native ant species were found at a higher proportion of the bait stations outside the *L. humile*-infested areas than inside, though this difference was statistically significant for only four species with large enough sample size: *F. moki*, *T. sessile*, *Prenolepis imparis*, and *Pheidole hyatti* (Table 2). The two native ant species found at stations deep within *L. humile* territory, *M. ergatogyna* and *S. molesta*, were both at a slightly higher proportion of bait stations outside the *L. humile* area than inside (for *M. ergatogyna*: 38.3% vs. 30.0%; for *S. molesta*: 5.6% vs. 4.3%).

Tree and soil/litter surveys

On 18 manzanita trees at Upper MariPro, we collected *L. humile* plus six native ant species: *C. marioni*, *C. hyatti*, *F. moki*, *Camponotus* sp. near *vicinus*, *C. clarithorax*, and *M. ergatogyna* (Figure 1). We found five of the native species on trees in uninfested areas. Three of these species (*F. moki*, *Camponotus* sp. near *vicinus*, and *C. hyatti*) also co-occurred with *L. humile* on border area trees. Only one species, *M. ergatogyna*, coexisted with *L. humile* on infested trees more than 10 m within the *L. humile*-infested area. At one border tree, B4, we collected no *L. humile*, although several days earlier we had observed *L. humile* on the tree. One ant species, *C. marioni*, had a mutually exclusive distribution with *L. humile*. It occurred on all seven trees without *L. humile* and on none of

Fig. 1. Number of ants collected from 18 manzanita trees at the Upper MariPro site on SCI, in areas immediately outside the area infested by *L. humile* (O1-O6), on the border of *L. humile* infested area (B1-B6), and more than 10m inside *L. humile* infested area (A1-A6).



the eleven trees with *L. humile* (Figure 1).

The very high numbers of *L. humile* workers on some manzanita trees (Figure 1) were associated with very high numbers of scale insects; large areas on the manzanita branches were completely covered by scale insects. All *L. humile* workers on these trees appeared to be tending the scale insects to feed on the honeydew they produce.

We found only two ant species in the six Berlese samples of soil and leaf litter from the Upper MariPro area. All six samples had *S. molesta* and one sample also had *L. humile*.

DISCUSSION

Numerous earlier studies indicate that *L. humile* has a great negative impact on native, epigeic (above-ground foraging) ants (**Erickson 1972 or1971?**; Ward 1987; Holway 1995; Holway 1998; Kennedy 1998), but that the impact shows spatial and temporal variation (Suarez *et al.* 1998; Parker *et al.* 1999). We found striking spatial variation in co-occurrence related to the distance from the edge of *L. humile*-occupied areas. Several native ant species co-occurred with *L. humile* at the outermost boundary of *L. humile*-occupied territory, but were absent from locations deeper than 10 m within *L. humile* territory. This pattern strongly suggests that these native ant species coexist only temporarily in areas recently invaded by *L. humile*, and are eventually excluded from these areas by *L. humile* (Holway 1999). Hattingh (1945) noted a similar pattern with exotic *L. humile* populations in South Africa. He wrote that "the indigenous ants have gradually disappeared until today not a single colony is to be found in areas heavily populated by the Argentine ant. In areas not heavily populated by this species, isolated nests of indigenous species may still be found. "Where [the] Argentine ant has only recently been introduced a mixed population occurs."

We found only two tiny ant species, *Monomorium ergatogyna* and *Solenopsis molesta*, persisting deep within *L. humile*-infested parts of SCI. Our study suggests little apparent impact of *L. humile* on *M. ergatogyna*. Overall, *M. ergatogyna*, the most common ant at baits, was only slightly less common at baits in *L. humile*-infested areas. In addition, the only manzanita tree on which we found *M. ergatogyna* also had extremely high numbers of *L. humile*. Holway (1998) found *M. ergatogyna* co-occurring with *L. humile* on mainland California, though in reduced numbers. In an area of Hawaii Volcano National Park dominated by extremely high densities of the long-legged ant, *Anoplolepis gracilipes*, the only other ant species found at tuna bait was another small *Monomorium* species, *Monomorium liliuokalanii* (formerly *M. minutum* var. *liliuokalanii*) (Wetterer 1998). *Monomorium ergatogyna* and other *Monomorium* species may be able to repel attacks by *L. humile*, by using their potent defensive secretions (Levins *et al.* 1973; Holway 1999; **S. Cover, pers. comm. not in References**).

Our bait station survey and our soil survey also suggested little impact of *L. humile* on *S. molesta*. Human & Gordon (1997) and Holway (1998) both found *Solenopsis molesta* in *L. humile*-infested areas of California, though in reduced numbers. Suarez *et al.* (1998) found *Solenopsis molesta* at 34 of 40 *L. humile*-infested sites. Interestingly, *Solenopsis molesta* is one of the few other ants species that persist at substantial densities in areas dominated by other tramp ants. In Biosphere 2, a 1.28-hectare closed greenhouse structure built in the Arizona desert, Wetterer *et al.* (1999) found that >99.9% of the ants coming to tuna and cookie bait were a single species, the crazy ant, *Paratrechina longicornis*. However, in soil and litter samples, one other ant species was also common, *Solenopsis molesta*. *Solenopsis molesta* may be able to coexist because of its largely subterranean habits (Ward 1987; Human & Gordon 1997; Holway 1998).

Although we found no overlap in the distributions of *C. ectopia* and *L. humile* the two exotic species on SCI, future coexistence may be expected. Gulmahamad (1997) found that "a number of behavioral strategies, in addition to a potent repellent chemical, probably allow *C. ectopia* to live in sympatry and synchrony with *Linepithema humile*."

The populations of *L. humile* in areas of SCI that it infested were often extremely high, as documented by the large numbers we collected from some manzanita trees. Whereas in native populations rival *L. humile* colonies defend individual territories, in invading populations, *L. humile* can achieve very high densities in part as a result of abandonment of intraspecific territorial aggression (Holway *et al.* 1998; Suarez *et al.* 1999). We noted that high populations of *L. humile* on SCI appeared to correlate with high populations of Homoptera. Numerous earlier studies have noted a positive relationship between populations of invasive ants and homopterans (e.g., Wetterer 1997; Wetterer *et al.* 1999; Green *et al.* 1999). Phillips & Sherk (1991) found that the presence of *L. humile* in vineyards correlated with great increases in mealybug populations, and that suppression of *L. humile* populations resulted in parallel decreases in mealybugs. This mutualistic relationship with homopterans may be of central importance in determining the distribution and impact of *L. humile* and other invasive ants. Extremely high densities of invasive ants, in general, may require high densities of homopterans to support their population, and they may only be able to invade areas with plants that can support high densities of homopterans, e.g., exotic weeds in disturbed environments (Wetterer 1998;

Wetterer *et al.* 1999). Conversely, the dearth of such vegetation may explain why invasive ants are often unable to penetrate relatively intact natural areas (Wetterer 1998). Such positive interactions among certain invading species may be of general importance for their successful invasion (Parker *et al.* 1999).

It is unclear what action should be taken concerning *L. humile* on Santa Cruz Island. If left unchecked, it seems likely that the *L. humile* populations will continue to spread until they occupy much of SCI, as they have on other islands of similar latitude that they have invaded, such as Madeira (32°45'N; Schmitz 1896) and Bermuda (32°20'N; Haskins & Haskins 1965, 1988). The *L. humile* populations on SCI continue to be monitored and the feasibility of controlling *L. humile* with chemicals is being investigated. *Linepithema humile* is now known to infest three other California Channel Islands as well. It is widespread on Santa Catalina Island, the only Channel Island with a large human population (Cockerell 1940; **Rentz & Weissman 1982 or 1981?**; **E. Hebard & N. Heller, pers. obs. not in References**), and occurs in three discrete populations around the Navy facilities on San Nicolas Island (E. Hebard & N. Heller, pers. obs.). There is also one record from San Clemente Island (Straughan 1982). Comprehensive ant surveys are needed on these and the other California Channel Islands to evaluate more fully the distribution and impact of this highly destructive invader and to study what action might be taken to eliminate or at least contain them while this is still a viable option.

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REFERENCES

Barber, E.R. 1916. The Argentine ant: distribution and control in the United

States. United States Department of Agriculture Bulletin, 377, 1-23.

Calderwood, J.A., A.M. Wenner, & J.K. Wetterer. 1999. Argentine ants (Hymenoptera) invade California's Santa Cruz Island. Proceedings of 5th California Islands Symposium, pp. 274-277. Santa Barbara Museum of Natural History, Santa Barbara.

Cockerell, T.D.A. 1940. The insects of the Californian Islands. Proceedings of the Sixth Pacific Science Congress, 4, 283-295.

Cole, F.R., A.C. Medeiros, L.L. Loope & W.W. Zuehlke 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. Ecology, 73, 1313-1322.

Collingwood, C.A., B.J.Tigar & D. Agosti 1997. Introduced ants in the United Arab Emirates. Journal of Arid Environments 37, 505-512.

Diamond, J.M. & Jones H.L. 1980. Breeding land birds of the Channel Islands. In: Power D (ed) The California islands: Proceedings of a Multidisciplinary Symposium, pp 597-612. Santa Barbara Museum of Natural History, Santa Barbara.

Erickson, J.M. 1971. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. Psyche, 78, 257-266.

Green, O.R. 1990. Entomologist sets new record at Mt. Smart: *Iridomyrmex humilis* established in New Zealand. The Weta, 13(1), 14-16.

Green, P.T., D.J. O'Dowd & P.S. Lake 1999. Alien ant invasion and ecosystem collapse on Christmas Island, Indian Ocean. Aliens, 9, 2-4.

Gulmahamad, H. 1997. Ecological studies of *Cardiocondyla ectopia* Snelling (Hymenoptera: Formicidae) in Southern California. Pan-Pacific Entomologist, 73, 21-27.

Haines, I.H., J.B. Haines & J.M. Cherrett 1994. The impact and control of the crazy ant, Anoplolepis longipes (Jerd.), in the Seychelles. Exotic Ants. Biology, Impact, and Control of Introduced Species (ed. by D.F. Williams) pp 206-218. Westview Press, Boulder.

Haskins, C.P. & E.F. Haskins 1965. *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda - equilibrium or slow replacement. Ecology, 46, 736-740.

Haskins, C.P. & E.F. Haskins 1988. Final observations on *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda. Psyche, 95, 177-184.

Hattingh, C.C. 1945. Argentine ant versus indigenous ants. Journal of the Entomological Society of South Africa, 8, 25-34.

Holway, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in Northern California. Conservation Biology, 9, 1634-1637.

Holway, D.A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. Oecologia, 116, 252-258.

Holway, D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology, 80, 238-251.

Holway, D.A.,, A.V. Suarez & T.J. Case 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. Science, 282, 949-952.

Human, K.G. & D.M. Gordon 1997. Effects of Argentine ants on invertebrate biodiversity in Northern California. Conservation Biology, 11, 1242-1248.

Junak, S., T. Ayers, R. Scott, D. Wilken & D. Young 1995. A Flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara.

Kennedy, T.A. 1998. Patterns of an invasion by Argentine ants (*Linepithema humile*) in a riparian corridor and its effects on ant diversity. American Midland Naturalist, 140, 343-350.

Levins, R., M.L. Pressick & H. Heatwole 1973. Coexistence patterns in insular ants. American Scientist, 61, 463-472.

Majer, J.D. 1994. Spread of Argentine ants (*Linepithema humile*), with special reference to Western Australia. Exotic Ants. Biology, Impact, and Control of Introduced Species (ed. by D.F. Williams) , pp 163-173. Westview Press, Boulder.

Miller, S.E. 1985. The California Channel Islands — past, present, and future: an entomological perspective. Entomology of the California Channel Islands (ed. by A.S. Menke & D.R. Miller) pp 3-27. Santa Barbara Museum of Natural History, Santa Barbara.

Parker, I.M., D. Simberloff, W.M. Lonsdale, K. Goodell, M. Wonham, P.M. Kareiva, M.H. Williamson, B. Von Holle, P.B. Moyle, J.E. Byers & L. Goldwasser 1999. Impact: towards a framework for understanding the ecological effect of invaders. Biological Invasions, 1, 3-19.

Phillips, P.A. & C.J. Sherk 1991. To control mealybugs, stop honeydew-seeking ants. California Agriculture 45 (2), 26-28.

Power, D.M. 1976. Avifauna richness on the California Channel Islands. Condor, 78, 394-398.

Rentz, D.C. & D.B. Weissman 1981. Faunal affinities, systematics, and bionomics of the Orthoptera of the California Channel islands. University of California Publications in Entomology, 94, 1-240.

Schmitz, E. 1896. As formigas da Madeira. Annaes de Sciencias Naturaes, 3, 55-58.

Skaife, S.H. 1961. The study of ants. Longmans, Green. London. 178 pp.

Snelling, R.R. 1974. Studies on California ants. 8. A new species of *Cardiocondyla* (Hymenoptera: Formicidae). Journal of the New York Entomological Society, 82, 76-81.

Straughan, D. 1982. Inventory of the natural resources of sandy beaches in Southern California. Technical Report of the Allan Hancock Foundation, University of Southern California, 6, 1-447.

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

Suarez, A.V., N.D. Tsutsui, D.A. Holway & T.J. Case 1999. Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. Biological Invasions, 1, 43-53.

Sugiyama, T. 2000. Invasion of Argentine Ant, *Linepithema humile*, into Hiroshima Prefecture, Japan. Japanese Journal of Applied Entomology Z

44: 127-129

Vega, S.J. & M.K. Rust 2001. The Argentine ant - A significant invasive species in agricultural, urban, and natural environments. Sociobiology, 37, 3-25.

Ward, P.S. 1987. The distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. Hilgardia, 55, 1-16.

Way, M.J., M.E. Cammell, M.R. Paiva & C.A. Collingwood 1997. Distribution and dynamics of the Argentine ant, *Linepithema* (*Iridomyrmex*) *humile* (Mayr) in relation to vegetation, soil conditions, topography and native competitor ants in Portugal. Insectes Sociaux, 44, 415-433.

Wenner, A.M. & D.L. Johnson 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? The California islands: Proceedings of a Multidisciplinary Symposium (ed. by D. Power) pp 497-530. Santa Barbara Museum of Natural History, Santa Barbara.

Wetterer, J.K. 1997. Ants on *Cecropia* in Hawaii. Biotropica, 29, 128-132.

Wetterer, J.K. 1998. Non-indigenous ants associated with geothermal and human disturbance in Hawai'i Volcanoes National Park. Pacific Science 52, 40-50.

Wetterer, J.K., P.C. Banko, L.P. Laniawe, J.W. Slotterback & G.J. Brenner 1998. Non-indigenous ants at high elevations on Mauna Kea, Hawaii. Pacific Science, 52, 228-236.

Wetterer, J.K., S.E. Miller, D.E. Wheeler, C.A. Olson, D.A. Polhemus, M. Pitts, I.W. Ashton, A.G. Himler, M. Yospin, K.R. Helms, E.L. Harken, J. Gallaher, C.E. Dunning, M. Nelson, J. Litsinger, A. Southern & T.L. Burgess 1999. Ecological dominance by *Paratrechina longicornis* (Hymenoptera: Formicidae), an invasive tramp ant, in Biosphere 2. Florida Entomologist, 82, 381-388.

Wetterer, J.K., P. S. Ward, A. L. Wetterer, J. T. Longino, J. C. Trager & S. E. Miller 2000. Ants of Santa Cruz Island, California. Bulletin of the Southern California Academy of Sciences, 99, 25-31.

Williams, D.F. (ed.) 1994. Exotic Ants. Biology, Impact, and Control of Introduced Species. Westview Press, Boulder.

Wilson, E.O. & R.W. Taylor 1967. Ants of Polynesia. Pacific Insects Monograph, 14, 1-109.

Woodward, C.W. 1908. The Argentine ant in California. University of California Agricultural Experiment Station Circular, 38, 1-11.