

## The History of Little Fire Ant *Wasmannia auropunctata* Roger in the Hawaiian Islands: Spread, Control, and Local Eradication

Casper Vanderwoude<sup>1</sup>, Michelle Montgomery, Heather Forester, Ersel Hensley, and Michael K. Adachi

Hawaii Ant Lab, Pacific Cooperative Studies Unit, University of Hawaii at Manoa, 16 E. Lanikaula St Hilo, Hawaii. <sup>1</sup>Corresponding author: casperv@hawaii.edu

**Abstract.** The islands of Hawaii have been the battleground for successive “invasion waves” by exotic ants for over a century. The arrival of *Pheidole megacephala* (Fabricius) (the big headed ant) in the late nineteenth century, was followed in 1939 by *Linepithema humile* (Mayr) (the Argentine ant) and *Anoplolepis gracilipes* (fr. Smith), (the longlegged Ant) in 1953. The most recent arrival is the little fire ant (*Wasmannia auropunctata* Roger) which was first recorded in 1999. This paper chronicles the subsequent spread of *W. auropunctata* through the Hawaiian archipelago. Initially introduced and spread via the import and sale of nursery plants, *W. auropunctata* is now well-established on the island of Hawaii. Ubiquitous on the windward side of Hawaii island, *W. auropunctata* are now being transported not only via nursery plants but also via non-agricultural products. The prevention, detection and response to *W. auropunctata* introductions is addressed by informal and *ad hoc* partnerships between a number of agencies, each contributing to preventing and reducing spread of this species. The draft Hawaii Inter-Agency Biosecurity Plan recognizes and strengthens these partnerships and will contribute positively to Hawaii’s biosecurity system.

**Key words:** invasive ants, Hawaii, *Wasmannia auropunctata*, biosecurity, biological invasions, Pacific, little fire ant

### Introduction

Native ants are thought to be naturally absent from the islands of the eastern Pacific, including those of the Hawaiian archipelago (Wilson and Taylor 1967). All ant species currently recorded in Hawaii are widespread cosmopolitan tramp species that have been introduced by human travel and commerce (Krushelnycky et al. 2005). The biota of Hawaii has evolved in the complete or nearly complete absence of ants, which most likely resulted in an ecological predisposition to invasions by exotic ant species along with increased impacts such invasions may cause (Reimer

et al. 1990). The number of new ant species has accumulated steadily over time to 47 (Krushelnycky et al. 2005), with the current number of species a little higher due mostly to taxonomic revisions.

Of these, four ant species are especially noteworthy due to their ecological and economic impacts worldwide, featuring prominently in the IUCN list of the world’s worst invasive species (Lowe et al. 2000). The bigheaded ant (*Pheidole megacephala* (Fabricius)) was first recorded in Hawaii as early as 1879 (Smith 1879), at which time it was already well established. In the years that followed,

entomologists lamented the dearth of native Coleoptera wherever *P. megacephala* had become established (Perkins 1913). Their association with mealybugs and other common plant pests caused crop losses, especially in pineapple (Beardsley et al. 1982, Jahn and Beardsley 1994). In the 1939, the Argentine ant (*Linepithema humile* (Mayr)) was detected on the island of Oahu (Zimmerman 1940, Reimer 1994). Primarily considered a nuisance species, Argentine ants spread quickly to the neighboring islands. The ensuing battle for territory between *L. humile* and *P. megacephala* saw the new invader restricted to higher elevation habitats where it caused considerable impacts to native ecosystems (Medeiros et al. 1986, Cole 1992, Krushelnicky and Gillespie 2008). In 1953, a new invader, *Anoplolepis gracilipes* (fr. Smith) (the longlegged ant, also known as the yellow crazy ant) arrived at the US Naval base, Pearl Harbor (Clagg 1953). A shade-tolerant species, *A. gracilipes* thrived in shaded lowland environments, preying on birds and invertebrates (Gillespie and Reimer 1993). Capable of episodic population explosions, *A. gracilipes* forms dense super-colonies that drive out other fauna and at some locations, can cause the collapse of plant communities (O'Dowd et al. 2003).

In 1999, the little fire ant (*Wasmania auropunctata* Roger) was detected on the island of Hawaii (Conant and Hirayama 2000). This ant species has a native range that includes South America and the Caribbean (Wetterer and Porter 2003), but has invaded many Pacific islands, West Africa, Australia, Florida, and Israel (Wetterer 2013). Genetic comparisons with material from native and introduced locations suggest Florida is the putative source of the Hawaii introduction (Mikheyev and Mueller 2007, Foucaud et al. 2010). Here, we describe the spread of this species through the Hawaiian islands

between 1999 and 2016 and discuss likely introduction pathways.

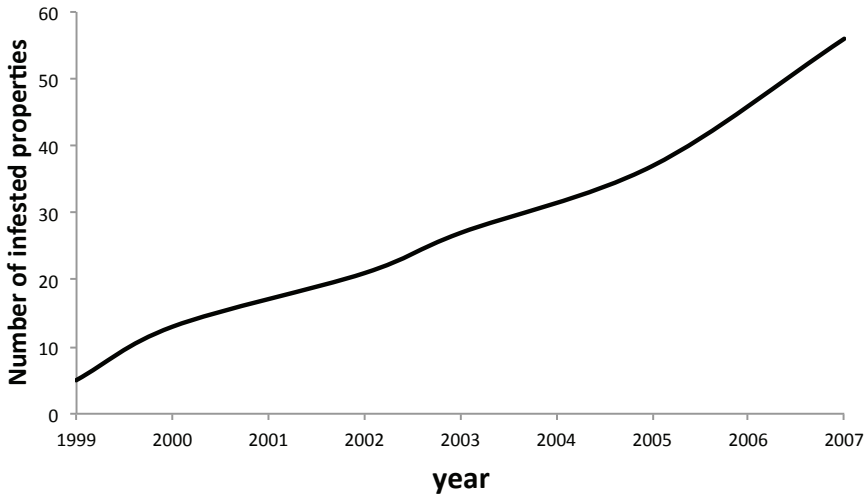
### Methods and Materials

We used published and unpublished literature as well as personal communications and observations from others involved with the response to this introduction to document the spread of *W. auropunctata* from the date of the initial detection to the present (2016).

### History of Introduction and Spread

The state of Hawaii is located in the central Pacific Ocean, approximately between longitudes 154–160° west, and latitudes 19–22° north. It is made up of eight separate islands, of which, six are accessible by the general public: Hawaii, Oahu, Maui, Kauai, Molokai, and Lanai. Since the initial discovery in 1999, *W. auropunctata* has become established on the four most populous islands (Oahu, Hawaii, Maui, and Kauai). The spread, to and within, each island, is detailed below.

**Hawaii island.** In 1999, Conant and Hirayama (2000) reported the presence of *W. auropunctata* at 13 locations in the South Hilo district on the island of Hawaii (the Big Island). Initially, *W. auropunctata* was observed on three infested properties in Hawaiian Paradise Park south of Hilo. Soon thereafter, additional infested locations were discovered at Kapoho and Paipaikou. Most infested locations were commercial nurseries or agricultural properties that had recently planted windbreaks of *Caryota* sp. (fish-tail palm) (P. Conant pers. com). Subsequent public outreach, e.g. Gruner (2000), and surveys revealed that *W. auropunctata* infestations were more widespread than first estimated, likely spread through the sale and movements of infested potted plants. Despite this challenge and a lack of resources, the Hawaii Department of



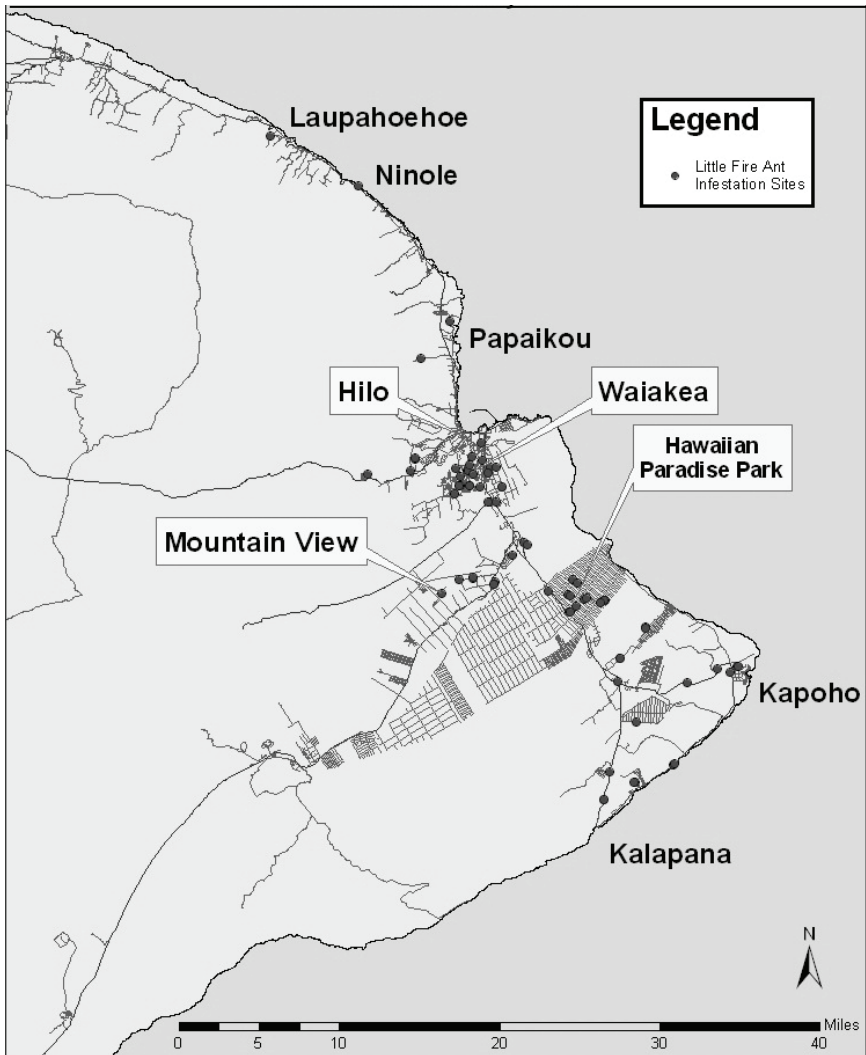
**Figure 1.** Number of known locations infested with *Wasmannia auropunctata* on Hawaii island between 1999 and 2007. Data sourced from Conant and Hirayama (2000); Motoki et al. (Motoki et al. 2013), P. Conant (pers. com.) and informal reports from Hawaii Department of Agriculture.

Agriculture (HDOA) responded by treating all known infested properties with baits. Between 1999 and 2007, the number of separate known infestations increased from an initial 3 properties to 56 by 2007 (Figure 1). These properties were scattered between Kalapana (30 miles SE of Hilo) and Laupahoehoe (25 miles NW of Hilo) (Figure 2) spanning some 55 miles to an elevation of 1,500 ft a.s.l.. However, the actual number of infested properties within these boundaries was probably much higher (P. Conant, pers. com.) as the number of known sites was a reflection of survey effort, increasing levels of public awareness and actual spread.

The widespread and mostly unknown distribution of *W. auropunctata*, along with an inability to treat colonies established in the tree canopy (Souza et al. 2008), resulted in the continued spread of this species. By early 2010, *W. auropunctata* had spread to several locations on the west coast of Hawaii island (Vanderwoude

et al. 2010). New infestations continued to be detected beyond the original Kalapana-Laupahoehoe area and now include most of the west side of Hawaii island, Waipio Valley, Hawi, Kapaau, Holualoa, Naalehu, Captain Cook, and Waimea. In districts with lower rainfall, *W. auropunctata* are limited to favorable microclimates near homes and other structures that feature artificial landscaping and irrigation (C.V. pers. obs.). This concurs with the observations of Vonshak in Israel (Vonshak et al. 2010). By end 2010, the estimated number of infested properties island-wide had exceeded 4,500, growing to an estimated 6,400 by end 2012 (Lee et al. 2015). Figure 3 shows areas on Hawaii island currently infested with *W. auropunctata*.

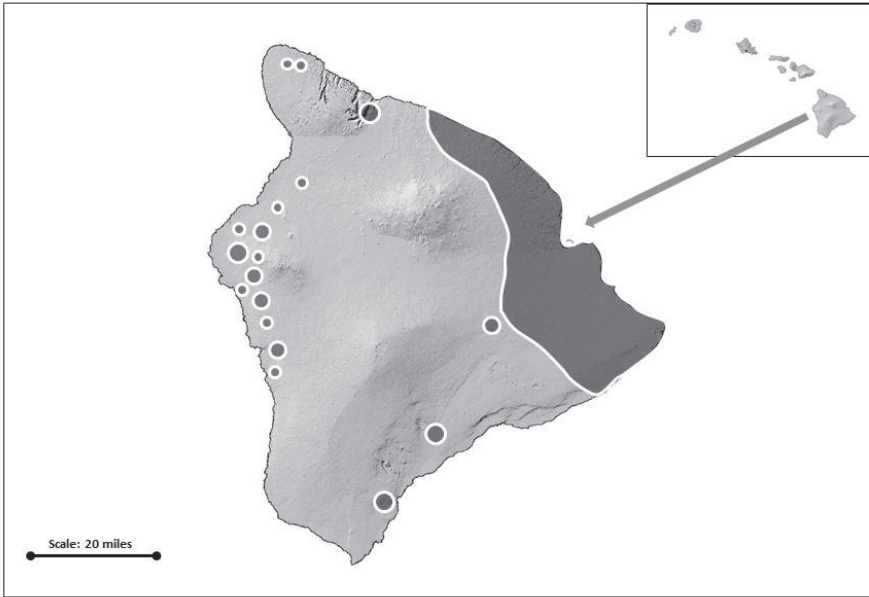
**Kauai.** At about the same time as the initial detection (October 1999), plants from an infested nursery on Hawaii had been shipped to the island of Kauai. These plants were infested with *W. auropunctata* colonies. The plants and adjacent



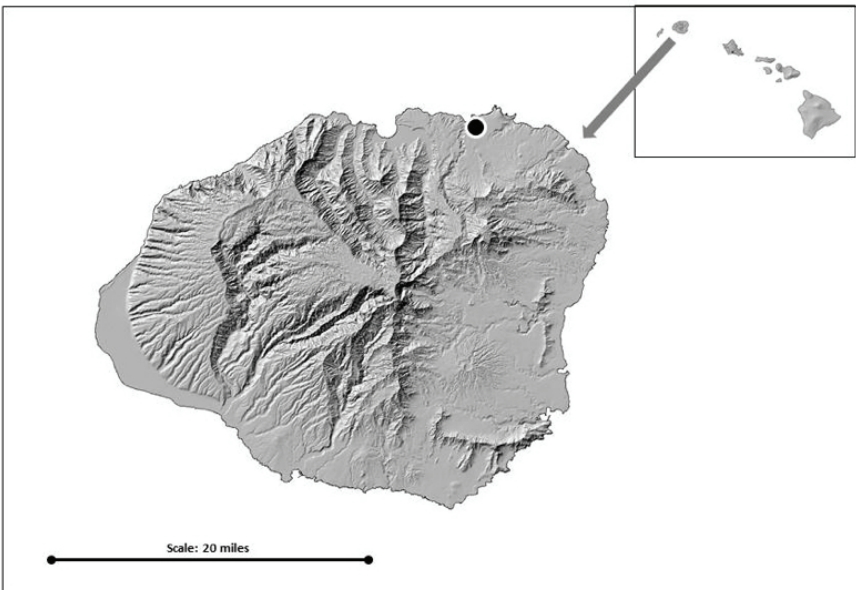
**Figure 2.** Location of properties infested with *Wasmannia auropunctata* in January 2007 prepared by Hawaii Department of Agriculture.

areas were immediately treated with baits to prevent further spread within Kauai (Conant and Hirayama 2000). This infestation was assumed eradicated. However, *W. auropunctata* were recorded in a follow-up survey at the site four years later in September 2003 (Null and Gundersen 2007). The infestation now covered five

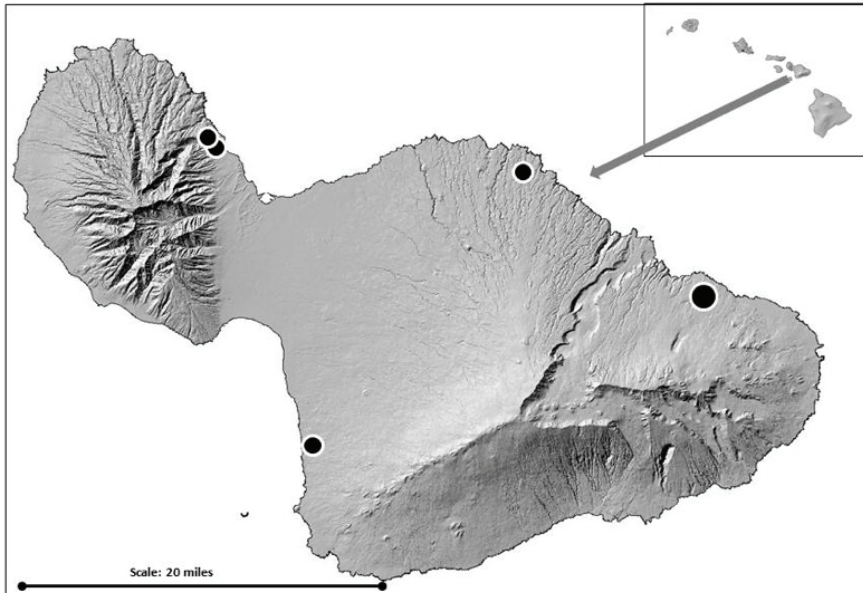
acres and had encroached onto an adjoining property (see Figure 4). The site was treated with granular baits followed by *ad hoc* retreatment and periodic surveys through to 2012. During these years, the infestation spread mostly westwards eventually spanning 12 acres and extending down a steep escarpment to Kalihiwai beach.



**Figure 3.** Areas of Hawaii island currently infested with *Wasmannia auropunctata* (2016). (Not all properties in the larger shaded section are infested).



**Figure 4.** Map of Kauai showing location infested by *Wasmannia auropunctata* (2012). Currently this site is putatively ant free.



**Figure 5.** Locations of all known sites on Maui infested with *Wasmannia auropunctata*.

In late 2012, a second eradication attempt was implemented. At this time, the critical issues of bait efficacy (Hara 2013, Hara et al. 2014, Montgomery et al. 2015) and arboreal treatment (Vanderwoude and Nadeau 2009) had been largely resolved. Due to the complexity of the site and regulatory issues, this attempt was divided into two phases: initially focusing on the readily accessible areas and later addressing the escarpment and taller vegetation. To date (late 2016), results are encouraging. The entire site is putatively free of *W. auropunctata* with only a single known active colony detected beneath a taller tree. Monitoring of this site and treatment of the known small colony continues.

**Maui.** *Wasmannia auropunctata* have been detected multiple times on the island of Maui (Figure 5). The first LFA infestation detected on Maui was located in Waihee, immediately west of the main city of Kahului, in September 2009. A

resident reported receiving painful stings from small ants on her property. Samples of these ants were submitted to the HDOA entomologist who confirmed it was *Wasmannia auropunctata*. An inter-agency taskforce was established, consisting of staff from the County of Maui, Maui Invasive Species Committee (MISC), HDOA, US Geological Survey, University of Hawaii, and the Hawaii Ant Lab (Hawaii Department of Agriculture 2009, Vanderwoude et al. 2010). Together they formulated an eradication plan which included treatment, outreach and delimiting elements (Vanderwoude et al. 2010). The ants were restricted to a single property and an island-wide delimiting survey of probable high-risk sites did not find additional infestations. The Waihee infestation was officially eradicated in April 2014.

In December 2013, a Maui resident, alerted by various outreach programs implemented by MISC, found *W. auropunc-*

*tata* on a hapuu log (*Cibotium* sp., a tree fern) purchased from a local landscaping supplier. The discovery prompted a larger investigation by HDOA who discovered that several shipments of hapuu logs, originating from the Big Island, were infested (Hawaii Department of Agriculture 2013). These shipments and subsequent distribution to retailers were located and inspected by quarantine officers. A number of these also had *W. auropunctata*. These were either destroyed or treated *in situ*. Two additional nascent infestations were found in south Maui (Wailea area) during the first half of 2014 and these have been eradicated by HDOA and MISC.

In September 2014, MISC field workers were stung by small ants while conducting other activities in Nahiku (near Hana, Maui). These ants were later identified as LFA and subsequent surveys found high density LFA in challenging rainforest terrain on both sides of the Hana Highway, extending 1½ miles along a drainage to the ocean. Four properties were involved. The infestation appeared to have spread downstream from an initial upstream establishment point to the ocean. The speed at which *W. auropunctata* spread downstream was substantially faster than normal lateral spread, most likely facilitated by the movement of infested debris during periodic flooding events. Due to the challenging nature of this infestation, agencies collaborating on the response (HAL, HDOA, Maui County and MISC) formulated a containment and aggressive control plan, first removing LFA from locations from which it would be likely to spread, then to later assess the possibilities for a more comprehensive approach. This plan is ongoing.

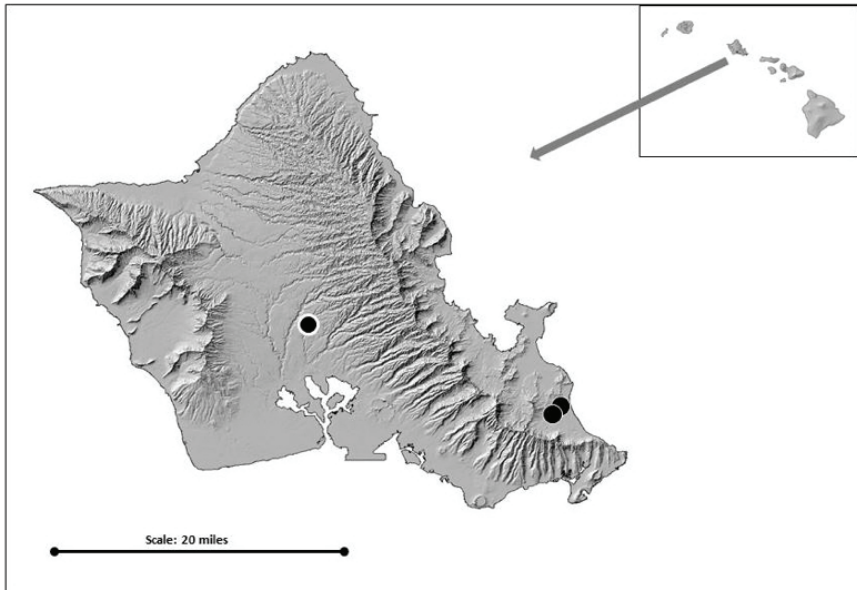
Another LFA discovery was made in Huelo in January 2015. An eradication plan has been developed and partly implemented. Activities at this site were hampered by the refusal of one resident

to allow treatment staff access. This resulted in the HDOA taking the unusual step of obtaining a court order (Hawaii Department of Agriculture 2016), and later declaring a quarantine on the property in order allow the eradication program to continue at this site. The delays to treatment activities have allowed *W. auropunctata* to recover and spread further into this property, necessitating additional treatment effort.

The site at Waihee, which had been ant-free since 2010, was surveyed repeatedly between 2010 and 2014. In 2016 another survey was conducted at this site. *W. auropunctata* were again detected in an area immediately adjacent to the original treatment area. It is possible that some infested plant trimmings may have been moved there before the original detection in 2009. Only spanning an acre or so, this site is now being treated again to ensure no live ants remain.

**Oahu.** The detection of infested shipments of hapuu in Maui prompted HDOA to investigate other shipments from the same supplier destined for Oahu and Lanai. Some of these were also infested, and as a result, HDOA staff systematically surveyed the retail stores that received these items. Several of these retail stores also had become infested, and these were systematically treated by HDOA staff (Hawaii Department of Agriculture 2013).

The increased publicity surrounding the infested hapuu led to the discovery of two well-established infestations on Oahu, each covering approximately five acres (Figure 6). One of these was located in abandoned agricultural land in Waimanalo and another in a suburban area of Mililani. Eradication plans were developed for each site and baits were applied repeatedly to both sites over the course of one year. One year after the last treatment was applied (2016), both sites are putatively free of LFA.



**Figure 6.** Locations of known sites on Oahu infested with *Wasmannia auropunctata*. (currently the infestation in Mililani and the original infestation in Waimanalo are putatively ant-free)

The movement of *W. auropunctata* to Maui and Oahu identified critical gaps in the biosecurity system. On Oahu, these gaps were addressed by implementing an ongoing island-wide survey of high-risk entry sites that began in January 2015 and continues to the present. This program was designed to complement existing regulation and inspection systems, with a goal to detect and eradicate infestations while small. During the past two years, this program has detected 16 nascent infestations at Oahu nurseries which were systematically treated. In late 2016 a large, 4-acre infestation was also discovered in Waimanalo (not linked to the original detection in the same district). Without this early detection, such infestations will grow too large to manage and become a source-point for jump-dispersal to new locations (Suarez et al. 2001).

## Discussion

The worldwide spread of invasive ants began at least as early as the 16<sup>th</sup> century (Gotzek et al. 2015). By the beginning of the 20<sup>th</sup> century, the ecological impacts caused by these invasions were becoming apparent as entomologists lamented the paucity of other invertebrate fauna in locations invaded by ant species such as *Pheidole megacephala* (Tryon 1912, Perkins 1913). These invasions are widely regarded as a consequence of human commerce (Wilson and Taylor 1967, Passera 1994, McGlynn 1999, Holway et al. 2002), and in this regard, the recent introduction and spread of *W. auropunctata* is no exception.

Queens and males in invasive *W. auropunctata* populations are mostly produced through thelytokous parthenogenesis (Fournier et al. 2005). Clonal reproduc-



tion allows global invasion pathways of this species to be accurately reconstructed (Foucaud et al. 2010). Thus, the origin of *W. auropunctata* in Hawaii can be attributed to *W. auropunctata* from Florida, as one population is a clonal subset of the other (Foucaud et al. 2010). Further, there is an unambiguous connection with the nursery trade as the original vector, both for the initial introduction and subsequent early spread within Hawaii island.

Potted plants are an ideal vehicle for the movement of this species. The spaces between the potting medium, plant roots and the wall of plant containers are convenient nesting sites, and forms a moisture gradient that optimizes brood development (Holldobler and Wilson 1990 p374). *W. auropunctata* colonies are small, interconnected and typically possess a worker:queen ratio between 250 and 500 (Ulloa-Chacon and Cherix 1990). This virtually assures every plant within an infested nursery houses a viable *W. auropunctata* colony which can remain largely undetected. Further, by their nature, plant nurseries are effective distribution points. Together, these factors contributed to the rapid spread of this species within Hawaii Island, mirroring the historical spread of this species through southern Florida via the movement of potted plants and balled citrus seedlings (Spencer 1941).

The pathways for movement of *W. auropunctata* between the Hawaiian islands have become more diverse as this species became increasingly ubiquitous. After the initial discovery in 1999, HDOA further regulated the movement of plants and propagative plant materials between islands. Regulatory intervention included a requirement for exporting nurseries to be certified by HDOA, or for each shipment to neighbor islands to be inspected before shipment. Without this increased watchfulness, the inter-island movement of *W. auropunctata* would undoubtedly

have been much more rapid. However, at least some of the multiple infestations detected on Maui and Oahu are not linked to the nursery trade in any way. For example, no links between the purchase of potted plants and infestations in Nahiku, Huelo, Waihee and Mililani could be found.

The majority of ant-infested agricultural commodities shipped between Hawaii Island and other islands is detected and prevented from arriving by means of a thorough and careful system of regulation and inspection implemented by HDOA. Inspection systems are based on a risk-management approach that utilize available resources to optimize risk reduction. However, not all infested commodities are (or can be) detected at the border. As *W. auropunctata* become increasingly ubiquitous on Hawaii island, the variety and proportion of infested cargoes increases beyond simply “nursery plants” to include non-agricultural items such as general cargo, household items and vehicles. A percentage of infested plants and other non-regulated material will continue to arrive as a result of slippage (Whyte 2006)—infested goods that bypass regulated pathways, escape detection or are in commodity categories that are not inspected.

By its very nature, slippage is difficult to quantify, and occurs in four commodity classes: those that bypass the biosecurity system, false negatives (infested material inspected and cleared), commodities excluded from inspection and commodities that do not fall within the HDOA mandate (Government of Hawaii 1973). Not all pathways are adequately regulated. Air passengers carrying plants and other propagative material between islands are not inspected due to a lack of resources. The rate of false negatives is likely to be very low, but remains largely unknown. Hawaii Administrative Rules (Hawaii Administrative Rules 2012) limit commodity

inspections to “plants and propagative material.” The rules also acknowledge that HDOA has legislative authority to inspect a wider range of commodities such as foliage, cut flowers and produce, but self-limits activities to “periodic random inspections.” Finally, there are no systematic inspections of other commodity classes (used vehicles, machinery, household effects etc.) because HDOA does not have legislative authority to do so.

Detection and response to these introductions demonstrates the complementary roles of prevention through regulation and inspection; early detection through increased awareness and surveillance, and rapid response through multi-agency collaboration. These elements of the Hawaii biosecurity framework are performed by different and sometimes multiple agencies (Kraus and Duffy 2010) often through semi-formal or *ad hoc* collaborations. Regardless of the multitude of funding partners, agency governance issues, obstacles to data sharing, complex legal considerations, and the often difficult operational impediments, these collaborations can be startlingly effective, as evidenced by the rapid detection, response, and treatment of multiple *W. auropunctata* infestations throughout Hawaii. Of the eight infestations on the neighbor islands of Oahu, Kauai and Maui, five sites are putatively free of *W. auropunctata* and the remaining three are contained and continue to be treated. A biosecurity plan that brings these agencies closer and recognizes these collaborations, is currently being drafted by the State of Hawaii (Anon 2016), and will serve as a blueprint for biosecurity activities in the next decade.

As *Wasmannia auropunctata* spread through the islands of Hawaii, the economic and ecological impacts are likely to be catastrophic. The predicted economic costs to the island of Hawaii alone are likely to exceed \$100 million annually

(Lee et al. 2015). Continued prevention, early detection and response to new incursions on islands other than Hawaii island is an invaluable investment in the future of the unique and fragile ecosystems that Hawaii has to offer.

### Acknowledgments

The Hawaii Department of Agriculture and Hawaii Invasive Species Council provide ongoing funding to the Hawaii Ant Lab. The authors sincerely acknowledge the contributions of HISC, HDOA, Forest and Kim Starr the various Invasive Species Committees, University of Hawaii, the Counties of Hawaii, Maui, and Kauai, City and County of Honolulu, the US Geological Survey, Department of Lands and Natural Resources, the Pacific Cooperative Studies Unit and all other agencies and individuals that contribute to the management of *Wasmannia auropunctata* in Hawaii. We thank P. Conant, N. Reimer, K. Onuma, D. Arakaki, C. Kaneshige and others who provided vital anecdotal information.

### Literature Cited

- Anon.** 2016. Draft Interagency Biosecurity Plan for Hawaii. Page 81. State of Hawaii, Honolulu Hawaii.
- Beardsley, J.W., S. Tsong Hong, F.L. McEwen, and D. Gerling.** 1982. Field investigations on the interrelationships of the big-headed ant, the gray pineapple mealybug, and pineapple wilt disease in Hawaii. Proceedings of the Hawaiian Entomological Society 24:51–67.
- Clagg, C.F.** 1953. Notes and exhibitions: *Anoplolepis gracilipes*. Proceedings of the Hawaiian Entomological Society 15:282.
- Cole, F.R., A.C. Medeiros, L.L. Loope, and W.W. Zuehlke.** 1992. Effects of Argentine ant on arthropod fauna of Hawaiian high elevation shrubland. Ecology 73:1313–1322.
- Conant, P., and C. Hirayama.** 2000. *Wasmannia auropunctata* (Hymenoptera:Formicidae): established on the Island of Hawaii. Bishop Museum Occasional Papers 64:21–22.

- Foucaud, J., J. Orivel, A. Loiseau, J. H. C. Delabie, H. Jourdan, D. Konghouleux, M. Vonshak, M. Tindo, J. Mercier, D. Fresneau, J. Mikissa, T. McGlynn, A. S. Mikheyev, J. Oettler, and A. Estoup.** 2010. Worldwide invasion by the little fire ant: routes of introduction and eco-evolutionary pathways. *Evolutionary Applications*:1–13.
- Fournier, D., A. Estoup, J. Orivel, J. Foucaud, H. Jourdan, J. Le Breton, and L. Keller.** 2005. Clonal reproduction by males and females in the little fire ant. *Nature* 435:1230–1234.
- Gillespie, R., and N. Reimer.** 1993. The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). *Pacific Science* 47:21–33.
- Gotzek, D., H. J. Axen, A. V. Suarez, C. S.H., and D.D. Shoemaker.** 2015. Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. *Molecular Ecology* 24:374–388.
- Government of Hawaii.** 1973. Chapter 150a. Plant and Non-domestic Animal Quarantine and Microorganism Import. Chapter 150a.
- Gruner, D.J.** 2000. Distribution of the Little Fire Ant *Wasmannia auropunctata* (Roger) in Hawaii: A partnership of K-12 schools, the University of Hawaii, and the Hawaii Department of Agriculture. University of Hawaii at Manoa. Hawaii, USA.
- Hara, A.H., K.L. Aoki, S.K. Cabral, and R.Y. Niino-Duponte.** 2014. Attractiveness of gel, granular, paste, and solid formulations of ant bait insecticides to the Little Fire Ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae). *Proceedings of the Hawaiian Entomological Society* 46:45–54.
- Hara, A.H., K.I. Aoki, S.K. Cabral, and R.Y. Niino-DuPonte.** 2013. Attractancy of bait insecticides to Little Fire Ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae). *Proceedings of the 2013 Imported Fire Ant Conference*:26–35.
- Hawaii Administrative Rules.** 2012. Plant and non-domestic animal quarantine, Plant intrastate rules. Page 15 in Hawaii Department of Agriculture, editor. Ch72 6(4), Honolulu.
- Hawaii Department of Agriculture.** 2009. Little Fire Ants found on Maui. HDOA press release NR-09-13. Honolulu, Hawaii.
- Hawaii Department of Agriculture.** 2013. Stinging ants found on plants sold at Oahu and Maui garden shops. HDOA Press release NR-13-17. Honolulu, Hawaii.
- Hawaii Department of Agriculture.** 2016. HDOA serves warrant to gain access to Maui property infested with Little Fire Ants. HDOA press release NR16-09. Honolulu, Hawaii.
- Holldobler, B., and E.O. Wilson.** 1990. *The Ants*. Springer-Verlag, USA.
- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui, and T. J. Case.** 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33:181–233.
- Jahn, G.C., and J.W. Beardsley.** 1994. Big-headed ants, *Pheidole megacephala*: interference with the biological control of gray pineapple mealybugs. Pages 199–205 in D. F. Williams, editor. *Exotic ants: biology, impact and control of introduced species*. Westview Press.
- Kraus, F., and D.C. Duffy.** 2010. A successful model from Hawaii for rapid response to invasive species. *Journal for Nature Conservation* 18:135–141.
- Krushelnicky, P.D., and R.G. Gillespie.** 2008. Compositional and functional stability of arthropod communities in the face of ant invasions. *Ecological Applications* 18:1547–1562.
- Krushelnicky, P.D., L.L. Loope, and N.J. Reimer.** 2005. The ecology, policy, and management of ants in Hawaii. *Proceedings of the Hawaiian Entomological Society* 37:1–25.
- Lee, D. J., M. Motoki, C. Vanderwoude, S.T. Nakamoto, and P.S. Leung.** 2015. Taking the sting out of Little Fire Ant in Hawaii. *Ecological Economics* 111:100.
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter.** 2000. 100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), Auckland, New Zealand.
- McGlynn, T.P.** 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* 26.

- Medeiros, A.C., L.L. Loope, and F.R. Cole.** 1986. Distribution of ants and their effects on endemic biota of Haleakala and Hawaii Volcanoes National Park: a preliminary assessment. Pages 39–53 Proceedings of the Sixth Conference of Natural Science, Hawaii Volcanoes National Park Cooperative National Park Resources Study Unit; University of Hawaii, Manoa.
- Mikheyev, A.S., and U.G. Mueller.** 2007. Genetic relationships between native and introduced populations of the little fire ant *Wasmannia auropunctata*. Diversity and Distributions:1-7.
- Montgomery, M.P., C. Vanderwoude, and A.J.L. Lynch.** 2015. Palatability of baits containing (S)-methoprene to *Wasmannia auropunctata* (Hymenoptera: Formicidae). Florida Entomologist 98:451–455.
- Motoki, M., D.J. Lee, C. Vanderwoude, L.J. Nakamoto, and P.S. Leung.** 2013. A bioeconomic model of Little Fire Ant *Wasmannia auropunctata* in Hawaii. 168, Pacific Cooperative Studies Unit, University of Hawaii, Honolulu Hawaii. Report number 186.
- Null, W., and K. Gundersen.** 2007. Little Fire Ant *Wasmannia auropunctata*: Its Presence on Kauai. Kauai Invasive Species Committee, Hawaii, USA.
- O’Dowd, D.J., P.T. Green, and P.S. Lake.** 2003. Invasional “meltdown” on an oceanic island. Ecology Letters 6:812–817.
- Passera, L.** 1994. Characteristics of tramp ants. Pages 22-43 in D. F. Williams, editor. Exotic Ants: Biology, Impact and Control of Introduced Species. Westview Press, Boulder, Colorado.
- Perkins, R.C.L.** 1913. Being a review of the land fauna of Hawaii. Fauna Hawaiensis 1:xv–ccxxviii.
- Reimer, N., J.W. Beardsley, and G. Jahn.** 1990. Pest ants in the Hawaiian islands. in R.K. Vander Meer, K. Jaffe, and A. Cedeno, editors. Applied myrmecology: a world perspective. Westview Press, Oxford.
- Reimer, N.J.** 1994. Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. Pages pp 11-22 in D. F. Williams, editor. Exotic Ants: Biology, Impact, and Control of Introduced Species. Westview Press, Boulder.
- Smith, F.** 1879. Descriptions of new species of aculeate Hymenoptera collected by the Rev Thos. Blackburn in the Sandwich Islands. Journal of the Linnean Society of London 4:674–685.
- Spencer, H.** 1941. The small fire ant *Wasmannia* in citrus groves - a preliminary report. Florida Entomologist 24:6–14.
- Suarez, A.V., D.A. Holway, and T.J. Case.** 2001. Patterns of Spread in Biological Invasions Dominated by Long-Distance Jump Dispersal: Insights from Argentine Ants. Proceedings of the National Academy of Sciences of the United States of America 98:1095–1100.
- Tryon, H.** 1912. The naturalization of an exotic ant (*Pheidole megacephala*, Fab.). Queensland Naturalist 9:225–229.
- Ulloa-Chacon, P., and D. Cherix.** 1990. The Little Fire Ant *Wasmannia auropunctata* (R.) (Hymenoptera: Formicidae). Pages 281–289 in R. K. Vander meer, K. Jaffe, and A. Cedeno, editors. Applied Myrmecology A World Perspective. Westview Press.
- Vanderwoude, C., and B. Nadeau.** 2009. Application methods for paste bait formulations in control of ants in arboreal situations. Proceedings of the Hawaiian Entomological Society 41:113–119.
- Vanderwoude, C., K. Onuma, 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.** 2013. Worldwide spread of the little fire ant, *Wasmannia auropunctata* (Hymenoptera: Formicidae). Terrestrial Arthropod Reviews:173–184.
- Wetterer, J.K., and S.D. Porter.** 2003. The Little Fire Ant, *Wasmannia auropunctata*: distribution, impact and control. Sociobiology 41:1–41.
- Whyte, C.** 2006. Science and biosecurity – monitoring the effectiveness of biosecurity interventions at New Zealand’s borders. Royal Society of New Zealand, Miscellaneous series 67:27–36.
- Wilson, E.O., and R.W. Taylor.** 1967. The ants of Polynesia. Pacific Insects Monograph 14:1–109.
- Zimmerman, E.C.** 1940. Argentine Ant in Hawaii. Proc. Hawaiian Entomol. Soc. 11:108.