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The odorous house ant, *Tapinoma sessile* (Hymenoptera: Formicidae), as a new temperate-origin invader

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Abstract

A population of the odorous house ant, *Tapinoma sessile*, was found at an upland site on Maui, Hawaii. Although *T. sessile* possesses many of the traits shared by most invasive ant species and is a significant urban pest in the continental USA, this represents the first confirmed record for this species outside its native North American range. Our survey of the site revealed a relatively large (ca. 17 ha) infestation with many closely spaced nests, possibly all belonging to a single supercolony as suggested by the lack of aggression or only occasional non-injurious aggression between workers from distant nests. The odorous house ant is currently abundant at this site, despite the presence of seven other introduced ant species, including the big-headed ant (*Pheidole megacephala*) and the Argentine ant (*Linepithema humile*). Based on its behavior at this site, *T. sessile* may successfully invade other temperate areas in the future, and should be watched for by biosecurity programs.

Key words: Invasive ants, odorous house ant, *Tapinoma sessile*, Hawaii.

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Introduction

Taxonomic patterns in the global spread of invasive species can shift over time (BLACKBURN & al. 2010). Among ants, for example, there is some evidence to suggest that an early wave of global invasion by species originating in tropical or subtropical climates has largely run its course, and that a new phase of invasions by temperate climate ant species may now be underway (SUAREZ & al. 2009). Over the past several decades, species such as *Lasius neglectus*, *Myrmica rubra* and *Pachycondyla chinensis* (see GARNAS & al. 2007, UGELVIG & al. 2008, GUENARD & DUNN 2010), have been spreading to or becoming invasive in new temperate areas. Many questions are raised by this potential trend. It is unclear, for example, why such a temporal lag in invasiveness for temperate ant species should exist (SUAREZ & al. 2009). In addition, while some aspects of the invasion process have been studied for some of these temperate species, it is too early to say whether these newer invaders typically employ the same mechanisms of invasion used by the handful of much more thoroughly-studied tropical or subtropical ant species that form the foundation of our knowledge on invasive ant biology (reviewed in HOLWAY & al. 2002, KRUSHELNYCKY & al. 2009). In this context, we report the first known established population of the odorous house ant, *Tapinoma sessile*, outside its native North American range, and make preliminary observations on its invasion of a mid-elevation, moderately temperate site in Hawaii that supports a number of other invasive ant species.

Tapinoma sessile is considered to be native to a large portion of North America, ranging from northern Mexico to southern Canada and occurring in each of the 48 continental US states (MENKE & al. 2010). It may have the "widest geographic range and greatest ecological tolerance of any ant in North America" (FISHER & COVER 2007), and can be found in a large variety of habitats. The odorous house ant is also unusual because recent work demonstrates that it is a highly plastic species with a flexible social structure (BUCZKOWSKI 2010, MENKE & al. 2010). In natural habitats, *T. sessile* has been reported as a subdominant species comprised of small, single-queen colonies (FELLERS 1987, BUCZKOWSKI 2010). In urban areas, however, *T. sessile* behaves very differently and exhibits the characteristics common to most invasive ant species: extreme polygyny (thousands of queens), extensive polydomy (multiple nests), unicoloniality, and ecological dominance over native ant species (BUCZKOWSKI & BENNETT 2008a, BUCZKOWSKI 2010, MENKE & al. 2010). The species is very opportunistic and will readily adapt to take advantage of human-modified environments. Indeed, as its common name suggests, in urban areas of the continental US it is considered a serious pest of homes and other structures (THOMPSON 1990, BUCZKOWSKI & BENNETT 2008b, KLOTZ & al. 2008). All of these attributes seemingly make *T. sessile* a perfect invader, but until now there was no evidence that it had succeeded in colonizing areas outside its native range.

In the course of a survey of ant species on the upper leeward slopes of Haleakala volcano, which forms east Maui, Hawaii, one of us (PDK) detected the presence of *Tapinoma sessile* at a single location in 2009. We subsequently conducted a more thorough survey of the site with the goals of delimiting the extent of the invasion, and making preliminary observations about the behavior of this new ant species in the archipelago.

Methods

Tapinoma sessile was first detected in Hawaii in June 2009 along Waipoli Road on the edge of the municipality of Kula, Maui, at an elevation of 1150 m. The area is occupied by small vegetable and flower farms, pastures, forest patches, and sparse residential housing. Initial observations suggested that the population might be limited in size, but the actual extent was unknown. To obtain fine-scale distributional information, we performed a detailed survey of the area. A roughly circular region radiating approximately 350 to 1000 m from the point where *T. sessile* was originally discovered was exhaustively sampled (20.74031° N - 20.73079° N to 156.33003° W - 156.31701° W; Fig. 1). A combination of baiting and visual searching was used to map *T. sessile* distributions over a period of 20 days, 13 - 22 June and 5 - 15 October 2010, between the hours of 9:00 am and 5:00 pm. Air temperatures during the survey period ranged from 18.1 to 23.7°C (obtained from a weatherstation located 2.5 km away from the study site, HALENET 2011). Note cards baited with a blend of canned tuna and corn syrup were placed on the ground at approximately 10 to 25 m intervals along numerous transects throughout the search site. We also surveyed along roads in the immediate vicinity that might act as avenues for *T. sessile* dispersal.

The bait cards were collected one hour after placement, the presence of *Tapinoma sessile* was recorded using a GPS, and species identity of other ants present on the baits was noted at a subset of the bait card survey points. This subset was selected haphazardly, and should provide an unbiased representation of the relative frequency of occurrence of the ant species in the area. In addition to baiting, visual searches for *T. sessile* were conducted throughout the site. This involved turning over rocks, inspecting debris on the ground, inspecting vegetation for ants that might be feeding on hemipteran honeydew, and looking for signs of ant activity on the ground.

We performed aggression tests between eight different sites spanning the majority of the invaded area (Fig. 1). We conducted tests for 15 different pairings of these eight sites, with the goal of representing a relatively complete gradient of distance between pairs (range = 23 m to 777 m, linear distance). At each site, we collected worker ants from one location, either a single bait card or foraging on a single plant. For each of the 15 pairings, we performed three replicate one-on-one aggression tests, in which single workers from each site were placed together in a 2 dram glass vial and observed for five minutes for maximum level of agonistic behavior according to the following scale (SUAREZ & al. 1999): 0 = ignore, 1 = touch, 2 = avoid, 3 = aggression (lunging, brief bouts of biting and/or pulling), 4 = fighting (prolonged aggression, also abdomen curling to deposit defensive compounds). We used the mean maximum score for each pairing, averaged across the three replicates, to test for a linear relationship between level of aggression and spatial distance (on a log scale).

Results and Discussion

We surveyed a total of at least 2,638 locations, covering just under 60 ha, around the site where *Tapinoma sessile* was first detected (Fig. 1). Colonies of *T. sessile* were found in an area totaling approximately 17 ha, an area much larger than we had initially anticipated. This population of colonies forms a relatively continuous aggregation in a single discrete area. Close inspection of several colonies revealed that all were highly polygynous (e.g., 20 queens were collected from one nest) and consisted of thousands of workers and brood. Of the 45 replicate aggression tests performed, all but two found no aggression (scores all equaled 1). In the remaining two tests, in which paired sites were 415 m and 777 m apart, leg and antennae pulling was observed (scores of 3). There was therefore no significant relationship between level of aggression and the log(distance) between sites where the workers were collected (Fig. 2). Although aggression assays do not always accurately reflect behavior at the colony level (ROULSTON & al. 2003), the lack of observed fighting or other prolonged aggression, together with the large and polygynous nature of inspected colonies, suggests that this population of colonies may exist as a single large supercolony, as has been documented in the native range. In the continental USA, *T. sessile* supercolonies of approximately 3 ha in area have been found in urban areas (BUCZKOWSKI & BENNETT 2008a). Additional genetic work is needed to conclusively determine the social structure of odorous house ants across the Maui site, but these behavioral results are similar to those found within supercolonies of the Argentine ant, *Linepithema humile* (see SUAREZ & al. 1999, 2002).

As can be seen in Fig. 1, there are large and small pockets within the 17 ha population where *Tapinoma sessile* appears to be absent. This absence could be due to competition from the existing ant community at this locality, due to abiotic unsuitability of these microsites, or a combination of the two. Of the 2,638 locations surveyed, *T. sessile* was detected at 338 of them, and non-*T. sessile* ant species identity was recorded at an additional 892 of the survey points. Of these 892 survey points, 448 (50%) had *Pheidole megacephala*, 98 (11%) had *Linepithema humile*, 28 (3%) had *Tetramorium caldarium*, 24 (3%) had *Ochetellus glaber*, 8 (1%) had *Cardiocondyla kagutsuchi*, 7 (1%) had *Plagiolepis alluaudi*, 7 (1%) had *Solenopsis papuana*, and 272 (30%) had no ants. Seven species therefore make up the ant community that *T. sessile* is invading in this area, with all seven species being found both inside and outside the polygon delineating the approximate *T. sessile* population boundary.

The big-headed ant (*Pheidole megacephala*) and the Argentine ant (*Linepithema humile*) were by far the most common non-*Tapinoma sessile* species at the site, and we encountered both species interspersed among locations where odorous house ants were present, often in close proximity (Fig. 3). Both the big-headed ant and the Argentine ant are dominant, aggressive invasive species, and typically are capable of displacing most other ant species in the areas they invade (HOLWAY & al. 2002, LACH & HOOPER-BUI 2009). They have been in Hawaii since at least 1879 and 1940, respectively (SMITH 1879, ZIMMERMAN 1941),

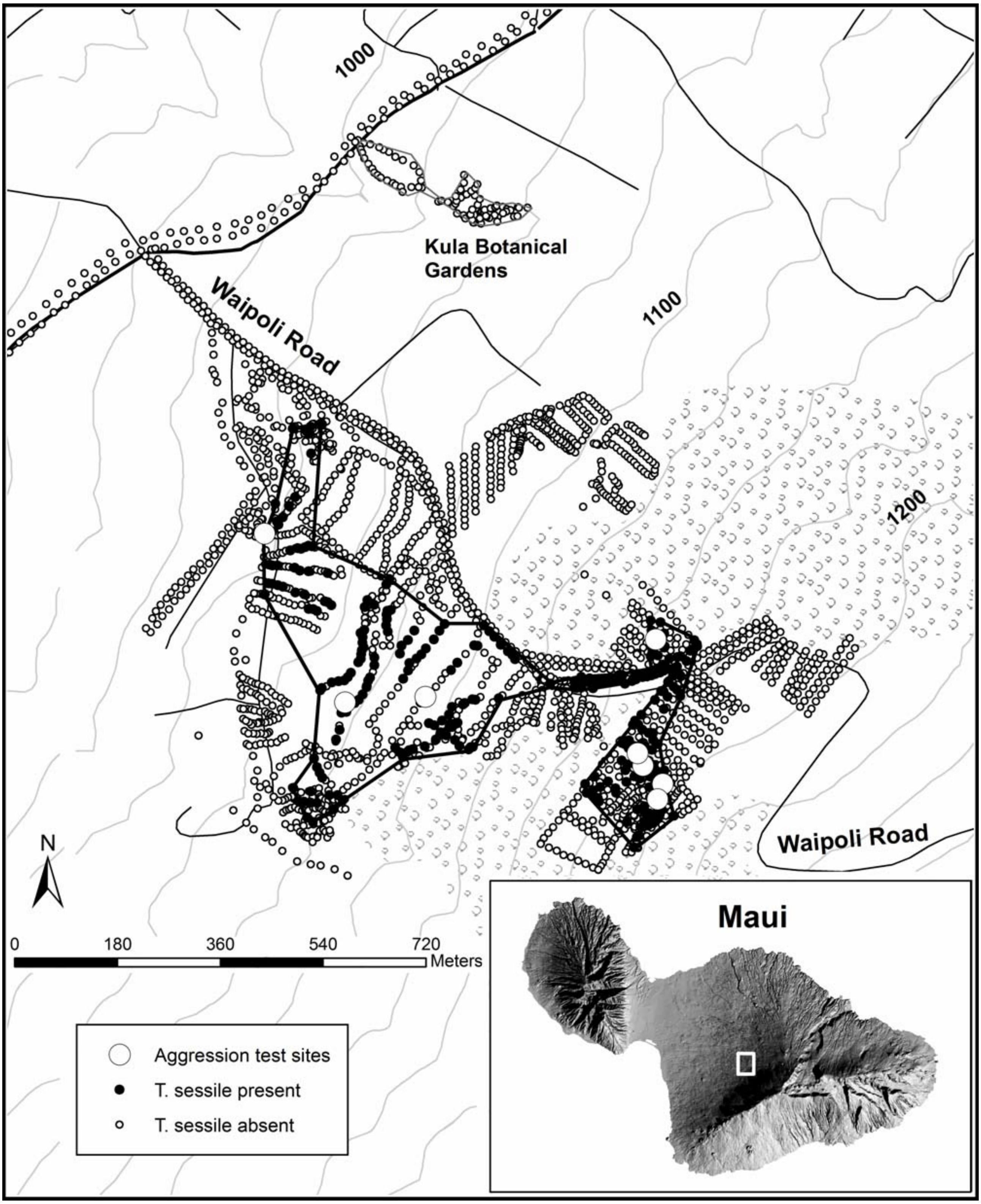

Fig. 1: Distribution of *Tapinoma sessile* at the study site, with inset showing the area of Maui enlarged in the main figure. Also shown are the eight sites used for aggression assays. The black polygon delineates the area known to be occupied by *T. sessile*, and the shaded areas illustrate approximate boundaries of heavily wooded habitat. Topographic lines are 25 m elevation contours.

and almost certainly already occurred at our study site when *T. sessile* arrived. They may therefore be preventing colonization by *T. sessile* of some of the microsites within the invaded area, and may also be slowing the outward spread of the *T. sessile* population. Studies of *T. sessile* within its native range have found it to be a subdominant species, often losing battles with other ant species (including the Argentine ant), especially at the colony level (FELLERS

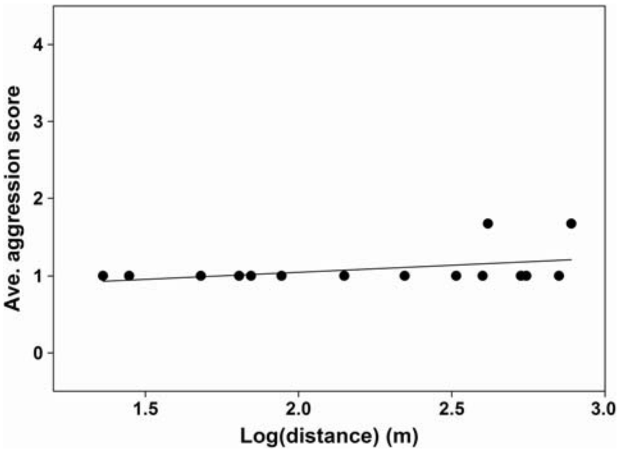

Fig. 2: Mean maximum aggression score between worker pairs as a function of distance between source sites (n = 15 nest pairings). A linear regression found no significant relationship between mean maximum aggression score and log(distance) [$r^2 = 0.164$, $p = 0.134$ for log(distance)].

1987, HOLWAY 1999, BUCZKOWSKI & BENNETT 2008b). Despite this competitive inferiority, it frequently manages to become dominant and form large, high density supercolonies in the urban environment (BUCZKOWSKI 2010). In what appears to be an analogous development, *T. sessile* has become established, spread and achieved high densities at this Maui site in spite of the presence of other dominant invasive ants. For instance, although it was absent from significant portions of the invaded area, where it did occur colonies were large and it recruited similar numbers of workers to baits as did *P. megacephala* and *L. humile*. Whether *T. sessile* gains ground against its competitors in the future, is pushed back, or persists in a similar condition wherein different species stake out territories interspersed among each other, will be of interest.

The majority of *Tapinoma sessile* colonies discovered within the search area were found nesting either under leaf litter or under kikuyu grass (*Pennisetum clandestinum*), which forms dense mats over the ground in pastures, roadsides and abandoned agricultural plots. Additional colonies were found in pastures nesting inside of dry cow dung, as well as in and around several residential buildings, where

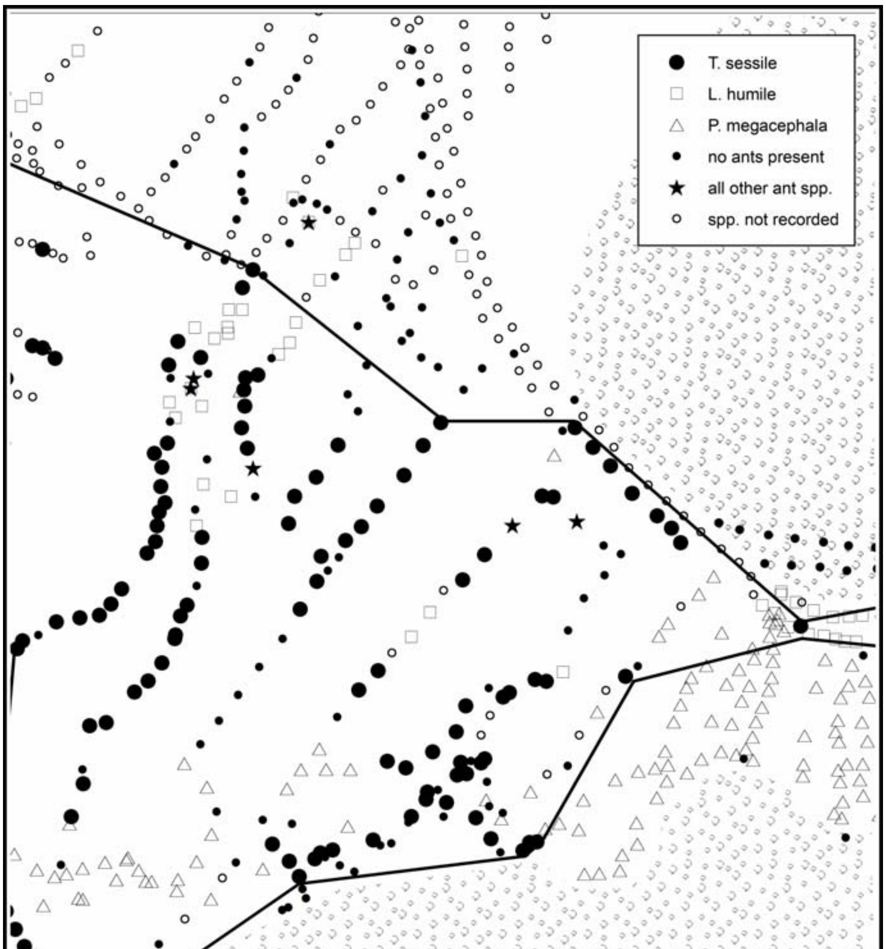

Fig. 3: Enlarged view of a portion of the study site, showing distributions of the most common ant species. Large filled circles indicate survey points where *Tapinoma sessile* was present, empty squares indicate presence of *Linepithema humile*, empty triangles indicate presence of *Pheidole megacephala*, filled stars indicate presence of all other ant species, small filled circles indicate that no ants were found, and small empty circles indicate locations where *T. sessile* was absent but other ant species presence or absence was not recorded. The black polygon delineates the area known to be occupied by *T. sessile*, and the shaded areas illustrate approximate boundaries of heavily wooded habitat.

foraging workers were viewed as new and conspicuous pests by the owners. Patches of black wattle (*Acacia mearnsii*) and *Eucalyptus* forest occur around the periphery of the *T. sessile* population, and these were always free of *T. sessile* and all of the other ant species that occur at the site (although small-colonied hypogaeic taxa such as *Hypoponera* spp. may well have escaped our attention). We surmise that relatively cold ground temperatures are the main factor responsible for the apparent unsuitability of thick forests at this elevation for all of the ant species at this locality, although abiotic factors limiting *T. sessile* spread need to be investigated more explicitly. In contrast, in successional areas sparsely wooded with black wattle, extrafloral nectaries on the wattle saplings, as well as honeydew from the Hemiptera that they host, could provide an abundant food source for *T. sessile*. We observed *T. sessile* visiting these nectaries and tending the introduced membracid *Vanduzeea segmentata* on wattle saplings. We also commonly observed *Pheidole megacephala* workers visiting wattle extrafloral nectaries.

Because the odorous house ant ranges as far north as southern Canada and occurs at elevations over 4000 m in North America (MENKE & al. 2010), there is serious cause for concern that, unlike most invasive ant species in Hawaii (REIMER 1994, KRUSHELNYCKY & al. 2005b), it will be capable of invading high elevation habitats. These areas support much of the archipelago's remaining intact native communities. Part of the unusually broad range in environmental tolerance exhibited by the odorous house ant in North America may be an artifact, however, in that *Tapinoma sessile* may actually represent a species complex with more regionally adapted variants (FISHER & COVER 2007, MENKE & al. 2010). Preliminary genotyping of specimens from Maui indicates that they are most closely related to colonies in western North America, and are most similar to those in southern California (S. Menke, unpubl.). The colonies on Maui may therefore not be as cold tolerant as those originating in more northern latitudes, but so far they appear to have similar requirements to those of Argentine ants, which have already demonstrated the ability to invade high elevation habitats on Maui (KRUSHELNYCKY & al. 2005a).

An unresolved question concerns the manner in which *Tapinoma sessile* is naturally dispersing on Maui, which can have strong effects on the course of its invasion. Most monogynous species disperse through mating flights, while most unicolonial invasive species disperse through short-distance budding (HOLWAY & al. 2002). Because *T. sessile* exhibits both colony arrangements in its native range, it is unknown whether it predominantly uses one or the other of these dispersal mechanisms, or perhaps both like the red imported fire ant, *Solenopsis invicta* (see TSCHINKEL 2006). On Maui, we were able to delimit the known *T. sessile* population with fairly high resolution, but its distribution on the remainder of the island is still unknown. The more or less contiguous nature of the Waipoli Rd. population suggests either budding dispersal or only short-distance mating flights at this site, although this is completely uninvestigated. Finding the answer to this question will not only allow a much better estimate of the likelihood that additional, distant colonies exist on Maui, but will also provide an expanded understanding of the biological attributes of invasive ants in general.

It is somewhat puzzling that no other established populations of *Tapinoma sessile* have been reported outside its native range, given that urban colonies possess most of the traits shared by most of the currently recognized invasive ant species, that *T. sessile* has such a broad distribution (i.e., source pool) in North America, and that the USA has been such a large source of commercial exports for many decades. It is possible that *T. sessile*, despite its biological and ecological similarity to other invasive ant species, may be less effective at being transported in human cargo. For example, among 451 ant interceptions on incoming cargo by the Hawaii Department of Agriculture between 1995 and 2003, only five were of odorous house ants, while 197 were of Argentine ants (N. Reimer, unpubl.). Similarly, *T. sessile* was never intercepted during regular quarantine activities at any ports of entry in New Zealand between 1955 and 2005, although it was intercepted during a special seven-month intensive screening of all ants arriving via all entry pathways in 2004 - 2005 (WARD & al. 2006). These figures, however, may simply indicate that the odorous house ant is not very common in the regions that ship the majority of goods to Hawaii and New Zealand. We have so far been unable to determine the pathway by which the Maui population was introduced, so this case can't yet provide insight into the question.

An alternative explanation for the only recent appearance of *Tapinoma sessile* outside its native range is that propagule pressure has been increasing in recent years. Although *T. sessile* has been a household pest in the USA for at least 80 years (SMITH 1928), some authors have reported that it has become a much more common urban nuisance over at least the past decade (SCHARF & al. 2004). The reasons for a recent increase in frequency and abundance in the urban environment are unclear (SCHARF & al. 2004, MENKE & al. 2010), but if this observation is accurate, then transportation of *T. sessile* to more areas around the world may also increase. Considering its ability to establish and persist among an impressive assemblage of invasive ant species at our study site in Hawaii, we believe that *T. sessile* should be watched for closely by quarantine officials, and viewed as a potential new invader of temperate zones.

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References

BLACKBURN, T.M., GASTON, K.J. & PARNELL, M. 2010: Changes in non-randomness in the expanding introduced avifauna of the world. – Ecography 33: 168-174.

BUCZKOWSKI, G. 2010: Extreme life history plasticity and the evolution of invasive characteristics in a native ant. – Biological Invasions 12: 3343-3349.

BUCZKOWSKI, G. & BENNETT, G.W. 2008a: Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile*. – Ecological Entomology 33: 780-788.

BUCZKOWSKI, G. & BENNETT, G.W. 2008b: Aggressive interactions between the introduced Argentine ant, *Linepithema humile* and the native odorous house ant, *Tapinoma sessile*. – Biological Invasions 10: 1001-1011.

FELLERS, J.H. 1987: Interference and exploitation in a guild of woodland ants. – Ecology 68: 1466-1478.

FISHER, B.L. & COVER, S.P. 2007: Ants of North America: a guide to the genera. – University of California Press, Berkeley, CA, 194 pp.

GARNAS, J.R., DRUMMOND, F.A. & GRODEN, E. 2007: Intercolony aggression within and among local populations of the invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in coastal Maine. – Environmental Entomology 36: 105-113.

GUENARD, B. & DUNN, R.R. 2010: A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. – Public Library of Science ONE 5: e11614. doi:10.1371/journal.pone.0011614.

HALENET 2011: HaleNet Haleakala Climate Network. – <http://climate.socialsciences.hawaii.edu/HaleNet/HaleNet.htm>, retrieved on 15 July 2010.

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

HOLWAY, D.A., LACH, L., SUAREZ, A.V., TSUTSUI, N.D. & CASE, T.J. 2002: The causes and consequences of ant invasions. – Annual Review of Ecology and Systematics 33: 181-233.

KLOTZ, J., HANSEN, L., POSPISCHIL, R. & RUST, M. 2008: Urban ants of North America and Europe: identification, biology, and management. – Cornell University Press, Ithaca, NY, 196 pp.

KRUSHELNYCKY, P.D., HOLWAY, D.A. & LEBRUN, E.G. 2009 [2010]: Invasion processes and causes of success. In: LACH, L., PARR, C. & ABBOTT, K. (Eds.): Ant ecology. – Oxford University Press, Oxford, UK, pp. 245-260.

KRUSHELNYCKY, P.D., JOE S.M., MEDEIROS, A.C., DAEHLER, C.C. & LOOPE, L.L. 2005a: The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. – Diversity and Distributions 11: 319-331.

KRUSHELNYCKY, P.D., LOOPE, L.L. & REIMER, N.J. 2005b: The ecology, policy, and management of ants in Hawaii. – Proceedings of the Hawaiian Entomological Society 37: 1-25.

LACH, L. & HOOPER-BUI, L.M. 2009 [2010]: Consequences of ant invasions. In: LACH, L., PARR, C. & ABBOTT, K. (Eds.): Ant ecology. – Oxford University Press, Oxford, UK, pp. 261-286.

MENKE, S.B., BOOTH, W., DUNN, R.R., SCHAL, C., VARGO, E.L. & SILVERMAN, J. 2010: Is it easy to be urban? Convergent success in urban habitats among lineages of a widespread native ant. – Public Library of Science ONE, 5:e9194. doi:10.1371/journal. pone.0009194.

REIMER, N.J. 1994: Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. In: WILLIAMS, D.F. (Ed.): Exotic ants: biology, impact, and control of introduced species. – Westview Press, Boulder, CO, pp. 11-22.

ROULSTON, T.H., BUCZKOWSKI, G. & SILVERMAN, J. 2003: Nestmate discrimination in ants: effect of bioassay on aggressive behavior. – Insectes Sociaux 50: 151-159.

SCHARF, M.E., RATCLIFF, C.R. & BENNETT, G.W. 2004: Impacts of residual insecticide barriers on perimeter-invading ants, with particular reference to the odorous house ant, *Tapinoma sessile*. – Journal of Economic Entomology 97: 601-605.

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 14: 674-685.

SMITH, M.H. 1928: The biology of *Tapinoma sessile* SAY, and important house-infesting ant. – Annals of the Entomological Society of America 21: 307-330.

SUAREZ, A.V., HOLWAY, D.A., LIANG, D., TSUTSUI, N.D. & CASE, T.J. 2002: Spatiotemporal patterns of intraspecific aggression in the invasion Argentine ant. – Animal Behaviour 64: 697-708.

SUAREZ, A.V., MCGLYNN, T.P. & TSUTSUI, N.D. 2009 [2010]: Biogeographic and taxonomic patterns of introduced ants. In: LACH, L., PARR, C. & ABBOTT, K. (Eds.): Ant ecology. – Oxford University Press, Oxford, UK, pp. 233-244.

SUAREZ, A.V., TSUTSUI, N.D., HOLWAY, D.A. & CASE, T.J. 1999: Behavioral and genetic differentiation between native and introduced populations of the Argentine ant. – Biological Invasions 1: 43-53.

THOMPSON, R.C. 1990: Ants that have pest status in the United States. In: VANDER MEER, R.K., JAFFE, K. & CEDENO, A. (Eds.): Applied myrmecology: a world perspective. – Westview Press, Boulder, CO, pp. 51-67.

TSCHINKEL, W.R. 2006: The fire ants. – The Belknap Press of Harvard University Press, Cambridge, MA, 747 pp.

UGELVIG, L.V., DRIJFHOUT, F.P., KRONAUER, D.J.C., BOOMSMA, J.J., PEDERSEN, J.S. & CREMER, S. 2008: The introduction history of invasive garden ants in Europe: integrating genetic, chemical and behavioral approaches. – BioMed Central Biology 6:11, doi:10.1186/1741-7007-6-11.

WARD, D., BEGGS, J.R., CLOUT, M.N., HARRIS, R.J. & O'CONNOR, S. 2006: The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. – Diversity and Distributions 12: 601-609.

ZIMMERMAN, E.C. 1941: Argentine ant in Hawaii. – Proceedings of the Hawaiian Entomological Society 11: 108.