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Prey specialization and chemical mimicry between *Formica archboldi* and *Odontomachus* ants

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Abstract

Formica ants are not known to be prey specialists on other ant species, however, for the past 60 years, field observations on *Formica archboldi* in the southeastern United States have noted that their nests are scattered with body parts of *Odontomachus* trap-jaw ants. This study investigates the relationship between *F. archboldi* and *Odontomachus*. Through a series of behavioral experiments and a descriptive study of their chemical ecology, I find: (1) behavioral evidence that *F. archboldi* are more capable predators of *Odontomachus* in comparison to other *Formica*. (2) *F. archboldi* match the cuticular hydrocarbon profiles of the native species of *Odontomachus* that they occur with. This includes *O. brunneus* and *O. relictus* and the intraspecific variation found across Florida populations of *O. brunneus*. (3) *F. archboldi* do not display a prey retrieval preference towards hydrocarbon-matching *Odontomachus* as compared to mismatching. (4) *F. archboldi* that match *Odontomachus* hydrocarbon profiles do not receive lower levels of aggression than mismatching *F. archboldi*. Beyond providing natural history insights into the relationship between these species, this study expands our knowledge of an important insect chemical phenotype. The intraspecific variability in *F. archboldi* cuticular hydrocarbon profiles is among the greatest reported for social insects and provides a unique case of how non-parasitic species can generate parasite-like chemical-mimic phenotypes.

Keywords Cuticular hydrocarbons · Predator–prey interactions · Social insects · Chemical deception · Social parasitism

Introduction

While many ants have a generalist diet, relatively few species are prey specialists. Many examples of prey specialization are found in the subfamily Ponerinae. For example, *Neoponera marginata* prey exclusively on termites, the genera *Plectroctena* and *Thaumatomyrmex* specialize on millipedes, and some *Leptogenys* are isopod hunters (Brandão et al. 1991; Dejean and Evraerts 1997; Hölldobler and Wilson 1990; Leal and Oliveira 1995). However, this degree of dietary specialization is relatively rare in crown group ants (e.g.,

subfamilies Formicidae, Myrmicinae, and Dolicoderinae) and few ants outside the subfamily Ecitoninae (e.g., the army ants) primarily prey on workers of other ant species.

Fourteen years after *Formica archboldi* Smith was formally described (Smith 1944), a peculiar natural history note was reported. Van Pelt (1958) wrote: "It [an *F. archboldi* nest] contained many heads of *Odontomachus haematoda insularis*, indicating that the *Formica* may take over *Odontomachus* nests, or that the *Odontomachus* is used as food". In subsequent decades, many authors have reported similar observations when describing the biology of *F. archboldi*, hypothesizing that the species is a prey specialist of *Odontomachus* ants (Fig. 1; Deyrup 2017; King and Trager 2007; Trager and Johnson 1985; Trager et al. 2007). The most detailed observations of *F. archboldi* and *Odontomachus* are from Trager and Johnson (1985) who published prey retrieval observations noting that *Odontomachus* were the most common prey item retrieved amongst all observed items, including other ants, other insects, and plant material. Additionally, they reported that "subterranean refuse heaps contained remains of numerous *Odontomachus* workers" (Fig. 1). These notes are peculiar because reports of prey

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Fig. 1 Natural history notes beginning in 1958 repeatedly mention the pictured scenario of: **a** *F. archboldi* workers from a freshly field-collected colony next to *Odontomachus* head and abdomen capsules found in their nest. **b** A complete collection of all insect heads found in a single *F. archboldi* nest collected in August of 2017 from Lecanto, FL. *Odontomachus* heads comprise the middle circle and are ringed by all other insect head capsules found in the nest, grouped by type

specialization in *Formica* ants are uncommon. Rarer still are reports of specialized predation on well-defended ant species such as trap-jaws of the genus *Odontomachus*.

Formica archboldi is restricted to the Southeastern United States, throughout the state of Florida and into Georgia and Alabama (Trager et al. 2007). Its range is completely congruent with the range of *Odontomachus brunneus*, a species thought to be native to the US (Deyrup 2017). The distribution of *F. archboldi* also overlaps with *Odontomachus relictus*, a species endemic to Florida, and *Odontomachus ruginodis*, a species thought to be introduced to Florida (Deyrup 2017; Macgown et al. 2014).

Odontomachus ants are commonly referred to as trap-jaw ants because of spring-loaded mandibles they snap shut for prey capture and predator avoidance (Larabee and Suarez 2014). The most abundant *Odontomachus* species in the Southeastern United States is *O. brunneus*. Several aspects of its biology have been studied in detail (e.g., Cerquera and Tschinkel 2010; Hart and Tschinkel 2012), but direct predator–prey-like interactions between *Odontomachus* and *F. archboldi* have not been reported (Trager and Johnson 1985). However, field observations of *Odontomachus* ants suggest that they may be particularly sensitive to chemical defenses of other ants, which has been the hypothesized mechanism through which they could be subdued by *F. archboldi* (Deyrup and Cover 2004).

The aim of this study is to investigate the relationship between *F. archboldi* and *Odontomachus* ants. In doing so, I have found that *F. archboldi* closely match the cuticular hydrocarbon profiles of *Odontomachus relictus* and *Odontomachus brunneus*, where they occur with those species. This finding has implications beyond the natural history of these species, expanding our knowledge of intraspecific variability in this insect chemical phenotype. Subsequently, many of the experiments herein are both in light of that

cuticular hydrocarbon finding as well as exploring the relationship between these species.

The cuticular hydrocarbon profile of *Odontomachus* ants in the Southeastern United States has been studied in detail (Smith et al. 2012, 2013, 2014, 2016). Cuticular hydrocarbons are a layer of non-volatile waxes coating the surface of an insect that, while likely originating for desiccation resistance, have been co-opted by many solitary and social insects for communication purposes (Blomquist and Bagnères 2010). In *Odontomachus* ants, they provide a means of discriminating nestmates from non-nestmates (Smith et al. 2013, 2015) and differentiating reproductive individuals from non-reproductives (Smith and Liebig 2017; Smith et al. 2012). In Florida, the *Odontomachus* hydrocarbon profile is variable between species (Smith et al. 2016) and high levels of population-level variation in the profile are found within *O. brunneus* (Smith et al. 2013). Intraspecific population-level variation in hydrocarbon profile, such as in *O. brunneus*, is thought to be uncommon across ants (Guillem et al. 2016). For example, species-specific profiles of *Formica* ants in Europe are stable across populations ranging from Finland to the British Isles (Martin et al. 2008).

Instances of one ant species matching the cuticular hydrocarbon profile of another are largely found in host–parasite scenarios (Bagnères and Lorenzi 2010). Obligate parasitic ant species can be close chemical mimics of their host ant species (Bauer et al. 2010; Kleeberg and Foitzik 2016). However, while mimicking most of the host profile, some obligate parasitic ant species also maintain hydrocarbon profile components that differentiate them from their hosts (Liu et al. 2003; Torres and Tsutsui 2016). *Formica* species are frequently the target of both obligate and facultatively parasitic ant species. Parasitism of *Formica* species has been shown to result in alteration of the host *Formica* cuticular hydrocarbon profile both as an immediate result

of a parasitism event (Torres and Tsutsui 2016; Włodarczyk and Szczepaniak 2017) and as an evolutionary response to parasitic ant species (Martin et al. 2011). *Formica archboldi* is known to be parasitized by the obligate dulotic ant species *Polyergus oligergus* (King and Trager 2007; Trager 2013); however, the chemical ecology of both species has not been studied.

This study describes the cuticular hydrocarbon profile of *F. archboldi* through sampling 21 colonies across three locations in Florida; one location where *Odontomachus relictus* is abundant and two locations where *Odontomachus brunneus* is abundant. For comparison, the cuticular hydrocarbon profile of the co-occurring *Odontomachus* species is also sampled from the same locations. Second, to better understand the potential predator–prey relationship between *F. archboldi* and *Odontomachus*, I performed a series of experiments with laboratory colonies of *F. archboldi* aimed at answering the following questions: are *F. archboldi* more capable predators of *Odontomachus* in comparison to other *Formica*? Do *F. archboldi* display a prey retrieval preference towards hydrocarbon-matching *Odontomachus* as compared to mismatching *Odontomachus*? Do *F. archboldi* that match *Odontomachus* hydrocarbon profiles receive lower levels of aggression than mismatching *F. archboldi*? While these experiments collect and analyze simple categorical response variables (e.g., "did the ants do this or that?"), finer-scale behavioral descriptions are reported from the interactions between these species observed during these experiments.

Methods

Chemical analysis

Cuticular hydrocarbons of *F. archboldi* workers were sampled from 21 colonies collected across three Florida locations in May 2016 and August 2017: 11 from the Citrus Tract of the Withlacoochee State Forest in Lecanto, five from the Croom Tract of the Withlacoochee State Forest in Brooksville, and five from the MacArthur Agro-ecology Research Center in Lake Placid. From each location, five colonies of the co-occurring *Odontomachus* species were also sampled (*O. brunneus* from Brooksville and Lake Placid, *O. relictus* from Lecanto). *Odontomachus ruginodis* is also locally abundant in the Lake Placid site. Its cuticular hydrocarbon profile was previously described from the same population (Smith et al. 2016), and preliminary sampling of *F. archboldi* revealed only matching of *O. brunneus*. Therefore, *O. ruginodis* was not collected and is not included in this study.

When complete colonies were accessible in the field, they were manually excavated, housed in the laboratory, and used for the behavioral experiments described below.

Sampling of cuticular hydrocarbon profiles was performed within 3 weeks of collection from the field. However, nine of the *F. archboldi* colonies were kept in the laboratory for 7 months on a diet of only sugar water and beetle larvae (*Tenebrio molitor*), without exposure to trap-jaw ants, prior to chemical sampling. This study does not specifically test the influence of laboratory conditions and standard diet on hydrocarbon profiles, but the samples that were kept in laboratory conditions are noted as such in the results and in the supplementary materials.

To sample cuticular hydrocarbons from both *Formica* and *Odontomachus*, three live worker ants were randomly selected from their colonies. They were freeze-killed and collectively immersed in 200 μl of hexane for 5 min. These crude, whole body extracts were then concentrated under a stream of nitrogen to a volume of approximately 25 μl, 1 μl of which was injected into an Agilent 7820A Gas Chromatograph (Agilent Technologies, Santa Clara, CA), equipped with a nonpolar column (HP-5; 30 m × 0.32 mm × 0.25 μm film; Agilent Technologies, Santa Clara, CA, USa), connected to a Flame Ionization Detector. The GC injection port was set to 280 °C and the transfer line to 315 °C. The column temperature was held at 60 °C for 2 min, increased to 220 °C at 40 °C/min, and then to 315 °C at 4 °C/min. Helium was used as a carrier gas at 1 ml/min, and samples were injected in splitless mode with a purge time of 2 min. For compound identification, a subset of samples, two from each species at each population, were subsequently analyzed with an Agilent 6890 GC coupled with an Agilent 5975 mass selective detector. The GC-MS was fitted with a DB-5MS column (30 m × 0.25 mm × 0.25 μm; Agilent). GC parameters were the same as listed above and a solvent delay of 3.2 min was used.

Straight-chain compounds were identified from their mass spectra, including the parent ion if present, and by matching retention times with authentic standards. Methyl-branched compounds were identified by a combination of their enhanced ions from fragmentation on either side of methyl branch points, and their retention indices relative to straight-chain hydrocarbon standards (Carlson et al. 1998). Alkenes and non-conjugated dienes were identified from their retention indices (slightly smaller than the corresponding alkanes on the DB-5 column), their parent ions, and their mass spectral fragmentation patterns. Identifications were confirmed by comparisons of retention times and mass spectra to those of authentic standards when available, as well as comparisons to previously described cuticular hydrocarbon profiles of *Odontomachus* from these populations (Smith et al. 2013, 2014, 2016).

Compounds were included in the results and graphical analysis if they occurred in ≥ 80% of the sampled individuals within at least one of the sample types (species and population). Compounds are presented in terms of relative

abundance within the entire profile (individual compound amount/sum of all compound amounts). I performed non-metric multi-dimensional scaling to visualize the similarity of profiles within and between populations (Primer 7, PRIMER-E Ltd., Ivybridge, UK). Chord (standardized Euclidean) distances were used to calculate the distance matrices. A stress value, representing how well the data are represented in two dimensions, was also calculated.

Experiment 1: Are *F. archboldi* more capable predators of *Odontomachus* in comparison to other *Formica*?

I compared aggressive behavior of *F. archboldi* toward live *Odontomachus* ants to that of a congeneric *Formica, F. pallidefulva*. *Formica pallidefulva* is a species whose range overlaps with that of the *Odontomachus* in this study. However, unlike *F. archboldi*, it is not known or hypothesized to be a specialist predator of *Odontomachus* ants. *Odontomachus*, with their spring-loaded mandibles and sting are well-defended ants. Therefore, because I was interested in comparing aggressive behavior of the *Formica* species, I immobilized the trap-jaw mandibles with glue in this experiment. Beyond their restrained mandibles, the *Odontomachus* ants used were normal functioning workers or a dealated gyne that was behaving as a worker in their natal nest. An *O. brunneus* delate gyne was used in one trial paired with an *F. pallidefulva* worker. In this species, dealated gynes are known to leave the nest and act as worker-like foragers (Hart and Tschinkel 2012).

The experiment consisted of introducing a live *Odontomachus* (either *O. relictus* or *O. brunneus*) and a live *Formica* into a 28 mm test arena and filming an aggressive interaction at high speed (500 frames per second with a Phantom Miro LC320s camera, Vision Research Inc., Wayne, NJ, USA) through a Vision Optics Laowa 60 mm f/2.8 2 × Ultra-Macro Lens. The *F. archboldi* were paired with a cuticular hydrocarbon-matching *Odontomachus* from the same population and the *F. pallidefulva* used were collected from urban locations around Raleigh, NC, well outside the range of *Odontomachus* ants. Each trial (paired design, $N=10$) used *Formica* and *Odontomachus* individuals from independent colonies and an individual ant was never used twice. Each *Odontomachus* colony used was paired with both *Formica* species.

Video recordings were made of the first aggressive interaction initiated by the *Formica* worker. The video observations, because they were made with a high-speed camera with limited memory, recorded a maximum of 12 s of interaction. The camera captured video via a post-trigger, meaning that it was constantly recording and could be triggered to save only the most recent 12 s. So, when aggression was first observed, the camera was recording and could be then told to stop and save. However, this was long enough to record an entire aggressive encounter. The ants were immediately separated after the recorded encounter. Post-trial normal-speed video recordings of the ants were made ~5 min after the trail to document the condition and mobility of the *Odontomachus* ants after receiving aggression. The test variable in this experiment was whether the *Odontomachus* ant, after receiving aggression from a *Formica*, was immobilized or able to walk around the test arena normally.

Next, I performed a gland-smearing experiment to document the effects of *Formica* chemical compounds on *Odontomachus*. The Dufour's and poison gland complex was dissected from 10 *F. archboldi* and *F. pallidefulva* workers originating from independent colonies. Both the Dufour's and the poison gland are secreted through the tip of the abdomen, which the high-speed video observations above revealed to be the source of excretions used in aggressive encounters. The Dufour's gland was included in this treatment along with the poison gland as it is known to be used by parasitic *Formica* and *Polyergus* species in aggressive encounters with other ants (D'Ettorre et al. 2000; Regnier and Wilson 1971). Each dissection was performed under de-ionized water and the gland complex was taken from the dissection and directly ruptured and smeared on the thorax and abdomen of live, restrained *O. brunneus* workers. Additionally, for every pair of *Formica* gland smears, a control *Odontomachus* was taken through the experimental protocol and treated with a sham smearing of water only. Each *Odontomachus* colony ($N=10$) used as a source of workers received each treatment. Post treatment, both gland-smeared ants and the control ant were filmed to document their condition and mobility. The test variable in this experiment was whether the *Odontomachus* ant, after receiving a *Formica* gland smear, was immobilized or able to walk around the test arena normally.

Experiment 2: Do *F. archboldi* display a prey retrieval preference towards hydrocarbon-matching *Odontomachus* as compared to mismatching *Odontomachus*?

I compared prey retrieval and in-colony treatment of *Odontomachus* workers through time-lapse video observations across 9 *F. archboldi* colonies housed in the laboratory. Laboratory *F. archboldi* nests consisted of 100 mm × 25 mm deep petri dishes with moistened dental plaster floors, interconnected to one another and to an open foraging arena by latex tubing. Nests were kept in constant light and the interior of the nest was filmed through the transparent lids to the petri dish nest chambers. Time-lapse video of the nest chambers was gathered at a frame rate of a frame every 3 s over a continuous 18-h period. The observation period began when the test *Odontomachus* ants were introduced into the

foraging arena. Colonies were simultaneously presented with a cuticular hydrocarbon-matching (same population) *O. brunneus* or *O. relictus* worker and a mismatching *O. brunneus* or *O. relictus* worker. Each trial presented ants from unique combinations of source colonies. The *Odontomachus* ants were first freeze-killed and then marked with dots of blue or white paint (Testors, USA) on the dorsal portion of the head, thorax, and abdomen to distinguish the matching from mismatch in the video observations. Ants were used in the experiment immediately after being freeze-killed and thawed. The test variable recorded from the video data was whether or not the *Odontomachus* ants were retrieved from the arena and brought into the nest chambers. Additionally, I report observations of how the ants were treated once they were brought into the nest.

Experiment 3: Do *F. archboldi* that match *Odontomachus* hydrocarbon profiles receive lower levels of aggression than mismatching *F. archboldi*?

I measured the aggressive responses (mandible strikes) of *Odontomachus brunneus* workers across 16 colonies in response to encountering either a cuticular hydrocarbon-matching *F. archboldi* worker, a mismatching *F. archboldi* worker (showing an *O. relictus* hydrocarbon profile), or a nestmate control worker. Motionless, cold-anesthetized but living, workers were presented in the foraging arena of the *O. brunneus* colonies. Each test colony was presented with each ant stimulus during the same 30 min period. Each stimulus ant was presented alone and the order in which colonies received the ants was random. Live *F. archboldi* workers used in this experiment originated from 15 different colonies. Each colony received a unique combination of match/mismatch *F. archboldi* stimuli ants. Physical encounters with the ant stimuli were video recorded for 5 min or until an observation of the maximum amount of aggression (mandible strikes from multiple workers) was observed. The test variable recorded in this experiment was whether or not the *F. archboldi* workers elicited mandible strikes from *Odontomachus* ants. Trials in which there were < 10 encounters with any of the test ants were excluded from data analysis. Trials that resulted in less than ten encounters only occurred twice during this experiment and resulted from the majority of those workers remaining in their nests and not actively patrolling their foraging arena.

Results

Field observations and chemical analysis

Field collections of whole *F. archboldi* colonies revealed what other authors have noted for the past 60 years:

Odontomachus body parts, particularly head capsules, are common in *F. archboldi* nests (Fig. 1a). However, as reported by Trager and Johnson (1985), *Odontomachus* are not the only insects collected by *F. archboldi* (Fig. 1b). While collecting *F. archboldi* samples, observations of foragers from two field colonies were made. Several natural encounters between *F. archboldi* and *O. brunneus* foragers were observed. None of the observed encounters resulted in predation or an aggressive interaction. The ants responded to antennal contact with one another with excited agitation and avoidance.

Cuticular hydrocarbon profiles of *F. archboldi* match profiles of *O. relictus* and *O. brunneus* across populations in Florida (Fig. 2; Table 1). Samples from Brooksville and Lake Placid indicate that *F. archboldi* also replicate the population-level variation previously reported in the hydrocarbon profile of *O. brunneus* (Smith et al. 2013). Graphical representation of the hydrocarbon profile samples separates each population and cluster *Formica* samples with *Odontomachus* (Fig. 3, stress values of 0.09 indicates a good graphical representation of the data, with "no real risk of drawing false inferences" [Clarke 1993]). Colonies that were sampled after being in the lab for 7 months without exposure to *Odontomachus* maintain their *Odontomachus*-like hydrocarbon profiles (Fig. 3).

Of the 44 compounds recorded for these species, across populations, all compounds produced by *Odontomachus* species were also collected from *F. archboldi* (Table 1; with single exception of 5-methylhentriacontane from two populations). While few qualitative differences (compounds found in all of one species and none of the other) were found between *F. archboldi* and *Odontomachus* samples within populations, qualitative differences in relative compound abundances between *Formica* and *Odontomachus* profiles were numerous (Table 1). However, across populations, *F. archboldi* appear to resemble their co-occurring *Odontomachus* more than *F. archboldi* from another population (Figs. 2, 3; Table 1).

Experiment 1: Are *F. archboldi* more capable predators of *Odontomachus* in comparison to other *Formica*?

Statistically, after being attacked by *Formica*, the ability of *Odontomachus* workers to move around the test arena was significantly more often impaired by *F. archboldi* attacks (10 of 10 impaired) than *F. pallidefulva* (1 of 10 impaired; McNemar's Chi-Square test, $\chi^2 = 7.1$, $p < 0.01$). High-speed video observations of aggressive interactions showed aggression from *Formica* workers (both *F. archboldi* & *F. pallidefulva*) consisted of either biting an appendage or climbing on top of the *Odontomachus* worker and curling the gaster underneath the body,
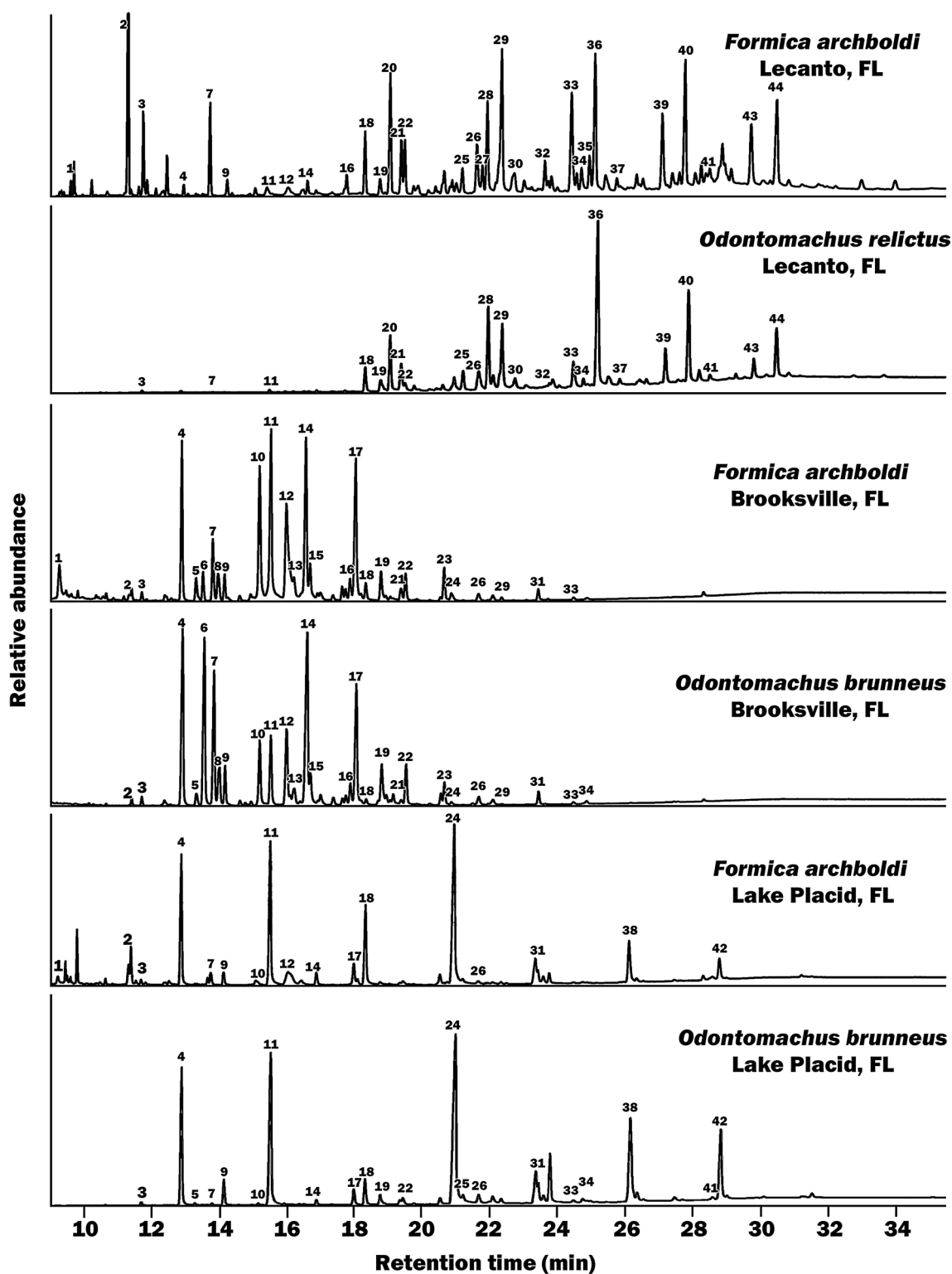
Fig. 2 Representative chromatograms of *Formica archboldi* and co-occurring *Odontomachus* worker cuticular hydrocarbon profiles across populations. Numbers above peaks correspond to the compounds presented in Table 1

pointing the tip directly at the target worker (Fig. 4a). In all 10 *F. archboldi* videos, fluid was seen either being sprayed from the tip of their gaster or pooling in a glob at the tip. Direct smearing of the tip of the gaster onto the

Table 1 Cuticular hydrocarbon compounds of workers of *Formica archboldi* and the co-occurring *Odontomachus* species across three Florida populations, Kovat's retention indices, and relative percent abundance

Peak number	Identification	Kovat's Retention Index	*Formica archboldi* Lecanto, FL	*Odontomachus relictus* Lecanto, FL	*Formica archboldi* Brooksville, FL	*Odontomachus brunneus* Brooksville, FL	*Formica archboldi* Lake Placid, FL	*Odontomachus brunneus* Lake Placid, FL
1	Unknown	22.09	0.45 (0, 1.43)	0 (0, 0)	2.99 (0.09, 7.21)	0.11 (0.04, 0.23)	1.53 (0.4, 3.39)*	0.01 (0, 0.03)
2	Unknown	23.7	2.68 (0.53, 5.75)*	0 (0, 0)	0.87 (0.31, 1.55)*	0.1 (0.06, 0.18)	0.85 (0.29, 1.31)*	0 (0, 0)
3	Tetracosane	24	1.62 (0.24, 3.85)*	0.08 (0.07, 0.1)	0.38 (0, 0.72)	0.16 (0.12, 0.22)	0.24 (0, 0.55)	0.15 (0.09, 0.24)
4	Pentacosane	24.99	0.24 (0, 0.59)	0 (0, 0)	6.62 (3.12, 12.27)	9.37 (8.14, 9.92)	3.83 (1.35, 5.68)*	10.43 (7.56, 13.14)
5	11- and 13-Methyl-pentacosane	25.33	0 (0, 0)	0 (0, 0)	1.79 (0.66, 2.75)	0.39 (0.24, 0.82)	0.02 (0, 0.09)*	0.3 (0.1, 1.07)
6	5-Methylpentacosane	25.49	0 (0, 0)	0 (0, 0)	1.5 (0.87, 2.04)*	6.44 (4.88, 11.87)	0 (0, 0)	0.09 (0, 0.33)
7	3-Methylpentacosane	25.73	1.02 (0, 2.01)	0.24 (0.08, 0.44)	4.56 (3.5, 5.48)	6.22 (5.29, 7.43)	0.45 (0.19, 0.99)	0.27 (0.11, 0.75)
8	5,8-Dimethyl-pentacosane	25.83	0 (0, 0)	0 (0, 0)	1.46 (1.19, 1.73)	1.85 (1.19, 3.29)	0.17 (0, 0.5)	0 (0, 0)
9	Hexacosane	25.98	0.27 (0, 0.71)	0.03 (0, 0.07)	1.1 (0.53, 1.9)	1.96 (1.69, 2.33)	0.36 (0, 0.6)*	1.22 (0.98, 1.74)
10	(Z)-9-Heptacosene	26.78	0.16 (0, 0.76)	0 (0, 0)	10.97 (8.96, 15.18)*	3.32 (2.55, 3.71)	0.44 (0, 1.01)	0.23 (0.11, 0.41)
11	Heptacosane	27	11.02 (0, 33.83)	0.25 (0.1, 0.5)	11.75 (7.55, 16.77)*	5.15 (3.67, 5.82)	22.31 (5.27, 49.7)	11.84 (9.96, 17.68)
12	11- and 13-Methyl-heptacosane	27.34	5.64 (0, 21.5)	0.16 (0.06, 0.31)	5.91 (2.85, 7.49)	4.59 (3.64, 7.08)	9.39 (0.33, 25.05)*	0.04 (0, 0.1)
13	5-Methylheptacosane	27.41	0 (0, 0)	0 (0, 0)	2.45 (0.28, 9.84)*	0.18 (0, 0.27)	0 (0, 0)	0 (0, 0)
14	3-Methylheptacosane	27.74	0.16 (0, 0.65)	0.08 (0, 0.14)	10.51 (6.3, 14.34)*	19.02 (15.48, 22.82)	0.8 (0, 1.89)	0.29 (0.2, 0.45)
15	5,19-Dimethyl-heptacosane	27.83	0 (0, 0)	0 (0, 0)	1.82 (1.61, 1.97)	1.16 (0, 2)	0.11 (0, 0.34)	0 (0, 0)
16	x,y-Nonacosadiene	28.68	0.43 (0, 1.21)	0.11 (0, 0.21)	1.08 (0.91, 1.33)	1.01 (0.88, 1.12)	0 (0, 0)	0 (0, 0)
17	(Z)-9-Nonacosene	28.8	0 (0, 0)	0.11 (0, 0.21)	14.14 (8.59, 28.49)	16.87 (9.27, 21.58)	4.47 (1.53, 6.83)	1.68 (0.99, 2.64)
18	Nonacosane	28.98	1.79 (0.63, 3.31)	2.43 (1.23, 4.43)	0.6 (0.34, 0.84)	0.36 (0.29, 0.43)	4.5 (0.98, 8.41)	1.12 (0.63, 1.44)
19	13- and 15-Methynonacosane	29.31	0.61 (0, 1.11)	1.41 (0.71, 1.9)	1.83 (1.05, 2.45)*	3.4 (2.71, 4.32)	0.09 (0, 0.47)	0.03 (0, 0.08)
20	5-Methylnonacosane	29.57	3.62 (2.12, 5.91)	5.91 (2.97, 10.49)	0.11 (0, 0.41)	0 (0, 0)	0 (0, 0)	0 (0, 0)
21	3-Methylnonacosane	29.7	1.95 (0.72, 3.12)	2.65 (1.83, 3.75)	0.38 (0, 0.53)	0.4 (0.29, 0.54)	0.15 (0, 0.53)	0.38 (0, 0.61)
22	5,12-Dimethyl-nonacosane	29.77	1.51 (0.27, 3.21)	0.59 (0.46, 0.8)	1.47 (1.28, 1.72)*	2.93 (2.19, 3.69)	0.71 (0, 1.27)	0.68 (0.56, 0.8)
23	x,y-Hentriacontadiene	30.63	0 (0, 0)	0 (0, 0)	2.07 (1.55, 2.73)	1.98 (1.22, 2.72)	0.32 (0, 1.14)	0 (0, 0)
24	(Z)-9-Hentriacontene	30.77	0 (0, 0)	0 (0, 0)	0.79 (0.62, 1.07)	0.46 (0.3, 0.76)	25.81 (4.75, 42.32)	26.75 (21.02, 31.09)

Table 1 (continued)

Peak number	Identification	Kovat's Retention Index	*Formica archboldi* Lecanto, FL	*Odontomachus relictus* Lecanto, FL	*Formica archboldi* Brooksville, FL	*Odontomachus brunneus* Brooksville, FL	*Formica archboldi* Lake Placid, FL	*Odontomachus brunneus* Lake Placid, FL
25	Hentriacontane	31	1.02 (0.27, 1.57)	2.12 (1.26, 3.11)	0.05 (0, 0.24)	0.04 (0.03, 0.05)	0.29 (0, 0.57)	0.4 (0.32, 0.55)
26	13- and 15-Methyl-hentriacontane	31.26	2.31 (0.95, 4.33)	2.8 (2.45, 3.22)	0.4 (0.27, 0.62)	0.22 (0.16, 0.27)	0.09 (0, 0.45)	0.19 (0.14, 0.25)
27	7-Methylhen-triacontane	31.4	1.28 (0.51, 1.98)*	0 (0, 0)	0.09 (0, 0.33)*	1.05 (0.82, 1.22)	0.04 (0, 0.19)*	1.06 (0.46, 1.35)
28	5-Methylhen-triacontane	31.48	3.68 (1.54, 5.21)*	8.56 (5.39, 10.92)	0 (0, 0)*	0.12 (0.1, 0.13)	0 (0, 0)	0.14 (0, 0.31)
29	3-Methylhen-triacontane	31.78	5.78 (0, 11.56)	7.2 (5.55, 9.27)	0.28 (0.26, 0.31)*	0.11 (0.09, 0.12)	0.3 (0, 0.49)	0.54 (0.44, 0.65)
30	Dotriacontane	32	1.31 (0, 2.02)	1.31 (1.1, 1.78)	0.02 (0, 0.1)	0.04 (0, 0.08)	0 (0, 0)	0 (0, 0)
31	x,y-Tritriacon-tadiene	32.59	0 (0, 0)	0 (0, 0)	1.72 (1.45, 2.21)	1.56 (0.91, 1.92)	3.08 (0.8, 6.2)	3.65 (1.96, 6.22)
32	Unknown	32.69	0.72 (0, 1.24)	1.27 (0.98, 1.81)	0.03 (0, 0.15)	0 (0, 0)	0.76 (0, 1.34)	0 (0, 0)
33	15- and 17-Methyltri-triacontane	33.26	2.87 (0.7, 4.06)	4.12 (3.65, 4.64)	0.12 (0, 0.31)	0.39 (0.27, 0.48)	0.04 (0, 0.2)*	0.43 (0.21, 0.54)
34	5-Methyltritri-acontane	33.47	1.23 (0, 2.79)	0.27 (0.14, 0.41)	0.08 (0, 0.38)*	0.6 (0.5, 0.73)	0.33 (0, 0.58)	0.43 (0.34, 0.58)
35	4-Methyltritri-acontane	33.65	1.1 (0, 1.8)*	0.04 (0, 0.22)	0 (0, 0)	0.01 (0, 0.03)	0 (0, 0)	0.09 (0, 0.15)
36	3-Methyltritri-acontane	33.77	6.01 (2.47, 9.85)*	20.09 (17.08, 23.87)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.08 (0, 0.26)
37	Unknown	34.25	1.09 (0, 2.59)	1.16 (0.9, 1.41)	0 (0, 0)	0 (0, 0.02)	0 (0, 0)	0.01 (0, 0.07)
38	x,y-Pentatriac-ontadiene	34.55	0 (0, 0)	0 (0, 0)	0.21 (0, 0.85)	0.13 (0.07, 0.28)	4.89 (0.94, 7.42)*	12.25 (9.71, 16.42)
39	15- and 17-Methyl-pentatriaco-ntane	35.26	2.84 (0.8, 4.76)	4.14 (3.71, 4.81)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0)
40	3-Methylpenta-triacontane	35.78	5.32 (1.71, 8.49)	7.93 (5.75, 9.78)	0 (0, 0)	0.06 (0, 0.09)	0 (0, 0)	0 (0, 0)
41	Unknown	36.28	0.96 (0, 3.63)	1.08 (0.67, 1.4)	0 (0, 0)	0.11 (0, 0.15)	0.07 (0, 0.33)	0.64 (0.52, 0.78)
42	x,y-Heptatriac-ontadiene	37.55	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.05 (0, 0.24)	2.26 (0, 3.64)	9.19 (7.73, 10.47)
43	17- and 19-Methyl-heptatriaco-ntane	37.23	2.78 (0, 5.11)	2.38 (2.18, 2.74)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.12 (0, 0.23)
44	3-Methylhepta-triacontane	37.75	3.99 (1.48, 6.02)	4.24 (3.19, 5.21)	0 (0, 0)	0 (0, 0)	0 (0, 0)	0.75 (0, 1.16)

Peak numbers correspond to the labels on Fig. 1. Data are means (minimums, maximums); $N = 11$ for each species in Lecanto, $N = 5$ for all other types. Asterisks indicate compound relative abundance ranges that are non-overlapping between *Formica* and *Odontomachus* samples within populations
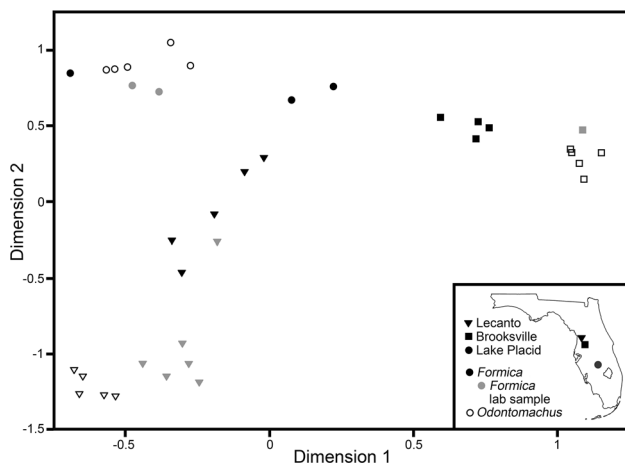
Fig. 3 Two-dimensional configuration of non-metric, multi-dimensional scaling of differences in cuticular hydrocarbon profiles of *Formica archboldi* (filled shapes) and co-occurring *Odontomachus* (open shapes) worker cuticular hydrocarbon profiles across populations. Filled gray shapes are samples that were taken after prolonged lab culture without exposure to *Odontomachus* ants (see methods). The stress value of this two-dimensional representation of the complete hydrocarbon data set is 0.09

Odontomachus was observed in two trials. In three of the *F. palidefulva* videos, fluid spray or a glob was visible, and direct smearing was also observed in two trials. Qualitatively, the amount of fluid sprayed by *F. archboldi* was greater than that of *F. pallidefulva* (Fig. 4a, Supplemental video 1). Post aggression, all ten of the workers attacked by *F. archboldi* were unable to walk around the 28 mm test arena, 7 of the 10 were completely immobilized and unable to stand. Only one of the *Odontomachus* attacked by

F. pallidefulva was unable to walk around the test arena, post attack, though this ant was not completely immobile.

Complete immobilization was a statistically significant effect of gland smearing (19 of 20 gland smears resulted in immobilization vs. 0 of 10 control treatments; Cochran's Q test, $\chi^2 = 18.2$, $p < 0.001$). Smearing *F. archboldi* and *F. pallidefulva* glands did not have a statistically different effect on *Odontomachus* (10 of 10 immobilized by *F. archboldi* glands, 9 of 10 immobilized by *F. pallidefulva; McNemar's* Chi-Square test with Yates correction for continuity, $p > 0.6$), but both treatments were statistically more effective at immobilizing *Odontomachus* than the control (McNemar's Chi-Square test with Yates correction for continuity, $p < 0.01$).

Experiment 2: Do *F. archboldi* display a prey retrieval preference towards hydrocarbon-matching *Odontomachus* as compared to mismatching *Odontomachus*?

All *Odontomachus* ants presented (9 of 9 hydrocarbon mismatching and matching ants) in this experiment were retrieved from the foraging arena and brought into the nest chambers of the 9 *F. archboldi* colonies tested (Fig. 4b). All expect for one hydrocarbon mismatch ant remained in the nest for the entire 18 h of observation. This exception was carried back out of the nest after 8 h. While in the nest, the *Odontomachus* ants were placed and arranged on the nest floor in a similar manner to the bits of beetle larvae that the colonies were regularly fed. The *Odontomachus* ants were frequently attended by *F. archboldi* workers who licked, bit, and moved the *Odontomachus* across the nest
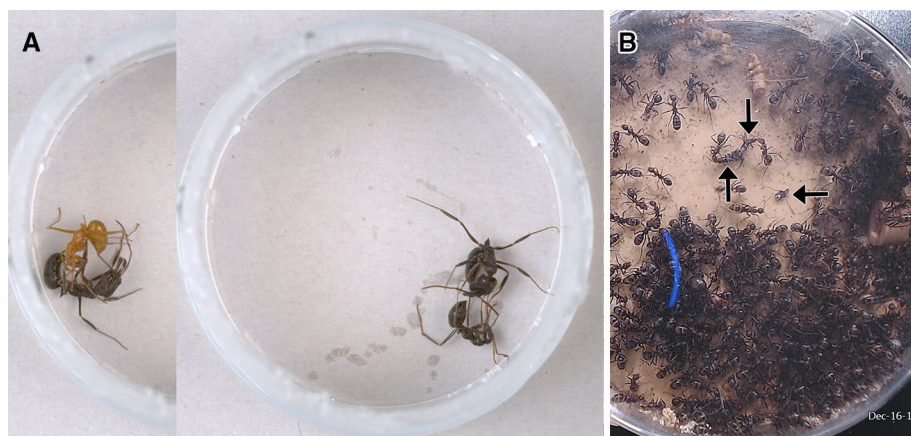

Fig. 4 a Still images from high-speed (500 frames per second) video observations of aggressive interactions between *Formica pallidefulva* (left), *Formica archboldi* (right), and *Odontomachus* workers. Both images display a stereotypical *Formica* aggressive behavior of appendage biting with a curled and gaster aimed at the opponent. *F. archboldi* image shows a trail of fluid sprayed by the *Formica* worker during the encounter. **b** Still image from time-lapse video observation showing two *Odontomachus* workers retrieved from the foraging arena and handled inside the laboratory nest (vertical arrows). Horizontal arrow shows a decapitated head of one of the retrieved *Odontomachus* workers. See supplemental materials for these videos

floor. Decapitation of *Odontomachus* workers was observed in 5 of the 9 colonies (Fig. 4b, Supplemental video 2). Four instances of decapitation were observed towards both hydrocarbon mismatch and matching *Odontomachus*. One instance of abdomen (gaster) removal (hydrocarbon matching/mismatching mark unclear) was observed and no other removals of appendages or body parts were observed.

Experiment 3: Do *F. archboldi* that match *Odontomachus* hydrocarbon profiles receive lower levels of aggression than mismatching *F. archboldi*?

Statistically, *F. archboldi* elicited significantly more strikes than nestmate workers (14 of 16 *Odontomachus* colonies performing mandible strikes towards *F. archboldi* vs. 0 of 16 performing mandible strikes towards nestmates, Cochran's Q test, $\chi^2 = 13$, $p < 0.01$). The distribution of strikes towards matches (10 of 16 colonies) vs. mismatches (9 of 16 colonies) was not statistically different (Chi-Square test with Yates correction for continuity, $p > 0.8$).

Discussion

This study revealed that an attack from *F. archboldi* can quickly immobilize an *Odontomachus* trap-jaw ant. *Formica archboldi* is more effective at immobilizing mandible-restrained *Odontomachus* than *Formica pallidefulva*, a *Formica* species with no known association with trap-jaw ants. Immobilization of the trap-jaw ant is likely due to chemical weaponry. However, the contents of the poison and Dufour's gland of *F. archboldi* are no more effective at immobilizing trap-jaws than those from *F. pallidefulva*. In the lab, *F. archboldi* will retrieve trap-jaw ants into their nests, treating them as retrieved prey items, and will decapitate intact ants. This behavior leads to the presence of trap-jaw ant head cases in their colony, like what has been reported for this species in field notes over the last 60 years.

All 21 *F. archboldi* colonies sampled for cuticular hydrocarbons in this study closely resemble the *Odontomachus* species with which they occur. Three distinct *F. archboldi* cuticular hydrocarbon profiles from Florida are described herein: one that matches *O. relictus* profiles in Lecanto, one that matches *O. brunneus* in Brooksville, and one that matches *O. brunneus* in Lake Placid. Matching an *Odontomachus* profile seems to have no effect (or one too subtle to be detected by these experiments) on how *F. archboldi* and *Odontomachus* interact. Matching and mismatching *F. archboldi* elicit equal amounts of aggression from trap-jaw ants. *Formica archboldi* are equally as likely to retrieve either matching or mismatching *Odontomachus* workers as a prey item into their nest.

This study's demonstration of the effectiveness of an *F. archboldi* attack at immobilizing an *Odontomachus* provides some support for the hypothesis that *F. archboldi* is a prey specialist on *Odontomachus*. The attack of an *F. archboldi* is more effective than that of *F. pallidefulva* likely due to behavioral differences between the *Formica* species, as the glandular contents of both species produce are equally devastating to the trap-jaws. While most reports of *Formica* species spraying are in the context of defense, some *Forimca* are known to deploy their formic acid spray in the context of prey capture (Ayre 1968). *Formica archboldi* may be a more proficient "sprayer" when attacking or may have a lower threshold for releasing their glandular contents when grappling with a trap-jaw ant as compared to other *Formica* species.

Perhaps the most intriguing finding of this study is the description of matching cuticular hydrocarbon profiles between *F. archboldi* and *Odontomachus* species. The degree to which *F. archboldi* match the profiles of *O. relictus* and *O. brunneus* is similar to that of some ant species that are obligate social parasites, wherein the parasite matches major compounds produced by the host species, but quantitative differences and minor components of the profile differentiate the species (Liu et al. 2003; Torres and Tsutsui 2016). There have been no reports of *Odontomachus* being parasitized by any ant species. Given the relatively large number of researchers who have studied *Odontomachus* in Florida, it is unlikely that *F. archboldi* is an unnoticed social parasite of the species. Beyond social parasitism, there are other scenarios in which one insect species will match the cuticular hydrocarbon profile of a social insect including, for example, cleptoparasitism and myrmecophily in which matching chemical profiles aid in avoiding aggression from the exploited species (Bagnères and Lorenzi 2010). However, the experiments in this study were unable to correlate any differences in behavior, aggressive or otherwise, with differences in matching and mismatching hydrocarbon profiles.

Interestingly, *F. archboldi* retained their *Odontomachus*-like hydrocarbon signature after 7 months in the lab without exposure to trap-jaw ants. Furthermore, *F. archboldi* that occurred in a field site with an abundance of both *O. brunneus* and *O. ruginodis* (Lake Placid collection site) only matched the hydrocarbon profile of *O. brunneus*, not *O. ruginodis* which is thought to be an exotic species in Florida. These two findings suggest that chemical matching is not a by-product of having a significant portion of their diet consist of the *Odontomachus* species found in their habitat. An insect-rich diet has been shown to alter the cuticular hydrocarbon profiles of some ant species (Buczkowski et al. 2005; Liang and Silverman 2000). Instead, I hypothesize that this matching is an evolved trait of *F. archboldi* corresponding to some

selective advantage gained by matching native *Odontomachus* species. The advantage could lie in increased proficiency in predator–prey interactions with *Odontomachus*. This study does not find any obvious evidence for that, but further experimentation could reveal more subtle advantages. Alternatively, the advantage of hydrocarbon matching might lie in the relationship between *F. archboldi* and its obligate social parasite ant *Polyergus oligergus* (Trager 2013). Social parasites are known drivers of evolutionary divergence in cuticular hydrocarbon profiles of their social insect hosts (Jongepier and Foitzik 2016; Lorenzi et al. 2014; Martin et al. 2011). An extraordinary alternative hypothesis is that *F. archboldi* have co-opted their *Odontomachus* feeding habits into a means of chemically camouflaging themselves from their parasites. Testing this would require research into how *Polyergus oligergus* recognizes its hosts and how it responds to encountering *Odontomachus* ants.

Regarding the evolution of phenotypic diversity in social insect cuticular hydrocarbons, *F. archboldi* could prove to be an especially useful study system for understanding the mechanisms behind the generation of chemical signal variation. The intraspecific hydrocarbon profile diversity of *O. brunneus* across Florida was already among the most diverse reported (e.g., see Guillem et al. 2016), and *F. archboldi* has herein been described as a species that generates an even great amount of chemical profile diversity. Comparing the expression patterns of hydrocarbon biosynthesis genes of these two species should provide unique insights into convergent evolutionary strategies for generating chemical signal variation. For instance, comparing biosynthesis genes between *O. relictus*-like and *O. brunneus*-like profiles in *Formica* to *Odontomachus* should prove insightful, particularly for gauging how species divergence (in *Odontomachus*) influences mechanisms of phenotypic diversity in comparison to how equivalent levels of diversity are generated within a single species (in *Formica*).

Many pieces of the natural history story between *F. archboldi* and *Odontomachus* remain left to be described. Field-based studies on *F. archboldi* could shed light on the relationship between these species and what the selective advantage of hydrocarbon matching might be. However, in pursuit of describing the relationship between these species, *F. archboldi* has revealed itself as an ant species that can uniquely inform our understanding of the evolution of cuticular hydrocarbon profiles, a broader issue in social insect biology.

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