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Regional and caste-specific variation in insecticide susceptibility in odorous house ants, *Tapinoma sessile* (Hymenoptera, Formicidae)

Kaitlyn Brill 💿 🕴 Grzegorz Buczkowski 💿

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Department of Entomology, Purdue University, West Lafayette, Indiana, USA

Correspondence

Grzegorz Buczkowski, Department of Entomology, Purdue University, West Lafayette, IN 47907, USA. Email: gbuczkow@purdue.edu

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Abstract

Ants consistently rank as the number one household pest, and many species are pests in agricultural and natural habitats. Despite economic and ecological impact of pest ants, effective management still faces many challenges and control failures with liquid spray insecticides are common. The odorous house ant (Tapinoma sessile Say) is an adaptive and widespread pest ant found in North America. This study examined regional variation in T. sessile insecticide susceptibility to three classes of insecticides commonly used in ant control. T. sessile showed significant regional variation in insecticide susceptibility on a relatively small geographic scale. A comparison of colonies collected in urban vs. natural areas showed no significant difference in susceptibility in tests with lambda-cyhalothrin and fipronil. In tests with dinotefuran, urban colonies were significantly more tolerant relative to natural colonies. These results suggest that habitat type and previous insecticide exposure do not reliably predict susceptibility levels in individual populations. Queens were significantly more tolerant relative to their worker counterparts across all insecticides. Higher insecticide tolerance in queens may explain why T. sessile is such a persistent pest in urban environments. The results provide a foundation for the development of more effective and efficient control methods for T. sessile and warrant further investigation of spatial and potentially temporal variability in insecticide susceptibility in ants.

K E Y W O R D S

insecticide resistance, odorous house ant, pest management, tapinoma sessile

1 | INTRODUCTION

Ants play critical roles in most ecosystems because they constitute a great part of animal biomass and act as ecosystem engineers (Folgarait, 1998). Despite their valuable contributions, many ant species are serious pests in urban, agricultural and natural environments (McGlynn, 1999; Suarez et al., 2010). Globally, the frequency of invasive ants is increasing due to various factors including urbanization (Buczkowski & Richmond, 2012), trade (Bertelsmeier et al., 2017) and climate change (Bertelsmeier et al., 2015). Numerous species such as the Argentine ant (*Linepithema humile*), red imported fire ant (Solenopsis invicta) and big-headed ant (Pheidole megacephala) thrive in urban environments, damage agricultural crops and cause ecological damage by displacing native organisms (Holway et al., 2002). The impact of pest ants is most frequently seen in urban areas where many ant species have attained major economic pest status and are serious household, structural and nuisance pests. Forty-one species of ants are considered pests in the United States (Hedges, 1998).

Pest ants are often numerous, persistent and difficult to eradicate (Hoffmann et al., 2016). Perimeter treatments with contact residual insecticides around the exterior foundation of the house are the most common management strategy to reduce the impact of pest ants in urban areas (Buczkowski et al., 2005; Rust et al., JOURNAL OF APPLIED ENTOMOLOGY

1996; Rust & Su, 2012; Scharf et al., 2004; Silverman & Brightwell, 2008). Residual spray applications, also known as barrier treatments, are the core of most ant control programmes because they are cost-effective and can be applied quickly over large areas using spray equipment. Spray applications typically provide fast knockdown of foraging ants, prevent them from establishing foraging trails across treated surfaces and provide efficacy for approximately 4-8 weeks (Rust & Knight, 1990; Scharf et al., 2004). Additionally, the efficacy of spray insecticides is greatly increased by insecticide movement from one ant to another by horizontal transfer (Buczkowski, 2019; Soeprono & Rust, 2004). Despite the tremendous economic and ecological impact of pest ants, effective management still faces many challenges and control failures with liquid spray insecticides are well-documented in urban (Rust et al., 1996) and natural areas (Hoffmann et al., 2016; Silverman & Brightwell, 2008). The prevailing treatment strategies and product label rate determinations are not entirely compatible with the biology of many species (Buczkowski, 2021; Silverman & Brightwell, 2008) for several reasons; (1) cryptic nesting behaviours prohibit the direct treatment of colonies (Rust & Su, 2012), (2) colonies are typically very numerous which limits treatment performance and confounds monitoring effects (Hoffmann et al., 2011), (3) largescale treatments in natural areas with broad-spectrum insecticides are problematic because of non-target effects (Buczkowski & Wossler, 2019; Schläppi et al., 2021) and (4) there is large variation in susceptibility to insecticides across different ant species (Buczkowski, 2021).

The odorous house ant (Tapinoma sessile Say) is considered one of the most adaptive and widespread ant species found in North America (Fisher et al., 2007: Buczkowski, 2010: Menke et al., 2010: Salyer et al., 2014). It has been recognized as an urban pest for nearly 100 years (Smith, 1928; Thompson, 1990). In natural environments, colonies are small and consist of a few hundred workers and one or a few gueens (Buczkowski, 2010; Menke et al., 2010). However, in urban environments, colonies tend to act as an invasive species and consist of millions of workers and thousands of queens spread across multiple nesting sites (Buczkowski, 2010; Menke et al., 2010). Recently, a non-native, supercolonial population of T. sessile was discovered in Hawaii, demonstrating its potential global threat (Buczkowski and Krushelnycky, 2012). Among ants, T. sessile is infamous for being very hard to control (Buczkowski, 2021; Paysen, 2019). Tapinoma sessile consistently ranks as the #1 "call-back" ant among pest management professionals (Robbins, 2015). A callback occurs when the applicator is called back because the initial treatment failed which necessitates re-application. In a national survey, PMPs reported that T. sessile was the most important ant driving sales and the most difficult ant to control (Paysen, 2019). Additionally, a recent study evaluated insecticide susceptibility in 12 species of urban pest ants, and T. sessile were consistently the least susceptible to all insecticides (Buczkowski, 2021). Comparatively, low susceptibility may be part of the reason why T. sessile is so persistent and so difficult to control.

The goals for this study were tri-fold. The first objective was to examine regional variation in T. sessile susceptibility to three classes of insecticides commonly used in urban ant control. The hypothesis was that T. sessile colonies collected across different towns within a county would show significant variation in insecticide susceptibility. The second objective was to compare insecticide susceptibility in T. sessile colonies collected in natural vs. urban areas. The hypothesis was that colonies from natural areas would be less tolerant because they are unlikely to have ever been exposed to insecticides, whereas colonies from urban areas would be more tolerant because they are frequently exposed to insecticides. The final objective was to assess insecticide susceptibility in workers vs. queens. The hypothesis was that gueens would be more tolerant due to their significantly higher body mass and potentially other genetic and behavioural factors that might affect susceptibility. The mean body mass of T. sessile workers is 0.79 mg vs. 2.43 mg for queens (Buczkowski, unpublished data). Additionally, recent evidence suggests that queens might have superior detoxification capabilities compared with workers (Schläppi et al., 2020), which could lower their ability susceptibility to insecticide treatments. The ultimate goal of this study is to provide a foundation for developing more effective and efficient control methods for T sessile

2 | MATERIALS AND METHODS

2.1 | Ant collections

To examine regional variation in insecticide susceptibility, a total of 30 T. sessile colonies were collected across different locations within a 80 kilometre radius (20,096 sg km) of Purdue University campus, Tippecanoe County, Indiana (40°25'26.40"N, -86°55'44.40"W). All colonies were separated by at least 4 km to limit the possibility they were nests of the same colony. For the purpose of this study, regional variation is defined as pertaining to colonies collected in different locations across the study area. Therefore, regional variation refers to intercolony variation across the 20,096 sq km sampling area. To compare insecticide susceptibility in natural vs. urban colonies, 15 colonies were collected in natural areas and 15 in urban areas (Buczkowski, 2010). Natural areas were large tracts of mixed hardwood forest that contained mature trees and were free of any anthropogenic influence or disturbance. Urban areas were various residential and commercial areas throughout Tippecanoe County. Most urban areas were known to receive insecticides applications with various frequencies ranging from quarterly to annually (Buczkowski, 2010; Buczkowski & Richmond, 2012). All colonies were brought to the laboratory and placed in plastic trays coated with Fluon to prevent escapes. The colonies were provided with drinking water and artificial nests consisting of Petri dishes filled with moist plaster. The colonies were maintained on a 20% sucrose solution and artificial diet (Bhatkar & Whitcomb, 1970).

2.2 | Residual exposure assays

The insecticide susceptibility of all 30 colonies was tested using residual exposure assays. The chemistries tested were as follows: (1) phenylpyrazole (Termidor SC, BASF Corporation, Research Triangle Park, NC, 9.1% fipronil), (2), pyrethroid (Demand CS, Syngenta Crop Protection Incorporated, Greensboro, NC, 9.7% lambda-cyhalothrin) and (3) neonicotinoid (Alpine WSG, BASF Corporation, Research Triangle Park, NC, 40% dinotefuran). The concentrates were diluted in water according to the label-recommended rates: 0.06% for fipronil, 0.015% for lambda-cyhalothrin and 0.1% for dinotefuran. For each experimental replicate, 0.42 mL of the dilution was pipetted onto a 10×10 cm glazed ceramic tile. This is equivalent to the label-recommended application volume of 4 mL of finished dilution per 1000 cm². Control tiles were left untreated. All tiles were allowed to dry overnight. The environmental conditions in the laboratory were as follows: $28 \pm 2^{\circ}$ C, $45 \pm 10\%$ relative humidity, and 14 light: 10 dark cycle. Insecticide susceptibility in urban colonies was evaluated in workers (6 replicates of 5 ants each) and queens (6 replicates of 1 ant each). Insecticide susceptibility in gueens vs. workers was compared with test the hypothesis that queens are more tolerant to insecticides relative to workers due to their significantly higher body mass. Control tests for urban colonies consisted of 2 replicates of 5 ants each for workers and 2 replicates of 1 ant each for queens. In contrast to urban colonies which contain multiple gueens, natural colonies are typically single queen which precluded testing on queens (Buczkowski, 2010). Therefore, insecticide susceptibility in natural colonies was tested on workers only (6 replicates of 5 ants each). For all tests, the ants were randomly selected from a stock colony using a toothpick and placed in a small holding cup. The inside of the cup was coated with Fluon to prevent escapes. When all ants needed for the trial were collected, they were gently tapped out of the cup and inside a plastic ring (9 cm diameter) placed on top of the tile. The inner wall of the ring was coated with Fluon to restrict the ants to the treated surface and to prevent escapes. The ants were continuously exposed to the treated tiles. Mortality assessments consisted of the number of ants that were either alive (moving) or dead (no movement when probed). Mortality counts were recorded at different time points depending on the insecticide, with no fewer than 9 time points per insecticide (lambda-cyhalothrin: every 5 min for the first hour, then every 10 min until 170 min; dinotefuran: every 5 min for the first hour, then every 10 min until 140 min; fipronil: every 30 min for 7 h).

2.3 | Data analysis

The median lethal time (LT_{50}) value was calculated for each replicate colony by using the probit analysis in R Development Core Team(2013). A goodness-of-fit test was performed for each probit model. ANOVA analysis (PROC GLM) was performed in SAS 9.4 (SAS 2008). Analysis of variance (ANOVA, PROC GLM) was performed in SAS 9.4 for each insecticide to examine the distribution of LT_{50} values across the different colonies. The ANOVA test was followed

by post-hoc Tukey's HSD tests to separate the means. Pairwise comparisons between workers collected in different habitats (natural workers vs. urban workers) and between castes (urban workers vs. urban queens) were performed using t-tests in Statistica (2017).

3 | RESULTS

All three insecticides resulted in 100% mortality of all colonies. However, T. sessile showed significant regional variation in insecticide susceptibility (Table 1). Workers collected in natural areas showed significant colony variation when exposed to residues of lambdacyhalothrin (mean LT_{50} value =37.2 ± 25.8 min, range: 17.7–92.1 min; ANOVA: F = 16.2, df = 14, p < 0.0001) and fipronil (mean LT₅₀ value =259.5 ± 47.0 min, range: 143.9-318.5 min; ANOVA: F = 10.3, df = 14, p < 0.0001), but not dinote furan (mean LT₅₀ value =18.3 \pm 6.0 min, range: 10.1-35.7 min; ANOVA: F = 1.4, df = 14, p = 0.20). Workers collected in urban areas showed significant colony variation when exposed to lambda-cyhalothrin (mean LT_{50} value =32.5 \pm 8.8 min, range: 21.3-45.9 min; ANOVA: F = 7.3, df = 14, p<0.0001) and fipronil (mean LT₅₀ value =217.1 ± 78.5 min, range: 106.8-333.0 min; ANOVA: F = 75.8, df = 14, p < 0.0001), but not dinotefuran (mean LT₅₀ value =65.9 \pm 6.1 min, range: 56.5-74.5 min; ANOVA: F = 4.3, df = 14, p = 0.07). Significant colony variation to all insecticides was observed in queens collected in urban areas: lambda-cyhalothrin (mean LT_{50} value =78.3 ± 33.0 min, range: 31.2–138.3 min; ANOVA: F = 6.3, df = 12, p < 0.0001), fipronil (mean LT₅₀ value =335.9 \pm 51.5 min, range: 259.1-448.6 min; ANOVA: F = 37.0, df = 12, p < 0.0001) and dinotefuran (mean LT_{50} value =92.6 \pm 33.4 min, range: 44.7–175.3 min; ANOVA: F = 20.3, df = 12, p < 0.0001).

Caste had a significant effect on insecticide susceptibility (Figure 1). Workers collected in urban habitats were significantly less tolerant to all insecticides relative to queens collected in urban habitats: lambda-cyhalothrin (mean LT_{50} value for workers =32.5 min vs. 78.3 min for queens; t-test: t = -4.4, df = 24, p < 0.0001), fipronil (mean LT_{50} value for workers =259.5 min vs. 335.9 min for queens; ttest: t = -4.9, df = 24, p < 0.0001), and dinotefuran (mean LT₅₀ value for workers =18.3 min vs. 92.6 min for queens; t-test: t = 2.9, df = 24, p=0.0008). Habitat type had a significant effect on insecticide susceptibility and workers collected in natural areas were significantly less tolerant relative to workers collected in urban areas when exposed to dinote furan (mean LT_{50} value for natural workers =18.3 min vs. 65.9 min for urban workers; t-test: t = -0.2, df = 28, p < 0.0001), but not lambda-cyhalothrin (mean LT50 value for natural workers =37.2 min vs. 32.5 min for urban workers; t-test: t = 0.7, df = 28, p=0.52) or fipronil (mean LT₅₀ value for natural workers =259.5 min vs. 217.1 min for urban workers; *t*-test: t = 1.8, df = 28, p = 0.08).

4 | DISCUSSION

Tapinoma sessile is one of the most widespread pest ants in North America and ranks as the number one household pest species 4

TABLE 1 Mean LT_{50} values (in min) and 95% confidence intervals for workers and queens of 15 colonies of odorous house ants collected in natural and urban habitats. For each insecticide within each column, LT_{50} means followed by the same letter are not significantly different based on Tukey's HSD test ($p \le 0.05$)

Insecticide	colony	Workers (natural)	Workers (urban)	Queens (urban)
λ-cyhalothrin	1	17.7 (16.3-19.0) e	39.1 (35.3–43.1) ba	not tested
	2	23.5 (19.5-27.5) edc	45.9 (41.3-50.9) a	99.4 (76.8–125.4) b
	3	19.5 (14.4-24.5) e	25.2 (23.4-27.0) bc	62.8 (41.2–58.3) c
	4	20.2 (14.0-26.3) ed	44.2 (37.1-52.2) a	80.4 (65.0-95.0) b
	5	42.7 (38.8-47.2) bdc	23.0 (14.4-31.3) bc	not tested
	6	27.3 (22.9-31.8) edc	30.2 (27.3–33.2) bac	39.7 (28.9–50.0) d
	7	18.3 (15.1-21.3) e	31.7 (26.4–37.3) bac	50.1 (39.8–59.8) c
	8	44.3 (39.5–49.4) bac	45.9 (41.6-50.6) a	123.7 (107.7-139.7) ab
	9	23.5 (18.9–28.2) edc	36.1 (32.8-39.6) bac	78.4 (59.6-97.3) b
	10	21.9 (19.3-24.4) edc	32.5 (29.93–35.2) bac	64.5 (42.3-85.1) c
	11	26.5 (22.5-30.6) edc	21.5 (19.8–23.2) c	110.3 (90.6 -130.9) ab
	12	92.1 (84.9-100.1) a	38.4 (35.9–41.1) ba	138.2 (118.5– 160.5) ab
	13	91.0 (78.2–108.4) a	23.4 (20.9–25.9) bc	49.3 (38.4–59.6) c
	14	21.0 (18.8-23.2) edc	21.3 (20.0–23.0) c	31.2 (24.1-39.3) d
	15	68.0 (59.7–78.1) ba	29.3 (26.7–31.9) bac	90.0 (76.3–103.1) b
Dinotefuran	1	22.0 (19.1–24.7) a	65.2 (30.6-70.1) a	not tested
	2	17.9 (0.4–31.9) a	66.8 (62.5-71.2) a	87.2 (73.3-101.4) bc
	3	14.9 (9.4–19.6) a	74.5 (66.8-83.2) a	61.6 (52.4–71.8) d
	4	10.1 (8.4–11.7) a	61.3 (57.6-65.3) a	75.2 (59.6–93.8) c
	5	20.11 (17.4–22.7) a	74.3 (70.1–78.6) a	not tested
	6	12.01 (8.1–15.5) a	56.5 (53.1–60.2) a	71.3 (59.6-83.7) d
	7	21.5 (19.0–23.8) a	74.3 (69.3–79.5) a	44.7 (37.0-53.4) e
	8	18.9 (16.3–21.4) a	72.8 (67.5–78.4) a	81.9 (69.3-94.5) bc
	9	15.6 (13.1-18.1) a	70.7 (63.4-78.8) a	127.3 (109.4–147.1) b
	10	15.9 (13.3–18.5) a	58.7 (54.9-62.7) a	72.5 (54.1-93.2) d
	11	21.0 (18.3-23.6) a	64.92 (60.5-69.6) a	175.3 (146.7- 236.) a
	12	35.7 (32.5-39.0) a	60.1 (56.2-64.3) a	116.6 (101.5– 131.1) b
	13	20.4 (14.6-26.1) a	60.9 (53.4-69.3) a	106.9 (91.4-112.2) b
	14	14.0 (11.5-16.4) a	62.7 (58.9-66.7) a	91.4 (79.5-102.2) bc
	15	14.2 (11.8–16.6) a	65.3 (60.74-70.2) a	92.1 (79.0–104.5)

TABLE 1 (Continued)

colony

1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

Insecticide

Fipronil

Workers (natural)

235.6 (223.8-247.5) ba

305.3 (261.9-376.9) a

285.1 (274.0-296.6) ba

279.5 (268.3-291.1) ba

143.9 (135.1-152.3) c

274.8 (263.9-286.0) ba

314.0 (303.8-324.4) a

268.6 (249.2-289.4) ba

238.0 (225.7-250.7) ba

300.3 (288.7-312.7) a

318 5 (295 7-348 3) a

208.0 (183.3-231.9) b

259.4 (246.8-272.5) ba

212.9 (201.5-224.0) b

249.3 (237.8-260.9) ba

Workers (urban)	Queens (urban)
262.5 (253.1-272.2) bdc	not tested
275.3 (265.9-284.9) bdac	318.4 (285.6– 351.8) c
333.0 (323.1-342.8) a	378.4 (347.0- 408.2) b
244.5 (223.9-265.5) dc	362.5 (326.5- 401.0) b

not tested

318.0 (281.8-

259.1 (233.8-

382.3 (354.1-408.6) b

372.1 (340.3-402.4) b

312.5 (278.3– 343.8) c 332.4 (300.3–

364.6) bc

277.3 (249.9-305.3) d

448.6 (412.8– 505.9) a 315.6 (284.9–

346.4) c

cd

289.3 (258.7-327.4)

285.2) d

356.4) c

303.5 (291.9-315.9) bac

235.9 (224.4-247.4) d

320.1 (310.0-330.2) ba

288.1 (276.1-300.8) bdac

167.9 (158.9-176.6) fe

177.9 (169.7-185.8) e

139.4 (131.6-146.7) fg

140.5 (131.9-148.6) fg

106.8 (99.0-114.1) h

126.0 (117.4-134.1) gh

134.4 (126.5-141.8) fgh

(Paysen, 2019). Field management of *T. sessile* is achieved mainly by using residual spray insecticides applied as perimeter treatments around structures. However, control failures are common and driven by multiple interacting factors. Results of this study demonstrate significant intraspecific and intercaste variation in insecticide susceptibility within *T. sessile*. Significant variation in insecticide susceptibility was found on a relatively small geographic scale, that is colonies collected within 80 km radius for fipronil and lambda-cyhalothrin, but not dinotefuran. It is likely that variation in insecticides and understanding the sensitivity of different ant colonies or populations will help in making decisions about appropriate chemical control.

Tapinoma sessile is abundant in a wide range of habitats and has a highly flexible social structure depending on habitat type (Buczkowski, 2010; Menke et al., 2010).. This study tested the hypothesis that colonies from natural areas would be less tolerant to insecticides because they are unlikely to have ever been exposed to insecticides, whereas colonies from urban areas would be more tolerant because they are frequently exposed to insecticides. However, no support was found for this hypothesis. Urban and natural colonies showed no significant differences in tests with lambdacyhalothrin and fipronil. In tests with dinotefuran, urban colonies were significantly more tolerant relative to natural colonies, with mean LT_{50} values of 18 \pm 6 and 66 \pm 6 min, respectively. The specific history of insecticide exposure for colonies used in this study is unknown except that most urban colonies have been used by Buczkowski et al. (unpublished data) for a wide range of insecticide efficacy trials between 2004 and 2022, and the majority of colonies have been exposed over multiple years to all insecticides tested in this study and several other insecticides applied in spray and bait form. Results suggest that habitat type and previous exposure to insecticides do not reliably predict susceptibility levels in individual populations. Rather, the results are insecticide and colony specific and may depend on various genetic, biological and other factors. Investigating these possible factors could be a worthwhile focus for future research efforts.

The insecticides evaluated in this study are used widely in the management of various urban pests including ants, bed bugs, cockroaches and termites. In non-social insects such as bed bugs and cockroaches, the widespread use of chemical control measures has resulted in insecticide resistance. Indeed, high levels of resistance to lambda-cyhalothrin, dinotefuran and fipronil have been documented in cockroaches (Gonzales-Morales et al., 2021) and bed bugs (Romero et al., 2007, Romero & Anderson, 2016). Intraspecific variation in insecticide susceptibility is commonly



FIGURE 1 Susceptibility of *T. sessile* workers (black bars) and queens (white bars) collected in urban areas to residual applications of (a) lambda-cyhalothrin, (b) dinotefuran, and (c) fipronil. Bars indicate mean LT_{50} values in minutes and each bar represents a different colony

observed in cockroaches (Fardisi et al., 2017,2019) and bed bugs (Romero & Anderson, 2016; Ashbrook et al., 2017; Gonzales-Morales et al., 2021) and is typically related to strain differences where field-collected strains are resistant and laboratory-reared strains are susceptible. Insecticide resistance in bed bugs and cockroaches often reaches extremely high levels and leads to control failures (Fardisi et al., 2019; Romero et al., 2007). In contrast to non-social insects, insecticide resistance has never been documented in social insects. This is despite widespread, persistent and repeated use of insecticides for the control of ants, termites and other social insects such as wasps (Jiang et al., 2014). It is thought that the unique reproductive biology of social insects (i.e. the caste system), is the main factor responsible for the lack of resistance. Individuals exposed to insecticide treatments are typically workers, which are sterile in most species of ants, and therefore do not pass resistance genes to the next generation. However, due to the possibility of horizontal transfer of insecticides to adult queens and immature queens (i.e. reproductive brood), it is highly plausible that insecticide resistance may act on the queens and lead to heritable changes in sensitivity of colonies.

The hypothesis of proportionality, which states that insecticides affect insects proportionally with their body weight (Robertson & Preisler, 1992), was supported in this study. Queens were significantly more tolerant relative to their worker counterparts across all three insecticides. Relative to workers, queens were 2.4 times more tolerant to lambda-cyhalothrin, 5.1 times more tolerant to dinotefuran and 1.3 times more tolerant to fipronil. Greater insecticide tolerance in the queens may explain why T. sessile is such a persistent pest in urban environments. Liquid spray insecticides applied as perimeter treatments around structures create a barrier that targets mostly foraging workers that trail across the treated areas. Unlike workers, gueens stay in the nest and are not directly exposed. Some mortality in the queens may occur indirectly through horizontal transfer when workers exposed to insecticide treatments return to the nest and share the insecticide with other members of the colony (Buczkowski, 2019; Buczkowski & Wossler, 2019; Soeprono & Rust, 2004). However, the amount of insecticide transferred may not be high enough to cause mortality. Additionally, urban populations of T. sessile are highly polygynous and contain numerous gueens (Buczkowski, 2010; Menke et al., 2010). Lack of direct exposure combined with reduced susceptibility and extreme polygyny may allow the queens to survive insecticide treatments and lead to quick regeneration of worker ants. Previous studies have suggested that the resurgence of polygynous ant colonies treated with baits may be explained by gueen survival resulting from sublethal doses due to a slowing of trophallaxis throughout the colony (Hooper-Bui et al., 2015).

Tapinoma sessile is unique among pest ants for a number of reasons. It has the widest geographic range and greatest ecological tolerance of any ant in North America (Fisher & Cover, 2007). It is highly opportunistic and inhabits a variety of nesting sites in natural and urban areas. In urban areas, T. sessile exhibits supercolony behaviours and becomes a dominant invasive pest (Buczkowski & Bennett, 2006,2008). It is capable of long-distance jump-dispersal and becoming established in areas previously invaded by other invasive ants (Buczkowski and Krushelnycky, 2012). Additionally, T. sessile has low susceptibility to insecticides relative to other pest ants (Buczkowski, 2021). The ability of T. sessile to invade new habitats, form large supercolonies, display elevated insecticide tolerance relative to other ants, display elevated insecticide tolerance in queens relative to workers, and display significant variation in insecticide susceptibility across colonies make T. sessile a strong contender in global invasions. Future studies should monitor both the pest and the invasive status of the species.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

GB designed the research, KB conducted the research, GB and KB analysed the data, wrote and revised the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at Purdue University Research Repository: https://doi.org/10.4231/ Z67M-1J74.

ORCID

Kaitlyn Brill D https://orcid.org/0000-0002-1211-1715 Grzegorz Buczkowski D https://orcid.org/0000-0001-9754-479X

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