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Comparison of Host-Seeking Behavior of the Filth Fly Pupal Parasitoids, *Spalangia cameroni* and *Muscidifurax raptor* (Hymenoptera: Pteromalidae)

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ABSTRACT The pupal parasitoids, *Spalangia cameroni* Perkins and *Muscidifurax raptor* Girault and Sanders, can be purchased for biological control of house flies *Musca domestica* L. and stable flies *Stomoxys calcitrans* (L.) (Diptera: Muscidae). Little is known about the odors involved in host-seeking behavior of these two species, so odors associated with house flies were investigated in the laboratory using a Y-tube olfactometer. Odor stimuli from house fly host puparia, larvae, pine-shavings bedding with horse manure, and developing flies in the pine-shavings-manure substrate were evaluated in bioassays using the two pteromalid species. In choice tests, naïve female *S. cameroni* were strongly attracted to odor from the substrate containing house fly larvae and secondarily from the uninfested substrate and substrate with puparia versus humidified and purified air. This species also selected the substrate with larvae versus the substrate with the house fly puparia or uninfested substrate. *Muscidifurax raptor* was attracted to odor from the substrate containing puparia, washed puparia, and substrate with puparia removed. The data suggest that coexistence between the two pteromalid parasitoids, *S. cameroni* and *M. raptor*, might be promoted by different host-seeking behavior.

KEY WORDS olfactometer, pteromalid, biological control, *Musca domestica*, *Stomoxys calcitrans*

Introduction

Spalangia cameroni Perkins and *Muscidifurax raptor* Girault and Sanders (Hymenoptera: Pteromalidae) are widely distributed filth fly ectoparasitoids (Taylor et al. 2006, Noyes 2014). These two species of pupal parasitoids are commercially available and often sold together to control house flies *Musca domestica* L. and stable flies *Stomoxys calcitrans* (L.), two pests of medical and veterinary importance. Although releases of pteromalid parasitoids as biological control agents for the control of pest muscoid flies associated with livestock have become more common in recent years (U.S. Department of Agriculture [USDA] 2006, Machtinger et al. 2012), their effectiveness has been variable (Meyer et al. 1990, Morgan and Patterson 1990, Geden et al. 1992, Andress and Campbell 1994, Petersen and Cawthra 1995, Weinzierl and Jones 1998, McKay and Galloway 1999, Crespo et al. 2002, Skovgård and Nachman 2004). Inconsistent fly control using pteromalid pupal parasitoids may result partially from an incomplete understanding of their host-seeking behavior. Because *S. cameroni* and *M. raptor* often are released together, comparative studies of the host-seeking behavior of these two parasitoids that share the same habitat could help with understanding their capacity for coexistence and improve their effectiveness in augmentative biological control programs (van Dijken and van Alphen 1998, de Moraes et al. 1999).

Volatile semiochemicals emitted from house and stable fly larval and pupal habitat, fly development stages, or interactions with associated microorganisms may serve as kairomones that attract parasitoids to their hosts (Vinson 1976, 1981, Elzen et al. 1983, Noldus 1988, Godfray 1994, Omacini et al. 2001, Mbata et al. 2004, Schulz and Dickschat 2007). The ephemeral nature and patchy distribution of some habitats of developing filth flies poses a challenge for newly emerged, adult pupal parasitoids to locate hosts. Odors emanating from host habitats can serve as long-range stimuli that are often highly detectable, whereas odors directly from hosts are a more reliable indication of host presence, but are generally less detectable from a distance (Laing 1937, Vet et al. 1991, Voss et al. 2009).

Early studies conducted on the effects of chemical stimuli on host finding in pteromalid filth fly parasitoids has produced inconsistent results. Some species are attracted to host habitat (Laing 1937), but more attracted to a combination of hosts and habitat (Edwards 1954, Wylie 1958, Stafford et al. 1984). Some species seem to use cues directly from the hosts, and host habitat without hosts is repellent (McKay and Broce 2003).

Understanding the host-seeking behavior of *S. cameroni* and *M. raptor* could increase the effectiveness of augmentative biological control programs by improving release and monitoring techniques. Taxonomic genus bias has been recorded with common

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monitoring methods; *Muscidifurax* spp. being recovered more frequently in laboratory-reared sentinel puparia, whereas *Spalangia* spp. are more abundant in wild-collected puparia (Petersen and Watson 1992). Analysis of odor-mediated behavior associated with host location could lead to monitoring strategies that are tailored to each parasitoid.

This study was focused on the responses of female *S. cameroni* and *M. raptor* to odors associated with developing hosts in an equine-generated substrate. Responses to odors of hosts as larvae or pupae with and without development substrate were tested in a Y-tube olfactometer.

Materials and Methods

House Fly and Parasitoid Rearing. House flies were obtained from a colony maintained at the USDA-ARS, Center for Medical, Agriculture and Veterinary Entomology (CMAVE) and reared as described in Machtinger and Geden (2013). Parasitoids used for this study were from colonies of *S. cameroni* and *M. raptor* established in 2012 from a source population on a dairy in Gilchrist County, FL. Colony maintenance consisted of providing parasitoids with 2-d-old house fly pupae as hosts at a host: parasitoid ratio of 5:1 twice weekly in 17.5 × 17.5 × 17.5-cm Bug Dorms (MegaView Science, Taiwan) held at 25°C and 80% relative humidity (RH) under constant light.

Experimental Substrates. The substrate used for the choice tests was 3-d-old pine shavings bedding (0.1–0.3-cm long) mixed with horse manure and urine. Both *S. cameroni* and *M. raptor* locate hosts in this medium (Pitzer et al. 2011, Machtinger and Geden 2013). The substrate was collected from a private equine facility in Reddick, FL. Shavings and manure were collected separately and frozen at −20°C for a minimum of 1 wk prior to testing to kill any existing arthropods. A standardized amount of substrate was used for each treatment (20 g total, 15 g of horse manure and 5 g pine shavings). This substrate was placed in a 5.5-oz plastic cup measuring 6 cm in height × 7.5 cm in diameter, hydrated to 70% by weight (Machtinger 2011), and mixed thoroughly. For a treatment with developing house flies, 30 eggs were applied to a moistened cloth placed on the surface of the substrate (Machtinger 2011). Substrate was also tested without developing fly larvae and puparia. Cups were covered with muslin, sealed with plastic rim lids, and maintained at 27°C and 80% RH under constant light. The entire contents of each cup were used only once for each test.

By random assignment, a variety of odor stimuli were presented in choice tests to both *S. cameroni* and *M. raptor*. The following odor treatments were tested at 4 d after initial set up in the cups: 1) substrate without developing house flies (uninfested substrate), 2) substrate with larvae that had developed from eggs to third instar (substrate with larvae), and 3) substrate in which the larvae had developed to third instar but were removed (substrate, larvae removed). Additionally, odor treatments were conducted with house fly puparia at 8 d after cup establishment, including substrate with house flies that had developed from eggs to puparia (substrate with puparia) and substrate in which house flies had developed to puparia but the puparia were removed (substrate, puparia removed). Larvae (washed larvae) and puparia (washed puparia) tested separately from substrate were removed from their respective substrates the morning of each bioassay. Individual larvae or pupae were rinsed twice with distilled water and air dried a minimum of 1 h prior to testing.

Substrate Bioassays. Bioassays were conducted at the USDA-ARS, CMAVE in an isolated laboratory illuminated with a 13 w CFL red light (195 lumens). They were performed using a glass Y-tube olfactometer constructed with a 16-cm-long central arm that was connected to two 8.5-cm-long lateral arms. The central and lateral arms were 2 cm in diameter. A removable 8-cm-long glass adaptor was inserted into each of the lateral arms and caped with 100-mesh plastic screen to prevent parasitoids from accessing the odor sources. Each glass adaptor was connected with Teflon tubing to a 35-cm-long × 4-cm-diameter glass chamber used to hold odor treatments for testing. Compressed air was humidified and purified with charcoal using a 2-port humidity and air delivery system (Model # OLFM-HAPS-ZAFMIC, Analytical Research Service, Inc., Gainesville, FL). In preliminary tests, the two parasitoid species differed in behavior movement with varying airspeed, so airflow was optimized for each species using a flowmeter set at 200 ml/min for *S. cameroni* and 130 ml/min for *M. raptor* (McKay and Broce 2003). The olfactometer was placed in a 47.5 × 47.5 × 47.5-cm^3 Bug Dorm (MegaView Science, Taiwan) with nylon (150 mesh) sides. The bug dorm sides were covered with black plastic to eliminate lateral light from the test area.

Parasitoids were standardized according to the protocol established by Mandeville and Mullens (1990). Male and female parasitoids were held in a 17.5 × 17.5 × 17.5-cm^3 bug dorm without hosts and provided with a 10% sucrose solution for 24 h prior to the bioassays. *S. cameroni* is autogenous, emerging with fully developed eggs (Gerling and Legner 1968, Morgan et al. 1989, King and King 1994), and disperses quickly after emerging (King 1990), so was tested at 1 d old. In preliminary tests, *M. raptor* required an additional 48 h before responding to odor treatments, so this species was held in the same conditions but tested at 3 d old. Both species were held in the bioassay room at 25°C and 80% RH in normal room light during the holding period.

Females were separated from males by immobilizing groups on a cooling table the morning of the bioassay and placing them in individual size 00 gelatin capsules. Individual capsules were opened and the parasitoids transferred to a 7-cm- × 1.5-cm-diameter tubular glass inlet adaptor to serve as a release chamber. The open end of the adaptor was covered with parafilm, and the parasitoid was given a minimum of 5 min to acclimate to the chamber to avoid an escape response. The chamber containing the wasp then was attached to the olfactometer with established airflow. The Y-tube was

positioned horizontally for *S. cameroni* but vertically for *M. raptor* because this species was more responsive with the vertical orientation and tested for 5 min. Parasitoids were scored as making a choice when they remained beyond a mark located 2 cm from the end of the Y-tube for 15 consecutive seconds. The latency time from initiation of the replicate to the parasitoid making a choice was recorded. If a parasitoid failed to make a choice within 5 min, it was removed and recorded as no choice. Tests were continued until 10 parasitoids made a choice for every treatment. Parasitoids that did not make a choice, varying between one and three parasitoids per odor treatment, were not included in the analysis. To ensure that wasps had no bias in movement toward either arm, the Y-tube was flipped for every other female. After each replicate, the olfactometer and associated glassware were washed thoroughly with water, rinsed with acetone, and allowed to dry for a minimum of 1 h before reuse (McKay and Broce 2003). Ten parasitoids were tested individually for each odor source in one arm of the Y-tube and clean air or another odor source in the other arm. Each odor test was replicated 10 times (total parasitoids, $n = 100$), each using a different generation of parasitoids.

Statistical Analysis. Odor treatments were tested in random order once to complete a block for each replication and tests conducted on different days. All odor treatments were randomly tested. Ten odor treatment combinations were shared between *S. cameroni* and *M. raptor*. Additional odor sources were tested for each individual species to further verify preferences. Initial analysis of treatment blocks (responses to individual odor sources) did not reveal replication effects, so data were pooled for each treatment. A chi-square goodness-of-fit test was used to determine conspecific differences in choice between odor sources. The responses to odors were compared between species using Fisher's exact test (FET). To analyze the response time of females to a given odor stimulus, data were subjected to a one-way ANOVA and presented means were separated within species using Tukey's HSD. Time data were subjected to log transformations for statistical analysis and back transformed for presentation in Table 2. In all cases, the level of significance testing was $\alpha = 0.05$. Statistical analysis was performed using JMP (v. 11, SAS Institute, Cary, NC.).

Results

Given a choice, the two pteromalid species, *S. cameroni* and *M. raptor*, selected different combinations of house fly larval substrate with and without fly larvae or puparia versus hydrated and purified clean air (Fig. 1). A highly significant number of *S. cameroni* moved toward the Y-tube arm with substrate containing house fly larvae versus clean air (Chi-square test: $\chi^2 = 43.56$, $P = < 0.0001$) but the parasitoid also was attracted to uninfested substrate ($\chi^2 = 6.76$, $P = 0.0093$), substrate with puparia ($\chi^2 = 6.76$, $P = 0.0093$), and substrate with puparia removed ($\chi^2 = 12.96$, $P = 0.0003$) versus clean air. *S. cameroni* did not differentiate between the washed larvae, washed puparia, and the substrate with puparia removed versus the clean air. Unlike *S. cameroni, M. raptor* did not distinguish between the substrate with larvae and the clean air control ($P = 0.0001$; FET). Similarly, *M. raptor* did not distinguish between the substrate and clean air control, but this species was attracted to the substrate with puparia over clean air ($\chi^2 = 11.56$, $P = 0.0007$). A significant number of *M. raptor* selected washed puparia ($\chi^2 = 5.76$, $P = 0.0164$), and substrate with the puparia removed ($\chi^2 = 4.00$, $P = 0.0455$) versus clean air.

When odor treatments were compared against other odors, *S. cameroni* and *M. raptor* responded differently to shared treatments. Similar to the behavior exhibited against clean air, *S. cameroni* was significantly attracted to the substrate with larvae over the substrate with puparia ($\chi^2 = 11.56$, $P = 0.0007$), the washed larvae over the washed puparia ($\chi^2 = 4.84$, $P = 0.0278$), and the substrate with larvae over the uninfested substrate ($\chi^2 = 4.00$, $P = 0.0455$). *M. raptor* was more attracted to the substrate with puparia than the substrate with larvae ($\chi^2 = 4.00$, $P = 0.0455$), the washed puparia over the washed larvae ($\chi^2 = 4.84$, $P = 0.0278$), and the uninfested substrate over the substrate with larvae ($\chi^2 = 4.00$, $P = 0.0455$). All of these comparisons were significantly different between species (substrate with larvae vs. substrate with puparia: $P = 0.0002$, FET; washed larvae vs. washed puparia: $P = 0.0028$, FET; substrate with larvae vs. substrate: $P = 0.0071$, FET).

Additional choice tests were conducted to verify the preference for house fly larval substrate by *S. cameroni* and for puparia by *M. raptor* (Table 1). The number of *S. cameroni* that moved toward the substrate with developing larvae removed was significantly greater than to clean air or washed larvae. Female parasitoids did not differentiate between the substrate with larvae and the substrate with larvae removed or between the uninfested substrate and washed larvae. For *M. raptor*, preferences were shown for washed puparia versus substrate containing larvae or substrate with puparia removed, and for substrate with puparia versus uninfested substrate.

The response latency time was varied between treatments for *S. cameroni* ($F = 2.20$; df = 9, 90; $P = 0.0292$); however, *M. raptor* was consistent across all odor tests (Table 2). The response time of *S. cameroni* to washed puparia versus clean air was significantly slower than the other odors, but this species responded most rapidly to the uninfested substrate versus substrate with larvae. *M. raptor* responded slowest to the substrate with larvae versus clean air and most rapidly to substrate with puparia removed or substrate that contained puparia versus clean air, although there were no statistically significant differences between odor tests for this species.

Discussion

This study showed that *S. cameroni* and *M. raptor* differed substantially in their responses to odors from house fly hosts and substrates associated with developing larvae and puparia. Although these two species

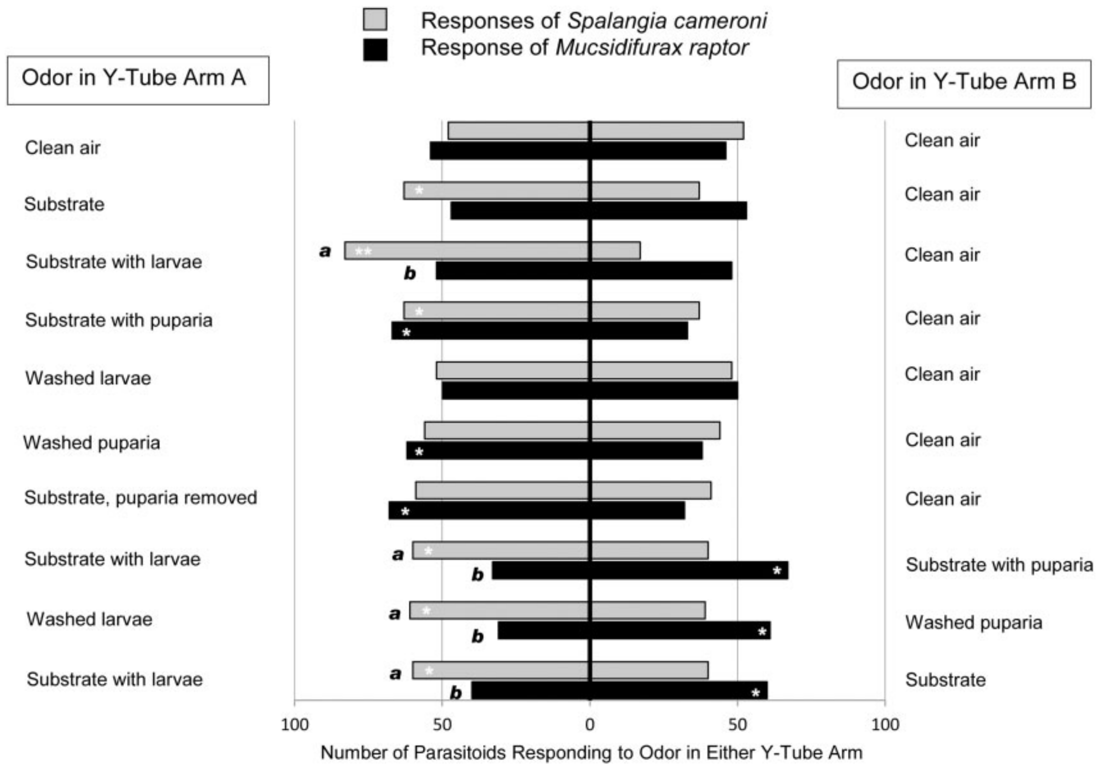

Fig. 1. Number of *S. cameroni* or *M. raptor* that responded in separate choice tests to odors from combinations of house fly larval substrate with and without fly larvae or puparia, or to clean air. The substrate consisted of 30 g of 3-d-old pine shavings mixed with equine manure and urine. The horizontal bars show the number of wasps that choose either odor source within 5 min from the start of the test. Asterisks indicate significant differences within a choice test: χ^2 test where $*P \leq 0.05$, $**P \leq 0.001$. Letters denote significant differences in the number of the two species of parasitoids that responded to a specific odor combination (Fisher's exact test, $P \leq 0.05$, $N = 100$, 10 parasitoids × 10 replicates).

Table 1. Number of *S. cameroni* and *M. raptor* that made a choice to odor emitted from a substrate consisting of 3-d-old pine shavings mixed with equine manure and urine only or used to rear house fly larvae and pupae, or washed larvae or pupae

Parasitoid Species	Odor in Y-Tube Arm A[a]	N	Odor in Y-Tube Arm B[b]	N	χ^2	P[c]
S. cameroni[d]	Substrate, larvae removed	80	Clean air	20	36.00	<0.0001**
	Substrate, larvae removed	70	Washed larvae	30	16.00	<0.0001**
	Substrate with larvae	57	Substrate, larvae removed	43	1.96	0.5485
	Substrate	57	Washed larvae	43	1.96	0.5485
M. raptor[d]	Substrate with larvae	36	Washed puparia	64	7.84	0.0051*
	Substrate with puparia	63	Substrate	37	6.76	0.0093*
	Substrate, puparia removed	40	Washed puparia	60	4.00	0.0455*

[a] Odor treatments and substrate collection as described in depth in the methods.
[b] Clean air was humidified and purified.
[c] Asterisks indicate significant differences within a choice test: χ^2 test where $*P \leq 0.05$, $**P \leq 0.001$ ($N = 100$, 10 parasitoids × 10 replicates).
[d] Colonies of *S. cameroni* and *M. raptor* established in 2012 were used in bioassays.

share some of the same habitats, their coexistence may rely on differences in host-seeking and relatively plastic foraging behavior (Vet et al. 1993, Wiskerke and Vet 1994, Geervliet et al. 1996, Cortesero et al. 1997, Harvey et al. 2013). *S. cameroni* was most attracted to odor stimuli originating from substrate and substrate with interactions with larvae, while *M. raptor* preferred odor associated with host puparia.

S. cameroni and *M. raptor* use many of the same habitats and hosts, but differences in life history and behavior, such as ovarian development, adult dispersal, and host seeking, enable them to coexist. *S. cameroni* was highly attracted to odor from substrates containing larvae. Similar positive responses to larvae in dry cattle manure over manure alone were observed with *S. endius* (Stafford et al. 1984), although the level of responsiveness depends on larval concentration. *S. cameroni* emerges as an adult with mature eggs and both males and females disperse rapidly in the laboratory, leaving the site of emergence within 3 h

Table 2. Latency (seconds to choice) of *S. cameroni* and *M. raptor* that made a choice to odors emitted from a substrate consisting of 3-d-old pine shavings mixed with equine manure and urine only or used to rear house fly larvae and pupae, or washed larvae or pupae

Odor in Y-Tube Arm A[a]	Odor in Y-Tube Arm B[b]	*S. cameroni*[c] time to response (s) Mean ± SE[d]	*M. raptor*[c] time to response (s) Mean ± SE[d]
Clean air	Clean air	83.18 ± 1.14ab	72.44 ± 1.18a
Substrate	Clean air	89.13 ± 1.17ab	66.07 ± 1.17a
Substrate with larvae	Clean air	83.18 ± 1.10ab	102.33 ± 1.12a
Substrate with puparia	Clean air	93.33 ± 1.09ab	66.07 ± 1.13a
Washed larvae	Clean air	107.15 ± 1.06ab	91.20 ± 1.10a
Washed puparia	Clean air	112.20 ± 1.09a	74.13 ± 1.16a
Substrate, puparia removed	Clean air	91.20 ± 1.10ab	58.88 ± 1.14a
Substrate with larvae	Substrate with puparia	79.43 ± 1.09ab	87.09 ± 1.21a
Washed larvae	Washed puparia	102.33 ± 1.09ab	69.18 ± 1.16a
Substrate	Substrate with larvae	70.79 ± 1.08b	89.13 ± 1.11a
Mean latency across all odor treatments (s)		90.37 ± 1.03	77.09 ± 1.04

[a] Odor treatments and substrate collection as described in depth in the methods.
[b] Clean air was humidified and purified.
[c] Colonies of *S. cameroni* and *M. raptor* established in 2012 were used in bioassays.
[d] Means in a column followed by the same letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$).

(Myint and Walter 1990). Additionally, *S. cameroni* prefers to oviposit on young hosts, less than 24 h old (King 1997). Because it is autogenous, *S. cameroni* does not need to immediately locate host puparia and host-feed before ovipositing. Likely females can disperse quickly from emergence sites to habitats with developing larvae, ensuring the detection of newly pupariated hosts. *Spalangia* spp. are flexible in locating puparia within their habitats, parasitizing hosts at depths up to 10 cm (Rueda and Axtell 1985, Geden 2002). After locating the appropriate habitat, *S. cameroni* may encounter close-range or contact chemicals that expose newly formed puparia.

Unlike *S. cameroni,* the dispersal behavior of *M. raptor* after emergence is not known. The bioassays suggested that this species requires a short latency period before responding to odors, preferring odors associated with the puparia. The primary attraction to host puparia was observed with another *Muscidifurax* spp., *Mucidifurax zaraptor* Kogan and Legner (McKay and Broce 2003). *M. zaraptor* is somewhat repelled by fresh and aged poultry manure alone but strongly attracted to host puparia. Both *M. zaraptor* and *M. raptor* parasitize older hosts than *S. cameroni* (Mandeville et al. 1988; King 1997). Moreover, *Muscidifurax* spp. primarily parasitize puparia near the substrate surface (Legner 1977) and generally search only within 3 cm from the surface of the host habitat (Rueda and Axtell 1985, Geden 2002). Perhaps *Muscidifurax* spp. have evolved the ability to locate hosts based on specific odors and the flexibility to parasitize puparia of different ages.

Both *S. cameroni* and *M. raptor* had the strongest responses to odor produced either directly or indirectly by the developing hosts. *S. cameroni* was not attracted to odor produced by washed puparia or washed larvae against clean air, but was highly attracted to odor from the substrate containing larvae. Additionally, this species did not differentiate between the substrate with the larvae and the substrate after the larvae were removed, suggesting that the attractant was some interaction between the developing larvae and the substrate. Kairomones produced by bacteria and fungi have been documented as attractants for several species of parasitoids (Davis et al. 2013). It is not known if *S. cameroni* responds to volatile compounds emitted from larval frass or microbial activity associated with fly larvae; however, fungal volatiles have been found to be important for host location by several other species of pteromalids. Examples include the parasitoid of stored product pests *Lariophagus distinguendus* Forster (Steidle and Scholler 1997, 2002) and the bark beetle parasitoids *Rhopalicus pulchripennis* (Crawford) and *Heydenia unica* Cook and Davis (Steiner et al. 2007, Boone et al. 2008). In the absence of substrate with larvae, *S. cameroni* was attracted to uninfested substrate, whereas *M. raptor* was not, suggesting that there is some odor stimulus from the substrate alone. *S. cameroni* may be more adaptable than *M. raptor* in responding to odors but is most responsive to substrates that contain or previously contained developing larvae. Short- and long-range attraction to odors associated with hosts may be different for these two species of parasitoids.

Filth fly augmentative biological control programs will be more effective if the existing and released pteromalid parasitoids and their hosts can be monitored accurately and efficiently. Currently, parasitoid monitoring is conducted using laboratory-reared sentinel or wild-type collected puparia, but bias by host genera has been observed with *Muscidifurax* spp. being recovered more frequently from the sentinel puparia and *Spalangia* spp. from wild-type puparia (Petersen and Watson 1992). These field observations are consistent with the current study in which *M. raptor* was attracted to laboratory-reared puparia and substrates containing these puparia. When laboratory-reared puparia are placed in the field, they may be more attractive to *M. raptor,* whereas *S. cameroni* may only parasitize them by chance, unless they are placed near developing larvae. Although both *S. cameroni* and *M. raptor* oviposit on house fly puparia, monitoring techniques should

integrate host puparia as well as developing larvae in substrate to recover the widest range of parasitoids.

Previous work examining competition between *Muscidifurax* spp. and *Spalangia* spp. has suggested that releases of these two taxanomic genera together may be beneficial and provide more control than a single species release (Rueda and Axtell 1985, Skovgård 2006). In some cases, biological control studies with introductions of multiple control agents have shown that often only a single agent is responsible for the control success (Myers et al. 1989, Denoth et al. 2002), likely because using multiple biological control agents has the potential to reduce the likelihood of control success through competitive exclusion (Ehler and Hall 1982). However, because of the complement of spatial separation in host seeking depth, age discrimination of pupal parasitization, and apparent differential host-seeking behavior, resource partitioning between these two species suggests that release in conjunction may provide cumulative control benefits. Fly control has been achieved by releasing both *Muscidifurax* spp. and *S. cameroni* (Geden and Hogsette 2006, Skovgård 2006, McKay et al. 2007). However, in all cases sentinel puparia alone were used to monitor parasitization, and control success was not measured against facilities with single-species releases. Further field studies are needed to assess the benefit of multiple-genera release of pupal parasitoids for filth fly control.

This study demonstrated that the two pupal parasitoid species, *S. cameroni* and *M. raptor*, use different strategies for host-seeking that may allow them to coexist in house fly habitats. Also, the negative effects of competition between these parasitoids might be mitigated by differences in their host utilization (Chesson 2000). Confirmation of the sources and identification of the volatile chemicals emanating from the developmental substrates, house fly larvae and puparia, or associated microorganisms that are involved in host-location by *S. cameroni* and *M. raptor* and further field studies assessing the benefit of multiple-genera releases should be explored to improve biological control using these parasitoids.

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