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CHEMICALLY MEDIATED ARRESTMENT OF THE PREDACEOUS MITE *PHYTOSEIULUS PERSIMILIS* BY EXTRACTS OF *TETRANYCHUS EVANSI* AND *TETRANYCHUS URTICAE*

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ABSTRACT

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Since *Tetranychus evansi* Baker and Pritchard had been observed to be unfavorable prey for several species of phytoseiid mite predators, a study was conducted to determine the possible existence of an allomone produced by this species against *Phytoseiulus persimilis* Athias-Henriot. Instead, *P. persimilis* was strongly arrested by extracts of eggs, adults and, especially, webbing plus excreta of *T. evansi*. Methanol extracts of *Tetranychus urticae* (Koch) showed a stronger arrestment than extracts of *T. evansi*.

INTRODUCTION

Tetranychus evansi Baker and Pritchard (Acarina: Tetranychidae) was originally described from specimens collected in Mauritius Island (Moutia, 1958), and later reported from the U.S.A. (Oatman et al., 1967), Brazil (Flechtmann and Baker, 1970), Islands of Seychelles, Rodriguez and Reunion (Gutierrez, 1974 and pers. commun., 1980), Puerto Rico (Medina Gaud and Garcia Tuduri, 1977) and Zimbabwe (Blair, pers. commun., 1983). It occurs mainly on wild and cultivated Solanacae, and frequently causes severe damage to these plants.

T. evansi has been reported to be affected by a pathogen and some species of predaceous insects (Moutia, 1958; Humber et al., 1981; Moraes et al., 1984). There are only two reports of phytoseiid mites associated with *T. evansi* and no indications that these predators significantly reduced its populations (Moutia, 1958; Moraes and McMurtry, 1983). In southern California and northeastern Brazil, the highest population levels of *T. evansi* occur during the dry, hot season, when fewest predators are associated with it.

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Phytoseiulus persimilis Athias-Henriot (Acarina: Phytoseiidae) has been reported to prefer species of tetranychid mite prey that produce copious amounts of webbing, especially *Tetranychus* spp. (McMurtry et al., 1970; Sabelis, 1981). Webbing probably acts as a physical arrestant for the predator. However, chemicals are also probably involved in this preference. Kairomones (Brown et al., 1970) produced by some tetranychids were reported by Sabelis and Van de Baan (1983) and Sabelis et al. (1984) to attract *P. persimilis*.

An organism may also produce compounds that act as allomones (Brown, 1968) which repel different organisms, e.g., potential predators (Fraenkel, 1959). It is also possible that in some cases there is no chemical communication between an organism and its potential predator.

Moraes and McMurtry (unpublished) conducted laboratory experiments to evaluate the oviposition rates of eight species of phytoseiid mites when offered *T. evansi* as prey. All of those species, including *P. persimilis*, had low oviposition and survivorship rates on *T. evansi*. The present study was conducted to determine whether an allomone is responsible for *T. evansi* being an unfavorable prey for *P. persimilis*, or whether no chemical communication exists between these two species. *Tetranychus urticae* (Koch) was also included in this study for comparison, as this prey species was shown by Sabelis and Van de Baan (1983) and Sabelis et al. (1984) to attract adult females of *P. persimilis*.

MATERIALS AND METHODS

Experiments were conducted in a laboratory at 25±3°C and 50±10% RH.

Stock colonies

T. evansi was collected from nightshade (*Solanum douglasii* Dunal) on the campus of the University of California, Riverside, during the course of the experiment. *T. urticae* was taken from a stock colony maintained on bean plants (*Phaseolus vulgaris* L.) for about one year. *P. persimilis* was taken from a stock colony reared on *Tetranychus pacificus* McGregor for about two years. This colony was started from individuals collected on strawberry, in Ventura County, California.

Extraction of the chemical cues

Some of the tests used extracts obtained from 2.0 × 2.0 cm pieces of leaves held on wet foam mats in stainless steel pans and infested with *T. evansi* or *T. urticae* for 48 h. In initial tests, the leaf pieces were infested with 60 females of either species. In all other tests, the leaves were infested with 200 females. In tests to evaluate the effect of the mechanical damage inflicted by the *Tetranychus* mites, leaves of the same dimensions, having

no prey, but punctured 800 times with a fine probe to simulate mite damage, were extracted. It is realized that this procedure only roughly mimics the real damage caused by the multiple insertions of the minute mite chelicerae.

Different concentrations of extracts of each stage of *T. evansi* and its webbing plus excreta were also tested. One to two-day-old eggs were first gently brushed free from the surrounding webbing and excreta and then collected for extraction. In one test, the eggs collected were squashed with a probe before extraction. Other stages or webbing and associated excreta were extracted after collection from the infested leaf pieces with a brush.

Extractions were done in 1.0 ml of either methanol, ethanol or water. The material was submerged for 4 min in either methanol or ethanol, and for 3 h in water. Immersion in the alcohols was brief to lessen the chances that these solvents might extract chemicals from inside the organisms, that would not be present externally under natural conditions but might alter the responses of the predators. Unless otherwise specified, the solvent used in these tests was methanol. When the material undergoing extraction consisted of webbing and excreta, the extract was centrifuged at 10 000 rpm for 3 min.

In addition, four choice tests were conducted to compare the response of *P. persimilis* to discs treated with extracts of either *T. evansi* or *T. urticae*, when both discs were placed on the same test arena. In the first two of these tests, whole leaves containing adults, eggs, webbing and excreta were extracted. In the third test, females, eggs and all the webbing and associated excreta that could be collected with a brush from the leaf pieces were extracted. In the fourth test, webbing and excreta were extracted at a concentration of 375 μg (fresh weight) per ml solvent.

Bioassay procedure

All tests were conducted by confining the predaceous mites in arenas of 4.0 × 4.0 cm pieces of bean leaves surrounded by a 0.5-cm wide strip of Cellucotton®. These arenas were placed on wet foam mats in stainless steel pans.

The bioassay used was based on the tendency of *P. persimilis* to rest under some obstacle when confined on various substrates in the laboratory. Filter paper discs (Whatman No. 1) 1.2 cm in diameter were impregnated with extracts of material suspected to contain the chemical cue, or with pure solvent. In the initial tests, impregnation involved submerging the discs in the extracts or solvents, whereas in all other tests, each disc received 20 μl of extract or solvent applied with a microsyringe. The discs were allowed to air-dry for ca. 40 min and then a treated and a control disc were placed in each arena in the center of two of its diagonally opposed quarters. In the comparative tests with *T. evansi* and *T. urticae*, one of

the two discs in the arena was treated with the extract of one species, and the other disc with extract of the other species. Ten well fed adult female *P. persimilis* were then put in each arena in order to determine whether they showed any preference for one of the paper discs under which to rest.

During the first few hours, it was observed that the predators walked randomly over the arenas, and some moved onto the wet foam mats. Therefore, the arenas were checked 2 h after introducing the predators and any females that had escaped were replaced. Counts of the females under each disc were made 5 and 8 h after the experiment was initiated. In some tests, the predators were left on the arenas for 24 h, after which the eggs under each disc were counted.

RESULTS

Initial tests

There were significantly more adult female *P. persimilis* under discs treated with extracts of leaves infested with either *T. evansi* or *T.urticae* than under the discs treated with only methanol at both the 5 and 8 h counts (Table 1). These results indicate that at least one of the components of the leaves infested with either tetranychid species contained one or more chemicals that arrested the predator. Also, considerably more predators were found under the discs treated with extracts of leaves with either of the two tetranychids than under those treated with an extract of leaves alone (Table 1). There was no indication that extracts of undamaged nightshade or bean leaves influenced the predators under the experimental conditions. There was a significantly larger number of predators under the discs treated with extracts of bean leaves mechanically damaged with a probe to simulate mite damage, compared to extracts of undamaged bean leaves at the 5 h count, but not at the 8 h count (Table 1). This result suggests that mechanical damage inflicted to bean leaves by the tetranychids may induce a positive response by the predator. However, there was no significant difference between the number of predators under discs treated with extracts of damaged and undamaged nightshade leaves. Therefore, it was assumed that other factor(s) responsible for the arrestment of *P. persimilis* could also be present either on the mites themselves or on their webbing or excreta. This assumption was supported by the positive response of the predators to discs treated with extract of a combination of females, eggs, webbing and excreta of *T. evansi* (Table 1). *P.persimilis* also showed a positive response to extracts of 300 adult female *T. evansi* in 1.0 ml of methanol or water, and to the methanol extract of webbing plus excreta produced by 300 female *T. evansi* in 24 h.

There were no significant differences between the number of predators under control discs and discs submerged in the extracts of 500 whole eggs

TABLE 1

Phytoseiulus persimilis females and eggs under filter paper discs treated with different extracts, as compared to controls (mean number under treated : mean number under control discs)

Material extracted[1] : control	Number of replicates	Females 5 h	Females 8 h	Eggs 24 h
T. evansi on nightshade : methanol	15	5.1 : 2.3**	5.7 : 2.1**	4.9 : 3.5
T. urticae on bean : methanol	15	6.0 : 1.3**	5.3 : 1.4**	7.2 : 1.6**
T. evansi on nightshade : nightshade	20	6.6 : 3.4**	7.0 : 2.8**	6.3 : 2.4**
T. urticae on bean : bean	20	6.8 : 2.1**	7.5 : 1.6**	10.0 : 2.5**
Undamaged nightshade : methanol	10	2.4 : 2.6	3.5 : 2.7	—
Undamaged bean : methanol	10	2.4 : 2.5	2.7 : 3.9	—
Damaged nightshade[2] : undamaged nightshade	20	2.4 : 2.6	2.3 : 2.7	—
Damaged bean[2] : undamaged bean	20	3.9 : 2.2**	3.6 : 2.7	—
Females, eggs, webbing, excreta : methanol	10	7.6 : 1.6**	8.7 : 1.2**	15.6 : 2.5**
300 females : methanol	10	7.9 : 2.2**	8.3 : 2.0**	8.7 : 1.9**
300 females : water	20	5.6 : 2.2**	6.2 : 2.1**	7.5 : 3.7**
500 whole eggs : methanol	10	4.9 : 4.5	6.0 : 3.8	7.3 : 5.1
1000 whole eggs methanol	10	6.1 : 3.5**	5.7 : 3.9	11.8 : 4.9**
1000 squashed eggs : methanol	10	4.5 : 1.6**	5.2 : 1.4**	6.2 : 1.8**
Webbing, excreta[3] : methanol	10	4.4 : 0.9**	8.0 : 0.9**	11.5 : 2.5**

[1]Extracted in same solvent as control. If not specified, solvent was methanol and prey species, *T. evansi.*
[2]Leaves punctured 800 times with a probe.
[3]Produced by 300 females in 24 h.
**= $P < 0.01$, Chi-square test for each ratio; — = eggs not recorded.

of *T. evansi*. However, significantly larger numbers of mites were found under discs treated with extract of 1000 whole eggs at the 5 h count, and 1000 squashed eggs at both the 5 h and the 8 h count.

In most tests where oviposition of *P. persimilis* was evaluated, significantly more eggs were laid under the treated discs. The exceptions were the tests comparing the extract of nightshade leaf infested with *T. evansi* to methanol and the extract of 500 whole eggs of *T. evansi* to methanol.

TABLE 2

Phytoseiulus persimilis females and eggs under filter paper discs treated with different extracts of *Tetranychus evansi* compared to control discs[1] (mean number under treated : mean number under control discs)

Treatment	Concentration[2]	Number of replicates	Females		Eggs
			5 h	8 h	24 h
Egg	1.0	10	4.4 : 4.0	5.3 : 4.2	—
	14.0	10	5.2 : 3.2	5.9 : 3.3*	—
	27.0	20	5.1 : 2.9**	5.9 : 2.9**	—
	40.0	20	5.3 : 3.4**	5.5 : 3.5**	—
Larva	3.0	10	4.7 : 3.5	5.6 : 4.2	—
	6.0	10	4.8 : 3.7	5.1 : 3.4	—
	9.0	10	4.6 : 3.4	4.8 : 4.4	—
	12.0	10	3.7 : 4.2	5.1 : 4.2	—
Protonymph	3.0	10	2.3 : 1.7	3.9 : 3.1	—
	6.0	10	2.4 : 2.7	5.4 : 3.4	—
	9.0	10	2.7 : 3.3	3.2 : 4.6	—
	12.0	10	4.9 : 3.7	5.8 : 4.0	—
Deutonymph	3.0	10	3.0 : 2.9	3.3 : 5.1	—
	6.0	10	5.7 : 3.0**	4.6 : 4.6	—
	9.0	10	3.9 : 3.4	4.2 : 4.1	—
	12.0	10	4.9 : 4.1	5.6 : 4.2	—
Male	3.0	20	2.5 : 2.9	2.2 : 1.5	—
	6.0	20	2.2 : 1.7	2.2 : 2.5	—
	9.0	20	3.0 : 2.7	2.2 : 2.4	—
	12.0	20	2.7 : 2.4	3.0 : 1.9	—
Female	1.0	20	4.3 : 2.8*	5.2 : 3.5**	—
	4.7	20	5.4 : 3.1**	5.7 : 3.4**	—
	8.3	20	5.0 : 2.7**	5.5 : 3.5**	—
	12.0	20	4.9 : 2.2**	5.9 : 3.1**	—
	12.0[3]	20	5.4 : 2.8**	6.5 : 2.5**	—
	12.0[4]	20	5.5 : 3.0**	5.5 : 3.5**	—
	12.0[5]	20	4.7 : 4.0	3.9 : 4.9	—
Webbing + Excreta	4.7	10	7.2 : 1.4**	7.4 : 1.7**	10.4 : 2.8**
	9.5	10	6.3 : 1.6**	7.0 : 2.2**	6.2 : 1.7**
	14.2	10	8.0 : 1.5**	6.7 : 1.2**	7.8 : 5.0*
	18.9	10	7.3 : 2.3**	7.9 : 1.7**	12.3 : 2.7**
	18.9[3]	20	5.4 : 2.0**	6.4 : 2.1**	—
	18.9[4]	20	6.0 : 2.1**	6.6 : 2.4**	—
	18.9[5]	20	6.9 : 2.5**	6.5 : 2.9**	—

Unless otherwise specified, solvent was methanol.

[1]Control = discs receiving 20 μl of same solvent as correspondending treated discs.

[2]Concentration = number of prey-equivalent/disc or μg-equivalent (webbing + excreta) per disc.

[3]Solvent = ethanol.

[4]Solvent = water.

[5]Treated and control (methanol) discs left on a hot plate (50—60°C) for 48 h beforehand.

* = $P < 0.5$, ** = $P < 0.1$, Chi-square test for each ratio; — = eggs not recorded.

Extractions of different life stages at various concentrations

P. persimilis did not show any significant preference for discs treated with extracts of larvae, protonymphs, deutonymphs or adult males at any concentration, except for the concentration of 6 deutonymph-equivalent per disc (5 h count). This exception could not be explained. Preferences for discs treated with extracts of eggs, adult females and webbing plus excreta were evident at some concentrations (Table 2).

The numbers of predators under the discs treated with the highest concentrations of the egg extract (27.0 and 40.0 egg-equivalent per disc) were significantly higher than under the control discs. A significant difference was also observed at the concentration of 14.0 egg-equivalent (5 h count). Although *P. persimilis* showed a significantly stronger preference for the discs treated with all concentrations of female extract in methanol, there was no significant preference for treated discs left on a hot plate (50—60°C) for 48 h before the test started. Discs treated with extracts of females in ethanol and water were also preferred by the predators.

A marked preference for discs treated with extract of webbing plus excreta was observed at all concentrations and with all solvents. The same result was obtained even when both treated and control discs were left on the hot plate (50—60°C) for 48 h before the beginning of the test.

Preference for treated discs for oviposition was evaluated only in the tests involving different concentrations of webbing plus excreta. Significantly more eggs were laid under the treated discs at all concentrations (Table 2). The number of eggs under the treated discs was ca. four times higher than that under control discs, except for the concentration of 14.2 μg-equivalent per disc, when the number of eggs under the treated disc was ca. 50% higher than under the control disc.

Choice tests with T. evansi *and* T. urticae

Discs treated with extract of *T. urticae* on nightshade leaves had a significantly higher number of predators than those treated with extract of *T. evansi* on nightshade after 8 h (Table 3). When *T. evansi* was on nightshade leaves and *T. urticae* was on bean leaves, this difference was more pronounced in both counts. When only the eggs, adults and webbing and excreta that could be collected from each infested leaf with a brush were extracted, the results were quite different. If both *Tetranychus* species were on nightshade leaves, there was no significant difference in the number of predators under each disc, but if *T. evansi* was on nightshade and *T. urticae* was on bean leaves, a stronger attraction was elicited by the discs treated with *T. evansi* extract.

To explain these seemingly conflicting results, we observed the number of eggs and the amount of webbing and associated excreta produced in 72 h by 20 adult female *T. urticae* on each of five leaves of both night-

shade and bean. An average of 132±50 and 276±23 eggs were oviposited on each nightshade and bean leaf, respectively, suggesting that bean is a more suitable host for *T. urticae*. A total of 136 μg and 68 μg of webbing plus excreta was collected with a brush from the five nightshade and bean leaves, respectively. These results indicate that *T. urticae* spent a longer time feeding and ovipositing and less time walking and webbing on bean leaves. This lesser amount of webbing and associated excreta probably resulted in a lower concentration of extracted kairomone, compared to that obtained from webbing and associated excreta collected from nightshade leaves. In the test with one of the discs treated with 7.5 μg-equivalent of webbing plus excreta of *T. evansi* or *T. urticae*, the predator showed a significant preference for discs treated with extract of the latter. This preference, however, was more pronounced after 5 h than after the 8 h count.

TABLE 3

Phytoseiulus persimilis females under filter paper discs treated with different extracts; counts at two different times after beginning the experiment

Hosts of *T. evansi* : *T. urticae*	Number of replicates	Mean number under disc treated with *T. evansi* : *T. urticae*	
		5 h	8 h
Nightshade : nightshade[1]	10	4.3 : 5.2	3.3 : 5.8*
Nightshade : bean[1]	10	1.4 : 8.0**	1.4 : 8.1**
Nightshade : nightshade[2]	20	4.3 : 3.4	4.5 : 4.2
Nightshade : bean[2]	20	3.6 : 1.7*	6.6 : 2.5**
Nightshade : bean[3]	20	1.9 : 4.6**	2.3 : 3.9*

[1]Extract of the leaves containing adult females, eggs, webbing and excreta.
[2]Extract of the adult females, eggs, webbing and excreta collected with a brush.
[3]Extracts of webbing and excreta at a concentration of 7.5 μg-equivalent per disc.
* = $P < 0.5$, ** = $P < 0.1$, Chi-square test for each ratio.

DISCUSSION

No evidence was found for the existence of an allomone produced by *T. evansi* which would act against *P. persimilis*. On the contrary, it was shown that *T. evansi* produces a kairomone which arrests the predator. However, the effectiveness of that kairomone seems to be less than that of *T. urticae*, as suggested in the choice test involving extracts of equal amounts of webbing plus excreta of both tetranychid species. Consequently, it seems that some other factor(s) must be responsible for the unfavorableness of *T. evansi* to *P. persimilis*. Results of other comparative studies involving the predation of phytoseiids on several tetranychids have shown reduced attraction or non-attraction to certain species (Hoy and Smilanick, 1981; Sabelis and Van de Baan, 1983), but no case of repellence has yet been reported.

There are at least two possible explanations for the preference of *P. persimilis* for discs treated with extracts of higher concentrations of *T. evansi* eggs over the control discs: (1) ovipositing *T. evansi* deposited an interspecific chemical messenger onto the eggs; (2) the eggs were contaminated with an interspecific chemical messenger present on the webbing or excreta. The significantly higher number of predators under the discs treated with the extract of squashed eggs was surprising. It has been observed (Moraes and McMurtry, unpublished) that when *P. persimilis* locates a *T. evansi* egg in an arena, it will not promptly consume the egg after probing it, which suggested the presence of a feeding deterrent inside the prey eggs. The significantly stronger preference of *P. persimilis* for discs treated with extracts of adult female spider mites was conceivably due to extraction of a kairomone present on the bodies of the prey females. No preference was shown by the predator for discs treated with extracts of larvae, protonymphs or deutonymphs. This is surprising because Sabelis et al. (1984) showed a significant attraction of each of the different stages of *T. urticae* to *P. persimilis*, by using a Y-tube olfactometer. However, it should be stressed that, aside from the difference in species involved in the present study and that of Sabelis et al., the methods used in this work evaluated only the arrestment of the predator. Moreover, a higher concentration of the extract of the immature stages than those used in this study could have arrested the predator.

In this study, water as well as methanol and ethanol was efficient in extracting the concerned kairomone. Working with *Metaseiulus occidentalis* (Nesbitt) and *T. urticae*, Hoy and Smilanick (1981) suggested the solubility in water of the kairomone present in the webbing plus excreta of *T. urticae*. Jackson and Ford (1973) noted that *P. persimilis* consumed only about half as many eggs of *T. urticae* that were washed with distilled water compared to unwashed eggs. This result led Jackson and Ford to postulate the presence of feeding stimulant on prey eggs.

The fact that *P. persimilis* did not show preference for discs treated with the extract of adult females of *T. evansi* after being left on the hot plate for 48 h, as opposed to the positive response to the discs treated with the extract of webbing plus excreta, after 48 h on the hot plate, suggests the existence of more than one factor involved in this interspecific communication. Apparently, the factor associated with the females is volatile whereas that associated with webbing plus excreta (the most active) is not. However, another explanation is that the factor associated with the females is more rapidly oxidized. Both factors may act as arrestants, whereas it is not clear whether the factor associated with the females also attracts the predator. According to Dethier et al. (1960), an attractant is a chemical that causes animals to make oriented movements towards its source, whereas an arrestant causes kinetic reactions that cause the animal to aggregate near the chemical source. Kennedy (1977a,b, 1978) elaborated on the limitations of those definitions, stating that the end result of the organism's

response depends upon central nervous integration of multiple inputs and outputs. Borden (1977) hypothesized that behavioral responses of insects to chemical messengers are accomplished in a sequence of genetically controlled behavioral events. He speculated that one of the means by which such chains of events could occur, with a beetle pheromone, was that a relatively nonvolatile host chemical (arrestant) could signal the immediate proximity of the source of a more volatile attractive chemical. The bioassay employed in this experiment did not evaluate the mechanisms involved in the preference for some discs over others. However, if the webbing plus excreta of different species of *Tetranychus* contains mainly a relatively nonvolatile arrestant, this could explain why Sabelis et al. (1984) found a weak response by *P. persimilis* to the fecal (= black) pellets and no significant response to webbing of *T. urticae* using a Y-tube olfactometer, whereas Schmidt (1976) reported the arrestment of *P. persimilis* on leaves containing webbing (plus excreta?) of the same prey.

Hoy and Smilanick (1981) reported the arrestment of *M. occidentalis* on leaves containing webbing plus excreta of six species of tetranychids, especially *Tetranychus pacificus* McGregor, *T. urticae* and *Eotetranychus willamettei* (McGregor), even when webbing plus excreta was aged for 72 h. The role of a kairomone was suggested by these authors since, when the leaves were washed, the webbing structure was retained but the arresting capacity was reduced. However, the excreta on the webbing and leaves may have been partially washed away in that experiment; therefore, a physical effect of the excreta cannot be disregarded as partially responsible for the arrestment of the predators. Hislop and Prokopy (1981) observed that contact with a kairomone apparently held *Phytoseiulus macropilis* (Banks) and *Amblyseius fallacis* (Garman) within the vicinity of a filter paper treated with extract of webbing plus excreta of *T. urticae*, even when the extract was up to 7 days old. However, they found little or no response by *A. fallacis* to air blown over those discs. These results agree with our evidence for the presence of a stable kairomone on the webbing plus excreta.

The possible reasons for *P. persimilis* being arrested by an unfavorable prey cannot be assessed in this study. Attraction and/or arrestment to an unfavorable prey is not inconceivable. Blum (1977) suggested that kairomones can be regarded as nothing more than pheromones or allomones that have evolutionarily boomeranged in some instances (in relation to the producer). It seems possible that the receiver (a predator or parasite), in the same manner, could also be betrayed in some cases by being attracted to an unfavorable prey. However, the literature indicates no overlap in the natural distributions of *P. persimilis* and *T. evansi*. (J. Chazeau, pers. commun. 1985, has recently found *P. persimilis* and *T. evansi* on Reunion Island. Any of these two species could, however, represent a relatively new introduction to the island.) Therefore, the attraction and/or arrestment of *P. persimilis* to an unfavorable prey might occur only under artificial laboratory conditions.

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