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Attraction to Ornamental Peony (*Paeonia lactiflora*, Paeoniaceae) by *Polistes dominulus* Christ (Hymenoptera: Vespidae) Demonstrated Using Olfactometers

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ABSTRACT: Observations were made of *Polistes dominulus* Christ (Hymenoptera: Vespidae) on budding *Paeonia lactiflora* plants (Paeoniaceae). Y-tube and parallel tube olfactometer experiments were performed on field-collected queens and workers to determine if peony odor is attractive to *P. dominulus*. In Y-tube olfactometer experiments, the wasps showed a significant orientation response toward peony bud odor but they did not show a significant response toward peony foliage odor, when compared to the control. Peony bud volatiles were collected in an adsorbent trap and tested in a parallel tube olfactometer for attractiveness to *P. dominulus* females. The wasp took significantly less time to travel upwind in the peony bud volatile tube compared to the control tube. Chemicals that produce peony bud odor could serve as a feeding attractant lure for trapping *P. dominulus*.

KEY WORDS: Vespidae, paper wasp, peony, attraction, flower, behavior

Polistes dominulus Christ (Hymenoptera: Vespidae), an old world polistine wasp, is extensively distributed in its native Palearctic region of Europe and North Africa (Guiglia, 1972; Carpenter, 1996). It was first recorded from Boston, Massachusetts as *Polistes gallicus* (L.) (Hathaway, 1981). The wasp is now well established in the northeastern USA (Hathoway, 1981; Staines and Smith, 1995), the Midwest (Judd and Carpenter, 1996), the western states of Washington and California (Landolt and Antonelli, 1999; Cervo *et al*., 2000), and the Canadian Province of British Columbia (Borkent and Cannings, 2004). Several reasons for the rapid spread of *P. dominulus* and its displacement of indigenous paper wasps have been hypothesized (Cervo *et al*., 2000; Gamboa *et al*., 2002, 2004). These hypotheses include, but are not limited to, shorter brood development time, less parasitism and usurpation, and more rapid and efficient foraging for nutrients.

Paper wasps, including *P. dominulus*, can be a stinging hazard to people, particularly when someone is close to an active nest. Nests of *P. dominulus* are often made within voids or spaces of man-made structures or objects (Jacobs, 2003), and this species may be more abundant around human habitations than other paper wasps (Cervo *et al*., 2000). For this reason, they may need to be controlled or managed under certain circumstances. Recommended control methods are with wasp and hornet sprays or insecticidal dusts (Jacobs, 2003). This wasp is not readily trapped with baits or chemical attractants. *Polistes dominulus* is not attracted to heptyl butyrate which has been shown to be highly attractive to several *Vespula* spp. (Davis *et al*., 1969; Landolt, 1998a; Reed and Landolt, 2002; Landolt *et al*., 2006). Although some *Polistes* species can be trapped with the combination of acetic acid and isobutanol, *P. dominulus* responds only weakly to acetic acid (Landolt, 1998b; Landolt *et al*., 1999; Reed and Landolt, 2002). With the rapid, invasive, and urban spread of *P. dominulus*, effective chemical attractants would aid in the monitoring and management of this wasp.

One possible source of an attractant is the peony, *Paeonia* spp. (Paeoniaceae). Field observations revealed *P. dominulus* making numerous visits to budding cultivated peonies

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throughout May and June 2004 in Yakima County, Washington. Wildflower peonies are native to the Northern Hemisphere in both the Old and New Worlds. The large herbaceous peony cultivars which originated in Asia are a major component of the ornamental flower industry (Halda and Waddick, 2004). Peonies exude a sticky substance from the undersurface of the flower buds that may serve as a feeding reward for insects, specifically ants (Keeler, 1978; Beckmann and Stucky, 1981; Halda and Waddick, 2004). Our observations indicate a strong presence of *P. dominulus*, in addition to ants, on the sticky areas of the buds.

The purpose of our experiments was to test the hypothesis that the odor from peony buds is attractive to *P. dominulus*. We report results concerning klinotaxic (directed turning based on stimulus concentration) and orthokinetic (rate of straight upstream movement depending on stimulus concentration) (Fraenkel and Gunn, 1940; Wyatt, 2003) orientation in *P. dominulus* in response to peony bud and peony foliage odors. Our experiments also address klinotaxic and orthokinetic responses to odor from extracted peony bud volatiles.

Materials and Methods

Between 14 May and 07 June 2004, observations of *P. dominulus* females on peony were conducted in Prosser (Benton County), Washington. Numerous peony plants (*Paonia lactiflora* Pallas) are planted and maintained in a garden area of the Washington State University Irrigated Agriculture Experiment Station, Prosser, Washington. Five plants were observed once a day during the late morning and early afternoon. This study was then replicated on five different days, using a new set of five peony plants each day. The plants were approximately 1.5 m high and 1.5 m wide with an estimated 65 buds per plant; wasps were counted regardless of their location on the plant. The date and time of day were recorded in addition to the number of wasps on each of the 25 plants.

Wasps used in olfactometer experiments were females that were netted at nests or while they were in flight. These were collected from mid-June into mid-August and were probably all workers, although they were not dissected to determine their mating status. The wasps were maintained in 30.5 cm^3-screened cages in a shaded greenhouse. They were provided water and a 1:10 molasses:water solution for nutrition. In order to ensure that the wasps were starved for these experiments, the molasses solution was removed from the cages forty-eight hours prior to the experiment.

Five different attraction experiments were conducted. A Y-tube olfactometer was used to test the klinotaxic response of the wasp to peony bud odor (Experiment 1) and to foliage odor (Experiment 2). The inside diameter of the Y-tube was 2.5 cm and the length of the tube, from stem base to Y-juncture, was 18 cm. A parallel tube olfactometer was used to test the orthokinetic response of the wasp to peony bud odor (Experiment 3), to peony foliage odor (Experiment 4), and to peony bud volatiles (Experiment 5). The inside diameter of the straight parallel tube was 2.5 cm and the length of the tube was 18 cm. The experiments were conducted in a controlled environment room at 24°C and 65% relative humidity. Olfactometer systems were placed horizontally on a table about 0.5 m below two, 1.2 m long, 34W fluorescent light bulbs (Osram Sylvania Corp., Danvers, MA). A J16 Digital Photometer (Tetronix Inc., Beaverton, OR) measured 27,663.48 lux (lumens/m^2) at the olfactometer surface. Olfactometer glassware (Ace Glass, Inc. Vineland, NJ), Teflon tubing, and steel tubing were washed in hot water with Micro-90 cleaning solution (International Products Corp., Burlington, NJ), and then rinsed with deionized water,

acetone, and hexane. Finally, the olfactometer parts were placed in a Precision Economy Oven (Thermo Electron Corp., Waltham, MA) at 180°C for more than 24 hours.

Y-Tube Olfactometer

Air moving through the olfactometer was from a compressed air source, purified through a hydrocarbon trap (Alltech Associates Inc., Deerfield, IL), and humidified with a gas diffusion bottle. Airflow was measured with a flow-meter (Aalborg Instruments, Monsey, NY) before and after passing through the treatment and control at 100 ml/min to ensure there were no air leaks in the system. Air passed over a treatment in a 960 ml jar, through one arm of the Y-tube, and out the stem of the Y-tube. Simultaneously, air passed through a 960 ml empty control jar, through the other arm of the Y-tube, and out the stem of the Y-tube.

A wasp was placed in the stem of the Y-tube and observed for a maximum of five minutes. If the wasp moved upwind to the Y-juncture it experienced air from the treatment through one arm, and air from the control through the other arm. If the wasp moved completely beyond the juncture of either of the arms, the assay was ended. Ten wasps were tested in succession using the same treatment. In order to eliminate a potential left or right turning bias, the positioning of the treatment and control was switched every 5 wasps. The experiments were repeated with a new set of 10 wasps, a clean olfactometer, and a fresh treatment. Experiment 1 was repeated 6 times ($n = 60$) and Experiment 2 was repeated 4 times ($n = 40$). Wasps were scored for entering the treatment arm, the control arm, or neither arm of the Y-tube. Numbers of wasps that entered the treatment arm (+) or the control arm (–) were analyzed using the chi-square goodness-of-fit test at $P < 0.05$.

Parallel Tube Olfactometer

The protocol for Experiments 3, 4, and 5 was similar to that of the Y-tube experiments, as was the pretreatment handling and feeding of the wasps. However, instead of being placed in the stem of a Y-tube, one wasp was placed in a straight tube downwind from the treatment and another wasp was placed in an identical tube downwind from the control. For every set of 10 wasps, the time it took for each wasp to cover the full forward distance was recorded and averaged. However, data from assay replicates for which the wasp did not move the 18 cm to reach the upwind end of the tube within the 5 minute observation period were not included in statistical analyses. Experiments 3 and 4 were repeated 4 times ($n = 40$) and Experiment 5 was repeated 8 times ($n = 80$). Treatment means were separated from control means using a paired t-test at $P < 0.05$.

In Experiment 5, peony bud volatiles were sampled using a volatile collection system (Landolt and Smithhisler, 2003), which included an electric air suction pump, flow meter, 3.8 liter gas sampling jar, and a Super Q trap. Forty flower buds were cut from *Paeonia lactiflora* shrubs on 2 June 2001 and were held on ice for transport to the laboratory. Volatile collections from those buds were started in the laboratory one hour after cutting. Air was pulled over the buds in the vacuum-sealed jar for 4 hr at a rate of 300 ml/min. The volatile collection trap contained 30 mg of Super Q adsorbant in a 0.6 cm diameter × 6.7 cm long borosilicate glass tube. A second trap with 10 mg of Super Q adsorbent was immediately downstream of the first trap. Each trap was extracted with 500 µl of methylene chloride, diluted to 1650 µl with the same solvent, and then separated into eight 200 µl aliquots. The aliquots were stored in a freezer for 1 week at −15°C. Immediately prior to conducting the experiment, the treatment (200 µl of extracted bud volatiles) and the control (200 µl of methylene chloride) were applied to 7 cm diameter, #2 Whatman

Table 1. Observations of female *P. dominulus* visiting 5 peony plants per day in 2004.

			P. dominulus	
Date	Time (hr)	Temperature (°C)	Total	Mean
14 May 2004	1200	26	18	3.6
19 May 2004	1300	23	10	2.0
25 May 2004	1100	27	15	3.0
01 June 2004	1200	23	17	3.4
07 June 2004	1000	21	22	4.4
			Sum = 82	Mean = 3.3

Filter Papers (Whatman International Ltd., Maidstone, England). These were aired for 5 minutes to permit the solvent to evaporate and were then sealed in 480 ml olfactometer jars. Experiment 5 was conducted and data were analyzed using the same protocol as Experiments 3 and 4.

Results

Observations

A total of 82 female wasps were observed on the peonies with a mean of 3.3 wasps per observation period (Table 1). Wasps were seen on upper and lower surfaces of buds and on leaves.

Y-tube Olfactometer

In Experiment 1, *P. dominulus* moved down the arm of the Y-tube with air from the peony bud odor significantly more than down the arm with air from the control (Table 2). In Experiment 2, the wasps did not move down the arm of the Y-tube with air from the peony foliage odor significantly more than down the arm with air from the control. Based on our 5-minute time limit, 3 of the wasps tested in Experiment 1 and 9 of the wasps tested in Experiment 2 did not move past the Y-tube juncture (Table 2).

Parallel Tube Olfactometer

In Experiment 3, the mean time (±SE) for *P. dominulus* to move upwind toward the peony buds (7.8 ± 1.1 sec) was significantly faster ($n = 4$, $P = 0.02$) than to the control (24.4 ± 3.0 sec) (Fig. 1). All of the 40 wasps tested to peony buds moved the 18 cm upwind to the end of the olfactometer tube during the 5 minute assay, while 38 of the 40 wasps tested to control airflow moved the 18 cm upwind. In Experiment 4, there was no significant ($n = 4$, $P = 0.564$) increase in the mean time (±SE) to move upwind in response to peony foliage (44.9 ± 7.5 sec) compared to the control (34.2 ± 10.9) (Fig. 1). Only 31

Table 2. *P. dominulus* response to peony buds and foliage compared to control in a Y-tube olfactometer analyzed using chi-square goodness-of-fit-test with Yates correction for continuity.[a]

	Bud	Control	Neither	$\chi_{experimental}$	*P*-value
Experiment 1 ($n = 60$)	39	18	3	7.018	$0.01 > P > 0.005$
	Foliage	Control	Neither	$\chi_{experimental}$	*P*-value
Experiment 2 ($n = 40$)	20	11	9	2.065	$0.25 > P > 0.10$

[a] $\chi^2_{theoretical(1,\ 0.05)} = 3.841$.

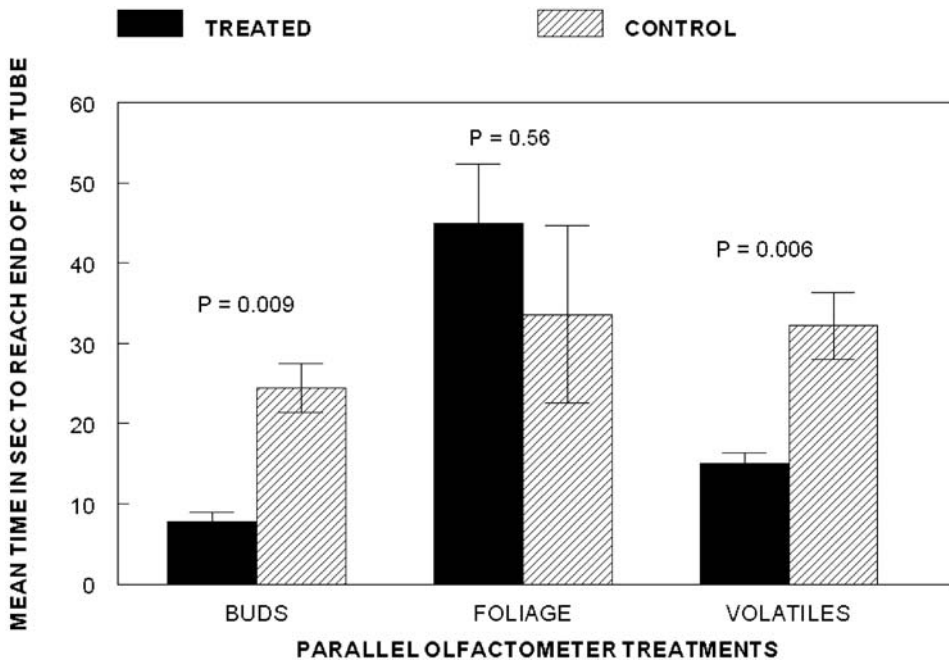

Fig. 1. Mean (±SE) time in seconds for wasps to traverse the 18 cm length of the olfactometer tube carrying airflow from over peony buds, peony foliage, peony volatile samples, or the system control.

of the 40 wasps tested to peony foliage moved the 18 cm upwind during the 5 minute assay, while 38 of the 40 wasps tested to control airflow moved the 18 cm upwind.

In Experiment 5, the mean time (±SE) for *P. dominulus* to travel toward the peony bud volatile collection sample (15.1 ± 1.3 sec) was significantly faster ($n = 8$, $P = 0.006$) than to the control (35.5 ± 3.8 sec) (Fig. 1). All of the 80 wasps tested to peony bud volatiles moved the 18 cm upwind during the 5 minute assay, while 77 of the 80 wasps tested to control airflow moved the 18 cm upwind.

Discussion

The principal objective of this study was to determine if *P. dominulus* is attracted to odor from peony buds using Y-tube and parallel tube olfactometers. Our results demonstrate that not only is *P. dominulus* attracted to peony, but also the source of attraction is from bud odor and not foliage odor. The wasps used in our olfactometer experiments were not taken from places near or on peony. Thus, the wasps were not expected to have been conditioned to peony odor from prior exposure to either the buds or the foliage.

Animals use two basic orientation mechanisms, kinesis and taxis, in response to a stimulus. Kinesis, or indirect guiding, refers to animal movement affected by the intensity of the stimulus, but the direction of the turn and movement are not related to gradients in the stimulus concentration. Conversely, taxis, or direct guiding, describes turning and moving that are related to the pattern of stimulus concentration (Fraenkel and Gunn, 1940; Wyatt, 2003). Odor from fresh peony buds elicited a positive klinotaxic

(directed turning based on stimulus concentration) response from *P. dominulus* in the Y-tube olfactometer (Table 2) and an orthokinetic (rate of straight upstream movement depending on stimulus concentration) in the parallel tube olfactometer (Fig. 1). The peony bud volatiles that were trapped in an air collection system and absorbed onto filter paper also elicited a significant orthokinetic response in the parallel tube olfactometer (Fig. 1). Y-tube and parallel tube experiments using peony foliage did not elicit a significant klinotaxic (Table 2) or orthokinetic response (Fig. 1), respectively.

We hypothesize that *P. dominulus* is attracted to peony odor because it signifies the presence of food. Plants with extrafloral nectaries often are attractive to insects or are heavily visited by insects. For example, *P. exclamans* (Viereck), *P. fuscatus*, *P. canadensis* (L.), *P. instabilis* (Saussure), *P. major* (Beauvois), and *Vespula maculifrons* (Buysson) frequent extrafloral nectaries of budding morning glories (*Ipomoea*, Convolvulaceae), but fewer ants and wasps were attracted to these plants with sealed nectaries (Keeler, 1978; Beckmann and Stucky, 1981). Koptur (1992) suggested that the sugar nutrients from extrafloral nectar and predation opportunities are feeding rewards once attraction of a predatory insect to the plant has occurred. In addition to extrafloral nectar, paper wasps are known to feed on other natural sugar sources such as insect honeydew, flowers, and ripe fruit (Rabb, 1960; Barrows, 1979; Beckmann and Stucky, 1981). None of these other sugar sources are associated however with these peony flower buds.

Peonies have formless nectaries on the floral bracts. These nectaries lack obvious structural specialization at the tissue or organ level but still secrete extrafloral nectar (Zimmerman, 1932). The only structural indication of nectaries in peonies is a separation of the epidermis from the underlying cells (Zimmerman, 1932; Elias, 1983; Pemberton, 1990). Chemical composition studies (Bentley, 1977; Koptur, 1992) on extrafloral nectar from a variety of plant sources reveal an aqueous solution of sugars, amino acids, lipids, and other organic compounds such as alkaloids, phenols, and non-protein amino acids. Studies show that sucrose, glucose, and fructose are by far the most abundant solutes in extrafloral nectar (Bentley, 1977; Koptur, 1992).

Social wasps have not been studied as thoroughly as ants and parasitoids with regard to their association with extrafloral nectar (Bentley, 1977; Beattie, 1985; Koptur, 1992; Bronstein, 1998). However, social wasps, like ants and parasitoids, reduce the number of herbivores on plants that produce extrafloral nectar (Dominguez *et al*., 1989; Cuautle and Rico-Gray, 2003). *Polistes* are known to show a type III functional response (Holling, 1966) when searching for nutrients. That is, there is a sigmoidal relationship between the numbers of prey items eaten by the paper wasp versus the number of prey available. For example, *Polistes* foragers have been observed fixating on areas of high prey density or past foraging successes and will not readily switch to new prey (Yamasaki *et al*., 1978; Gould and Jeanne, 1984; Stamp and Bowers, 1988; Raveret Richter, 2000; Schenk and Bacher, 2002). McPheron (1996) found that *Mischocyttarus flavitarsis* (Saussure) (Hymenoptera: Vespidae) foragers preferred olfactory cues to visual cues from both prey and plants damaged by prey.

As the geographical range of *P. dominulus* continues to rapidly expand in the urban and suburban landscape throughout the USA, an effective chemical attractant is needed to trap this wasp. Heptyl butyrate attracts *Vespula* species but not *Polistes* species (Davis *et al*., 1969; MacDonald *et al*., 1973; Landolt, 1998a; Landolt *et al*., 2003), and acetic acid with isobutanol attracts a number of *Vespula* and *Polistes* species, but not the invasive *P. dominulus* (Landolt, 1998a, b; Landolt *et al*., 1999; Landolt *et al*., 2000; Reed and Landolt, 2002). Perhaps the volatile chemicals emitted from peony flower buds will

provide a feeding attractant for *P. dominulus* wasps that will be useful in monitoring and management.

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