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Olfaction-based mate-odor identification by jumping spiders from the genus *Portia*

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Abstract. Jumping spiders (Salticidae) are known for having good eyesight, but the extent to which they also rely on olfaction is poorly understood. We report here new information on the olfactory abilities of the salticid genus *Portia*. We investigated for the first time the ability of adult males and females of four *Portia* species (*P. africana*, *P. schultzi*, *P. fimbriata* and *P. labiata*) to discriminate between mate and non-mate odor. In a Y-shape olfactometer, males of all four species chose the odor from an opposite-sex conspecific significantly more often than they chose a no-odor control, but the number of males that chose the odor from an opposite-sex heterospecific or the odor from a same-sex conspecific was not significantly different from the number of males that chose the control. The number of female test spiders that chose the odor from an opposite-sex conspecific or the odor from a same-sex conspecific was not significantly different from the number of females that chose the control. The implications of these findings for understanding *Portia*'s mating system are discussed.

Keywords: Olfaction, mate-identification, mating systems, pheromones, Salticidae

Jumping spiders (Araneae: Salticidae) are renowned for having unique, complex eyes (Land & Nilsson 2002), eyesight based on exceptional spatial acuity and intricate vision-based behavior. Yet chemoreception also plays an important role in salticid predatory and mating behavior, either in conjunction with or as alternatives to vision-based signals (Pollard et al. 1987; Clark et al. 2000; Jackson et al. 2002, 2005). In particular, it may be common for salticid males to gain information about the presence of potential mates by detecting chemical traces (i.e., chemical signpost signals) left behind on draglines or nest silk (Jackson 1987; Clark & Jackson 1994a, b; 1995a, b; Taylor 1998; Clark et al. 1999). Considerably less is known about the extent to which salticid mating strategies depend on the detection and identification of volatile compounds (i.e., olfaction), with most of what we currently know having come from a single species, *Evarcha culicivora* Wesolowska & Jackson 2003. This unusual salticid from East Africa feeds indirectly on blood by targeting blood-carrying mosquitoes as preferred prey (Cross & Jackson 2010a), and experiments have shown that *E. culicivora* can identify this prey even when restricted to using sight alone or olfaction alone (Jackson et al. 2005). Human odor and the odor of particular plant species are also salient to this spider (Cross & Jackson 2009a, 2011b). Moreover, even when restricted to using olfaction alone, each sex of *E. culicivora* can identify potential mates (Cross & Jackson 2009b, c) and also determine whether a potential mate has recently fed on a blood-carrying mosquito or whether it has fed on something else (Cross et al. 2009).

Here we report on an experimental study of olfaction-based mate-identification behavior by *Portia africana* (Simon 1886), *Portia schultzi* Karsch 1878, *Portia fimbriata* (Doleschall 1859) and *Portia labiata* (Thorell 1887), species that are only distantly related to *E. culicivora*. Salticid systematics remains poorly understood, but three major taxa are generally recognized, the Salticoida, Spartaeinae and Lyssomaninae (Maddison & Hedin 2003). *E. culicivora*, along with most salticids, is a salticoid. *Portia* belongs to the subfamily Spartaeinae, and spartaeines are known for having unusual predatory strategies (Su et al. 2007). Although most salticids probably prey primarily on insects (Richman & Jackson 1992), most spartaeines that have been studied specialize at feeding on other spiders (i.e., they are 'araneophagic'). Part of what 'araneophagy' means is that these salticids adopt prey-specific tactics for capturing other spiders, and also that they express a strong, active preference for eating other spiders (Jackson & Pollard 1996; Li & Jackson 1996; Nelson & Jackson 2011). For an araneophagic salticid, making use of olfactory cues from prey may often be especially advantageous because another spider is not only potential prey but also a potential predator. Earlier research has provided experimental evidence of olfactory prey identification by two araneophagic spartaeines, *Portia fimbriata* (Jackson et al. 2002) and *Cyrba algerina* (Lucas 1846) (Cerveira & Jackson 2011).

Owing to how encounters between opposite-sex conspecifics can end in cannibalism, the prey-choice and mate-choice decisions of salticids may often be intertwined (Elgar 1992; Jackson & Pollard 1997). The overlap between predatory and mating strategies may be especially evident when we consider *Portia* and other araneophagic salticids. Encountering *Portia* females may be especially dangerous for *Portia* males (Jackson & Hallas 1986), a risk made all the worse by how with *Portia*, as is commonly the case in animals (Trivers 1972), males are more active than females in initiating courtship. Taken together, this suggests that *Portia* is a salticid in which, for males, early identification of conspecific females would be especially advantageous.

From earlier work on two *Portia* species (*P. africana* and *P. fimbriata*), there is indirect evidence that males, but not females, identify the odor of potential mates (Willey & Jackson 1993; Cross et al. 2007a; Cross & Jackson 2009b). Here we investigate directly for the first time the hypotheses that spiders from the genus *Portia* can identify the odor of potential mates on the basis of olfaction alone and that this is an ability expressed strongly by males but only weakly, if at all, by females.

METHODS

All test spiders were taken from laboratory cultures (second and third generation). The origins of these cultures were Mbita Point (Kenya) for *P. africana*, Malindi (Kenya) for *P. schultzi*, Cairns (Australia) for *P. fimbriata* and Los Baños (Philippines) for *P. labiata*. Voucher specimens were deposited at the National Museums of Kenya (Nairobi), the Museum of Natural History (Wroclaw University, Poland) and the Florida State Collection of Arthropods (Gainesville, Florida).

Standard spider-laboratory rearing and testing procedures were adopted (for details, see Jackson & Hallas 1986). No test spider had prior experience with other *Portia* individuals. For standardization, all test and source spiders were unmated adults that had matured 2–3 wk before testing and all were of a standard body length (accurate to nearest 0.5 mm): males 8 mm, females 10 mm. Hunger level was also standardized, with each test and each source spider fasting for four days prior to testing. Testing was carried out between 0900 and 1200 h (laboratory photoperiod 12L:12D, lights on 0800 h).

Testing was carried out using a Y-shaped olfactometer (Fig. 1) with air pushed by a pump independently into two chambers, an experimental chamber and a control chamber. Airflow was adjusted to 1500 ml/min using Matheson FM-1000 flow meters, and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on the test spider's behavior. Each chamber was a glass cube made from 5-mm thick glass (inner dimensions, 70 × 70 × 70 mm), with a removable lid. There were two holes (20 mm diam.) situated opposite each other on the cube, each hole being plugged with a rubber stopper. There was a hole in each stopper through which a glass tube (45 mm length, 4 mm diam.) passed, enabling air to move in and out of the chambers. On the stopper, a nylon-netting screen ensured that the test spider could not enter the chamber. New netting was used for each test. From the chambers, air moved independently into the two arms of the Y (the control and the experimental arm).

The odor source (a spider) was in the experimental chamber. There was no odor source in the control chamber. A series of experiments was carried out with each of the four *Portia* species: male tested with conspecific female odor, male tested with heterospecific female odor, male tested with conspecific male odor, female tested with conspecific male odor, female tested with conspecific female odor (see Table 1). Testing *Portia* females with the odor of heterospecific males might have also been of interest, but this would have meant addressing questions somewhat tangential to our specific objective in this study of investigating *Portia*'s ability to discriminate between mate and non-mate odor. We found that the odor of opposite-sex conspecifics was salient to males but not to females (see Results), and this gave us a clear rationale for testing whether *Portia* males had specifically responded to mate odor or whether they had responded to the odor of opposite-sex salticids in general. However, there was no comparable rationale for also investigating this for *Portia* females.

A test spider was confined to a holding chamber at the far end of the test arm for 2 min before testing began. A removable metal grill fit into a slit in the chamber roof, blocking access to the rest of the olfactometer. The grill was lifted to start a test. Once the spider left the holding chamber, it was given 30 min in which to make a choice, with the operational definition of 'choosing' being that it entered either the control arm or the experimental arm of the olfactometer and remained there for 30 s. Each spider usually walked about actively in the olfactometer and we recorded which of the two arms it chose. As a precaution against the possibility that test spider behavior was influenced by traces left by spiders that had been tested previously, the olfactometer was dismantled and cleaned with 80% ethanol and then with distilled water between tests.

Data for each experiment were analyzed using chi-square tests for goodness of fit (null hypothesis: probability of making one of the two choices same as probability of making other choice). Using chi-square tests of independence (null hypothesis: choices made by one group of test spiders same as choices made by other group of test spiders), comparisons were also made between different groups of test spiders. Bonferroni adjustments were applied whenever there was repeated testing of the same data sets (alpha 0.05, adjusted alpha 0.013: see Howell 2002). For data analysis, individuals that failed to choose were ignored. For each experiment, $n = 30$.

RESULTS

For each of the four *Portia* species, the number of males that chose the odor of conspecific females was significantly more than the number of males that chose the no-odor control (Tables 1 & 2). The number of females that chose the odor of conspecific males was not significantly different from the number of females that chose the control. In all other experiments, there was no significant difference between the number of test spiders (male or female) that chose the experimental odor and the number that chose the control.

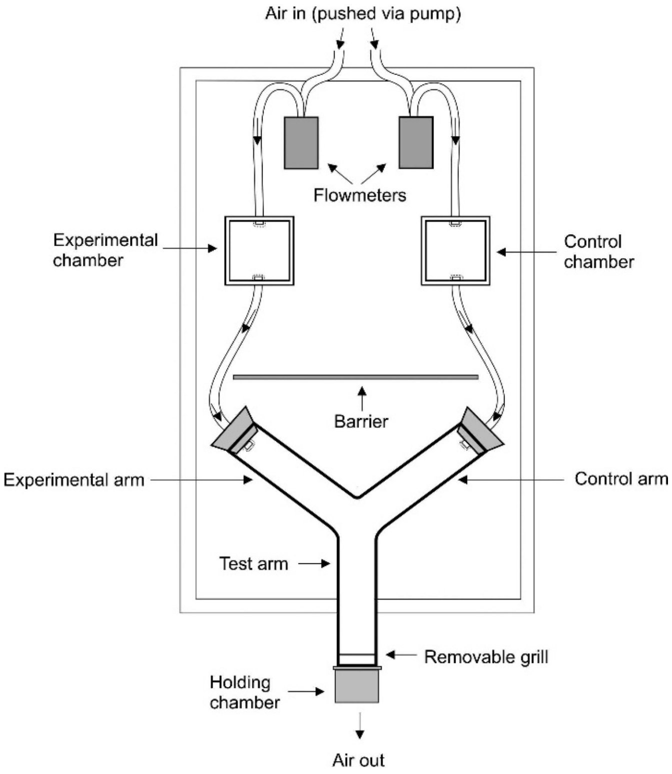

Figure 1.—Olfactometer (not drawn to scale). Arrows indicate direction of airflow. Holding chamber (location of test spider at start of test): 25 mm length, 25 mm inner diam. Start of test: test spider in holding chamber; grill removed, giving access to test arm, control arm and experimental arm. Dimensions of test arm, control arm and experimental arm: 90 mm length, 20 mm inner diam. Opaque barriers prevent test spider from seeing odor source.

Males made significantly different choices when the experimental odor was from an opposite-sex conspecific instead of an opposite-sex heterospecific (*P. africana*: $X^2 = 9.32$, $P = 0.002$; *P. schultzi*: $X^2 = 13.61$, $P < 0.001$; *P. fimbriata*: $X^2 = 8.52$, $P = 0.004$; *P. labiata*: $X^2 = 20$, $P < 0.001$) and they made significantly different choices when the experimental odor was from an opposite-sex conspecific instead of a same-sex conspecific (*P. africana*: $X^2 = 19.20$, $P < 0.001$; *P. schultzi*: $X^2 = 13.61$, $P < 0.001$; *P. fimbriata*: $X^2 = 13.02$, $P < 0.001$; *P. labiata*: $X^2 = 23.72$, $P < 0.001$). Choices made by males were also significantly different from choices made by females when the experimental odor was from an opposite-sex conspecific (*P. africana*: $X^2 = 13.87$, $P < 0.001$; *P. schultzi*: $X^2 = 10.33$, $P = 0.001$; *P. fimbriata*: $X^2 = 11.43$, $P < 0.001$; *P. labiata*: $X^2 = 20$, $P < 0.001$). Choices made by females when the experimental odor was from an opposite-sex conspecific instead of a same-sex conspecific were not significantly different (*P. africana*: $X^2 = 0.27$, $P = 0.605$; *P. schultzi*: $X^2 = 0.07$, $P = 0.793$; *P. fimbriata*: $X^2 = 0.07$, $P = 0.796$; *P. labiata*: $X^2 = 0$, $P = 1.00$).

DISCUSSION

There is abundant evidence that dragline-associated chemical cues assist salticids with the task of identifying potential mates (e.g., Pollard et al. 1987; Clark & Jackson 1995b; Taylor 1998). However, until now, the only direct evidence of olfactory mate identification by salticids has come from *Evarcha culicivora* (Cross & Jackson 2009c; Cross et al. 2009). Both sexes of *E. culicivora* expressed olfactory mate identification. The results of our present study are different because we found evidence for *Portia* males, but not for *Portia* females, of olfactory mate identification.

Table 1.—Summary of findings from experiments testing four *Portia* species for ability to discern mate odor. Sample size 30 for each species in each cell. (1) For each species, the number of individuals that chose the odor was significantly different from the number that chose the no-odor control. (2) For each species, the number of individuals that chose the odor was not significantly different from the number that chose the no-odor control. (3) Not tested.

	Odor of opposite-sex conspecific	Odor of same-sex conspecific	Odor of opposite-sex heterospecific
Male test spider	(1)	(2)	(2)
Female test spider	(2)	(2)	(3)

Previous work has shown that one of the salticid species we investigated here, *Portia fimbriata*, makes use of olfaction in the context of predation (Jackson et al. 2002). Previous work has also shown that males, but not females, of *P. fimbriata* and *P. africana* escalate conflicts with same-sex rivals when the odor they detect comes from opposite-sex conspecifics instead of from opposite-sex heterospecifics (Cross et al. 2007a; Cross & Jackson 2009b). More specifically, it has been shown that, for these two species, competition for access to mates becomes more intensive for males than for females when odor from opposite-sex conspecifics is present. This is consistent with a simplistic interpretation of Trivers' (1972) argument that sex roles are qualitatively different, with only one sex (usually the male) doing the active courting and competing for access to mates and with only one sex (usually the female) being especially choosy. Recent work with a population of *P. fimbriata* from Queensland (Australia) has shown that males and females of this species may place different emphasis on different resources, with access to potential mates being more important for males (Cross & Jackson 2009b) and with access to a particular prey species (*Jacksonoides queenslandicus* Wanless 1988, a common salticid species in *P. fimbriata*'s habitat) being more important for females (Cross & Jackson 2011a).

Whether mate odor is salient to salticid females may depend, in part, on the mating system of the species in question. For example, *E. culicivora*'s mating system differs from that of the four *Portia* species we tested, as *E. culicivora* is a salticid species in which mutual mate choice is expressed especially strongly (Cross et al. 2007b). Besides mate odor being salient to males and to females of this species (Cross & Jackson 2009c), both sexes also escalate conflict with a same-sex rival when they are presented with the odor of a potential mate (Cross & Jackson 2009b).

Although we demonstrated olfactory mate identification for males but not for females in the present study, non-significant findings do not, of course, simply prove that *Portia* females are indifferent to male odor. Perhaps the female's response to male odor drops to a level below the sensitivity of our choice-test design. Maybe another experimental design would be more effective. However, regardless of how these non-significant findings are interpreted, our findings imply an interesting male-female difference. Early detection of odor from a potential mate seems to be of greater importance to the males than to the females of *Portia*. This in turn suggests that females are more important as a resource to males (i.e., as potential mates) than males are as a resource to females. However, *Portia* females may also be more dangerous to males (i.e., as potential predators) than males are to females (Jackson & Hallas 1986), and this might in turn make early detection of mate odor more important for males than for females. Being prepared for encounters with a conspecific female may have an especially important self-defense role for males.

Yet caution is needed when basing conclusions on olfactometer data. The basic conclusion implied by our findings is that the odor of conspecific females is salient to *Portia* males. It may be tempting to conclude that *Portia* males are also attracted to female odor, but the biologically relevant effects of female odor on males may be considerably different. The hypothesis we are currently investigating for *Portia* is that, when the odor of a conspecific female is detected, a primary effect on the male is the triggering of selective visual attention (i.e., he becomes prepared to see a conspecific female). There is evidence that prior exposure to the odor of a specific prey (*Jacksonoides queenslandicus*) prepares *P. fimbriata* to see this particular prey species (Jackson et al. 2002). Experiments have also

Table 2.—Choices made by adult males and females of four *Portia* species in Y-shaped olfactometer. Odor source in experimental chamber: adult source spider. Control chamber: no odor source present. $n = 30$ for each row. Choice defined by arm of olfactometer entered and remained in for minimum of 30 s.

				Test for goodness of fit	
Test spider	Source spider	Chose experimental	Chose control	χ^2	P
Portia africana male	*Portia africana* female	28	2	22.533	< 0.001
Portia africana male	*Portia schultzi* female	18	12	1.200	0.273
Portia africana male	*Portia africana* male	12	18	1.200	0.273
Portia africana female	*Portia africana* male	15	15	0.000	1.000
Portia africana female	*Portia africana* female	13	17	0.533	0.465
Portia schultzi male	*Portia schultzi* female	25	5	13.333	< 0.001
Portia schultzi male	*Portia africana* female	11	19	2.133	0.144
Portia schultzi male	*Portia schultzi* male	11	19	2.133	0.144
Portia schultzi female	*Portia schultzi* male	13	17	0.533	0.465
Portia schultzi female	*Portia schultzi* female	12	18	1.200	0.273
Portia fimbriata male	*Portia fimbriata* female	27	3	19.200	< 0.001
Portia fimbriata male	*Portia labiata* female	17	13	0.533	0.465
Portia fimbriata male	*Portia fimbriata* male	14	16	0.133	0.715
Portia fimbriata female	*Portia fimbriata* male	15	15	0.000	1.000
Portia fimbriata female	*Portia fimbriata* female	14	16	0.133	0.715
Portia labiata male	*Portia labiata* female	30	0	30.000	< 0.001
Portia labiata male	*Portia fimbriata* female	15	15	0.000	1.000
Portia labiata male	*Portia labiata* male	13	17	0.533	0.465
Portia labiata female	*Portia labiata* male	15	15	0.000	1.000
Portia labiata female	*Portia labiata* female	15	15	0.000	1.000

shown that the odor of preferred prey (i.e., blood-carrying female mosquitoes) makes *E. culicivora* selectively attentive to the odor and appearance of this particular prey, and that the odor of a potential mate makes *E. culicivora* selectively attentive to the odor of potential mates (Cross & Jackson 2009d, 2010b). We are currently investigating whether the odor of conspecific females also influences selective visual attention by *Portia* males to the appearance of conspecific females.

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