

Love is in the air: olfaction-based mate-odour identification by jumping spiders from the genus *Cyrba*

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Abstract Jumping spiders (Salticidae) are known for having good eyesight, but the extent to which they rely on olfaction is poorly understood. Here we demonstrate for the first time that olfactory pheromones are used by two species from the salticid genus *Cyrba* (*C. algerina* and *C. ocellata*). Using a Y-shape olfactometer, we investigated the ability of adult males and females of both species to discriminate between mate and non-mate odour. A hidden spider or a spider's draglines (no spider present) were used as odour sources. There was no evident response by females of either *Cyrba* species to any tested odour. Males of both species chose odour from conspecific females, or their draglines, significantly more often than the no-odour control, but there was no evident response by males to any of the other odours (conspecific male and heterospecific female). Our findings demonstrate that *C. algerina* and *C. ocellata* males can make sex- and species-specific discriminations even when restricted to using olfaction alone. Also, by showing that draglines can be a source of olfactory pheromones, our findings illustrate

the difficulty of ruling out olfaction when attempting to test for chemotactile cues.

Keywords Olfaction · Mate identification · Mating systems · Pheromones · Salticidae

Introduction

Specific compounds or blends of compounds, known as pheromones, often function as signals that mediate interactions between conspecific individuals (Shorey 1976; Maynard Smith and Harper 2003; Carde and Millar 2004; Bradbury and Vehrencham 2011). Perhaps all animals rely to some extent on chemoreception (Wyatt 2003; Steiger et al. 2011), but the literature is dominated by research on insects, with spiders being comparatively neglected. Symonds and Elgar (2008) have estimated that about 80 % of all pheromone research has been on insects, whereas only about 1 % has been on spiders.

With spiders, as with animals in general, it is customary to distinguish between contact-chemoreception (chemotactile) and olfactory pheromones (Barth 2001; Foelix 2011), but most experiments pertaining to pheromone use by spiders have allowed for contact with webs, nests or silk draglines (Trabalon and Bagnères 2010), leaving unresolved the question of whether chemotactile or olfactory pheromones, or both, mediated the spider's response. A more limited number of studies have been based on testing design that ruled out contact and thereby showed that specifically olfaction mediated the spider's response (Blanke 1972; Schulz and Toft 1993; Searcy et al. 1999; Papke et al. 2000, 2001; Gaskett 2007; Cross and Jackson 2009a; Aisenberg et al. 2010; Jerhot et al. 2010; Chinta et al. 2010; Xiao et al. 2010).

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As a step toward a fuller understanding of olfactory communication by spiders, we investigated *Cyrba algerina* and *C. ocellata*, two species from the family Salticidae. Although salticids are better known for their unique eyes and complex vision-based behaviour (Land and Nilsson 2002; Jackson and Cross 2011a; Harland et al. 2012), numerous studies have illustrated the use of acoustic, percussive (seismic), silk-borne and tactile signalling during salticid intraspecific interactions (Edwards 1981; Gwynne and Dadour 1985; Maddison and Stratton 1988; Jackson and Pollard 1997; Noordam 2002; Elias et al. 2003, 2005, 2010, 2012; Sivalingham et al. 2010). Salticids are also known to make extensive use of chemoreception. Examples include experiments showing that salticids can use chemoreception for discriminating between conspecific and heterospecific individuals, familiar and unfamiliar rivals and own and other conspecific individuals' eggs and draglines, as well as determining whether a potential mate is reproductively mature, determining what a potential mate has been eating and even determining the fighting ability of a rival (Jackson 1987; Pollard et al. 1987; Clark and Jackson 1994a, b, 1995a, b; Taylor 1998; Clark et al. 1999; Cross et al. 2009; Jackson and Cross 2011a, b). Moreover, some salticid species are known to escalate conflict with conspecific rivals when they detect odour from potential mates (Cross et al. 2007; Cross and Jackson 2009b), whilst others are proficient at using chemoreception for identifying their preferred prey (Clark et al. 2000a, b; Jackson et al. 2002, 2005). However, with most salticid species used in research pertaining to chemoreception, whether the spider used chemotactile or olfactory pheromones, or both, has been uncertain because the testing design adopted did not prevent contact with the stimulus source. Currently, there are only five salticid species for which the experimental design have provided evidence of specifically olfactory pheromones being used (Willey and Jackson 1993; Cross and Jackson 2009a; Jackson and Cross 2011b).

Here our objective is to investigate the ability of *C. algerina* and *C. ocellata* to use specifically olfactory pheromones for species and sex identification. That these species might be especially likely to use olfactory pheromones is suggested by their microhabitats. Salticids are typically found in the open where, even if in dense forest, the ambient light level is conducive to seeing detail. However, *C. algerina* and *C. ocellata* normally encounter prey and conspecific individuals under and around the lower edges of stones on the ground (Jackson and Hallas 1986; Jackson 1990; Guseinov et al. 2004; Cerveira and Jackson 2011), a structurally complex and dimly lit microhabitat where proficiency at using olfaction could be especially advantageous.

Taxonomic considerations also suggest that use of olfactory pheromones by *C. algerina* and *C. ocellata* is likely. *Cyrba* belongs to the subfamily, Spartaeine, widely regarded as being a basal clade in the family Salticidae (Maddison and Hedin 2003; Su et al. 2007), and to which four (Jackson and Cross 2011b) of the five species known to use olfactory pheromones belong. It is also of note that *Cyrba*, along with four other spartaeine genera (*Portia*, *Cocalus*, *Gelotia* and *Mintonia*) are characterised by having mytiliform organs, situated in clusters of 35–50, and located on the spider's dorsal abdomen and though to function as a source of pheromones (Wanless 1984).

Materials and methods

Standard spider-laboratory rearing and testing procedures were adopted (see Jackson and Hallas 1986; Cerveira and Jackson 2011). All test spiders were taken from laboratory cultures (2nd and 3rd generation; origin for *C. algerina* Sintra, Portugal; for *C. ocellata* Mbita Point, Kenya). After dispersal from the egg sac, spiders were kept individually in an enriched environment (see Carducci and Jakob 2000): a spacious cage fitted with a cardboard harmonium provided adequate substrate for nest building and hunting.

All testing was carried out between 0800 and 1200 hours (laboratory photoperiod 12L:12D, lights on 0700 hours). None of the spiders had prior encounters with other salticids. For standardization, all test and source spiders were unmated adults that had matured 2–3 weeks before testing, and all test and source spiders were kept without food for 4–5 days before testing.

Testing was carried out using a Y-shaped olfactometer (Fig. 1) with air pushed by a pump independently into two chambers: a stimulus chamber and a control chamber. Whether the stimulus chamber was on the left or the right was determined at random. There was an odour source in the stimulus but not in the control chamber. Using Matheson FM-1000 flow meters, airflow was adjusted to 1500 ml/min, and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on the test spider's behaviour. Each chamber was a glass tube (length 90 mm, inner diameter 15 mm, each end plugged by a rubber stopper). Smaller glass tubes (length 45 mm, diameter 4 mm) that passed through a hole in each stopper, and silicone tubing, connecting these glass tubes to each other and to the pump, allowed air to move through the olfactometer. For confining spiders, there was a nylon-netting screen over the inner side of each stopper, with new netting being used for each trial. From the control and stimulus chambers, air moved independently into the two arms of the Y (i.e. the control and the stimulus arm).

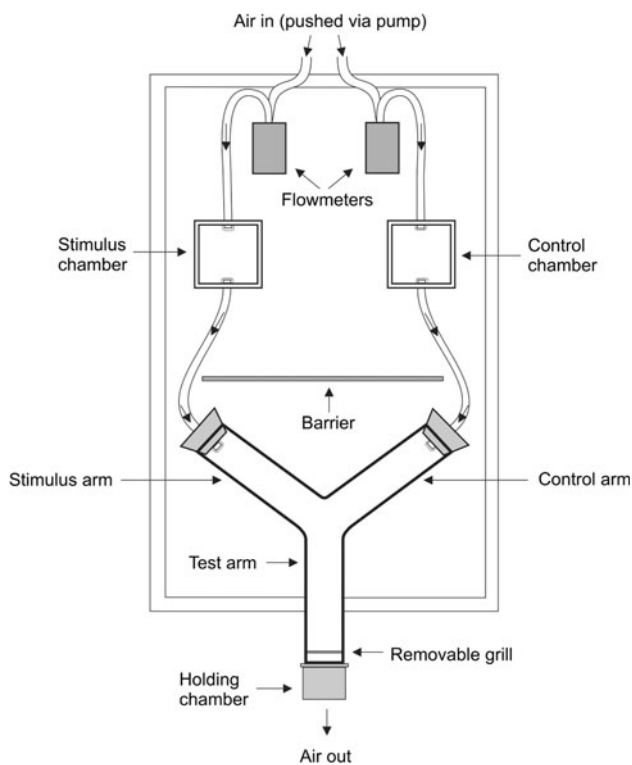


Fig. 1 Olfactometer (not drawn to scale) used for testing *Cyrrba algerina* and *C. ocellata*. Arrows indicate direction of airflow. Holding chamber (location of test spider at start of test). Start of test: test spider in holding chamber; grill removed, giving access to test arm, control arm and stimulus arm. Opaque barriers block test spider's view of odour source

Since previous research (Cerveira and Jackson 2011) indicated that testing *C. algerina* and *C. ocellata* under bright, direct lighting is problematic, we placed the olfactometer inside a cardboard box (length 500 mm, width 500 mm, height 500 mm), with the interior being made accessible by a window (width 150 mm, height 150 mm up from floor, top of window 350 mm from top of box) cut out of the front end of the box.

Before testing began, the test spider was confined for 2 min to the holding chamber at the far end of the test arm. A metal grill that fitted into a slit in the chamber's roof blocked the test spider's 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, the test spider's 'choice' being defined as the arm of the Y it entered and stayed in for 30 s. During testing the test spider could not see or touch the odour source.

Individual spiders from both sexes of the two *Cyrrba* species were used in experiments as odour sources. Whenever there was olfactometer evidence that a given odour elicited a response, we also used the draglines of individual spiders (spider absent) as odour sources. The

odour source (spider or draglines) was put in the experimental chamber 15 min before testing began.

For collecting draglines, we used a glass Petri dish (diameter 60 mm) with a circle of blotting paper (diameter 60 mm) covering the inside bottom of the dish and another circle (60 mm) covering the inside top. At 0700 hours, the source spider was put in the dish, and the dish was then oriented upright and held in place by a clamp so that neither of the two circles of blotting paper was above the other. Blotting paper was held in place on the glass by four squares (each side 10 mm) of double-sided sticky tape spaced evenly around the inside perimeter of the dish. On the following day, 15 min before testing began, the Petri dish was opened, the source spider and sticky tape were removed and one of the two pieces of blotting paper (chosen at random) was rolled up loosely and inserted into the experimental chamber (either on the right or the left side of the olfactometer, decided at random).

As a precaution against the possibility of test spider behaviour being influenced by traces left by spiders used previously as test or source spiders, the olfactometer was dismantled and wiped clean with 80 % ethanol followed by distilled water and then dried between tests. No spider was used as a test spider or source spider more than once. Data from choice testing were analyzed using chi-square tests for goodness of fit (null hypothesis: equal probability of choosing any one arm over the other). Comparisons between odour types were done using chi-square tests for independence.

Results

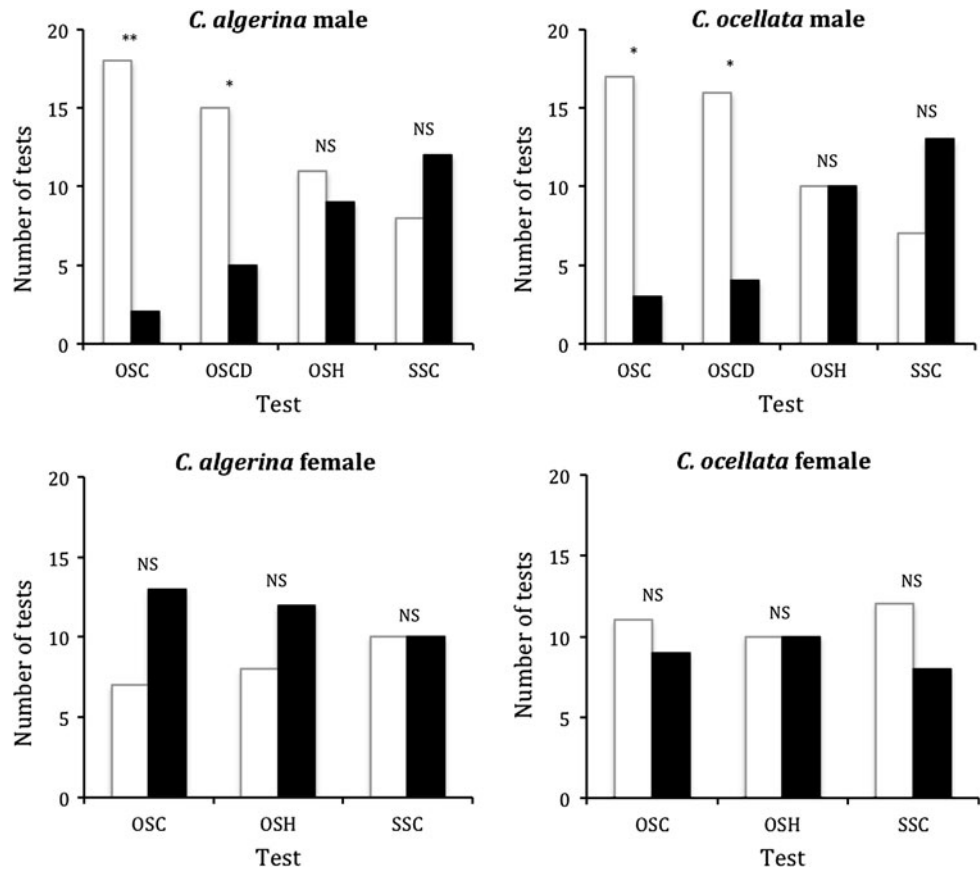
Males of both *Cyrrba* species chose the stimulus arm significantly more often than the control arm when the odour source was a conspecific female or the female's draglines, but not when the odour source spider was a heterospecific female or a conspecific male. Females chose none of the odours significantly more often than the no-odour control (Fig. 2).

The number of males that chose the odour of conspecific females did not differ significantly between tests with female spiders present and tests with only the female's draglines present (test of independence; *C. algerina*: $\chi^2 = 1.558$, $df = 1$, $P = 0.211$, $N = 40$; *C. ocellata*: $\chi^2 = 0.173$, $df = 1$, $P = 0.677$, $N = 40$).

Discussion

Our findings show that *C. algerina* and *C. ocellata* males can identify conspecific females on the basis of specifically olfactory stimuli (i.e. reliance on chemotactile stimuli was

Fig. 2 Results for both sexes of *Cyrrba algerina* and *C. ocellata* tested with Y-shape odour olfactometer (Fig. 1). *White bars* test spiders that chose stimulus arm. *Black bars* test spiders that chose control arm (no odour). Odour source in stimulus chamber: *OSC* opposite-sex conspecific individual, *OSCD* only the draglines of opposite-sex conspecific individual, *OSH* opposite-sex heterospecific individual, *SSC* same-sex conspecific individual. Chi-square goodness of fit (null hypothesis: experimental arm and control arm chosen equally often). ** $P < 0.001$; * $P < 0.05$; ^{NS} $P > 0.05$



ruled out because our test design prevented contact with the stimulus source). Our findings also show that, even when the female is not present, males respond to olfactory stimuli from the female's draglines. Evidence of draglines functioning as a source of olfactory pheromones may have important methodological implications. It has been traditional to permit contact in experiments aimed at determining whether draglines are pheromone sources (Gaskett 2007), and the spider's response in these experiments is routinely envisaged as being evidence of chemotactile pheromones. Yet the designing of experiments that can clearly distinguish between olfaction and contact chemoreception is a challenging, but rarely acknowledged, problem. Ruling out contact chemoreception when testing for olfaction is comparatively straightforward, but testing for specifically chemotactile pheromones requires more than just allowing for contact. Knowing that silk can be a source of odour, we need to consider the possibility that the spider, even when it can touch the silk, is nonetheless relying on olfactory instead of, or in addition to, chemotactile signals.

Although the sense organs that mediate chemoreception by spiders are not fully understood, tarsal organs (i.e. small pits, or sometimes rods, on the dorsal side of each leg tarsus) appear to function as primary olfactory receptors (Foelix and Chu-Wang 1973; Dumpert 1978; but see Ehn

and Tichy 1996), and specialised hairs (tip pore sensilla) on the distal segments of the spider's palps and forelegs appear to function as primary contact chemoreceptors (Foelix 1970; Harris and Mill 1973; Jiao et al. 2011; Tichy et al. 2001). Determining the sense organs that respond to *Cyrrba* pheromones would be of particular interest.

We found no evidence of odour from heterospecific females or conspecific males being relevant to *Cyrrba* males, nor any evidence of any tested odour being relevant to *Cyrrba* females. These findings are consistent with our impression that *C. algerina* and *C. ocellata* follow a common trend among animals (Trivers 1972; Andersson 1994), including salticids (Jackson and Pollard 1997) and other spiders (Huber 2005), of males having a more active role in mate searching and courting, and females placing greater emphasis on active mate choice behaviour.

In this initial study, we standardised spider age and reproductive status (i.e. all test and source spiders were unmated adults that had matured 2–3 weeks before testing). However, as a next step, it would be of interest to determine whether males of *C. algerina* and *C. ocellata* discriminate by olfaction between conspecific females that have and have not already mated. Previously mated *Cyrrba* females sometimes mate again. However, as with many salticids and other spiders (Jackson 1981; Jackson and Pollard 1997; Huber 2005; Cross et al. 2007), prior mating

seems to make *Cyrba* females less receptive to courting males, which might, in turn, make previously mated females less attractive to males (see Baruffaldi and Costa 2010). Sperm competition may also predispose males to being less attracted to females that have already mated, as first-male sperm priority appears to be the prevailing pattern when salticid females mate more than once (Jackson 1982; Huber 2005).

With the present study, *Cyrba* joins *Evarcha* and *Portia* (Willey and Jackson 1993; Cross and Jackson 2009a; Jackson and Cross 2011b) as one of only three salticid genera for which there is evidence of species and sex identification on the basis of olfaction alone. However, when spiders can contact silk (draglines or nests), evidence of mate identification exists for many salticid species (Jackson 1987; Clark and Jackson 1995b; Taylor 1998). On this basis it would be tempting to conclude that chemotactile pheromones are more common than olfactory pheromones in the Salticidae. However, as the only published experiments designed specifically for detecting use of olfactory pheromones are those on *Cyrba*, *Evarcha* and *Portia*, this conclusion would be premature.

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