# Widespread reliance on olfactory sex and species identification by lyssomanine and spartaeine jumping spiders

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Jumping spiders (Salticidae) are renowned for their exceptional vision, but this does not preclude use of other senses. Here we provide evidence that olfactory pheromones are widespread in the Spartaeinae and Lyssomaninae, two subfamilies regarded as basal clades within the Salticidae. Pheromone use by salticids was tested in a series of experiments: males were tested with the odour of conspecific females, heterospecific females, and conspecific males, and females were tested with the odour of conspecific males. With seven of the 29 species tested, we also tested males using the draglines of conspecific females (spider absent) as the odour source. Males of all species tested were attracted to the odour of conspecific females and to the odour of the draglines of conspecific females. There was no evidence of males responding to the odour of heterospecific females or conspecific males, or of females responding to the odour of conspecific males. These findings suggest that it is primarily males that respond to olfactory sex pheromones, consistent with the apparent trend within spiders of males more actively searching for females and females placing greater emphasis on mate-choice decisions. Compared with most salticid groups, lyssomanines and spartaeines are unusually sedentary and this lifestyle may favour olfactory mate searching. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **107**, 664–677.

ADDITIONAL KEYWORDS: communication – chemoreception – olfaction – pheromones – Salticidae.

## INTRODUCTION

Specific chemical compounds or blends of compounds, known as pheromones, often function as signals that govern how conspecifics interact (Shorey, 1976; Maynard Smith & Harper, 2003; Bradbury & Vehrencamp, 2011). Among invertebrates we know a considerable amount about this subject in insects (Carde & Millar, 2004), but considerably less is known about the role of pheromones in spiders. Distinguishing between chemotactile (based on contact-chemoreception from the web, nest, or dragline silk) and olfactory pheromones is customary in the spider literature (Barth, 2001; Foelix, 2011), but most research has focused on chemotactile signal use (e.g. Baruffaldi *et al.*, 2010). However, olfactory communication, which depends on an animal responding to volatile compounds, has been demonstrated in a few spiders (Gaskett, 2007).

While mutual mate choice (Andersson, 1994; Kokko & Johnstone, 2002) is seen in some spiders (e.g. Rypstra *et al.*, 2003; Cross, Jackson & Pollard, 2007,

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2008), search and courtship behaviour appears to be more strongly expressed by males than by females (Huber, 2005). Male search behaviour can be elicited by pheromones released by females (Schulz & Toft, 1993; Papke *et al.*, 2000; Papke, Riechert & Schulz, 2001; Xiao, Zhang & Li, 2009; but see Xiao, Zhang & Li, 2010), but almost all studies to date have focused on web-building spiders (i.e. spiders that use a web for prey capture). Another group of spiders, the hunting spiders, typically do not build webs. Many species of hunting spider actively range through the environment, and these species may rely more heavily on chemotactile pheromones to elicit courtship (Foelix, 2011). Yet, as illustrated by the well-known example of thomisid spiders that sit on flowers waiting to ambush insects that arrive to gather pollen or nectar (Morse, 2007), being relatively sedentary does not require living in webs. Given that activity levels of spiders probably lie on a continuum, we might expect female sex pheromones (mate-attraction pheromones) to be more prevalent among species at the more sedentary end of the continuum, irrespective of web use.

As a step toward clarifying the role of pheromones in a large group of hunting spiders, we carried out olfactory-pheromone experiments on 29 species from the spider family Salticidae (jumping spiders). Although salticids are better known for their intricate vision-based behaviour made possible by complex eyes supporting exceptional spatial acuity (Land & Nilsson, 2002; Harland, Li & Jackson, 2012; Nagata *et al.*, 2012), numerous studies have illustrated that salticids also make extensive use of acoustic, seismic, silk-borne, and tactile signalling during intraspecific interactions (Edwards, 1981; Gwynne & Dadour, 1985; Maddison & Stratton, 1988; Noordam, 2002; Elias *et al.*, 2003, 2005, 2010, 2012; Sivalinghem *et al.*, 2010). The ways in which salticids rely on chemoreception are especially varied (Jackson & Cross, 2011), but experimental evidence of response to specifically olfactory sex pheromones has come from only seven salticids – *Evarcha culicivora*, two *Cyrba* species, and four *Portia* species (Willey & Jackson, 1993; Cross & Jackson, 2009; Jackson & Cross, 2011; A. M. Cerveira & R. R. Jackson, unpubl. data). The vast majority of the Salticidae, including *Evarcha*, belong to a well-defined clade, the Salticoida (Maddison & Hedin, 2003), but *Cyrba* and *Portia* are from the subfamily Spartaeinae. Along with the lyssomanines, cocalodines, hisponines, and lapsiines, spartaeines are regarded as basal clades within the Salticidae (Maddison, 2006, 2009; Maddison & Needham, 2006; Maddison & Zhang, 2006; Su *et al.*, 2007). The salticids we consider here all belong to two of these basal clades, the Lyssomaninae and Spartaeinae.

Despite being referred to as hunting spiders, there are salticid species that build webs (Jackson, 1986) and even an individual salticid may sometimes be both a web spider and a hunting spider. For example, the building of large prey-capture webs is characteristic of the spartaeine *Portia*, but with individuals alternating between using their webs and making prey-capture forays away from, and then returning to, their webs (Jackson & Blest, 1982). Specialized predation on other spiders (araneophagy), expressed by invading other spiders' webs, by gleaning spiders off the edges of their webs or by making ambushing attacks completely away from webs, is common in the Spartaeinae (Jackson & Pollard, 1996; Nelson & Jackson, 2011), with the spartaeine tending to remain at fixed locations for extended periods. Less is known about lyssomanine behaviour, but these species build, and appear to spend much of their time under, silk sheets (rudimentary webs) on leaves, from which they launch attacks on insects that land on the silk or nearby (e.g. Hallas & Jackson, 1986; Jackson, 1986). On the whole, their lifestyles (Su *et al.*, 2007; Table 1) may predispose spartaeines and lyssomanines to be unusually sedentary as compared with other salticids. On this basis, it seemed especially likely that we would find species that rely on olfactory mate-locating pheromones in these two subfamilies. Our experiments were also designed to investigate whether attraction to olfactory pheromones by spartaeines and lyssomanines tends to be expressed primarily by males instead of by females.

## MATERIAL AND METHODS
### GENERAL

For each species, all individuals used (Table 2) were from laboratory cultures (2nd and 3rd generation) and, after dispersal from the egg sac, none of these individuals had encounters with other salticids. For rearing and maintenance, we adopted the standard procedures routinely used in our laboratory for salticid research (see Jackson & Hallas, 1986a; Cerveira & Jackson, 2011), with all tests beginning between 0800 and 1500 h (laboratory photoperiod 12L:12D, lights on at 0700 h) and no individual spider being used more than once as a test spider or source spider, a source spider being an individual which provided the potential pheromones to which the test spider was exposed. All test and source spiders were unmated adults that had matured 2–3 weeks before testing and had fasted for 4–5 days before use.

We used two olfactometer procedures that were identical to those adopted in numerous previous studies (retention testing, see Cross, Jackson &

**Table 1.** Characteristics of salticid genera tested for olfactory sex pheromones

| Genus | Resting site built by the spider | Predatory strategy | Reference(s) |
|---|---|---|---|
| *Asemonea** | Silk sheets across underside of leaves | Captures insects on and near silk sheet | Jackson (1990e) |
| *Brettus** | Silk sheets across undersides of leaves | Araneophagic web-invading aggressive mimics | Jackson & Hallas (1986b) |
| *Cocalus** | Silk sheets on tree trunks | Araneophagic web invaders | Jackson (1990a) |
| *Cyrba** | Silk sheets across underside of stones on ground | Araneophagic web-invading aggressive mimics | Jackson & Hallas (1986b); Jackson (1990b) |
| *Goleba†* | Silk sheets across underside of leaves | Captures insects on and near silk sheet | Jackson (1990e) |
| *Gelotia** | Hangs dead leaf below other spiders' webs | Araneophagic web-invading aggressive mimics | Jackson (1990c) |
| *Holcolaetis** | Sits on tree trunks, often under other spiders' webs | Araneophagy by ambushing and slow stalking | Su *et al.* (2007) |
| *Lyssomanes†* | Silk sheets across underside of leaves | Captures insects on and near silk sheet | Jackson (1990e) |
| *Meleon** | On leaves, often under other spiders' webs | Araneophagic web invaders | R. R. Jackson, unpubl. data |
| *Neobrettus** | On leaves, often under other spiders' webs | Araneophagic web-invading aggressive mimics | Su *et al.* (2007) |
| *Onomastus†* | Silk sheets across underside of leaves | Captures insects on and near silk sheet | Jackson (1990e) |
| *Paracyrba** | Inhabits bamboo internodes. Minimal silk use | Pulls aquatic insects from water in bamboo internodes | Zabka & Kovac (1996) |
| *Phaeacius** | Silk sheets webs on tree trunks | Araneophagy by ambushing and slow stalking | Jackson & Hallas (1986b); Jackson (1990d) |
| *Portia** | Large, three-dimensional web | Araneophagic web-invading aggressive mimics | Jackson & Hallas (1986a); Li, Jackson & Barrion, (1997) |
| *Spartaeus** | Rudimentary sheet webs on tree trunks | Captures insects on web | Jackson & Pollard (1990) |

*Spartaeinae; †Lyssomaninae.

Pollard, 2009; choice testing, see Jackson, Nelson & Sune, 2005), with airflow always set at 1500 mL min$^{-1}$ (Matheson FM-1000 airflow regulator). With retention tests, we determined how long a test spider remained in a holding chamber when exposed to specific odours; the underlying rationale was an expectation that test spiders would remain in the holding chamber longer when it could detect a preferred odour and would more quickly leave when there was no odour source in the odour chamber (see Cross *et al.*, 2009). In choice tests, we used Y-shaped glass olfactometers with the two ends of the Y each connected to an odour source toward which the spider could move if attracted to the odour.

Odour chambers (see Fig. 1 for dimensions), a feature common to both testing procedures, were glass tubes. There was a rubber stopper at each end of each tube. Smaller glass tubes (length 45 mm, diameter 4 mm) 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. The source spider, or its draglines, was put in the odour chamber 30 min before testing began. Spiders were confined to the chamber by nylon netting that covered the inner sides of the glass tubes extending through the stoppers. New netting was used for each trial. Between trials, olfactometers were dismantled and cleaned with 80% ethanol followed by distilled water and then dried.

To collect draglines, we used a glass Petri dish (diameter 60 mm) with blotting paper affixed with double-sided tape to the bottom and inner top of the dish. At 0700 h, the source spider was put in the dish and the dish was then oriented upright and held in place by a clamp. On the following day, 15 min before testing began, the Petri dish was opened, the source spider was removed, and one of the two circles of blotting paper (chosen at random) was loosely rolled up (silk-side outwards) and inserted into the odour chamber.

**Table 2.** Origin of salticid species tested for olfactory sex pheromones and choice-test results for males tested with conspecific females (odour 1) and males (odour 2); two-tailed binomial tests

| Test spider species | Locality | N | Chose odour 1 | P |
|---|---|---|---|---|
| *Asemonea murphyae* | Kenya (Nairobi) | 30 | 25 | < 0.001 |
| *Asemonea tenuipes* | Sri Lanka (Kandy) | 30 | 23 | 0.005 |
| *Brettus adonis** | Sri Lanka (Kandy) | 20 | 16 | 0.012 |
| *Brettus albolimbatus* | Sri Lanka (Kandy) | 30 | 20 | 0.099 |
| *Cocalus gibbosus* | Australia (Queensland) | 20 | 20 | < 0.001 |
| *Cyrba algerina* | Portugal (Sintra) | 20 | 17 | 0.003 |
| *Cyrba ocellata* | Kenya (Kisumu) | 20 | 19 | < 0.001 |
| *Cyrba simoni* | Kenya (Kisumu) | 20 | 19 | < 0.001 |
| *Goleba puella* | Kenya (Malindi) | 30 | 25 | < 0.001 |
| *Gelotia lanka* | Sri Lanka (Galle) | 20 | 17 | 0.003 |
| *Holcolaetis vellerea* | Kenya (Kisumu) | 20 | 18 | < 0.001 |
| *Lyssomanes patens* | Costa Rica (Finca La Selva) | 30 | 24 | 0.001 |
| *Lyssomanes viridis* | USA (Florida) | 30 | 22 | 0.016 |
| *Meleon solitaria* | Uganda (Entebbe) | 30 | 29 | < 0.001 |
| *Neobrettus nangalisagus* | Philippines (Luzon) | 20 | 19 | < 0.001 |
| *Onomastus nigricauda* | Sri Lanka (Negombo) | 30 | 28 | < 0.001 |
| *Paracyrba wanlessi* | Malaysia (Kuala Lumpur) | 30 | 22 | 0.016 |
| *Phaeacius malayensis* | Singapore | 20 | 18 | < 0.001 |
| *Phaeacius wanlessi* | Sri Lanka (Kandy) | 20 | 16 | 0.012 |
| *Portia africana* | Kenya (Kisumu) | 30 | 28 | < 0.001 |
| *Portia albimana* | Sri Lanka (Kandy) | 20 | 20 | < 0.001 |
| *Portia fimbriata* | Australia (Queensland) | 30 | 23 | 0.005 |
| *Portia jianfengensis* | China (Hainan) | 20 | 17 | 0.003 |
| *Portia labiata* | Sri Lanka (Kandy) | 30 | 24 | 0.001 |
| *Portia* cf. *orientalis†* | Philippines (Luzon) | 30 | 28 | < 0.001 |
| *Portia quei* | China (Yunan) | 20 | 18 | < 0.001 |
| *Portia schultzi* | Kenya (Malindi) | 30 | 29 | < 0.001 |
| *Spartaeus spinimanus* | Singapore | 30 | 24 | 0.001 |
| *Spartaeus thailandicus* | Thailand | 20 | 19 | < 0.001 |

*Previously *Brettus cingulatus*.
†Previously *Portia labiata*.

### RETENTION TESTS

Retention tests followed a paired design, with each test spider being tested twice: with odour from one source spider on one day and with a no-odour control on the next or previous day (sequence determined at random). For each species, one set of males was tested with odour of conspecific females, another set with heterospecific females and yet another with conspecific males, and females were tested with the odour of conspecific males. With seven of these species, we also tested males using as the odour source the draglines of conspecific females with the females absent. No test spider was used in more than one pair of tests.

Air in retention test olfactometers was pushed successively through an odour chamber, the holding chamber, and an exit chamber (Fig. 1A). The holding chamber was a glass tube (identical to the odour chamber). The test spider was confined in the holding chamber for 2 min before testing began, with each end plugged by a stopper (no holes in stoppers). We began testing by un-plugging the two sides of the holding chamber, connecting one side to the odour chamber and the other to an exit chamber, making sure that the tests began with the test spider in the half of the holding chamber furthest from the exit chamber. The exit chamber was a glass cube with two holes (diameter 20 mm) opposite each other. When connected, the open end of the holding chamber fit into one of the hole in the exit chamber (flush with the inner wall of the exit chamber), the other end being plugged with a rubber stopper and, via a small glass tube through this stopper, air could move in from the odour chamber. As there was nylon netting over the inner opening in the small tube going through the stopper, the only way the test spider
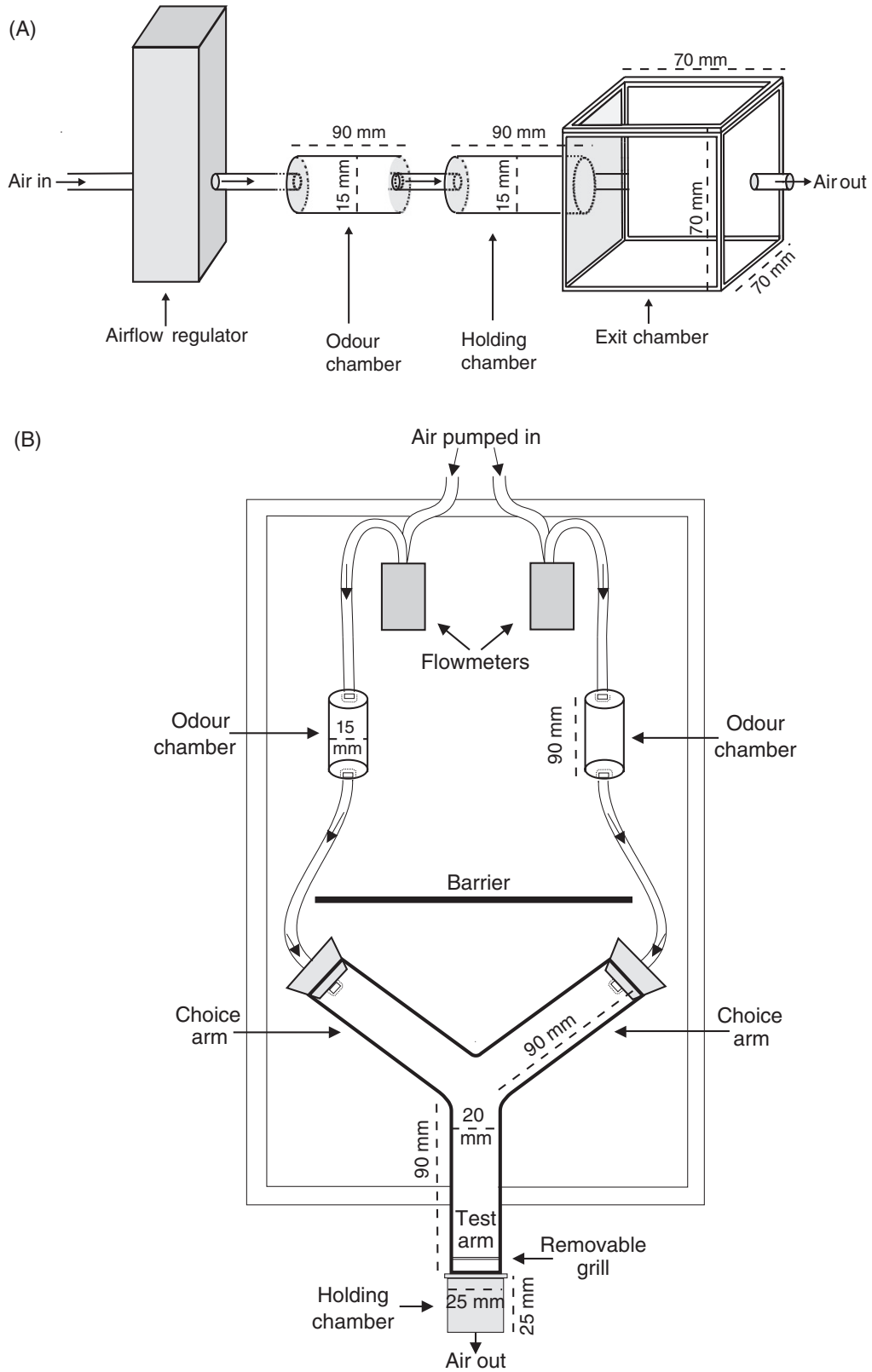
**Figure 1.** Olfactometers used for (A) retention testing (view of odour source obstructed by black paper taped to outside of odour chamber wall that faced holding chamber) and (B) choice testing (view of odour source obstructed by opaque barrier). Dashed arrows indicate direction of airflow. Not drawn to scale.

could leave the holding chamber took it into the exit chamber.

We recorded the time elapsing between the beginning of each test and the test spider entering the exit chamber. Maximum test duration allowed was 60 min, with latency to leave being recorded as 60 min whenever the 60-min test period ended with the test spider still in the holding chamber.

## CHOICE TESTS

Choice testing was carried out using a Y-shaped olfactometer (Fig. 1B) with a pump pushing air independently into two odour chambers. From the two odour chambers, air moved independently into the two arms of the Y. With both sexes of all 29 species, experiments were carried out (Table 2) using different pairings of odours in the two chambers (both conspecific, opposite sex in one chamber, same sex in the other; both opposite sex, conspecific in one chamber, heterospecific in the other). Before testing began, the test spider was confined for 2 min to a holding chamber at the far end of the test arm. A metal grill that fit 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. No spider was used in more than one test. In previous research on two *Cyrba* species (A. M. Cerveira & R. R. Jackson, unpubl. data) and four *Portia* species (Jackson & Cross, 2011), the same choice-testing olfactometer was used, but with an odour source in only one stimulus chamber, the other chamber being empty (no-odour control), unlike here where we use choice testing specifically to test for olfactory species and sex discrimination.

## ANALYSIS

Data for retention tests were analysed using Wilcoxon matched-pairs tests comparing the latency of the spider to exit the holding chamber ('retention time') during the odour test and the no-odour control. These data are presented as boxplots depicting the retention time when with odour minus the retention time when with no-odour control. Data from choice tests were analysed using binomial tests comparing the number of spiders that went into each of the two choice arms of the olfactometer ($H_o = 50/50$).

## RESULTS

In retention tests, when a stimulus chamber contained the odour of a conspecific female or her draglines, retention times for males of all species were significantly longer than when tested with the no-odour control. However, for males of all species, retention times when with the odour of a heterospecific female or a conspecific male were not significantly different from retention times when with the no-odour control. For all species, retention times for females with the odour of a conspecific male and with the no-odour control were not significantly different (Table 3, Fig. 2).

In choice tests, significantly more males of all species chose the odour of conspecific females than chose the odour of conspecific males (Table 2) or heterospecific females (Table 4), but the number of females that chose the odour of conspecific males was not significantly different from the number that chose the odour of conspecific females (Table 5).

## DISCUSSION

Our objective was to investigate pheromone use in a large sample of two of the smaller salticid subfamilies, the spartaeines and lyssomanines. Prior to this study, there was evidence from many salticid species of males responding to sex pheromones when experimental design permitted contact with draglines (Jackson, 1987; Clark & Jackson, 1995; Taylor, 1998), but there was evidence from only seven species (*Evarcha culicivora*, two *Cyrba* species, and four *Portia* species: Willey & Jackson, 1993; Cross & Jackson, 2009; Jackson & Cross, 2011; A. M. Cerveira & R. R. Jackson, unpubl. data) of males responding to sex pheromones when experimental design permitted olfaction alone. With this report, the number of salticids shown to use olfactory sex pheromones has increased to 30 species and 17 genera. Moreover, we are aware of no instances in which appropriate experiments with large sample sizes have failed to reveal the use of olfactory pheromones.

There are 184 extant species from eight genera for lyssomanines and 193 species from 18 genera for spartaeines (Prószyński, 2011). Our data are based on four (50%) of the lyssomanine genera and 12 (66.7%) of the spartaeine genera. Obtaining very consistent evidence for the use of olfactory pheromones by the males of every species we tested, we have a strong basis for suggesting that, despite considerable variation in lifestyle and predatory strategy (Table 1), reliance on mate-searching olfactory pheromones (including detection of odour from draglines in the absence of females) is a widespread, and perhaps universal, characteristic of lyssomanines and spartaeines, independent of whether a given species is a web builder (e.g. *Portia*) or not (e.g. *Phaeacius*).

It is known that the females of species from two salticoid genera, *Evarcha* (Jackson *et al.*, 2005) and *Naphys* (Clark, Jackson & Cutler, 2000), and two spartaeine genera, *Cyrba* and *Portia* (Clark, Harland

**Table 3.** Sample size and test statistics (Wilcoxon matched-pairs tests) from olfactometer retention tests using 29 salticid species

| Species | N | Females tested with odour of conspecific males | | Males tested with odour of conspecific males | | Males tested with odour of heterospecific females | | Males tested with odour of conspecific females | | Males tested with odour of conspecific female draglines | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | W | P | W | P | W | P | W | P | W | P |
| *Asemonea murphyae* | 25 | −20.0 | 0.786 | 30.0 | 0.638 | 17.0 | 0.819 | 232.0 | 0.002 | 203.0 | 0.004 |
| *Asemonea tenuipes* | 25 | −28.0 | 0.716 | −23.0 | 0.767 | 71.0 | 0.346 | 222.0 | 0.002 | — | — |
| *Brettus adonis* | 20 | −15.0 | 0.794 | 13.0 | 0.823 | −30.0 | 0.588 | 115.0 | 0.013 | — | — |
| *Brettus albolimbatus* | 20 | 0.0 | 1.000 | −30.0 | 0.527 | 4.0 | 0.955 | 134.0 | 0.007 | — | — |
| *Cocalus gibbosus* | 20 | −27.0 | 0.571 | 2.0 | 0.984 | 30.0 | 0.527 | 110.0 | 0.010 | — | — |
| *Cyrba algerina* | 20 | 33.0 | 0.519 | −10.0 | 0.845 | −36.0 | 0.481 | 134.0 | 0.007 | 120.0 | 0.005 |
| *Cyrba ocellata* | 20 | −34.0 | 0.537 | −9.0 | 0.881 | 59.0 | 0.206 | 160.0 | 0.001 | 167.0 | <0.001 |
| *Cyrba simoni* | 20 | −30.0 | 0.526 | −25.0 | 0.654 | −36.0 | 0.513 | 168.0 | <0.001 | — | — |
| *Gelotia lanka* | 19 | −7.0 | 0.896 | 11.0 | 0.813 | −34.0 | 0.506 | 131.0 | 0.005 | — | — |
| *Goleba puella* | 25 | −25.0 | 0.731 | −40.0 | 0.577 | 46.0 | 0.520 | 184.0 | 0.003 | 189.0 | 0.011 |
| *Holcolaetis vellerea* | 30 | 39.0 | 0.695 | 46.0 | 0.608 | 87.0 | 0.301 | 322.0 | <0.001 | 189.0 | 0.011 |
| *Lyssomanes patens* | 25 | −10.0 | 0.904 | 88.0 | 0.213 | 78.0 | 0.299 | 223.0 | <0.001 | — | — |
| *Lyssomanes viridis* | 30 | 93.0 | 0.293 | 91.0 | 0.144 | −54.0 | 0.501 | 378.0 | <0.001 | — | — |
| *Meleon solitaria* | 25 | −23.0 | 0.737 | 104.0 | 0.117 | 45.0 | 0.411 | 278.0 | <0.001 | 189.0 | 0.011 |
| *Neobrettus nangalisagus* | 30 | −66.0 | 0.459 | 133.0 | 0.132 | −123.0 | 0.163 | 431.0 | <0.001 | — | — |
| *Onomastus nigricauda* | 30 | −80.0 | 0.392 | 53.0 | 0.484 | −59.0 | 0.530 | 404.0 | <0.001 | — | — |
| *Paracyrba wanlessi* | 30 | −82.0 | 0.356 | 17.0 | 0.862 | 30.0 | 0.753 | 310.0 | <0.001 | — | — |
| *Phaeacius malayensis* | 25 | −15.0 | 0.820 | 57.0 | 0.394 | −13.0 | 0.872 | 323.0 | <0.001 | — | — |
| *Phaeacius wanlessi* | 25 | −10.0 | 0.898 | 16.0 | 0.840 | 7.0 | 0.927 | 227.0 | 0.001 | — | — |
| *Portia africana* | 25 | 0.0 | 1.000 | −38.0 | 0.617 | −50.0 | 0.426 | 207.0 | 0.003 | 189.0 | 0.011 |
| *Portia albimana* | 25 | −81.0 | 0.252 | 63.0 | 0.404 | 91.0 | 0.225 | 241.0 | <0.001 | — | — |
| *Portia fimbriata* | 25 | 87.0 | 0.246 | 4.0 | 0.958 | 42.0 | 0.532 | 268.0 | <0.001 | — | — |
| *Portia jianfengensis* | 25 | −25.0 | 0.732 | −18.0 | 0.808 | 90.0 | 0.203 | 202.0 | 0.007 | — | — |
| *Portia labiata* | 25 | 53.0 | 0.429 | −14.0 | 0.808 | 45.0 | 0.529 | 210.0 | 0.003 | — | — |
| *Portia cf. orientalis* | 25 | −21.0 | 0.775 | 47.0 | 0.511 | −70.0 | 0.353 | 272.0 | <0.001 | — | — |
| *Portia quei* | 25 | 38.0 | 0.573 | −15.0 | 0.851 | 6.0 | 0.939 | 223.0 | <0.001 | — | — |
| *Portia schultzi* | 25 | 34.0 | 0.616 | −10.0 | 0.898 | −43.0 | 0.548 | 211.0 | 0.005 | — | — |
| *Spartaeus spinimanus* | 25 | −64.0 | 0.306 | −54.0 | 0.419 | 6.0 | 0.943 | 213.0 | 0.001 | — | — |
| *Spartaeus thaliandicus* | 25 | 21.0 | 0.775 | 73.0 | 0.303 | 51.0 | 0.447 | 271.0 | <0.001 | — | — |
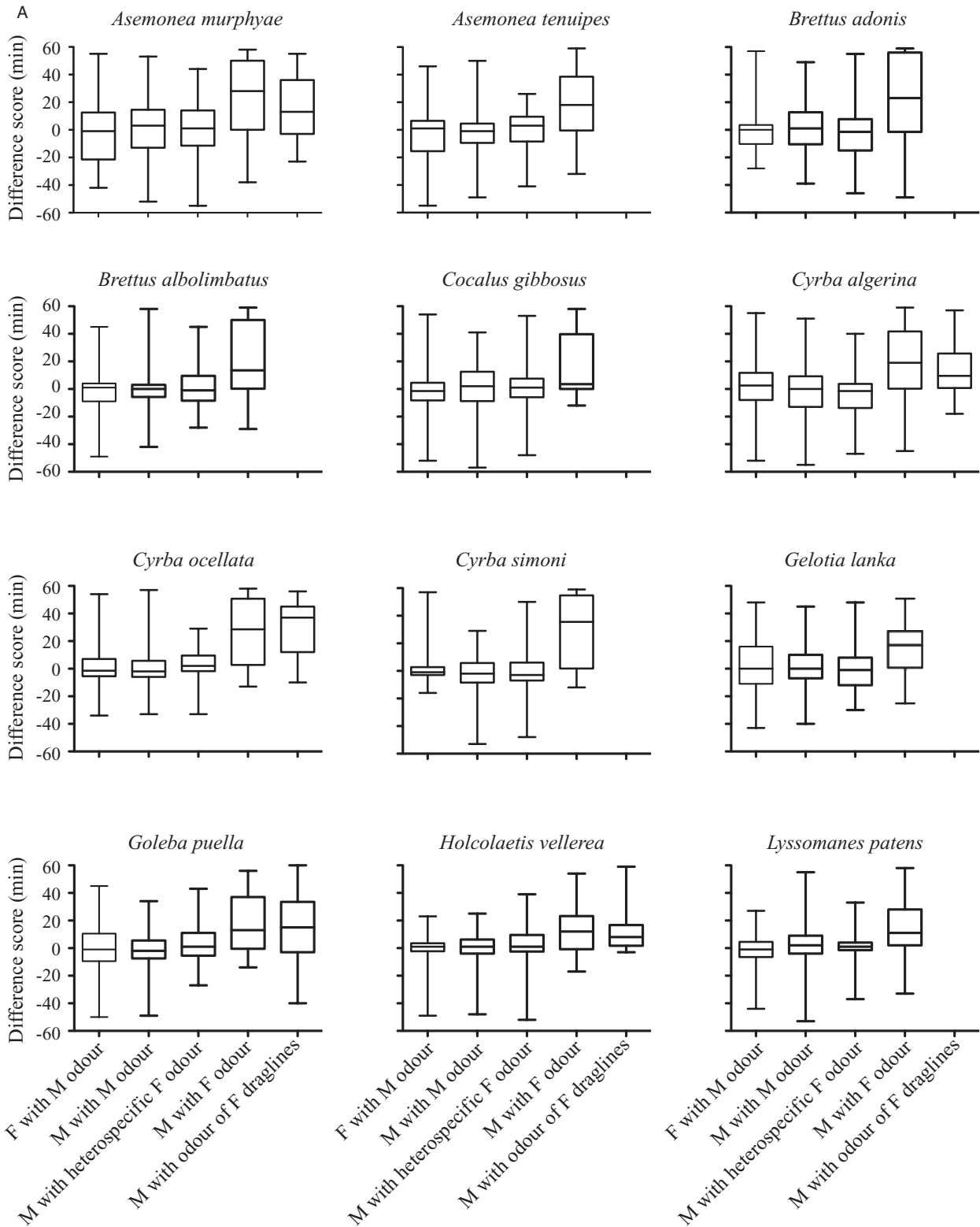
**Figure 2.** Boxplots (median and quartiles) with whiskers (min. and max.) depicting scores [retention time when with odour minus retention time when with no-odour control for 29 species of lyssomanine and spartaeine salticids (positive, spider spent longer within holding chamber with odour; negative, spider spent longer within holding chamber with control)]. All tested with conspecific odour unless specified in legend. M, male; F, female.
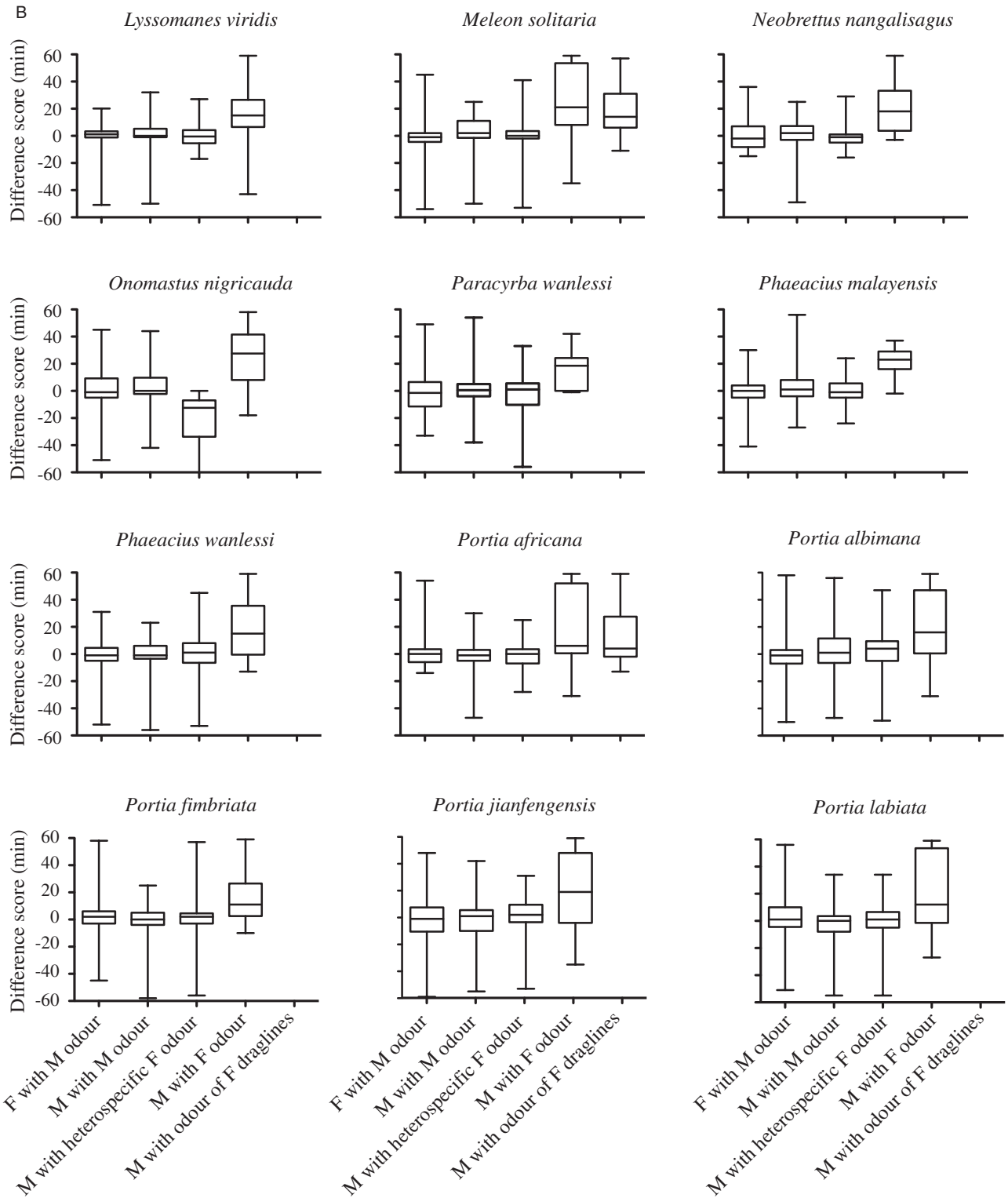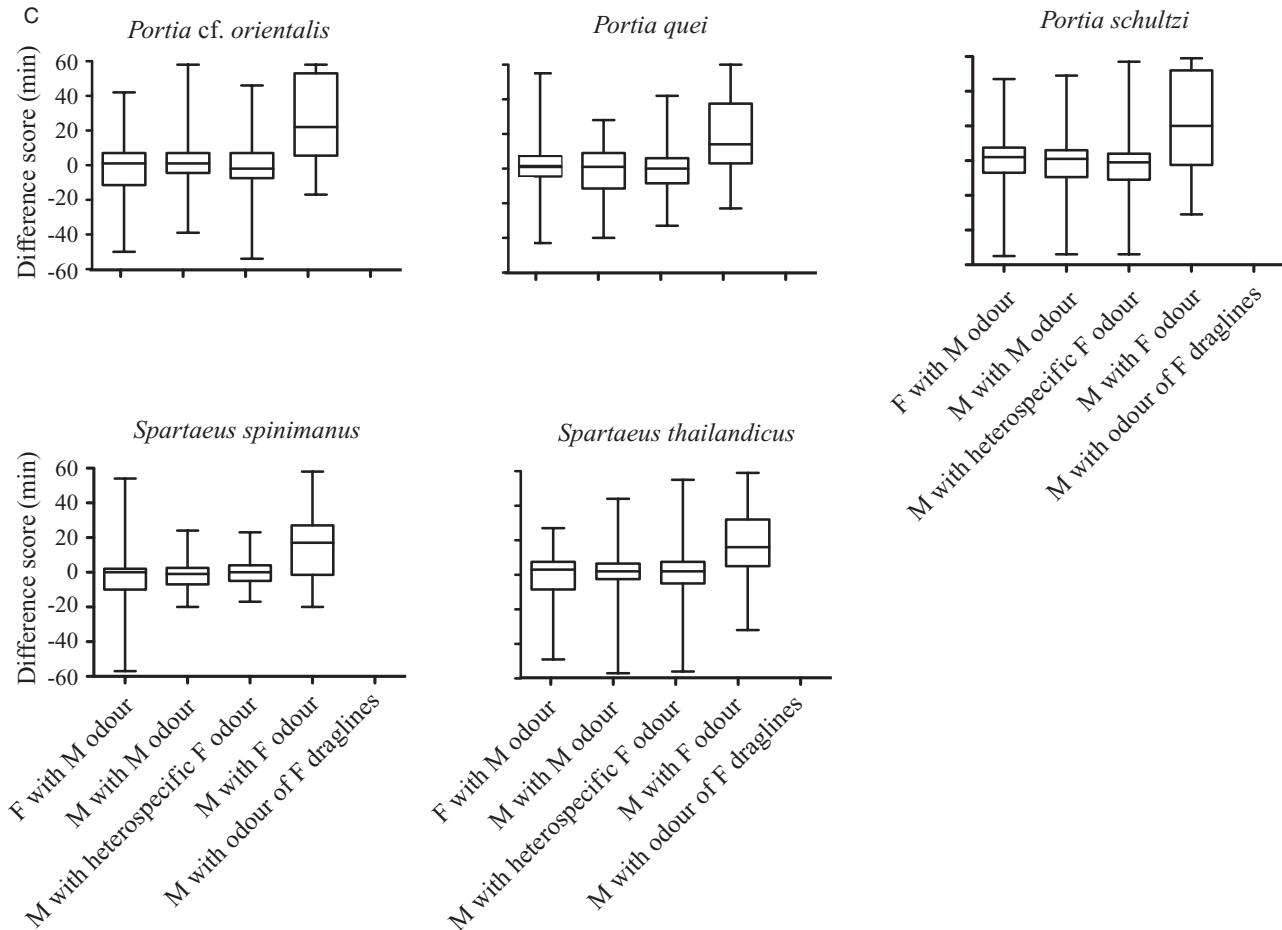
**Figure 2.** *Continued*

**Figure 2.** *Continued*

& Jackson, 2000; Jackson, Clark & Harland, 2002; Cerveira & Jackson, 2011), can identify the odour of particular types of prey. Other contexts in which lyssomanine and spartaeine females, as well as males, might make use of olfactory cues should also be considered. For example, some lycosid spiders are alerted by chemical cues from specific predators (Persons & Rypstra, 2001; Persons *et al.*, 2001; Schonewolf *et al.*, 2006; Eiben & Persons, 2007; Rypstra *et al.*, 2007). Other contexts in which *Portia* females have been shown to use chemical cues include discriminating between its own and another spider's eggs and draglines and even determining the fighting ability of a rival (Clark & Jackson, 1994a, b; Clark, Jackson & Waas, 1999). In these studies, *Portia* females could touch draglines from the source spider and the behavioural effects were referred to as being mediated by contact chemoreception.

Many of the species tested here use their silk to capture prey, and so may have less need to move about than many of the more modern salticids that hunt prey away from their nests, where they can often be seen to encounter opposite sex conspecifics and begin courtship behaviour. While this may be solely visually mediated, evidence to date suggests that pheromones (contact or airborne) are also involved (Jackson, 1987; Clark & Jackson, 1995; Taylor, 1998; Cross & Jackson, 2009). Sexually mature male salticids tend not to be especially motivated to feed, seemingly more 'intent' on searching for a mate (Jackson & Pollard, 1997; Zurek *et al.*, 2010). We suggest that a strong reliance on olfactory mate searching pheromones by males is associated with a tendency to be sedentary, based on our observations spanning several decades (R. R. Jackson, unpubl. observ.) that the lyssomanines and spartaeines subfamilies are, compared with other salticids, relatively sedentary. This hypothesis remains to be explicitly tested in these two groups and in the wider range of salticoid species, including the salticoids known to build webs (see Harland *et al.*, 2012), but future work in this area may be productive, as our current knowledge lends some support to this idea. The only salticoid that has been shown to use olfactory sex

**Table 4.** Choice-test results for males tested with conspecific females (odour 1) and heterospecific females (odour 2); two-tailed binomial tests

| Test spider species | *N* | Odour 2 | Chose odour 1 | *P* |
|---|---|---|---|---|
| *Asemonea murphyae* | 20 | *Asemonea tenuipes* | 19 | < 0.001 |
| *Asemonea tenuipes* | 20 | *Asemonea murphyae* | 16 | 0.012 |
| *Brettus adonis* | 20 | *Brettus albolimbatus* | 18 | < 0.001 |
| *Brettus albolimbatus* | 20 | *Brettus adonis* | 20 | < 0.001 |
| *Cocalus gibbosus* | 20 | *Portia fimbriata* | 16 | 0.012 |
| *Cyrba algerina* | 20 | *Cyrba ocellata* | 16 | 0.012 |
| *Cyrba ocellata* | 30 | *Cyrba simoni* | 29 | < 0.001 |
| *Cyrba simoni* | 30 | *Cyrba ocellata* | 23 | 0.005 |
| *Goleba puella* | 30 | *Asemonea murphyae* | 27 | < 0.001 |
| *Gelotia lanka* | 20 | *Portia labiata* | 16 | 0.012 |
| *Holcolaetis vellerea* | 20 | *Portia africana* | 18 | < 0.001 |
| *Lyssomanes patens* | 30 | *Lyssomanes viridis* | 27 | < 0.001 |
| *Lyssomanes viridis* | 30 | *Lyssomanes patens* | 25 | < 0.001 |
| *Meleon solitaria* | 20 | *Portia africana* | 18 | < 0.001 |
| *Neobrettus nangalisagus* | 20 | *Portia labiata* | 17 | 0.003 |
| *Onomastus nigricauda* | 20 | *Asemonea tenuipes* | 19 | < 0.001 |
| *Paracyrba wanlessi* | 20 | *Portia labiata* | 16 | 0.012 |
| *Phaeacius malayensis* | 20 | *Phaeacius wanlessi* | 18 | < 0.001 |
| *Phaeacius wanlessi* | 20 | *Phaeacius malayensis* | 17 | 0.003 |
| *Portia africana* | 20 | *Portia schultzi* | 20 | < 0.001 |
| *Portia albimana* | 20 | *Portia labiata* | 18 | < 0.001 |
| *Portia fimbriata* | 20 | *Portia labiata* | 17 | 0.003 |
| *Portia jianfengensis* | 20 | *Spartaeus spinimanus* | 18 | < 0.001 |
| *Portia labiata* | 20 | *Portia fimbriata* | 16 | 0.012 |
| *Portia* cf. *orientalis* | 20 | *Portia quei* | 19 | < 0.001 |
| *Portia quei* | 20 | *Portia* cf. *orientalis* | 17 | 0.003 |
| *Portia schultzi* | 20 | *Portia africana* | 19 | < 0.001 |
| *Spartaeus spinimanus* | 30 | *Spartaeus thailandicus* | 24 | 0.001 |
| *Spartaeus thailandicus* | 20 | *Spartaeus spinimanus* | 17 | 0.003 |

pheromones is *E. culicivora* (Cross & Jackson, 2009), both sexes of which are active participants in courtship, are attracted to the odour of conspecific opposite-sex individuals (Cross & Jackson, 2009), and exhibit mutual mate-choice (Cross *et al.*, 2007, 2008) – although its movement patterns are relative to other salticioids is unknown. In the species tested here, males responded to the odour of conspecific females, but there was no evidence of females responding to the odour of conspecific males, consistent with these being species more reliant on female mate choice and male mate searching.

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**Table 5.** Choice-test results for females tested with con-specific males (odour 1) and females (odour 2); two-tailed binomial tests

| Test spider species | N | Chose odour 1 | P |
|---|---|---|---|
| *Asemonea murphyae* | 30 | 13 | 0.585 |
| *Asemonea tenuipes* | 30 | 16 | 0.856 |
| *Brettus adonis* | 20 | 12 | 0.503 |
| *Brettus albolimbatus* | 30 | 10 | 0.099 |
| *Cocalus gibbosus* | 20 | 11 | 0.824 |
| *Cyrba algerina* | 20 | 12 | 0.503 |
| *Cyrba ocellata* | 20 | 10 | 1.000 |
| *Cyrba simoni* | 20 | 10 | 1.000 |
| *Goleba puella* | 30 | 13 | 0.585 |
| *Gelotia lanka* | 20 | 9 | 0.824 |
| *Holcolaetis vellerea* | 20 | 10 | 1.000 |
| *Lyssomanes patens* | 30 | 17 | 0.585 |
| *Lyssomanes viridis* | 30 | 14 | 0.856 |
| *Meleon solitaria* | 30 | 18 | 0.362 |
| *Neobrettus nangalisagus* | 20 | 8 | 0.503 |
| *Onomastus nigricauda* | 30 | 16 | 0.856 |
| *Paracyrba wanlessi* | 30 | 15 | 1.000 |
| *Phaeacius malayensis* | 20 | 12 | 0.503 |
| *Phaeacius wanlessi* | 20 | 10 | 1.000 |
| *Portia africana* | 30 | 15 | 1.000 |
| *Portia albimana* | 20 | 9 | 0.824 |
| *Portia fimbriata* | 30 | 17 | 0.585 |
| *Portia jianfengensis* | 20 | 10 | 1.000 |
| *Portia labiata* | 30 | 14 | 0.856 |
| *Portia* cf. *orientalis* | 30 | 13 | 0.585 |
| *Portia quei* | 20 | 8 | 0.503 |
| *Portia schultzi* | 30 | 14 | 0.856 |
| *Spartaeus spinimanus* | 30 | 13 | 0.585 |
| *Spartaeus thailandicus* | 20 | 10 | 1.000 |

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