

Mode of use of sexually dimorphic glands in a Neotropical harvestman (Arachnida: Opiliones) with paternal care

G.P. Murayama and R.H. Willemart*

Laboratório de Ecologia Sensorial e Comportamento de Artrópodes (LESCA), Escola de Artes Ciências e Humanidades, Universidade de São Paulo, São Paulo, Brazil

(Received 10 March 2014; accepted 2 January 2015; first published online 18 February 2015)

Males of *Iporangaia pustulosa* (Arachnida: Opiliones) have a sexually dimorphic metatarsus IV, which is thicker and with more glandular pores in males. Here we tested the hypothesis that this glandular area is used by males to leave chemicals in the environment, predicting that the animals would rub the metatarsus IV against the substrate. We have made recordings both in the field and in the laboratory, in several distinct contexts during the day and at night, comprising 67 hours of observations. We also experimentally tested the reaction of both sexes to a filter paper rubbed on the metatarsus gland, with adequate controls. We report and describe for the first time that the metatarsal gland of *I. pustulosa* is used to leave chemicals on the substrate by rubbing or touching it against the substrate. We also provide evidence that males can control the release of secretions of the metatarsal gland IV.

Keywords: chemical communication; gonyleptidae; mate finding; pheromone; Progonyleptoidellinae

Introduction

Animals of different taxa have sexually dimorphic glands that produce secretions differing between the sexes (arachnids: Juberthie-Jupeau and Lopez 1991; mammals: Kruuk et al. 1984; Hoh et al. 1984; Cangussu et al. 2002; amphibians: Wabnitz et al. 1999), usually with sexual functions (Andersson 1994; Jaffe et al. 2007). These glands may be used in several ways including airborne release (Wedell 2005; Allen et al. 2012), rubbing on the substrate (Atkeson and Marchinton 1982) or rubbing directly against conspecifics (Ralls 1971; Hutchings and White 2000).

Chemicals released by such glands may have several roles, such as attracting the opposite sex and stimulating courtship (Suter and Renkes 1982; Olsson et al. 2006; Gaskett 2007; Brum et al. 2012), providing information on the size of the individual (Carazo et al. 2011), social status (Martín et al. 2007), physiological state (Ibáñez et al. 2012) and territory marking (Gosling and Roberts 2001; Khannoon et al. 2011). The behavioural reaction of males and females towards conspecific chemicals also varies: when males find chemicals of conspecific males, the responses are avoiding the site (Melville et al. 2003; Miller and Formanowicz 2011), running away or becoming aggressive (Khannoon et al. 2011). When females detect chemicals of conspecific males, they often spend more time on the spot (Wabnitz et al. 1999; Pearl et al. 2000;

*Corresponding author. Email: willemart@usp.br

Steiner and Ruther 2009). Such behaviours are obviously only possible in animals that have an accurate sense of smell or taste, and that is true for some arachnids including species in the order Opiliones (Willemart et al. 2009).

The use of chemicals is particularly important for harvestmen. Chemoreception is used for finding back shelters (Donaldson and Grether 2007; Teng et al. 2012; Santos et al. 2013), food and predator detection (Willemart and Chelini 2007; Chelini et al. 2009; Costa and Willemart 2013), detection of alarm pheromones (Machado et al. 2002) and conspecific recognition (Willemart and Hebets 2012).

In the harvestman *Iporangaia pustulosa* Mello-Leitão 1935 (Gonyleptidae, Progonyleptoidellinae), males take care of eggs (Requena et al. 2009). A male can copulate with several females, which will add eggs to the batch the male is guarding on the inferior part of leaves (Machado et al. 2004; Requena et al. 2009). This species has a sexually dimorphic metatarsus IV that is thicker and darker in males, which bear more of such glandular pores than females. The small pores are widely spread on that specific region of the metatarsus (Willemart et al. 2007). The mode of use of these glands is unknown. There is no mention of use of these glandular openings during copulation (Requena and Machado 2014). It is not known if males are capable of attracting the female to themselves or the egg batch. Because some harvestmen species have been observed to drag body parts against the substrate possibly leaving chemicals (Willemart and Hebets 2012; Willemart et al. 2007, 2009; Fernandes and Willemart 2014), we tested the hypothesis that this glandular area is used by males to leave chemicals in the environment, predicting that the animals would rub the metatarsus IV against the substrate. We also tested how both sexes react to a filter paper rubbed on the metatarsus gland. Finally, we report a putative use of a gland on the tarsus I that is also absent in females.

Methods

Collection and maintenance in the laboratory

We collected the animals in Parque Estadual de Intervalos, in Ribeirão Grande, South of the State of São Paulo (24°14'S, 48°04'W). We conducted the fieldwork from February to April 2012, which is the reproductive season for this species (Requena et al. 2009). For both the preliminary trials and the actual experiments we collected a total of 68 males and 72 females and brought them to the laboratory. All the animals were maintained in individual plastic containers (20 cm diameter × 8 cm height) with a retreat, a wet cotton ball and soil on the bottom. The animals were maintained at room temperature, with the natural day–night cycle, and fed once a week with moistened dog food.

Data collection

We conducted the experiments and behavioural observations in the morning, afternoon and at night. Including preliminary experiments, the total sampling times of the descriptive parts were 51 h in the laboratory and 16 h in the field. These aimed at identifying how the metatarsal gland of legs IV is used. We used a Sony Handycam HDR-XR550 (Sony Corporation, Tokyo, Japan) with 'nightshot' when necessary.

Field recordings

We recorded individuals of *I. pustulosa* in the morning (06.00–12.00), afternoon (12.00–16.30) and at night (19.00–05.30), between 21 February and 3 April 2012. We used focal animal sampling with continuous recording (Martin and Bateson 2011) for 10 minutes, with 84 males randomly selected. This is in addition to other recordings that did not last 10 minutes because the animals were not observable after some minutes ($n = 25$). Typically, all the animals were wandering or stationary on the vegetation.

Laboratory recordings

We recorded the animals in the morning (09.00–10.15), afternoon (13.30–16.00) and at night (21.00–02.00) between 21 March and 2 April 2012. A male and a female ($n = 18$) were introduced in the same terrarium (31 cm \times 27 cm; height 35 cm) with humid soil on the bottom and a 40 cm plant in the centre. Five minutes after introducing the two individuals in the terrarium, we started recording continuously, for 30 min per pair.

Behavioural experiment

In this experiment we tested the reaction of conspecifics to a filter paper rubbed against the metatarsal gland IV ($n = 9$ males and 14 females). We ran the trials in the morning (07.30–10.30), afternoon (12.30–18.00) and at night (18.00–22.00), between 23 February and 24 March 2012.

The tested animal was introduced in an arena (15 \times 15 \times 15 cm) with paper towel on the bottom and a wet cotton ball to provide humidity. While we kept the specimen in a vial where it acclimated for five minutes, we rubbed a 1 \times 1 cm filter paper against both metatarsi IV of one male. We repeated the procedure with a second piece of filter paper rubbed against the exact same region of a female. We then introduced both filter papers and a third blank one side by side, in a row, separated by approximately one cm. They were placed in front of the tested animal, at one cm from the vial. The position of the three filter papers was systematically pre-determined so that the sequence would vary between trials. We released the animal and recorded it for 15 minutes, one individual at a time.

Harvestmen usually attempt to touch a chemical stimulus source they have detected (Willemart et al. 2009). We predicted that more males and females would touch the filter paper rubbed against males. Individuals that did not touch the filter papers were retested until they touched at least one of the three filter papers. Each tested individual had two secretion donors (a male and a female) and each donor only gave secretions for one tested individual. Not all donors were used as subjects in the experiment. The combinations were made in a way that most individuals (males and females) were donors and subjects. Chi square was used to test for differences between treatments in the trials.

Results

Field recordings

We have observed two ways of using the metatarsal gland IV: when gently touching the substrate, the leg would make contact with the substrate only once and then be taken

off the substrate; when the leg was rubbed on the substrate, the animal would clearly drag it against the substrate. Repeatedly touching the metatarsus IV on the substrate was observed only in one male, which touched the glandular region on the margins of a leaf for 44 s and then again on the same leaf for 24 s (Figure 1). Tibia, calcaneus and tarsus also touched the leaf. Rubbing the metatarsus IV dorsoventrally was observed in two males: the first one rubbed the metatarsus IV against a twig while it was walking, three times in 1.51 s. Another male did it against a leaf margin, once in 1.8 s.

Laboratory recordings

Two males were observed dragging the metatarsus IV: while walking, the male would lean downwards to one side, extending the leg IV of the same side and dragging the metatarsal gland IV (Figure 2). Chelicerae and legs II occasionally touched the substrate. Legs I either supported the body or were not touching the substrate. One male did it five times in an interval of 4 min 18 s (mean = 3.7 s \pm 2.30 s standard deviation [SD]). Another male did it nine times in an interval of 13 min 11 s (mean: 2.6 s \pm 1.29 s SD). Another behavioural category observed in the laboratory was similar to one observed in the field, in which the male legs III and IV of one side would support the body while the metatarsus from the other side would gently touch the substrate. Legs I and II did not touch the substrate. This behaviour was observed once and its duration was 1 s.

Experiment: reaction of conspecifics to secretions of the metatarsus IV

None of the individuals displayed any stereotyped behaviour before or after touching the filter paper, irrespective of the stimulus on it. They just wandered in the arena



Figure 1. *Iporangaia pustulosa* male touching the metatarsal gland IV on a leaf (seta).



Figure 2. *Iporangaia pustulosa* male rubbing the right metatarsus IV against the substrate (seta).

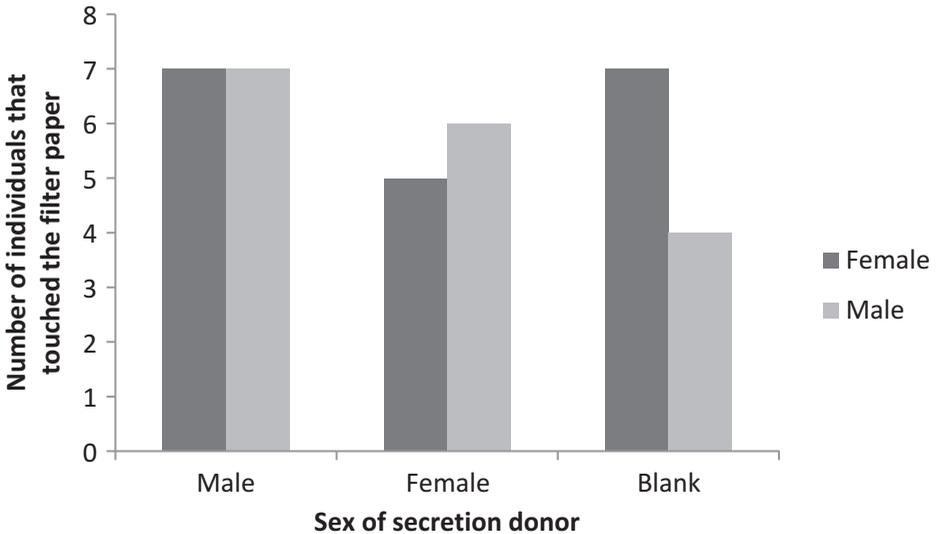


Figure 3. Number of males and females of the harvestman *Iporangaia pustulosa*, tested separately, that touched three 1×1 cm pieces of filter paper available simultaneously. The filter papers were rubbed against the sexually dimorphic proximal portion of the metatarsus IV, where males bear lots of pore glands. One piece of filter paper was rubbed against the two metatarsi of a male, the other one on the same regions of a female and the last one was blank.

tapping their surroundings with legs I and II, including the filter paper. None of the stimuli was touched preferentially (males: $\chi^2 = 0.819$; $p > 0.05$; DF = 2; females: $\chi^2 = 0.422$; $p > 0.05$; DF = 2) (Figure 3).

Other observations

In captivity, one male was observed rubbing the tarsus IV: when walking, the male twisted the right tarsus IV from left to right, keeping it in contact with the substrate and gently dragging it at the end of the behaviour (Figure 4). Males of *I. pustulosa* also bear glandular openings on the tarsi I (Willemart et al. 2010), and its mode of use is unknown. In the field, we recorded a male on the inferior side of a leaf displaying rapid dorsoventral whipping movements with a leg I. Occasionally, the male displayed leg-threading, passing this same tarsus between the chelicerae and pedipalps, and then restarted the whipping movements.

Discussion

We have described how *I. pustulosa* uses the metatarsal gland to leave chemicals on the substrate. We also provide evidence that males can control the release of secretions of the metatarsal gland IV and report a possible use of the gland in tarsus I of males, which is also sexually dimorphic. This is the first field observation on how a sexually dimorphic gland is used in the order Opiliones. The low sample size of our observations reflects the fact that the behaviours described herein are very hard to notice and last a few seconds. This species has been studied for about 10 years in the field (Machado et al. 2004; Requena et al. 2009, 2012), we have recorded and analysed videos of 136 males for 27 h and these herein are the only reports of such behaviours. As these behaviours are hard to spot and because of the implications discussed below, we consider their description very relevant.

In non-opilionid taxa, rubbing has also been observed, either directly on conspecifics or on the substrate. Other animals leave faeces and urine for marking. In every case, marking is somehow related to communication (Ralls 1971; Peters and Mech 1975; Atkeson and Marchinton 1982; Erlinge et al. 1982; Hutchings and



Figure 4. *Iporangaia pustulosa* male twisting the right tarsus IV, rubbing it against the substrate (seta).

White 2000; Barja et al. 2004; Jarau et al. 2004). Rubbing, pressing and dragging body parts has been observed in invertebrates (insects: Jarau et al. 2004; Bhadra et al. 2007; Roux et al. 2010) and vertebrates (amphibians: Teodecki et al. 1998; mammals: Kruuk et al. 1984; Pereira and Oliveira 2010; Mertl-Millhollen 2007). Previous papers have reported rubbing body parts against the substrate in other harvestmen species: Willemart et al. (2007) observed males and females of *I. pustulosa* and *Neosadocus* sp., rubbing legs III and IV on the substrate while they walk. Willemart and Hebets (2012) reported *Leiobunum vittatum* rubbing the lateral, ventral and dorsal regions of the body and Donaldson and Grether (2007) described *Prionostemma* sp. rubbing the dorsal region of the body against the substrate. Adding to these previous descriptions, here we described the twisting of tarsus IV, which can be a way of rubbing the non-sexually dimorphic tarsal aggregated pores (Willemart et al. 2007; Gainett et al. 2014), openings of glands of unknown function. However, none of these papers had reported sexually dimorphic glands being rubbed except for the very recent paper of Fernandes and Willemart (2014). The implication of rubbing sexually dimorphic glands is that harvestmen seem to leave chemicals not only for putative orientation in the environment or aggregation formation but also for sexual purposes (see Andersson 1994).

Males of some harvestmen species take care of eggs and may leave the batch unprotected in some periods of the day (Mora 1990; Hara et al. 2003; Machado et al. 2004; Proud et al. 2011). Three hypotheses have been raised to explain this behaviour: (I) males leave the batch to forage; (II) males patrol the batch at a distance as a way of repelling predators or other males; and (III) males are looking for females to copulate with (Machado et al. 2004). Based on our findings, we suggest a fourth hypothesis, which is indirectly related to the third one: males leave the batches to mark the surroundings and therefore maximize female attraction. If females can match males' scent to the scent of their secretion or if males also mark the leaf where they are (or the eggs recently laid by females if they are already guarding eggs), these could be clues to where males are located (see discussion in Wyatt 2003). Moreover, it is known that *I. pustulosa* females prefer males guarding eggs recently deposited by other females (Requena et al. 2012; see also Tallamy 2001). Our data allow us to suggest that female evaluation of males could also happen in the absence of the male or the eggs, since chemicals could provide information about the physiological state of the male (Rentala et al. 2002; Martín and López 2011). Finally, chemicals left by males may also repel male competitors, therefore avoiding direct fights with conspecifics for females (Martín et al. 2007; Ibáñez et al. 2012).

The non-significant results we obtained in the experiment suggest that the production of secretion by the metatarsal gland IV may be interrupted even during the reproductive season (when we collected our data). Such interruption is not related to the hour of the day since we have made observations in the morning, afternoon and at night. Males may produce chemicals only when they are going to use the secretion or they might have interrupted it because of our manipulation. Because harvestmen have contact chemoreceptors, because they have been reported to use contact chemoreception in several contexts, and because sexually dimorphic glands are typically used in intraspecific communication (Wyatt 2003; Willemart et al. 2009), we do not believe *I. pustulosa* would have failed to detect any chemicals if they were on the filter papers.

The behaviour of whipping legs I (where another sexually dimorphic gland is present) after passing it through the chelicerae could potentially be another form of communicating to conspecifics. Males may be diluting the secretions from the glands with water coming out of their mouth, just like they do with their defensive secretions (Gnaspini and Hara 2007). By quickly whipping the leg, it could be that secretions are dropped down to the soil, in the surroundings of the plants where the male is standing. This would be similar to what aphids do (Del-Claro and Oliveira 1996) to attract ants.

The proximal data we provide herein not only complement studies with ultimate approaches but may also help to answer ultimate questions such as why males leave their batches. We therefore hope to have helped in the understanding of this interesting system, which has contributed to the comprehension of the evolution of mating systems and parental care (Requena et al. 2009, 2012).

Acknowledgements

We thank all the members of LESCA (Laboratory of Sensory Ecology and Behavior of Arthropods) for carefully revising the manuscript: Guilherme Gainett, Guilherme Pagoti, Jessica Dias, Júlio Segovia, Norton Silva-Santos and Thaiany Costa. Julio Segovia, Guilherme Gainett, Norton Silva-Santos and Faustino Avelino Ribeiro also helped in the field. Júlio Segovia also helped with the laboratory experiments. We also thank Afonso Pelli for kindly letting us use laboratory space. Gustavo Requena and Kleber Del-Claro are thanked for the useful suggestions and discussions that helped to improve the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was supported by [grant FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo) 2010/00915-0] to RHW; and [2012/12863-0] to GPM.

References

- Allen LE, Barry KL, Holwell GI. 2012. Mate location and antennal morphology in the praying mantid *Hierodula majuscula*. *Aust J Entomol.* 51:133–140.
- Andersson M. 1994. *Sexual Selection*. Princeton: Princeton University Press.
- Atkeson TD, Marchinton RL. 1982. Forehead glands in White-Tailed Deer. *J Mammal.* 63:613–617.
- Barja I, Miguel FJ, Bárcena F. 2004. The importance of crossroads in faecal marking behaviour of the wolves (*Canis lupus*). *Naturwissenschaften.* 91:489–492.
- Bhadra A, Iyer PL, Sumana A, Deshpande SA, Ghosh S, Gadagkar R. 2007. How do workers of the primitively eusocial wasp *Ropalidia marginata* detect the presence of their queens? *J Theoretic Biol.* 246:574–582.
- Brum PED, Costa-Schmidt LE, Araujo AM. 2012. It is a matter of taste: chemical signals mediate nuptial gift acceptance in a neotropical spider. *Behav Ecol.* 23:442–447.

- Cangussu SD, Vieira FG, Rossoni RB. 2002. Sexual dimorphism and seasonal variation in submandibular gland histology of *Bolomys lasiurus* (Rodentia, Muridae). *J Morphol.* 254:320–327.
- Carazo P, Font E, Desfilis E. 2011. The role of scent marks in female choice of territories and refuges in a lizard (*Podarcis hispanica*). *J Comp Psychol.* 125:362–365.
- Chelini M-C, Willemart RH, Hebets EA. 2009. Costs and benefits of freezing behaviour in the harvestman *Eumesosoma roeweri* (Arachnida, Opiliones). *Behav Proc.* 82:153–159.
- Costa TM, Willemart RH. 2013. First experimental evidence that a harvestman (Arachnida: opiliones) detects odors of non-rotten dead prey by olfaction. *Zoologia (Curitiba).* 30:359–361.
- Del-Claro K, Oliveira PS. 1996. Honeydew flicking by treehoppers provides cues to potential tending ants. *Anim Behav.* 51:1071–1075.
- Donaldson ZR, Grether GF. 2007. Tradition without social learning: scent-mark-based communal roost formation in a Neotropical harvestman (*Prionostemma* sp.). *Behav Ecol Sociobiol.* 61:801–809.
- Erlinge S, Sandell M, Brinck C. 1982. Scent-marking and its territorial significance in stoats, *Mustela erminea*. *Anim Behav.* 30:811–818.
- Fernandes NS, Willemart RH. 2014. Neotropical harvestmen (Arachnida, Opiliones) use sexually dimorphic glands to spread chemicals in the environment. *Compt Rend Biol.* 337:269–275.
- Gainett G, Sharma PP, Pinto-da-Rocha R, Giribet G, Willemart RH. 2014. Walk it off: predictive power of appendicular characters toward inference of higher-level relationships in Laniatores (Arachnida: opiliones). *Cladistics.* 30:120–138.
- Gaskett AC. 2007. Spider sex pheromones: emission, reception, structures, and functions. *Biol Rev.* 82:27–48.
- Gnaspini P, Hara MR. 2007. Defense Mechanisms. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: the Biology of Opiliones*. Cambridge, MA: Harvard University Press; p. 374–399.
- Gosling LM, Roberts SC. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Adv Stud Behav.* 30:169–217.
- Hara MR, Gnaspini P, Machado G. 2003. Male egg guarding behavior in the neotropical harvestman *Ampheres leucopheus* (Mello-Leitão 1922) (Opiliones, Gonyleptidae). *J Arachnol.* 31:441–444.
- Hoh JH, When-L L, Nadakavukaren MJ. 1984. Sexual dimorphism in the Harderian gland proteins of the golden hamster. *Comp Biochem Physiol.* 77:729–773.
- Hutchings MR, White PCL. 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mamm Rev.* 30:157–169.
- Ibáñez A, López P, Martín J. 2012. Discrimination of conspecifics' chemicals may allow Spanish terrapins to find better partners and avoid competitors. *Anim Behav.* 83:1107–1113.
- Jaffe K, Mirás B, Cabrera A. 2007. Mate selection in the moth *Neoleucinodes elegantalis*: evidence for a supernormal chemical stimulus in sexual attraction. *Anim Behav.* 73:727–734.
- Jarau S, Hrnčir M, Zucchi R, Barth FG. 2004. A stingless bee uses labial gland secretions for scent trail communication (*Trigona recursa* Smith 1863). *J Comp Physiol.* 190:233–239.
- Juberthie-Jupeau L, Lopez A. 1991. Sexual dimorphism of gnathocoxal glands of the spider *Leptyphantes sanctivincentii*. *Tiss and Cell.* 23:423–426.
- Khannoon ER, El-Gendy A, Hardege JD. 2011. Scent marking pheromones in lizards: cholesterol and long chain alcohols elicit avoidance and aggression in male *Acanthodactylus boskianus* (Squamata: lacertidae). *Chemoecol.* 21:143–149.
- Kruuk H, Gorman M, Leitch A. 1984. Scent-marking with the subcaudal gland by the European badger, *Melesmeles* L. *Anim Behav.* 32:899–907.
- Machado G, Bonato V, Oliveira P. 2002. Alarm communication: a new function for the scent-gland secretion in harvestmen (Arachnida: opiliones). *Naturwiss.* 89:357–360.

- Machado G, Requena GS, Buzatto BA, Osses F, Rosseto LM. 2004. Five new cases of paternal care in harvestmen (Arachnida: opiliones): implications for the evolution of male guarding in the Neotropical family Gonyleptidae. *Sociobiol.* 44:1–22.
- Martín J, López P. 2011. Pheromones and reproduction in Reptiles. In: Norris DO, Lopez KH, editors. *Hormones and reproduction of vertebrates*. Vol. 3. Reptiles. San Diego, California: Academic Press; p. 141–167.
- Martín J, Moreira PL, López P. 2007. Status-signalling chemical badges in male Iberian rock lizards. *Funct Ecol.* 21:568–576.
- Martin P, Bateson P. 2011. *Measuring behaviour, an introductory guide*. Cambridge: Cambridge University Press.
- Mello-Leitão CF. 1935. Alguns novos opilões do Estado de S. Paulo e do Districto Federal. *Archos Mus Nac.* 36:9–37.
- Melville JM, Tallarovic SK, Brownell PH. 2003. Evidence of Mate Trailing in the Giant Hairy Desert Scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae). *J Ins Behav.* 16:97–115.
- Mertl-Millhollen AS. 2007. Lateral bias to the leading limb in an olfactory social signal by male ring-tailed lemurs. *Am J Primatol.* 69:635–640.
- Miller AL, Formanowicz DR. 2011. Friend or foe: behavioral responses to conspecifics in the northern scorpion, *Paruroctonus boreus* (Scorpionida: vaejovidae). *J Ethol.* 29:251–256.
- Mora G. 1990. Paternal care in a neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: gonyleptidae). *Anim Behav.* 39:582–593.
- Olsson P-O, Ryne C, Wallén R, Anderbran O, Löfstedt C. 2006. Male-produced sex pheromone in *Tribolium confusum*: behaviour and investigation of pheromone production locations. *J Stor Prod Res.* 42:173–182.
- Pearl CA, Cervantes M, Chan M, Ho U, Shoji R, Thomas EO. 2000. Evidence for a mate-attracting chemo signal in the Dwarf African Clawed frog *Hymenochirus*. *Horm Behav.* 38:67–74.
- Pereira RLA, Oliveira MAB. 2010. Etograma de *Eira barbara* (Carnivora: mustelidae) em cativo. *Rev Etol.* 9:45–57.
- Peters RP, Mech LD. 1975. Scent-marking in wolves. *Am Scient.* 63:628–637.
- Proud DN, Viquez C, Townsend Jr VR. 2011. Paternal care in a Neotropical harvestman (Opiliones: cosmetidae) from Costa Rica. *J Arachnol.* 39:497–499.
- Ralls K. 1971. Mammalian Scent Marking. *Science.* 171:443–449.
- Rentala MJ, Jokinen I, Kortet R, Vainikka A, Suhonen J. 2002. Do pheromones reveal male immunocompetence? *Proc Roy Soc London.* 269:1681–1685.
- Requena GS, Buzatto BA, Martins EG, Machado G. 2012. Paternal care decreases foraging activity and body condition, but does not impose survival costs to caring males in a Neotropical arachnid. *Plos One.* 7:e46701.
- Requena GS, Buzatto BA, Munguía-Steyer R, Machado G. 2009. Efficiency of uniparental male and female care against egg predators in two closely related syntopic harvestmen. *Anim Behav.* 78:1–8.
- Requena GS, Machado G. 2014. Mating behavior of a Neotropical arachnid with exclusive paternal care. *Acta Ethol.* 17:23–30.
- Roux O, Billen J, Orivel J, Dejean A. 2010. An overlooked mandibular-rubbing behavior used during recruitment by the African weaver ant *Oecophylla longinoda*. *Plos One.* 5:1–6.
- Santos GC, Hogan JA, Willemart RH. 2013. Associative learning in a harvestman (Arachnida, Opiliones). *Behav Proc.* 100:64–66.
- Steiner S, Ruther J. 2009. Mechanism and behavioral context of male sex pheromone release in *Nasonia vitripennis*. *J Chem Ecol.* 35:416–421.
- Suter RB, Renkes G. 1982. Linyphid spider courtship: releaser and attractant functions of a contact sex pheromone. *Anim Behav.* 30:714–718.
- Tallamy DW. 2001. Evolution of exclusive paternal care in arthropods. *Ann Rev Entomol.* 46:139–165.

- Teng B, Dao S, Donaldson ZR, Grether GF. 2012. New communal roosting tradition established through experimental translocation in a Neotropical harvestman. *Anim Behav.* 84:1183–1190.
- Teodecki EE, Brodie Jr ED, Formanowicz Jr DR, Nussbaum RA. 1998. Head dimorphism and burrowing speed in the African caecilian *Schistometopum thomense* (Amphibia: gymnophiona). *Herpetologica.* 54:154–160.
- Wabnitz PA, Bowie JH, Tyler MJ, Wallace JC, Smith BP. 1999. Aquatic sex pheromone from a male tree frog. *Nature.* 401:444–445.
- Wedell N. 2005. Female receptivity in butterflies and moths. *J Exp Biol.* 208:3433–3440.
- Willemart RH, Chelini M-C. 2007. Experimental demonstration of close-range olfaction and contact chemoreception in the Brazilian harvestman *Iporangaia pustulosa*. *Entomol Exp App.* 123:73–79.
- Willemart RH, Chelini MC, Andrade R, Gnaspini P. 2007. An ethological approach to a SEM survey on sensory structures and tegumental gland openings of two neotropical harvestmen (Arachnida, Opiliones, Gonyleptidae). *Ital J Zool.* 74:39–54.
- Willemart RH, Farine J-P, Gnaspini P. 2009. Sensory biology of Phalangida harvestmen (Arachnida, Opiliones): a review, with new morphological data on 18 species. *Acta Zool.* 90:209–227.
- Willemart RH, Hebets EA. 2012. Sexual differences in the behavior of the harvestman *Leiobunum vittatum* (Opiliones, Sclerosomatidae) towards conspecific cues. *J Ins Behav.* 25:12–23.
- Willemart RH, Pérez-González A, Farine JP, Gnaspini P. 2010. Sexually dimorphic tegumental gland openings in Laniatores (Arachnida, Opiliones), with new data on 23 species. *J Morph.* 271:641–653.
- Wyatt TD. 2003. Pheromones and animal behavior, communication by smell and taste. Cambridge: Cambridge University Press.