

Brève note – *Short note*

Larval aggregations of the blister beetle *Stenoria analis* (Schaum) (Coleoptera: Meloidae) sexually deceive patrolling males of their host, the solitary bee *Colletes hederæ* Schmidt & Westrich (Hymenoptera: Colletidae)

NICOLAS J. VEREECKEN ⁽¹⁾ & GILLES MAHÉ ⁽²⁾

⁽¹⁾ Eco-Ethologie Evolutive, Université Libre de Bruxelles CP 160/12, Av. F.D. Roosevelt 50, B-1050 Bruxelles, Belgique;
Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

⁽²⁾ 18, Rue de la Matte, F-44600 Saint-Nazaire, France

Abstract. We here report on observations on the parasitism of the solitary bee *Colletes hederæ* Schmidt & Westrich (Hymenoptera: Colletidae) by triungulins (first instar larvae) of the European beetle *Stenoria analis* (Schaum) (Coleoptera: Meloidae). Our observations carried out in western France provide behavioural evidence that patrolling males of *C. hederæ* hover in front of, and are strongly drawn to, larval aggregations of *S. analis* in a manner reminiscent of approaching flights to emerging, conspecific females. Not only were the male bees strongly attracted to clusters of newly hatched triungulins, but they also attempted copulation (i.e., *pseudocopulation*) with the latter, which regularly resulted in small groups of triungulins being transferred onto the thorax of the male bees. Decent-sized groups of triungulins were exclusively found on the thorax of male bees, which suggests that triungulins of *S. analis* lure only males of the targeted host species, presumably by mimicking the female pheromonal cues of *C. hederæ*. This is to our knowledge the first record of this kind of interaction for the whole West-Palaeartic, and only the second account on sexual deception between blister beetles and wild bees described to date.

Résumé. Des agrégats de larves du méloé *Stenoria analis* (Schaum) (Coleoptera : Meloidae) trompent sexuellement les mâles de leur hôte *Colletes hederæ* Schmidt & Westrich (Hymenoptera : Colletidae). Nous fournissons ici des observations relatives au parasitisme de l'abeille solitaire *Colletes hederæ* Schmidt & Westrich (Hymenoptera : Colletidae) par les triungulins (larves de premiers stades) du coléoptère méloé européen *Stenoria analis* (Schaum) (Coleoptera : Meloidae). Nos observations comportementales menées dans l'ouest de la France révèlent que les mâles de *C. hederæ* sont fortement attirés par les agrégations larvaires de *S. analis*, pratiquant des vols d'inspection rappelant leur comportement à l'approche de femelles émergentes conspécifiques. L'attraction des amas de triungulins est importante au point que les mâles de *C. hederæ* engagent occasionnellement des tentatives de copulation (i.e., *pseudocopulation*) avec ceux-ci, ayant pour conséquence immédiate le transfert de petits groupes de triungulins sur le thorax des mâles d'abeilles. Des groupes de triungulins n'ont jusqu'ici été trouvés que sur les mâles, ce qui suggère que les triungulins de *S. analis* leurrent exclusivement les mâles de l'espèce hôte, vraisemblablement en imitant les signaux phéromonaux émis par les femelles de *C. hederæ*. Il s'agit là, à notre connaissance, du premier cas de ce type pour l'ensemble de l'Ouest Paléarctique et du second exemple de leurre sexuel d'abeilles sauvages par des larves de méloés décrit à ce jour.

Keywords: pheromones, deception, cleptoparasitism, triungulins.

Among the various insects known to be cleptoparasites (from *clepto* in Greek, meaning “conceal” or “steal”) of wild bees' nests are blister beetles (Coleoptera: Meloidae), a diverse group of ca. 2,500 species distributed worldwide and sometimes characterised by a very restricted spectrum of hosts (Bologna 1991;

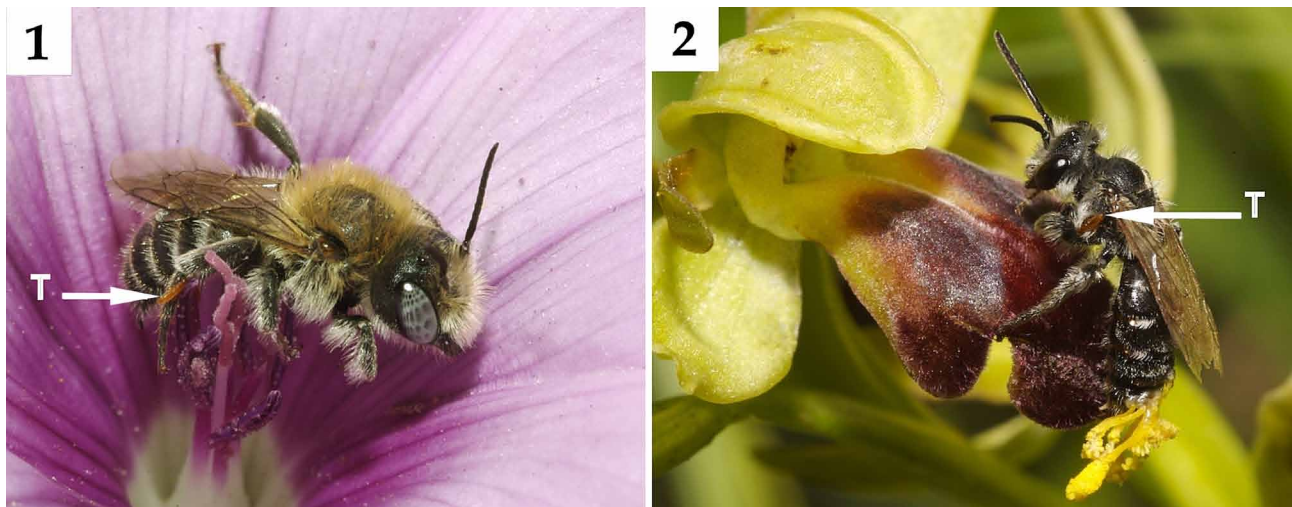
Bologna & Pinto 2002). Females of blister beetles with wild bees as hosts are generally assumed to lay eggs in groups on a variety of substrates, both above and below ground, and in the neighbourhood of their hosts' nests. Data on the reproductive biology of blister beetles are remarkably scarce, and the knowledge of the ecology of host-parasite interaction of most species is scanty (Lückmann & Assmann 2005). Yet it is generally postulated that soon after hatching, early instar larvae (i.e., triungulins) disperse haphazardly on neighbouring

E-mail: nicolas.vereecken@ulb.ac.be, nicolas.vereecken@systbot.uzh.ch
Accepté le 8 octobre 2007

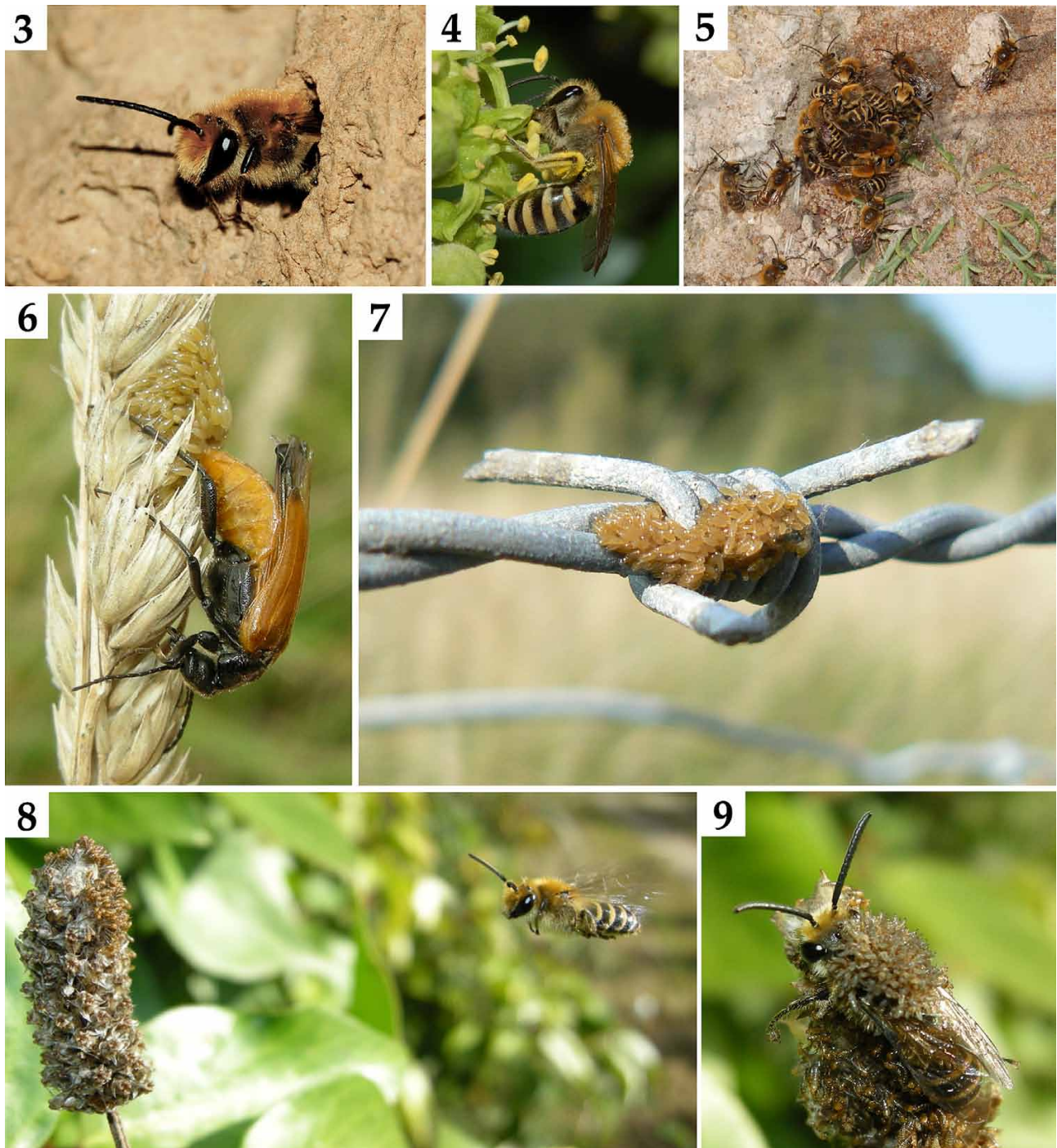
flowers, where a few fortunate individuals ultimately hitch a ride on a passing foraging bee, a phenomenon known as *phoresy* (Askew 1971). This hypothesis has been supported many times by field observations of flower-visiting wild bees (both males and females) bearing one or a few triungulins on different parts of their bodies (Figs 1–2). These bees eventually fly back to their nest where the beetle larvae jump off and gain access to the suitable resources accumulated in the bees' brood cells.

The nature of the relationship between the Ivy bee, *Colletes hederæ* Schmidt & Westrich (Hymenoptera: Colletidae) (Figs 3–4), and the blister beetle *Stenoria analis* (Schaum) tells us a very different story: our observations suggest that clusters of newly hatched triungulins of *S. analis* sexually deceive patrolling males of their host. Although the first account of the biological cycle of *S. analis* was provided more than 130 years ago (Mayet 1875), the *modus operandi* of the phoretic behaviour in this blister beetle species has hitherto never been described. Males of *C. hederæ* usually emerge a few days or weeks before the females, and engage in very conspicuous male-male competitions to access virgin females emerging from their underground natal cell. The formation of these spectacular "mating balls" (Fig. 5) suggests that female sex pheromone might be responsible for mate location and recognition in this species (Vereecken *et al.* 2006), as was recently described in a closely-related species, *C. cunicularius* (L.) (Mant *et al.* 2005). A current monitoring programme on the distribution of *C. hederæ* in western Europe has allowed us to gather

gather several observations of *C. hederæ* males bearing not just one or a few, but literally tens to hundreds of triungulins of *S. analis* clinging to the hairs covering the bees' thoraces. These records have encouraged more in-depth investigations and monitoring of the different cycles of *S. analis* in an attempt to uncover how triungulins of this species managed to find their way to the nests of *C. hederæ*. Females of *S. analis* were found copulating from mid-August onwards and laying batches of eggs above ground on dried stems of weeds or even on barbed wire (Figs 6–7). Newly hatched triungulins remained at their emergence site and formed coherent groups (no dispersal was recorded) that triggered approaching flights of patrolling *C. hederæ* males (Fig. 8). Since no contact was observed between the larval aggregations of *S. analis* and the male bees, we undertook a translocation of several larval aggregations from a neighbouring meadow to the near vicinity of the nesting/emergence site of *C. hederæ*. This experiment turned out to be highly illuminating: a few males instantaneously approached the larval clusters and attempted copulation (i.e., *pseudocopulation*) with the latter, collecting small groups of triungulins on their body in the process (Fig. 9). Our observations illustrate that *C. hederæ* males are drawn to larval aggregations of *S. analis* by means of an olfactory cue, in a manner reminiscent of approaching flights to emerging, conspecific females. This hypothesis constitutes a striking parallel to results of recent studies carried out on the American blister beetle *Meloe franciscanus* Van Dyke and its host, the solitary bee *Habropoda pallida* (Timberlake)



Figures 1–2
Male bees carrying early instar larvae of blister beetles (triungulins, T). **1**, *Hoplitis perezii* (Ferton) (Hymenoptera, Megachilidae) on a flower of *Convolvulus altheoides* L. (Convolvulaceae) (beetle larva on hind right leg); **2**, *Andrena ovatula* (Kirby) (Hymenoptera, Andrenidae) on the labellum of the sexually deceptive orchid *Ophrys sulcata* Devillers-Terschuren & Devillers (Orchidaceae) (beetle larva on left side of the thorax) (Photos N.J. Vereecken).



Figures 3–9

Natural history of the Ivy bee, *Colletes hederæ* Schmidt & Westrich (Hymenoptera, Colletidae), and its parasite, *Stenoria analis* (Schaum) (Coleoptera, Meloidae). **3**, male bee at the entrance of its underground nest (Photo N.J. Vereecken); **4**, female bee collecting pollen on Ivy, *Hedera helix* L. (Araliaceae) (Photo N.J. Vereecken); **5**, cluster of male bees attempting copulation with a single emerging female (i.e., “mating ball”) (Photo N.J. Vereecken); **6**, female beetle laying eggs on a dead stem of *Dactylis glomerata* L. (Poaceae) (Photo G. Mahé); **7**, cluster of newly hatched beetle larvae on barbed wire (Photo A. Lachaud); **8**, approaching flight of the patrolling male bee to the cluster of beetle larvae on a dried inflorescence of *Plantago lanceolata* L. (Plantaginaceae) (Photo G. Mahé); **9**, male bee attempting copulation with the mass of blister beetle larvae and transferring some of the latter onto its thorax (Photo G. Mahé).

(Hymenoptera, Apidae). In this system, Hafernik & Saul-Gershenz (2000) described triungulins grouping together and releasing sex pheromone-mimicking compounds that triggered pseudocopulations of male bees with the larval aggregations “[...] so swiftly that the action can only be followed in any detail with a slow-motion camera” (Attenborough 2005). Once on board the male bee, the beetle larvae are then transferred onto the body of conspecific female bees during “genuine” copulations, and they are ultimately brought back to the bee’s nest as the female bee discharges its pollen load to provision its brood cells (Hafernik & Saul-Gershenz 2000). The *Meloe-Habropoda* interaction differs from the *Stenoria-Colletes* system in many respects, notably in the fact that the patrolling flights of *C. hederæ* males are regularly interrupted by frequent trips back to the nests (NJ Vereecken, pers. obs.), which provide an additional opportunity for triungulins to jump off their host and gain access to the bees’ nests.

Saul-Gershenz & Millar (2006) have recently described the chemistry of the interaction between *Meloe* and *Habropoda* and proposed long-chained alkenes (mono-unsaturated hydrocarbons) as likely candidates for the female sex pheromone in *H. pallida*. These results are consistent with previous studies on pollinator-attracting odour signals in *Ophrys* orchids (e.g. Mant *et al.* 2005) and on female sex pheromones in *C. cunicularius* (Mant *et al.* 2005, Vereecken *et al.* 2007) that report that blends of mono-unsaturated alkenes are the primary male attractants in this solitary bee species. The key role of cuticular hydrocarbons and their derivatives in triggering mating behaviour in male solitary bees has also been documented in studies on *Amegilla dawsoni* (Rayment) (Simmons *et al.* 2003), *Andrena flavipes* Panzer (Schiestl & Ayasse 2002; Vereecken *et al.* unpublished data), *Andrena nigroaenea* (Kirby) (Schiestl *et al.* 1999), *Megachile rotundata* (Fabricius) (Paulmier *et al.* 1999), and *Osmia rufa* L. (Ayasse *et al.* 2000). Ongoing investigations on female sex pheromone differentiation among species in the *Colletes succinctus* group (which includes *C. hederæ*, Kuhlmann *et al.* 2007) suggest that virgin females in these bee species also produce alkenes as mate attractants (Vereecken *et al.*, unpublished data). We are currently investigating whether clusters of triungulins of *S. analis* emit sex pheromone-mimicking odour blends and whether larval aggregations attract only males *C. hederæ* as hosts or, as is the case in the *Meloe-Habropoda* system (L. Saul-Gershenz, pers. comm. 2007), if related species, such as *C. succinctus* (see Villemant 2001), can constitute alternative hosts for triungulins.

Acknowledgements. We are grateful to Darren Mann (Oxford University Museum, UK), Leslie Saul-Gershenz (Center for Ecosystem Survival, San Francisco, California, USA) and Johannes Lückmann (University of Lüneburg, Germany), for sharing thoughts and material during this study. Stuart P.M.

Roberts (University of Reading, UK) and Anne C. Gaskett (Macquarie University, Australia) kindly commented on an earlier version of the manuscript. NJV received financial support from two Belgian institutions, namely the “Fonds pour la formation à la Recherche dans l’Industrie et l’Agriculture” (F.R.I.A.) and the “Académie Royale des Sciences, des Lettres et des Beaux-Arts (Fondation Agathon de Potter).”

References

- Attenborough D. 2005. *Life in the Undergrowth*. BBC Books, London, 288 p.
- Askew R.R. 1971. *Parasitic Insects*. American Elsevier Publishing Co., New York, 316 p.
- Ayasse M., Dutzler G., Schiestl F.P., Ibarra F., Francke W. 2000. Identification of female and male sex pheromone in the solitary bee *Osmia rufa* (Hymenoptera: Megachilidae), p. 21 in: *International Congress of Entomology, Chemistry and Physiological Ecology Symposium and Poster Session, Brazil, Abstract Book II*.
- Bologna M.A. 1991. *Fauna d’Italia: Coleoptera Meloidae*. Ed. Calderini, Bologna, 541 p.
- Bologna M.A., Pinto J.D. 2002. The Old World genera of Meloidae (Coleoptera): a key and synopsis. *Journal of Natural History* 36: 2013–2102.
- Hafernik J., Saul-Gershenz L.S. 2000. Beetle larvae cooperate to mimic bees. *Nature* 405: 35–36.
- Kuhlmann M., Else G.R., Dawson A., Quicke D.L.J. 2007. Molecular, biogeographical and phenological evidence for the existence of three western European sibling species in the *Colletes succinctus* group (Hymenoptera: Apidae). *Organisms, Diversity & Evolution* 7: 155–165.
- Lückmann J., Assmann T. 2005. Reproductive biology and strategies of nine meloid beetles from Central Europe (Coleoptera: Meloidae). *Journal of Natural History* 39(48): 4101–4125.
- Mant J.G., Brändli C., Vereecken N.J., Schulz C., Francke W., Schiestl F.P. 2005. Cuticular hydrocarbons as source of the sex pheromone in *Colletes cunicularius* (Hymenoptera: Colletidae) and the key to its mimicry by the sexually deceptive orchid *Ophrys exaltata* (Orchidaceae). *Journal of Chemical Ecology* 31(8): 1765–1787.
- Mayet V. 1875. Mémoire sur les moeurs et métamorphoses d’une nouvelle espèce de Coléoptère de la famille des Vésicants, le *Staris colletis*. *Annales de la Société Entomologique de France* 5: 64–92.
- Paulmier I., Bagnères A.-G., Afonso C.M.M., Dusticier G., Rivière G., Clement J.-L. 1999. Alkenes as sexual pheromone in the alfalfa leaf-cutter bee *Megachile rotundata*. *Journal of Chemical Ecology* 25(3): 471–490.
- Saul-Gershenz L.S., Millar J.G. 2006. Phoretic nest parasites use sexual deception to obtain transport to their host’s nest. *Proceedings of the National Academy of Sciences of the USA* 103(38): 14039–14044.
- Schiestl F.P., Ayasse M., Paulus H.F., Löfstedt C., Hansson B.S., Ibarra F., Francke W. 1999. Orchid pollination by sexual swindle. *Nature* 399: 421–422.
- Schiestl F.P., Ayasse M. 2002. Do changes in floral odor cause speciation in sexually deceptive orchids? *Plant Systematics and Evolution* 234: 111–119.
- Simmons L.W., Alcock J., Reeder A. 2003. The role of cuticular hydrocarbons in male attraction and repulsion by female Dawson’s burrowing bee, *Amegilla dawsoni*. *Animal Behavior* 66: 677–685.
- Vereecken N.J., Toffin E., Michez D. 2006. Observations relatives à la biologie et à la nidification d’abeilles psammophiles d’intérêt en Wallonie. 2. Observations estivales et automnales. *Parcs et Réserves* 61(4): 12–20.
- Vereecken N.J., Mant J., Schiestl F.P. 2007. Population differentiation in female sex pheromone and male preferences in a solitary bee. *Behavioral Ecology and Sociobiology* 61: 811–821.
- Villemant C. 2001. Les Coléoptères Méloïdés cleptoparasites de nids d’abeilles solitaires. *Insectes* 121: 7–10.