Beetle larvae cooperate to mimic bees

These parasites get into bees' nests by fooling males into trying to mate with them.

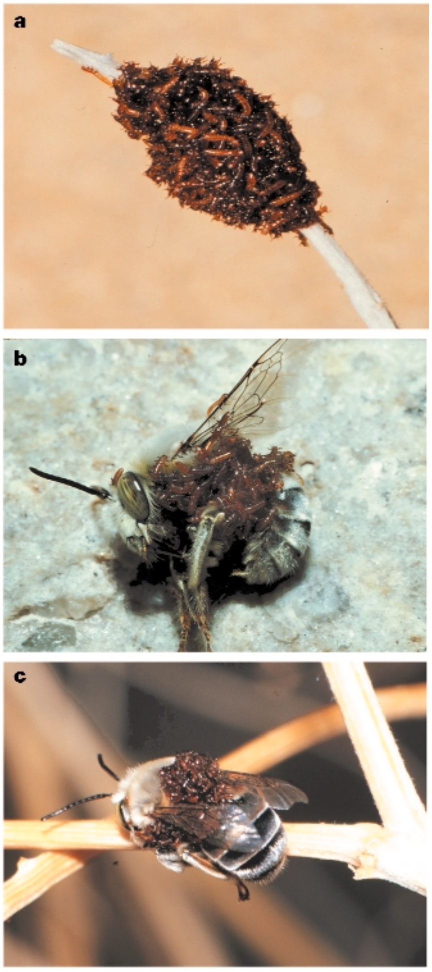

Figure 1 Interaction of *Meloe franciscanus* triungulin aggregations and the bee *Hapropoda pallida*. **a,** Triungulins aggregated on a dried twig. Aggregations sampled in 1992 included 120–2,359 larvae (mean, 549; $n = 19$; s.d. = 460) and crudely resembled perching bees in shape, as well as their abdomen colour. From 17 April to 18 May 1999, we monitored 36 triungulin aggregations ranging in size from 1.3 to 0.3 cm from 08:00 to 17:00 each day. We concentrated observations on a 10 m × 6 m portion of an area that contained eight aggregations. In addition, one of us periodically checked the status of aggregations in other areas and monitored the activity associated with them. Although aggregations appear reddish to humans, bees are red-blind and confuse red with black[10]. Triungulin aggregations and models, as well as bees and *Astragalus lentiginous* var. *borreganus* flowers, were photographed with a Kodak 18 A filter to detect ultraviolet reflectance patterns to which bees might respond. Only flowers showed an ultraviolet pattern different from that at visible wavelengths. **b,** Male bee with triungulins on its underside. In 1992, we collected male bees from sleeping aggregations and as bees visited *Astragalus* flowers. We tested the null hypothesis that triungulins had attached to bees at random by computing the index of dispersion, I_D, of triungulins on bees: $I_D = s^2(n-1)/\bar{X}$, which is approximately distributed as χ^2 with $n-1$ degrees of freedom[11]. Triungulins were highly aggregated on male bees (mean, 53 triungulins per bee; $n = 26$, s.d. = 80; range, 4–369; $I_D = 6{,}100$, 23 d.f., $P < 0.0001$). **c,** Female bee with triungulins on its dorsal surface. The abdomen of females and the aggregations are similar in size (mean, 0.69 cm; $n = 6$ for abdomens; mean, 0.63 cm; $n = 29$ for aggregations).

The life cycles of parasites often involve complex behavioural and morphological adaptations in order to find a host. Here we report a remarkable mode of host-finding by the blister beetle *Meloe franciscanus*, in which young larvae aggregate together on vegetation to mimic the appearance of a female bee, luring male bees to land on them and collect the aggregation as a unit for transmitting to females during real matings. Although cooperative behaviour is common among highly social insects, particularly bees[1–3], to our knowledge it has not been reported before in blister beetles, nor has it been associated with mimicry.

Although some mites[4] also parasitize their hosts by venereal transmission, this behaviour is not seen in other *Meloe* species, whose larvae disperse to flowers and attach individually to passing bees whose nests they parasitize. Young *Meloe* larvae (triungulins) are highly adapted for grasping bees, structurally resembling lice rather than beetle larvae (so much so, that Linnaeus described a triungulin as a louse rather than a beetle[5]). *Meloe* triungulins drop off when they arrive at the bee's nest, however, and develop primarily on pollen provided by the bee[6–8].

We investigated the interaction of bees and triungulin aggregations at the Kelso Dunes in California's Mojave Desert during April 1992 and April and May 1999. Triungulins cooperated in forming aggregations and in holding onto vegetation (Fig. 1a). They collectively responded to outside stimuli, such as nearby movements, by waving their front legs or by contracting as a unit. They also moved as a unit, sometimes forming living bridges between adjacent grass blades. Long-lasting aggregations (mean, 5.4 days; $n = 36$; range, 1–15 days) were found on grass and twigs, but there were no aggregations or individual triungulins on or near 1,256 flowers inspected in 1999.

Activities of the anthophorid bee *Habropoda pallida* were positively associated with the aggregations. We observed 98 instances in which bees hovered within a few centimetres of an aggregation and nine instances in which bees landed on an aggregation. These bees often flew away with all or most of an aggregation attached to their ventral surface. All of the bees that were orientated towards masses and could be sexed ($n = 42$) were male. We determined the fate of 22 of the triungulin aggregations: of these, five were removed by a bee, seven were killed by adverse weather conditions, nine died of old age and one was eaten by a spider. In addition, ten masses disappeared in a way consistent with removal by bees. We estimate that bees removed 42% of the masses.

All male bees sampled in 1992 carried triungulins (Fig. 1b). Most (26 of 27) carried them on their underside, where they would be transferred to the dorsal surface of a female during attempted matings in which males typically mount females. All females that we observed with triungulins ($n = 7$) carried them on their dorsal surface (Fig. 1c), and we saw a female that apparently acquired newly deposited triungulins immediately after copulating.

We believe that male bees confuse triungulin masses with female bees, which often perch on vegetation in positions similar to those presented by the masses, because males approach and land on masses and females in the same way. This phenomenon could be mediated in a way similar to pseudocopulation in orchids[9] and probably involves both visual and olfactory mimicry. The importance of olfactory cues is supported by our observation of four males landing on or hovering next to groups of triungulins before their formation into discrete aggregations, and by the fact that bees ignore painted models of aggregations placed nearby.

Females of *Meloe* species produce up to 3,000 larvae per clutch[6]. Such a high reproductive rate is usually associated with high larval mortality and low individual success in host-finding. We believe that the mimicry practised by *M. franciscanus* larvae, together with their subsequent venereal transmission, enhances their chance of finding a bee's nest. This may apply particularly in highly variable environments such as our desert study site, where bee numbers and the location and frequency of flowering plants vary widely from year to year.

John Hafernik, Leslie Saul-Gershenz
Center For Ecosystem Survival
699 Mississippi Street, Suite 106
San Francisco, California 94107
California 94132, USA
e-mail: lsaul@meer.net

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LESLIE SAUL-GERSHENZ
CENTER FOR ECOSYSTEM SURVIVAL
699 Mississippi Street, Suite 106
San Francisco, CA 94107
e-mail: lsaul@meer.net
Phone: 415.648.3390
Fax: 415.824.6526