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Small hive beetles survive in honeybee prisons by behavioural mimicry

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Abstract We report the results of a simple experiment to determine whether honeybees feed their small hive beetle nest parasites. Honeybees incarcerate the beetles in cells constructed of plant resins and continually guard them. The longevity of incarcerated beetles greatly exceeds their metabolic reserves. We show that survival of small hive beetles derives from behavioural mimicry by which the beetles induce the bees to feed them trophallactically. Electronic supplementary material to this paper can be obtained by using the Springer LINK server located at <http://dx.doi.org/10.1007/s00114-002-0326-y>.

Introduction

Small hive beetles (SHB), *Aethina tumida* Murray, are ubiquitous, facultative social parasites of colonies of honeybees (*Apis mellifera*) and are endemic to sub-Saharan Africa. SHB feed on pollen, honey and brood, and reproduce in honeybee nests of honeybees but seldom inflict serious damage on the colonies (Lundie 1940; Hepburn and Radloff 1998). As a defence against the SHB, honeybees construct cells of propolis (plant resins) into which they drive the beetles and imprison them (Neumann et al. 2001). Incarcerated beetles lack access to the combs because worker bees continuously guard

the entrances of such cells and prevent many attempted escapes of beetles. Nonetheless, despite no access to food in the combs, imprisoned beetles may survive for 2 months or longer (Neumann et al. 2001). However, their survival is not due to metabolic reserves, because starved beetles die within a fortnight (Ellis et al. 2001; Neumann et al. 2001). So how do beetles spend their tenure as honeybee prisoners deprived of foodstuffs?

While documenting bee–beetle interactions, we observed what appeared to be trophallactic encounters between guard bees and imprisoned beetles (Fig. 1). The beetles characteristically approach guard bees, extend their heads towards and make antennal contact with guard bees (mimicking normal honeybee trophallaxis). This behaviour of the beetles often elicits aggressive reactions from the guard bees, which try to grab the beetles with their mandibles. However, if the beetles are persistent enough, they seem to induce the bees to regurgitate a drop of honey, which the beetles appear to take directly from the mouthparts of the bees. Here we report the results of a simple experiment to determine whether long-term survival of incarcerated beetles derives from a form of behavioural mimicry which induces honeybees to feed them by trophallaxis (Fig. 1 and see electronic supplementary material).

Methods

To test the bee–beetle trophallaxis hypothesis, we set up a three-frame observation hive with 100 SHB confined to the upper third of the hive. The lower two-thirds of the hive housed a feeder, a normal comb, and a small but robust colony of Cape honeybees, *Apis mellifera capensis*. The colony was partitioned between the upper third and the lower two-thirds by metal gauze that prevented mingling of bees and beetles, but did allow antennal and mouthpart contact, hence trophallaxis, between bees and beetles through the gauze mesh. The bees were fed a sugar/water solution containing the vital stain Rose Bengal. The beetles were confined to the upper chamber, and had no direct access to any source of the dyed sugar solution except by being fed trophallactically through the metal gauze by the bees. Twenty-four hours after their introduction, we collected a sample of 50 beetles and squeezed them to discharge their viscera which were analysed by UV-spectroscopy.

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Fig. 1 Sequence of interactions between a honeybee worker and two imprisoned small hive beetles resulting in eventual trophallaxis. The frames sample 3.5 s (photography by Gerald Kostberger and Otmar Winder)

Results

Twenty out of the 50 SHB sampled showed red-stained emissions that were analysed spectrophotometrically (Fig. 2). The spectral analysis indicated that the emis-

sions were indeed stained with Rose Bengal, unequivocally establishing that Cape honeybee workers trophalactically feed the beetles.

Discussion

The video sequence (Fig. 1, see also electronic supplementary material) and the spectrograms (Fig. 2) confirm that SHB use behavioural mimicry to induce trophallaxis from honeybees. The SHB are not always successful in

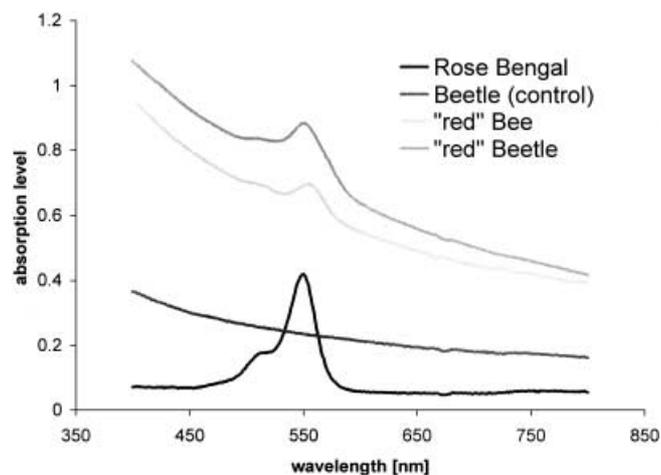


Fig. 2 UV spectrograph of a Rose Bengal standard, “red bees”, “red beetles” and a control beetle. Rose Bengal has a characteristic peak at 550 nm, the red bee at 551 nm, red beetle at 551 nm (the latter two being within error range of the spectrophotometer) and the control beetle no peak at all

soliciting food and it often takes them more than five attempts to induce trophallaxis. Moreover, after 24 h only 20 out of the 50 beetles sampled contained signs of the Rose Bengal. So the behavioural mimicry of the SHB, while adaptive, is clearly not fail-safe. Antennation of honeybees by SHB is easily observed behaviour; but this does not exclude the possibility that bee–beetle interactions are also modulated perhaps by chemical mimicry as occurs, for example, in the death's head hawkmoth (Moritz et al. 1991).

To place the behavioural mimicry of the SHB in a wider context, it must be remembered that there are many other cases where social insects, particularly ants, are tricked by beetles into feeding them. In more evolved instances, such as in some ant–aphid interactions, the relationship is one of virtual aphid husbandry by the ants (Hölldobler and Wilson 1990; Schmid-Hempel 1998). In contrast, the behaviour of the small hive beetle is simply a case of honeybee exploitation, albeit of a novel kind.

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