together with other independent but overlapping pathways, such as PIP$_3$ signalling, to produce co-ordinated changes in the cell structure. Indeed, different combinations of signals may also make the cell respond differently, resulting in a decision to either extend, divide, stabilise or withdraw a particular region of the cell. Perhaps each signalling pathway can independently regulate different aspects of the mechanics of cell migration, such as adhesion, vesicle fusion, or actin nucleation. Such a mechanism would be robust as well as flexible, allowing the cell to change its motile behaviour at different stages of development.

Recent work has shown that, at least in shallow gradients, cells steer by splitting existing pseudopods and then retaining the most accurate pseudopod [16]. The selection process could be mediated by integrating the relative combinations of signalling molecules present in different regions of a bifurcated pseudopod, which means that it will be interesting to learn to what extent PIP$_3$ signalling and phosphorylated PKBR1 colocalise. Indeed, one of the limitations of the paper by Kamimura *et al.* [6] is that they only show the localised phosphorylation of PKBR1 in very steep gradients of chemoattractant. As cells are most sensitive to inhibition of PI 3-kinase in shallow gradients [17], it will also be important to know the relative contribution of PKBR1 signalling in more shallow gradients and even in waves of stimulation, such

as those encountered during *Dictyostelium* aggregation.

The presence of multiple parallel mechanisms is compelling us to think in new ways about how cells direct their migration. The next challenge will be to understand how these pathways interact and co-operate with each other to produce a finely tuned response like chemotaxis.

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CR-UK Beatson Institute for Cancer Research, Switchback Road, Bearsden, Glasgow G61 1BD, UK.
*E-mail: j.king@beatson.gla.ac.uk

# Mutualism: Wasp Keeps Watchdogs to Protect Young

The adaptive value of acarinaria — specialized structures in some wasps and bees that harbour symbiotic mites — has long been elusive. A new study has now shown that the mites are actually beneficial to their host by actively defending it against parasitoids.

Daniel J.C. Kronauer

The conceptual framework of studies in evolutionary biology generally assumes that the systems and structures we observe have adaptive properties. While this view has also been criticized, it has produced a wealth of fruitful and successful tests of evolutionary theory, unlike any other approach [1]. Some structures in nature are in fact so elaborate that they seem to demand an adaptive interpretation. Striking examples are the specialized domatia developed by *Acacia* trees, which provide nest sites for ants [2], and the cuticular crypts of fungus-growing ants that contain filamentous *Pseudonocardia* bacteria [3]. In both cases, the structures serve to harbour coevolved mutualistic partners: the ants protect the trees against herbivores and receive nectar and housing in return, while the *Pseudonocardia* bacteria produce antibiotics to control fungus-garden pests and are in turn apparently nourished by glandular secretions from the ants.

A similarly complex and fascinating relationship has now been unveiled by Kimiko Okabe and Shun'ichi Makino [4]. In their recent paper, they

report that a supposedly parasitic mite, *Ensliniella parasitica*, actually increases the fitness of its host, the solitary eumenine wasp *Allodynerus delphinalis*, in an unsuspected way: if a brood cell containing an immobile wasp pupa or prepupa is accessed by the small parasitoid wasp *Melittobia acasta*, the predominant natural enemy of *A. delphinalis*, adult mites rush to attack and kill the intruder (videos can be viewed online at http://dx.doi.org/10.1098/rspb.2008.0586).

As in the above examples, the adult *A. delphinalis* wasps have evolved derived structures, so-called acarinaria, or mite pockets, to shelter their symbionts [5] (Figure 1). Acarinaria occur over a wide taxonomic range: in several genera of eumenid wasps, as well as in different bees of the families Apidae (subfamily Xylocopinae), Halictidae and Stenotritidae [6]. But given that haemolymph-sucking mites are among the most destructive parasites of Hymenoptera — think of the devastating effects that *Varroa* mites are having on honeybee populations [7] — it has been a puzzle why some wasps and bees should actively shepherd the bloodsuckers and even transfer them to their brood. Unlike the association of phoretic and parasitic mites with their hosts — these mites use special attachment organs and hook-shaped pretarsal claws to adhere to the host body — the settlement of mites in acarinaria involves mutual specificity and an apparently coevolved interaction, and this has prompted researchers repeatedly to predict a mutualistic relationship between the two parties (for example [5,6,8]). Circumstantial evidence suggested that certain predatory mites could serve the host by diminishing the populations of harmful arthropods or nematodes in brood cells, and mites feeding on detritus could keep fungal and bacterial infestations in check [5,8]. The nature and quantifiable benefits of such suspected mutualisms, however, have remained elusive. The alternative suggestion has been made that mite pockets simply serve to concentrate harmful mites on infested hosts and to hinder transmission between brood chambers [9]. The new study [4] now finally sheds some light on the
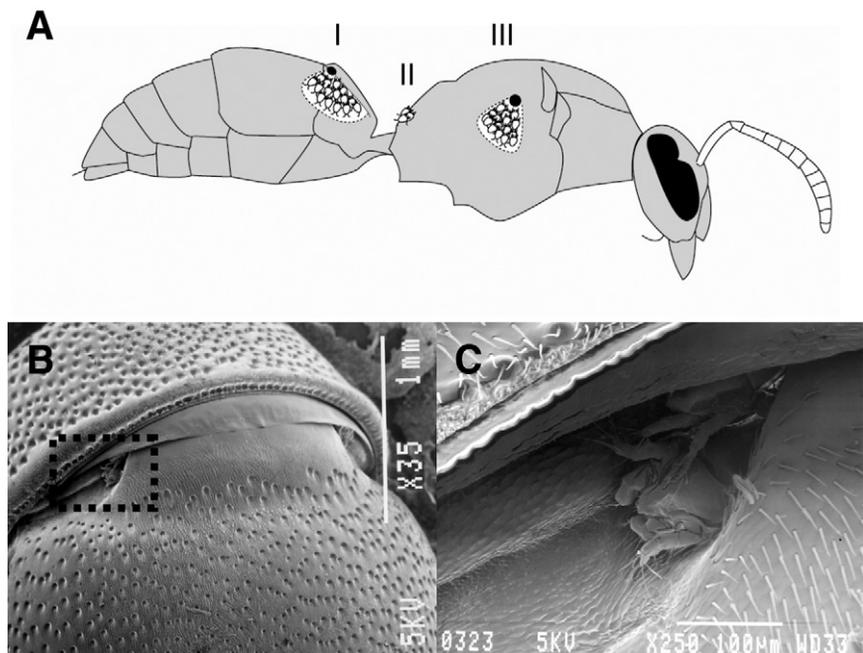


Figure 1. Mite pockets of a female *Allodynerus delphinalis* wasp.

(A) Metasomal (I), propodeal (II), and scutellar (III) mite pocket; black dots indicate openings (reprinted with permission from [4]). (B) Detail of the metasomal mite pocket. The rectangle is enlarged in (C) and shows mites at the pocket entrance. Part (A) adapted with permission from [10]; pictures courtesy Kimiko Okabe.

true evolutionary significance of acarinaria.

After mating, female *A. delphinalis* wasps excavate dead plant stems in which they construct up to seven brood cells. A single egg is laid in each cell and provisioned with a paralyzed lepidopteran larva before the cell is sealed. During this process, deutonymphs, the dispersal state of the mite, leave the acarinaria on the mother wasp and enter the nest chambers, where they soon moult into tritonymphs and then into adults. The prevalence of mites is high, with over 90% of wasp brood cells being infested, and each cell containing approximately six mites on average [10]. The mites initially suck haemolymph from the lepidopteran prey, and later also from the developing wasp itself [4,10]. Under controlled conditions the presence of mites did not adversely affect wasp development and survival [10], but it seems not unlikely that the wasps pay some, albeit small, cost for having the mites around, which may become more apparent under less benign circumstances. Upon host pupation, the mites begin ovipositing, and by the time the adult wasp ecloses, the next generation of mites has

developed into deutonymphs which hurry into the acarinaria. Evidently, as is true of many symbionts that rely on their host for dispersal, the mite's life-cycle is tightly attuned to that of the wasp [10].

Mated females of the parasitoid wasp *M. acasta*, about a tenth the size of the host wasp, enter the brood cell and initially puncture the *A. delphinalis* prepupa or early pupa with their ovipositor. They then feed on the oozing body fluids and, after one or two days, begin to lay eggs. If the invasion is successful, the larvae of *M. acasta* continue to feed voraciously on haemolymph, and the host pupa finally dies [4,11]. This in turn also dooms the mite brood, which will not be able to develop and disperse [4]. Perhaps not surprisingly then, the adult mites do everything in their power to fight off the parasitoid, and the battle is indeed one of life and death for both sides. Upon contact, the mites cling to the intruder and apparently attempt to pierce soft spots of its cuticle with their mouthparts, while the attacked wasp responds by biting the little offenders. The chances of success from a mite's point of view depend strongly on the number of allies: while three mites in a cell

succeeded in killing the parasitoid in only about ten percent of the cases, ten mites are sufficient to swing the outcome of the fray consistently in their favour [4]. Clearly, it pays for *A. delphinalis* to include a small army of watchdog mites when provisioning for its young.

Unlike eusocial Hymenoptera, where adult workers continuously care for the developing offspring, solitary wasps abandon their brood at an early stage. This means that measures against future threats have to be in place at the time the brood cell is sealed. An earlier study [12] on the European beewolf, another solitary hunting wasp, demonstrated that defence can be efficiently achieved by transferring symbionts with a protective function to the offspring. Female beewolves inoculate their brood chambers with antibiotic-producing bacteria of the genus *Streptomyces*, which protects the young from fungal infections and significantly increases their chance of survival [12]. The new work of Okabe and Makino [4] shows that solitary wasps have repeatedly employed mutualists to safeguard their offspring, which suggests that this could be a more general and widespread mechanism that has so far been largely overlooked.

Symbioses between different organisms are often categorized as parasitic, commensal, or mutualistic, while in fact the potential outcomes of species interactions form a continuum and even the nature of a particular relationship can change over time and space [13–15]. One of the central questions is therefore how the interests of the different parties become aligned so that mutualisms are evolutionarily stabilized [13,14]. This general point is nicely illustrated by the present example [4]. First, the preliminary data suggest that parasitoid load fluctuates greatly over time. In the first year of the study, hardly any brood cells were infested, while in the second year, *M. acasta* was the predominant cause of host death [4]. This means that the mite–wasp association might classify as parasitic in one year, but mutualistic in the other. While we can still assume that, averaged over the years, the host wasp profits from the symbiosis, this probably helps to explain why it has been so difficult to unravel quantifiable benefits. Second, just as in the above mentioned

*Acacia*–ant mutualism, the fitness of both partners is tightly coupled, because the survival and dispersal of the mite is directly dependent on the survival of the wasp host. In other words, disproportionate exploitation by the mite, or cheating, which decreases the survival probability of the wasp pupa, would directly backfire on the mite's own fitness. Such directed reciprocation with partner fidelity feedback offers one of the most straightforward mechanisms for the evolution and maintenance of mutualisms [14].

The strength of partner fidelity feedback, as well as the long-term stability and specificity of a given mutualism, is thought to be directly related to the mode of symbiont transmission [14]. In the cases of mutualistic bacteria associated with beewolves and fungus-growing ants, young females carry the microbial strain of their mother [3,12]. This uniparental vertical transmission of symbionts maximizes fitness feedback, facilitates coevolution between the two parties, and minimizes wasteful competition between different symbiont strains [14,16]. In the present example [4], the mites are likewise transmitted vertically from mothers to daughters, but also to sons, and some transfer occurs from males to females during copulation [10]. This implies mixing of symbiont strains. Other wasp–mite symbioses strikingly differ in this respect: in one especially curious case, female but not male wasp larvae kill all mites in their brood cell, so that mites only disperse on males, followed by venereal transmission back to females [17]. Assuming that females mate only once, symbiont transmission would then indeed be strictly male-mediated uniparental and vertical. How such differences affect the outcome of the symbiosis could be subject to comparative analyses in the future. As a first step, however, additional systems have to be investigated in more detail. As the study by Okabe and Makino [4] shows, such endeavours promise not only fascinating and unanticipated insights into the natural history of wasp-mite associations, but will also significantly advance our understanding of the evolution and maintenance of mutualisms.

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Département d'Écologie et Évolution, Université de Lausanne, Quartier UNIL-Sorge, Bâtiment Biophore, 1015 Lausanne, Switzerland.
E-mail: djckronauer@bio.ku.dk