Butterflies that trick ants with sound

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Larvae of parasitic *Maculinea* butterflies use acoustic mimicry to induce host ants to adopt and care for them.

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The nests of ant colonies contain mature ants, their brood, and stored food—valuable commodities to a predator. Those nests, therefore, are aggressively defended by colony members, who employ a complex, finely tuned system to discriminate between nestmates and strangers.

Nonetheless, numerous ant-sized organisms called myrmecophiles ("ant lovers") thrive within the ant society and perhaps exploit its resources, if only for a short part of their lives. The interactions that have evolved between myrmecophiles and ants range from loose associations to utter dependency for one or both partners. Some 10 000 arthropod species live as ant parasites and have evolved to intercept and exploit their host's communication code. Among the most fascinating of those adaptations is the acoustic strategy that parasitic *Maculinea* butterflies use to deceive ants into letting them enter and live undisturbed in a host colony.

Meet the *Maculinea*

The large blue butterflies *Maculinea* have attracted much public attention because of conservation efforts on their behalf and their extraordinary life cycle. Each *Maculinea* species depends on a specific food plant and on a specific species of *Myrmica* ant for its survival. Once hatched, *Maculinea* caterpillars feed on floral buds for 10–15 days. After their third molt, the larvae drop to the ground and wait until a *Myrmica* worker finds them. While aground, the *Maculinea* caterpillars secrete a simple mixture of chemical compounds that, to a worker ant, seems similar to that given off by ant larvae. The chemical subterfuge deceives foraging workers, who bring the parasites into the ant nest. Thanks to their ability to mimic the colony's "odor," the parasites live in the ant nest for at least 11 months, during which time they gain more than 90% of their ultimate biomass. The larvae pupate in the upper chambers of the nest, and a month later adult butterflies emerge and leave the colony.

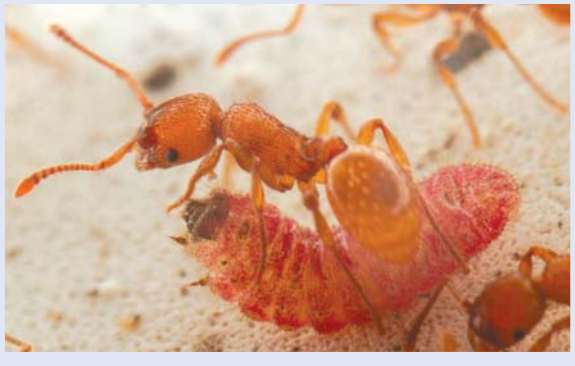

Figure 1. A worker *Myrmica scabrinodis* in its nest feeds a larva of the butterfly species *Maculinea alcon*.

Maculinea species differ in their feeding strategy inside the ant colony. Some, such as *M. alcon* and *M. rebeli*, use a so-called cuckoo strategy—that is, they are fed directly by attending workers, as shown in figure 1. Others, such as *M. arion* and *M. teleius*, are predators that prey on ant brood; they want to lay low while in the nest.

Acoustic deception

The idea that *Maculinea* butterflies could augment their chemical trickery with acoustic deception came to Jeremy Thomas some 20 years ago, after he and Philip DeVries recorded the sounds of *Maculinea* caterpillars and worker ants. In 2009 we worked with Thomas, Karsten Schönrogge, and other colleagues to expand on those preliminary experiments. We used a new recording device to capture the stridulations (sounds made by rubbing body parts together) of both worker and queen ants. In addition, we performed behavioral tests on the ants.

Entomologists had long known that acoustic communications play a wide range of roles in ants' social behavior. Before our work, however, there was no direct evidence showing that acoustic communication signaled social status. Our findings revealed that different members of an ant society produce distinctive caste-specific stridulations and induce patterns of benevolent behavior either in fellow caste members or in other castes. Moreover, the ants' complex system of intracolony acoustic recognition can be exploited by a butterfly social parasite as a means to become well integrated into the colony.

Last year our research group found that fully grown *M. alcon* larvae can mimic the sounds produced by *M. scabrinodis* queens, as shown in figure 2; thus they and other cuckoo species obtain high status in the host colony. Cuckoo caterpillars are rescued ahead of the ant brood when a colony is disturbed, and they are fed in preference to host ant larvae when food is scarce. They almost literally get the royal treatment. Neither chemical mimicry nor begging, a peculiar position held by an ant larva to manipulate workers into giving it more food, explains why *M. alcon* caterpillars are preferred over host ant brood. Our argument is that acoustical cues make the difference.

In addition to analyzing the similarity of the sounds emitted by *Maculinea* and *Myrmica*, we observed the behavior of the ants to better understand the role of acoustical emissions in the ant–butterfly relationship. Not surprisingly, playback experiments

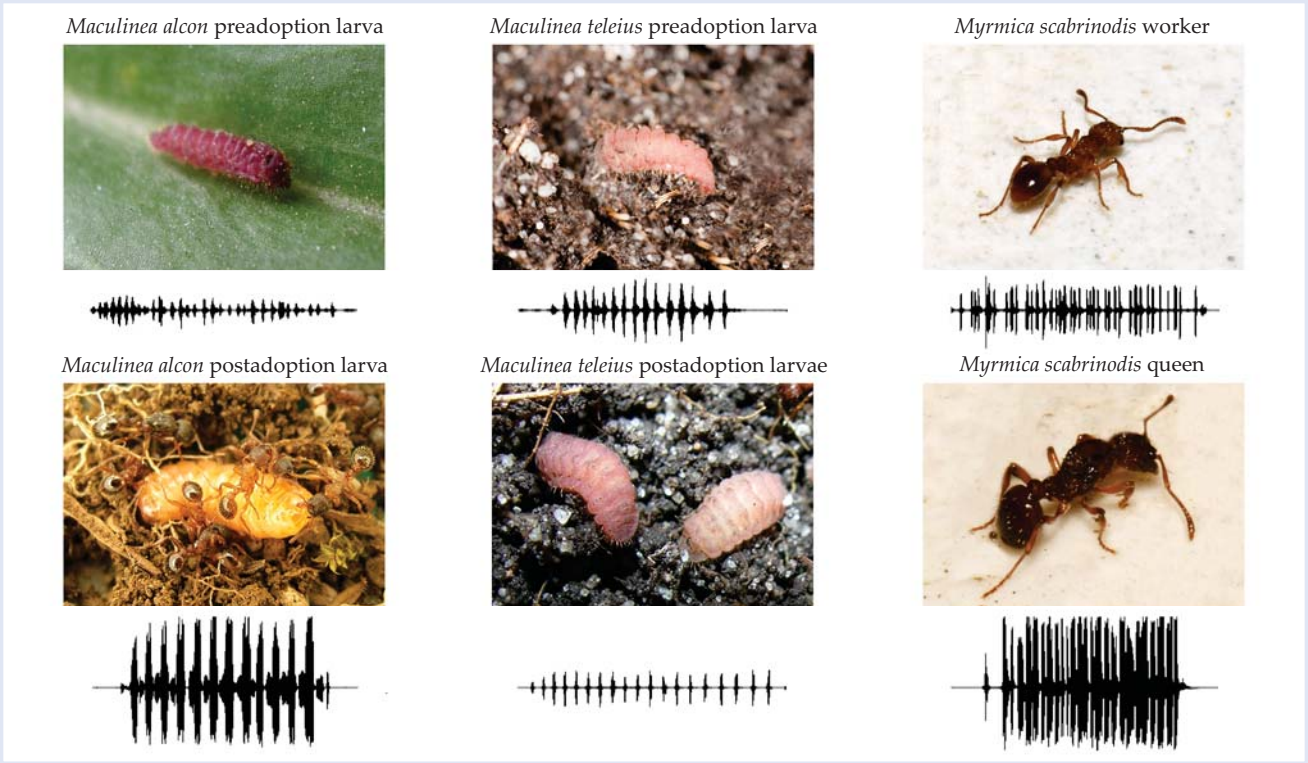

Figure 2. *Maculinea alcon* and *M. teleius* parasite larvae use chemical and acoustic mimicry to trick *Myrmica scabrinodis* worker ants into carrying the larvae to their ant nest. But once inside the colony, the *M. alcon* change their tune to sound more like the queen ant; in that manner the parasites gain high social status and are fed in preference to ant larvae. *M. teleius*, by contrast, are predators that eat ant brood; they do not want to draw attention to themselves when in the nest. The audio waveforms shown here were obtained over a period of two seconds. (Photo of *M. teleius* preadoption larva courtesy of Piotr Ślipiński.)

revealed that sounds produced by queen ants elicited the highest responses in workers—for instance, inducing the workers to assume the on-guard position they hold when defending their queen. But the experiments also showed that parasites' acoustic stimuli may even cause more frequent reactions in workers than the workers' own stridulations. When we compared the sounds of *Maculinea* species using different strategies to obtain food—cuckoo *M. alcon* versus predatory *M. teleius*—we observed differences not only in the features of the calls emitted but also in the reactions provoked.

The calls of the cuckoo species, as we have discussed, are essential once the larvae are already inside the ant nest. But the predatory species need to avoid being discovered by ants during their raids on the ant broods. Their calls, it seems, are more effective in the preadoption phase, when the predatory larvae reach the highest degree of interaction with the host ants, because they need to be touched, adopted, and taken into the nest. The predators do not chemically mimic ant larvae as precisely as cuckoos do, and the cuckoo species are adopted in preference to predatory species. We conjecture that the predatory larvae use sounds to supplement their less effective chemical mimicry.

Do ants hear?

Although we have talked about sounds produced by arthropods, we confess that scientists have only a scant understanding of the structures involved in the production of their acoustic signals and perhaps even less of a handle on how those signals are received. In particular, the community is engaged in a lively debate about the nature of ant hearing. Some, such as acoustician Robert Hickling and entomologist Richard Brown, have argued that ants can hear airborne acoustic waves over short distances; others insist that ants perceive only vibrations transmitted by a substrate, a view supported by the discovery of the so-called subgenual organ in carpenter ants. In our work, we have steered clear of the issue and have used methods of recording and playback compatible with either means of transmission.

Further studies of the structures responsible for the formation and perception of sound in ants would help clarify the role of acoustics in the world of social insects. So would further investigations of the sounds themselves. In our work, we played back the full repertoire of butterfly and ant sounds, but it may be that a single sound component is more important than the others. In future studies, we hope to use computer-synthesized acoustic stimuli and modify individual sound parameters to assess whether messages are conveyed through particular features in acoustic signals. Meanwhile, we can only marvel at the remarkable survival strategies of the *Maculinea* butterflies.

We thank our supervisor Emilio Balletto and Simona Bonelli for gratifying research collaborations and Karsten Schönrogge and Jeremy Thomas for introducing us to the acoustic world of Maculinea *and* Myrmica.

Additional resources

▶ P. J. DeVries, R. B. Cocroft, J. Thomas, "Comparison of acoustical signals in *Maculinea* butterfly caterpillars and their obligate host *Myrmica* ants," *Biol. J. Linn. Soc.* **49**, 229 (1993).
▶ F. Barbero et al., "Queen ants make distinctive sounds that are mimicked by a butterfly social parasite," *Science* **323**, 782 (2009).
▶ M. Sala et al., "Variation in butterfly larval acoustics as a strategy to infiltrate and exploit host ant colony resources," *PLOS ONE* **9**, e94341 (2014).