The Guests of Ants: How Myrmecophiles Interact with Their Hosts

By Bert Hölldobler and Christina L. Kwapich. 2022. Belknap Press. 576 pages, 205 colour photos, and 16 colour illustrations, 90.95 CAD, Hardcover.

I had high expectations for *The Guests of Ants* given that Bert Hölldobler and E.O. Wilson's *The Ants* (Belknap Press, 1990) won a Pulitzer Prize in 1991 and their subsequent ant-related books were great reads. I was not disappointed. And I certainly wasn't surprised,



as Dr. Hölldobler is one of the world's leading authorities on ants, and Dr. Kwapich also has an impressive publication record on ants and myrmecophiles. But just what is a myrmecophile?

A myrmecophile is literally an "ant-lover", an organism that spends at least part of its life cycle with ant colonies. To narrow the scope somewhat, The Guests of Ants does not attempt to discuss ants that exploit other ant societies, nor the interactions between ants and honeydew-producing insects such as aphids. That still leaves a staggering diversity of actors, with thousands of known myrmecophiles. Most are typically arthropods, but there are also myrmecophile bacteria, fungi, worms, and vertebrates. Their relationships with ants run the gamut from living in or on ant bodies (symbiotically or otherwise), stealing booty from foraging ants outside the colony, living in the margins of ant nests while feeding on discarded refuse, or even penetrating the inner sanctum of the nest to prey upon ant eggs and larvae. How myrmecophiles take advantage of ant colonies is a big part of the book, which includes discussions of risks to the myrmecophiles as well as costs to the ant colonies.

The diversity of taxa and relationships poses a challenge for how to best synthesize and present the information without overwhelming the reader. Fortunately, the first chapter is a primer on how ant societies work, from reproduction to division of labour. A much-needed glossary (with more than 200 definitions) introduces the reader to new terms—such as mermithergate, "an aberrant worker form in ants, caused by infection with nematode parasites in the genus *Mermis*" (p. 489)—and serves as a memory jog for others. This large format (24 cm \times 24.5 cm) book is brought to life by more than 200 spectacular fullcolour macro photographs, scanning electron microscope images, and illustrations of tiny organisms that we rarely get to see up close. More than mere eye candy, many photos even capture intimate interactions between myrmecophiles and their ant hosts, both in the lab and nature.

Myrmecophiles have diverse morphological, behavioural, chemical, and other mechanisms that allow them to exploit ant societies. For example, adults of the aptly-named phorid fly Vestigipoda myrmolarvoidea lack functional legs (and wings) and are dead ringers for the larvae of Aenictus army ants, whose colonies they inhabit. In contrast, despite not resembling their host, the ant cricket Myrmecophilus albicinctus uses its legs and palps to drum on the mouthparts of host Anoplolepis ants to induce them to regurgitate the liquid food (in an exchange called trophallaxis) upon which it depends. Even more remarkable is the chemical subterfuge used by myrmecophiles to hijack the olfactory communication used by ant societies in order to take advantage of them for room and/or board. Some guests have cuticular scent profiles that mimic those of host ant colonies (often acquired from living in close proximity to ants or from consuming ants) that allow them to hide in plain sight. Some staphylinid (rove) beetles produce appeasement chemicals that can temporarily distract ant workers while the beetles make their getaway, or they spray noxious compounds as a deterrent of last resort. Yet other myrmecophiles have larvae that are preferentially fed by their host ants to the detriment of their own ant broods, similar to avian cuckoos. The final chapter of the book is on vertebrate myrmecophiles and covers more well-trodden ground, like the relationship between army ants and antbirds (which eat the invertebrates flushed by the ants, rather than the ants themselves). There were still surprises, such as Painted Ant-nest Frog (*Lithodytes lineatus*) laying its eggs deep inside leafcutter ant nests or snapping turtles nesting in *Formica* ant mounds and enjoying the added benefit of leech removal services.

One minor quibble: over 1000 references are cited in the main text using the author-date (Harvard) format. This format makes for rather dense reading at times, compared to using superscripted numerals for in-text references. The references are essential if the reader wishes to dive deeper into the primary literature, which is made all the more useful by Hölldobler and Kwapich's critiques (where appropriate) of the cited study designs or findings. As the authors point out, there is still much to learn about numerous myrmecophile species and the nature of their relationships with host ants.

While books on ants seem almost as numerous as their subjects, the same cannot be said about books on myrmecophiles. *The Guests of Ants* fills this niche and is an essential reference for any myrmecologist or entomologist. It is also an interesting read for any naturalist interested in social insects and their ecology. This book serves as an inspiration to further explore myrmecophiles; after all, a journey of a thousand steps begins with a single ant column.

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