risk of harm to non-target species. As a potential biocontrol model for rodents, the group of Paul Thomas at the University of Adelaide, Australia, developed a novel gene-drive method designed to spread a genetic variant that makes females infertile (Proc. Natl. Acad. Sci. USA (2022) *119*, e2213308119).

Inspired by gene-drive methods developed for mosquito control in the fight against vector-borne diseases like malaria, this is the first time such a method has been used against a mammalian species. The researchers used the super-Mendelian transmission of the t haplotype in mice achieved with CRISPR–Cas9 gene editing, an approach that edits the animal's DNA *in vivo* and enables it to spread gene variants that would normally reduce their fitness (Nature (2019) *566*, 105–109). This way the researchers produced genetically engineered mice that would be able to spread infertility traits in a population. Using computer modelling with a range of realistic, field-based parameters, the authors show that releasing 250 gene-modified mice among an invasive island population of 200,000 would be sufficient to eradicate the invasive population within 20 years.

Further work will be required to rule out any possibility of the targeted population evolving resistance to the manipulated gene as well as a possible escape of the engineered trait to non-target populations. Bioethical concerns will have to be addressed, but the very remote nature of those islands that are more likely to have unique biodiversity vulnerable to rodent invasion may make this a model case for the use of gene-drive methods in the service of conservation efforts.

The biodiversity summits have a poor track record in that none of the targets have been reached so far. Keeping rodents away from small islands with vulnerable ecosystems at least appears to be a goal that is feasible and can make a considerable contribution to the overall protection of global biodiversity.

Michael Gross is a science writer based at Oxford. He can be contacted via his web page at www.michaelgross.co.uk

Book review

The bank most tangled

Joseph Parker

The Guests of Ants
Bert Hölldobler and Christina L. Kwapich
(Harvard University Press, Cambridge, Massachusetts; 2022)
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As chance would have it, you are reading this at a time when about 3.7 billion years of biological evolution have passed. To gauge how far we've come in the great unfolding of our biosphere, I urge you to immerse yourself in *The Guests of Ants* — the new book by myrmecologists Bert Hölldobler and Christina Kwapich. For here, laid out in 559 pages, is evolution at its maximal contemporary expression — organismal phenotypes at their most exaggerated extremes; Darwin's 'bank' at its most tangled.

The book's subjects are 'myrmecophiles' — organisms that make their living from the societies of ants. The past 50 million years have witnessed the reshaping of swathes of the natural world by an ant hegemony — a major biotic episode, with deep reaches into how contemporary ecosystems function and how the phylogenetic tree of extant life appears. *The Guests of Ants* is an account of how these pervasive social insects have impacted biological diversity most directly. In exquisite and sometimes uncomfortable detail, we are shown the spectrum of lifeforms that have become so entangled with ants that they now depend on them. What Hölldobler and Kwapich have produced is a carnival of the extraordinary; a relentless and stunningly illustrated parade of the myriad organisms that have gained footholds in virtually every aspect of ant biology. Such is the ecological preponderance of ants that no domain of life has been exempted from their reach.

First up are the microbes that have entrenched themselves within their hosts' metabolism. Next, the endoparasites — cestodes, nematodes, trematodes, and infamous *Ophiocordyceps* fungi that gain control of worker behavior, eventually blowing them up to scatter their spores. Phorid flies follow, and we learn to pity the ants as they fend off these flies' attempts to oviposit into them. If the ants succumb, the phorid larva will hatch within them, decapitate them, and use their head capsule as a pupal chamber. Inevitably, we pass through groups of parasitoid wasps before encountering mites, so miraculous that they are known only from the narrowest anatomical niches on ant bodies, their modified forms affixing with ergonomic precision.

Yet, all of these are just the opening acts, and soon we are deep into the realm of that new and most specialized form of life for which social insects must take full credit: the social parasite — evolution's inevitable response to the emergence of resource-rich ant colonies. One by one, we are fed examples of the thousands of animal species — both invertebrate and vertebrate — that have evolved to exploit ants and infiltrate their colonies in the most perplexingly intricate ways. Some of these impostors seem better at playing ants than the ants themselves. *The Guests of Ants* is a careening ride through the natural history, ecology and evolution of these ever more bewildering organisms — miniature tank-like haeteriine clown beetles and cremastocheiline scarabs that invade colonies to feed on the ants' brood; ant-mimicking diapriid wasps and aleocharinae rove beetles (Figure 1) that walk unnoticed in army ant columns; lycaenid and riodinid butterfly caterpillars that chemically appease ants for protection, reneging on the deal by evolving into predators and cuckoo-like nest parasites; reduviid bugs that sport invisibility cloaks woven from ant cadavers; jaw-droppingly convincing myrmecomorph spiders that are also myrmecophagous (ant-eating); ant crickets (Myrmecophilidae) that scrape ant bodies for nutrition and inexplicably scale their body size to different host ant species; eyeless *Claviger* beetles fed trophalactically (mouth-to-mouth) by the ants and dragged around nests like insect corpses; *Attaphila* cockroaches confined to the subterranean depths of leaf cutter ant fungus gardens — only to hitch high altitude flights on the gasters of winged reproductives.

Each myrmecophile comes with its own brand of chemical and behavioral chicanery to deceive its unknowing host. Each has found a solution to the perennial challenge of how to propagate and disperse while tied to a host and living under its radar. Viewed from one perspective, this book may appear a compilation of some of evolution's greatest avant-garde productions. But make no mistake — myrmecophiles are not mere biological curiosities. They are the archetype of complex symbionts, with everything to teach us about how phenotypes transform — and evolutionary strategies switch — as organisms forge obligate relationships with other species.

The book is structured to highlight specific myrmecophile groups that encapsulate fundamental aspects of interspecies relationships. One chapter, covering the ecology and behavior of aleocharine rove beetles, traces how myrmecophiles may originate from free-living ancestors. In this hugely species-rich clade of tiny beetles, numerous lineages have transitioned from litter-dwelling predators into sophisticated colony impostors. Taking a comparative approach, the authors infer the stepwise evolutionary changes in chemistry and behavior that have seamlessly integrated some aleocharines into the social organization of ant colonies. The beetles' abdomens, adorned with exocrine glands, have been key to this process — a substrate for evolutionary innovation whereby defensive secretions have been superseded by exudates that promote acceptance and adoption. These biochemical changes have arisen in concert with elaborate behaviors that enable the beetles to solicit trophallaxis. The beetles' larvae, too, develop inside nests — raised by workers whom they chemically manipulate to obtain preferential treatment.

Another chapter, on lycaenid butterflies, walks us along the knife edge between cooperation and exploitation that exists in many interspecies partnerships. What appear at first to be equitable mutualisms — sugary secretions in return for protection — may obscure a more dynamic and in some cases dishonest reality — a pressure to

Figure 1. Imitation without flattery.
Three different army ant genera (on the left) facing their corresponding rove beetle myrmecophiles. The beetles convergently evolved into social parasites that mimic their hosts. Ants, top to bottom: *Nomamyrmex*, *Aenictus* and *Neivamyrmex*. Beetles, top to bottom: *Ecitocryptus*, *Giraffaenictus*, *Diploeciton*. Photos from Maruyama and Parker (2017). Curr. Biol. *27*, 920–926.

take as much as possible while sacrificing as little as possible. This tension plays out in the caterpillars' secretions themselves: spiking in valuable amino acids helps cement ant attendance, but what if the secretion were further modified with narcotics? Such appears to be the case in the lycaenid *Arhopala japonica*, the larva's secretions lowering dopamine in the brains of attendant ants, coercing them to protect it. Perhaps an immediate adaptive pull of selfishness explains why the ancestral mutualism has repeatedly broken down in Lycaenidae, giving way to nest intruders that are fed trophalactically (*Phengaris*) and voracious ant predators (the terrifying *Liphyra*). Elsewhere, chapters focus on how certain features of ant biology have catalyzed the evolution of different kinds of myrmecophiles, and we come to view the ant colony as an ecosystem in its own right. Far from being the impenetrable fortress, vulnerabilities are many, each offering an entry point for exploitation. Among many contenders, the giant *Bengalia* flies may represent the ne plus ultra, swooping down to siphon off regurgitated food as foraging workers engage in trophallaxis with each other.

This book has had a long gestation period. Introduced as a boy to the world of myrmecophiles by his myrmecologist father, the book's first author went on to produce a seminal piece of Tinbergenian ethology that to this day stands out among studies of myrmecophile–host interactions. In a series of clever experiments, Hölldobler teased apart how adults and larvae of the rove beetles *Lomechusa* and *Lomechusoides* integrate into host colonies by way of glandular secretions that modify host behavior. His fascination with myrmecophiles never wavered (how could it?), and a precursor of this book materialized as a chapter in *The Ants* (1990), co-authored by Hölldobler and the late Edward O. Wilson. As Hölldobler recounts, following the publication of this Pulitzer prize-winning opus, Wilson encouraged him to produce an entire book dedicated to the biology of myrmecophiles. Thirty-two years later, in conjunction with ant ecologist and fellow myrmecophile aficionado Kwapich, it has arrived.

The wait seems appropriate. The intervening years have seen a slew of new discoveries that span the natural history, ecology, chemistry, taxonomy and phylogenetic relationships of myrmecophiles. Hölldobler and Kwapich are to be applauded for distilling this mass of literature into a comprehensive and digestible work. A real strength of the book is the scrutiny the two authors have paid to all these pieces of literature. Repeatedly, shortcomings are highlighted, gaps in knowledge emphasized, alternative hypotheses floated, and ideas for experiments suggested. One senses that despite the volume of research that now exists on various myrmecophiles, we have still barely scratched the surface of this phenomenon. There is virtually everything to learn about how these relationships originate and persist evolutionarily; how they feed back into the life histories and population genetics of these symbiotic animals; how the behavioral interactions we see are fashioned from underlying chemical, cellular and neurobiological processes; and how, reciprocally, playing host to tens of thousands of myrmecophile species has impacted the diversification and present-day ecology of the ants themselves. What the authors have done is lay out much of what we've observed while conveying how little of it we truly understand.

The writing is matter-of-fact, and devoid of superlatives. Why is any hype needed when the biology is already this rich? In the decades since the publication of *The Ants*, insect photography too has evolved. Throughout, *The Guests of Ants* is decorated with exceptional shots from some of the world's foremost insect macrophotographers. Numerous pictures from Taku Shimada in particular — a photographer with an apparent sixth sense for tracking down rare myrmecophiles — capture remarkable behavioral interactions for the first time, and with emotive clarity.

If I have one miniscule gripe it is with the authors' insistence on restricting the term 'social parasite' solely to ants that subjugate the workers of other ant species. Their rationale is unconvincing, and in my view, any organism that exploits a social niche that ants have created is unavoidably a social parasite, analogous to a classical parasite infecting an organismal host. To be sure, this point is trivial when considered in the context of this incredible book's entirety. But to leave it unsaid risks suppressing a valuable term used widely among myrmecophile workers.

Who, then, is this book for? Perhaps for no one in particular, but also for everyone. Because at whichever page the book falls open, the myrmecophiles' seductive beauty, intricacy and intrigue pour out. The curious layperson will feel themselves inside of nature. The entomologist, ecologist and evolutionary biologist will fixate until they dog ear the corners and bend the spine (as I have done with my copy already). As a landmark reference on the biology of myrmecophiles, it will be the quintessential resource for generations of researchers to come, and will surely inspire many to find their own niches within this vast and richly rewarding biological terrain (as the publication of *The Ants* did for myrmecology). And as the tendrils of molecular biology, genomics and modern behavioral neuroscience spread into new frontiers, *The Guests of Ants* is a clarion call. For the history of biology has shown that the starting point for path-breaking discoveries is observational natural history. What secrets lurk enmeshed within this most tangled of banks one can only speculate. But they are waiting to be found, and *The Guests of Ants* provides us with many signposts.

Division of Biology and Biological Engineering, California Institute of Technology, 1200 E. California Boulevard, Pasadena, CA, USA.
E-mail: joep@caltech.edu

Q & A

Noah Whiteman

Noah Whiteman is Professor of Integrative Biology and of Molecular and Cell Biology at the University of California, Berkeley. He studies the mechanistic basis of adaptations that arise from species interactions, particularly between host and parasite, and between plant and animal. He received a 2020 Guggenheim Fellowship and is an elected fellow of the Royal Entomological Society and the California Academy of Sciences.

What turned you on to biology in the first place? It was partly innate and partly the influence of my parents. My father was an amazing naturalist and my mother encouraged me through reading and by listening to the knowledge I accumulated. I was one of those kids who just observed nature and tried to understand it, often by catching animals and bringing them home, alive, to show my family. My mother had what she called a 'three-foot rule' that meant I couldn't come closer than three feet if I was holding an animal, and if I wanted a new 'pet' I had to read about it first by going to the library and finding books on the subject. I credit them both with fostering my innate curiosity about nature that was just insatiable.

My biophilia was also undoubtedly influenced by the fact that, from about the age of 10 onwards, I lived in the middle of nowhere, at the edge of the vast Sax-Zim Bog in between Duluth and the Iron Range cities in Minnesota, within the southern limits of the Boreal forest. That bog is a huge relic peatland covered in rafts of sphagnum peat moss, studded with black spruce and tamarack trees, like the taiga, and below them, legions of carnivorous pitcher plants and tiny sundews. Prior to that we lived in Duluth, on the northern shore of Lake Superior.

What I didn't realize at the time was that the Sax-Zim Bog was also known as the 'Arctic Riviera' by birders because many different bird species from Canada, including great grey owls and northern hawk owls, would make their way down to the bog in the winter when rodent populations up north were waning. Because it was inland,