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Evolution: Shape-Shifting Social Parasites

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Ants exploit differences in body surface chemistry to distinguish nestmates from colony intruders. Socially parasitic ants in Madagascar have convergently evolved morphological similarities to host worker anatomy, implying that body shape may also be surveilled. Studies of tactile behaviors in ant societies are now needed.

Since their emergence during the early Cretaceous, ants have diversified into ecologically dominant insects that impact the biosphere in ways unmatched by most animal groups [1]. Ant colonies police landscapes, regulate nutrient flows and control the abundance of other life forms. Key to this ecological hegemony is social cohesion, manifested in a division of labor among workers, and between workers and reproductives [2]. As in all eusocial insects, the emergent behaviors of ant colonies depend on chemical cues that enable reliable nestmate recognition [3]. The integral compounds are cuticular hydrocarbons (CHCs): long chain alkanes and alkanes, which are secreted onto the ant body surface in complex blends [4,5]. When encountering another insect, ant workers will sense the insect's CHCs and compare them to their own, colony-specific profile. If there is a mismatch, the insect is recognized as foreign, and the ants will respond aggressively to extinguish the threat. This CHC-based model of nestmate recognition is broadly accepted and has spawned a consensus view that olfaction is the predominant sensory modality underlying colony cohesion [4,5]. Indeed, ants provide an archetypal model for how chemosensory information controls social behavior that is now being examined at the neurobiological level [6]. However, a new study by Georg Fischer, Evan Economo and colleagues in this issue of *Current Biology* [7] challenges

the absolute explanatory power of this chemocentric view. Their findings indicate that tactile sensing of external anatomy may represent a parallel information channel for nestmate recognition.

To reach this controversial conclusion, Fischer and colleagues [7] report evidence from a newly discovered group of 'socially parasitic' ants. Social parasites are animals that make a living inside ant colonies. Bountiful, climatically controlled ant nests are targeted by a veritable zoo of such intruders, including thousands of species of 'myrmecophiles' — non-ant arthropods such as beetles, flies, crickets and butterfly caterpillars that are specialized for colony infiltration [8,9]. In addition, there are more than 400 socially parasitic ant species that are obligately dependent on the social environment provided by host colonies of other ant species [10]. Social parasites employ diverse strategies to evade detection inside nests. Many species are able to assimilate into the ant society by mimicking how their hosts recognize and interact with each other, a phenomenon termed 'Wasmannian mimicry', after Erich Wasmann, the Austrian entomologist who pioneered the study of myrmecophile biology [8]. Social parasites that are integrated in this way provide valuable windows into how ants communicate: their Wasmannian adaptations reveal fundamental phenotypic traits that are necessary to be treated as a nestmate.

Studies of both ant and non-ant social parasites indicate that chemical deception is paramount, with many social parasites capable of mimicking their hosts' CHC profiles [11].

The new study of Fischer and colleagues [7] suggests that all may not be so straightforward. The authors inferred the phylogenetic relationships of 80 Malagasy species of the large ant genus *Pheidole*. Within the Malagasy *Pheidole* radiation, they recovered a single origin of social parasitism with 13 descendent species. Crucially, each species within this clade has evolved to target another, distantly related free-living species within the Malagasy *Pheidole* clade (Figure 1). These replicate instances of social parasitism on phylogenetically distinct hosts provide an opportunity to ask a simple question: what happens to a social parasite's body plan as it adapts to a novel host? To answer this question, the authors used micro-CT scans to build 3D anatomical reconstructions of workers of ten social parasite–host pairs (parasite and host queens were also examined in this way if specimens were available). They then quantified anatomical similarities between host and parasite, employing both linear measurements of body structures and geometric morphometrics to estimate multivariate shape parameters. Plotting measurements of host versus parasite across species, striking correlations emerged: social parasite workers show
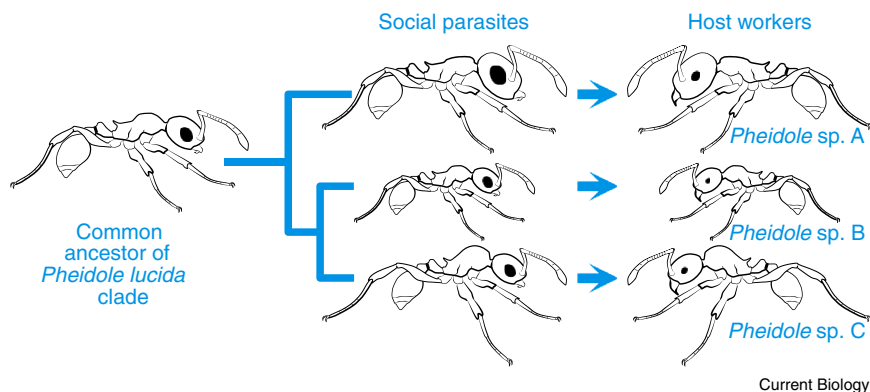
Figure 1. Malagasy *Pheidole* social parasites match host worker anatomy.
Social parasitism evolved once in the common ancestor of the *Pheidole lucida* species group. Each social parasite has evolved to target a different *Pheidole* species (A, B, C). In 10 such cases, the social parasites have evolved similar body, head, thorax, leg and antennal size to their hosts, as well as comparable head and thorax shapes. The social parasites also retain certain traits typical of their lifestyle, such as larger eyes and smaller mandibles.

marked similarities to host worker morphology, both in terms of the linear sizes of individual body and appendage segments, as well as shape parameters of the head and thorax (Figure 1). To a significant degree, the parasites have evolved to 'mirror' their hosts' anatomies. The fact that many lineages have convergently evolved in this way implies that such changes are adaptive.

What value might this similarity of form serve? The authors propose that it represents a novel mode of Wasmannian mimicry: the social parasites are fooling their hosts. They do so not by appearing to be visually similar — *Pheidole*'s eyesight is far too poor, and the social parasites are also likely to dwell within the dimly illuminated nest — but rather by feeling similar to the touch. This daring proposition demands that, in addition to being highly sensitive to CHCs, *Pheidole* ants are able to detect the sizes and shapes of creatures, incorporating tactile assessment into nestmate recognition. Through changes in body proportions, the authors argue, the social parasites have evolved to conform morphologically to the host's worker caste, enabling them to pass this extra level of surveillance. The impostor ants may thus have exposed a distinct and unappreciated sensory mechanism of colony cohesion.

Could there be alternative explanations? Perhaps the parasites have adapted to the same microhabitat conditions as their hosts, reflected in their convergent morphology. Maybe mimicry helps the social parasite avoid being eaten by a

visual predator, considering that many arthropods mimic ants for this reason, thus conforming to Batesian rather than Wasmannian mimicry. However, these alternatives seem doubtful given that social parasite workers are believed to stay inside the nest, leaving the heavy lifting and the risky outdoors to their hosts [10]. Still, precious little is currently known about the behavior of these Malagasy *Pheidole* social parasites, and the authors' inferences about their biology are based on limited studies of other socially parasitic ants that retain a worker caste (most inquiline socially parasitic ants are simply queens evolved to be without workers).

What other evidence is there for morphological sensing? Anatomical mimicry has not been reported for other socially parasitic ants; however, this may stem from the fact that such species tend

to target hosts that are their close relatives, and in rare cases the social parasites evolve directly from their future hosts [12]. Hence host and parasite are already morphologically very similar — a phenomenon known as Emery's rule [10]. Instead, support for morphological sensing may be found with non-ant social parasites, specifically the rove beetles (Staphylinidae) [13]. Many species of rove beetle have evolved to socially parasitize large, nomadic colonies of army ants. As well as chemically mimicking their hosts [14,15], these beetles display dramatic anatomical mimicry (Figure 2A). This morphological mimicry has evolved at least a dozen times independently [16], indicating its adaptive nature. Some of these beetles differ markedly in color to their hosts (Figure 2B), which are virtually blind, subterranean and nocturnal, rendering visual or Batesian mimicry unlikely and instead representing Wasmannian mimicry [9,16,17]. Indeed, these beetles are amongst the most highly integrated myrmecophiles known and interact with their hosts extremely intimately.

However, there are legions of non-ant myrmecophiles that are accepted inside nests without resembling their hosts at all [8,9]. One explanation might be that these species are not pretending to be nestmates, but playing a different game. Many myrmecophilous beetles and butterflies, for example, secrete 'appeasement compounds'. These secretions are not CHCs, but may be psychoactive or at least attractive to host workers [18,19]. If this doping strategy is effective, perhaps 'feeling like an ant' is less critical for such social parasites.
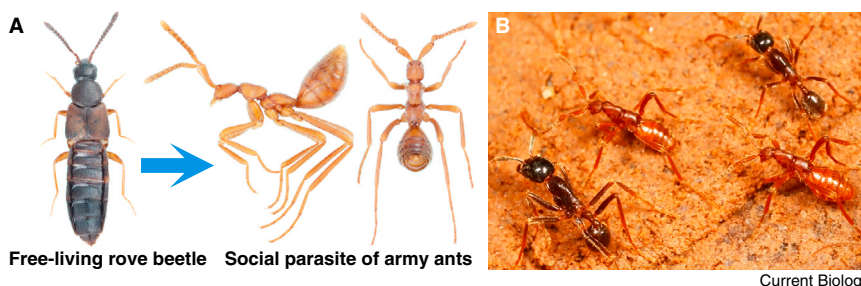

Figure 2. Wasmannian mimicry in rove beetle myrmecophiles.
(A) Over a dozen lineages of aleocharine rove beetle have evolved from free-living species with generalized morphology (beetle on left) into social parasites that live inside army ant colonies and mimic their hosts' body shapes (beetle on right). (B) In some genera such as *Pseudomimeciton*, beetle morphology is ant-like but coloration differs strongly to the host (*Labidus*), arguing against Batesian mimicry in these cases (photo credit: Taku Shimada).

If morphological sensing is real, what purpose does it serve? Direct touch has been shown to be non-essential for nestmate recognition [20], implying that at least some CHCs are sensed over short distances and can influence worker interaction. However, this observation does not negate the fact that tactile interactions can and do occur, and may allow for reliable assessment of identity. Unlike CHC profile, however, body anatomy is far less variable within a given ant species. Shape is hence unlikely to enable perceptual determination of nestmates from non-nestmates of the same species. Nevertheless, even if shape conveys coarser information about species identity, it may be adaptive, assisting in detection of uninvited ant or arthropod guests. Clearly, ant worker behavior must now be studied with tactile sensing in mind. What is the degree of aggression versus acceptance towards CHC-coated objects of different shapes? Do experimental manipulations of worker shape lead to quantifiable effects on inter-worker aggression inside nests? If morphological sensing occurs, it is presumably performed during antennation. Do ants possess the ability to simultaneously perceive the smell and shape of the objects they antennate? Clever experiments may yield answers to these questions and determine whether we need to update our view of nestmate recognition.

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Neuroscience: A New Pathway to Make Us Smarter and Happier

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Treatments that improve cognition and decrease depression converge on decreasing phosphorylation of eukaryotic elongation factor 2 (eEF2). This decrease is sufficient to lead to altered levels of proteins that cause an increase in new neurons, improved cognition and less depression.

A translational regulon describes a group of mRNAs that contain a common motif allowing for coordinated translational regulation to achieve a physiological function [1]. For example, some mRNAs encoding proteins important for the induction of the integrated stress response contain upstream open reading frames that allow for translational activation when eukaryotic initiation factor 2 alpha (eIF2α) phosphorylation is increased [2]. In contrast, translational regulons corresponding to changes in the rates of translation elongation, such as ones mediated by the phosphorylation of eukaryotic elongation factor 2 (eEF2), have