Chemical strategies to deal with ants: a review of mimicry, camouflage, propaganda, and phytomimesis by ants (Hymenoptera: Formicidae) and other arthropods

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Abstract

Chemical tactics by ant social parasites, including myrmecophiles, often relate to ant nestmate recognition and alarm communication. The strict nestmate recognition system in ants can be disrupted by chemical imitation of the nestmate recognition pheromone, which consists of cuticular hydrocarbon components. Social parasites often acquire these components through direct body contact, but occasionally synthesize them even before ant adoption. Such an imitation of the host cuticular chemicals causes species-specific adoption of the parasites, which are then often taken care of by ants for long terms. In contrast, transient invaders often use a propaganda allomone that induces panic alarm responses in ants. The allomone occasionally even causes fighting among nestmate ants, and seems to disrupt the ant nestmate recognition. These two chemical strategies are to modify the ant responses after ant detection. A third chemical strategy taken by some insect species is to avoid the detection itself, and is evidenced in the chemical phytomimesis by geometriid twig-like caterpillars. Since this counts upon the ants not to respond to the "invasion", it usually does not cause visible responses when it works effectively. Appropriate evaluation methods are necessary to evaluate the ant responses induced by the parasites to reveal the underlying mimetic strategy.

Key words: Chemical mimicry, camouflage, propaganda, crypsis, phytomimesis, cuticular hydrocarbons, review.

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Introduction

Ants are generally omnivorous or carnivorous, and characterized by their organized social structure with labor division. They have well-developed chemical communication systems that maintain their societies. Ants are therefore formidable predators of various animals, particularly mobile terrestrial insects. Numerous insect groups, including ants, must avoid ant attack to survive (ELMES 1996), and many have developed various chemical defenses. It is likely that such chemical tactics are effective because ants rely on chemical signals to sense their environment. In interactions with ants, survival strategies are roughly separated into two classes: avoiding ant detection and dealing with ants after being detected (Tab. 1). The former can be an effective strategy to avoid ant attack, and "crypsis" is known as a primary defense mechanism in animals in general (EDMUNDS 1974, RUXTON & al. 2004). Chemical crypsis can be confirmed in the animals that adopt this strategy. In contrast, there are at least two different strategies to deal with ants after detection. One is based on evasion, including so-called "propaganda", which is adopted by several social parasitic ants and wasps (REGNIER & WILSON 1971, BLUM & al. 1980, LLOYD & al. 1986, THOMAS & al. 2002). The other strategy is to pose as nestmates for acceptance by the host ants. This strategy is presumably the most frequent and best studied of the interactions between myrmecophiles and host ants.

To understand the background of these three strategies, it is important to review briefly how the ants rely on chemical communication to sense their biotic environment. Since ants live in colonial societies with numerous members, they are always required to communicate in order to maintain their social life (HÖLLDOBLER & WILSON 1990, YAMAOKA 1990, VANDER MEER & ALONSO 1998, LENOIR & al. 1999). Ant colony members can usually discriminate their nestmates from alien species and conspecific foreigners. With nestmates, ants can discriminate their task, caste and fertility. Outside the nest, they judge food sources, share food information, warn of foraging dangers, and recruit nestmates if necessary. The means of these communications are chemical signals that operate in a sophisticated communication network. But this reliance on chemical signals has also enabled myrmecophiles and social parasites to develop adaptive chemical tactics to deceive the ants (DETTNER & LIEPERT 1994, VANDER MEER & MOREL 1998, LENOIR & al. 2001). Ironically, the strict exclusivism of the ant colonies provides social parasites safe ecological niches if they successfully deceive hosts with their chemical tactics.

This is a review of the chemical strategies that surround ants, with reference to my research on myrmecophilous insects (AKINO & al. 1996, 1999, AKINO 2002, ELMES & al. 2002), parasitoid wasps (AKINO & YAMAOKA

Tab. 1: Classification of main chemical strategies to deal with ants. See detailed explanations in the text.

Category	What to achieve ultimately	Chemical strategy	Proximate effect
Primary defense	Avoid detection by ants	Chemical mimesis (including chemical phytomimesis)	Being "invisible" by background-matching
Secondary defense	Avoid attacks by ants	Chemical mimicry and camouflage	Pretending to be nestmates
Attack	Induce panic alarm response in host ants	Propaganda	Disturbing the host nestmate recognition

1998, THOMAS & al. 2002), and phytomimetic caterpillars (AKINO & al. 2004a, AKINO 2005). There are excellent recent reviews on chemical strategies after ant detection (VANDER MEER & MOREL 1998, LENOIR & al. 1999, 2001, HOWARD & BLOMQUIST 2005). This review starts with the known strategies by myrmecophiles and ant social parasites, and then focuses on the chemical crypsis that is employed to avoid ant detection. The latter element has perhaps not yet received enough attention.

Pretending to be nestmates to avoid ant attack

The chemical mimicry and camouflage used to assume the identity of ant nestmates are the most frequent chemical strategies employed by ant parasites. Chemical mimicry entails the parasites' active synthesis of the host cues. In chemical camouflage, parasites obtain cues from the host through passive and active acquisition (HOWARD 1993, DETTNER & LIEPERT 1994). These strategies are not mutually exclusive and can coexist in the same species (LENOIR & al. 2001). They are secondary defenses because both change ant responses after host detection.

Ants have an ability to discriminate their conspecific nestmates from foreigners, and they generally share safety and food only among the formers. If social parasites successfully imitate nestmates of the host ants, they can avoid ant attack and also attain protection and food inside the nest. This strategy relies on ant nestmate recognition and has been applied by various myrmecophilous insects and social parasitic ants (VANDER MEER & al. 1989, HOWARD 1993, DETTNER & LIEPERT 1994, AKINO & al. 1996, 1999, AKINO & YAMAOKA 1998).

Ant nestmate recognition has been considered to be based on chemical signals, i.e., "nestmate recognition pheromone". Nestmate recognition is common in eusocial insects, including not only ants but also bees, wasps, and termites. There are several recent reviews on the subject (BREED 1998, SINGER & al. 1998, VANDER MEER & MOREL 1998, LENOIR & al. 1999, 2001, HOWARD & BLOMQUIST 2005, HEFETZ 2007). There has been controversy as to which chemicals serve as the pheromone in each group. Cuticular hydrocarbons are considered to be the most likely components in ants (VANDER MEER & MOREL 1998, LENOIR & al. 1999, HOWARD & BLOMQUIST 2005, HEFETZ 2007).

Cuticular hydrocarbons as the nestmate recognition pheromone in ants

Hydrocarbons are major lipid compounds of the ant cuticular waxes, although relatively small amounts of polar lip-

ids are also present. The hydrocarbon compositions generally differ among species, i.e., each species has its own composition. Furthermore, the relative amounts of each component of the cuticular hydrocarbon profiles within species are usually specific to colonies. In other words, colony members share almost identical profiles that differ from those of conspecific foreigners. These two characters are the basis of the "hydrocarbon hypothesis" suggesting the active role of the cuticular hydrocarbons as nestmate recognition pheromones. This hypothesis is widely supported by many indirect correlative lines of evidence as recently summarized by HEFETZ (2007). However, much of this evidence is at the best circumstantial, based on either correlation studies or bioassays using removal and replacement of cuticular compounds by solvent extraction (BREED 1998). Behavioral experiments using artificial blends with authentic hydrocarbons are necessary to prove the critical link between cuticular hydrocarbons and nestmate recognition. However, ant cuticular hydrocarbons are generally complex mixtures of various methyl-branched alkanes, including mono-, di-, and tri-methyl alkanes (HOWARD & BLOMQUIST 2005). This complexity makes it difficult to conduct behavioral experiments in most ant species to test the "hydrocarbon hypothesis" by direct comparison of artificial and natural blends of the hydrocarbons.

This obstacle was, however, overcome in Japan's most common ant, *Formica japonica*, as reported by AKINO & al. (2004b). This species apparently has an ability of nestmate recognition, which is most likely based on cuticular hydrocarbon profiles (YAMAOKA 1990). The profiles were shared by workers and queens in each colony, but significantly differed between colonies (YAMAOKA 1990, AKINO & al. 2004b). It was fortunate that the cuticular hydrocarbons consisted of pairs of n-alkanes and respective (Z)-9-alkenes of odd numbers from C25 to C33. Furthermore, the absence of branched alkanes makes the composition much simpler than that in many other ant species. This simple composition enabled us to prepare all the hydrocarbons commercially and synthetically, and also to obtain artificial hydrocarbon blends that matched natural blends. Complete artificial blends of n-alkanes and 9-alkenes, as well as the natural blends of a certain *F. japonica* colony, caused worker aggression in foreign colony workers but not in nestmate workers. This indicates that those hydrocarbons actually serve as the nestmate recognition pheromone in *F. japonica*, and that these ten hydrocarbons are sufficient for nestmate discrimination. In contrast, single blends of either n-alkanes or (Z)-9-alkenes caused no ag-

gression in foreign workers. This diminishes the possibility that single active compounds can activate nestmate recognition, but suggest that it is the combinations of these two classes of hydrocarbons that provide this function. Similarly, nestmate recognition relies not on particular hydrocarbon components but complex hydrocarbon profiles in *Linepithema humile* and *Aphaenogaster cockerelli* (GREENE & GORDON 2007). In contrast, the nestmate recognition in *Formica exsecta* does depend on particular components (MARTIN & al. 2008).

Simple hydrocarbon compositions are rare in ant species. It is difficult to test the "hydrocarbon hypothesis" in most ant species with a classical pheromonal approach. Instead, a neurophysiological approach was recently attempted for *Camponotus japonicus*, and demonstrated the existence of particular sensilla on the antennae that specifically responded to foreign cuticular hydrocarbon profiles (OZAKI & al. 2005). This indicates that the sensilla can discriminate between nestmate hydrocarbon profiles and foreign hydrocarbon profiles immediately after direct contact, although the details of such a physiological perception mechanism remain unknown. Such an immediate discrimination of the minute differences in the complex hydrocarbon profiles is considered to be necessary for nestmate recognition behavior, which is induced immediately after body contact between individual workers. Therefore, the existence of such sensilla strongly supports the "hydrocarbon hypothesis". Thus, a neurophysiological approach can be quite effective to verify the "hydrocarbon hypothesis" and to explore if a similar perception system is common in ant species.

On the other hand, recent studies suggest additional functions of the ant cuticular hydrocarbons, e.g., signals for caste, task, and fertility recognition (reviewed by HEFETZ 2007). However, most of them are based on quantitative comparison of the cuticular hydrocarbons that correspond to ant behavior and physiological states, and few include hydrocarbon manipulation. It is necessary to organize results in ways that illuminate the details of caste, task, and fertility recognition. Other verification methods to test the hypothesis directly should also be developed. Although the classical pheromonal study approach is presumed to be effective for verification of the expanded "hydrocarbon hypothesis", the complexity of the ant cuticular hydrocarbon compositions prevents the execution of behavioral bioassays with pure chemicals.

Chemical mimicry and camouflage by cuticular hydrocarbons

It is most likely that the chemical signal for ant nestmate recognition consists of cuticular hydrocarbons, as indicated by many lines of circumstantial evidence and several direct ones. Chemical mimicry (in which the parasite actively biosynthesizes the host cues) and camouflage (in which the parasite obtains cues from the host both by passive and active acquisition) are practiced by various insects that take advantage of ant social systems (VANDER MEER & al. 1989, HOWARD 1993, DETTNER & LIEPERT 1994, AKINO & al. 1996, 1999, AKINO & YAMAOKA 1998, 2000, AKINO 2002). This includes not only myrmecophilous insects but also social parasitic ants. The ethological role of cuticular hydrocarbons in this strategy in ants has often been highlighted (HOWARD 1993, DETTNER & LIEPERT 1994, SINGER & al.

1998, VANDER MEER & MOREL 1998, LENOIR & al. 1999, 2001, HOWARD & BLOMQUIST 2005).

Chemical camouflage

The cases of the tiny *Myrmecophilus* cricket and the aphidiid wasp *Palaripsis eikoae* are noteworthy as examples of chemical camouflage because of the chemical adjustment ability and the characteristic behavior for acquiring the ant hydrocarbons, respectively.

The species ecology of the myrmecophilous cricket *Myrmecophilus* sp. is closely connected to several ant species. It is believed that this cricket has an ability to switch host ant species. Comparative GC-MS analyses revealed resemblances in the cuticular hydrocarbon compositions and profiles between the crickets and their corresponding host ants (AKINO & al. 1996). Transfers of the crickets between conspecific colonies resulted in initial aggression by host ants against the foreign crickets, but this decreased within a week. This was also confirmed in transfer of the crickets between different species, for example, between *Lasius nipponensis* and *Formica japonica*, and between *F. japonica* and *Lasius fuji*. The crickets escaped from the initial ant attacks through physical agility. Then they approached the ant workers repeatedly, and successfully adjusted their cuticular hydrocarbon compositions and profiles to fit those of the new host ant species and colonies within approximately a week. This ability to adjust their cuticular hydrocarbons requires direct body contact with the host ants that show high hostility at the beginning. Preventing direct body contact with the host ants results in drastic decrease of ant-like hydrocarbons in the crickets. Such chemical resemblance by acquisition is known in the beetles *Myrmecaphodius excavaticollis* (see VANDER MEER & WOJCIK 1982), *Pella comes* and *Diaritiger fossulatus* (see AKINO 2002), and the spider *Cosmophasis bitaeniata* (see ELGAR & ALAN 2006).

Another example is the aphidiid parasitoid wasp, *Paralipsis eikoae*, which is a specialist parasitoid of the wormwood root aphid *Sappaphis piri* tended by *Lasius niger*, as reported by TAKADA & HASHIMOTO (1983, 1985). Presumably because the wasp requires upbringing by ants to mature its ovaries after eclosion, it acquires the ant cuticular hydrocarbons through direct body contact after invading the ant colony to let the ants feed it (AKINO & YAMAOKA 1998). The direct body contact occurs as the wasp mounts on the ant's back and then repeatedly rubs the ant abdomen with its midlegs in "rubbing" behavior (TAKADA & HASHIMOTO 1983). The *Lasius* ants do not move during this process, as if they were paralyzed. The wasp may use some appeasement signals to facilitate this docility (this will be discussed in a later section). After the rubbing behavior, cuticular hydrocarbon compositions and profiles of the wasps change and become similar to those of the host *Lasius* ants (AKINO & YAMAOKA 1998). Thus, *P. eikoae* acquires the host ant cuticular hydrocarbons, by which it avoids ant attack. In contrast, the related European species *Paralipsis enervis* is known to imitate the host ant aphid cuticular hydrocarbons to avoid attack by the aphid-attending ants (VÖLKL & al. 1996). This may be considered as a "background-matching" strategy (discussed in a later section), when the aphids are regarded as a background of the wasps, which enables avoidance of ant detection. Despite being related species, these two *Paralipsis* wasps have se-

lected different modes of imitation to avoid ant attack.

Acquisition through direct contact facilitates the imitation of host ant hydrocarbons, but it also entails the risk and cost of attack by ants during the initial encounter. Therefore, it is also important for myrmecophiles and parasites to evade this initial danger. Myrmecophilous crickets avoid the initial ant attack by quickness and agility (AKINO & al. 1996), and the aphidiid parasitoid wasp *P. eikoae* presumably does so by rubbing behavior (TAKADA & HASHIMOTO 1983, AKINO & YAMAOKA 1998). In addition to such behavioral actions, chemical mimicry is often adopted as the strategy to avoid initial danger.

Chemical mimicry

Some myrmecophiles are known to exude chemical signals to appease the host ants before their direct interactions. Myrmecophilous lycaenid butterfly caterpillars possess ant-like hydrocarbons even in the pre-adoption stages (AKINO & al. 1999, ELMES & al. 2002, SCHLICK-STEINER & al. 2004, SCHÖNROGGE & al. 2004). In the habitat of the Mountain Alcon Blue, *Maculinea rebeli* (hereafter treated as *Phengaris alcon*, following recent phylogenetic and taxonomic study by FRIC & al. 2007), there are several sympatric *Myrmica* ant species, but ELMES & al. (1998) showed *Myrmica schencki* to be the most frequent host. In some populations, *M. schencki* seems to be the only host that provides complete rearing for *P. alcon*, which requires the latter to actively seek adoption by *M. schencki* workers. Presumably, this causes the caterpillars to synthesize series of particular hydrocarbons that are specific to *M. schencki* even before adoption by the ants. *M. schencki* workers carried glass dummies treated with *Phengaris* pre-adoption hydrocarbons, as well as those with their own hydrocarbons (AKINO & al. 1999). Thus, the pre-adoption hydrocarbons seem to promise positive preferable interactions with *M. schencki* to the Mountain Alcon Blue caterpillar. Cuticular hydrocarbon resemblance between pre-adoption *P. alcon* and *M. schencki* was independently confirmed by different analyses (ELMES & al. 2002, SCHLICK-STEINER & al. 2004). Because the caterpillars successfully imitate complete sets of the host ant cuticular hydrocarbons instead of pre-adoption hydrocarbons after adoption, AKINO and co-workers (1999) hypothesized that the caterpillars acquired them through direct body contact with the host ant workers and brood. Further detailed studies on the chemical acquisition after adoption revealed, however, that the caterpillars not only acquire the ant hydrocarbons but also synthesize additional mimetic hydrocarbons (ELMES & al. 2002, SCHÖNROGGE & al. 2004). SCHÖNROGGE and co-workers (2004) revealed that the *P. alcon* caterpillars had an ability not only to acquire the host ant hydrocarbons but also to synthesize several hydrocarbons that matched those of their natural host *M. schencki*. According to NASH & al. (2008), there are geographic variations in such species-specific interactions on hydrocarbon resemblance between *P. alcon* and *Myrmica* ant species.

It is not certain, however, how the social parasites generate imitation of the host ant hydrocarbons, even when chemical resemblance is confirmed between the parasites and host ants. For example, caterpillars of the lycaenid butterfly *Niphanda fusca*, which is known to have a species-specific relation with *Camponotus japonicus*, imitate the host ant cuticular hydrocarbons after adoption (HOJO & al.

2007). It is curious that the cuticular hydrocarbon composition of the caterpillars specifically resembled those of male ants rather than those of worker ants, because the former rarely spend times with the latter inside the colonies. Such resemblances could not occur if the caterpillars acquired the hydrocarbons through direct body contact with the ant colony members. This suggests that the *N. fusca* caterpillars connately have an ability to synthesize host ant hydrocarbons and to adjust the profiles to be similar to those of male ants after adoption.

Cuticular hydrocarbon resemblances are also confirmed between social parasitic ants and host ants, e.g., between the cuckoo ant *Leptothorax kutteri* and its *L. acervorum* host (FRANKS & al. 1990), and between the slave maker *Polyergus* and its *Formica* slaves (YAMAOKA 1990, HAVERSETZER 1993, HAVERSETZER & BONAVITA-COUGOURDAN 1993, BONAVITA-COUGOURDAN & al. 1996, 1997, D'ETTORRE & al. 2002). Some of these parasitic ants lose the host-like cuticular hydrocarbons after isolation from host colonies (YAMAOKA 1990). Although this suggests that the parasitic ants do not synthesize but acquire the host-like hydrocarbons from the host ants, it does not invalidate an alternative hypothesis, in which the parasitic ants have an ability to control biosynthesis of their own cuticular hydrocarbons.

Chemical camouflage or mimicry?

The improvement of the gas chromatograph (GC) and gas chromatograph-mass spectrometer (GC-MS) has made it easier to confirm the cuticular chemical resemblance between host ants and their social parasites, but it is still difficult to identify its causes. Chemical tracing by isotope labeling with ^{14}C might be helpful for this purpose. This technique has been applied to investigate the nestmate recognition signals of *Cataglyphis niger* (see SOROKER & al. 1994, 1995, SOROKER & HEFETZ 2000) and *Pachycondyla apicalis* (see SOROKER & al. 1998). Although it was originally developed to investigate hemolymph lipophorin in *Locusta migratoria* (see KATASE & CHINO 1984), Soroker and co-workers proved the technique's utility for ants. Injection of [1-^{14}C] sodium acetate into the ant abdomen through the intersegmental membrane produces various ^{14}C-labelled hydrocarbons in the cuticle. It appears to be necessary to inject such labelled sodium acetate into the social parasites' bodies to investigate whether they synthesize or acquire the host-like hydrocarbons. Further improvement of the technique may be necessary because the social parasites are usually much smaller than the host ants; nevertheless, it can be applied to identify the causes of the chemical resemblance in question.

Usage of repellent to avoid ant attack
Repellent allomone

The repelling of ants is another effective way to avoid ant attack, even after ant detection. This strategy is also classified as secondary defense. It is often applied, not only by insects but also by plants. Such repellent chemicals may presumably become available for control of pest ant species. Leaf-cutting ants are generally polyphagous and attack various plants to obtain the leaves for culturing their symbiotic fungus. Several native plants, however, escape the leaf-cutter ant attack, because of their repellent chemicals. *Astronium graveolens* (Anacardiaceae) contains sev-

eral volatile chemicals that are effective repellents against leaf-cutter ants *Atta cephalotes* (see CHEN & al. 1984). Because most ants that prefer flower nectars are potential nectar thieves of insect-pollinated flowers (HERRERA & al. 1984), some plants contain ant repellent chemicals in the nectars (FEINSINGER & SWARM 1978, GUERRANT & FIEDLER 1981). Various insects, e.g., stinkbugs (Pentatomidae), secrete repellent chemicals that are effective against ants. Also, it is well established that *Polistes* paper wasps secrete repellent chemicals when constructing their nest petiole (POST & JEANNE 1981, KOJIMA 1993). These studies showed how petioles were coated with a rubbery chemical layer of secretion that included ant-repellent-like chemicals. When it was removed, ants easily invaded the wasp nests to steal brood and stocked food. Ant repellent impedes ant invasion and attack of both insects and plants.

Transitory intruders of ant societies also use ant repellent allomone to endure the attacks of other ants during intrusion. BLUM & al. (1980) demonstrated that the thief ant *Solenopsis fugax* emitted host ant repellent alkaloids from the poison gland to disperse brood-nursing workers away before robbing the host broods. Queens of the temporary social parasite ant *Bothriomyrmex syrius* emit volatile chemicals that match a host alarm pheromone. This distracts the host workers during the queen's invasion (LLOYD & al. 1986). Such repellent allomone was also found in bumblebees. Females of an obligate social parasite *Bombus* (*Psithyrus*) *norvegicus* possess large quantities of a pure volatile ester on the cuticle, which shows a strong repellent effect on host *Bombus* (*Pyrobombus*) *hypnorum* workers (ZIMMA & al. 2003).

Propaganda allomone

American slave maker *Formica sanguinea* workers emit mixtures of volatile alkyl ketone, alkane, and acetates when invading host ant nests. Those chemicals induce panic responses in defenders (REGNIER & WILSON 1971). Such offensive chemical signals are also found in the slave making ant *Harpagoxenus sublaevis* and the workerless inquiline ant *Leptothorax kutteri* (see ALLIES & al. 1986), the European slave making ant *Polyergus rufescens* (see VISICCHIO & al. 2000), and the Japanese slave maker *Polyergus samurai* (T. Akino, unpubl.). Although the effect of these chemicals is similar to that of repellent allomone, the host workers occasionally attack each other, as if they had lost the nestmate recognition signal of their colonies. REGNIER & WILSON (1971) therefore developed the term "propaganda" for these offensive signals, which should now also be classified as belonging to the allomone category of allelochemicals.

Such powerful propaganda chemicals are also utilized by the parasitoid wasp *Ichneumon eumerus* of the myrmecophilous lycaenid butterfly *Phengaris alcon* (THOMAS & al. 2002). Because the host *P. alcon* larvae are tended inside the *Myrmica schencki* nest, the wasp must invade the ant for its oviposition even though ant attack responses are inevitable. Even if the wasp succeeds in oviposition, the parasitized *P. alcon* larvae remain to grow inside the ant nest, and the wasp offspring must emerge inside the ant nest. The wasp needs to avoid ant aggression to survive, so the wasp emits a series of allyl alcohols and aldehydes, which cause *M. schencki* workers to attack each other instead.

Appeasement allomone

In the American slave maker ant *Polyergus breviceps* (TOPOFF & al. 1988) and the European slave maker *P. rufescens* (D'ETTORRE & al. 2000, MORI & al. 2000a, b), the Dufour's gland secretion is found not to induce panic alarm but to reduce aggression of the resident workers. The secretion is therefore named appeasement allomone.

Both propaganda and appeasement allomones commonly disrupt nestmate recognition in the host ant species, but the physiological mechanism is unknown. Because nestmate recognition is the most basic communication to maintain ant societies, such allomone chemicals might be used as social communication disruption agent against harmful ants.

Chemical phytomimesis: ant "invisibility"

The basis of propaganda and appeasement allomones is to modify ant reactions by chemical signals after ant detection. These strategies aim to deter attacks by ants that detect the intruders. In contrast, the third strategy is basically to avoid ant detection itself. This strategy presumably exists in animals that do not have necessity to maintain long interactions with ants, and it includes chemical background-matching.

Background-matching is one of several common strategies in animals to avoid predator attack (EDMUNDS 1974, ENDLER 1988). There are many reports on animals that seem adapted to physiologically match their visual appearance to their environment (GREENE 1989, MCFALL-NGAI & MORIN 1991, MESSENGER 1997, CHIAO & HANLON 2001), and that behaviorally select backgrounds that match their appearance (ENDLER 1984, MARSHALL 2000). It is likely that such background-matching in animals could reduce predation risk (FELTMATE & WILLIAMS 1989). These studies are based on visual matching, because the predators seek and capture preys through visual information.

The case of the giant geometer, *Biston robustum*, can be a good example for chemical background-matching, or phytomimesis. Presumably, this occurs to avoid ant attack, though it is also a typical example of visual background-matching (AKINO & al. 2004a, AKINO 2005). This species is a close relative of *B. betularia*, well known for industrial melanism (KETTLEWELL 1955), and is univoltine with a long larval stage of more than 5 months from the end of March to early October in Japan (NAKASHIMA 1912). Larvae are typical twig-like caterpillars that pretend to be motionless host plant twigs in the day. A key to their survival is background-matching. Their visual appearance strongly resembles the host plant twigs, and is characterized by a combination of color, the presence of horns and markings on the body that look like buds and scars on the twigs, the absence of abdominal legs except for hind grasping pairs, and a habit of resting in an unusual position with the body stretching out at an angle from the branch. The caterpillars change their appearance according to their host plant species including colors and marks (AKINO & al. 2004a). They also change their feeding and resting behaviors as they grow (AKINO & al. 2004a, AKINO 2005). It is highly likely that such visual phytomimesis is effective to avoid avian predators as generally suggested (RUITER 1958, HEINRICH 1993).

Their motionless life style that avoids feeding in the day is presumably compensated by long larval periods. How-

ever, it increases the danger of becoming prey to terrestrial predators, including ants such as *Lasius*, *Formica*, *Camponotus*, *Crematogaster*, and *Pristomyrmex*. These ant forager workers were often observed on the tree twigs where the caterpillar perched in the day, but they rarely attacked the latter even when walking on them (AKINO & al. 2004a). Passing over the caterpillars' bodies initiated no interest in the ants, even after antennation, very much as if they were dealing with real twigs. Comparative GC and GC-MS analyses revealed that the caterpillars possessed cuticular chemicals identical to those of host-twig surfaces, in both composition and relative ratios. The caterpillar and the tree twig are indistinguishable by their surface chemicals, which suggests that the ants cannot discern between the two. Additional host plant exchange experiments indicated the ability of the caterpillars to adjust their cuticular chemicals to match new host plant surface chemicals, although this required molting(s). As this cuticular chemical adjustment required feeding on the new host plant leaf, it is obviously triggered by diet and ingestion (AKINO & al. 2004a, AKINO 2005). All of the caterpillars tested preferred to perch on twigs with the surface chemicals that they were imitating at the time (AKINO & al. 2004a). Thus, the caterpillars have a potential ability to confuse the ant workers even though they have excellent chemical sense.

Diet-induced visual phytomimesis is also known in another geometer, *Nemoria arizonaria* (GREENE 1989). The caterpillars of the spring brood develop into mimics of the oak catkins which they feed upon, while those of the summer brood develop into mimics of oak twigs. This developmental polymorphism is considered to be triggered by the variable concentration of a defensive secondary compound, tannin, in the larval diet, and it enables the visual phytomimesis of this caterpillar. Another example of diet-induced body color change is reported in the spider *Theridion grallator* (GILLESPIE 1989). These diet-induced visual polymorphisms may be more widespread in herbivores than we currently know, because of high predation pressure by avian and mammalian predators that rely on visual information. It is adaptive for herbivores to be able to evade predation through visual background-matching. Dietary cues are closely related to the native habitat for herbivores (WOODHEAD & CHAPMAN 1986, MALONEY & al. 1988, VARELA & BERNAYS 1988), so they can be a useful signal to induce appropriate background-matching in morphs and behaviors for predator avoidance.

This reasoning also can apply to diet-induced chemical background-matching, where the predators rely on chemical instead of visual information to seek their prey. Ants typify this mechanism (e.g., ESPELIE & BERNAYS 1989), and provide high predation pressure to herbivores. The case of *Biston robustum* shows sophisticated chemical phytomimesis to avoid ant detection because of the ability to chemically adjust to various host plants (AKINO & al. 2004a). Although there are few reports on chemical phytomimesis in herbivores, it may be widespread to avoid the high predation pressures of ants.

Such chemical "invisibility" seems effective to avoid ant attack, and chemical phytomimesis is not the only context in which it should be considered. The absence of a cuticular chemical signal in freshly emerged ants is another phenomenon that precludes adult ant attack (LENOIR & al. 1999, 2001). Freshly emerged callow ants usually possess small amounts of hydrocarbons that are not specific to colonies, and low levels of the cuticular hydrocarbons presumably reduce aggression of the adult workers. Different kinds of background, including inorganic substances, would be available for chemical mimesis, but there are no reports on such background-matching that I am aware of. However, preliminary experiments suggest that myrmecozelinid caterpillars might use such chemical mimetic tactics (T. Akino, unpubl.). The caterpillars usually hide inside their cocoons, and are often found near ant nests. The ant workers aggressively attack the naked caterpillars, but pay no attention to the cocoons. These responses were also confirmed by the respective chemical extracts. These observations are still insufficient to argue that this ant unresponsiveness is the result of chemical mimetic tactics of the caterpillars, although it is suggestive. A similar phenomenon is confirmed in ant interactions between lycaenid larvae and ants (Y. Hagiwara, pers. comm.). Probably we need to identify which chemicals trigger / suppress ant aggressive responses, and to construct proper bioassay methods to evaluate "unawareness" of ants for further clarification of this topic. Such verification might suggest generalities of this "silent" chemical mimesis by insects that appear to have less interaction with ants.

Where to from now?

Chemical mimesis is presumably one of the effective strategies for animals to avoid ant attacks because ants are highly sensitive to chemical signals. The animals that use chemical mimesis (including phytomimesis) are difficult to identify because they do not always necessarily use visual mimesis simultaneously. *Biston robustum* caterpillars happen to use both visual and chemical phytomimesis (AKINO & al. 2004a). Visual mimesis is visually obvious to human observers, but most animals using chemical mimesis may not have been identified.

For example, small white butterfly *Pieris* caterpillars are often hunted by various ants. In contrast, the pupae are relatively untouched in spite of their immobilized vulnerability; it is not known why. These pupae do not contain any toxic compounds, though several aposematic lepidopteran pupae do so to avoid predation (NISHIDA 1994). According to KANEKO & KATAGIRI (2004), the cuticular wax components of *Pieris* pupae mainly consist of odd-numbered n-alkanes. One may conjecture that since such simple sets of hydrocarbons are generally found in the plant surface chemicals, they may efficiently confuse ants seeking prey. Thus, it is necessary to compare the surface chemicals of the animals not preyed upon by ants with the environmental agent that can become the background in order to verify the possibility of a chemical mimetic strategy.

However, there is another difficulty for the study of chemical mimesis even after chemical resemblance is successfully confirmed between the target animals and their background, namely that of a proper evaluation by behavioral bioassays. A proper bioassay would identify this "unawareness" by lack or presence of chemical signals. If we properly focus on this phenomenon, comparative analyses of chemicals and behavior in herbivores, their host plants, and corresponding predators may alter our recognition of chemical phytomimesis.

Because ants are so abundant, and sensitive to chemical signals, the chemical mimicry, camouflage, and propa-

ganda in insects that have close interactions with ants have been well studied and summarized. These strategies are very impressive because they modify the ant behavioral responses very clearly after the ants detect intrusion and also involve great risk if the modifications fail to occur. The chemical mimetic strategy is less dramatic, as the ants usually do not present clear responses to the social parasites. This is presumably one of the reasons why the strategy appears to have garnered little attention.

Since ants generally pose a risk of harm for most insects, the mimetic strategy would be safer than applying chemical mimicry, camouflage, and repellents. Despite the difficulty of evaluation, the chemical features to mimetic strategists should be carefully evaluated to their "silent odors" against ants.

Acknowledgements

Zusammenfassung

Chemische Strategien von Sozialparasiten von Ameisen, einschließlich Myrmecophile, knüpfen oft an die Nestgenossenerkennung und die Alarmierungskommunikation der Ameisen an. Das strikte Nestgenossenerkennungssystem von Ameisen kann durch die chemische Imitation des Nesterkennungspheromons geknackt werden, welches aus kutikulären Kohlenwasserstoffen besteht. Sozialparasiten eignen sich diese Substanzen oft durch direkten Körperkontakt an, aber synthetisieren sie in selteneren Fällen sogar noch vor der Adoption durch die Ameisen. Solche Imitation wirtsspezifischer, kutikulärer chemischer Substanzen bedingt artspezifische Adoption der Parasiten, welche dann häufig von den Ameisen langfristig umsorgt werden. Im Gegensatz dazu setzen nicht-permanente Invasoren häufig Propagandaallomone ein, die bei den Ameisen panische Alarmreaktionen hervorrufen. Die Allomone lösen fallweise sogar Kämpfe zwischen Ameisennestgenossen aus und scheinen die Nestgenossenerkennung der Ameisen zu stören. Die beiden eben umrissenen chemischen Strategien zielen darauf ab, die Reaktion der Ameisen nach der Entdeckung durch die Ameisen zu modifizieren. Eine dritte chemische Strategie, die sich bei manchen Insekten findet, ist, die Entdeckung selbst zu vermeiden, nachgewiesen etwa für die chemische Phytomimese von zweigähnlichen Geometridenlarven. Da diese Strategie bewirkt, dass die Ameisen nicht auf die "Invasion" reagieren, ruft sie normalerweise keine sichtbare Antwort hervor, wenn sie effektiv ist. Geeignete Evaluierungsmethoden werden notwendig sein, um die Reaktion von Ameisen auf die Parasiten zu ergründen und so die zugrundeliegende mimetische Strategie im Detail zu klären.

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