



Male stump-tail macaques from Thailand. Despite a clear dominance hierarchy stump-tail macaques are tolerant and reconcile frequently after conflicts. (Photos by Oliver Schülke, MPI-EVA.)

social relationships or dominance styles to variation in food resource characteristics, such as the distribution, abundance and quality of food resources. If resources are of high quality and spatially clumped, for example, they are monopolizable by an individual, which usually leads to a dominance effect on food intake, because higher ranking individuals have preferred access. In this case, it will pay to be of high rank and maintain despotic dominance relationships. More egalitarian relationships are expected, for example, if low quality resources are more evenly scattered in the environment and hence fighting for access is not worth the effort.

Given the lack of long-term field studies on macaque species — with only very few examples — a thorough test across species is still pending. An alternative model, the phylogenetic hypothesis, on the contrary proposes that the variation in social relationships is a consequence of phylogeny, with more closely related species showing more similar social patterns. So far, three broad species groups have been identified, the *silenus-sylvanus* group, which presumably is the oldest lineage, the *sinica-arctoides* group and the *fascicularis* group, which presumably includes all the nasty, despotic species. Cross-species comparison of captive macaques indeed shows evidence for conservative traits, such as rank

acquisition or dominance relations between the sexes, which suggest at least some phylogenetic inertia. The possible influence of ecology, however, has not been tested in these studies on captive groups. So the debate continues.

**Is there a macaque genome project?** After the chimpanzee, rhesus macaques are the second non-human primate whose genome sequence now is available. A multi-centered team just recently deposited a draft version into databases accessible to the public. The rhesus genome shares about 92–95% of its sequence with that of humans and more than 98% with the chimpanzee genome.

#### Where can I find out more?

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## Primer

# Communication in ants

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Social insects have several advantages over solitary insects. The presence of many individuals can increase system reliability, and work can also be organized more efficiently through division of labour and task partitioning. Another advantage is the possibility of sharing information, especially communicating where food can be found. But research is increasingly showing that foraging communication does more than merely direct nestmates to food. It also allows the colony to regulate total foraging activity, to retain a memory of previously rewarding locations, and to select among locations of different profitability. In this primer, we first provide a brief historical perspective, then focus on recent research that has uncovered remarkable richness and sophistication in ant foraging communication, and finally identify some key questions for further research.

The study of foraging communication in social insects has a long history. In the 1880s the eminent Victorian John Lubbock (Baron Avebury) showed that ants used odour trails in foraging. His contemporary Wassmann even believed that ants had a sophisticated language encoded by antennal tapping, somewhat like Morse code. Far-fetched as Wassmann's idea may seem, the subsequent discovery by Karl von Frisch that honeybee foragers use waggle dances to communicate both direction and distance of food sources showed sophistication in communication that seemed barely credible for an animal, let alone an insect. Von Frisch went on to win the 1973 Nobel Prize for physiology or medicine for this discovery.

Research into chemical communication developed rapidly in the 1960s following the identification of the first two

pheromones: queen substance in the honeybee and the male attractant of female silk moths. Investigation of numerous ant species demonstrated that a wide range of chemicals are used to mark pheromone trails and are produced by several different glands. Research published by E.O. Wilson in 1962 demonstrated that ant pheromone trails provide positive and negative feedback to organise foraging at the colony level. A colony forms a trail when successful foragers deposit pheromone on their return to the nest, with the trail gaining in strength as more and more workers add pheromone to it, so providing positive feedback. The trail decays when the food runs out because foragers refrain from reinforcing it on their return and the existing pheromone evaporates, so providing negative feedback.

In the 1980s the new field of self-organisation adopted ant pheromone trails as a paradigm to illustrate emergent processes, where the activities of many 'agents' responding only to local information leads to a global adaptive process. Mathematical and computational models showed how worker ants, which were credited with minimal individual intelligence, could work together to solve problems such as selecting the shorter of two paths between food and nest, or selecting the better food source when presented with two of differing quality. These models showed that adaptive global solutions can arise in a system with a single trail pheromone providing positive feedback. From a biological perspective, however, this may have oversimplified things. Most trail-using ants employ multiple trail pheromones secreted from one or more glands. But why use many pheromones if one is apparently sufficient? Recent research into the roles of multiple pheromones has uncovered remarkable sophistication of communication in ant foraging trail networks. In Pharaoh's ants, for example, a suite of trail pheromones complement each other by providing a long-term memory of previously used trails, short-term attraction to currently rewarding trails, and



Figure 1. In the Malaysian ponerine army ant, *Leptogenys distinguenda*, emigration takes place along a pheromone trail to a new temporary nest site.

Workers communicate the initiation of emigration with audible 'clicking' sounds made by rattling their mandibles against each other, the sound resonating on dry leaves. (Image courtesy of Alex Wild.)

a 'no entry' signal to unrewarding branches. The geometry of the trail system also provides information, and there is worker specialization in trail laying and detection.

#### Foraging communication

Natural selection will favour communication if it helps nestmates to forage more efficiently. In social insects, workers collect the food for the colony. So if worker A helps worker B to collect more food, this is as good to worker A as if she collected it herself, because the food is brought back to the same nest to feed the same larvae. Nevertheless, many species of social insects do not share foraging information. In some cases this may be because foragers have no useful information to share. For example, desert ants (*Cataglyphis* spp.) collect dead insects, but there would be little point in directing nest-mates to the site of a discovery if no food remains. Communication is most useful when food resources are found that are larger than can be exploited by a single forager, or that need defending. Large or renewable feeding sites would be well worth communicating to nest-mates, such as the location of a group of aphids secreting honeydew or a patch of flowers.

In a general sense, social insect colonies live in a dynamic, competitive environment in which food sources of variable quality are constantly changing in location. Most ant species are dependent

upon ephemeral food finds. In such an environment, there is an advantage to sharing information if it can help the colony direct its workers quickly to the best food sources. Persistent or recurring food sources may also be available, such as the aphids or scale insects 'farmed' by many ant species. The best strategy is often to remember rewarding foraging sites but also to be flexible enough to exploit newly discovered food and to select the better sources from those available. To this end, information directing nestmates to food also enables them to select the highest quality food find when multiple resources are available.

Different ant species employ a range of communication methods for directing nestmates to foraging sites. The simplest is 'tandem running', where a successful forager leads a recruit. Recruitment is faster when the successful forager leads a group of recruits. The recruit or recruits follow the leader by physical contact or pheromone from the leader. The most spectacular use of trail pheromones is in mass foraging. Here the recruitment and guiding aspects of foraging communication are usually decoupled. The pheromone trail provides only the route to food, whilst recruitment of additional foragers is caused by other behaviours, such as dances or direct physical contact in the nest. In honeybees, the waggle dance recruits additional foragers but also directs them to the food. However,



Figure 2. Pharaoh's ants, *Monomorium pharaonis*, form branching networks of pheromone trails.

Here the network has been formed on a smoked glass surface to aid visualisation. (Image courtesy of Duncan Jackson.)

honeybees have another dance, the vibratory signal, which helps recruit more foragers but does not guide them to food. Decoupling means that mass foraging ants broadcast guidance information widely, potentially to all foragers, in the form of a trail network marked with varying amounts and types of pheromone. In contrast, the broadcast range of the honeybee waggle dance is limited to workers in contact with the dancer.

#### Multi-pheromone trails

Ant pheromone trails contain many chemicals that differ greatly in their persistence. Trail pheromones are also secreted from a diverse range of glandular sources, such as the Dufour's gland, poison gland, anal glands, glands on the feet, and glands on the thorax or abdomen. The use of multiple trail pheromones by a single ant species means that foraging communication can be more complex than is possible with a single pheromone.

Many foraging insects, for example a worker honeybee, can individually remember where they have foraged and can return to rewarding sites. However, for trail-following ants this memory need not be an individual memory encoded in the brain. Instead, it can be a group memory encoded externally in the pheromone trail system. The use of several trail pheromones that differ in their persistence provides memory over differing time scales. In particular, a non-volatile pheromone can provide a longer-term memory,

while a volatile pheromone can allow rapid choice among potential feeding locations by quickly 'forgetting' depleted locations.

The traditional view of ant pheromone trails as short-lived signals designed for rapid effect is often illustrated by the swarm raids of army ants. Raiding army ants certainly use short-lived trails to coordinate their lightning raids. But recent research has detected a more complex array of pheromone signals. For example, in the Malaysian ponerine army ant, *Leptogenys distinguenda* (Figure 1), distinct roles have been assigned to trail pheromones from two glands (poison and pygidial).

Temporal and spatial variation in the use of three trail pheromones communicates context-specific information in directing and organizing raids. The poison gland of *L. distinguenda* contains two pheromone components. One elicits a strong short-term attraction to prey items. The other guides workers from foraging sites to the colony, but only weakly. The prey-attraction component directs more ants to prey encountered during raiding to ensure that the prey is swiftly overwhelmed. The number of foragers attracted is a non-linear function of pheromone concentration, such that a trail laid by just a few ants leads to a rapid increase in workers attacking the prey. In this way a small number of workers encountering prey can rapidly attract enough nestmates to capture the prey. This prey-attraction pheromone is highly volatile and lasts only 5 minutes,

ensuring that ants are not attracted long after the prey item has been captured.

In contrast, the pygidial gland of *L. distinguenda* produces a longer-lasting trail pheromone (approximately 25 minutes). When attacking prey, workers often become detached from the trail network and this pheromone guides them back to the trail, or the colony. The pygidial gland is responsible for maintaining the spatial organisation of raiding ants, helping them explore the environment for prey in a systematic manner. Raiding parties advance in a single direction on the trail, only departing when locating prey or when signalled to do so by the poison gland pheromone. Thus, the longer-lived trail pheromone forms a well-connected network from which all raiding excursions are made. The trail network ensures rapid and reliable communication between foragers and enables the rapid transport of prey items back to the colony.

Our second example is the Pharaoh's ant, *Monomorium pharaonis* (Figure 2). Pharaoh's ants are common in human habitations and are an introduced pest worldwide. They are generalist foragers, taking a wide range of foods. Recent research has shown distinct short-lived and long-lived attractive trail pheromone effects, and also a short-lived repellent pheromone effect. The short-lived attractive trail pheromone (approximately 20 minutes) is used to guide foragers to currently rewarding feeding sites. Again, like *L. distinguenda*, Pharaoh's ants also make use of a longer-lived trail network to organise foraging and maintain foraging cohesion. In contrast to *L. distinguenda*, however, the long-lived trails of Pharaoh's ants can persist for several days. The long-lived pheromone means that the trail network can be explored from day to day. Sections of the network leading to food can be reinforced with the short-lived trail pheromone. The negative pheromone is placed locally in the network, immediately after trail bifurcations on the non-rewarding branch. These three effects seem to have complementary

roles. The long-lived attractive pheromone is a memory. The short-lived attractive pheromone marks out routes to current food sources. The short-lived repellent pheromone is a 'no entry' signal to unrewarding branches in rewarding trail sections. There are probably additional complementary effects. For example, the presence of both attractive and repellent short-lived trail pheromones may help ants chose the more rewarding branch at a trail bifurcation, and may also allow more rapid changes in directing foragers to particular locations.

#### Caste-specific communication

Division of labour, in which different workers do different tasks, is universal in insect societies. For example, some workers forage and others nurse the brood. Within the foragers there is also specialization. In the honeybee, most foragers collect nectar but some specialize in collecting pollen, water or tree resin. Most are guided by waggle dances to known food sources but some scout out new sources. Recent research shows that individual specializations also exist in relation to ant pheromone trails.

In Pharaoh's ants, only workers that walk with their antennae in contact with the substrate can detect the long-lived trail pheromone. Although it is not possible to individually mark Pharaoh's ant workers because they are so small (body length approximately 2 mm), ants that are individually confined for several hours show consistent behaviour with approximately 17% being able to detect a previously established trail that has been unused for 24 hours. These 'pathfinder' ants are probably a behaviourally specialized sub-caste of foragers that help re-establish existing trails. That is, they convert a long-term memory into a more easily detected signal. In addition, approximately 40% of the Pharaoh's ant foragers on an active trail make repeated U-turns. They walk with their sting extended indicating that they are maintaining the trail by laying additional pheromone. Thus, in Pharaoh's ant trail networks there is specialization for both laying and detecting trail pheromones.



Figure 3. Leafcutter ants, *Atta cephalotes*, form dense foraging columns when transporting leaves back to the nest along pheromone trails. (Image courtesy of Alex Wild.)

Pharaoh's ant workers are all of the same size. But some cases of individual differences in relation to trail pheromones involve different size castes. In the physically dimorphic *Pheidole embolopyx* the minor workers specialize in laying trail pheromone (from their poison gland), but both major and minor workers follow trails in foraging. Major workers do not lay trails but do most of the food transporting. Both castes actively cooperate in defending food finds. The two castes also have different defensive roles. Minors bite the legs of competitors whilst majors attack the heads. During foraging minor workers also guard food finds whilst majors transport food back to the nest.

Specialization in pheromone communication among different worker castes also extends beyond foraging trails. For example, *Atta* leafcutter ants (Figure 3) use alarm pheromones to signal predators or other dangers. The different size castes in *Atta* possess different blends of the same overall alarm pheromone components, but worker castes respond differently to the blends produced by other worker castes.

#### Multimodal communication

Chemical communication is of great importance in ant foraging organization. But foraging ants also use other modalities to communicate, and signals of different modalities may combine in promoting the organization of a colony's foraging system, and in other areas of colony life such as defence. Close behind chemical communication in overall

importance is the use of tactile communication, either through substrate-borne vibration or direct contact. Direct contacts may take the form of ritualised movements in communication, such as displays, dances, wagging and jerking. Physical displays by returning foragers of many ant species often serve a similar excitatory/recruitment role to that observed in honeybee waggle dances. The commonest form of physical contact is mutual antennation. This is seen very frequently when ants pass in opposite directions on a trail but has yet to be assigned a purpose. It probably does not comprise a 'language', as suggested by Wassmann, but it is hard to believe that no information is transmitted.

In contrast to the widely broadcast information of pheromone trails, the use of sounds, physical contacts and displays are primarily mechanisms whereby information can be communicated to near neighbours. In some situations, however, the message is passed from ant to ant and so travels further. *Camponotus senex* live in large arboreal nests built from larval silk. If a small area of the nest is disturbed physically, or by carbon dioxide, then the ants affected produce an alarm response by drumming their abdomens on the nest substrate. This stimulates other ants to follow suit, resulting in the communication of alarm throughout the entire nest, which can be up to 1 m in length. The volume of a medium-sized colony drumming is greater than human speech.



Figure 4. Foragers of *Aphaenogaster albisetosus* use stridulation and a poison gland pheromone to attract additional foragers when they locate prey they cannot capture alone. Transport of the prey back to the nest is via highly volatile trails. (Image courtesy of Alex Wild.)

Multiple pheromones, displays, contacts and sounds are often used in combination. This is probably not to provide backup mechanisms (redundancy) but to communicate a wider repertoire of messages. For example, *Aphaenogaster albisetosus* (Figure 4) modulate the recruitment pheromone by rubbing their abdominal tergites together to make sound. When individual *A. albisetosus* workers locate large prey items, such as dead insects, they release a poison gland pheromone and audibly stridulate to attract workers in the locale. The stridulation encourages other workers to release further pheromone and this feedback leads to rapid trail recruitment to the prey site. *A. albisetosus* retrieves prey items significantly faster when stridulation is present.

#### Future research

Research shows that ants, and also honeybees and other species of social insects, use several pheromones or other signals in organizing their foraging system. Two important and connected questions, therefore, are to determine why multiple signals are needed and how they work together. Some progress has been made in the honeybee, where four dances and a pheromone are known to be involved. The role of most of these signals is known. The waggle dance directs foragers to food and recruits them to foraging, the vibratory dance prepares

foragers for work by causing them to move into the dance floor area where returning foragers make waggle dances, and the tremble dance recruits additional workers to the task of unloading nectar foragers. But what is not known is precisely how they work together and why five signals (and maybe more) are needed. Why not four?

One possibility is that some of these signals are fine tuning. Multiple signals may be needed because of inherent limitations in the signals used. For example, the short-lived attractive and repellent trail pheromones used by Pharaoh's ants can direct foragers to the rewarding branch at a trail bifurcation but a single one of these pheromones can only direct about 75% to the rewarding branch. Perhaps the presence of two pheromones can increase this to 90%.

We also need to understand communication mechanisms in relation to the foraging method. The solid substrate upon which ants walk from nest to food is suitable for depositing trail pheromones to guide nestmates. A trail pheromone is obviously less useful for flying social insects, such as honeybees. However, some stingless bees do mark routes to food with pheromone, which they deposit on vegetation as discrete beacons rather than a continuous trail. The use of a trail pheromone means channels of communication may be continuously open for ants, because they are capable of

a continual, reactive exchange of information with nestmates whilst foraging. This is in marked contrast with the honeybee, where the signals used to organize foraging are communicated in the nest. Foraging is a dynamic process and an important role of communication is to recruit or direct nestmates rapidly to a food source. But the need to do more than this, for example to retain a longer term memory, may require additional pheromones or signals.

The multiple signals used in social insect communication provide shared information and enable the colony (or system) to be more responsive or better regulated, so that it functions better. Similar complexity is found at other biological levels, such as cell signalling pathways, where positive and negative feedback provide the capacity for control at multiple levels and enable greater flexibility in system responsiveness. A major interdisciplinary challenge in modern biology is to understand how complex adaptive systems function, and how they function robustly yet flexibly. One goal in this research is to determine if there are any general principles underlying adaptive biological systems. The focus of this research, and the funding, is usually directed at the organismal level or below, particularly cells in a multicellular organism, or molecules within cells. Insect societies provide another level of organization for comparison.

#### Further reading

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