

Recognition Systems in the Social Insects

A. Payne and P. T. Starks, Tufts University, Medford, MA, USA

© 2010 Elsevier Ltd. All rights reserved.

Introduction: A Wide-Angle View of Recognition Systems

Readers of scientific journals are no strangers to recognition: a recent keyword search by the authors turned up over 100 000 papers related to that subject. Of these, only a fraction were from the animal behavior literature; the balance came from journals of molecular biology, immunology, cellular medicine, or cognitive psychology. There were papers on human facial recognition and on the immune detection of viral proteins, papers on nepotism in ground squirrels, and on the specificity of restriction enzymes – papers, in other words, from almost every branch of biology. The only question was what, if anything, they had in common.

During the last 15 years, some researchers have begun to converge upon an answer. They argue that these studies are united both by a common theme and by the need for a common framework, and that the time has come for a unified approach to the study of recognition. They point out that all recognition research, no matter what the model system, is about explaining how evaluators identify and discriminate among entities. To these scientists, it makes little difference whether that evaluator is a red-tailed hawk or a human lymphocyte; both bird and blood cell have evolved to recognize significant entities accurately and efficiently. In this expanded view – what we call the ‘wide-angle’ approach to recognition – all biological recognition systems are variations on a theme, a theme best understood through a shared vocabulary and a common theoretical framework.

And yet, despite the promise of new insights and new collaborations, this wide-angle perspective remains rare. Even after well-reasoned arguments published by Blaustein and Porter in 1996 and Sherman and colleagues in 1997, many still think of kin recognition not as a limited case, but rather as the *only* case, of animal recognition. While this may be due to poor coverage in the textbooks – recognition is often given little more than a short mention in a chapter on kin selection – it also owes something to long-standing inconsistencies in the technical language, inconsistencies that persist despite efforts at standardization.

In this review, we explore how students of behavioral ecology might benefit by adopting the wide-angle approach. We offer a quick review of current terms and make the case for recognition as a ubiquitous biological process. We then illustrate the approach by bringing it to bear upon the study of social insects, and by showing how

four seemingly unrelated behaviors – selecting nest sites, choosing mates, recognizing relations, and detecting parasites – all depend on the ability to recognize and discriminate.

Describing Recognition: The Need for a Common Vocabulary

Despite its widespread use in the literature, ‘recognition’ remains a vague term. Almost all of us have some sense of what it means to ‘recognize an opportunity’ or to ‘recognize a face in a crowd,’ but few, if pressed, could provide a rigorous definition. What do we really mean when we say we recognize an old friend on the train? For that matter, what do we mean when we say that a honeybee recognizes olfactory cues, or that a restriction enzyme recognizes a nucleotide sequence? If we expect to get a handle on recognition systems, we must first get a handle on the terms we use to describe them.

To that end, we propose the following definition: recognition occurs whenever an evaluating entity, regardless of its level of biological organization, identifies another entity with reference to a previously existing template. In short, the ability to recognize is the ability to identify encountered entities. While no one would argue that an enzyme identifies its substrate through the same mechanisms that we use to identify a car in a parking lot, the overall structures and the ultimate outcomes of those processes are the same. A recognition system does not require cognitive processing to achieve these goals: Neither gated channels nor restriction enzymes nor tRNA molecules require ghosts in the machines – or in this case, in the alpha helices – to meet the basic requirements for recognition.

Any attempt at synthesis must also designate those features that all recognition systems share. Perhaps the most obvious of these is the condition of having two or more participants, one that does the recognizing and at least one other that gets recognized. Following Liebert and Starks, we call these the ‘evaluator’ and the ‘cue bearer,’ respectively. These terms are particularly helpful as they replace a confusing set of words (‘signaler’ vs. ‘receiver’; ‘recipient’ vs. ‘actor’) that grew out of the exigencies of communication and kin recognition work.

The act of recognizing also means that evaluators must possess criteria against which to judge cue bearers. Taken together, these criteria form the ‘template,’ a term we use

regardless of whether those criteria are learned or fixed. Learned templates may crystallize early on or they may require constant updates throughout the evaluator's lifetime, but either way they only form after exposure to example stimuli, the so-called referents. For example, one of the first things that newly emerged *Polistes* paper wasps are exposed to is the odor of the natal nest. This unique hydrocarbon signature becomes the referent by which the wasps form nestmate recognition templates, and future interactions between adults depend on how well newly encountered wasps and those templates match (see section 'Recognizing kin').

Though we usually think of recognition as a single behavior, it is often helpful to break it down into three essential components: expression, perception, and action. The expression component refers to the production or acquisition of identity cues by the cue bearer, the perception component to the detection and interpretation of those cues, and the action component to all those behaviors elicited by recognition on the part of the evaluator. Expression thus falls to the cue bearer (which need not be a biological entity), while the other two are exclusive to the evaluator. Each of these components is explored in detail elsewhere by Starks.

There is one more subtle distinction in the terms used to describe recognition systems, namely the difference between 'discrimination' and 'recognition.' While authors have sometimes used them interchangeably, the former properly refers to observable behavioral changes, while the latter refers only to an invisible process occurring inside the evaluator. In other words, only one, discrimination, is amenable to traditional behavioral analysis. Some organisms almost certainly recognize objects or other individuals without outwardly changing their behavior, but short of brain-imaging assays or EEGs, we have no way of knowing for sure. (These techniques are, however, becoming more common. See the discussion of pheromone detection in section 'Identifying Mates.')

In the next sections, we show how these terms apply to some behaviors of the social insects and how the wide-angle view helps us make sense of those behaviors.

Evaluating Nest Sites

This is a common enough scene in the summertime forests of North America: a swarm of honeybees, *Apis mellifera*, is dangling from the high branches of a tree, a compact mass made up of thousands of homeless workers. Hours before, this swarm split from its parent hive, leaving the old nest in the hands of a young queen and striking out for a new place to call home. Now, it hangs in a moment of indecision, exploring its surroundings, weighing its options, and figuring out where to begin the task of building a new colony.

This decision is not to be taken lightly. Many hives do not survive their first year, and much of their success or failure depends on finding a quality nest site. But how do the bees even begin to decide? The forest and surrounding fields are full of potential homes: every tree cavity, every old stump, every farmer's empty bee box is a possibility. To complicate matters, most workers are inexperienced at choosing real estate; hardly any of them are more than a few weeks old, and for many the swarm marks the first real journey into the outside world. What's more, this corporation of workers must arrive at a decision without the help of central management because the queen, buried deep within a writhing mass of bees, is in no position to affect the process.

So how to begin? First, the scout bees, the workers charged with finding the new nest site, must know what to look for and how to rank the cue-bearing sites they encounter. In other words, it must possess a nest template. Seeley and Morse first investigated this template in the late 1970s by evaluating the nest sites of feral bees in the forests around Ithaca, New York. They found that bees tended to prefer tree cavities that fell within a circumscribed range of volumes, usually between thirty and sixty liters, and that they tended to choose cavities with small exterior openings over those with larger entrances. The data did not imply any preference for one tree species over another and suggested only a small preference for living versus dead trees.

Following their forest observations, Seeley and Morse designed a series of experiments to see what other cues might influence nest site preference. The researchers built a series of side-by-side nest boxes, each modified according to a single variable, and presented them as choice experiments to bee swarms. Scout bees would encounter both cue-bearing boxes at the same time, evaluate the cues with reference to the nest site template, and then convince the swarm to settle in one of the two boxes. When one type of box was chosen significantly more often than another, the researchers interpreted this as evidence of a preference.

The results showed that scout bees possess far more complicated templates than one might expect given their small brains. As it turns out, the scout bees were looking not only at cavity volume and entrance diameter, but also at nest height (higher boxes were preferable to lower ones), distance from the previous nest (somewhere between 400 and 1000 m was ideal) and nest entrance direction (south facing was better than north facing). Data for nest entrances supported the previous observation that bees preferred small over large holes, but the bees showed no preference when it came to the shape of the entrance. Meanwhile, the position of that entrance, either near the bottom or the top of the nest box, did seem to matter, while the bees showed no preference when it came to cavity shape, dryness, or draftiness. Through

careful observation and well-designed experiments, Seeley and Morse were beginning to shed light on the nature of the honeybee nest template.

Of course, there is more to the perception component of a recognition system than just the template; on an even more fundamental level, evaluators must first be able to perceive identity cues. In another project, Seeley investigated the proximate mechanisms behind the scout bees' ability to perceive differences in nest site cavity volume. Clearly, the bees were able to accurately and consistently discriminate between cavity sizes, but the means by which they did so were far from clear. Seeley had previously observed that the bees spent a great deal of time walking and flying around the interior of the nest cavity; through a series of elegant experiments, he was able to demonstrate that this movement was actually a method for measuring and calculating interior volumes. When the bees were deprived of visual information by means of a light baffle over the cavity entrance, they were still able to choose those nests closest to the ideal volume. However, when Seeley placed rotating cylinders inside the nest boxes and created a sort of treadmill for incoming bees, he was able to confuse their spatial assessments. Regardless of whether the bees were forced to do more or less walking than the cavity size required, their perceptions of volume correlated to the distances they walked, and not to the real size of the cavity. Thus, Seeley showed that the bees measured not with their eyes, as one might expect, but rather through a complex calculus of distances walked and angles turned.

Recent studies by Seeley and colleagues have begun to shed light on the action component of nest site recognition, the decision-making process that leads a swarm to move into a site. Removing colonies to a mostly treeless island off the coast of Maine, the researchers offered scout bees their choice of several nest boxes, only one of which was a high quality site. Previous studies had demonstrated that individual scouts visit only a single site, evaluate it thoroughly, and then return to the hive to share their assessment with the other workers. The scout bees then advertise their site through a series of waggle dances containing information about both the location and the quality of the cue bearer. Stronger dances lead more bees to investigate the sites, until eventually the swarm becomes a miniature political convention, each faction dancing in support of its nest site choice. When a quorum is reached, the scouts begin to make faint piping noises, and the swarm takes off in the direction of their new home. (Pratt covers this process in more detail and with a specific focus on collective decision making in another chapter in this volume.)

The problem of finding a nest site is not, of course, limited to bees. Starks investigated some of the same questions using European paper wasps, *Polistes dominulus*, and found that they too recognize quality nest sites. Given a

choice between long, medium, and short nest boxes, the wasps preferred to initiate nests in the medium ones. While several foundresses started nests in the small boxes, almost none chose the large ones, perhaps because more exposed sites raise the risk of predation by birds or brood parasites. Unlike honeybees, however, these wasps had no preference for higher versus lower nest sites and settled equally often into boxes at all elevations in the enclosure. Thus, as expected, recognition templates vary between species and almost certainly reflect the unique selection pressures faced by each.

As an interesting side note, Starks found that female wasps emerging from hibernation preferentially stopped to perch on fragments of the nests they were raised on, even when those fragments had been moved from their original sites. Since these nest materials were in new locations and had been cut up into smaller pieces, the wasps must have used chemical cues to discriminate between them. It is well known that wasps acquire hydrocarbon signatures from their nests and use those signatures as referents when creating nestmate recognition templates; Starks suggests that returning to the nest may be a way of reconnecting with the previous season's sisters or of updating a learned template by new exposure to the original referent. Either way, returning to the natal nest may be a proximate mechanism by which wasps facilitate cooperation between kin, a behavior that is facilitated in turn by the ability to recognize.

Despite advances such as these, we still have much to learn about the expression, perception, and action components of nest site recognition systems. While we now know that honeybees possess a nest cavity template that includes ideal measurements of volume, entrance size, and height, we know practically nothing about the development of that template. Somehow, by the time scout bees are searching the landscape for appropriate nest cavities, they have developed a Platonic vision of their ideal home; how they and other insects are able to form such templates, sometimes in the absence of clear referents, is an exciting area for future research.

Identifying Mates

Among the social insects, sex tends to be a limited affair. For the workers who make up the bulk of any given colony, life is a chaste, and often brief, exercise in altruism. That much is to be expected. But even among reproductives – the winged queens and frenetic males that fill the skies in early spring and autumn – the mating season is often little more than a brief interlude in a longer life cycle.

Of course, we must not mistake brief for boring; more often than not, these mating periods are every bit as extravagant as they are short. Reproductive female paper

wasps fly out to meet some of their male counterparts on high, well-lit structures where the latter congregate en masse. Honeybees meet each other high above the ground where males hone in on and mate with polyandrous queens midflight. Winged reproductive ants rendezvous in swirling, carousing clouds, several hundred strong, and naturalists lucky enough – or unlucky enough – to wander into them do not soon forget the experience. In the high stakes game of finding a mate under such chaotic conditions, recognition is a critical component of fitness.

This is especially true for males. With the exception of one genus of ant (*Cardiocondyla*, see later), all social Hymenoptera species seem to have sperm-limited males with life expectancies that are significantly shorter than their queens'. Once the males' sperm supplies are exhausted, so too is their biological relevance, and selection seems to favor individuals who bow out gracefully (though "gracefully" may be too charitable a word for a species like the honeybee: its drones are famous for explosively rupturing immediately after they mate.) Honeybee males not only mate just once before they die; they also have just one *opportunity* to mate, a single high-altitude flight in which they must compete with hundreds of other males to find and inseminate a new queen. It makes sense for them to maximize that opportunity and to locate receptive females as quickly as they can.

To this end, selection has favored honeybee males with large eyes and large antennae to serve as well-honed, queen-detection devices. Recent studies by Wanner and colleagues investigated the perception component of queen recognition and showed that drones possess sex-specific odorant receptors that respond to a chemical (9-oxo-2-decenoic acid (9-ODA)) found in the queen retinue pheromone. Meanwhile, using calcium-imaging techniques, Sandoz demonstrated that brain regions found only in the males respond specifically to this and to two other components of the queen pheromone. These long-distance chemical signals, along with a highly developed detection apparatus, help drones perceive flying cue bearers long before they can detect them visually. Their sterile sisters, meanwhile, recognize and respond to some of the same chemicals, but with an entirely different behavior: in their case, recognition of 9-ODA leads them to gather around the queen and to suppress the development of their ovaries. The same expression component, the production and emission of 9-ODA, leads to two very different action component outcomes in the honeybee.

While males have a lot invested in finding females, they do sometimes misinterpret cues. An interesting example comes from *Cardiocondyla obscurior*, an ant species that exhibits strong dimorphism within the male population of each nest. Some males are wingless, or ergatoid, individuals who stay within their natal nests, mate with their relatives, and produce sperm throughout their lives.

Others are winged, sperm-limited dispersers who mate with the same females as the ergatoids, but who also leave the nest to mate. Interestingly, while ergatoid males show extreme aggression toward each other and often kill new males before they emerge, they are highly accepting of the winged males. In fact, they not only tolerate them, but also frequently mount them in attempts at copulation. Cremer and colleagues have recently shown that the wingless males escape the lethal aggression of their nestmates by mimicking the chemical signatures of virgin queens. By covering themselves in mimicked cues, these ants are able to fool the ergatoid recognition system, thus escaping aggression while still competing for mates.

While hymenopteran males must do everything they can to maximize their reproduction, most of them do not, at least, have to live with the consequences. Not so their newly inseminated queens, who can live years or even decades longer than their mates. While some species, notably the honeybee and some bumblebees, are able to mate multiply with different males, many hymenoptera appear to be monandrous and to store their sperm for life. This leads to the curious instance, rare among animals, of sperm outliving the males that created them. It should also lead to a great deal of pickiness on the part of the females, and to the development of highly precise mechanism for recognizing quality males. Unfortunately, the high-altitude nature of the nuptial flights means that we know far less than we would like about female mate choice in these species. Baer provided tantalizing details in a recent review of bumblebee male sexual selection – apparently females in laboratory settings show a great deal of choosiness among potential mates and occasionally sting undesirable males to death – but much of the necessary research remains to be done.

For termites, lifetime mating and the continuous production of sperm create a different set of selection pressures, but the need to recognize and evaluate potential mates remains the same. In a recent study of the damp-wood termite, *Zootermopsis nevadensis*, Shellman-Reeve demonstrated that they were able to recognize and avoid close relatives during laboratory mating trials. Although termites often replace dead mates with offspring or other close relatives, they appear to avoid such inbreeding during initial colony formation.

As a result of their haplodiploid reproductive system, some hymenopteran species suffer disastrous consequences after inbreeding. When these females mate with close relatives, they increase their chances of producing diploid offspring that are homozygous at the complementary sex-determination locus; since heterozygosity at the *CSD* (complementary sex determination locus) is required to develop as a female, these individuals grow up to become genetically abnormal males. If they do not die early or get identified and removed from the nest (as in honeybees), they may mate with females, produce sterile

triploid offspring, and thus increase the colony's genetic load. We know that several of these species demonstrate some form of kin recognition, and so we expect some of them to recognize and avoid close relatives when choosing mates. Intriguingly, this kin discrimination may relax under extreme circumstances, such as those found in the genetic bottlenecks associated with invasions. A study by Keller and Fournier tested whether or not nonnative French populations of Argentine ant *Linepithema humile* avoided inbreeding with siblings. They concluded that these individuals did not recognize their siblings in mate choice situations, but suggested that this might not be true of the populations in the native range.

Of course, inbreeding avoidance is just one way that animals benefit from the ability to recognize their kin. In the next section, we look at some more ways that the social insects rely on these abilities to survive, reproduce, and maintain their fitness advantages.

Recognizing Kin

Few evolutionary quandaries have caused as much puzzlement, or as much grief, as the question of how altruism persists in a Darwinian world. Consider, for instance, how long it took for an elegant and, more importantly, a mathematically rigorous solution to emerge. In the early 1960s, over a hundred years after Darwin hinted at it in the *Origin*, William Hamilton published his vision of inclusive fitness, a gene-centered view of natural selection that explains why some animals sacrifice so much for their relatives. The concept is simple: Hamilton argued that an altruism promoting gene could spread through a population so long as it caused organisms to preferentially direct care toward their relatives. If an organism sacrifices its own fitness, and if that sacrifice means that more copies of the sacrifice-inducing gene wind up in the next generation via the reproduction of close relatives, then the altruistic gene has an evolutionarily successful strategy. Inclusive fitness is the lens that clarifies, and allows us to see for the first time, the true nature of altruism.

Hamilton also suggested that if an animal could recognize its relatives and then discriminate between them and other individuals, then that ability to recognize would play a central role in the evolution of altruism. In the decades since the debut of inclusive fitness, behavioral ecologists have confirmed that kin recognition exists in multiple species and that it seems to be adaptive in ways predicted by theory. In fact, the recognition system framework described in this chapter largely grew out of that work and has blossomed most fully within it; while the examples that follow are covered by the authors elsewhere in this volume, it is worthwhile to briefly revisit them here in the context of social insect recognition.

Many insects are, it turns out, surprisingly smelly creatures – at least to other individuals of the same species. Most of the scent cues studied so far belong to a class of molecules found embedded in the waxy outer surfaces of their exoskeletons and known to biochemists as cuticular hydrocarbons (CHCs). These molecules have proven to be quite diverse, and the normal variability found between species and even between individuals is sufficient to provide high-resolution signals of identity. As such, CHCs are well suited to act as the cues by which insects recognize differences between kin and nonkin.

As predicted, researchers have indeed uncovered a central role for CHCs in the recognition systems of social insects. A classic example comes from the work of Gamboa and his colleagues on recognition in the primitively eusocial *Polistes* paper wasps. Females of the temperate species emerge in the spring and found nests dominated by a single reproductive queen; often this queen also receives a great deal of help from nonreproductive assistants who do everything from collect food to defend and enlarge the nest. By Hamiltonian logic, this kind of altruistic behavior makes little sense unless it is directed toward close relatives and leads to an increase in the helper's inclusive fitness, even as she reduces her personal fitness. Paper wasps, like most other animal altruists, would do well to tell relatives apart from other reproductive females.

This discrimination between kin and nonkin, or more accurately between nestmates and non-nestmates, is based on recognizing CHC cues specific to wasps from the same natal nest group. While there is some evidence to suggest that genetics may play a role in these chemical signatures, by far the most important influence appears to come from the papery nest itself. *Polistes* wasps are much more likely to accept individuals that eclosed on their own nest than they are to associate with foreign wasps, even if those foreign individuals are more genetically related to themselves. Experimental manipulation of larval origin supports these findings and shows that wasps preferentially associate with nestmates even when overall relatedness is low. The nest carries the cues which, when acquired by a female, provide a passport to interacting with nestmates found off the original nest. While this kin recognition system is clearly susceptible to error, nestmate status is probably linked to kinship status often enough in nature that nest origin serves as a decent proxy.

There are at least two proximate mechanisms at work in *Polistes* nestmate recognition: first, the acquisition of cues by newly eclosed wasps (an expression component mechanism), and second, the learning of cues and the formation of a nestmate template by evaluator wasps (a perception component mechanism). For the expression component, each wasp appears to acquire and then bear the specific odor cues of the nest material on which it was raised; this means that while odor cues are

homogenized across nestmates, no meaningful intracolony distinctions can be made on the basis of CHC dissimilarity. Experiments bear this out and demonstrate that wasps appear to follow an 'all-or-none' rule when encountering previously unmet individuals: when other wasps smell like nestmates, they are accepted as kin, but when they do not, they are treated as intruders and often met with aggression.

When it comes to the perception component, wasps seem to develop their nestmate templates in much the same way that they develop their own chemical cue profiles, namely through exposure to the natal nest. The nest odor itself appears to be a mixture of environmental- and wasp-based odors, and taken together these cues form the referent on which the nestmate recognition template is based. In this way, an inanimate referent (the nest) ends up having a profound effect on the way a wasp evaluates and discriminates between animate cue bearers (other wasps).

Of course, this particular model of cue expression and template formation is not applicable across all social insects: that polyphyletic taxon is simply too diverse to allow for generalizations. Ants, for instance, seem to have evolved an array of different expression mechanisms that result in nest- or colony-specific CHC profiles. In some groups, for example in species of the genus *Camponatus*, the queens appear to be the sole source of colony-specific odors; in others, for example, *Cataglyphis iberica* and *C. niger*, the queen has little influence on the cues, and the colony's odor is derived instead from a 'gestalt' mixture of individual worker-produced chemicals. For the vast majority of species, the mechanisms remain unknown; while research continues, the only conclusion we can draw so far is that there are no easily generalizable conclusions.

It appears that insects need not rely solely on chemical cues to recognize differences between conspecific individuals. To return to *Polistes* wasps, Tibbetts studied the mechanisms by which females identify individuals and maintain dominance hierarchies. After observing that individual brown paper wasps, *P. fuscatus*, varied greatly in individual facial markings, she decided to modify these markings with paint and then observe how other wasps responded. All focal individuals received paint treatments on their faces, though those treatments did not affect the previously existing patterns on control wasps. As it turned out, individuals with altered facial patterns received more aggression from their nestmates than the controls did. None received aggression of the sort that would be used against non-nestmates – presumably because they still bore chemical cues that tied them to that specific nest – but they did lose their places in the dominance hierarchy and had to fight to regain positions of power. After a short span characterized by aggressive interactions, the wasps sorted themselves back into the previous dominance order, apparently familiarizing themselves with the new facial patterns. It seems that the wasps have flexible and

updatable visual templates for who is in charge in the colony; when the disconnect between facial cues and other indicators of status, such as aggression and fighting ability, becomes too great, the wasps learn to look for a different set of cues.

While the existence of visual templates raises intriguing questions for future research, chemical recognition still seems to be the sine qua non of insect kin recognition. It also plays a vital role in another set of recognition systems, systems that have evolved to protect those resources that social insects work so hard to accumulate.

Avoiding Parasites

Social insect colonies are centers of wealth in the insect world; with hidden food stores, nutritious larvae, and armies of committed workers, they are cities ripe for pillaging. The committed workforce is particularly appealing, and often essential, to a certain type of insect opportunist, the so-called social parasite. These organisms steal workers and occasionally the entire nests of other species, and use those resources to benefit their own offspring. But such coups require a certain delicacy. Most social insects have highly developed mechanisms by which to recognize and discriminate against other species, and the successful parasite must somehow find a way to subvert these systems. The means with by which they do so are the focus of this section.

While social parasites exist in many different groups of insects, nowhere have they evolved to such an extraordinary degree as in the ants. In some of these species, the so-called dulotic or slave-making ants, workers routinely leave their own nests to make raids on the pupae of neighboring species. The captured pupae are returned to the slave-makers' nests, where they emerge as adults and, using their new masters as referents for template formation, quickly accept their faux nestmates as kin. Thus, an action component behavior suitable under normal conditions becomes terrifically maladaptive after a recognition error.

In one genus of dulotic ants (*Polyergus*), the slave makers are so highly specialized to their raiding tasks that they have lost most of the abilities required to take care of themselves and have thus become obligatory social parasites. *Polyergus* species often raid the nests of closely related *Formica* species, returning the pupae to eclose inside their own colonies; occasionally, however, they have been observed to enter queen-right host colonies, kill the host queen, and usurp her position among the workers. Recent work by Tsuneoka investigated the nature of these usurpations by the Japanese pirate ant, *Polyergus samurai*, against its host, *Formica japonica*.

Tsuneoka introduced *P. samurai* queens into *F. japonica* colonies raised in the laboratory and observed the parasite

queens' behaviors under three experimental conditions: in queen-right, queenless, and workerless host colonies. Under none of these circumstances did the slave-making queen physically attack her host workers; instead, in both the queen-right and queenless colonies, she was able to stave off *F. japonica* attacks by raising her gaster and presumably emitting behavior modifying pheromones (which immobilized and sometimes killed host workers). Within a few hours, the host workers gradually ceased to attack the parasite and instead accepted her presence.

The relatively low level of aggression directed toward host workers was not seen in interactions between the queens in worker-filled colonies. When *P. samurai* females entered queen-right nests, they attacked the *F. japonica* queen immediately upon contact, grasping and biting the host with their mandibles. During these attacks, the parasite queens also directed their gasters toward the host queens, and spent some time after the attack licking their victims and grooming their own bodies; shortly after, the workers gradually accepted the new queen. In queenless colonies, meanwhile, *P. samurai* queens appeared to have more difficulty usurping colonies. Finally, in workerless colonies, most introduced queens simply ignored the host queens, presumably avoiding conflicts in which there were no workers to be gained.

All this adds up to a picture of *P. samurai* as a highly skilled chemical cue mimic, a not uncommon type among the social parasites. Indeed, some social insects seem to use similar methods against their own species: the Cape honeybee, *Apis mellifera capensis*, has become a major pest for South African beekeepers who rely on colonies of its host, *A. m. scutella*. The workers of *A. m. capensis* are unusual among honeybee subspecies in their ability to lay diploid female eggs via asexual reproduction; most honeybee workers are only able to lay haploid male eggs and even then only successfully in colonies without queens. In queen-right colonies, workers usually police each other's egg-laying and remove eggs that they have not laid themselves. Thus, not only have Cape honeybees managed to evolve a novel method of asexual reproduction, but they have also developed a way to avoid detection by African honeybee workers intent on policing. Presumably they do so by means of chemical mimicry of queen-laid eggs.

Finally, the mixing and the acceptance of hetero-specifics are not limited to parasitic relationships. Mixed colonies of ants often live together in fungus gardens, symbiotic associations between ants and certain species of epiphytes; Orivel and colleagues investigated one such

relationship between two species of ant, *Crematogaster limata parabiatica* and *Odontomachus mayi*. These two species coexist peacefully inside their ant gardens, sharing food resources and odor trails, but keeping their broods separate. Remarkably, the relationship between these species goes beyond tolerance of each other to the exclusion of any individual not associated with the ant garden. Indeed, both species will readily attack members of their own species if these individuals come from outside the shared nests. Equally remarkable is that each of these species manages to maintain distinct hydrocarbon profiles throughout their association. This implies that these ants are able to build recognition templates using the individuals around them as nonexclusive referents and, in this respect, they share some aspects of their behavior with those ants that fall prey to dulotic parasites.

Conclusions

This article provides only a limited tour of the many recognition behaviors performed by social insects; it does not address the identification of foreign debris within the nest, the recognition of specific floral odors, or the discovery and removal of diploid male larvae, to name but a few. Nevertheless, each of these – and scores of other behaviors – are best understood as acts of recognition.

The recognition systems framework first developed to study kin recognition is still the best way to approach these topics. Future research will no doubt reveal even more applications, and will hopefully explore the mechanisms behind template formation, cue expression, and behavioral modification in even more detail.

See also: Collective Intelligence.

Further Reading

- Hölldobler B and Carlin NF (1991) The role of the queen in ant nestmate recognition: Reply to Crosland. *Animal Behaviour* 41: 525–527.
- Seeley TD and Morse RA (1978) Nest site selection by the honey bee, *Apis mellifera*. *Insectes Sociaux* 25: 323–337.
- Sherman PW, Reeve HK, and Pfennig DW (1997) Recognition systems. In: Krebs JR and Davies NB (eds.) *Behavioural Ecology: An Evolutionary Approach*. Oxford: Blackwell Science.
- Starks PT (2004) Recognition systems: From components to conservation. *Annales Zoologici Fennici* 41: 689–690.
- Wilson EO (1971) *The Insect Societies*. Cambridge, MA: Harvard University Press.