1 Ants – Individual and Social Cognition

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Species Description

The total number of ants is estimated to be between one and ten million billion, which makes them a very successful life form (Hölldobler and Wilson, 1990). Ants are characterized by a very specific social evolution, perennial life cycle, unusual genetic method of sex determination and exceptional forms of collective decision-making.

Brain

Perhaps the first question about ants' individual cognition is whether their tiny brains are sufficient for solving intellectual problems. Darwin (1981) recognized this and considered the brain of an ant as 'one of the most marvellous atoms of matter in the world, perhaps more so than the brain of man'. Like some other animals with small brains, ants express behaviours and sensory capacities comparable to large-brained animals, despite the high energetic costs for maintaining a relatively large brain in small-bodied animals (e.g. Seid *et al*., 2011). Unlike social vertebrates, which have larger brains and cerebral cortices than solitary species, ant brains are not larger than those of solitary insects, but they are more specialized (Gronenberg, 2008).

The central brain structures in insects are the mushroom bodies (Strausfeld *et al*., 1998). Ant brains are equipped with structures and mechanisms that allow advanced learning and memory, including learning landmarks, odours and changes in their environment (Gronenberg, 2008). However, neural network analyses made by Chittka and Niven (2009) have shown that cognitive features found in ants and bees, such as numerosity, attention and categorization-like processes, may require only very limited neuron numbers. Moreover, there is no strong correlation between the volume of the mushroom body and cognitive abilities. A recent study (Groh *et al*., 2014) revealed that in the highly polymorphic leaf-cutting ant *Atta vollenweideri*, mini workers have significantly larger mushroom bodies to total brain ratios, and synaptic densities play a much more important role than the relative size of the brain.

Perception

Antennae and compound eyes are the main sensory organs, with representations in the optic and the antennal lobes of the ant brain. Most ant species are guided mainly by

smell and touch, and some species rely mainly on visual navigation, including the polarization pattern of the skylight and landmarks, and possibly magnetic cues (Hölldobler and Wilson, 1990). The demand on different sensory systems varies among species with different foraging strategies. For example, members of the *Cataglyphis* genus and bull ants of the genus *Myrmecia* forage individually and do not use odour trails, whereas fungi-growing ants of the tribe Attini have a highly developed olfactory system, necessary to meet the demands of complex olfactory-guided tasks such as pheromone communication or substrate selection.

Even within one ant colony, members of physical subcastes differ in their tasks and, correspondingly, in their sensory equipment (e.g. numbers of ommatidia in their eyes and sensilla on their antennae). In the desert ant *Cataglyphis bicolor*, the larger workers with 1200 ommatidia show better visual orientation abilities and serve as foragers, whereas the smaller workers (600 ommatidia) remain inside the nest (Menzel and Wehner, 1970). Despite the modest visual capabilities of ants in general, even ants with small eyes (e.g. *Leptothorax albipenni*s; 60 ommatidia) are able to use bold landmarks as beacons (McLeman *et al.*, 2002). For visual navigation, ants can use not only landmarks but also stars, including sun and moon at night, and sky polarization (Wehner and Müller, 2006). They also have visual snapshots of what the area looks like, taken from some distance away and from several positions. This path integrator is more or less fixed and does not improve with training (Merkle and Wehner, 2009). Forest ants can memorize the entire canopy structure above them (Ehmer, 1999) and landmarks of different sizes, from grass and bushes to trees (Rosengren and Fortelius, 1986). The neotropical rainforest ant *Gigantiops destructor*, the ant species with the largest eyes (Gronenberg and Hölldobler, 1999), can travel individually through 20 m of rainforest – with all the trees and other objects in the scenery – without using any chemicals (Beugnon *et al.*, 2001). Ants have long been considered unique among Hymenopterans for having only two spectral classes of photoreceptors, while most bees and wasps have three (Briscoe and Chittka, 2001). A recent electrophysiological study (Ogawa *et al.*, 2015), however, demonstrated that the diurnal *Myrmecia croslandi* and the nocturnal *Myrmecia vindex* also enjoy trichromatic colour vision.

As in other insects, antennae are complex sensory arrays studded with different types of sensilla, which process a range of inputs in different modalities, including mechanical, odour and chemical stimuli, which can be referred to as taste, signals of humidity, temperature and CO_2 level. The majority of sensilla on the antenna contains olfactory neurons that respond to particular subsets of odorants or chemical compounds (Gronenberg, 2008; Ramirez-Esquivel *et al.*, 2014). In social Hymenoptera, individual olfactory sensilla on the antennae are generally equipped with a higher number of olfactory neurons and glomeruli as compared to other insects, possibly reflecting the rich diversity of olfactory-guided behaviours and the complexity of a social organization based on olfactory communication and chemical recognition (see Kelber *et al.*, 2009).

Social Characteristics

There are more than 12,000 ant species in the world, with different colony sizes (from tens to millions of individuals), social life and styles of cooperation, from single

foraging to mass recruiting. All known ant species are eusocial, meeting the following criteria: reproductive division of labour and cooperative alloparental brood care, overlap of adult generations and lifelong philopatry. Like other members of the order Hymenoptera, including wasps and bees (from which not all are eusocial), ants are haplodiploid. Ant colonies consist of one or more reproductive females (queens) and a large number of female workers, which are either permanently or temporarily sterile and share the same diploid genome with queens. Males develop from unfertilized eggs, making them haploid. Haplodiploidy has important consequences that affect social behaviour and derive from different levels of relatedness among fertilized females (which can mate more than once), their daughters and sons. For instance, haplodiploidy opens the way for the evolution of a worker caste, devoted to helping their mother, although conflicts between the queen and the workers over who lays the male eggs in a nest are common (Walter and Heinze, 2015).

Caste polyphenism is rather expressive in some ant species, which harbour special castes of particularly large workers, 'soldiers' or 'majors', which play the main roles in colony defence, cutting up or carrying large objects. Morphology, physiology and behaviour thus differ profoundly between subcastes of workers. In leaf-cutting ants, for instance, tiny 'mini workers' cultivate fungi in the subterranean nest to feed the larvae. Other workers have an up to 200-fold increased body weight, leaving the nest for long foraging trips and bringing back leaves which are used as substrate for the fungi (Wilson, 1980). Remarkably, however, each female embryo has the potential to become either a queen or a major or a minor worker – all can be moulded from the same genome and regulated by epigenetic and nutritional factors (Chittka et al., 2012).

Ant reproductive females may live hundreds of times longer than non-social insects of similar body size. Queens in some ant species live for up to three decades, whereas winged males are quite short-lived and survive only a few weeks, and workers live from a few days to 3 years (see Kramer et al., 2015). Many researchers consider a colony of social Hymenopterans a 'superorganism', where workers represent the soma and the queen the germ line of the colony. However, cognitive responsibilities, if any, are distributed among relatively short-living sterile workers. One can hardly imagine a multicellular organism in which cells (unfertilized workers in an ant case) possess their own intelligence, and there is no central control of behaviour from a supreme brain.

In many ant species, complex dominance hierarchies and high levels of intracolonial aggression have been demonstrated. For example, in the Indian jumping ant *Harpegnathos saltator*, colonies are founded by a single queen, but after queen senescence, workers compete in a ritualized dominance tournament to establish the new group of reproductives, the gamergates. After mating with their brothers, gamergates display dominant behaviour and serve as the sole egg-layers in the colony (Peeters et al., 2000). They also undergo extreme internal changes triggered by changes in dopamine levels: their brains shrink, their ovaries expand and their life expectancy jumps from about 6 months to several years (Penick et al., 2014).

Many ant species are highly territorial animals (Adams, 2016). Hölldobler and Lumsden (1980) distinguished three types of ant territories: (1) absolute territories, in

which the entire foraging space is defended regardless of food location; (2) trunk trail territories, in which defence is concentrated around long-lasting trails; and (3) spatio-temporal territories, in which defended regions shift from day to day according to where the ants are foraging. Territorial behaviour in ants includes recognition, avoidance, vigilance, demonstrations of aggression and fighting. Ants use odour cues to mark boundaries and ritual displays to solve conflicts (van Wilgenburg *et al.*, 2005). For instance, colonies of meat ants *Iridomyrmex purpureus* establish territories in which the boundaries are lined by workers engaged in pairwise ritual displays, sweeping legs and heads (Ettershank and Ettershank, 1982). While all these behaviours need not necessarily be cognitive, they are complex and flexible, and amazingly similar to territorial demonstrations in highly intelligent mammals and birds.

Interspecific hierarchies also emerge among ant communities of different species (Reznikova, 1980; Vepsäläinen and Pisarski, 1982; Savolainen *et al.*,1989; Stuble *et al.*, 2017). Interrelations between dominating *Formica* and subdominating *Serviformica* species, for instance, are behaviourally flexible, being directly related to both trophic competition and sophisticated 'cooperation' (Stebaev and Reznikova, 1972; Reznikova, 1975, 1982, 2007a). Dominant ants use members of the subdominant species as 'guides' while searching for prey, stealing their 'know-how'. At the same time, sub-dominants scrounge the prey from dominants and use their aphid colonies to obtain honeydew. Thus, 'cooperation' between dominant and subdominant ant species is based on reciprocal kleptoparasitic relations, which may require cognitive resources.

Ant colonies also interact through 'interspecific social control': dominant species actively regulate the level of the dynamic density of the subdominant species, exterminating 'superfluous' individuals or whole populations (Reznikova, 1999, 2003). In a manipulation experiment, for example, a sharp increase in the size of three *Formica picea* (subdominant) families was caused by adding 300 conspecific pupae in each family during 3 days and additional food sources only accessible to this species. Despite no decrease in food availability for the dominant species, *Formica uralensis* responded to an increase in the abundance of the subdominant species by killing and bringing into their nest about 250 *Formica picea* ants. Importantly, the number of subdominants killed by the dominant ants was close to the number of extra pupae added by the researchers to the subdominant species. This suggests that members of the dominant species can estimate number of encounters with subdominants quite precisely.

State of the Art

The majority of models consider cognitive skills and individual interactions in social insects redundant, and assume that their behaviour is based on what is called 'swarm intelligence', that is, it is only governed by collective decision-making (Miller *et al.*, 2013). These models are used to describe reactions of large groups as a whole to relatively simple stimuli from the environment. Indeed, there are many specific

behaviours performed by ants collectively, such as nest architecture and nest climate control, consensus building, slave-making, agriculture and well-coordinated territorial wars (Hölldobler and Wilson, 2009). However, ants and bees are known to combine highly integrative colony organization with sophisticated cognitive skills implemented by individual tiny brains.

To date, ant ethograms are still scarce and mainly refer to few behavioural domains (e.g. within-nest behaviour, hunting, recruitment to food sources). Moreover, most cognitive studies have been conducted in laboratories and not in the wild (but see Reznikova and Bogatyreva, 1984). The number of behaviours recorded in ants (38 in Wilson, 1976; 40 in Villet, 1990), however, is comparable to that of other species (e.g. 22 in American moose, *Alces alces*; 44 in De Brazza monkeys, *Cercopithecus neglectus*; 123 in bottlenose dolphins, *Tursiops truncatus*: Changizi, 2003; 59 in honeybees, *Apis mellifera*: Chittka and Niven, 2009) and can largely vary across casts of workers (Brown and Traniello, 1998; but see Sempo and Detrain, 2010).

Social hymenopterans are capable of abstraction, extrapolation and simple arithmetic, and can solve rather sophisticated discrimination tasks, in a way comparable to dogs and monkeys (Reznikova, 2007a, 2017; Dornhaus and Franks, 2008; Loukola *et al.*, 2017; Perry *et al.*, 2017). These studies have mainly been carried out on just ants (Reznikova and Ryabko, 1994, 2011) and bees (see Chapter 3). In particular, there is evidence that ants are good at maze learning (Cammaerts Tricot, 2012), complex route learning (Rosengren and Fortelius, 1986; Czaczkes *et al.*, 2013) and visual discrimination of shapes (Cammaerts and Cammaerts, 2015). Moreover, highly social ant species possess sophisticated intelligent communication (*sensu* Reznikova, 2017; see below). With such a variety of ant species differing in social and foraging styles, however, it is clear that cognitive abilities may differ enormously across species, and also across colonies and individuals, due to task allocation and 'professional specialization' of individuals.

Individual Recognition

Ants use hydrocarbon labels to distinguish between members of their own and alien colonies at the inter- and intraspecific level, and between members of different casts and ages. Ants evolved a 'gestalt' organ (the postpharyngeal gland, Soroker *et al.*, 1995), which helps to homogenize recognition cues among colony members, through grooming and trophallaxis (mouth-to-mouth food sharing), shaping an internal representation of their own colony odour (Lenoir *et al.*, 2009; Bos and d'Ettorre, 2012). In *Myrmica rubra*, newly hatched ants attract adults via 'cuticular chemical insignificance' determined by underdeveloped postpharyngeal glands and ovaries (Lenoir *et al.*, 2009; Atsarkina *et al.*, 2017). However, these behaviours are fixed and do not require cognitive skills. Moreover, invertebrates are usually thought to be incapable of individually identifying conspecifics (but see Tibbetts, 2002). Field experiments with *Formica pratensis* ants showed that permanent units of ants patrolling the boundaries of their feeding territories differentiate at least between members of their own family, acquainted guards from neighbouring families and individuals from more remote areas (Reznikova, 1974, 2007a). This system of individual or at least group identification is

cognitively demanding, and allows personally acquainted neighbours to establish boundaries, share resources and form a temporal society in which informative signals are shared (Fox and Baird, 1992; Godard, 1993).

Recognition of Competitors and Symbionts

One of the vital tasks faced by animals is to recognize, categorize and appropriately react to the stimuli encountered: whether it is prey, a dangerous predator, a competitor which should be driven away or a possible symbiotic organism. Red wood ants (*Formica aquilonia*), for instance, can recognize images of competitors, such as ground beetles (Dorosheva *et al.*, 2011; Reznikova and Dorosheva, 2013). By using live beetles and mock models in field and laboratory experiments, we showed that ants respond selectively to features of competitors like dark coloration, the presence of 'outgrowths' (legs, antennae), body symmetry, rate of movement and scent, even without previous experience. This suggests that red wood ants possess an innate template for recognition of potential competitors, although the ability to single out the key features, complete the integral image and display the behavioural patterns of guarding and defence appears to increase with experience, and thus requires learning and memory.

Recognition of symbionts, instead, is especially important in ants suckling Hemiptera species (e.g. aphids). The ants look after the symbionts, protect them from adverse conditions, carry them to new feeding sites and take care of their eggs. In return, the ants 'milk' the aphids, whose sweet excretions are one of their main sources of carbohydrates (Addicott, 1978; Novgorodova, 2015). Our experiments revealed that naïve red wood ants encountering aphids for the first time perceive aphids as any other unknown object, until they accidentally touch a drop of the aphid's excretion, which triggers the whole pattern of aphid milking: the ant gradually stops tapping at the aphids and begins to stroke them with folded antennae to obtain its excretion, then stopping and milking other aphids in the colony (Reznikova and Novgorodova, 1998; Reznikova, 2007a). Interestingly, this trophobiotic behaviour becomes more efficient with experience, completely developing in 60–90 minutes after the first contact with aphids. This can be considered a form of guided learning (*sensu* Gould and Marler, 1984), which requires the ability to integrate wired behaviours and acquired experience.

Communication

Ants largely communicate to recruit others, in the following contexts (Jackson and Ratnieks, 2006; Reznikova, 2007b, 2017; Leonhardt *et al.*, 2016): (1) tandem running, where a successful forager leads a recruit; (2) mass recruitment, by which recruiters returning from a food source to the nest lay a chemical trail that guides their nestmates to the source; (3) group recruitment, where the scout first lays a chemical trail upon return to the nest and subsequently leads a small group of recruits along this trail to the source; and (4) group-retrieving mode of foraging, based on distant homing

(i.e. transferring messages about remote events from a scouting individual to foragers, without other cues such as a scent trail or direct guiding; see: Reznikova, 2008, 2017). The most striking examples of distant homing are the honeybee dance language (see Chapter 3) and the symbolic 'language' of highly social ant species (Reznikova 2007a, 2007b, 2017). In these species, distant homing confers productivity (i.e. the ability to generate a potentially unlimited number of messages on the basis of a finite number of signals) and flexibility (i.e. interlocutors grasp regularities in their environment and use them to optimize messages). Ant 'language' has been explained through information theory (Ryabko and Reznikova, 1996, 2009), which allows investigating the very process of information transmission, by measuring the time which animals spend on transmitting messages of definite length and complexity. The main point of this approach is that it is not necessary to 'decipher' ants' messages and understand how they represent information. As we show, analysing the duration of information transmission – provided the information content is (precisely) known to us – is sufficient to uncover many facts about ants' 'language' and their intellectual abilities (see below).

Red wood ants (*Formica rufa* group) are possibly the most promising and underestimated group for studying cognitive aspects of communication. They have hundreds of times more individuals per colony than other sympatric species, more spacious feeding territories, and face more complex vital problems (e.g. finding and possibly memorizing locations of thousands of aphid colonies in a three-dimensional space). Members of this group of species are able to transfer messages about the exact coordinates of a food source (Reznikova and Ryabko, 1990, 1994, 2012), and use distant homing to transfer exact information about remote events, like honeybees do (Reznikova, 2007a, 2007b, 2017; Tautz, 2008). Observing them solving complex search problems may be revealing to understand the processes of information transmission and task allocation between members of the ant society.

Cognitive Differences between Mass Foraging and Solitary Foraging Species

In many ant species, fairly simple interactions among individuals generate complicated group behaviour. For instance, many species of the subfamily Myrmicinae show *mass foraging*, that is, they broadcast guidance information to potentially all foragers, in the form of a trail network marked with varying amounts and types of pheromone (see Hölldobler and Wilson, 1990). However, as demonstrated in *Temnothorax albipennis* (Dornhaus, 2008), although workers differ in their ability to perform different tasks (e.g. foraging, collection of nest-building material, brood transporting), they are allocated to different tasks independently of their skills. Possibly, members of mass-foraging species, although they display variable capacities preceding 'professional specialization', have not further developed this system in their colonies, and so there may be no differences in cognitive responsibilities within families of mass-foraging ant species (Dornhaus and Franks, 2008). Members of *solitary foraging* species (e.g. desert *Cataglyphis* ants, solitary hunters of the genus *Myrmecia*, many species of the subgenus *Serviformica*), in contrast, are much more flexible than members of mass foraging
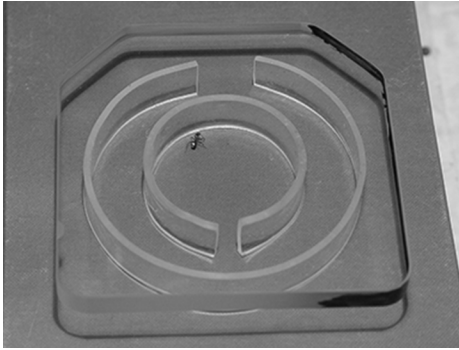
Figure 1.1. A round maze with three circles.
Photo by Ivan Iakovlev.

species, individually searching for food and making decisions. In field experiments with *Cataglyphis*, Wehner (2003) revealed that the same ant could flexibly learn different routes for the outward and homeward journeys and for journeys leading to different feeding sites.

A striking example of the difference between solitary foraging and mass foraging ant species lies in their ability to navigate 'round mazes'. In field experiments, ants were presented with mazes consisting of one to three concentric circles placed one inside the other in such a way that their entrances were placed on the opposite sides, and the inner circle contained food pellets (Figure 1.1): although in solitary foraging species (*Formica cunicularia*) nearly all foragers could successfully solve the maze, only 10 per cent of the mass-foraging ants (*Formica pratensis*) successfully navigated mazes (and only after observing *Formica cunicularia*). Interestingly, *Formica cunicularia* is also subdominant to *Formica pratensis*, and serves as a scout to the latter, being much more successful in learning new ways to search for food (see above; Reznikova, 1975, 1982, 2007a).

Cognitive Specialization within Colonies of Group-Retrieving Species

In group-retrieving species such as red wood ants, colonies include stable teams with one scout and four to eight foragers (Reznikova and Ryabko, 1994; Reznikova, 2007a, 2007b). Only scouts (but not foragers) are able to solve complex problems and pass information to other team members: they can memorize and transfer information about a sequence of turns toward a goal, grasp regularities in these sequences and also perform simple arithmetic operations (Reznikova and Ryabko, 2011). This cognitive specialization is based on the ability of some specific individuals to learn faster within specific domains, and it likely increases effectiveness at solving problems while searching for food (Reznikova, 2007a, 2012).

For instance, hungry ants can locate food on one of several 'leaves' in a 'binary tree' maze (Figure 1.2). In each trial, one scout was placed on a certain leaf of the binary tree, with food, and could then return to the foragers in the nest. The scout contacted one to
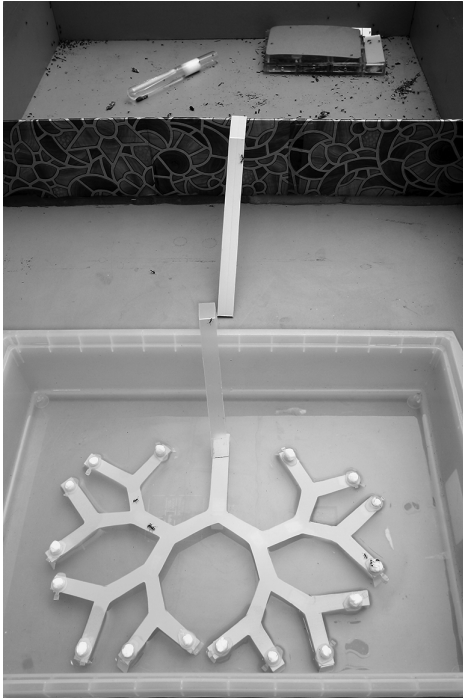
Figure 1.2. A laboratory arena divided into two parts, containing an artificial ant nest and a binary tree maze placed in a bath with water. This binary tree has four forks.
Photo by Nail Bikbaev.

four foragers, and the time the scout spent on 'informative contacts' was used as the main feature of ants' communicative means. All experiments were so devised as to eliminate all possible cues that could help the ants find the food (e.g. odour tracks), except for information contacts with the scout. If the group reached the correct point, they were immediately presented with the food. Crucially, scouts shared information about the discovered food only with members of their team (Reznikova and Ryabko, 1994, 2011; Reznikova, 2017).

Like honey bees, *Formica* scouting individuals do not bear any distinctive morphological traits. It is known that scouting bees constitute a very specific group in a hive, although, in contrast to *Formica* scouts, they transfer information not to the members of their own team but rather to anyone that is interested (see Chapter 3; Tautz, 2008). Some of the molecular underpinnings of their behaviour relative to foragers have been revealed (Liang *et al.*, 2012). Yet we know nothing about the peculiarities of the brains of scouting ants. For this reason, we designed the first battery of behavioural tests examining scouts' levels of aggression (estimating the variety of interactions with ground beetles), exploratory activities (recording ethograms of ants interacting with artificial models of natural objects) and spatial cognition (assessing the ability to memorize the path in a binary tree maze; Figure 1.3A–C), in comparison with members
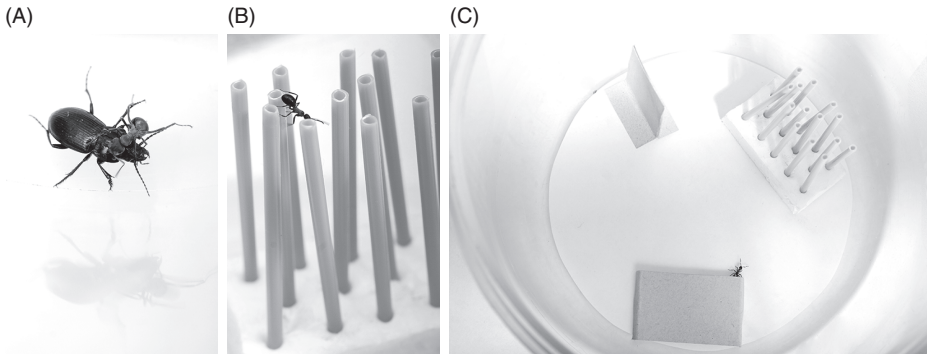
Figure 1.3. A piece of 'artificial world' designed for studying ants' exploratory activity and aggressiveness. (A) Test of aggressiveness: an ant is biting a beetle; (B) an ant is exploring 'grass'; (C) a shelter ('litter setup'), 'tree trunk' and grass stems imitated by 'brushes' made of plaster bars.
Photos by Nail Bikbaev.

of other task groups such as aphid milkers, guards and foragers. Both scouts and foragers were overall more exploratory than other out-nest workers, and scouts more than foragers. In unfamiliar situations, scouts more readily switched between different activities. Scouts and foragers displayed nearly equal levels of aggressiveness, more than aphid milkers and closer to guards, but never attacked beetles directly. The most distinctive feature of scouts was their high exploratory activity of novel items. Scouts also seem to form spatial memory faster and keep information longer and more precisely than foragers (Atsarkina *et al*., 2014).

It is worth noting, however, that learning is costly for insect brains. Replicate *Drosophila* populations selected for improved learning lived on average 15 per cent shorter than the corresponding unselected control populations, and long-lived selected flies showed an almost 40 per cent reduction in learning ability early in life (Burger *et al*., 2008). In our study (Reznikova and Ryabko, 1994, 2011), we observed scouts performing their tasks during up to 8–10 weeks, which is extremely long in comparison with, for example, *Cataglyphis* ants, having only about 6 days to perform feats of orientation (Schmid-Hempel, 1984). In ant species with a relatively low level of social organization, however, specialization does not predict individual efficiency. In our experiments with mass recruiting *Myrmica rubra* and solitary foraging *Formica cunicularia*, we did not find any evidence of distant homing (Reznikova and Ryabko, 1994). However, in *Myrmica* ants we found a system of distributed learning responsibilities, which possibly decreases the cost of learning at both individual and family levels (Reznikova and Panteleeva, 2008). In particular, the spreading of complex hunting behaviours towards jumping springtails appeared to be based on relatively simple forms of social learning, such as social facilitation, which triggers relevant behavioural patterns when these are encountered with sufficient frequency. This system of 'distributed social learning' can be considered alternative to individual cognition in ant societies.

All for One and One for All
Box 1.1 Cognition in Eusocial Species

Felicity Muth

Ants and bees are essentially cousins: they are both in the order Hymenoptera and are more closely related than ants are to social wasps like yellowjackets. While there are 20,000 species of bees, most of what we know about their cognition comes from three species: *Apis mellifera* (honeybees) and two bumblebee species: *Bombus impatiens* and *Bombus terrestris*. Given the intense interest in the cognitive abilities of these three eusocial species (most bee species are actually solitary), it is perhaps surprising that there has not been more investigation into the cognitive abilities of ants, which are all eusocial.

Working with species that live in colonies of tens to thousands of closely related individuals carries some common methodological challenges. For example, it is often important when studying cognition to be able to recognize individuals, to differentially manipulate their experiences. With ants, this is most often done through paint-marking individuals: each individual might have one colour mark on the head, one on the thorax and two on the abdomen: this allows for hundreds to thousands of individuals to be uniquely identifiable. More recently, ants have also been tagged using Radio-Frequency Identification (RFID) tags. In experiments on bee behaviour, both of these methods of tagging have been used, as well as thorax tags and more advanced tracking systems, such as transponders that allow radar tracking over much larger spatial scales (Riley *et al.*, 1996; Woodgate *et al.*, 2016).

Somewhat similar methods have also been used to address cognition in ants and bees: associative learning has long been studied in bees through the proboscis extension response (PER), where the bee is held in a harness and trained to learn an association through pairing a conditioned stimulus (e.g. a colour or scent) with a reward (sucrose, presented to the bee's proboscis; Bitterman *et al.*, 1983; see Chapter 3). An adaptation of this protocol has since been used for ants, where the ant's antennae are stimulated with sucrose, causing the ant to extend its maxilla-labium (Guerrieri and D'Ettorre, 2010). Many free-moving protocols also exist for testing bee and ant learning, although for bees this mostly consists of visiting artificial flowers, whereas for ants it often consists of learning about nest sites or landmarks. We recently designed a method to address learning in wild-caught bees (Muth *et al.*, 2018), which we believe could also be adapted for looking at learning in nectivorous ants.

Given the social structure of ants and social bees, individuals often explore and learn individually, but then share information with the colony. Ant behaviour is often studied in terms of how individual decisions lead to colony-level behaviour (Robinson *et al.*, 2011; Sasaki and Pratt, 2012). While similar questions have been asked in honeybees (Seeley, 2010), bee cognitive abilities are also often addressed on the individual rather than colony level (Perry *et al.*, 2017). Looking ahead, the large species diversity of ants and bees offers a useful opportunity for comparative

(*cont.*)

analyses: we could test hypotheses about which life-history traits favour particular cognitive abilities. Indeed, there are particular cognitive abilities that may be associated with sociality, diet breadth or resource specialization: for example, we might expect ant and bee species with a wider dietary breadth to be better at learning novel associations with food rewards.

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Field Guide

Depending on the research question, different ant species should be used. Although *Lasius, Temnothorax* or *Myrmica* species are easier to keep in the laboratory, species with distant homing (e.g. *Formica rufa, Formica sanguinea* and several *Camponotus*) should be preferred, for instance, when using communication as a tool for studying cognition.

   To study communication and cognition, a laboratory should host at least 1000 specimens, although smaller groups can be used in complementary studies, such as deprivation experiments. Ideally, experiments should be performed with more

laboratory groups on separate arenas. The laboratory groups should be taken from a typical colony in nature and hosted in one artificial nest (recommended size: $10 \times 15 \times 12$ cm). Plain, transparent nests divided into several internal cameras should be preferred, as they allow observation of contacts among individuals. Ants should be gradually accustomed to light in the laboratory. Normal room temperature is suitable for ants ($21-23°C$), and a wet cotton tampon should be placed in one camera to give a certain moisture within the nest. The recommended size of the foraging arena is 150×50 cm, and its rims should be about 15 cm high and covered with a sticky substance (such as Vaseline) to prevent ants from escaping. The arena should be divided into two parts: a small living one and a part containing an experimental device (Figure 1.2). Laboratory mazes can be easily made from plastic folders and other materials at hand. Sugar syrup and immobilized small insects can be used to feed the ants in the living part of the arena. However, during the experiments, ants may be more strongly motivated by only receiving food in a certain point of a maze, once every 2–3 days.

The idea of using the natural communication of animals to study their cognitive capacities is based on an information-theoretic approach: experimenters force animals to transfer a predetermined quantity of information, and then measure the duration of the time spent by the subjects to transfer this information (Ryabko and Reznikova, 1996, 2009). Comparing time durations required for information transfer in different situations, one can reason about certain key characteristics of the communication system under study. This system may be potentially applied to other species such as bees (having a symbolic dance language) and possibly some highly social vertebrates, including those which have been language-trained (Savage-Rumbaugh and Lewin, 1994; Pepperberg, 2009; Herman, 2010), but could be tested using their natural signals rather than artificial intermediary languages. The crucial idea is that experimenters know exactly the quantity of information (in bits) to be transferred (for instance, the number and sequence of turns toward food). In ants, this system is based on two main experimental schemes: investigation of ants' ability to memorize and transfer sequences of turns in a binary tree maze, and of their ability to use the numbers of branches in the 'counting' mazes.

First, it is necessary to reveal the composition of the working teams (i.e. distinguishing between scouts and foragers: Reznikova, 2017; http://reznikova.net/research/ant-language), by administering preliminary familiarization trials lasting 2–3 weeks, in which ants have free access to the set-up and syrup. All active ants should be labelled individually by applying drops of paint to different parts of their bodies in different combinations of colours (Holbrook, 2009). In the course of the main experiments, then, one of the scouts actively moving on the living part of the arena can be placed in the maze with food, until it returns to the nest by itself. All contacts between the scout and its team should then be observed and measured in seconds. Usually, members of a team are waiting for 'their' scout on the living part of the arena (Figure 1.2) and their contacts can be easily video-recorded. However, recording contacts within a transparent nest is also possible. The experiments should be devised so as to eliminate all possible ways for the members of each foraging team to find the target, except for information contact with their scout. The set-up should be replaced with a fresh one, with all troughs filled

Table 1.1. Essential experimental tools required to study ants and their function.

Tool	Function
Forceps and a special trap to catch ants	To catch ants and manipulate them. I suggest to cut a hole in the bottom of a small retort and use it as a special trap to catch individual ants in the field (Reznikova, 2009), before labelling or manipulating them (e.g. releasing them in another part of their feeding territory for studying navigation and spatial memory)
Paint applicator (e.g. toothpick or bristle from paintbrush)	To mark individuals with a distinct colour code and track their movements in the field and laboratory. Recently, thin radio-trackers have been suggested (www.york.ac.uk/news-and-events/features/ant-behaviour/); however, in many cases researchers use simpler equipment
Sandwich boxes (24 × 30 × 1 cm, or so)	To keep live ants in the field and transport them to the lab or into alien territories
Field round mazes	To compare individual characteristics such as searching activity and ability to find a way across different colonies and species. Mazes can be easily made from plastic folders and other materials at hand
Field troughs	To study searching activity, navigation and memory in ants in the field. Round disposable plastic dishes (diameter from 2 to 4 cm) are recommended. Use 3 ml of 30% sucrose solution as carbohydrate food and pieces of tuna baits as protein food
Numbered pins or toothpicks	To track the route and record time and length of each foraging path, in order to investigate individual foraging strategies and spatial memory. As the ant walks, a numbered pin can be placed on the ground along its route, each 60 seconds. Each path can then be converted into a smaller grid on paper, digitized and overlapped with the other paths (see Pie, 2004)
Digital voice recorder	To record behavioural data for later transcription
Video-camera	Any camera capable of recording high-quality video
Video analysis	Relevant tools for video analysis should be chosen, such as The Observer 10 XT (Noldus Information Technology) and VLC media player, reducing the playback speed when necessary to 1/8

with water, while the scout is in the nest; if the foraging team reaches the correct branch in a compact group, then the water-filled trough is replaced with one with syrup as a reward. Each scout can master up to three trials per day. When working with the 'binary tree' maze, it should be taken into account that even those ant species which do use distant homing only do so when confronted with complex mazes, and not with the T maze.

Tree-mazes can also be used to assess whether ants grasp regularities in the information available: if food can be reached by turning right and left four times (RLRLRLRL), and ants grasp regularities, they should transmit this information more quickly (4LR) than random sequences like LRRLRLLR. *Formica sanguinea* ants, for instance, spent less time transferring information about more regular sequences of turns (e.g. transferring LLLLLL was quicker than transferring LRLRLR, which was in turn
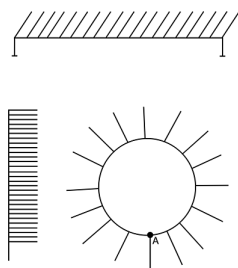
Figure 1.4. 'Counting mazes': a *horizontal trunk*, a *vertical trunk* and a *circle*.

quicker than transferring LRLLRL). This means that the ants are able to grasp regularities within these sequences, and the time spent transmitting information depends on its complexity (Ryabko and Reznikova, 1996, 2009; Reznikova, 2017). Interestingly, ants begin to use regularities to compress information only when sequences are rather long.

Given that ants can pass exact information about a target in a maze, in 'counting' experiments (Reznikova and Ryabko, 2011, 2012) scouting individuals can be required to transfer information to foragers about which branch of a special 'counting maze' they had to go to in order to obtain syrup (Figure 1.4): by estimating how much time individual ants spend on transferring information about index numbers of branches, experimenters can judge how ants represent numbers. The first variant of the counting maze is a comb-like set-up consisting of a long horizontal plastic trunk with 25–60 equally spaced plain plastic branches, each of them 6 cm in length. Each branch ends with an empty trough, except for one filled with syrup, and ants come to the initial point of the trunk over a small bridge. The second variant is a set-up with 60 vertically aligned branches. In order to test whether the time of transmission of information about the number of a branch depends on its length, as well as on the distance between the branches, a similar vertical trunk can be used, in which the distance between the branches is twice as large, and the branches themselves are three times and five times longer. The third variant is a circular trunk with 25-cm long branches. As before, all actively foraging ants are individually marked with coloured paint, strongly motivated scouts are placed directly on the trough and the time spent on 'informative contacts' with their teams once they are back in the nest is measured.

In red wood ants *Formica polyctena*, the teams left the nest after they were contacted by scouts and moved towards the trough by themselves on 152 trials. In 117 cases, the team immediately found the correct path to the trough, and in the remaining cases, ants came to the empty troughs and began looking for food by checking neighbouring branches, supporting the idea that scouts transmit information (Reznikova and Ryabko, 2011; Reznikova, 2017). The likely explanation of the results concerning ants' ability to find the 'right' branch is that they can evaluate the number of the branch in the sequence of branches in the maze and transmit this information to each other. Presumably, a scout can pass messages not about the number of the branch, but about the distance to it or about the number of steps. What is important is that even if ants operate with distance

or with the number of steps, they are able to use quantitative values and pass on exact information about them. Moreover, scouts perform simple operations of addition and subtraction: as the 'special' branches can only be referred to by their numbers (i.e. as no other visual or olfactory cues are available), scouts placed on, say, branch 17 and heading to branch 20 have to correctly calculate that 17 is three branches away from 20. Similarly, when placed on the branch 23, the scout has to correctly compute that this branch is three branches away from branch 20, which, in the absence of any mark on the branch 20, requires addition. Overall, our studies show that ants can show impressive cognitive skills, although this may only be true for specific ant species with especially complex and flexible communication systems.

Wild vs. Lab

Box 1.2 Understanding the Nature of Ant Cognition by Studying Ant Cognition in Nature

Neil D. Tsutsui

Ants are fascinating and productive model systems for illuminating cognition and behaviour due to the sophisticated, coordinated behaviours they display. In addition, eusocial insects offer unparalleled opportunities to study systems that simultaneously display behaviour at multiple levels: individual organism (ant) and superorganism (colony).

Although field studies of ants are prominent in ecological research, behavioural studies tend to be more laboratory-oriented. This is due, in part, to the inherent challenges of studying ant behaviour in the field, which include small size (often minute), the anonymity of individual workers within the teeming masses of the colony, and the inordinate amount of time that ants spend in the inaccessible reaches of colonies underground or in fallen or standing deadwood. However, it is essential to complement laboratory-based studies of ants with corresponding data from the field. Important stimuli that occur in nature may be absent in the lab, or laboratory environments may introduce artificial variables or stressors that do not occur in the wild.

Ants are chemically oriented creatures, but studying chemical ecology in natural environments can be challenging, due to the abundance of confounding or contaminating natural odorants. At the same time, removing ants from their environment may produce stress and/or unnatural behaviours. In some cases, a hybrid approach may be fruitful. Youngsteadt and colleagues (2008), for example, combined olfaction experiments in the field with laboratory chemical analyses, to identify the specific chemicals that *Camponotus* ants use to locate and recognize seeds of their epiphyte mutualist.

Social interactions may also differ between the field and lab, both qualitatively and quantitatively, and these interactions shape the behaviours of both individuals and colonies. In Argentine ants (*Linepithema humile*), for example, a single fight with a worker from a different colony increases the likelihood of aggression in

(*cont.*)

subsequent encounters (van Wilgenburg *et al.*, 2010), and, in the wild, this significantly affects intercolony interactions (Thomas *et al.*, 2005). Because such sensitive responses to social stimuli can produce large-scale consequences, it is essential to complement laboratory-based assays with field studies.

In the future, chemical and genetic manipulations will be increasingly used in the field as powerful approaches for disentangling the determinants of behaviour and cognition. RNA interference (RNAi), for example, has been used for targeted gene silencing in a carpenter ant (*Camponotus floridanus*; Ratzka *et al.*, 2013) and the red imported fire ant (*Solenopsis invicta*; Cheng *et al.*, 2015), making it likely that such approaches will soon be taken outdoors to assess how the altered expression of candidate genes affects behaviour in the wild.

It is likely that many colony-level phenotypes are only expressed in natural substrates and foraging environments, which would be exceedingly difficult to replicate in the lab. The physical architecture of ant nests, for example, is an important determinant of harvester ant (*Veromessor andrei*) foraging behaviour (Pinter-Wollman, 2015). By combining cutting-edge imaging techniques for quantifying structural variation in the field with manipulative lab experiments, we will likely gain exciting new insights into how the built environment shapes the behaviour of social organisms, including ourselves (Pinter-Wollman *et al.*, 2017).

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Resources

Popular books on ants:

- Hölldobler, B., and Wilson, E. O. (1994). *Journey to the ants: a story of scientific exploration*. Cambridge, MA: Harvard University Press.
- Hölldobler, B., and Wilson, E. O. (2009). *The superorganism: the beauty, elegance, and strangeness of insect societies*. New York, NY: W.W. Norton and Company.
- Reznikova, Z. (2017). *Studying animal languages without translation: an insight from ants*. Cham, Switzerland: Springer.

Popular books on individual and social cognition:

- Reznikova, Z. I. (2007). *Animal intelligence: from individual to social cognition*. Cambridge: Cambridge University Press.
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior.* Oxford: Oxford University Press.
- Menzel, R., and Fischer, J. (2011). *Animal thinking: contemporary issues in comparative cognition*. Cambridge, MA: MIT Press.
- Wynne, C. D. (2001). *Animal cognition: the mental lives of animals*. London: Macmillan.
- Bekoff, M., Colin, A., and Burghardt, G. M. (2002). *The cognitive animal: empirical and theoretical perspectives on animal cognition*. Cambridge, MA: MIT Press.

Some ant labs:

- www.uni-regensburg.de/biologie-vorklinische-medizin/evolutionsbiologie/
- www.bristol.ac.uk/biology/research/behaviour/antlab/
- http://en.nencki.gov.pl/laboratory-of-ethology
- http://reznikova.net/labs/
- http://icouzin.princeton.edu/
- https://web.stanford.edu/~dmgordon/
- www.schoolofants.net.au/our-team/
- http://sydney.edu.au/science/biology/socialinsects/
- http://ucanr.edu/sites/ucrurbanpest/Research/Ant/
- http://pratt.lab.asu.edu
- www.iiserkol.ac.in/~antlab/lab_members.html
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- www.rockefeller.edu/our-scientists/heads-of-laboratories/988-daniel-kronauer/
- https://wurmlab.github.io
- www.life.illinois.edu/suarez/

Profile

Zhanna decided to study ants as a first-year student at Novosibirsk State University. Ants allowed her to observe fragments of a 'civilization', asking questions through experiments, and getting answers, often for the first time in the world. Zhanna grew up in the Soviet Union behind the 'iron curtain' and was not allowed to go abroad until 1991 (for her first international conference in Kyoto, right after the 'August revolution', which she joined on her way to the conference). However, she always exchanged letters with researchers all over the world. The KGB only once gave her the approval to publish a paper outside the 'socialist camp' (in 1982, in *Behaviour*), so that many pioneering results remained long unknown to most scientists. Although she presently leads the laboratory of community ethology and develops comparative cognitive studies on rodents, birds and other wonderful creatures, ants remain her passion, being uniquely clever and enigmatic.

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