Animal Cognition
https://doi.org/10.1007/s10071-020-01423-x

REVIEW

Spatial cognition in the context of foraging styles and information transfer in ants

Zhanna Reznikova[1,2]

Received: 4 December 2019 / Revised: 13 May 2020 / Accepted: 13 August 2020

Abstract

Ants are central-place foragers: they always return to the nest, and this requires the ability to remember relationships between features of the environment, or an individual's path through the landscape. The distribution of these cognitive responsibilities within a colony depends on a species' foraging style. Solitary foraging as well as leader-scouting, which is based on information transmission about a distant targets from scouts to foragers, can be considered the most challenging tasks in the context of ants' spatial cognition. Solitary foraging is found in species of almost all subfamilies of ants, whereas leader-scouting has been discovered as yet only in the *Formica rufa* group of species (red wood ants). Solitary foraging and leader-scouting ant species, although enormously different in their levels of sociality and ecological specificities, have many common traits of individual cognitive navigation, such as the primary use of visual navigation, excellent visual landmark memories, and the subordinate role of odour orientation. In leader-scouting species, spatial cognition and the ability to transfer information about a distant target dramatically differ among scouts and foragers, suggesting individual cognitive specialization. I suggest that the leader-scouting style of recruitment is closely connected with the ecological niche of a defined group of species, in particular, their searching patterns within the tree crown. There is much work to be done to understand what cognitive mechanisms underpin route planning and communication about locations in ants.

Keywords Spatial cognition · Ants · Communication · Navigation · Memory · Solitary foraging · Leader-scouting

Introduction

Spatial cognition can be seen as a set of mental abilities to cope with the physical dimension of space and includes spatial coding, landmark anchoring, and route planning. A plethora of studies on spatial cognition and its consequences for animal behaviour have emerged since the second half of the nineteenth century. Recent experimental findings and theoretical models provide insight into the mechanisms that link sensory systems to spatial representations and to large-scale natural navigation (Geva-Sagiv et al. 2015). Cognitive aspects of insect navigation have been experimentally studied since the first half of the twentieth century (Santschi 1913; Schneirla 1933; Tinbergen and Kruyt 1938). Since then, displacement experiments (reviews in Collett et al. 2013; Giurfa 2015) and maze observations (review in Saar et al. 2017) have become the most popular methods to study spatial cognition in insects. Recent techniques enabling the recording of visual scenes from the perspective of the insect, such as an ant or a bee, provide some insights into their ability to see landmarks and recognize scenes (Zeil et al. 2003; Wystrach and Graham 2012; Narendra et al. 2013a, b; Stürzl et al. 2015; Freas et al. 2017a, b).

Remembering landmarks and estimating directions and distances travelled over a particular amount of time could be cognitively demanding tasks. What is even more sophisticated is to share this information with members of one's social group. There are only a few examples of animals transferring "messages" about spatial coordinates of distant goals using their natural communication means. E. Menzel's (1973) experiments showed that chimpanzees could retain

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10071-020-01423-x) contains supplementary material, which is available to authorized users.

✉ Zhanna Reznikova
zhanna@reznikova.net

[1] Institute of Systematics and Ecology of Animals, Siberian Branch RAS, Frunze 11, Novosibirsk 630091, Russia

[2] Novosibirsk State University, Pirogova 2, Novosibirsk 630090, Russia

and transmit information to group members about object quality, the quantity of food, and location. Later, similar results have been obtained with lexigram-competent bonobos (Menzel et al. 2002); however, details of their natural communication still remain unknown. Honeybees use the “dance language” to inform others about the coordinates of a food source (von Frisch 1923, 1967; reviews in Dyer 2002; Tautz 2008; Seeley 2009; Barron and Plath 2017). Curiously, some individuals will spontaneously dance in the night when no foraging takes place, which means that bees can retrieve the memory of a location they had visited the day before (Chittka 2017). Use of such methods such as the robotic bee (Michelsen et al. 1992; Landgraf et al. 2011) and harmonic radar (Riley et al. 2005) has provided a quantitative description of how efficiently bees translate the code in the dance into flight to their destinations. However, essential cognitive aspects of communication in bees, such as how the dance is read and what neural mechanisms it is based on, remain unclear. One other highly social group, namely, leader-scouting ant species (*Formica rufa* group) were also found to be able to transfer abstract information about remote events, to grasp regularities, and to use them to optimise their messages (Reznikova and Ryabko 1994, 2000, 2011; Reznikova 2008, 2017). Until recently, both in ants and honey bees, their abilities for transferring messages about remote targets, have been considered in terms of communication, separately from their spatial cognition. In this review, I consider spatial cognition in ants in the context of their foraging strategies and information transfer.

Navigation in the context of foraging strategies in ants

Like many animals, ants, except for those of nomadic army species, are central-place foragers: they carry food items back to a central place to store, eat, or feed their offspring. Central-place foraging theory predicts that foragers invest more effort to harvest more valuable resources at greater distances from the central place (Orians and Pearson 1979). Many species as diverse as honey bees (Kacelnik et al. 1986), chipmunks (Giraldeau and Kramer 1982), grasshopper sparrows (Kaspari 1991), Norway rats (Mellgren et al. 1984) and others show positive load-distance relationships in empirical studies. In ants, this pattern occurs frequently where workers control load size (Harkness and Maroudas 1985; Roces 1990; Bonser et al. 1998; Wright et al. 2000), but is less prevalent where resource size is fixed (e.g., seeds, Bailey and Polis 1987; Brown and Gordon 2000). However, although in terms of energy costs, members of some ant species do not fit the theory (reviews in Gibb et al. 2016; Alma et al. 2017) in terms of spatial cognition, they perform central-place foraging. The need to return to the nest requires the ability to encode and memorise relationships between features in an environment to return home successfully. In this section, I will consider how the distribution of cognitive responsibilities within an ant colony depends on the species-specific modes of foraging and recruiting.

In more than 13,000 ant species (Bolton 2016), foraging strategies display a continuum from individual forms, in which foragers leave the nest in random directions, and each ant procures food on its own, to cooperative arrangements mediated by different means of transferring information (reviews in Hölldobler and Wilson 1990; Detrain et al. 1999; Jackson and Ratnieks 2006; Heinze 2008; Leonhardt et al. 2016; Reznikova 2017). Members of cooperatively acting ant species first send out individual scouts to find a new resource (nest/food), and later the scout ants return to the nest to recruit nestmates. There are different methods of classification of modes of recruitment in ants (Lanan 2014; Reeves and Moreau 2019). In this review, I refer to the following four main categories of recruitment strategy (1) Mass recruitment, in which scouting individuals broadcast guidance information to all potential foragers in the form of a trail network marked with varying amounts and types of pheromone. For example, Pharaoh’s ant, *Monomorium pharaonis* uses a short-lived (approximately 20 min) attractive trail pheromone to guide foragers to the rewarding feeding sites, and a long-lived pheromone to maintain the trail network which can be explored over several days. The negative pheromone (repellent) is placed locally in the network immediately after trail bifurcations on a non-rewarding branch, thus playing the role of an additional, “no entry” signal (Jackson and Ratnieks 2006). In mass recruitment systems in general, patterns of interactions among individuals are governed by rules of self-organisation, and fairly simple units generate complicated behaviour at the group level. However, individual learning and explorative activity can be important factors for colony foraging success (Pasquier and Grüter 2016). (2) Tandem running, where a pair of workers consisting of a successful scout and a recruit leave the nest, and the scout leads the recruit to the resource found earlier (Wilson 1959). Since only one nestmate is recruited at a time, tandem running has been considered to be a primitive form of recruitment, which, however, is prevalent across the ant phylogeny (review in Schultheiss et al. 2015). Although tandem running seems to be costly, as walking speed of followers is low compared to solitary foraging ants, studies on the rock ant *Temnothorax albipennis* (Franklin et al. 2012) and the Australian “sugar ant” *Camponotus consobrinus* (Schultheiss et al. 2015) showed that the experience gained improves navigational success both for leaders and followers and thus shows effectiveness of this recruitment strategy. (3) Group recruitment: a scouting ant may lead a group of several nestmates to a goal (Hölldobler 1971). For example, in different species of the genus *Polyrhachis* one to four recruited ants at a time followed closely behind a leader ant to the target area (Hölldobler and Wilson 1990). (4) "Leader—scouting" systems in which a scout communicates a distant location to foragers. In this system, messages about distant targets come from the scouting individual, without relying on any other cues such as scent trails or direct guidance. Here a scout plays the role of a permanent "cognitive leader," transferring information about remote targets using tactile contacts with the members of a constant group of foragers (reviews in Reznikova 2008, 2017). This system has been revealed in several species of the *Formica* group that have large colonies and spacious feeding territories (Reznikova and Ryabko 1994, 2011).

Most ant species employ only a single foraging strategy, but some species use several, and they can also switch between different strategies depending on external (environmental) stimuli, such as the size of the available food sources, as well as internal stimuli, such as colony growth. For example, *Formica cunicularia* ants can switch from individual foraging to mass recruitment depending on the size of the prey available (Reznikova 1975). Similar results have been obtained by Cerdá et al. (2009) on the gypsy ant *Aphaenogaster senilis*. As another example, generalist predators *Ectatomma ridium* select between solitary hunting, cooperative hunting, and group hunting with recruitment, depending on the prey weight and its distance from a nest, all without trail laying (Schatz et al. 1997; Lima and Antonialli-Junior 2013). The tree-dwelling African ant *Polyrhachis laboriosa* uses individual foraging when the food resource is small, whereas for large permanent food sources scouts use group recruitment. In this case, the choice of the foraging strategy is determined by the first forager, which modifies its behaviour according to the volume of the food supply (Mercier and Lenoir 1999; review in Reeves and Moreau 2019).

For a further analysis of spatial cognition in the context of foraging styles, it is worth comparing the mass-recruiting and the leader-scouting systems. Recent studies have demonstrated that in mass-recruiting species, scouting individuals neither play a leading role nor do they bear the central part in taking cognitive responsibilities and making decisions. Instead, when an informational conflict occurs, recruited foragers may prefer the private navigational information (memory) to social information (trail pheromone) from scouting ants (Grüter et al. 2011). Distributed leadership in mass-recruiting species is rather ephemeral and depends on the activity and motivation of individuals at the moment. For example, individual marking of *Tetramorium caespitum* showed that the same individual rarely leads groups of recruits towards the food source more than once, and recruiting ants can be successively observed both as group leaders and as non-leaders during the same foraging experiment (Collignon et al. 2014). Experiments with another mass recruiting species, *Temnothorax albipennis* revealed no difference in task allocation within the colony, although workers appeared to differ in their ability to perform different tasks. Surprisingly, this variation is not utilised by the colony: worker allocation to tasks is unrelated to their ability to perform them (Dornhaus et al. 2008). Further experiments with another *Temnothorax* species demonstrated that inactive workers act as a pool of "reserve" labour (Charbonneau et al. 2017), and colonies of this species can withstand removal of highly active individuals (Pinter-Wollman et al. 2012). In contrast to the mass recruiting system, the leader-scouting one is based on permanent relations between scouting ants and members of their teams. Furthermore, these teams have a constant composition, and a colony can hardly withstand the removal of active scouting individuals (see details in the next sections, and also in: Reznikova 2007a, 2017, 2018).

It is clear now that solitary foraging and leader-scouting are the most challenging tasks in the context of ants' spatial cognition, as these systems require individual exploration, learning, and memory. In this review, I concentrate on how spatial cognition works in two disparate foraging systems. Members of solitary foraging species navigate individually, lacking any cooperation between foraging individuals. Neotropical ant*s Gigantiops destructor*, which are extremely solitary in their foraging, even fight for prey with nestmates (Beugnon et al. 2001). In contrast, highly social leader-scouting red wood ants (*Formica rufa* group) possess a sophisticated communication system that is based on an intricate cooperation within stable individualised teams, and scouting in these species reflects cognitive specialization within the colony (Reznikova 2008; Iakovlev and Reznikova 2019).

Spatial cognition in solitary foraging ant species

Visual and idiothetic navigation in solitary foraging ant species

Solitary foraging, found in species of all the different subfamilies of ants, except for the army ants, is a strategy in which a worker will discover, capture and transport the food without any systematic cooperation or communication with other nestmates (Beckers et al. 1989; Hölldobler and Wilson 1990). Recent theory suggests that solitary foraging is the ancestral foraging behaviour of the Formicidae, and that cooperative behaviours have arisen independently multiple times within each subfamily (Reeves and Moreau 2019). Solitary foraging may be efficient within a given environment due to the unpredictable distribution of small food sources, substrate surface temperature, and many other factors (review in Lanan 2014). The desert genera *Cataglyphis*, *Melophorus*, and some others, which undertake long-distance trips to bring home small dead items, have become a model system for studying animal navigation (Wehner 2009; Wystrach et al. 2012; Mangan and Webb 2012; Narendra et al. 2013a, b; Schwarz et al. 2017; Heinze et al. 2018; Jayatilaka et al. 2018). In the North-African desert ant *Cataglyphis fortis* the total lengths of foraging trips may exceed 1500 m with maximal foraging distances of more than 350 m away from the nest entrance. This is equivalent to several thousand times of the ants' own body length (Ronacher 2008). Members of the genus *Cataglyphis* do not lay pheromone trails (Wehner 2003). However, *Cataglyphis* ants use olfactory cues and anemotactic orientation to pinpoint food sources (Wolf and Wehner 2000) and food plume to orient. These ants combine high sensitivity toward food odours with crosswind runs (Buehlmann et al. 2014), and they use olfactory landmarks for orientation to find the nest entrance (Steck et al. 2010). Yet the main mechanisms of orientation in individually foraging ants are visual (reviews in Wehner et al. 2014; Knaden and Graham 2016; Freas and Schultheiss 2018), and different species use slightly different implementations of the same navigational toolkit. For example, the Neotropical rainforest ant *Gigantiops destructor* can travel individually through 20 m of rainforest with trees and other objects in the scenery without using any trail pheromones (Beugnon et al. 2001). With these feats of individual navigation in mind, the question arises about the role of spatial cognition in the search for food and nests.

In my early field experiments with *Cataglyphis aenescens* in the semi-desert of Kazakhstan (Reznikova 1983), I offered red wings of locusts to individual ants. The ants readily seized the wings and immediately started to carry them to the nest. The locust wing looks like a red flag, making it possible to observe from a distance the trajectories of the ants carrying them. Thus there was no need to mark the ants with paint. This trick was also used to identify distances between colonies and the range by which foragers moved away from the nest. It is noteworthy that ants made choreographed rotations about the vertical body axis. In those days I denoted these movements in my field records as "minuets." They were later named, perhaps more precisely, ''pirouettes'' (reviews in Grob et al. 2019; Zeil and Fleischmann 2019), and it was also suggested in other *Cataglyphis* species (Wehner et al. 2004; Fleischmann et al. 2016), Namibian *Ocymyrmex robustior* (Müller and Wehner 2010), and the Australian jack jumper ant *Myrmecia croslandi* (Jayatilaka et al. 2018) that short stopping phases during rotations of the body allow individuals to integrate snapshot memories from different positions around their nest.

Path integration (PI) is a strategy used by many animals to return home by the shortest possible route. In PI, animals continuously combine odometric and compass information into a vector that can be used to find a direct path home, even across a previously unvisited terrain (Wehner and Srinivasan 2003; Graham and Mangan 2015). PI is more or less fixed and does not improve with training (Merkle and Wehner 2009) but plays a vital role in the whole process of learning of visual information (Collett et al. 1998; Knaden and Wehner 2005; Narendra et al. 2007; Heinze et al. 2018). In ants, vector information is first stored as a short-term working memory that is systematically updated and "reset to zero" at the end of the foraging task when an ant returns home (Ziegler and Wehner 1997). Ants can also store vector information in the long-term memory presumably by averaging PI vectors of various lengths and thus optimising over the course of multiple homing runs (Wehner et al. 1996, 2006; reviews in Beugnon et al. 2005; Heinze et al. 2018). For accurate route guidance and homing, ants complement PI with visual information learnt from panoramic scenes (Collett et al. 2007; Buehlmann et al. 2018, 2020). An ant's path is thus controlled by a combination of its vector memories, its visual memories and a continuously updated PI state (Collett 2012). Ants that live in slightly cluttered landscapes learn visual landmark information and establish individual routes that lead them to their food sources and back to the nest (Kohler and Wehner 2005; Mangan and Webb 2012). Ants occupying landmark-rich habitats trust visual cues to the extent that they follow their home vector only for a short distance when displaced to unfamiliar locations (Narendra et al. 2007).The degree to which ants rely on their path integrator when placed in an unfamiliar location thus inversely correlates with the availability of landmarks in their habitat (Cheung et al. 2012).

Further in this section, I am trying to highlight how different solitary foraging species use slightly different implementations of the same navigational toolkit. Below, I consider the life histories of several model groups of ants of solitary foraging species in light of their spatial cognition. Among them are highly visual diurnal species, as well as nocturnal ones that manage to use the same visual and idiothetic navigational means. The diurnal species belonging to *Serviformica* subgenus merits a separate consideration as a model group for comparing spatial cognition in solitary foraging and group foraging ants.

Spatial cognition in highly visual solitary foraging ant species

The genus *Cataglyphis* is a favourable experimental model for the study of how spatial cognition works in adult foragers and how it develops ontogenetically. In *Cataglyphis*, PI employs a skylight compass using the sky polarization pattern, sun position and chromatic cues of the sky to integrate the directions travelled and a stride integration mechanism for measuring distances of path segments (review in: Rössler 2019). In cluttered landscapes, PI interacts with other, more cognitively demanding navigational strategies, such as the learning and encoding of landmarks. There is some evidence of flexible switching between the methods of orientation in *Cataglyphis*. Field experiments show that *C. fortis* could learn both the direction and distance of a route segment towards a food source. M. Collett and T. Collett (2009) trained ants along an L-shaped route in order to show that ants can learn local vectors on the way to a food site. The sharp turn appears to present particular difficulties for the ants. When low bushes 20–30 m from the route were removed, local vectors were briefly unaffected, but then deteriorated. The vectors improved again once the missing bushes were replaced by artificial landmarks. The fragility of local vector memories may permit an ant the flexibility to adapt its route to fluctuations in the distribution of resources. Recent experiments (Wolf et al. 2018) with selectively covering eye regions responsible for optic flow input in odometry showed that the two odometers (stride and optic flow integration) possibly have separate distance memories that interact in determining homing distance, which makes a system more flexible.

The individual life history of ants of the genus *Cataglyphis* offers unique experimental model as these ants undergo a robust behavioural transition from performing tasks inside the dark nest to outside solitary foraging over long distances in bright sunlight, and they have to learn much about the external world during a rather short life outside the nest (Wehner and Rössler 2013; Rössler 2019; Zeil and Fleischmann 2019). Prior to their first foraging trips naïve *Cataglyphis* ants perform several learning walks to learn panoramic cues for navigation, as demonstrated in displacement experiments (Fleischmann et al. 2018). Given an average total foraging period in *Cataglyphis* of about 7 days (1984), the investment of 2–3 days into learning walks emphasizes that this behaviour represents a crucial element in the ontogeny of successful navigation (reviews in: Rössler 2019; Zeil and Fleischmann 2019). Naive ants walk relatively slowly in loops around the nest while performing distinct scanning movements. Successive learning walks extend further and further out from the nest, reaching distances of up to 4 m. One possible interpretation of this behaviour is that it serves for calibrating and re-calibrating skylight cues using the information from the panoramic scenery (Müller and Wehner 2010). This is supported by a recent study demonstrating that *Cataglyphis* ants also use the earth's magnetic field as a compass cue and directional reference for path integration during naïve learning walks (Fleischmann et al. 2018). Ants also store memories of nest-associated visual landmarks, which last for the entire lifetime (Ziegler and Wehner 1997). A study on *C. fortis* (Pfeffer et al. 2015) revealed one more flexible component of ants' orientation, that is, the so-called "food vector" used by ants during their foraging trips. While the parameters of nest searches are relatively constant and improve little with experience, food searches, by contrast, are more pliable and depend on the reliability of food encounters over several visits.

The Amazonian *Gigantiops destructor* is another formicine solitary foraging highly visual ant. *Gigantiops* has the largest eyes of any ant species and a volume ratio of the optic lobes to antennal lobes about 4.75 times higher than in *Cataglyphis bicolor* (Gronenberg and Hölldobler 1999). This species lives in partially sunny zones, such as forest edges and the banks of streams. Foragers navigate daily back and forth along familiar routes between the nest and a preferred feeding site, using both landmark and celestial information (Beugnon et al. 2001). The search for prey can last several hours; such intensive search patterns result in very long and sinuous paths (Chagné and Beugnon 2001). Similarly, the search for extra-floral nectaries on a given tree can also last several hours and involve climbing to heights of up to 40 m (Beugnon et al. 2001). Naive *Gigantiops* foragers probably depend on the output of their path-integrator during their first foraging trips before they adopt site fidelity for a given foraging area. Experienced ants seem to avoid using a continuously running path-integrator likely to be prone to an accumulation of errors during extended foraging periods (Beugnon et al. 2005). Laboratory experiments with diverse beacons (Macquart et al. 2006) showed that *G. destructor* foragers develop individually distinctive landmark routes. Each ant *en route* to the goal slalomed in an idiosyncratic distinctive way around different midway landmarks from a foraging trip to the next, which induced a variability of the path shapes in their intermediate parts. The use of a "rectangular arena" (Cheng 1986) showed that *Gigantiops* individuals partially update their route memory after each trial (Wystrach et al. 2011). It is possible that panoramic views are favoured over landmarks in this species. By reducing the number of landmark recognition-triggered responses, this strategy may be helpful in the Amazonian forest where many prominent landmarks are alike (Macquart et al. 2006).

Spatial cognition in nocturnal solitary foraging ants

The Australian nocturnal bull ant, *Myrmecia midas*, has to cope with navigation problems in conditions contrasting to those of the diurnal species, including a diurnal member of the same genus, jack jumper bull ant *M. croslandi* (Jayatilaka et al. 2018). Nocturnal ants forage and navigate during periods of reduced light, making detection of visual cues difficult, yet they are skilled visual navigators. These foragers retain visual panoramic memories both around the nest and along known routes for later use, be it to return to previously visited food sites or to the nest (Freas and Cheng 2019). *M. midas* occupy highly cluttered environments and establish nests at the base of a tree on which they forage and in addition, they also forage on nearby trees (Freas and Schultheiss 2018). Foragers of this species do not move far away from the nest area on the ground, and they are unable to orient to the nest after small local displacements (5 m; Freas et al. 2017a). When *M. midas* foragers navigate to the nest on the ground, albeit over short distances, they rely primarily on landmark cues (Freas et al. 2017b), and they also use polarised skylight pattern to compute a homeward vector while on-route (Reid et al. 2011). *M. midas* display active navigation along vertical foraging route on the nest tree (Freas and Schultheiss 2018). Since their bodies are oriented perpendicularly to the ground, these ants solve an entirely different navigation problem. Experiments have shown that when *M. midas* ants were released on non-foraging trees near the nest, displaced foragers again travelled around the tree to the side facing the nest. All the displaced foragers reached the correct side of the tree well before reaching the ground. However, when the terrestrial cues around the tree were blocked, foragers were unable to orient correctly, suggesting that the surrounding panorama is critical to successful orientation on the tree. Through analysis of panoramic pictures, the authors demonstrated that views acquired at the base of the foraging tree nest can provide reliable nest-ward orientation up to 1.75 m above the ground (Freas Schultheiss 2018). Using an opportunity to slightly modify the natural visual environment around the nest of the nocturnal *M. pyriformis* by felling three dead trees, Narendra and Ramirez-Esquivel (2017) found that immediately after the trees were removed, ants walked slower and were less directed. Their foraging success decreased and they looked around more, including turning back to look towards the nest. An image difference analysis showed that the change in the overall panorama following the removal of these trees was relatively small, however, these subtle changes disrupt visual navigation in a nocturnal bull ant. A recent study, on the example of *M. midas* (Freas and Cheng 2019) revealed that spatial cognition plays a different role in the navigation process according to how far from the nest individuals forage. Multiple metrics of forager navigational performance turned out to correspond with the degree of similarity between the release site panorama and panoramas of previously visited sites.

In sum, for nocturnal ants foraging in highly cluttered environments, where scenes change rapidly over short distances, the views acquired near the nest are only useful over a small area, and memories acquired along foraging routes become critical.

Spatial cognition in solitary foraging *Serviformica* ants

A striking example of the difference between spatial cognition in solitary foraging and cooperatively foraging ant species comes from members of the subgenus *Serviformica* and their superb ability to navigate mazes. In my early field experiments (Reznikova 1975, 1982, see also: 2007a, 2018), ants were presented with round mazes consisting of one to three concentric circles placed one inside the other in such a way that their entrances were on opposite sides, and the inner circle contained food pellets. Although in solitary foraging species (*Formica cunicularia*) nearly all foragers could successfully solve the maze, only 10 percent of the cooperatively foraging ants (*F. pratensis*) successfully navigated mazes. Moreover, in the latter species successful navigation was only observed when these ants had an opportunity to observe *F. cunicularia* ants solving this problem.

Interestingly, *F. cunicularia* takes the second place after the dominant *F. pratensis* in the hierarchical system within inter-species communities in which several other species of the genera *Lasius*, *Myrmica*, *Tetramorium* and *Leptothrax* play roles of "influents" (Reznikova 1980, 1999, 2003). It is worth noting here that inter-specific hierarchy in ant communities was originally described by Kaczmarek (1953) who coined the terms "dominants", "subdominants" and "influents". However, his claims were only based on measurements made by cutting with an entomological net and lacked a rigorous experimental proof. The first experimental demonstration of inter-specific hierarchy was made with the use of baiting observations (Reznikova 1980). Hierarchical structure of ant communities has been later investigated by many myrmecologists (Savolainen and Vepsäläinen 1988; Palmer 2003; Sanders and Gordon 2003, and others). In the steppe ant inter-species communities the subdominant species serves as a scout to the dominant, being much more successful in searching and remembering new ways to find food. Dominant ants use members of the subdominant species as "guides" while searching for prey, stealing their "know-how". At the same time, subdominants scrounge the prey from dominants and use their aphid colonies to obtain honeydew (Reznikova 1982, 2007a).

This phenomenon gives rise to parallels with slavery as one of the forms of social parasitism in ants (review in: Buschinger 2009). In the case of the slave-making or dulotic ants, the young queen has to penetrate a host species nest, eliminate the host colony queen and take over her workers and the brood. They attack independent, neighbouring colonies of the slave species, fight against the defenders, and finally carry back the brood to the slave-maker's nest. Thus, the slave stock may be replenished several times a year (Buschginger 1980). It is known that agile and explorative members of solitary foraging species of the subgenus *Serviformica*, (sensu: Romiguier et al. 2018; but see: Bolton 2016) such as *F. cunicularia*, *F. rufibarbis*, *F. fusca* and *F. lemani* serve as slaves to the dulotic ant *F. sanguinea,* being more successful in out-nest tasks including foraging and scouting (Reznikova 1980; Buschinger 1986; Hölldobler and Wilson 1990; Romiguier et al. 2018). To my mind, this also indicates a deep resemblance between styles of navigation in *Serviformica* and *Cataglyphis*. This hypothesis is based on observations I made in Kazakhstan, where *C. aenescens* served as slaves for *F. sanguinea*. Navigating landscapes much better than *F. sanguinea*, *Cataglyphis* ants played the role of scouts for their "hosts", similarly to the *Serviformica—F. pratensis* species pair (Reznikova 1983). The latter relations could be considered the "light variant" of social parasitism: dominant species do not engage in kidnapping of the subdominant ants but they permanently depend on subdominants to forage successfully.

Still, very little is known about the abilities of ants of the *Serviformica* species to navigate and remember landmarks. Field experiments on *F. japonica*, belonging to the same subgenus *Serviformica*, showed that these ants use the distant skyline and landmark cues for navigation (Fukushi 2001; Fukushi and Wehner 2004). A recent study (Piqueret et al. 2019) on olfactory learning in *F. fusca* showed that they learn very rapidly, their memory lasts up to 3 days, decreases slowly over time and is highly resistant to extinction, even after a single conditioning trial. I suggest that members of the subgenus *Serviformica* are underestimated as a model for studying cognitive aspects of navigation in solitary foraging ants.

To summarise the whole section on spatial cognition in solitary foraging ant species, it is worth noting that across different ants there are more cognitive similarities than differences. Despite the diversity of life histories, all species share such traits as flexible components of orientation, the capacity for learning and encoding landmarks, and the ability to adapt their routes to fluctuations in the distribution of resources. Taking into account the extremely low individual variability of searching skills in Serviformica, I can conclude that relative cognitive equality within a colony is typical for all solitary foraging species, whereas highly cooperative species, such as red wood ants, display dramatic inter-individual differences in their cognitive capacities.

Spatial cognition in red wood ants as a group of highly social species

Red wood ants (*Formica rufa* group) have impressed researchers for more than a century with marvels of engineering, management within their colonies, and the enormous impact on forest ecosystems (Dlussky 1967; Hölldobler and Wilson 1990; Iakovlev et al. 2017). Among many taxonomic groups, red wood ants are possibly the most promising and a surprisingly underestimated group for studying cognitive aspects of navigation and communication. Every day these ants face more complex vital problems than many other species: for example, in order to obtain honeydew, the basic food for adults (review in: Stadler and Dixon 2005), red wood ants have to find and possibly memorise locations of many aphid colonies within a huge three-dimensional space, as a tree is for an ant; in addition, each colony has to find, kill and transport thousands of invertebrates in order to feed larvae (reviews in: Reznikova 2008; Iakovlev et al. 2017). Dobrzanska (1958) demonstrated that in red wood ants, groups of individuals return repeatedly to approximately the same parts of the colony's feeding territory and work together there. Studying site allegiance in the *Formica rufa* group, Rosengren and Fortelius (1986) characterised them as "replete ants" storing not lipids in their fat-bodies but habitat information in their brains.

There is much evidence of extremely long- lasting storage of spatial information in red wood ant foragers, which is based mainly on visually perceived objects (Rosengren 1971, 1977; Fourcassie and Beugnon 1988; Nicholson et al. 1999), although these ants use trail communication as well (Rosengren and Fortelius 1986; Hölldobler and Wilson 1990). It is likely that the visual component involved in site location can be stored in the memory of individual foragers during ever a 6-month hibernation period (Salo and Rosengren 2001).

Laboratory experiments have revealed excellent visual landmark memories in red wood ants (Harris et al. 2005; Fernandes et al. 2015), in contrast to mass recruiting *L. niger* ants, which learn odour associations more rapidly than visual cues (Oberhauser et al. 2019). A detailed analysis of the walking trajectories of the *F. rufa* foragers revealed that, when leaving a newly discovered feeding site, they repeatedly turn back and face the landmarks positioned close to the feeder (Judd and Collett 1998; Nicholson et al. 1999). Similar turn-back-and-look behaviour was first described for honeybees (Becker 1958; Vollbehr 1975; Lehrer 1993), but ants and honeybees move differently when searching for a goal within an array of transformed landmarks (Nicholson et al. 1999). In ants, contrary to flying hymenopterans, body orientation and direction of travel are collinear, so that an ant approaching an object always looks at it with frontal visual field (Durier et al. 2003). *F. rufa* can also acquire landmark information for building their homeward path while running their food-bound path, and this information may be picked up when ants briefly reverse direction and retrace their steps for a short distance (Nicholson et al. 1999; Graham and Collett 2006). When *F. rufa* were trained to walk parallel to an extended landmark (a wall), they maintained a desired distance from the wall by keeping the image of the top of the wall at a particular retinal elevation (Graham and Collett 2002). In general, red wood ants appear to take several snapshots of the visual landmarks from different vantage points.

Experiments in which *F. rufa* were trained in a channel to perform either a single short foraging route or two foraging routes in opposite directions showed that ants remember the length of their route and can link memories of direction and distance (Fernandes et al. 2015). By shifting the starting position of the route within the channel, but keeping the direction and distance fixed, experimenters tried to ensure that the ants would rely upon vector memories rather than visual memories to decide where to stop. The homeward memories that the ants formed were revealed by placing fed or unfed ants directly into a channel and assessing the direction and distance that they walked without the prior performance of the food-ward leg of the journey. This procedure prevented the distance and direction walked being affected by a home vector derived from path integration. Ants that were unfed walked in the feeder direction. Fed ants walked in the opposite direction for a distance related to the separation between the start and the feeder. Vector memories of a return route can thus be primed by the ants' feeding state and expressed even when the ants have not performed the food-ward route (Fernandes et al. 2015).

In general, members of the *Formica rufa* group, although enormously different from solitary foraging species in their foraging style and levels of sociality, have many common traits of individual navigation, such as the primary use of visual navigation, excellent visual landmark memories, and the subordinate role of odour orientation. It is worth noting that all the experiments discussed above concerned red wood ants regardless of their task-group membership. However, in red wood ants navigation and learning dramatically differ among members of different task groups based on cognitive specialisation (Reznikova 2007a, b, 2008; Iakovlev and Reznikova 2019), and scouting behaviour can be considered to be most challenging task in these aspects (Reznikova 2018). In the next section I will consider spatial cognition in members of differed task groups in the context of information transfer.

Spatial cognition in the context of information transfer

Specificity of recruitment to food in red wood ants

As noted above, red wood ants can transfer exact information about remote events from a scouting individual to foragers, without other cues such as a scent trail or direct guiding (Reznikova 2008, 2017). Why should red wood ants use such a sophisticated communication system? Indeed, one can hardly imagine a *Formica* ant running from the borders of a feeding territory toward an anthill like a bee flying into a hive to tell the whereabouts of a food source. Red wood ants forage for food as much as 100 m away from their nests (review in: Véle and Modlinger 2016). This distance is far too great for a scout to walk to the nest and mobilise foragers from there.

For a long time, very little was known about recruitment to a food source in species belonging to the *Formica rufa* group. Rosengren and Fortelius (1987), on the example of *F. truncorum*, described the elementary mode of recruitment where, upon finding food, scouts attracted workers roaming in the vicinity by making alerting movements. This mode of recruitment, called "kinopsis" (Stüger 1931; Dlussky 1967; Reznikova 1982) or "directional recruitment" (Rosengren and Fortelius 1987), is considered a rather primitive mode of communication in ants (Hölldobler and Wilson 1990). In *F. truncorum* a scout also can lay a short pheromone trail to attract foragers (Rosengren and Fortelius 1987).

To elucidate the question about recruitment to food in red wood ants, two issues must be considered: levels of social organisation and cognitive specialisation of individuals. Levels of social organisation in ants serve as an essential factor for determining the choice of foraging strategies connected with colony growth. In *Formica* species the lower level is the use of a feeding territory by a colony inhabiting a single domicile, and on the highest level is the super-colony. A super-colony in *Formica* ants is an association of polygynous colonies inhabiting single nests and connected with food—and brood-exchanging routes (Dlussky 1967; Rosengren 1985; Fortelius et al. 1993; Ellis and Robinson 2014). One of the largest examples of super-colonies in *Formica* is an enormous polydomous population of the Japanese ant *F. yessensis*, which covered an area of 2.7 km^2 and contained an estimated 306 million workers and one million queens (Higashi 1983). A super-colony of *F. lugubris* in Switzerland consisted of about 1200 interconnected nests occupying an area of 70 ha (Cherix 1980). I found a super-colony of polygynous *F. pratensis* with similar forager densities in the vicinity of the southern borders of the geographic area of this species in South Kazakhstan (Reznikova 1983). In the central parts of its area in steppe and forest-steppe zones *F. pratensis* inhabits single nests, and each monogynous colony protects its own territory (Reznikova 1979).

It is of particular interest that *F. pratensis* displays a rather peculiar mode of group-foraging (Reznikova 1979, 1983). Inhabiting a single domicile, a colony uses trench-like foraging routes. Some ants go along these routes towards their individual foraging plots in the foraging territory, whereas others circulate along segments of the route waiting to be mobilised by scouts that have found food sources in the territory. These workers circulating along the routes constitute the "candidate pool" for being called on by scouts. That this communication between scouts and foragers is based on information transmission, has been demonstrated much later in laboratory experiments (Novgorodova 2006). In my early field experiments using manipulation of ant density (Reznikova 1979, 1983, see also: Reznikova 2017), I placed barriers along one of the foraging routes, which forced ants to concentrate within a relatively small territory. In response, ants set up auxiliary stations along the route, resembled polydomy, and they even accepted several fertilised mating queens to these stations. The colony thus changed its status to "temporal polygyny." After that, the ants readily switched their recruitment mode in accordance with their new territorial organisation. Scouts stopped mobilising ants from the route. Instead, upon finding food on foraging plots, scouts attracted workers roaming in the vicinity by "directional recruitment," as described above. Amazingly, this reconfiguration took only several weeks. It is likely that "directional recruitment" in *Formica rufa* group works well when the density of workers on the feeding territory is rather high, and in this situation there is no need for distant homing.

A typical situation in the field in which red wood ants cooperate to perform a specific task and use a contact mode of communication is honeydew collection by foragers in the tree crown. In this case, the task is to find an aphid colony, inform other ants about the new food source and organise honeydew collection and its transportation to the nest. Studies at the individual level reveal deep specialisation, that is, considerable behavioural differences between members within the task group of aphid tenders. This group turned out to include specialised subgroups such as scouts, aphid milkers ('shepherds'), aphid guards, and carriers transporting honeydew to an anthill or the intermediate auxiliary nests (Reznikova and Novgorodova 1998; Reznikova 2007a, b, 2008). A particular aphid tending team (sensu: Reznikova 2007a) includes about ten shepherds, several guards, and one scout. It is rather difficult to observe in nature how a scout attracts its team to a new aphid colony, and we succeeded in doing this only twice. In both cases the scouts found a female aphid that had established a new colony and then by means of distant homing recruited members of their teams who were waiting for them at another branch of the same tree.

Using spatial tasks and information theory for studying the transfer of information about distant targets in ants

Our long-term experimental laboratory studies based on a "binary tree" paradigm model a situation of transferring information about a new aphid colony. These experiments allowed us to evaluate the capabilities of ants' "language" through measuring the rate of information transmission. A "binary tree" is the first experimental paradigm for investigating spatial coding in ants. More precisely, it is used to measure their abilities to share information about the location of distant resources with nestmates. The idea of the experiments is that we know exactly the quantity of information (in bits) to be transferred, and can measure the time that ants spend transferring it. The binary tree maze presents a situation in which, in order to obtain food, ants have to transmit the information about the sequence of turns towards a target. The target is a trough filled with syrup, located on one of the leaves of a binary tree; all the other leaves of the tree contained empty troughs. The leaf with the reward was chosen randomly by tossing a coin for each fork in the path. The simplest design is a tree with one fork and two leaves, that is, a Y-shaped maze (Fig. 1 shows the trees with four forks). It represents one binary choice which corresponds to one bit of information. In this situation, a scouting animal should transmit one bit of information to other individuals: to go to the right (R) or to the left (L). In other experiments the number of forks of the binary tree increased up to six. Since the rewarded leaf on which to put the trough with syrup was chosen uniformly at random, the number of bits necessary to choose the correct way is equal to the number of forks, that is, the number of turns to be taken. Red wood ants were found to be able to transfer exact information about a remote target, to grasp regularities, and to use them to optimise their messages (see: Reznikova and Ryabko 1994, 2000, 2011; Reznikova 2007a, 2008, 2017). Here, in terms of spatial cognition, it means that red wood ants can remember and transfer to their nestmates a sequence of turns

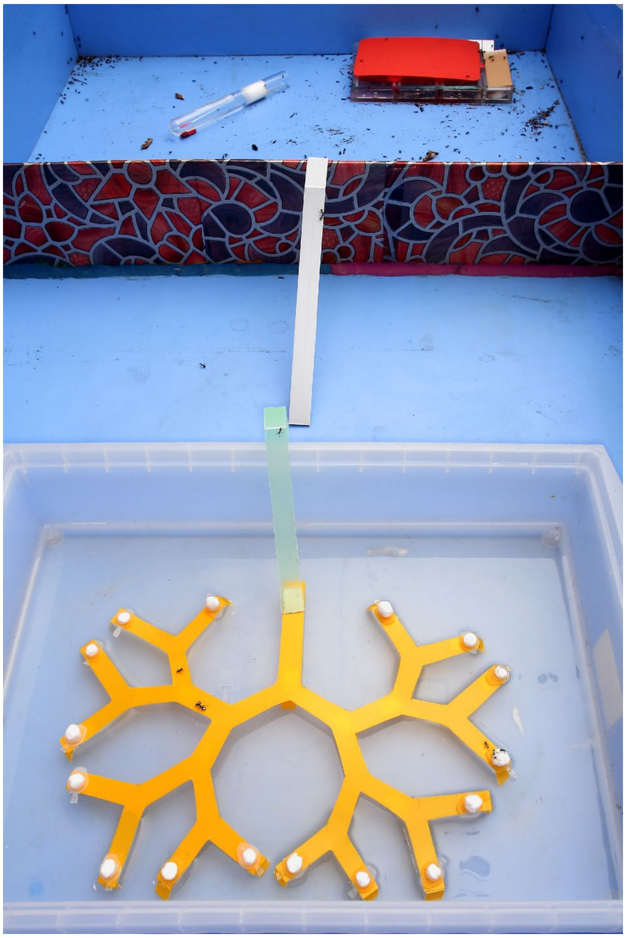

Fig. 1 A laboratory arena divided into two parts, containing an artificial ant nest and a binary tree maze placed in a bath with water. This binary tree has four forks. Photo by Nail Bikbaev

towards a goal. These abilities dramatically differ between scouting individuals and foragers.

In the "binary tree" experiments, hungry ants can locate food on one of several "leaves" in a maze (Fig. 1). The laboratory colonies were found to include teams of constant membership, each of which consisted of one scout and four to eight recruits (foragers): the scout mobilised only members of its own team to the food. The composition of the teams was revealed during special run-up experiments. During the main course of experiments, in each trial, one scout was placed on a certain leaf of the binary tree, with food, and could then return to the foragers waiting on the arena or within the nest. Returning to the group, the scout contacted one to four foragers one by one, or, sometimes, two of them simultaneously. It is worth to note that the scout did not contact any other ants except members of its own group. Contacts were followed by numerous antennal and fore-tarsi movements and touches (supplementary 1). We used the time the scout spent on "informative contacts" as the main measure to study ants' communication means. The contact was considered to begin when the scout touched the first forager ant, and to end when the first two foragers left the nest for the maze. When the scout repeatedly returned to the trough alone (supplementary 2), each of its contacts with foragers was measured. However, only the duration of the contact after which the foragers left the nest was taken into account. These contacts were hypothesised to be "informative" because they preceded the foragers' trip to the maze. Note that only seldom did the "informative" contacts include food exchange ("trophallaxis") as a part.

The experiments were designed to investigate the characteristics of ants' communication of a distant target, so after the scout had contacted members of its team, it was isolated for a while, and the foragers had to search for the food by themselves. All experiments were so devised as to eliminate all possible cues that could help the ants to find the food (including olfactory cues), except for contacts with the scout. To avoid the use of an odour track, the experimental set-up was replaced by an identical one when the scout was in the nest or on the arena contacting its group. All troughs in the fresh maze contained only water to avoid the possible influence of the smell of syrup. If the group reached the correct leaf of the binary tree (supplementary 3), they were immediately presented with the food.

Analysis of empirical data consisted of two parts: (1) evidence of the transfer of information about distant targets in ants and (2) analysis of ants' communication means. The evidence of information transmission from scouts to foragers comes from experiments of two types: first, from the statistical analysis of the number of times the group found the target correctly, and second, from a special series of control experiments with "uninformed" ("naïve") and "informed" foragers. The statistical analysis of the number of times of finding the target correctly was carried out by comparing the hypothesis H_0 (ants find the leaf containing the food by chance) with the hypothesis H_1 (they find the target thanks to the information obtained), proceeding from the fact that the probability of finding the correct way by chance when the number of forks is i is $(1/2)^i$. We analysed series of experiments separately for 2, 3, 4, 5 and 6 forks. The control experiments were organised so as to compare searching results of the ants that had and did not have a previous possibility to contact the scout (the "informed" and "naïve" ants, respectively). The "naïve" and "informed" ants were tested one by one. Each ant was allowed to search for the food for 30 min. In sum, the difference between frequencies of findings of naive and informed ants, as well as the time spent for searching the target by them, were completely different. The obtained data confirm information transmission about the distant goal in red wood ants and exclude any orientation mechanism except the use of information transmitted by the scouts. Similar results were obtained later on *F. pratensis* (Novgorodova 2006).

Analysis of ants' communication involves comparing the duration of "informative" contacts between scouts and foragers when solving different spatial tasks. As already noted, in the binary tree, the number of turns towards a goal (Left, L and Right, R) corresponds to the amount of the information (in bits) to be transferred (in terms of Shannon 1948). It is worth noting that this information theory approach provides a way for studying essential characteristics of animal communication, such as the rate of information transmission (bits per minute) and the potential flexibility of communication systems. Ants appeared to be able not only to memorise and pass to each other up to 6 bits of information but also to grasp regularities in the "text" to be transferred and use these regularities to optimise their messages. The regular sequence (such as LLLLLL) is "simpler" than a random one (say, LLRLR), and the time the ants spent transmitting the information about the sequence of turns (Table 1) appeared to increase with complexity (in terms of Kolmogorov 1965). Statistical analysis of these data were described in detail in: Ryabko and Reznikova 1996, 2009; Reznikova 2007b, 2008, 2017. Note that in cases of "complex" sequences the continuation of "informative contacts", that is, contacts preceding foragers' trip to the maze, can reach up to 200 s. This exceeds many times the average duration of usual contacts between ants, including food exchange (trophallaxis). Contacts of this latter type need to be minimized to make the process of food exchange as fast as possible (Quque et al. 2020). A similar approach of discriminating between two types of contacts ("informative contacts" and "trophallaxis") based on the same "binary tree" paradigm (Frasnelli et al. 2012) provided the first evidence of lateralization in antennal contacts in red wood ants at the population level.

Table 1 Duration of transmitting information on the way to the trough by scouts to foragers (no. 1–8 regular turn pattern; no. 9–15 random turn pattern)

No.	Sequences	Mean duration (s)	SD	Numbers of experiments
1	LL	72	8	18
2	RRR	75	5	15
3	LLLL	84	6	9
4	RRRRR	78	8	10
5	LLLLLL	90	9	8
6	RRRRRR	88	9	5
7	LRLRLR	130	11	4
8	RLRLRL	135	9	8
9	LLR	69	4	12
10	LRLL	100	11	10
11	RLLR	120	9	6
12	RRLRL	150	16	8
13	RLRRRL	180	22	6
14	RRLRRR	220	15	7
15	LRLLRL	200	18	5

It is worth noting that attempts to analyse elements of the so-called "antennal code" (sensu: Wasmann 1899) as the primary means of the "ant language" have been made for a long time (review of the early works in Hölldobler and Wilson 1990). The first attempt to use information theory to evaluate sequences of antennal movements led Lenoir (1982) to conclude that ants do not possess an "antennal language." However, he used records of ants' movements during trophallaxis only, and apparently did not use data that would include informative contacts. More recent studies confirmed that trophallaxis plays an initiating rather than an informational role (Mc Cabe et al. 2006; Mailleux et al. 2011). In our experiments described above, the ideas of information theory were applied purposefully for studying a process of information transfer during the execution of a spatial task and evaluating ants' communicative means quantitatively.

The transfer of information about distant targets seems to be a privilege of leader-scouting ant species that possess highly social and rather specific organisation. A negative result to this effect has been obtained for mass recruiting *Myrmica rubra* (Reznikova and Ryabko 1994; Reznikova 2008, 2017). However, that young *Myrmica rubra* ants gain the experience of antennal communication from adults (Atsarkina et al. 2017) raises the possibility that tactile contacts in mass recruiting species can include informative components. Attempts to check whether *Lasius* species can communicate the location of resources in a maze through tactile communication showed null results (Popp et al. 2018) due to the fact that mass recruiting species, like *Lasius* and *Myrmica*, use pheromone trails as primary means of communication.

The transfer of information about distant targets can be considered in the context of differences in spatial cognition between scouts and recruited foragers. Unlike in honeybees, which do not transfer information only to the members of their own team but rather to any worker that is interested (see details in: Tautz 2008; Seeley 2009), each scouting ant attracts to the feeder only members of its fixed team. The recruited foragers can only memorise and not transfer the information. The composition of the working teams remained constant in each colony from several days to even several weeks, that is, during the whole period when a given scout was actively working (Reznikova 2008). Notably, not all of the scouts managed to memorise the way to the correct leaf of the maze. The number of scouts that succeeded in memorising the way decreased with increasing complexity of the task. In the case of two forks all active scouts and their groups (up to 15 per colony) were successful whereas in the case of six forks, only one or two coped with the task (Reznikova 2008, 2017). This means that spatial cognition dramatically varies between individuals within red wood ants' colonies.

To study the mental states of scouting ants, we designed a battery of behavioural tests examining scouts' levels of aggression (by recording 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), in comparison with members of other task groups such as aphid milkers, guards and foragers (Atsarkina et al. 2014; Reznikova 2018). 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. Of particular interest here is the effect of isolating the scouts from their colonies. Again, in contrast to mass recruiting species in which colonies can easily withstand the removal of highly active individuals (Pinter-Wollman et al. 2012), laboratory colonies of red wood ants fell into collapse in response to the removal of scouting individuals. This removal of the intellectual elite from the ant society resembles the famous philosopher's steamboat, which transported intellectuals expelled from Soviet Russia in 1922.

In sum, unique life-history traits of red wood ants favour particular cognitive specialisations within their colonies. Only scouts (but not foragers) are able to memorize and transfer exact information about a sequence of turns toward a goal, grasp regularities in these sequences and even perform simple arithmetic operations (Reznikova and Ryabko 2011). This cognitive specialisation is possibly 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. Ants' abilities to encode sequences of turns along a binary tree maze can be considered a specific cognitive adaptation closely connected with their searching patterns within the tree crown. These peculiar traits of spatial cognition in red wood ants can give a possible explanation of why *F. rufa* failed to learn a sequence of visual features encountered at different stages along a route (Riabinina et al. 2011), as reported earlier for honeybees (Zhang et al. 1999). Yet there is an open question whether specialized members of a colony, such as scouts and foraging team members possess brains of different size and capacity, and correspondingly have various capabilities of learning.

Conclusion

Ants are good candidates for studying cognitive aspects of navigation, because they are central-place foragers, always returning to a nest, which demands the ability to encode relationships between features in an environment or an individual's path through the landscape. The distribution of these cognitive responsibilities within a colony depends on ants' foraging style. I argue that relative cognitive equality within a colony is typical for all solitary foraging species, whereas cooperatively foraging ants can display essential inter-individual differences in cognitive abilities. Solitary foraging and leader-scouting are the most challenging tasks in the context of ants' spatial cognition requiring exploration, learning, and memory. Solitary foraging was found in species of almost all subfamilies of ants, whereas distant homing based on leader-scouting has been discovered as yet only in the *Formica rufa* group of species (red wood ants). Surprisingly, these two systems, although enormously different in their levels of sociality, have many common traits of individual cognitive navigation, such as the primary use of visual navigation, excellent visual landmark memories, and the subordinate role of odour orientation. However, in contrast to *Cataglyphis*, the model genus for studying cognitive navigation, in which chronological age and physiological development strongly determine their short life outside the nest, red wood ants live long, and workers lack pronounced age polyethism. Numerous experiments on spatial cognition in red wood ants have failed to take into account their task-group membership. However, in the leader-scouting species, spatial cognition and abilities to transfer information about a location dramatically differ among scouts and foragers, suggesting cognitive specialisation. The ability of scouting individuals to encode sequences of turns along the "binary tree" maze and share this information with foragers can be considered a specific cognitive adaptation closely connected with their searching patterns within the tree crown. Still, it is unknown how red wood ants translate the code in their communication into a trip to their destinations. There is much work to be done to understand what cognitive mechanisms underpin route planning and communication about locations in ants. Studying cognitive navigation in the context of information transfer can provide new insights into spatial cognition in social animals.

Acknowledgements I am grateful to Daniil Ryabko for the helpful discussion and useful comments. I appreciate the efforts and valuable comments of the editors and two anonymous reviewers that helped me to improve the manuscript.

Funding This work was funded by Russian Fund for Basic Research (No. 20-04-00072) and by The Federal Fundamental Scientific Research Program for 2013–2021 No. VI.51.1.10. (AAAA-A16-116121410120-0) (Grant No. 0-109-2018-0074).

References

Alma AM, Farji-Brener AG, Elizalde L (2017) A breath of fresh air in foraging theory: the importance of wind for food size selection in a central-place forager. Am Nat 190(3):410–419. https://doi.org/10.5061/dryad.n0g90

Arnan X, Gaucherel C, Andersen AN (2011) Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. Oecologia 166(3):783–794. https://doi.org/10.1007/s00442-011-1919-y

Atsarkina N, Iakovlev I, Reznikova Zh (2014) Individual behavioural features of scouts and recruits in red wood ants (Hymenoptera: Formicidae). Euroas Entomol J 13(3):209–218

Atsarkina NV, Panteleeva SN, Reznikova ZhI (2017) *Myrmica rubra* ants are more communicative when young: do they need experience? J Comp Psychol 131(2):163–173. https://doi.org/10.1037/com0000067

Bailey KH, Polis GA (1987) Optimal and central-place foraging theory applied to a desert harvester ant, *Pogonomyrmex californicus*. Oecologia 72:440–448. https://doi.org/10.1007/BF00377577

Barron AB, Plath JA (2017) The evolution of honey bee dance communication: a mechanistic perspective. J Exp Biol 220(23):4339–4346. https://doi.org/10.1242/jeb.142778

Becker L (1958) Untersuchungen über das Heimfindevermögen der Bienen. Zur Vergleich Physiol 41(1):1–25. https://doi.org/10.1007/BF00340239

Beckers R, Goss S, Deneubourg JL, Pasteels JM (1989) Colony size, communication and ant foraging strategy. Psyche AJ Entomol 96(3–4):239–256. https://doi.org/10.1155/1989/94279

Beugnon G, Chagné P, Dejean A (2001) Colony structure and foraging behavior in the tropical formicine ant, *Gigantiops destructor*. Insect Soc 48(4):347–351. https://doi.org/10.1007/PL00001788

Beugnon G, Lachaud JP, Chagné P (2005) Use of long-term stored vector information in the neotropical ant *Gigantiops destructor*. J Insect Behav 18(3):415–432. https://doi.org/10.1007/s10905-005-3700-8

Bolton B (2016) Bolton world catalog ants. AntWeb: ants of Bolton world catalog. https://www.antweb.org/project.do?name=worldants. Accessed 4 Dec 2019

Bonser ROB, Wright PJ, Bament S, Chukwu UO (1998) Optimal patch use by foraging workers of *Lasius fuliginosus*, L. *niger* and *Myrmica ruginodis*. Ecol Entomol 23(1):15–21. https://doi.org/10.1046/j.1365-2311.1998.00103.x

Brown MJ, Gordon DM (2000) How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. Behav Ecol Sociobiol 47(3):195–203. https://doi.org/10.1007/s002650050011

Buehlmann C, Graham P, Hansson BS, Knaden M (2014) Desert ants locate food by combining high sensitivity to food odors with extensive crosswind runs. Curr Biol 24(9):960–964. https://doi.org/10.1016/j.cub.2014.02.056

Buehlmann C, Fernandes ASD, Graham P (2018) The interaction of path integration and terrestrial visual cues in navigating desert ants: what can we learn from path characteristics? J Exp Biol 221(1):jeb167304. https://doi.org/10.1242/jeb.167304

Buehlmann C, Mangan M, Graham P (2020) Multimodal interactions in insect navigation. Anim Cogn. https://doi.org/10.1007/s10071-020-01383-2

Buschinger A (1986) Evolution of social parasitism in ants. Trend Ecol Evol 1(6):155–160. https://doi.org/10.1016/0169-5347(86)90044-3

Buschinger A (2009) Social parasitism among ants: a review (Hymenoptera: Formicidae). Myrmecol News 12(3):219–235

Chagné P, Beugnon G (2001) Familiar routes and spatial memory in the tropical ant *Gigantiops destructor*. In: Proceedings Meeting European Sections IUSSI. Berlin, p. 63

Charbonneau D, Sasaki T, Dornhaus A (2017) Who needs 'lazy' workers? Inactive workers act as a "reserve" labor force replacing active workers, but inactive workers are not replaced when they are removed. PLoS ONE 12(9):e0184074. https://doi.org/10.1371/journal.pone.0184074

Cheng K (1986) A purely geometric module in the rats spatial representation. Cognition 23(2):149–178. https://doi.org/10.1016/0010-0277(86)90041-7

Cherix D (1980) Note preliminaire sur la structure, la phenologie et le regime alimentaire d'une super-colonie de *Formica lugubris*. Insect Soc 27(3):226–236. https://doi.org/10.1007/BF02223666

Cheung A, Hiby L, Narendra A (2012) Ant navigation: fractional use of the home vector. PLoS ONE 7(11):e50451. https://doi.org/10.1371/journal.pone.0050451

Chittka L (2017) Bee cognition. Curr Biol 27(19):1049–1053. https://doi.org/10.1016/j.cub.2017.08.008

Cerdá X, Angulo E, Boulay R, Lenoir A (2009) Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. Behav Ecol Sociobiol 63(4):51–562. https://doi.org/10.1007/s00265-008-0690-5

Collett M (2012) How navigational guidance systems are combined in a desert ant. Curr Biol 22(10):927–932. https://doi.org/10.1016/j.cub.2012.03.049

Collett M, Collett TS (2009) The learning and maintenance of local vectors in desert ant navigation. J Exp Biol 212(7):895–900. https://doi.org/10.1242/jeb.024521

Collett M, Collett TS, Bisch S, Wehner R (1998) Local and global vectors in desert ant navigation. Nature 394(6690):269–272. https://doi.org/10.1038/28378

Collett M, Collett TS, Chameron S, Wehner R (2003) Do familiar landmarks reset the global path integration system of desert ants? J Exp Biol 206(5):877–882. https://doi.org/10.1242/jeb.00176

Collett TS, Graham P, Harris RA (2007) Novel landmark-guided routes in ants. J Exp Biol 210(12):2025–2032. https://doi.org/10.1242/jeb.000315

Collett M, Chittka L, Collett TS (2013) Spatial memory in insect navigation. Curr Biol 23(17):789–800. https://doi.org/10.1016/j.cub.2013.07.020

Collignon B, Valdivieso LEC, Detrain C (2014) Group recruitment in ants: who is willing to lead? Behav Proc 108:98–104. https://doi.org/10.1016/j.beproc.2014.09.033

Detrain C, Deneubourg JL, Pasteels JM (1999) Information processing in social insects. Birkhäuser, Basel. https://doi.org/10.1007/978-3-0348-8739-7

Dlussky GM (1967) Ants of the genus *Formica* (Hymenoptera, Formicidae). Biology, practical importance and use, keys for the species founded in USSR (in Russian). Nauka, Moscow.

Dobrzanska J (1958) Partition of foraging grounds and modes of conveying information among ants. Acta Biol Exp 18:55–67

Dornhaus A, Holley JA, Pook VG, Worswick G, Franks NR (2008) Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. Behav Ecol Sociobiol 63(1):43–51. https://doi.org/10.1007/s00265-008-0634-0

Durier V, Graham P, Collett TS (2003) Snapshot memories and landmark guidance in wood ants. Curr Biol 13(18):1614–1618. https://doi.org/10.1016/j.cub.2003.08.024

Dyer FC (2002) The biology of the dance language. Annu Rev Entomol 47(1):917–949. https://doi.org/10.1146/annurev.ento.47.091201.145306

Ellis S, Robinson EJH (2014) Polydomy in red wood ants. Insect Soc 61(2):111–122. https://doi.org/10.1007/s00040-013-0337-z

Fernandes ASD, Philippides A, Collett TS, Niven JE (2015) Acquisition and expression of memories of distance and direction in navigating wood ants. J Exp Biol 218(22):3580–3588. https://doi.org/10.1242/jeb.125443

Fleischmann PN, Christian M, Müller VL, Rössler W, Wehner R (2016) Ontogeny of learning walks and the acquisition of landmark information in desert ants, *Cataglyphis fortis*. J Exp Biol 219(19):3137–3145. https://doi.org/10.1242/jeb.140459

Fleischmann PN, Grob R, Müller VL, Wehner R, Rössler W (2018) The geomagnetic field is a compass cue in *Cataglyphis* ant navigation. Curr Biol 28(9):1440–1444. https://doi.org/10.1016/j.cub.2018.03.043

Fortelius W, Rosengren R, Cherix D, Chautems D (1993) Queen recruitment in a highly polygynous supercolony of *Formica lugubris* (Hymenoptera, Formicidae). Oikos 67(2):193–200. https://doi.org/10.2307/3545463

Fourcassie V, Beugnon G (1988) How do red wood ants orient when foraging in a three dimensional system? I Laboratory experiments. Insect Soc 35(1):92–105. https://doi.org/10.1007/BF02224142

Franklin EL, Robinson EJ, Marshall JA, Sendova-Franks AB, Franks NR (2012) Do ants need to be old and experienced to teach? J Exp Biol 215(8):1287–1292. https://doi.org/10.1242/jeb.064618

Frasnelli E, Iakovlev I, Reznikova Z (2012) Asymmetry in antennal contacts during trophallaxis in ants. Behav Br Res 232(1):7–12. https://doi.org/10.1016/j.bbr.2012.03.014

Freas CA, Cheng K (2019) Panorama similarity and navigational knowledge in the nocturnal bull ant *Myrmecia midas*. J Exp Biol 222(11):jeb193201. https://doi.org/10.1242/jeb.193201

Freas CA, Narendra A, Cheng K (2017a) Compass cues used by a nocturnal bull ant, *Myrmecia midas*. J Exp Biol 220(9):1578–1585. https://doi.org/10.1242/jeb.152967

Freas CA, Narendra A, Lemesle C, Cheng K (2017b) Polarized light use in the nocturnal bull ant, *Myrmecia midas*. R Soc Open Sci 4(8):170598. https://doi.org/10.1098/rsos.170598

Freas CA, Schultheiss P (2018) How to navigate in different environments and situations: lessons from ants. Front Psychol 9:841. https://doi.org/10.3389/fpsyg.2018.00841

Fukushi T (2001) Homing in wood ants, *Formica japonica*: use of the skyline panorama. J Exp Biol 204(12):2063–2072

Fukushi T, Wehner R (2004) Navigation in wood ants *Formica japonica*: context dependent use of landmarks. J Exp Biol 207(19):3431–3439. https://doi.org/10.1242/jeb.01159

Geva-Sagiv M, Las L, Yovel Y, Ulanovsky N (2015) Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. Nat Rev Neurosci 16(2):94–108. https://doi.org/10.1038/nrn3888

Gibb H, Andersson J, Johansson T (2016) Foraging loads of red wood ants: *Formica aquilonia* (Hymenoptera: Formicidae) in relation to tree characteristics and stand age. PeerJ 4:e2049. https://doi.org/10.7717/peerj.2049

Giraldeau LA, Kramer DL (1982) The marginal value theorem: a quantitative test using load size variation in a central place forager, the eastern chipmunk, *Tamias striatus*. Anim Behav 30(4):1036–1042. https://doi.org/10.1016/S0003-3472(82)80193-0

Giurfa M (2015) Learning and cognition in insects. Interdiscip Rev Cogn Sci 6(4):383–395. https://doi.org/10.1002/wcs.1348

Graham P, Collett TS (2002) View-based navigation in insects: how wood ants (*Formica rufa* L.) look at and are guided by extended landmarks. J Exp Biol 205(16):2499–2509

Graham P, Collett TS (2006) Bi-directional route learning in wood ants. J Exp Biol 209(18):3677–3684. https://doi.org/10.1242/jeb.02414

Graham P, Mangan M (2015) Insect navigation: do ants live in the now? J Exp Biol 218(6):819–823. https://doi.org/10.1242/jeb.065409

Grob R, Fleischmann PN, Rössler W (2019) Learning to navigate—how desert ants calibrate their compass systems. Neuroforum 25(2):109–120. https://doi.org/10.1515/nf-2018-0011

Gronenberg W, Hölldobler B (1999) Morphologic representation of visual and antennal information in the ant brain. J Comp Neurol 412(2):229–240. https://doi.org/10.1002/(SICI)1096-9861(19990920)412:2<229:AID-CNE4>3.0.CO;2-E

Grüter C, Czaczkes TJ, Ratnieks FL (2011) Decision making in ant foragers (*Lasius niger*) facing conflicting private and social information. Behav Ecol Sociobiol 65(2):141–148. https://doi.org/10.1007/s00265-010-1020-2

Harkness RD, Maroudas NG (1985) Central place foraging by an ant (*Cataglyphis bicolor* Fab.): a model of searching. Anim Behav 33(3):916–928. https://doi.org/10.1016/S0003-3472(85)80026-9

Harris RA, de Ibarra NH, Graham P, Collett TS (2005) Ant navigation: priming of visual route memories. Nature 438(7066):302. https://doi.org/10.1038/438302a

Harrison JF, Fewell JH, Stiller TM, Breed MD (1989) Effects of experience on use of orientation cues in the giant tropical ant. Anim Behav 37(5):869–871. https://doi.org/10.1016/0003-3472(89)90076-6

Heinze J (2008) The demise of the standard ant (Hymenoptera: Formicidae). Myrm News 11:9–20

Heinze S, Narendra A, Cheung A (2018) Principles of insect path integration. Curr Biol 28(17):1043–1058. https://doi.org/10.1016/j.cub.2018.04.058

Higashi S (1983) Polygyny and nuptial flight of *Formica (Formica) yessensis* Forel at Ishikari Coast, Hokkaido, Japan. Insect Soc 30(3):287–297. https://doi.org/10.1007/BF02223986

Hölldobler B (1971) Recruitment behavior in *Camponotus socius* (Hym. Fromicidae). Z Vergl Physiol 75(2):123–142. https://doi.org/10.1007/BF00335259

Hölldobler B, Wilson EO (1990) The ants. Springer-Verlag, Berlin Heidelberg, Cambridge. https://doi.org/10.1046/j.1420-9101.1992.5010169.x

Iakovlev I, Reznikova Z (2019) Red wood ants display natural aversive learning differently depending on their task specialization. Front Psychol 10:710. https://doi.org/10.3389/fpsyg.2019.00710

Iakovlev IK, Novgorodova TA, Tiunov AV, Reznikova ZI (2017) Trophic position and seasonal changes in the diet of the red wood ant *Formica aquilonia* as indicated by stable isotope analysis. Ecol Entomol 42(3):263–272. https://doi.org/10.1111/een.12384

Jackson DE, Ratnieks FL (2006) Communication in ants. Curr Biol 16(15):570–574. https://doi.org/10.1016/j.cub.2006.07.015

Jayatilaka P, Murray T, Narendra A, Zeil J (2018) The choreography of learning walks in the Australian jack jumper ant *Myrmecia croslandi*. J Exp Biol 221(20):1jeb85306. https://doi.org/10.1242/jeb.185306

Judd SPD, Collett TS (1998) Multiple stored views and landmark guidance in ants. Nature 392(6677):710–714. https://doi.org/10.1038/33681

Kacelnik A, Houston AI, Schmid-Hempel P (1986) Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. Behav Ecol Sociobiol 19(1):19–24. https://doi.org/10.1007/BF00303838

Kaczmarek W (1953) Badania nad zespołami mrówek leśnych. Ekol Polska 1(2):69–96

Kaspari M (1991) Central place foraging in grasshopper sparrows: opportunism or optimal foraging in a variable environment? Oikos 60(3):307–312. https://doi.org/10.2307/3545072

Knaden M, Graham P (2016) The sensory ecology of ant navigation: from natural environments to neural mechanisms. Annu Rev Entomol 61:63–76. https://doi.org/10.1146/annurev-ento-010715-023703

Knaden M, Wehner R (2005) Nest mark orientation in desert ants *Cataglyphis*: what does it do to the path integrator? Anim Behav 70(6):1349–1354. https://doi.org/10.1016/j.anbehav.2005.03.030

Kohler M, Wehner R (2005) Idiosyncratic route-based memories in desert ants, *Melophorus bagoti*: how do they interact with path-integration vectors? Neurobiol Learn Mem 83(1):1–12. https://doi.org/10.1016/j.nlm.2004.05.011

Kolmogorov AN (1965) Three approaches to the quantitative definition of information. Probl Inf Transm 1(1):3–11

Lanan M (2014) Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). Myrm News 20:53–70

Landgraf T, Rojas R, Nguyen H, Kriegel F, Stettin K (2011) Analysis of the waggle dance motion of honeybees for the design of a biomimetic honeybee robot. PLoS ONE 6(8):e21354. https://doi.org/10.1371/journal.pone.0021354

Leonhardt SD, Menzel F, Nehring V, Schmitt T (2016) Ecology and evolution of communication in social insects. Cell 164(6):1277–1287. https://doi.org/10.1016/j.cell.2016.01.035

Lehrer M (1993) Why do bees turn back and look? J Comp Physiol A 172(5):549–563. https://doi.org/10.1007/BF00213678

Lenoir A (1982) An informational analysis of antennal communication during trophallaxis in the ant *Myrmica rubra* L. Behav Proc 7:27–35

Lima LD, Antonialli-Junior WF (2013) Foraging strategies of the ant *Ectatomma vizottoi* (Hymenoptera, Formicidae). Rev Bras Entomol 57(4):392–396. https://doi.org/10.1590/S0085-56262013005000038

Macquart D, Garnier L, Combe M, Beugnon G (2006) Ant navigation en route to the goal: signature routes facilitate way-finding of *Gigantiops destructor*. J Comp Physiol A 192(3):221–234. https://doi.org/10.1007/s00359-005-0064-7

Mailleux AC, Buffin A, Detrain C, Deneubourg JL (2011) Recruitment in starved nests: the role of direct and indirect interactions between scouts and nestmates in the ant *Lasius niger*. Insect Soc 58(4):559–567. https://doi.org/10.1007/s00040-011-0177-7

Mangan M, Webb B (2012) Spontaneous formation of multiple routes in individual desert ants (*Cataglyphis velox*). Behav Ecol 23(5):944–954. https://doi.org/10.1093/beheco/ars051

Mc Cabe S, Farina WM, Josens RB (2006) Antennation of nectar-receivers encodes colony needs and food-source profitability in the ant *Camponotus mus*. Insect Soc 53(3):356–361. https://doi.org/10.1007/s00040-006-0881-x

Mellgren RL, Misasi L, Brown SW (1984) Optimal foraging theory: prey density and travel requirements in *Rattus norvegicus*. J Comp Psychol 98(2):142–215. https://doi.org/10.1037/0735-7036.98.2.142

Menzel EW (1973) Chimpanzee spatial memory organization. Science 182(4115):943–945. https://doi.org/10.1126/science.182.4115.943

Menzel CR, Savage-Rumbaugh ES, Menzel EW (2002) Bonobo (*Pan paniscus*) spatial memory and communication in a 20-hectare forest. Int J Primatol 23(3):601–619. https://doi.org/10.1023/A:1014925802015

Mercier JL, Lenoir A (1999) Individual flexibility and choice of foraging strategy in *Polyrhachis laboriosa* F. Smith (Hymenoptera, Formicidae). Insect Soc 46(3):267–272. https://doi.org/10.1007/s000400050145

Merkle T, Wehner R (2009) Repeated training does not improve the path integrator in desert ants. Behav Ecol Sociobiol 63(3):391–402. https://doi.org/10.1007/s00265-008-0673-6

Michelsen A, Andersen BB, Storm J, Kirchner WH, Lindauer M (1992) How honeybees perceive communication dances, studied by means of a mechanical model. Behav Ecol Sociobiol 30(3–4):143–150. https://doi.org/10.1007/BF00166696

Müller M, Wehner R (2010) Path integration provides a scaffold for landmark learning in desert ants. Curr Biol 20(15):1368–1371. https://doi.org/10.1016/j.cub.2010.06.035

Narendra A, Ramirez-Esquivel F (2017) Subtle changes in the landmark panorama disrupt visual navigation in a nocturnal bull ant. Philos Trans R Soc Lond B Biol Sci 372(1717):20160068. https://doi.org/10.1098/rstb.2016.0068

Narendra A, Si A, Sulikowski D, Cheng K (2007) Learning, retention and coding of nest-associated visual cues by the Australian desert ant, *Melophorus bagoti*. Behav Ecol Sociobiol 61(10):1543–1553. https://doi.org/10.1007/s00265-007-0386-2

Narendra A, Reid SF, Raderschall CA (2013a) Navigational efficiency of nocturnal *Myrmecia* ants suffers at low light levels. PLoS ONE 8(3):e58801. https://doi.org/10.1371/journal.pone.0058801

Narendra A, Gourmaud S, Zeil J (2013b) Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. Proc Biol Sci 280(1765):20130683. https://doi.org/10.1098/rspb.2013.0683

Nicholson DJ, Judd SP, Cartwright BA, Collett TS (1999) Learning walks and landmark guidance in wood ants (*Formica rufa*). J Exp Biol 202(13):1831–1838

Novgorodova TA (2006) Experimental investigation of information transmission in *Formica pratensis* (Hymenoptera, Formicidae) using "binary tree" maze. Entomol Rev 86(3):287–293. https://doi.org/10.1134/S0013873806030043

Oberhauser FB, Schlemm A, Wendt S, Czaczkes TJ (2019) Private information conflict: *Lasius niger* ants prefer olfactory cues to route memory. Anim Cogn 22(3):355–364. https://doi.org/10.1007/s10071-019-01248-3

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell DR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, pp 155–177

Palmer TM (2003) Spatial habitat heterogeneity influences competition and coexistence in an African acacia ant guild. Ecology 84(11):2843–2855. https://doi.org/10.1890/02-0528

Pasquier G, Grüter C (2016) Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant. Behav Ecol 27(6):1702–1709. https://doi.org/10.1093/beheco/arw079

Pinter-Wollman N, Hubler J, Holley JA, Franks NR, Dornhaus A (2012) How is activity distributed among and within tasks in *Temnothorax* ants? Behav Ecol Sociobiol 66(10):1407–1420. https://doi.org/10.1007/s00265-012-1396-2

Piqueret B, Sandoz JC, d'Ettorre P (2019) Ants learn fast and do not forget: associative olfactory learning, memory and extinction in *Formica fusca*. R Soc Open Sci 6(6):190778. https://doi.org/10.1098/rsos.190778

Pfeffer SE, Bolek S, Wolf H, Wittlinger M (2015) Nest and food search behaviour in desert ants, cataglyphis: a critical comparison. Anim Cogn 18(4):885–894. https://doi.org/10.1007/s10071-015-0858-0

Popp S, Buckham-Bonnett P, Evison SE, Robinson EJH, Czaczkes TJ (2018) No evidence for tactile communication of direction in foraging Lasius ants. Insect Soc 65(1):37–46. https://doi.org/10.1007/s00040-017-0583-6

Quque M, Bles O, Bénard A, Héraud A et al (2020) Hierarchical networks of food exchange in the black garden ant *Lasius niger*. Insect Sci. https://doi.org/10.1111/1744-7917.12792

Reeves DD, Moreau CS (2019) The evolution of foraging behavior in ants (Hymenoptera: Formicidae). Arthropod Syst Phylo 77(2):351–363. https://doi.org/10.26049/ASP77-2-2019-10

Reid SF, Narendra A, Hemmi JM, Zeil J (2011) Polarised skylight and the landmark panorama provide night active bull ants with compass information during route following. J Exp Biol 214:363–370. https://doi.org/10.1242/jeb.049338

Reznikova Z (1975) Non-antagonistic relationships of ants occupying similar ecological niches. Zoologicheskii Zhurnal 54(7):1020–1031 **(in Russian with English summary)**

Reznikova Z (1979) Different forms of territoriality in ants Formica pratensis Retz. Zoologicheskii Zhurnal 58:1490–1499 **(in Russian with English summary)**

Reznikova Z (1980) Interspecies hierarchy in ants. Zoologicheskii Zhurnal 59:1168–1176 **(in Russian with English summary)**

Reznikova J(Z) (1982) Interspecific communication among ants. Behaviour 80(1–2):84–95. https://doi.org/10.1163/156853982X00454

Reznikova Z (1983) Interspecies relations in ants (in Russian). Nauka, Novosibirsk

Reznikova Z (1999) Ethological mechanisms of population density control in coadaptive complexes of ants. Russ J Ecol 30(3):187–192

Reznikova Z (2003) A new form of interspecies relations in ants: hypothesis of interspecies social control. Zoologicheskii Zhurnal 82:816–824 **(in Russian with English summary)**

Reznikova Z (2007a) Animal intelligence: from individual to social cognition. Cambridge University Press, Cambridge. https://doi.org/10.1016/j.intell.2009.04.004

Reznikova Z (2007b) Dialog with black box: using Information Theory to study animal language behaviour. Acta Ethol 10(1):1–12. https://doi.org/10.1007/s10211-007-0026-x

Reznikova Z (2008) Experimental paradigms for studying cognition and communication in ants (Hymenoptera: Formicidae). Myrm News 11:201–214

Reznikova Z (2017) Studying animal language without translation: an insight from ants. Springer Nature, Cham. https://doi.org/10.1007/978-3-319-44918-0

Reznikova Z (2018) Ants. Individual and social cognition. In: Bueno-Guerra N, Amici F (eds) Field and laboratory methods in animal cognition: a comparative guide. Cambridge University Press, Cambridge, pp 8–30. https://doi.org/10.1017/9781108333191.003

Reznikova Z, Ryabko B (1994) Experimental study of the ants communication system with the application of the Information Theory approach. Mem Zool 48:219–236

Reznikova Z, Novgorodova T (1998) The importance of individual and social experience for interaction between ants and symbiotic aphids. Dokl Biol Sci 359(1):173–175

Reznikova Z, Ryabko B (2000) Using Information Theory approach to study the communication system and numerical competence in ants. In: Meyer JA, Berthoz A, Floreano D, Roitblat H, Wilson SW (eds) From animals to animats 6: Proceeding of the sixth international conference on simulation of adaptive behaviour. The MIT Press, Cambridge (MA), pp 501–506

Reznikova Z, Ryabko B (2011) Numerical competence in animals, with an insight from ants. Behaviour 148(4):405–434. https://doi.org/10.1163/000579511X568562

Riabinina O, de Ibarra NH, Howard L, Collett TS (2011) Do wood ants learn sequences of visual stimuli? J Exp Biol 214(16):2739–2748. https://doi.org/10.1242/jeb.058537

Riley JR, Greggers U, Smith AD, Reynolds DR, Menzel R (2005) The flight paths of honeybees recruited by the waggle dance. Nature 435(7039):205–207. https://doi.org/10.1038/nature03526

Roces F (1990) Leaf-cutting ants cut fragment sizes in relation to the distance from the nest. Anim Behav 40(6):1181–1183. https://doi.org/10.1016/S0003-3472(05)80185-X

Romiguier J, Rolland J, Morandin C, Keller L (2018) Phylogenomics of palearctic *Formica* species suggests a single origin of temporary parasitism and gives insights to the evolutionary pathway toward slave-making behaviour. BMC Evol Biol 18(1):40. https://doi.org/10.1186/s12862-018-1159-4

Ronacher B (2008) Path integration as the basic navigation mechanism of the desert ant *Cataglyphis fortis* (Forel, 1902) (Hymenoptera: Formicidae). Myrm News 11:53–62

Rosengren R (1971) Route fidelity, visual memory and recruitment behaviour in foraging wood ants of genus *Formica* (Hymenoptera, Formicidae). Acta Zool Fenn 133:1–106

Rosengren R (1977) Foraging strategy of wood ants (*Formica rufa* group) I. Age polyethism and topographic traditions. Acta Zool Fenn 149:2–30

Rosengren R (1985) Internest relations in polydomous *Formica* colonies (Hymenoptera, Formicidae). Mitteilungen der deutschen Gesellschaft für allgemeine und angewandte Entomologie 4:288–291

Rosengren R, Fortelius W (1986) Ortstreue in foraging ants of the Formica rufa group—-hierarchy of orienting cues and long-term memory. Insect Soc 33(3):306–337. https://doi.org/10.1007/BF02224248

Rosengren R, Fortelius W (1987) Trail communication and directional recruitment to food in red wood ants (*Formica*). Annales Zoologici Fennici. University of Helsinki, Helsinki pp 137–146.

Rössler W (2019) Neuroplasticity in desert ants (Hymenoptera: Formicidae)—importance for the ontogeny of navigation. Myrm News 29:1–20

Ryabko B, Reznikova Z (1996) Using Shannon Entropy and Kolmogorov complexity to study the communicative system and cognitive capacities in ants. Complexity 2(2):37–42

Ryabko B, Reznikova Z (2009) The use of ideas of information theory for studying "language" and intelligence in ants. Entropy 11(4):836–853. https://doi.org/10.3390/e11040836

Saar M, Gilad T, Kilon-Kallner T, Rosenfeld A, Subach A, Scharf I (2017) The interplay between maze complexity, colony size, learning and memory in ants while solving a maze: a test at the colony level. PLoS ONE 12(8):e0183753. https://doi.org/10.1371/journal.pone.0183753

Salo O, Rosengren R (2001) Memory of location and site recognition in the ant *Formica uralensis* (Hymenoptera: Formicidae). Ethology 107(8):737–752. https://doi.org/10.1046/j.1439-0310.2001.00702.x

Sanders NJ, Gordon DM (2003) Resource dependent interactions and the organization of desert ant communities. Ecology 84(4):1024–1031. https://doi.org/10.1890/0012-9658(2003)084[1024:RIATOO]2.0.CO;2

Santschi F (1913) Comment s'orientent les fourmis. Rev Suisse Zool 21:347–425

Savolainen R, Vepsäläinen K (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51(2):135–155. https://doi.org/10.2307/3565636

Schatz B, Lachaud JP, Beugnon G (1997) Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*. Behav Ecol Sociobiol 40(6):337–349. https://doi.org/10.1007/s002650050350

Schmid-Hempel P (1984) Individually different foraging methods in the desert ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). Behav Ecol Sociobiol 14(4):263–271. https://doi.org/10.1007/BF00299497

Schneirla TC (1933) Motivation and efficiency in ant learning. J Comp Psychol 15(2):243–266. https://doi.org/10.1037/h0072289

Schultheiss P, Raderschall CA, Narendra A (2015) Follower ants in a tandem pair are not always naïve. Sci Rep 5:10747. https://doi.org/10.1038/srep10747

Schwarz S, Mangan M, Zeil J, Webb B, Wystrach A (2017) How ants use vision when homing backward. Curr Biol 27(3):401–407. https://doi.org/10.1016/j.cub.2016.12.019

Seeley TD (2009) The wisdom of the hive: the social physiology of honey bee colonies. Harvard University Press, Cambridge (MA)

Shannon CE (1948) A mathematical theory of communication. Bell Sys Tech J 27(3):379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Stadler B, Dixon AF (2005) Ecology and evolution of aphid–ant interactions. Annu Rev Ecol Evol Syst 36:345–372. https://doi.org/10.1146/annurev.ecolsys.36.091704.175531

Steck K, Knaden M, Hansson BS (2010) Do desert ants smell the scenery in stereo? Anim Behav 79(4):939–945. https://doi.org/10.1016/j.anbehav.2010.01.011

Stüger R (1931) Uber das Mitteilungsvermgen der Waldameise beim Auffinden und Transport eines Beutesttickes. Z Wiss Ins 26:125–137

Stürzl W, Mair E, Grixa I, Narendra A, Zeil J (2015) Three-dimensional models of natural environments and the mapping of navigational information. J Comp Physiol A 201(6):563–584. https://doi.org/10.1007/s00359-015-1002-y

Tautz J (2008) The buzz about bees: biology of a superorganism. Springer-Verlag, Berlin. https://doi.org/10.1007/978-3-540-78729-7

Tinbergen N, Kruyt W (1938) On the orientation of the digger wasp, philanthus triangulum fabr, III. Selective learning of landmarks. The animal in its world. Harvard University Press, Cambridge, pp 146–196

Véle A, Modlinger R (2016) Foraging strategy and food preference of *Formica polyctena* ants in different habitats and possibilities for their use in forest protection. Lesn Cas For J 62(4):223–228. https://doi.org/10.1515/forj-2016-0026

Vollbehr J (1975) Zur Orientierung junger Honigbienen bei ihrem I. Orientierungsflug Zool Jb Physiol 79(1–2):33–69

von Frisch K (1923) Über die Spräche der Bienen. Zool Jahrb Abt allg Zool Physiol Tiere 40:1–119

von Frisch K (1967) The dance language and orientation of bees. Harvard University Press, Cambridge

Wasmann E (1899) Die psychischen Fähigkeiten der Ameisen. Zoologica 26(2):1–133

Wehner R (2003) Desert ant navigation: how miniature brains solve complex tasks. J Comp Physiol A 189(8):579–588. https://doi.org/10.1007/s00359-003-0431-1

Wehner R (2009) The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae). MyrmNews 12:85–96

Wehner R, Srinivasan MV (2003) Path integration in insects. In: Jeffery KJ (ed) The neurobiology of spatial behaviour. Oxford University Press, Oxford, pp 9–30. https://doi.org/10.1093/acprof:oso/9780198515241.003.0001

Wehner R, Rössler W (2013) Bounded plasticity in the desert ant's navigational tool kit. In: Menzel R, Benjamin (eds) Handbook of behavioral neuroscience invertebrate learning and memory, Elsevier, Amsterdam, pp 514–529

Wehner R, Michel B, Antonsen P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. J Exp Biol 199(1):129–140

Wehner R, Meier C, Zollikofer C (2004) The ontogeny of foraging behaviour in desert ants, *Cataglyphis bicolor*. Ecol Entomol 29(2):240–250. https://doi.org/10.1111/j.0307-6946.2004.00591.x

Wehner R, Boyer M, Loertscher F, Sommer S, Menzi U (2006) Ant navigation: one-way routes rather than maps. Curr Biol 16(1):75–79. https://doi.org/10.1016/j.cub.2005.11.035

Wehner R, Cheng K, Cruse H (2014) Visual navigation strategies in insects: Lessons from desert ants. In: Werner JS, Chalupa LM (eds) The new visual neurosciences. MIT Press, Cambridge, pp 1153–1163

Wilson EO (1959) Communication by tandem running in the ant genus *Cardiocondyla*. Psyche 66(3):29–34. https://doi.org/10.1155/1959/29093

Wolf H, Wehner R (2000) Pinpointing food sources: olfactory and anemotactic orientation in desert ants, *Cataglyphis fortis*. J Exp Biol 203(5):857–868

Wolf H, Wittlinger M, Pfeffer SE (2018) Two distance memories in desert ants—modes of interaction. PLoS ONE 13(10):e0204664. https://doi.org/10.1371/journal.pone.0204664

Wright PJ, Bonser R, Chukwu UO (2000) The size-distance relationship in the wood ant *Formica rufa*. Ecol Entomol 25(2):226–233. https://doi.org/10.1046/j.1365-2311.2000.00253.x

Wystrach A, Graham P (2012) What can we learn from studies of insect navigation? Anim Behav 84(1):13–20. https://doi.org/10.1016/j.anbehav.2012.04.017

Wystrach A, Cheng K, Sosa S, Beugnon G (2011) Geometry, features, and panoramic views: ants in rectangular arenas. J Exp Psychol 37(4):420–435. https://doi.org/10.1037/a0023886

Wystrach A, Beugnon G, Cheng K (2012) Ants might use different view-matching strategies on and off the route. J Exp Biol 215(1):44–55. https://doi.org/10.1242/jeb.059584

Zeil J, Fleischmann PN (2019) The learning walks of ants (Hymenoptera: Formicidae). Myrm News 29:93–110. https://doi.org/10.25849/myrmecol.news_029:093

Zeil J, Hofmann MI, Chahl JS (2003) Catchment areas of panoramic snapshots in outdoor scenes. J Opt Soc Am A 20(3):450–469. https://doi.org/10.1364/josaa.20.000450

Zhang SW, Lehrer M, Srinivasan MV (1999) Honeybee memory: navigation by associative grouping and recall of visual stimuli. Neurobiol Learn Mem 72(3):180–201. https://doi.org/10.1006/nlme.1998.3901

Ziegler PE, Wehner R (1997) Time-courses of memory decay in vector-based and landmark-based systems of navigation in desert ants, *Cataglyphis fortis*. J Comp Physiol 181(1):13–20. https://doi.org/10.1007/s003590050088