Searching behavior in social Hymenoptera

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ABSTRACT

The movement pattern of a searching animal affects how it interacts with the environment, thus playing an important role in many environmental processes. Social hymenopteran foragers make good models for studying search patterns because their only role is to search for food and bring it back to the nest or hive. Search patterns in ants and bees, the most studied social hymenopterans, consist of loops around the origin of search that expand in size as the search goes on. Different factors influence search structure, including the type and distribution of the resource that is targeted, and the kind and amount of information available for navigation. In the distributions of the lengths of search segments, bees exhibit a Lévy walk pattern, which follows a power law in which occasional long segments are interspersed within many short segments, and yet longer segments are interspersed within the long segments. Such a scale-free and heavy-tailed distribution has been shown to be optimal in searching for sparse targets. Ants on the other hand show a composite Brownian search distribution, composed of two exponential distributions at different scales. We argue that such composite Brownian searches serve to approximate a Lévy walk. Both Lévy walks and composite Brownian searches are found in a range of other animals, including hunter–gatherer humans. These patterns may be ancient, as they have been found in fossils dating to at least 50 million years.

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Searching behavior plays a central part in the everyday lives of almost all animals. It is displayed whenever an animal needs to locate specific resources, such as food, mates, nesting sites or hosts (Bell, 1991). While these resources provide clear benefits for an individual's survival and reproduction, there are also costs attached to searching behavior (Pyke, 1984). Not only does a searching animal have to invest time and energy, but it may also be exposed to predation or other threats. Natural selection should therefore favor efficient search strategies that minimize the amount of time and energy invested, and maximize the encounter rate with the resource in question (Stephens & Krebs, 1986; Ydenberg, 1998). Three main factors play a role in shaping the structure of searching behavior: (1) physiological or anatomical constraints of the animal, (2) external environmental factors such as resource availability and distribution or the risks involved, and (3) internal factors such as motivation, experience and reproductive state (Bell, 1990). The complex interplay of these different factors can be difficult to disentangle. For example, a searching animal may simultaneously be looking for food resources and mates; or its searching behavior may change over time as a result of changes in resource distribution, or as a result of changes in the level of motivation.

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In many regards, social insects such as ants, bees and wasps constitute a particularly useful system for the study of searching behavior. Due to their eusocial organization, some of the factors outlined above do not always apply or can be readily controlled for in experiments. By definition, social insects live in colonies, often located at the same place for a number of years (Wilson, 1971). These colonies are organized into castes (behavioral or morphological) that practice a division of labor. Female reproduction is limited to the queen (or in some cases queens) of the colony, while the entire female worker caste remains sterile throughout their lives. All duties outside of the nest are performed by workers, with foraging duties usually relegated to a separate group of 'foragers' that perform no other tasks. These foragers collect not only food for their own purposes, but also food for the entire colony. This food is either carried back to the nest or collected in a separate 'social stomach', from which it is shared with other colony members by trophallaxis. This specialized force of female, sterile workers thus always forages in the same general area and often returns to the colony or nest. They are singularly motivated to search for food on outbound foraging journeys and to search for the nest at the end of the inbound journey, without being 'distracted' by their own reproductive interests. In addition, foragers are the colony members who have to interact most with the external environment, find their way around, locate food items, and find the nest again. For these reasons, much of the research on the searching behavior of social insects has focused on the behavior of foraging workers.

The searching behavior of social insects is shaped by this central-place foraging lifestyle. As the foragers need to return to the colony at the end of their foraging trips, they have become expert at pinpointing the nest entrance. In close vicinity of the nest, the forager restricts her search to a small area, which is therefore searched intensively. This is achieved by systematically looping back to the assumed nest location (Wehner & Srinivasan, 1981). The same search pattern can also be used in a foraging context, when attempting to locate a previously visited food location (Wolf, Wittlinger, & Bolek, 2012). If the forager does not know the exact location in space, such as when looking for distributed food items, it will engage in a more freely ranging search, in order to encounter one or more of these resource items. We will deal with these two types of search, the focused systematic search and the exploratory search, in turn.

In the final section, we will then investigate the efficiency of searching behavior in social hymenopterans, and in other animals. Depending on the context of the search, certain movement strategies are predicted to lead the searching animal to the goal faster than other strategies, and thus be more efficient. Common movement strategies of animals are the Brownian walk, where the distances traveled between consecutive significant turns are exponentially or Gaussian distributed, and Lévy walks, where the distances traversed between significant turns come from distributions with power-law tails. Lévy walks, named after the French mathematician Paul Lévy, arose in a purely mathematical context in the first half of the last century (Lévy, 1937). They first entered the biological literature when Shlesinger and Klafter (1986) proposed that they can be observed in the movement patterns of foraging ants, and in subsequent biological and ecological literature are often called Lévy flights. Shlesinger and Klafter (1986) recognized that Lévy walks can be advantageous when searching for sparsely distributed resources and this has given rise to the 'Lévy flight foraging hypothesis' which states that since Lévy flights can optimize search efficiencies, natural selection should have led to adaptations for Lévy flight foraging (Viswanathan, Raposo, & da Luz, 2008). Brownian walks and Lévy walks can be equally effective when resources are abundant (Viswanathan et al., 1999). This may explain why, for example, some marine predators (sharks, tuna, billfish and ocean sunfish) switch between Lévy and Brownian movement as they traverse different habitat types with Lévy movements being prevalent in less productive waters and Brownian movements being associated with productive shelf and convergence-front habitats in the oceans (Humphries et al., 2010). The Lévy flight foraging hypothesis is now amply supported by a plethora of empirical observations (Harris et al., 2012; Hays et al., 2012; Humphries, Weimerskirch, Sims, & Freckleton, 2013; Korobkova, Emonet, Vilar, Shimizu, & Cluzel, 2004; Osborne et al., 2013; Raichlen et al., 2014; Reynolds, Smith, Menzel, et al., 2007; Reynolds, Smith, Reynolds, Carreck, & Osborne, 2007; Sims et al., 2008, 2014), but, until our studies (Reynolds, Schultheiss, & Cheng 2014; Schultheiss & Cheng, 2011, 2013; Schultheiss, Wystrach, Legge, & Cheng, 2013), whether ants exhibit Lévy walks had not been determined, although it had been suggested years ago by Shlesinger and Klafter (1986).

Systematic search as a navigational back-up mechanism

Navigation is of utmost importance for central-place foragers like social hymenopterans, as they have to find the way back to the nest at the end of every journey, even the very first one. The main sensory modalities employed in navigation in these insects are vision and olfaction. In social insects, particularly in ants, olfaction is often used for the communication of information between individuals, such as in nestmate recognition and pheromone trails (Hölldobler, 1984). However, the use of olfactory cues in navigation has not been well studied in social insects (but see Steck, Hansson, & Knaden, 2009, 2011), and here we will limit ourselves to visual navigation. Visual cues for navigation fall into two broad categories: celestial cues and terrestrial cues (Cheng, 2006). Celestial cues such as the position of the sun or the pattern of polarized light in the sky are very distant, and do not appear to change as the animal moves around. Due to this apparent immutability over short time periods, such cues are only useful for compass orientation. Several species of bees and ants are able to re-locate specific locations in space by combining this celestial compass with an odometer mechanism in a process called path integration (Wehner & Srinivasan, 2003). In flying honeybees, this odometer relies primarily on the perceived optic flow across the eyes (Srinivasan, Zhang, & Bidwell, 1997), while in walking ants the odometer consists primarily of a step-counting mechanism (Wittlinger, Wehner, & Wolf, 2006, 2007). At any point during its journey, the forager is able to integrate all the different directions and distances it has moved and 'compute' a straight-line vector back to its origin, often the nest entrance (Wehner & Srinivasan, 2003). Path integration can be performed on the very first foraging run, and does not improve with experience
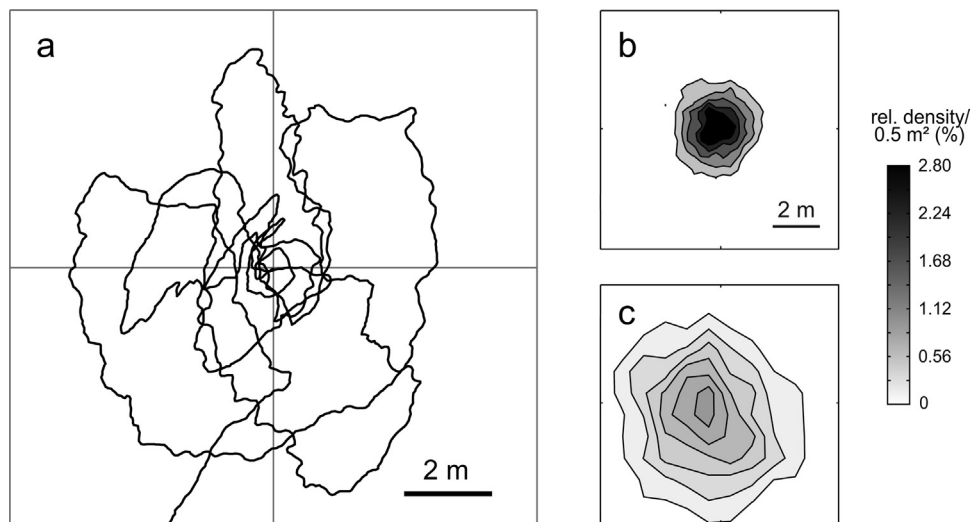
Fig. 1. Systematic search of the Australian desert ant *Melophorus bagoti*. The nest entrance is located at the center of each panel. (a) Example path of an ant searching for the nest entrance. (b and c) Search density plots showing the expansion of the systematic search over time. Panel b shows the search density of the first 20 m of search path, panel c shows the density of the next 20 m of path (*n* = 83 ants). Panel a is modified from Cheng (2012), panels b and c are modified and reprinted from *Animal Behaviour*, 81, Patrick Schultheiss and Ken Cheng, Finding the nest: inbound searching behaviour in the Australian desert ant, *Melophorus bagoti*, pp. 1031–1038, copyright 2011, with permission from Elsevier.

(Merkle & Wehner, 2009; Narendra, Cheng, & Wehner, 2007). In addition, many bees, wasps and some ants are able to use terrestrial visual features such as trees, bushes or buildings for navigation (Collett, 1992). The shape and arrangement of these features change in a predictable fashion as the animal moves among them, such that each position in space is characterized by a specific arrangement of visual landmarks. With experience, foragers can learn to navigate using these visual cues, and often develop habitual routes (Kohler & Wehner, 2005; Mangan & Webb, 2012; Wehner, Michel, & Antonsen, 1996).

While these processes enable a forager to navigate toward specific locations in space, they are far from fail-safe. Even small errors in path integration will accumulate over the distance that is integrated, and terrestrial visual navigation also has its limitation when attempting to pinpoint a small target like the nest entrance. In these cases searching behavior can act as a back-up mechanism when other navigational mechanisms fail. Such a search for a very specific target has a systematic structure, as it is made up of loops of increasing size (Wehner & Srinivasan, 1981; Wolf, 1927). The entire search path is centered on the expected target location, to which the searcher repeatedly returns (Fig. 1). Searching behavior thus also depends on integrating the path during the search (Wehner & Srinivasan, 1981).

Müller and Wehner (1994) modeled the production of search loops by having a model agent travel in spirals that increase in size. To simulate the ant's (*Cataglyphis*) behavior, such spiraling is occasionally broken off, with the agent returning to the starting point of search. Occasionally, the spiral changes 'sign' as well, that is, switching from a clockwise direction to a counterclockwise direction or vice versa. The authors called their proposal "the hidden spiral" (Müller & Wehner, 1994).

Wehner and Srinivasan (1981) provided some functional reasons for the search pattern of increasing loop size with occasional returns to the area where search started. Intuitively, the idea is that after search initiation, the path extends into a distance range that maximizes the probability of encountering the goal, in this case the ant's nest. They assume that at the start of search, some two-dimensional Gaussian distribution describes the probability of finding the nest as a function of location, relative to the start of search. The nest is most likely nearby, and the ant accordingly starts searching with small loops. As these loops continue without nest encounter, however, the probability of finding the nest nearby decreases, so that the unsearched area beyond becomes the most probable area. After searching that band, however, the probability value in that band decreases, and the area close to the origin of search once again becomes the most probable area for finding the nest, and the ant returns to search near the start of its search. This dynamic probabilistic scenario iterates, with the ant searching in a more and more distant range of distances from its start as the search wears on.

The overall size of such a systematic search, i.e., the area that is covered, is flexible and reflects the navigational certainty of the animal (Merkle, Knaden, & Wehner, 2006; Wehner, 1992). In North African *Cataglyphis fortis* desert ants (Wehner, 2003) navigating by path integration, the size of the systematic search path increases steadily with the length of the preceding vector, reflecting the cumulative error of path integration with length of travel (Merkle & Wehner, 2010). In Central Australian *Melophorus bagoti* desert ants (Cheng, Narendra, Sommer, & Wehner, 2009), this size adaptation to the cumulative error of path integration is also seen (Schultheiss & Cheng, 2011). Search size is sensitive to the length of the return path to the nest, even though the ants were simultaneously navigating by terrestrial visual landmarks, a process that does not accumulate errors over time or distance, although it will have other, non-cumulative errors attached to it.

In regard to terrestrial visual navigation, the size of the systematic search is influenced by the amount of navigational information that can be gleaned from the surrounding visual panorama. In *M. bagoti* ants searching for the nest in an

information-rich setting, visual navigation can be very precise and the systematic search path is constrained to a small area around the assumed target; in a visually more impoverished environment, the size of the search path is increased accordingly (Schultheiss et al., 2013).

Apart from navigational mechanisms, other factors can also influence the size of the search. In a setting where the length of path integration and visual surrounding were not manipulated, *M. bagoti* ants were trained to revisit a feeder with either protein-rich or carbohydrate-rich food. Subsequent systematic searches for the (now removed) feeder were smaller for the carbohydrate food than for the protein food (Schultheiss & Cheng, 2013). Under natural conditions, carbohydrate food sources (e.g., flower nectar) are far more likely to be renewable than protein sources (e.g., dead insects), and the ants appear to adjust their search path accordingly. The ant *Formica pallidefulva* (previously *F. schaufussi*) shows a similar pattern after only one visit to the feeder, and this pattern does not change notably with further experience (Fourcassié & Traniello, 1993, 1994).

Searching for distributed resources

Before a hymenopteran forager heads out to forage for food, it typically conducts a number of learning walks or learning flights to learn about the panoramic terrestrial cues. Wasps conduct orientation flights consisting of increasing arcs backing away from their nest, facing the direction in which they expect to face the nest on their return (Zeil, 1993a, 1993b). Honeybees perform orientation flights consisting mostly of heading straight out in one direction and returning again (Capaldi et al., 2000). Over repeated trips, they head off in different directions. Ants conduct what has been called learning walks around the area of their nest before going on foraging excursions (*Cataglyphis*: Wehner, Meier, & Zollikofer, 2004; Southern African *Ocymyrmex*: Müller & Wehner, 2010). Such insects are presumed to learn their landscapes in such walks and flights, although what they learn and how they do it are far from clear.

On its first foraging trip outside the nest, a forager will have no previous knowledge about the distribution or specific locations of resource items and will typically engage in a freely ranging search. Searches of such naïve (inexperienced) ants will mostly be guided by internal, inherited strategies. But during this first, and all subsequent journeys, the animal will gain experience about the structure of the environment, and of the spatial and temporal distribution of resources within that environment. This knowledge can then in turn be used to shape searching behavior in a way that maximizes resource encounter. For example, by simply being able to monitor its position in space, the forager can avoid searching the same area repeatedly and move into unexplored regions instead.

A forager searching for an unpredictably distributed food resource will have no specific knowledge of the spatial and temporal distribution of the separate items. Even locations that previously offered a food reward may not be worth revisiting, either because the location does not offer a repeated reward (a so-called 'destructive' foraging scenario), or because it could have been visited by a competitor. Nonetheless, detailed experience of the distribution pattern of a resource can be very useful in predicting the probability of finding the next reward. For example, even though the exact location of many food items such as seeds or fruits will be unpredictable, such items often occur in patches. A freely ranging forager that switches to a local search strategy upon encounter with the first food item will therefore have a much greater chance of success than if it continued with its freely ranging search. The structure of the search can thus be adapted to different types of resource distributions, resulting in increased searching efficiency. If resources can be considered to have typical distribution patterns, this even opens up the possibility that certain searching strategies might be intrinsic to the animal. To locate, say, a resource that is naturally distributed in a sparse but patchy manner, natural selection would favor those individuals that search with an appropriate and efficient intrinsic strategy. This area of research has become a topic of great interest to theoretical ecologists, as it implies that species are capable of optimizing their movement strategies to increase efficiency and reduce costs.

Optimal foraging theory

In a theoretical approach to animal movement, an animal is usually considered to move in a straight line for a certain distance, before reorienting and heading off in a new direction. For a model searcher, the lengths of movements and the sizes of reorientation angles are drawn from certain theoretical distributions. The efficiency of such artificially created movement strategies, i.e., usually the time until discovery of a target or the number of targets discovered per unit of time, is then evaluated for different target distributions. The overall aim is to identify optimal solutions for specific foraging scenarios, and eventually identify such optimal strategies in actual animal movement data. In many cases, the movement lengths can be approximated by Brownian random walks, i.e., by a succession of random steps. The step-length distribution is typically exponential and turning angles are typically drawn from a uni-modal distribution that is peaked around zero degrees.

In recent years, there has been a strong interest in so-called Lévy walks. Lévy walks comprise clusters of many short steps with longer steps between them. This pattern is repeated across all scales with the resultant clusters creating fractal patterns that have no characteristic scale. Being scale-free, the overall length of a Lévy walk is dominated by the longest step and the step-length variance grows over time but nonetheless remains finite even when unbounded by biological and ecological considerations. Lévy walks are also superdiffusive, meaning that they spread out faster than normal random walks (Fig. 2). The scale-free and superdiffusive characteristics of Lévy walks can be advantageous when searching because they
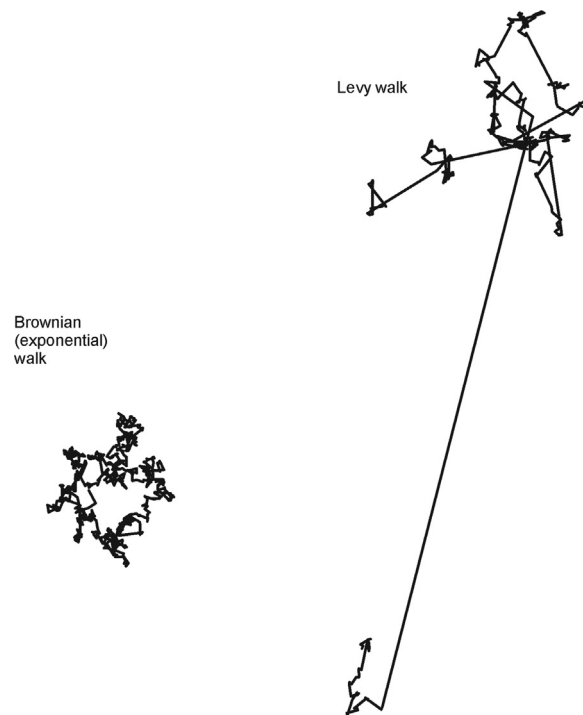
Fig. 2. An example of a Lévy walk with Lévy exponent $\mu = 2$ and a Brownian walk with exponentially distributed step-lengths. The two walks have the same overall length.

limit needless over-sampling (revisiting of locations) without requiring sophisticated cognitive abilities (Viswanathan et al., 1999). Natural selection may therefore lead to adaptations for Lévy walk searching patterns.

The hallmark of a Lévy walk is a step length distribution with a 'heavy' power-law tail: $P(l) \sim l^{-\mu}$, $1 < \mu \leq 3$, where P is the probability, l is the length of a search segment, and μ is the exponent of the power-law distribution; "$\sim$" is read as "is distributed as". Initial evidence for Lévy walks in the flight patterns of wandering albatrosses (Viswanathan et al., 1996), together with the realization that these movement patterns can be advantageous in random search scenarios (Viswanathan et al., 1999), led to an explosion of interest in Lévy walks as models of animal movement patterns. Nonetheless, Lévy walks became contentious when it was found that they had been wrongly attributed to the wandering albatross and many other species through the employment of inappropriate statistical techniques and through misinterpretation of the data (Edwards, 2011; Edwards et al., 2007).

More recent studies have, however, provided seemingly compelling evidence that many organisms do have search patterns that can be approximated by Lévy walks. These have been identified in human T cells (Harris et al., 2012), *Escherichia coli* (Korobkova et al., 2004; Tu & Grinstein, 2005), honeybees and bumblebees (Osborne et al., 2013; Reynolds, Smith, Menzel, et al., 2007; Reynolds, Smith, Reynolds, et al., 2007), a diverse range of marine predators including bony fish and sharks (Hays et al., 2012; Humphries et al., 2010; Sims et al., 2008), hunter-gatherer-humans (Hadza: Raichlen et al., 2014), and even fossilized animals, as determined from the tracks that they left (Sims et al., 2014). And it is now clear that the wandering albatross does after all search the skies using a Lévy strategy (Humphries et al., 2013). This evidence has shifted the debate from 'do animals perform Lévy walks' to 'when do they and why' (Buchanan, 2008).

Hymenopteran searching behavior and the question of optimality

While the searches of honeybees and some bumblebees show Lévy walk characteristics, the distribution of movement lengths in desert ants cannot be modeled as a Lévy walk. Like other hymenopterans, foragers of the Australian desert ant *M. bagoti* adopt a stereotypical search pattern when attempting to locate their nest. These searches begin at the location where the ant expects to find the nest, and comprise loops that start and end at this location, and are directed in different azimuthal directions. Loop lengths are exponentially distributed when searches are in visually familiar surroundings (Schultheiss et al., 2013). However, in unfamiliar landscapes, movements are best described by a mixture of two different exponentials (Schultheiss & Cheng, 2011). Compared to a simple exponential movement strategy, long movements occur much more often in this bi-exponential; the second exponential effectively adds on long movements at the tail end of the distribution (see Fig. 3, in which the probability distribution of a single exponential, a bi-exponential and a power-law are shown). This intrinsic bi-exponential approximates a power-law distribution, the hallmark of an advantageous Lévy search (Reynolds et al., 2014), and it is displayed by desert ants when a Lévy search pattern is advantageous, i.e., in an unfamiliar environment (Narendra, Cheng,
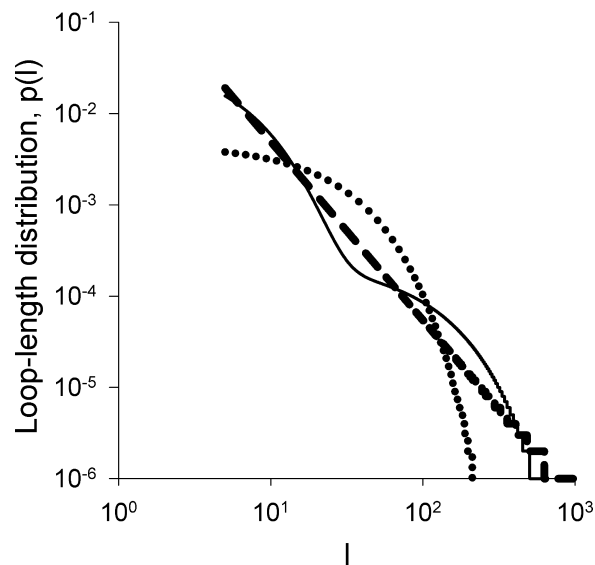
Fig. 3. An example of a bi-exponential distribution (solid-line) that resembles an inverse-square power-law (dashed line), the hallmark of an optimized Lévy walk, and is distinctly different from the best-fit single exponential distribution (dotted line). Figure modified and reprinted from *Journal of Theoretical Biology*, 340, Andy M. Reynolds, Patrick Schultheiss, and Ken Cheng, Does the Australian desert ant *Melophorus bagoti* approximate a Lévy search by an intrinsic bi-modal walk? pp. 17–22, copyright 2014, with permission from Elsevier.

Sulikowski, & Wehner, 2008; Reynolds et al., 2014; Schultheiss & Cheng, 2011). The ability of bi-exponentials to approximate power-law distributions is illustrated in Fig. 3. Analogous behavior has been identified in the movement patterns of mussels during the formation of patterned beds (Jansen, Mashanova, & Petrovskii, 2012; Reynolds, 2014a). Mussels approximate a Lévy walk by adapting an intrinsic tri-modal random walk.

Lévy-loop search patterns are evident in the flight patterns of honeybees when searching for their hive after becoming lost, and when searching for new food sources (Reynolds, Smith, Menzel, et al., 2007; Reynolds, Smith, Reynolds, et al., 2007). In this case Lévy search patterns can be derived from the Weber-Fechner law in a bee's odometer (Reynolds, Schultheiss, & Cheng, 2013). This law refers to the observation that the error in estimating a distance is proportional to the distance being estimated, at least in the range tested (Cheng, Srinivasan, & Zhang, 1999). This suggests that errors in the estimation of distance can be implicitly involved in shaping the structure of systematic search behavior and should not be regarded as merely deficiencies in the odometer. In desert ants, the errors of odometry are of a different kind, as their proportionality to the distance estimated only holds for relatively short journeys. At longer distances, the errors appear to 'level off' and do not increase further (*Cataglyphis fortis*, Sommer & Wehner, 2004). In other words, Weber's law breaks down at longer distances in desert ants, and Lévy search patterns can therefore not be derived from these errors. The composite Brownian search that they do exhibit is an approximation to a Lévy search (Reynolds et al., 2014). This pattern is closer to a power-law distribution than to a single exponential distribution.

It is currently not understood why errors of distance estimation in honeybees, but not those seen in desert ants, follow the Weber-Fechner law, but it might be a consequence of differences in locomotion. Foraging ants walk whereas foraging bees fly, which might have led to the evolution of the different cognitive strategies by which bees and ants estimate distances. For walking ants, proprioceptive cues (in the form of the stride integrator) provide a sufficiently accurate measure of their movements relative to the substrate, with which they are in direct physical contact. Accordingly, a stride integrator has been found to be a major cue for odometry in ants (Wittlinger et al., 2006, 2007). Flying bees on the other hand are not in direct contact with the substrate anymore. Any proprioceptive measures such as energy expenditure or the count of wing beats would be susceptible to outside influences such as wind, and would be unreliable. Accordingly, optic-flow has been shown to be a major cue for distance traveled in honeybees (Srinivasan et al., 1997). But it is unclear why these differences in the principal means of odometry should lead to the absence vs. the presence of the Weber-Fechner law. Nonetheless, the theoretical analyses of Reynolds et al. (2013, 2014) make it clear that the programming for Lévy walks does not need to be very sophisticated or clever on the bee's and ant's part.

Discussion

Ants adapt an innate behavior, a multiphasic walk, to mimic a Lévy walk (Reynolds et al., 2014). Mussels too seem to adopt a similar strategy (Reynolds, 2014b). We suggest that because Lévy walks are advantageous under the right circumstances, natural selection will shape mechanisms that produce Lévy walks (as in bees) or those that approximate them (as in ants and mussels). In the case of bees, because they get Lévy walks 'for free' from the Weber-Fechner law in odometry, natural

selection might well have acted to prevent the loss of this pattern (Reynolds et al., 2013). Such adaptation of innate behaviors has ancient origins as evident, for example, in the preserved form of tracks made by organisms that occupied ancient sea beds exhibiting Lévy walk characteristics (Sims et al., 2014). These 'trace fossils' (ichnofossils) are the only direct record of the behavior of ancient organisms and thus provide critical indications of the early evolution of movement patterns, dated to at least 50 million years ago but perhaps even older. The bi-modal movement patterns may be sufficient to mimic a Lévy walk over the duration of their searches. If the searches continue without success then it is possible that other (higher) modes will be activated. This would be interesting to examine experimentally.

Even big-brained animals might resort to approximating Lévy walks with composite Brownian searches. In Raichlen et al.'s (2014) study of the foraging searches of hunter-gatherers, such composite Brownian searches were found in great frequencies along with Lévy searches characterized by power-law distributions. As hunter-gatherers are the closest we have to ancient hominids, it is possible that a combination of Lévy walks and composite Brownian searches characterizes our lineage as well.

We end with some more speculative considerations on the theoretical developments in Lévy processes. Lévy loop search appears to be very similar to "fast simulated annealing", a powerful stochastic search algorithm for locating a global maximum that is hidden among many poorer local maxima in a large search space (Szu & Hartley, 1987). The algorithm has found widespread application in engineering and physics (Van Laarhoven & Aarts, 1987) and has also been exploited in artificial neural networks (e.g., Bechtel & Abrahamsen, 1991). Basically the searcher selects a step length from a Lévy distribution, jumps to the new location, and relocates to that position if it is better than the last position; otherwise it tends to go back (loop back) to the last location and repeats the process. When there is a single maximum (like a nest) then fast simulated annealing is just like Lévy loop searching. But if there are poorer local maxima, then the simulated annealing does not center on the origin of the search. It is possible that ants searching for the nest are actually implementing fast simulated annealing, but we cannot distinguish between this strategy and a pure Lévy looping search. Intriguingly, there is evidence that the jellyfish *Rhizostoma octopus* uses this strategy when searching the water column to locate the richest prey strata (Reynolds, 2014b).

Summary

Social Hymenoptera such as ants and bees make good models for the study of searching because foragers of these species are frequently motivated to find their home again after finding forage. As they represent a specialized caste within the colony, they are unlikely to have other motivations. Ants and bees exhibit area restricted search patterns that regularly loop back to the origin of the search. As search time goes on, the loops expand in size. When we look at the distributions of the lengths of movement segments, bees, both honeybees and bumblebees, show a power-law Lévy search distribution, with occasional long segments interspersed with many short segments. Such a distribution with a heavy tail has been shown to be optimal for searching for sparse targets, such as a single nest when the surrounding scene is unfamiliar. Desert ants, on the other hand, do not show the Lévy search distribution, but instead a composite of multiple exponential distributions characteristic of random walks at multiple scales. We have argued that such composite Brownian searches serve to approximate Lévy walks. Across the animal kingdom, quite a number of animals exhibit either Lévy walks or composite Brownian walks.

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