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Beginnings of a synthetic approach to desert ant navigation

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ABSTRACT

In a synthetic approach to studying navigational abilities in desert ants, we review recent work comparing ants living in different visual ecologies. Those living in a visually rich habitat strewn with tussocks, bushes, and trees are compared to those living in visually barren salt pans, as exemplified by the Central Australian *Melophorus bagoti* and the North African *Cataglyphis fortis*, respectively. In bare habitats the navigator must rely primarily on path integration, keeping track of the distance and direction in which it has travelled, while in visually rich habitats the navigator can rely more on guidance by the visual panorama. Consistent with these expectations, *C. fortis* performs better than *M. bagoti* on various measures of precision at path integration. In contrast, *M. bagoti* learned a visually based associative task better than *C. fortis*, the latter generally failing at the task. Both these ants, however, exhibit a similar pattern of systematic search as a 'back up' strategy when other navigational strategies fail. A newly investigated salt-pan species of *Melophorus* (as yet unnamed) resembles *C. fortis* more, and its congener *M. bagoti* less, in its path integration. The synthetic approach would benefit from comparing more species chosen to address evolutionary questions.

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Contents

1. Introduction

On a January day in 2001, two of the authors (KC, RW) and Sibylle Wehner pulled in at the parking lot at Simpson's Gap, a gorgeous desert place in the West MacDonnell ranges ~18 km west of Alice Springs, Australia. As the group stepped out of the car, a red ant with long legs dashed quickly across the hot bitumen. Eureka! Thus began the study of navigation, foraging, and learning in the thermophilic red honey ant *Melophorus bagoti* (Cheng et al., 2009). More than a decade later, the study of *M. bagoti* now complements research on the far more studied desert ants of North Africa, genus *Cataglyphis* (see Wehner, 2013, for a personal historical account), as well as desert ants in southern Africa, genus *Ocymyrmex* (Wehner, 2003). We have learned something about its foraging ecology (Muser et al., 2005; Schultheiss and Nooten, 2013), its use of the surrounding panorama (Graham and Cheng, 2009; Wystrach et al., 2011a, 2012), its route following

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(Kohler and Wehner, 2005; Narendra, 2007b; Sommer et al., 2008; Wystrach et al., 2011b), and compared its performance with other desert ants (Bühlmann et al., 2011; Schwarz and Cheng, 2010). The study of *Melophorus* ants has now expanded to a species (as yet unnamed) that lives on the salt pans of South Australia (Schultheiss et al., 2012). Comparing ants in different habitats that fill a similar ecological niche of a thermophilic scavenger has yielded interesting similarities and differences that form the topic of the present account.

Research on navigation in desert ants on different continents reflects to a large extent Kamil's (1987) synthetic approach to the study of animal intelligence, especially in the comparisons between species. The synthetic approach focuses on intelligent behaviour that an animal needs to use in its natural life, much more so than on laboratory tasks that experimenters can impose in standardized conditions. Lab work is not eschewed, but often inspired and informed by field work in the natural habitats of the animals. A wider range of intelligent behaviour was called for in Kamil's (1987) paper, including numerical, timing, and spatial abilities, as well as placing the animal's behaviour in an appropriate ecological and evolutionary context.

In Kamil's own work on food-storing corvids for example, the interest started with field observations suggesting excellent spatial memory in the food-storing Clark's nutcracker (*Nucifraga columbiana*; Tomback, 1980), which stores and retrieves tens of thousands of food caches over a winter (Vander Wall and Balda, 1977). Lab work inspired by such findings confirmed the role of spatial memory (Kamil and Balda, 1985). Further comparative work with a number of corvids showed that the Clark's nutcracker, the most prolific food-storer among North American corvids, performs best on lab tasks of spatial memory, but did not stand out in a lab task requiring memory for colour (Olson et al., 1995). Birds that are more prolific food storers also remember caches stored in the lab for longer (Bednekoff et al., 1997). More recent work has expanded to compare corvids on other kinds of tasks, such as transitive inference (Bond et al., 2010).

The work on desert ant navigation focuses on an important task in their natural life, that of finding their way to food sources solitarily – for desert ants are solitary foragers – and then finding their way back home again after suitable prey has been found. Most of the research takes place in the ants' natural habitats, in the form of field experiments, but lab work complements the enterprise when it is needed, for example in examining the eyes (Schwarz et al., 2011b) or the brains of ants (Stieb et al., 2010). The subjects of study travel the scale of distance in the range of their normal travels on foraging excursions, unlike, for example, the much smaller and restricted arenas typically foisted on lab rodents in the study of rodent navigation. Functional and mechanistic questions have both been entertained in the course of the research. And with the most recent comparisons across genera, questions of evolution are beginning to be addressed about the navigational toolkit of these animals. In our account, we will show that all desert ants possess a basic navigational toolkit. Natural selection from living in different habitats, however, has drawn different emphases and specializations. We discuss briefly the bases for such specializations. First, however, we need to present the key players in the story.

2. Thermophilic scavengers and their navigational toolkits

The desert ants of the genera *Cataglyphis* (in North Africa), *Ocymyrmex* (in southern Africa), and *Melophorus* (in Australia) all fill the niche of thermophilic scavengers (Wehner, 1987; Wehner and Wehner, 2011). These ants specialize in heat tolerance, with one of our study species, *M. bagoti*, being the most heat tolerant ant on its continent (Christian and Morton, 1992). This allows the ants to forage in the heat of the day in summer, when it is too hot for other foragers. *M. bagoti*, for example, shares a geographic niche with other ants (of the genera *Iridomyrmex*, *Camponotus*, and others), but when the ground temperature exceeds about 50 °C, only they are out foraging (Schultheiss and Nooten, 2013). They forage solitarily, running on long legs (Sommer and Wehner, 2012) and scavenging dead animal bits, largely arthropods (Wehner et al., 1983). In ants that live in plant-rich habitats, plant materials are also collected (Muser et al., 2005; Schultheiss and Nooten, 2013; Schultheiss et al., 2012). One species, *Cataglyphis floricola* in south-western Spain, even uses the latter in the form of petals as its main food source (Cerdá et al., 1992).

Their navigational toolkit includes a number of what Wiener et al. (2011) called spatial primitives, such as the encoding of compass direction, based on both celestial and terrestrial cues, and distance travelled or odometric measure. It is possible that the more complex level of spatial constructs is also encoded. The major systems in the toolkit are generally recognized as path integration, use of the visual panorama, and systematic searching (Wystrach et al., 2013b), although a fourth system of backtracking has just been proposed for *M. bagoti* (Wystrach et al., 2013b). Less well investigated are the use of cues of other modalities, including vibrational, magnetic (Buehlmann et al., 2012) and olfactory ones (Buehlmann et al., 2012; Steck et al., 2009; Wolf and Wehner, 2000), and a different compass mediated by the ocelli (Schwarz et al., 2011a, 2011c) rather than the dorsal rim area of the compound eyes (Wehner, 1994).

In path integration, the navigator keeps track of the straight-line distance and direction that it has travelled from a starting point (typically home), and uses the calculated vector for homing (Wehner and Srinivasan, 2003). This system depends on registering the direction in which the ant is travelling, the distance travelled *en route* (odometry), and importantly, integrating the two kinds of information, so that the traveller encodes which direction a particular step has moved in. The directional component is based largely, but not solely, on a celestial compass derived from the pattern of polarized light in the sky. Light is scattered in a systematic fashion as it enters the Earth's atmosphere (Wehner, 1994). A visual system with appropriate receptors and processing systems can perceive a pattern in the polarized light that indicates the direction of the sun. The position of the sun itself is also used as a cue (Wehner and Müller, 2006), as are spectral patterns (Wehner, 1994). The latter refer to the distribution of different wavelengths of light reflected by terrestrial objects as a function of the position of the sun. The pattern of polarized light, spanning the entire sky, is not surprisingly weighted more than the position of the sun (Wehner and Müller, 2006). Odometry is dependent largely on a stride integrator that functions like a step counter (Wittlinger et al., 2006, 2007), although the pattern of optic flow beneath the ant is also used to some small extent (Ronacher and Wehner, 1995). These studies were all on the North African *C. fortis*.

In using the visual panorama, some visual cues in the surrounding panorama are used to determine a direction of travel. These cues might encompass large segments or the entire visual surround (Graham and Cheng, 2009; Wystrach et al., 2011a, 2012). Thus, the skyline is used by *M. bagoti* as a terrestrial compass source (Graham and Cheng, 2009). The skyline is a record of the heights of terrestrial objects in the visual panorama. Graham and Cheng (2009) showed that desert ants would follow the dictates of an artificially constructed skyline made of black cloth. The contour of the cloth enclosure matched roughly the skyline heights measured at the feeder to which the ants were trained to visit, with the elevations matched at 15° intervals. Even large landmarks, obvious and prominent to human observers, might not be used by the ants when the rest of the visual panorama is unfamiliar (Wystrach et al., 2011a). This and other results led to proposals that the entire panoramic