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Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants

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Collective behaviours are influenced by the behavioural composition of the group. For example, a collective behaviour may emerge from the average behaviour of the group's constituents, or be driven by a few key individuals that catalyse the behaviour of others in the group. When ant colonies collectively relocate to a new nest site, there is an inherent trade-off between the speed and accuracy of their decision of where to move due to the time it takes to gather information. Thus, variation among workers in exploratory behaviour, which allows gathering information about potential new nest sites, may impact the ability of a colony to move quickly into a suitable new nest. The invasive Argentine ant, *Linepithema humile*, expands its range locally through the dispersal and establishment of propagules: groups of ants and queens. We examine whether the success of these groups in rapidly finding a suitable nest site is affected by their behavioural composition. We compared nest choice speed and accuracy among groups of all-exploratory, all-nonexploratory and half-exploratory–half-nonexploratory individuals. We show that exploratory individuals improve both the speed and accuracy of collective nest choice, and that exploratory individuals have additive, not synergistic, effects on nest site selection. By integrating an examination of behaviour into the study of invasive species we shed light on the mechanisms that impact the progression of invasion.

Collective behaviour emerges from individual-based local rules without central control. Traditional models of collective behaviours assume that all the system's components follow identical behavioural rules (Couzin, Krause, James, Ruxton, & Franks, 2002; Seeley & Buhrman, 1999). However, individual variation is prevalent in animal groups (Jandt et al., 2014; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) and can have a great impact on the emergence of collective behaviour. For example, variation in connectivity may affect the speed at which information is transmitted among individuals (Pinter-Wollman, Wollman, Guetz, Holmes, & Gordon, 2011) and certain individuals may act as leaders (Conradt & Roper, 2005) and influence the actions of other group members.

In social insects, individual variation in behaviour among workers has great implications for the collective behaviour of the colony. Variation in which task each individual performs (i.e. division of labour) can improve colony productivity (Beshers & Fewell, 2001; Oster & Wilson, 1978) and efficiency (Dornhaus, 2008), similar to division of labour in factories (Smith, 1776). Individual variation in social insects is not confined to which task a worker performs. Within a task, there is much behavioural variation in how well it is performed (Jaisson, Fresneau, & Lachaud, 1988). For example, some workers are highly diligent in performing their task, yet others are not (Pinter-Wollman, Hubler, Holley, Franks, & Dornhaus, 2012). Such behavioural variation within a task is often overlooked, despite its potential impact on colony collective behaviour, on which natural selection acts (Jandt et al., 2014; Pinter-Wollman, 2012).

Variation among colonies in their collective behaviour may arise from differences in worker composition. Colonies may vary in their collective behaviour because the mean behaviour of their workers differs, because of differences in the distribution of worker performance, or because of variation in both mean and distribution of worker performance (Pinter-Wollman, 2012). Thus, colony behaviour may be the outcome of additive effects (i.e. a colony's collective behaviour reflects the simple mean behaviour of its workers). For example, bumblebee colony thermoregulatory behaviour is a result of the average response threshold of its workers (Jandt & Dornhaus, 2014). Alternatively, a few individuals may influence how others

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behave, leading to synergistic effects on colony behaviour. Such individuals have been termed 'key individuals' (Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014; Robson & Traniello, 1999) and may act as catalysts (i.e. increase the activity of other workers). For example, exploratory ants (Modlmeier & Foitzik, 2011) or bold individuals (Pruitt, Grinsted, & Settepani, 2013) affect how the colony responds collectively to changes in its environment. Such variation in the distribution of behavioural types within a colony can influence both the fitness of the individuals (Pruitt & Riechert, 2011) and the longevity of the colony (Pruitt, 2012, 2013).

Social insect colonies often relocate to new nest sites (Smallwood, 1982). The process of choosing a new nest site (i.e. when to move and where to settle) has been studied extensively in both honeybees (Seeley, 2010) and rock ants (Franks, Dechaume-Moncharmont, Hanmore, & Reynolds, 2009; Franks, Mallon, Bray, Hamilton, & Mischler, 2003). Nest site selection can be performed by workers of different tasks; for example, scouts locate the new nest and transporters assist in moving the colony (Franks, Mallon, et al., 2003; Seeley & Buhrman, 1999). Further variation among workers within a task group, such as experience (Langridge, Sendova-Franks, & Franks, 2008) or diligence (Pinter-Wollman et al., 2012), affects the speed of nest relocations. When making collective decisions of selecting a new nest site, there is an inherent trade-off between the speed and accuracy of the decision due to the time it takes to gather information (Chittka, Skorupski, & Raine, 2009; Franks, Dornhaus, Fitzsimmons, & Stevens, 2003). In ants, nest quality varies based on attributes such as darkness and entrance size (Franks, Mallon, et al., 2003), so colonies that make more accurate decisions are safer after relocation. In addition, the speed of relocation can affect the survival of the moving ants that are unprotected while outside the nest.

Invasive ant species expand their range through establishing new nest sites; thus, the collective process of nest selection in these species and the effects of individual variation among workers on this process have important ecological consequences. For example, behaviours such as the propensity to explore novel environments (Liebl & Martin, 2012; Rehage & Sih, 2004; Sih, Cote, Evans, Fogarty, & Pruitt, 2012) and quickly control new resources (Davidson, 1998; Holway, 1998; Holway & Case, 2001) play an important role in invasion success (Holway & Suarez, 1999). Furthermore, behavioural variation within a group determines its collective exploratory tendency (Brown & Irving, 2014). Thus, variation within a colony in the exploration and aggression of its workers may determine how well the colony as a whole expands its range.

The invasive Argentine ant, *Linepithema humile*, has been introduced from its native range in Argentina throughout the world (Holway, 1995; Suarez, Holway, & Case, 2001; Vogel, Pedersen, Giraud, Krieger, & Keller, 2010) and has detrimental impacts on the ecology of its introduced range (Fisher, Suarez, & Case, 2002; Human & Gordon, 1996; Peterson, Kus, & Deutschman, 2004; Suarez, Richmond, & Case, 2000). The spread of these ants at a global spatial scale is human mediated (Suarez et al., 2001), but at a local spatial scale, of a few hundred metres per year (Heller & Gordon, 2006; Markin, 1970), Argentine ants increase their range through budding: a propagule consisting of an inseminated queen and workers leaves an established nest site on foot and establishes a new nest nearby (Hee, Holway, Suarez, & Case, 2000). Propagules can disperse during any season, with or without queens (Aron, 2001), and their size (Sagata & Lester, 2009) and the number of queens (Hee et al., 2000) predict their establishment success. However, Argentine ant workers vary in their aggressive behaviour (Van Wilgenburg, Clemencet, & Tsutsui, 2010), so colonies, and potentially propagules, are composed of a behaviourally heterogeneous work-force. Thus, it is important to understand how the behavioural composition of the workers of a propagule, and not only their numbers, influences the spread of this invasive species. In addition, when choosing a new nest site, the speed–accuracy trade-off may affect how Argentine ant propagules extend the invasion range because they may be competing with other species over nest sites and other resources.

To examine how variation in exploratory behaviour of workers affects the collective speed and accuracy of choosing a new nest site by groups of Argentine ants, we induced nest relocation using nest flooding (Scholes & Suarez, 2009). We examined the choice of groups varying in composition of exploratory and nonexploratory individuals between two alternative nest sites of different quality. We asked whether exploratory individuals increase the speed of a group's search for a new nest site or improve the accuracy of distinguishing between alternative nest sites, whether there is a trade-off between the speed and the accuracy of selecting a new nest site, and whether the effect of exploratory individuals on group behaviour is additive or synergistic.

METHODS

We collected 400 Argentine ant foragers from a foraging trail at the UCSD Biology Field Station on 1 March and 17 May 2013. Ants were housed in the laboratory on a 12:12 h dark:light cycle in two fluon-lined circular boxes (diameter = 25 cm, height = 13 cm) and were provided with water and sugar-water ad libitum.

Individual Exploration Assay

To determine the exploratory behaviour of individual workers, each ant was placed at the centre of an eight-arm maze and its behaviour was observed for 5 min, as in Modlmeier and Foitzik (2011). The maze comprised eight petri dishes (height = 10 mm) connected to one central dish using tygon tubes (Fig. 1a). Each of the eight dishes contained approximately 0.2 ml of a different spice (chili, cinnamon, garam masala, garlic, ginger, oregano, pilau and sage), providing novel stimuli for the ants to explore (Fig. 1a). After an ant was placed in the central chamber, we counted the number of spices it explored during 5 min. Exploring a spice was defined as entering the tube leading to a spice dish, whether or not an ant reached the spice itself. We did not observe a bias towards exploring a particular spice (all spices were visited at a similar frequency). In a preliminary test of 118 workers, we found that ants explored up to four spices (mean = 1.3 spices, median = 1 spice; Fig. 1b). Based on the distribution of the number of spices visited in these preliminary trials (Fig. 1b), we set the median number of spices visited as a threshold and defined an exploratory worker as an ant that visited two or more spices, and an ant that visited no spices or one spice as nonexploratory.

Group Nest Choice Assay

To examine the effect of group composition on their collective behaviour, we assembled three types of groups of 10 workers each. Hee et al. (2000) showed that as few as 10 workers accompanying a fertile queen were able to establish in a new nest site. Workers were scored for individual exploratory behaviour as described above and placed in one of three groups: 100% exploratory (all-exploratory), 50% exploratory and 50% nonexploratory (half-and-half) and 100% nonexploratory (all-nonexploratory). A new set of 10 workers was tested in each trial, and we replicated each type of group composition eight times, for a total of 24 group trials using 240 workers. At the end of each experiment, ants were placed in a different box from which they were previously housed in to ensure that they were not used more than once and were provided with water and sugar-water ad libitum until they died naturally. Ants were not