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Harvester ants use interactions to regulate forager activation and availability

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Social groups balance flexibility and robustness in their collective response to environmental changes using feedback between behavioural processes that operate at different timescales. Here we examine how behavioural processes operating at two timescales regulate the foraging activity of colonies of the harvester ant, *Pogonomyrmex barbatus*, allowing them to balance their response to food availability and predation. Previous work showed that the rate at which foragers return to the nest with food influences the rate at which foragers leave the nest. To investigate how interactions inside the nest link the rates of returning and outgoing foragers, we observed outgoing foragers inside the nest in field colonies using a novel observation method. We found that the interaction rate experienced by outgoing foragers inside the nest corresponded to forager return rate, and that the interactions of outgoing foragers were spatially clustered. Activation of a forager occurred on the timescale of seconds: a forager left the nest 3–8 s after a substantial increase in interactions with returning foragers. The availability of outgoing foragers to become activated was adjusted on the timescale of minutes: when forager return was interrupted for more than 4–5 min, available foragers waiting near the nest entrance went deeper into the nest. Thus, forager activation and forager availability both increased with the rate at which foragers returned to the nest. This process was checked by negative feedback between forager activation and forager availability. Regulation of foraging activation on the timescale of seconds provides flexibility in response to fluctuations in food abundance, whereas regulation of forager availability on the timescale of minutes provides robustness in response to sustained disturbance such as predation.

Complex biological systems are regulated by processes that operate at multiple time scales, providing flexibility in the shorter term and robustness in the longer term in response to changing conditions (Flack 2012). For example, the activation of neuron cells relies on the release of neurotransmitters at the synapse on the timescale of seconds, allowing rapid response to fluctuating environments. On a longer timescale of hours, gene regulation increases the stability and predictability of a neural response by determining which neurotransmitters are available to be released (Zupanc 2004). Negative feedback, in the form of neurotransmitter depletion by their release from the cell, prevents the system from entering a runaway process of perpetual signalling (Alon 2006).

Recent work suggests that feedback between processes that operate at multiple timescales is as important in animal behaviour as it is in other biological systems. For example, in primate societies, individuals that differ in functional role and demographic class vary in the timescale at which they decide to join or avoid fights, reducing social uncertainty about the outcome of conflict (DeDeo et al. 2011). Furthermore, the foraging behaviour of gulls in the intertidal zone is best described by models that combine immediate encounter rate with prey as well as the longer-term effect of tide cycles on prey availability (Suraci & Dill 2013). More generally, hierarchical models of foraging show that integrating information from processes occurring on short and long timescale maximizes energetic return (Lucas 1983).

Studies of social insects show that regulation of foraging occurs at different timescales, but little is known about how and why these different timescales are linked. The foraging activity of colonies of the honeybee, *Apis mellifera*, is regulated on the timescale of minutes through the temporal distribution of forager arrivals, leading

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to adjustment in foraging activity in response to short-term changes in food availability (Fernández et al. 2003). On a longer, seasonal timescale, honeybee foraging is regulated through vibration dances that vary seasonally in frequency and intensity, producing stable seasonal patterns of foraging activity (Schneider et al. 1986). The synergy between these two regulation mechanisms may help bee colonies to collectively balance flexibility and stability. In the ant *Temnothorax albipennis*, task allocation is determined by factors that are regulated at two different timescales. An ant's location in the nest, which changes on a short timescale of hours, and its fat and water stores, which change on a longer timescale of days, both influence the task it performs (Robinson et al. 2009), allowing the colony to balance robustness and flexibility in task allocation.

Here we examine how colonies of the red harvester ant, *Pogonomyrmex barbatus*, combine processes on the timescale of seconds and minutes to regulate foraging activity in response to changes in their environment. Previous work has shown that foragers search for scattered seeds, distributed by wind and flooding (Gordon 1993). A forager searches until it finds a seed, so search time corresponds to food availability (Beverly et al. 2009) (Fig. 1b) and is constrained by the risk of desiccation while searching (Feener & Lighton 1991). Foraging activity can be disturbed by predation by horned lizards (Munger 1984), which stay near foraging trails and consume foragers as they pass by. These short-term changes in foraging activity operate in the context of longer-term changes in food availability and weather, on the timescale of days (Gordon 1991; Gordon et al. 2013) and on the timescale of years, as colonies grow older and larger (Gordon 1991, 1992). Here we ask how processes operating at different timescales of seconds and minutes are linked through positive and negative feedback to allow an ant colony to balance behavioural robustness and flexibility (Fig. 1a).

First, we consider how the rate of forager return corresponds to the rate of interaction between returning and outgoing foragers. Previous work has shown that the rate at which outgoing foragers leave the nest depends on the rate at which successful foragers return with food (Gordon 1991; Schafer et al. 2006; Gordon et al. 2008, 2011, 2013; Prabhakar et al. 2012). This previous work is consistent with the hypothesis that foraging activity is regulated by interactions between returning and outgoing foragers inside the nest. However, these interactions have never been directly observed. Observations of laboratory -housed colonies have shown that collective behaviour of other social insects is regulated through interactions inside the nest: foragers are activated by biting in wasps (O'Donnell 2001) and by other interactions in honeybees (Fernández et al. 2003; Gruter & Farina 2009; Balbuena et al. 2012), and relocation to new nest sites is regulated by interaction rate in wasps (Sonnentag & Jeanne 2009), honeybees (Camazine et al. 1999) and rock ants (Pratt 2005). However, whether foraging regulation of harvester ants in field colonies is mediated by interactions among workers has not yet been directly observed. Here we investigate for the first time whether foraging activity depends on the interactions of foraging harvester ants inside nests in the field.

Second, we consider how forager return rate influences the probability, on the timescale of seconds, that an ant leaves the nest to forage. The more quickly a forager can find food, the lower the cost in desiccation (Lighton & Feener 1989). Thus, colony flexibility on the timescale of seconds is important for balancing the trade-off between desiccation and obtaining food. Whether a worker performs a certain task can be the result of environmental cues that lead it to reach a response threshold (Robinson 1987; Theraulaz et al. 1998; Beshers et al. 1999). We examined whether an outgoing forager requires a threshold number of interactions to become an active forager and leave the nest. Outgoing forgers may interact with both returning foragers and with other task workers inside the nest. Previous work has shown that successful, but not unsuccessful, foragers returning to the nest influence foraging activity (Schafer et al. 2006), and that the combined chemical odour of both seeds and foragers stimulates foraging, but the odour of foragers or of seeds alone does not (Greene et al. 2013). Therefore, we asked whether interactions with returning foragers with seeds were more likely to stimulate outgoing foragers to leave the nest than interactions with other ants. Because a previous study of laboratory colonies showed that interactions are not homogenously distributed in space (Pinter-Wollman et al. 2011), we also asked whether, in colonies in the field, there are interaction 'hotspots' close to the nest entrance, similar to those observed in the laboratory.

Third, we investigate the process on the timescale of minutes that determines how many foragers are available to interact with returning foragers. In colonies of honeybees (Anderson & Ratnieks 1999) and wasps (Jeanne 1986), workers queue near the nest entrance to receive food or building material from returning individuals, creating a pool of available workers. In harvester ants, foraging may stop for minutes when a predator, the horned lizard,

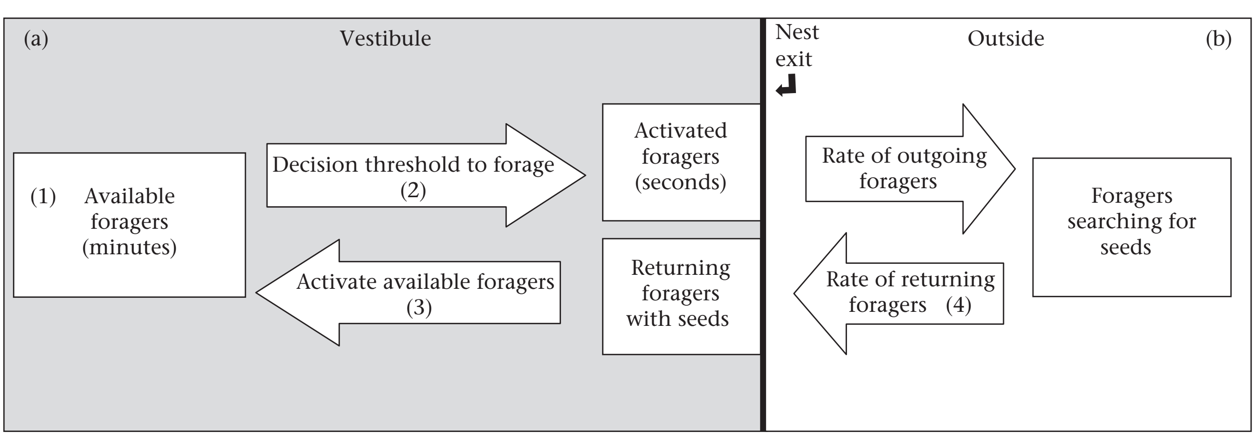

Figure 1. Diagram of the regulation of foraging behaviour in harvester ants. (a) Processes identified in the current study as occurring inside the nest vestibule. (b) Processes known from previous work to occur outside the nest. (1) Forager availability (numbers of ants) in the vestibule changes on the timescale of minutes. (2) An available forager's decision whether to leave the nest depends on its interactions with returning foragers on the timescale of seconds. (3) Interactions of returning foragers with available foragers activate the available foragers. In addition, a returning forager can become an available forager once it drops off the food item it brought into the nest. (4) The rate at which foragers return to the nest depends on food availability.