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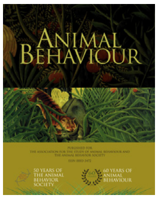

Individual and social information gathering are fine-tuned to the internal state of the group

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It is well known that the environment a group inhabits influences the frequency at which its members use information gained from one another, that is, social information. However, the potential link between internal state (i.e. individual and social physiology) and use of social information has received little attention. This is surprising as it is known that internal state has profound effects on group behaviour in many group-living animals and especially eusocial insects. Energy reserves are a particularly important determinant of internal state and have been predicted to affect the use of social information. However, empirical studies on foraging dynamics of ants subjected to different durations of food deprivation supply conflicting evidence. We investigated how information is gained by the tandem-running ant, *Temnothorax albipennis,* when the colony had been fed compared to when it had been deprived of food. Our results indicate that both individual and social information gathering occurred significantly more when the colony had been deprived of food and that both were fine-tuned to internal state. We found no strong evidence that social information gathering increased more quickly with an increased perceived level of starvation. We suggest that differences between colonies in their internal state can be an explanation for the inconsistencies among previous studies regarding whether low food availability increases or decreases the benefit of acquiring social information.

Many empirical and theoretical studies (reviewed in Seeley 1995; Devouche 1999; Chittka & Leadbeater 2005; Galef & Laland 2005; Rieucau & Giraldeau 2011) have focused on the effect of the environment on the frequency at which members of a group make use of information from one another, that is, social information transfer (SIT). Intriguingly, although SIT, in general, is considered highly beneficial (Rendell et al. 2010), in certain species in which group living is the norm, members of groups do not always use SIT but rather may engage exclusively in individual information acquisition (IIA): information obtained through each individual's own experience (reviewed in Seeley 1995; Leadbeater & Chittka 2007). While there has been extensive research on the effect of the environment on the frequency at which a group makes use of information obtained from others, the potential link between the internal state (i.e. physiology; Barnard 1983, page 72) of the group and the use of social information transfer has scarcely been studied empirically. Theoretical studies in this field point out that the level of energy reserves might be a particularly important state variable that can affect the use of social information (Barta & Giraldeau 2000) particularly in the context of group foraging tactics.

In many vertebrates (primates, *Macaca mulatta:* Loy 1970; cats, *Felis catus*: Crowell-Davis et al. 2004; fish, *Fundulus diaphanus:* Hensor et al. 2003) the internal state of the group may lead to individuals leaving the group. Eusocial insect species, however, do not have such a choice and typically the lives of such social insects are dedicated to colony survival and efficiency. Thus, in such systems individuals are frequently exposed to social information (Leadbeater & Chittka 2007; Gruter et al. 2010) and hence they may decide to act on such information or to obtain personal information. In this study, we examined how information about food location is gained by ant colonies. In ants, knowledge of food location is initially gained through IIA (exploration), but can then be transferred to other individuals through recruitment behaviour. It is commonly assumed that recruitment always increases the colony's net energy gain (Ydenberg & Schmid-Hempel 1994). However, it is known that the level of SIT can vary within and between colonies (Sherman & Visscher 2002; Dechaume-Moncharmont et al. 2005), in response to environmental conditions such as food quality and quantity, distance to food source, risk of predation and competition (Portha et al. 2002; Cassill 2003). For example, the theoretical study of Dechaume-Moncharmont et al. (2005) and certain empirical studies (e.g. Dornhaus & Chittka 2004) have suggested that the

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availability of food can affect the level of recruitment. When food sources are ephemeral, waiting to gain information by social interaction may not be beneficial. Under these circumstances, the optimum strategy may therefore be to acquire individual information via exploration.

Most studies have investigated the effect of food availability and quality on the way information is acquired, that is, via individual and/or social interactions. Only a few studies have dealt with the way this information is acquired in relation to the internal state of the colony (Mailleux et al. 2006, 2010b, 2011). Starvation level is one of the most important parameters affecting foraging behaviour in ants (Roces & Holldobler 1996; Blanchard et al. 2000; Robinson et al. 2009), honeybees, *Apis mellifera* (Seeley 1995) and bumblebees (Cartar & Dill 1990). Thus, it seems likely that the form of acquiring information may be affected by the level of starvation. When a colony has been subjected to food deprivation, recruitment behaviour is predicted to be the optimal method of foraging, rather than individual exploration. When individuals are starved, the cost of exploring (and not finding food) may outweigh the cost of waiting for potentially valuable social information from successful foragers (Cassill 2003; Richardson et al. 2010). Nevertheless, empirical studies on foraging dynamics provide contradictory evidence of the effect of starvation on the way information is acquired (reviewed in Mailleux et al. 2010a). In all of these studies the starvation level was defined by the duration of time the ants were deprived of food, rather than how the colony perceived food deprivation, that is, its internal state. However, it is known that the perception of food deprivation for the same time period can vary both between and within species owing, for example, to the proportion of brood items in the colony (Blanchard et al. 2000). Thus, in order to derive a general concept of the effect of food deprivation on the level of social and individual information acquisition, it is crucial to assess the internal state of colonies.

We investigated the possible effect of the degree of food deprivation, as perceived by colonies of the ant *Temnothorax albipennis*, on the way information is acquired. *Temnothorax albipennis* ants do not lay recruitment trails and all SIT is in the context of tandem running: transferring information from a knowledgeable individual to a naïve individual (Franks & Richardson 2006). The assessment and collection of food are undertaken on behalf of the colony by the foragers, acting as part of their society's alimentary canal, that is, both the collective mouth and to some degree part of its guts (Dussutour & Simpson 2009). By doing so, social insects maintain the supply of an appropriate balance of nutrients at both the individual and the collective level. Thus, assessing the relative importance of social information can be accomplished at the individual level (by following the ants that find food and counting those that recruit nestmates, SIT, and those that keep the information to themselves, IIA) or, as in this study, at the colony level. We considered the number of tandem runs as a measure of SIT at the colony level and the number of ants that could potentially find a food source irrespective of the way information would be shared with nestmates later, or whether it would be shared at all, as the degree of IIA at the colony level. We measured the level of food deprivation perceived by the colony as the difference between the number of ant feeding events when colonies had been food deprived compared to when they had been fed. This measure is likely to be positively correlated with both IIA and SIT since there is a high probability that ants exploring or engaging in tandem running will eventually visit the food. However, we aimed to elucidate the relative rather than the absolute investment in IIA and SIT in relation to the perceived level of starvation by the colony. We predicted that (1) information gathering activity would be higher when colonies had been food deprived, (2) there would be more social than individual information gathering when the colonies' perceived starvation levels were higher, and (3) although the period of food deprivation was the same for all colonies, those with more brood items would perceive higher starvation levels.

METHODS

Ten queenright *T. albipennis* ant colonies were collected in Dorset, U.K. on 25 February 2012 (number of workers: median = 73, interquartile range, IQR = 57.25; number of brood: median = 72.5, IQR = 59.25). Each colony was provided with an artificial nest with a perimeter of cardboard 1 mm thick, sandwiched between two microscope slides. This formed a single cavity measuring 45 × 36 mm, area 1620 mm^2, with an entrance 2 mm wide and 7.5 mm long. Each nest was covered by a red filter and placed in a petri dish (10.5 × 105 mm and 20 mm high). The walls of the petri dish were painted with Fluon to prevent the ants escaping. We kept the colonies at a constant temperature of 24 °C and under a natural light:dark regime. We photographed the colonies every week to monitor the number of workers and brood in each colony.

To exclude any possible effects of previous starvation in the field, each colony received a water tube, two drops of honey solution (1 part honey in 10 parts water) and two *Drosophila* flies, for 2 weeks after their collection from the field (Fig. 1). After these 2 weeks of habituation to laboratory conditions, five colonies (group 1) were deprived of water and food for 2 weeks. After monitoring the activity in the arena, group 1 received food for 3 weeks and was once again monitored. Group 2 ($N = 5$) was first monitored after an additional week of feeding. Group 2 was again monitored after 2 weeks of feeding followed by 2 weeks of food deprivation. Dividing the colonies into two groups allowed us to control for any effect of the order of the treatments: first food deprivation and then access to food or vice versa. The experimental design was paired so that each of the 10 experimental colonies underwent both a fed and a food-deprived treatment.

All experiments were carried out between 14 March and 22 April 2012. At the beginning of each experiment, we placed the focal colony in a 1 × 1.5 m arena with five landmarks (3 × 2.5 cm) located haphazardly within the arena. After 30 min, we placed two droplets of honey solution, soaked in a piece of cotton, at a distance of 1 m from the nest entrance. All ants were allowed to explore the arena for 7 h. Every 10 min we counted the ants in the arena (and the ants in the nest to make sure all ants were accounted for), the number of tandem runs and the number of ants feeding on the honey solution. These counts were used for our measures of IIA, SIT and level of perceived food deprivation, respectively (see Data Analysis).

Ethical Note

Temnothorax ant colonies can survive 8 months of starvation (Rueppell & Kirkman 2005). During the food deprivation phase we monitored the experimental colonies and in none was the death

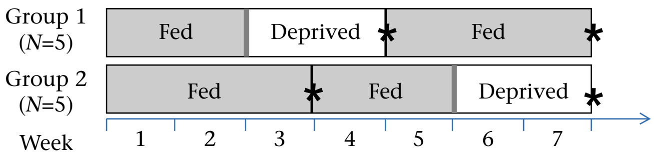

Figure 1. Experimental schedule: colonies were allocated to two groups to control for the order of treatment. Group 1 was first monitored (*) after food deprivation and the second time after 3 weeks of feeding. Group 2 was treated in the reverse chronological order. In both cases we used a paired design, namely each colony underwent each of the two treatments: food deprived and fed.