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ORIGINAL ARTICLE

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# Improvement in collective performance with experience in ants

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**Abstract** We show that entire ant colonies can improve their collective performance progressively when they repeat the same process. Colonies of *Leptothorax albipennis* can reduce their total emigration times over successive emigrations. We show that this improvement is based on experience and some memory-like process, rather than a coincidental developmental change or an increased general level of arousal. We demonstrate that the benefits of experience can be lost (i.e. forgotten) if the interval between successive emigrations is too long. We also show that the benefits of experience are more likely to be retained over a longer period if the collective performance has been repeated several times. This is a new demonstration of a process akin to learning in ants and we briefly discuss how it may involve not only improvements in individual performance but also improvements in the ways in which the ants interact with one another.

**Keywords** Ant · Collective performance · Experience · Learning · *Leptothorax*

## Introduction

Natural selection has promoted innovation by repeatedly favouring new combinations of existing life forms. Thus, eukaryotic cells have evolved, in part, from symbiotic associations of prokaryotes (Margulis 1981; Dyer and Obar 1994). Metazoans have evolved from assemblages of single celled animals, and animal societies have evolved from coalitions of individual organisms. Such events have been termed the major evolutionary transitions (Maynard Smith and Szathmáry 1997). Certain social insect colonies are supreme exemplars of such a transition and consequently they have been termed superorganisms (Wheeler 1910; Wilson 1971, 1990; Franks 1989; Seeley 1989).

Many single-celled organisms and countless metazoan individuals have been shown to improve their performance of tasks as a result of learning (Thorpe 1963; Corning et al. 1973; Pearce 1999). Learning by most metazoans can be attributed to changes in individual cells and changes in interactions among cells (Kandel et al. 1991). By analogy, if an entire society improves its collective performance, this might arise not only through individuals learning to improve their own performances but also through them learning to interact with one another more efficiently.

In this paper, we consider whether complete societies can improve their collective performance when they must accomplish the same process repeatedly. Although there have been a number of classical demonstrations of learning by individual ants in the context of solitary foraging decisions (see, for example: Schneirla 1943, 1953; Johnson 1991; Schatz et al. 1994; Judd and Collett 1998; Collett and Collett 2002), to the best of our knowledge this is the first study to focus on whole colonies of ants. We specifically chose to analyse the emigrations of complete colonies, from a disrupted nest site to a new one, because this task is not only vital to colony survival, but it also involves the whole colony. Furthermore, we could measure collective performance, i.e. the performance of whole colonies, which involves the need for cooperation, rather than average the performance of individual colony members (see, for example: Johnson 1991).

Our model societies are *Leptothorax albipennis* ant colonies. They are small, with less than 500 monomorphic workers and a single queen. Colonies occupy preformed cavities in rocks. Using any small particles available to them, the workers build a wall that encloses the queen, brood and nest workers (Franks et al. 1992). They can be

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cultured in the laboratory in nests formed from two microscope slides separated by a cardboard perimeter delineating the nest chamber (Sendova-Franks and Franks 1995). This allows detailed observations to be made of all colony members.

Emigration is a highly structured process that consists of a number of components: discovery, assessment and transport (see Methods for a definition of these terms). Improvement in collective performance in each or any of these components is possible. Recent studies have examined, in detail, the various elements of *L. albipennis* emigrations and have shown that they have a sophisticated organisation involving multiple interactions among the members of the colony (Mallon et al. 2001; Franks et al. 2002; Pratt et al. 2002; Sendova-Franks et al. 2002; Franks et al. 2003). For example, individual workers are able to assess the floor area of a potential new nest site (Mallon and Franks 2000; Mallon et al. 2001; Mugford et al. 2001) and colonies can choose the best nest among many, as determined by a diversity of cues, by using an additive decision-making strategy (Franks et al. 2002, 2003). After such exploration and initial decision-making, scouts begin to recruit most quickly to the best available nest (Mallon et al. 2001). Individual scouts also use a quorum-sensing procedure, based on their assessment of the number of their nest mates already present in a potential new nest site, to determine when to increase their recruitment rate (Pratt et al. 2002). In this way, the decisions of many members of the colony are collated. The single queen, who is "the vital organ of the society" (Franks and Sendova-Franks 2000), is moved during the middle of the emigration. At this optimum point, the queen can be carried quickly between the protection offered by half of her workers in the old nest and half of her workers in the new nest (Franks and Sendova-Franks 2000). In addition, individuals can learn the positions of both small and extended landmarks on the route between the old and new nest, thus facilitating the transport of brood and passive adults (Pratt et al. 2001; McLeman et al. 2002). All of these studies strongly suggest that the emigration behaviour of *L. albipennis* colonies and their individual members has been strongly selected, at both the colony level and the individual level, to favour efficiency.

In the field, colonies may emigrate frequently (Partridge et al. 1997) not only because their nest sites are fragile but also because colonies can choose to move to better nest sites even if their old one is intact (Dornhaus et al. 2004). During an emigration, speed is important because the whole colony is exposed to potential predators (Franks et al. 2003). Furthermore, workers of *L. albipennis* are long-lived. In the laboratory, individually marked workers can survive for more than 3 years (Sendova-Franks, personal observations). Thus, even though workers may live much shorter lives in the field, they may engage in several colony emigrations not only during their lifetime but also within a single spring or summer.

Here we ask: can entire *L. albipennis* colonies improve their performance over successive emigrations and consequently move between nest sites more quickly? However, an improvement in performance might not be attributable to the experience gained. It might occur as a consequence of other factors. We suggest that there are five possible explanations for an improvement in performance. These are: (1) development; (2) priming; (3) activation; (4) facilitation; and (5) learning. With the first, a colony's abilities might have improved due to some developmental change occurring in individuals that simply coincides with the time over which the task repetition occurs. The second alternative, colony "priming", could also lead to an improvement in performance if workers that have participated actively in an emigration retain a certain level of arousal and, as a result, begin to respond more rapidly in a subsequent emigration. Colony "activation", the third alternative, could also result in an improved performance if increasing numbers of workers are stimulated to participate actively in successive emigrations. That is, a lowering of individual response thresholds might increase, for example, the number of workers that become transporters. Fourth, a recent emigration may facilitate another. A second emigration could occur before a colony had become fully established in a new nest. It might, therefore, be able to move again more easily. Finally, an improved performance could arise from the modification of individual or collective behaviour after a colony's experience of a previous emigration. Here, learned skills would be memorised in the short- term, but might be forgotten over longer periods. Furthermore, if a colony experiences a substantial number of repeated trials, with short intervals between each and then an extended interval before a final trial, its final performance may be only partially diminished by the hiatus. This might occur if the behavioural improvement is "reinforced" strongly by repetition.

We designed a series of three experiments to discriminate between these possibilities. The aim of the first experiment was to test if *L. albipennis* colonies can improve their performance with experience. Do colonies reduce their emigration times over successive emigrations (when such successive emigrations occur at relatively short intervals) and is any reduction in emigration time the result of a reduction in all or just some of its components? The aim of the second experiment was to establish if any such improvement in performance is lost if the interval between successive emigrations is too long. Is there an inter-trial interval beyond which the emigration time fails to improve? Such an interval is likely to exist if the underlying mechanism for improved performance involved facilitation or (a decaying) memory rather than a merely coincidental developmental change. The aim of the third experiment was to discriminate between facilitation and learning. Facilitation would be ruled out and learning would be favoured if memories were retained for longer if they were strongly "reinforced" by repeated experience.

## Methods

### Collection and culturing of experimental colonies

*L. albipennis* colonies were collected from Portland Bill, Dorset, U.K. in 1998, 1999 and 2002. All were queen-right and had brood at different developmental stages. They were housed in artificial nests consisting of two microscope slides separated by a perimeter of cardboard, to provide a nest cavity of either 54×33×1 mm (experiment 1) or 63×31×1 mm (experiments 2 and 3). Two different nest designs were used for technical reasons that are irrelevant here because we only compare emigration times for emigrations to similar nest types. For details of the method used to maintain colonies under laboratory conditions see Sendova-Franks and Franks (1995). Within all three experiments, the lighting conditions, temperature and position of the experimental arenas were kept constant. For all emigrations, in all three experiments, each occupied nest was removed from its home arena and placed in a pre-marked position within the experimental arena 6 cm from, and parallel to, a new nest (Fig. 1). Emigration was induced by the removal of the top slide of the old nest. Any outside workers remaining in the home arena were also transferred to the experimental arena. At the end of each emigration, the new nest, and any ants present in the experimental arena, were returned to the colony's home arena. We cleaned the floor of each experimental arena with water and alcohol after each emigration to remove any trail pheromones. Colonies were given an ad libitum supply of honey solution, dead *Drosophila* and water. They were deprived of access to water and food for a maximum of 4 h when they were in the experimental arenas.

### Statistical analysis

All statistical analyses, except Page's trend test for ordered alternatives, were carried out with the Minitab statistical package. Since Page's trend test is always one-tailed, the *P*-values for it and all post hoc tests were one-tailed. We used non-parametric methods because the distributions of a substantial proportion of our data sets were significantly different from normal even after transformation.

### Experiment 1: does emigration time decrease with successive emigrations?

To test whether emigration time decreases with successive emigrations, 30 colonies collected in 1998 were each emigrated 3 times at 1-day intervals. The interval length separating emigrations refers to the number of whole days between the days on which the colonies emigrated. For example, a 1-day interval would mean that a colony would emigrate on day 1 and then again on day 3. Three colonies were emigrated at a time in identical experimental arenas, each with an area of 24×24 cm and a perimeter wall 7.5 cm high. Each colony was emigrated once in each of the three experimental arenas. We randomised both the order in which colonies were emigrated and the order of the three experimental arenas in which each colony was emigrated.

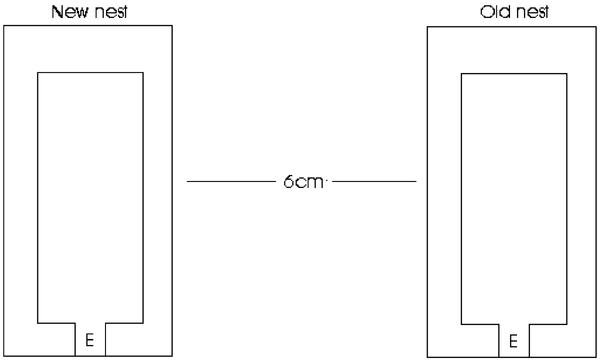

**Fig. 1** Diagrammatic representation of the relative positions of the old and new nests within the experimental arenas. The distance between the two nests was 6 cm in all experiments. The entrances to both nests (*E*) always faced the observer

For each colony we recorded: (1) the emigration time (the interval from the time the old nest was opened to the time the last brood was transported into the new nest) and (2) its three components: (a) the discovery time (the interval from the time the old nest was opened to the time the first worker entered the new nest); (b) the assessment time (the interval from the time the first worker entered the new nest to the time the first brood or adult was transported into the new nest); and (c) the transport time (the interval from the time the first brood or adult was transported into the new nest to the time the last brood was transported into the new nest).

To test whether a reduction in emigration time could result simply from an increasing number of workers becoming active transporters in successive emigrations, we estimated the number of transporters from another five colonies collected and emigrated 4 times at 1-day intervals in 1999. Every worker in each of these colonies was individually marked (Sendova-Franks and Franks 1993). However, individual identification of all transporters was not always possible and, therefore, an estimated average number was calculated. The estimated average number represents the middle of the range between the minimum and maximum possible number of transporters. The minimum number was the number of workers individually identified as transporting at least one item during an emigration. The maximum number was the number of workers individually identified as transporting at least one item during an emigration plus the number of unidentified transporters.

### Experiment 2: is there a time interval beyond which improvement is lost?

In order to determine an interval over which memory loss might occur, we carried out a series of trials with different intervals between the first and second emigrations. The 30 colonies used in this experiment were all collected on the same day and emigrated for the first time on 1 February 2002. The colonies were randomly allocated to three groups of ten. One group was emigrated a second time after 6 days. Another group was emigrated a second time after 14 days and the third group after 20 days.

### Experiment 3: does repetition reinforce?

To test for enhanced learning through repetition, 13 colonies collected in 2002 were emigrated 5 times over 14 days. A 1-day interval separated emigrations 1 through 4, and a 6-day interval separated emigrations 4 and 5.

## Results

### Experiment 1: does emigration time decrease with successive emigrations?

Emigration time decreases in successive emigrations that are separated by a 1-day interval. Among the 30 colonies emigrated, 21 (70%) achieved their fastest emigration time in their third emigration. Emigration times decreased significantly from the first to the third emigration (Page's trend test for ordered alternatives, $Z$=6.07, $n$=30, $P$<0.001; Meddis 1984; Siegel and Castellan 1988). This trend resulted from the following significant differences between emigrations. Emigration

2 was significantly faster than emigration 1 (Wilcoxon signed ranks test, *T*=5.0, *n*=30, *P*<0.001). Emigration 3 was not significantly faster than emigration 2, but emigration 3 was significantly faster than emigration 1 (Wilcoxon signed ranks test, *T*=137.0, *n*=30, *P*=0.025; *T*=5.0, *n*=30, *P*<0.001, respectively, Bonferroni correction: alpha=0.05/3=0.017; Sokal and Rohlf 1995; Fig. 2).

There was also a reduction in the time recorded for each component of emigration time over successive emigrations. In pair-wise comparisons between emigrations, the discovery, assessment and transport times for the second emigration were significantly faster than those for the first (Wilcoxon signed ranks test, *T*=39.0, *n*=30, *P*<0.001; *T*=100.0, *n*=30, *P*=0.003; *T*=20.0, *n*=30, *P*<0.001, respectively). The times for these components for the third emigration were not significantly faster than those for the second (Wilcoxon signed ranks test, *T*=271.5, *n*=30, *P*=0.792; *T*=182.0, *n*=30, *P*=0.152; *T*=157.0, *n*=30, *P*=0.061, respectively), but were significantly faster than those for the first (Wilcoxon signed ranks test, *T*=87.5, *n*=30, *P*=0.001, *T*=71.0, *n*=30, *P*<0.001 *T*=5.0, *n*=30, *P*<0.001, respectively; Bonferroni correction: alpha=0.05/3=0.017; Fig. 2).

The emigration times for the five colonies emigrated in 1999, in which all workers were individually marked, reduced significantly over four successive emigrations (Page's trend test for ordered alternatives, *L*=137, *n*=5, *P*=0.05), thus following the same trend as that shown by colonies in experiments 1 and 3 (first four emigrations, see later) where the inter-trial interval was 1 day. The estimated average number of transporters in each emigration also reduced significantly over the four emigrations (Page's trend test for ordered alternatives, *L*=145.5, *n*=5, *P*<0.01). This is the opposite trend to the one expected under the activation hypothesis (Table 1).

### Experiment 2: is there a time interval beyond which improvement is lost?

The second emigration was not significantly faster than the first when the inter-trial interval was 6 days (Wilcoxon signed ranks test, *T*=24.0, *n*=10, *P*=0.380), 14 days (Wilcoxon signed ranks test, *T*=27.0, *n*=10, *P*=0.541) or 20 days (Wilcoxon signed ranks test, *T*=35.0, *n*=10, *P*=0.793) (Table 2). Therefore, there is no evidence that emigration time changed with successive emigrations when the emigration interval was 6 days or longer. This suggests that the colonies involved were behaving as if they had had no previous experience of emigration.

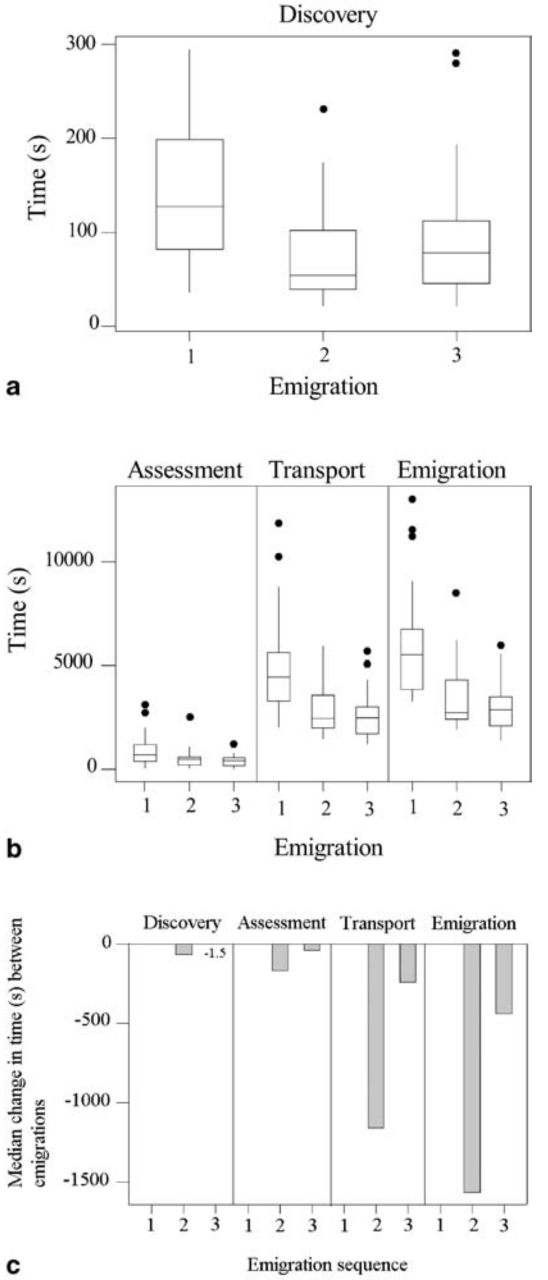

**Fig. 2 a–c** Results for the three successive emigrations of the 30 colonies in experiment 1: **a** discovery times; **b** assessment, transport and emigration times. The *numbers* 1, 2, 3 refer to the first, second and third emigration respectively. The *box* encompasses the inter-quartile range, the *line* across the *box* is the median, *whiskers* are drawn to the nearest value within 1.5 times the inter-quartile range and all remaining outlying points are marked with *black circles*; **c** median change in discovery, assessment, transport and emigration time between emigrations. The value of the median change in time for discovery between emigrations 2 and 3 is shown as a number, due to its small size

### Experiment 3: does repetition reinforce?

Emigration time decreased significantly from the first to the fourth emigration (Page's trend test for ordered alternatives, *Z*=5.38, *n*=13, *P*<0.001) (Fig. 3). This trend resulted from successive reductions in time across emigrations separated by a 1-day interval. Emigration 2 was faster than emigration 1 (Wilcoxon signed ranks test, *T*=13.0, *n*=13, *P*=0.013), emigration 3 was significantly faster than emigration 2 (Wilcoxon signed ranks test, *T*=1.0, *n*=13, *P*<0.001) and emigration 4 was faster than emigration 3 (Wilcoxon signed ranks test, *T*=12.0, *n*=13,

**Table 1** Emigration times of four emigrations by five colonies of *Leptothorax albipennis*, collected and emigrated in 1999, and estimated average number of transporters transporting in each emigration. Each row of data corresponds to a different colony. To allow tracking of individual behaviour during emigrations, all of the workers in each colony were marked with distinctive combinations of paint marks on the thorax and gaster

| Emigration 1 | | Emigration 2 | | Emigration 3 | | Emigration 4 | |
|---|---|---|---|---|---|---|---|
| Emigration | Av. no. | Emigration | Av. no. | Emigration | Av. no. | Emigration | Av. no. |
| Time (s) | Transporters | Time (s) | Transporters | Time (s) | Transporters | Time (s) | Transporters |
| 1,970 | 27.0 | 1,270 | 21.5 | 838 | 20.0 | 826 | 22.5 |
| 4,229 | 53.0 | 3,074 | 45.5 | 5,562 | 23.0 | 3,280 | 36.5 |
| 3,670 | 41.0 | 1,166 | 39.0 | 2,030 | 37.5 | 2,961 | 21.5 |
| 3,544 | 43.0 | 3,989 | 31.5 | 2,817 | 28.5 | 2,779 | 27.5 |
| 6,438 | 45.0 | 3,030 | 43.5 | 2,945 | 43.5 | 4,599 | 28.5 |

**Table 2** Emigration times for the two successive emigrations of colonies used in experiment 2. Each row of data corresponds to a different colony. Intervals between the first and second emigration were 6, 14, or 20 days

| 6-day interval | | 14-day interval | | 20-day interval | |
|---|---|---|---|---|---|
| Emigration times (s) | | Emigration times (s) | | Emigration times (s) | |
| 1st | 2nd | 1st | 2nd | 1st | 2nd |
| 4,295 | 3,655 | 5,247 | 5,972 | 5,422 | 7,881 |
| 12,538 | 9,578 | 5,818 | 8,075 | 6,458 | 6,874 |
| 5,699 | 6,793 | 10,827 | 7,938 | 3,294 | 7,614 |
| 9,000 | 7,309 | 4,451 | 4,984 | 6,846 | 16,857 |
| 7,002 | 3,696 | 4,762 | 5,642 | 3,981 | 4,004 |
| 7,779 | 6,596 | 15,608 | 8,709 | 5,886 | 7,142 |
| 10,307 | 15,240 | 6,827 | 7,080 | 6,055 | 5,015 |
| 9,973 | 11,161 | 9,681 | 7,101 | 4,257 | 3,325 |
| 8,187 | 9,052 | 16,418 | 16,899 | 8,992 | 6,507 |
| 5,550 | 5,763 | 4,353 | 5,546 | 5,512 | 4,736 |

$P$=0.011, Bonferroni correction: alpha=0.05/5=0.01, see two more comparisons below).

By contrast, after a 6-day inter-trial interval, the fifth emigration was not significantly faster than the fourth (Wilcoxon signed ranks test, $T$=64, $n$=13, $P$=0.908) yet was significantly faster than the first (Wilcoxon signed ranks test, $T$=0.0, $n$=13, $P$=0.001, Bonferroni correction: alpha=0.05/5=0.01, Fig. 3c). These results suggest that memories can be "reinforced" by repeated experience.

## Discussion

Our results demonstrate that whole ant colonies can improve their collective performance with experience (experiment 1). When the inter-trial interval is short, the emigration time of *L. albipennis* colonies decreases over successive emigrations (experiments 1 and 3). The existence of a time interval, longer than 1 day and shorter than or equal to 6 days, beyond which the benefits of a single earlier experience are lost, strongly suggests that a developmental process is unlikely to account for the improvement in performance (experiment 2).

The "primed" hypothesis, would predict a reduction in emigration time that resulted from workers responding more quickly in a subsequent emigration because they retain a certain level of arousal from an earlier emigration. However, if workers were "primed" by an earlier emigration, this could explain, for example, the reduction in the discovery and assessment times, but not necessarily the reduction in the transport time. However, analysis of the components of emigration time (discovery, assessment and transport times) in experiment 1 showed that there was a reduction in all of them. Sendova–Franks et al. (2002) found that the activity levels of *L. albipennis* workers during emigration quickly declined after transport had finished, reaching a lower asymptote between 6 and 7 h after transport began. In addition, if workers retained a certain level of arousal from an earlier emigration, one would expect all potential transporters to start transporting soon after the end of the assessment phase. When recording the behaviour of individually marked *L. albipennis* ants during emigration, Mallon et al. (2001) found that individual workers begin transporting throughout an emigration. These data were obtained from colonies that were only emigrated once and it is possible that this behaviour may have changed over repeated emigrations. However, our observations of colonies of individually marked workers during repeated emigrations with 1-day intervals suggest that transporters continue to begin transporting throughout an emigration (Langridge, personal observation). Therefore, although this hypothesis cannot be completely excluded, we consider it to be unlikely.

The "activation" hypothesis predicts a reduction in emigration time resulting from an increasing number of workers being recruited to the status of transporter in successive emigrations, possibly as a result of lower individual response thresholds. However, results from the emigrations of marked colonies showed that numbers of transporters do not progressively increase with successive emigrations. On the contrary, there is evidence that they decrease. Therefore, any reduction in transport time over a number of repeated emigrations cannot be explained by an increase in the number of transporters. There are, however, several other means by which the transport time could be reduced. For example, transporters could spend less time at the old nest choosing and picking up adults and brood or they could return more quickly to the old nest after leaving a transported item in the new nest.

In experiment 2, we established that 6 days are sufficient for colonies to forget the experience of a single

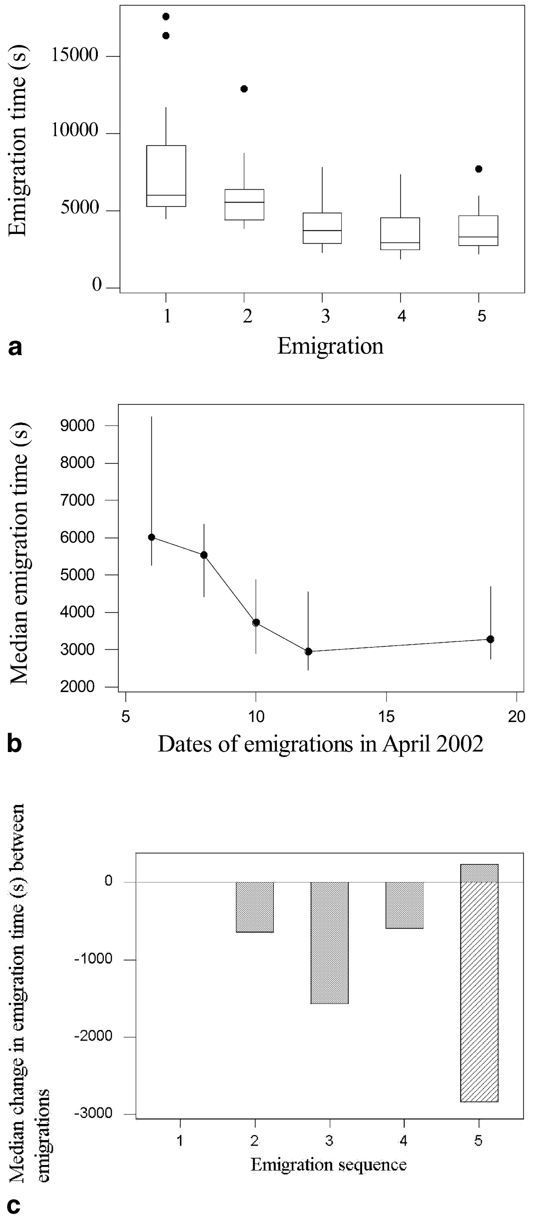

**Fig. 3a-c** Results for the five successive emigrations of the 13 colonies in experiment 3: **a** *box plots* of emigration times. Colonies were emigrated four successive times with 1-day inter-trial intervals and then for a fifth time after a 6-day interval. The *box plots* are drawn as in Fig. 2; **b** median emigration time plotted against date of emigration to illustrate the relationship between the inter-trial interval and the subsequent emigration time. *Lines* denote the inter-quartile range; **c** median change in emigration time between emigrations. Median changes between emigrations 2 and 1, 3 and 2, 4 and 3, 5 and 4 are shown as *filled bars*; median change between emigrations 5 and 1 is shown as a *hatched bar*

earlier experience. However, the results from experiment 3 suggest that, given sufficient repetition, the improvement in collective colony performance is not lost completely after a single prolonged inter-emigration interval. The fifth emigration in experiment 3 occurred after a 6-day interval and yet was significantly faster than the first emigration. Evidence from studies of brood sorting (Franks and Sendova-Franks 1992), building (Franks and Deneubourg 1997) and worker activity (Sendova-Franks et al. 2002) all suggest that colonies are fully established in new nests within 24 h of an emigration. Yet, in experiment 3 the colonies emigrated faster in their fifth emigration than they had done in their first emigration. This suggests that facilitation plays a lesser role than learning.

Taken together, our findings suggest that some form of memory and hence learning is involved in the reduction in colony emigration times and the associated improvement in collective performance. There have been many demonstrations in other animals that repeated practice could improve memory and prolong its retention at an individual level (Manning 1979; Schmidt 1982; Shettleworth 1998; Pearce 1999; Slater 1999). Our demonstration that there are longer term benefits of experience from repeated emigrations, also at a collective level, may be important in the field where colonies may emigrate frequently at one time of year and then only emigrate again after a considerable delay (Partridge et al. 1997).

So far studies of learning in social insects have focused entirely on improvement made by individuals acting in isolation and changes in individual performances have been quantified and compared (see, for example: Schneirla 1943, 1953; Schatz et al. 1994; Judd and Collett 1998; Collett and Collett 2002; Pratt et al. 2001; McLeman et al. 2002). Johnson (1991), in a pioneering study of improvements in the handling of novel seeds by harvester ants, used the terms “colony memory” and “learning at the colony level” because not only foragers but also nest workers had the possibility of learning to handle novel seeds that were first encountered by foragers and then passed onto nest workers. However, Johnson’s (1991) use of these terms when describing forager behaviour differs from the meaning that we place on these terms in our study. His focus was entirely on the behaviour of individual foragers and nest workers and quantification of “colony memory and foraging efficiency” involved the summation of data from 100 individual foragers. In contrast, our study quantified the performance of whole colonies in a process, colony emigration, in which every colony member takes part. Consequently, our data (emigration and component times) are the product of the actions of all colony members and, therefore, are a measure of the performance of the entire colony.

The tremendous collective abilities of certain insect societies have lead to them being called superorganisms (see Seeley 1989). Many recent studies have shown that such collective abilities are not merely the sum of the performances of the individual organisms that are their constituents, but that they depend on the interactions between the constituent parts (Camazine et al. 2001). The next step in our investigation of improvement in collective performance with experience will be to determine if this is attributable not just to individuals learning to improve their own performances but also to them learning to interact with one another more efficiently, e.g. swifter exchanges of items to be transported (Möglich 1978; Pratt et al. 2002; personal observations). The improved performance of whole colonies could be due to the sum of improved individual performances and/or to improved interactions and communication. Colony emigration involves many concurrent tasks. Any improvement in the performance of these tasks may need to be synchronised for colony level performance to improve. In theory, such concurrent processes might 'improve' separately, but in ways that would cause mutual interference and lead to a reduction in colony-level performance. We focused this study on an activity in which the whole colony is engaged and we showed that collective performance could improve with experience. This raises, for the first time, the possibility that collective intelligence (see Franks 1989) may involve collective learning.

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