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Author(s): Mark J. F. Brown and Deborah M. Gordon
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INDIVIDUAL SPECIALISATION AND ENCOUNTERS BETWEEN HARVESTER ANT COLONIES

by

MARK J.F. BROWN[1] and DEBORAH M. GORDON[2]
(Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA)

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Summary

This study examined how individual specialisation contributes to neighbour-stranger discrimination in the red seed-harvesting ant, *Pogonomyrmex barbatus*. The following hypothesis was tested: is there a group of ants (detectives) that specialise in interacting with non-nestmates and thus have the opportunity to learn the colony-specific odour of neighbouring colonies? Encounters were staged between laboratory colonies. Ants were marked and observed in successive encounters. There is no specialisation for interaction; the results showed that all ants were equally likely to interact with non-nestmates. The frequency of fighting between *P. barbatus* colonies varies from day to day. The following hypothesis was tested: do some ants (fighters) specialise in fighting when they interact with non-nestmates. There is specialisation for fighting; a few ants tended to fight when they met non-nestmates. There was no day-to-day effect of encounters on the number of foragers in the laboratory arena. Without specialised detectives, neighbour recognition must arise either from frequent interactions between foragers of neighbouring colonies or from communication among nestmates about the odour of neighbours. Shifts in the number of specialised fighters present in the foraging pool may underlie the day-to-day variation in fighting intensity observed in the field.

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[1] Corresponding author; e-mail: mark@ants.stanford.edu

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Introduction

Animals compete for space in which to mate, raise offspring, or obtain resources. Encounters between animals can mediate such competition (Stamps, 1994). In many ant species, colonies compete for resources (reviewed in Hölldobler & Wilson, 1990) and there are frequent encounters between neighbouring colonies (Hölldobler, 1981; Adams, 1990; Gordon, 1992). The outcome of an encounter depends on how individual workers behave when they meet non-nestmates. Here we investigate the role of individual specialisation in the behaviour of workers during encounters between colonies of the seed-harvesting ant, *Pogonomyrmex barbatus*. This species does not have morphological castes, but individual specialisation nevertheless plays an important role in the response of colonies to environmental conditions (Gordon, 1987, 1989b). In this study we ask how individual specialisation contributes to two aspects of encounter behaviour, neighbour-stranger discrimination and fighting.

As in other ant species, colonies of *P. barbatus* compete for foraging area (Gordon, 1992, 1993) and a colony's foraging behaviour is influenced by encounters with conspecific colonies (Hölldobler, 1976; Gordon, 1989a, 1989b, 1991, 1992). When foragers of neighbouring colonies meet, colonies immediately (within an hour) reduce the number of foragers traveling out towards the site of the encounter. This response appears to involve neighbour recognition: experiments showed that foraging is more strongly reduced in an encounter with ants from a neighbour colony, than in one with ants from a distant, previously unknown colony (Gordon, 1989a). Social insects discriminate nestmates (kin) from non-nestmates (non-kin) by means of colony-specific odours carried in cuticular hydrocarbons (Brill *et al.*, 1985; Bonavita-Courgourdan *et al.*, 1987; Vander Meer, 1988; Nowbahari *et al.*, 1990). Because new colonies are founded after queens disperse at random from a mating aggregation, colonies of *P. barbatus* are unlikely to be more closely related to neighbours than to more distant colonies. Thus, neighbour-stranger discrimination probably requires that ants learn the colony-specific odour of ants from neighbouring colonies.

Ants might learn the odours of neighbours in the course of repeated interactions. There is considerable day-to-day turnover in a colony's foraging force (Gordon, 1989b, 1991). This raises the question of which foragers learn to recognise neighbours through repeated interactions. There are two possibilities. First, interactions might be distributed randomly amongst all a colony's foragers. In this case, only those ants that, by chance, had enough interactions to learn a neighbour colony's odour would be able to discriminate between neighbours and strangers. Reduction of foraging in response to an encounter with neighbours would require those ants that could discriminate neighbours to disseminate information that would reduce the flow of all foragers. However, Gordon & Kulig (1996) showed that, on average, each forager has very few interactions with non-nestmates, suggesting that few ants would have enough opportunities to learn neighbour odours.

The second possibility is that a group of ants we will call 'detectives' specialise in interacting with non-nestmates. These detectives might choose to interact with non-nestmates, whilst other ants might avoid interactions (Gordon *et al.*, 1993). The detectives would be responsible for disseminating information to their nestmates, during an encounter with a neighbouring colony, that would reduce the flow of foragers to the encounter site.

Fighting is an important aspect of encounter behaviour between ant colonies (Lumsden & Hölldobler, 1983; reviewed in Hölldobler & Wilson, 1990). Interactions between non-nestmates of *P. barbatus* sometimes end in a fight but often do not (Hölldobler, 1976; Gordon, 1991, 1992; Gordon & Kulig, 1996). Two different hypotheses could explain the low frequency of fighting. First, it may be that all ants fight, but in most interactions they choose not to do so. Second, one group of workers might specialise in fighting ('fighters'), whilst other workers tend not to fight. Then only interactions that involve fighters would result in fights. Specialised fighters might be better at winning and surviving aggressive interactions, thus enabling a colony to compete more effectively. However, fighters might be less efficient foragers due to time spent fighting.

Here we exposed laboratory colonies to encounters with conspecific colonies. By following uniquely marked workers through successive encounters, we investigated whether there were specialised detectives and specialised fighters, or whether all exterior workers were equally likely to interact with and fight with non-nestmates.

In the course of these experiments, we investigated whether encounters changed the number of foragers in the arena from one day to the next. Ants in laboratory colonies of *Lasius pallitarsis* and *Myrmica incompleta* change where they forage depending upon encounters with a *Formica subnuda* worker (Nonacs & Dill, 1988, 1991). In field experiments with *P. barbatus*, an encounter with another colony on one day influences the number of ants that forage towards the encounter site on the following day (Gordon, 1992; Gordon & Kulig, 1996).

Methods

Subjects

We used two sets of laboratory colonies of *P. barbatus* for the experiments. The first set consisted of three colonies (P1, P2 and P3), each of which had a queen, brood, and 700-1100 workers (colony size fluctuated during the study). These three colonies will be referred to as the 'home' colonies. The second set consisted of five colonies (A, B, C, D and E) each of which had a queen, brood, and 75-200 workers. These five colonies will be referred to as the 'visitor' colonies. We tracked the behaviour of ants in the home colonies during encounters with ants from the visitor colonies. All eight colonies were collected from SE Arizona (for details of the collection site see Gordon, 1986) and were maintained in the laboratory on a modified version of the Keller *et al.* (1989) artificial diet. Prior to the study, P1, P2 and P3 had been kept in the laboratory for 1.5, 2.5 and 1.5 years, respectively. Visitor colony A had been in the laboratory for 2.5 years, and colonies B, C, and D had been in the laboratory for 1.5 years when they were introduced to home colony P1. Visitor colony A was 3.5 years old when it was introduced to P2 and P3, whilst colonies B, C, D, and E were 2.5 years old when they were introduced to P2 and P3. Before the study, ants from the home colonies had never met ants from the visitor colonies.

During an experiment, the home colony was kept in six plastic boxes (18 × 8.5 cm) connected by Tygon tubing. Five boxes were half-filled with Kerr Hydrock/Rapidstone dental plaster, and two of these were kept warm and moist for the queen and brood. The plasterless box was connected by Tygon tubing to an arena 30 cm above the colony boxes (Fig. 1a). The arena consisted of a nest area (119 × 58 cm), a bridge (74 × 9 cm), and a foraging area (125 × 54 cm). The arena was surrounded by plastic walls coated with Fluon so that ants could not climb out. The foraging area was connected to a second arena by a doorway in the end wall. The visitor colony was kept in a plastic box (18.5 × 8.5 cm) half-filled with dental plaster, which box was kept in the second arena. Visitor-colony ants had access to their arena through a length of Tygon tubing (Fig. 1b). The colonies were kept in a 12 : 12 hour light : dark cycle, at an ambient temperature of 85°F.

Experimental procedure

We ran the experiment 10 times, with the three home colony replicates, P1, P2 and P3 paired with four, three and three visitor colonies, respectively. Each experiment consisted of exposing one home colony to a series of encounters (or 'visits') with ants from one visitor colony on successive days. In each visit we allowed one ant from the visitor colony to enter and wander freely around the home colony's arena. In the field, encounters frequently occur between colonies of very different sizes (Gordon & Kulig, 1996), and ants from at

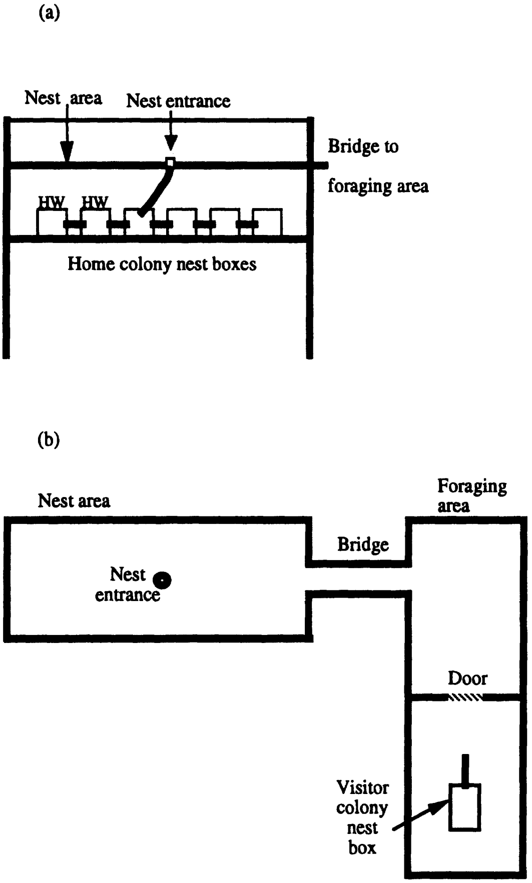

Fig. 1. (a) A vertical section through the home colony nest. HW = boxes that were heated and watered; the brood and queen lived here. The dark lines are Tygon tubing, connecting the boxes to each other and the non-plaster box to the nest entrance. (b) View from above of the arena.

least one of the colonies are likely to be familiar with the area where the encounter occurs. In these ways, conditions in our experiment resemble those of some encounters in the field.

Visits took place during a 30-min period at approximately the same time each day. A visit ended (i) when a home-colony ant fought with the visitor-colony ant, (ii) when the visitor-colony ant came within 10 cm of the home colony's nest entrance, or (iii) when the 30-min period was over. If (i) or (ii) occurred, we allowed further visits that day (with five min gaps between them) until the 30 minutes were over. In experiments with P1, an experiment ended when no visitor-colony ants entered the home colony's arena for two consecutive days. In experiments with P2 and P3, an experiment ended after 13 days. For the number of days and the total number of visits for each experiment, see Table 1.

During a visit, we tracked each visitor-colony ant's movement and her interactions with home-colony ants. In experiments with P1, an interaction was considered to occur when the antennae of one ant touched any part of the body of another ant. During most interactions, both ants involved antennated each other. However, in a small proportion of interactions, only one ant actively antennated the other. Consequently, the interaction experience of a few home-colony ants was increased, due to interactions in which they did not antennate the visitor-colony ant. To correct for this, in experiments with P2 and P3, an interaction was considered to occur only if the home-colony ant antennated the visitor-colony ant. Interactions were classified as (1) 'meet and separate', when one ant antennated the other and then moved on; or (2) 'fight', when the interaction was followed by a fight between the visitor-colony ant and the home-colony ant. In a fight, at least one ant gripped the other with its mandibles and curled its gaster as if to sting; sometimes both ants did this.

For each home-colony ant in an interaction we noted the type of interaction and the ant's interaction history. To keep track of home-colony ants and record their interaction history, we marked them with paint. We found that marking had a negligible effect on interaction and fighting behaviour (see 'Effects of marking protocol' below). To discriminate home-colony ants and visitor-colony ants, we marked all ants in the visitor colony before each experiment. Visitor-colony ants were immobilized with ice or carbon dioxide, and then marked on the gaster with Pactra fuel-proof model airplane paint. Ants of the home colony were marked only after they interacted with a visitor-colony ant. After each interaction between a home-colony ant and a visitor-colony ant, the home-colony ant was taken from the arena and marked with Unipaint oil-based paint using a colour-code that represented the type of interaction ('meet and separate' or 'fight') and the interaction history of that individual. For example, one colour signified a 'meet and separate' interaction, a second colour a 'fight' interaction. A paintmark on an ant's head would represent her first interaction, the one on her thorax, the second, and the one on her gaster, the third. For further interactions we began at the head again, with the second layer colour signifying not only the interaction type, but also the mark that was painted over. At the end of each day, we returned all newly marked home-colony ants to the home colony's foraging area.

On each day we counted the number of home-colony ants, marked and unmarked, in the arena before the first visit. These data were used both in the analysis of individual specialisation, and to measure whether the colony responded to repeated encounters with a change in the number of ants at the encounter site from one day to the next.

Statistical analysis

To test whether any ants of the home colony specialised in interacting with ants from the visitor colony, we calculated the log odds ratio (adapted from Sokal & Rohlf, 1981) for each day of each experiment. The log odds ratio is the natural logarithm of the ratio of the observed proportion of interactions between visitor-colony ants and experienced (*i.e.* marked) home-colony ants to the expected proportion of such interactions, given the known proportion of experienced home-colony ants in the foraging arena at the start of a day's visits. Thus, the log odds ratio compares the history of those home-colony ants that did interact with visitor-colony ants to the history of all home-colony ants that could have done so on a particular day. The null hypothesis is that all ants in the home colony's foraging arena have the same probability of interacting with a visitor-colony ant, regardless of their previous interaction history. In this case, the log odds ratio would be zero. If home-colony ants that have met visitor-colony ants on a previous day show a preference for interacting again with visitor-colony ants, the log odds ratio would be positive; if they prefer not to interact again with visitor-colony ants, the log odds ratio would be negative. To test whether there is individual specialisation for interaction, that is, whether the log odds ratio was consistently positive or negative, we used the Wilcoxon sign test. To test for a change over time in the preference of home-colony ants to interact with visitor-colony ants, that is, whether the log odds ratio changed linearly over successive days, we calculated for each experiment the Spearman's rank correlation coefficient using log odds ratio versus experimental day.

To test whether any ants of the home colony specialised in fighting with ants from the visitor colony we used an ordered contingency test. First we calculated the Mann-Whitney U-statistic (Moses *et al.*, 1984) for each day on which fighting occurred. For each day, the ants were divided into two groups, the 'fighters' and the 'meet-and-separaters'. The statistic compares the entire interaction history of the home-colony ants that fought with visitor-colony ants to the history of the home-colony ants that interacted with, but did not fight visitor-colony ants on each experimental day. A value greater than 0.5 means that home-colony ants who fought had previously experienced more fights than home-colony ants who did not fight. A value less than 0.5 means that the home-colony ants who did not fight had already experienced more fights than those home-colony ants that did fight. If all ants are equally likely to fight, these scores should be distributed symmetrically between zero and one with a mean of 0.5; the distribution of scores was tested using a 2-tailed sign test (Sokal & Rohlf, 1981, p. 449).

To test whether the home colony responded to encounters by changing the number of ants in the arena (the site of interactions), we looked for a consistent change in the number of ants in the home-colony's foraging arena between visit and post-visit days. We used both the Runs test (Sokal & Rohlf, 1981, p. 786) and Spearman's rank correlation coefficient to test whether changes in pre-visit counts of ants in the arena, from visit to post-visit experimental days, were consistently positive or negative.

Effects of marking protocol

Previous work (Gordon, 1989b) showed that paint-marking does not visibly affect the behaviour of *P. barbatus* ants. However, the marking protocol used in this study could conceivably affect both interaction and fighting behaviour. Repeated marking of ants might influence the probability that they will interact with non-nestmates during visits. We compared the distribution of interactions amongst individuals when all ants were marked prior to the experiment, with that distribution when ants were marked repeatedly during the experiment. The frequency distribution of interactions is the number of home-colony ants that met with each of one, two, ..., N visitor-colony ants during an experiment. For the comparison we used the combined data from all four experiments with P1 in which ants were marked repeatedly (the first four columns of Table 2), and data from an earlier experiment with P1 in which all the P1 ants were marked prior to the experiment. We compared the two distributions using the Kolmogorov-Smirnov two-sample test (Sokal & Rohlf, 1981, p. 441). The distribution of interactions did not differ between the two marking protocols (N_1 for the repeated-marking experiments $= 501$, N_2 for the pre-marked experiment $= 67$, $D = 0.09$, $p > 0.8$). Repeated marking did not affect the probability that an ant interacts with non-nestmates.

Repeated marking might affect the probability that an ant fights during an interaction with a non-nestmate. To test this, we carried out the following experiment. One hundred and eighty ants from P1 were marked and then tested for fighting behaviour in controlled trials. Each ant was placed in a Petri dish, divided in half by a plastic partition, with a non-nestmate from a novel colony. The ants were given one minute to acclimatise to the Petri dish before the partition was removed and they were allowed to interact. The trial continued for five minutes. If the P1 ant initiated a fight within this time, the ants were removed and the P1 ant was assigned to one of two groups. Group 1 ants were marked again, whilst Group 2 ants were not marked. The next day, a second trial was conducted for all ants in both groups. We recorded whether the ants initiated a fight in this second trial. Only 23 out of the 180 ants tested initiated fights in their first encounter. Of these, 22 were split into two groups of 11. Repeated marking had no effect on the probability that an ant initiated a second fight (eight of the Group 1 ants initiated a fight, versus nine of the Group 2 control ants; G-test, adjusted $G = 0.24$, $p > 0.05$).

Results

In the course of the 10 experiments, there were 2621 interactions between a home-colony ant and a visitor-colony ant (Table 1). Approximately 10% of the home-colony ants interacted with visitor-colony ants in each experiment. Home-colony ants that interacted with visitor-colony ants met one to nine visitor-colony ants in an experiment (Table 2). Most home-colony ants engaged in only one type of interaction; of 661 home-colony ants that interacted with more than one visitor-colony ant, 637 engaged in only one type of interaction (628 engaged in ‘meet and separate’ only, and 9 engaged in ‘fight’ only).

There was no individual specialisation to interact with visitor-colony ants (Fig. 2). Seven of the 10 experiments had a log odds ratio distribution consistent with the hypothesis that there was no preference for some home-colony ants to repeat interactions with visitor-colony ants (Wilcoxon signed-ranks test, P1-A, P1-B, P1-C, P1-D, P2-B, P3-D, P3-A, all $p > 0.05$). Of the three distributions that differed significantly from the null hypothesis, two, from the same home colony (P2), were in opposite directions, with one indicating significant specialisation for interaction (Wilcoxon signed-ranks test, P2-A, $N = 12$, $z = -2.67$, $p = 0.008$) and the other indicating that ants from P2 avoided repeated interactions (Wilcoxon signed-ranks test, P2-D, $N = 12$, $z = -2.82$, $p = 0.005$). The third, from home colony P3, had a marginally significant positive distribution indicating a

TABLE 1. *The number of days on which visits occurred, the number of visits, and the number and type of interactions for each replicate of the experiment*

	P1				P2			P3		
	A	B	C	D	A	B	D	D	E	A
# days	8	9	16	10	13	13	13	13	13	13
# visits	30	13	27	12	17	14	13	14	13	15
# interactions	159	260	293	137	248	479	420	180	223	222
m + s	127	251	279	137	240	478	420	180	223	218
fights	32	9	14	0	8	1	0	0	0	4
	(28)	(7)	(12)		(8)	(1)				(4)

P1, P2 and P3 are the home colonies. A, B, C, D and E are the visitor colonies. Each column of data represents one home/visitor experiment. Column order is the order in which experiments were done. m + s = meet and separate. Values in parentheses show the number of fights that were initiated by home-colony ants.

TABLE 2. *The distribution of interactions with visitors amongst home colony ants*

	P1				P2			P3		
# visitors interacted with	A	B	C	D	A	B	D	D	E	A
1	76	119	68	18	65	74	87	47	33	50
2	26	48	32	19	23	49	42	25	19	21
3	9	11	31	13	19	34	28	10	10	14
4	2	3	11	9	10	20	22	7	9	6
5			5	0	8	15	7	5	7	6
6				1		2	3		3	3
7						3	0		1	1
8						1	3		0	1
9						1			3	

P1, P2 and P3 are the home colonies. A, B, C, D, and E are the visitor colonies. Each column shows the number of home ants that interacted with a given number of visitors during an experiment. Column order is the order in which experiments were done.

slight specialisation for repeated interactions (Wilcoxon signed-ranks test, P3-E, $N = 12$, $z = -1.99$, $p = 0.047$).

There was no consistent temporal trend in the preference of home-colony ants to repeat interactions with visitor-colony ants on successive days. Of the ten experiments, nine showed no temporal change in the preference of marked ants to interact with visitor-colony ants (Spearman's rank correla-

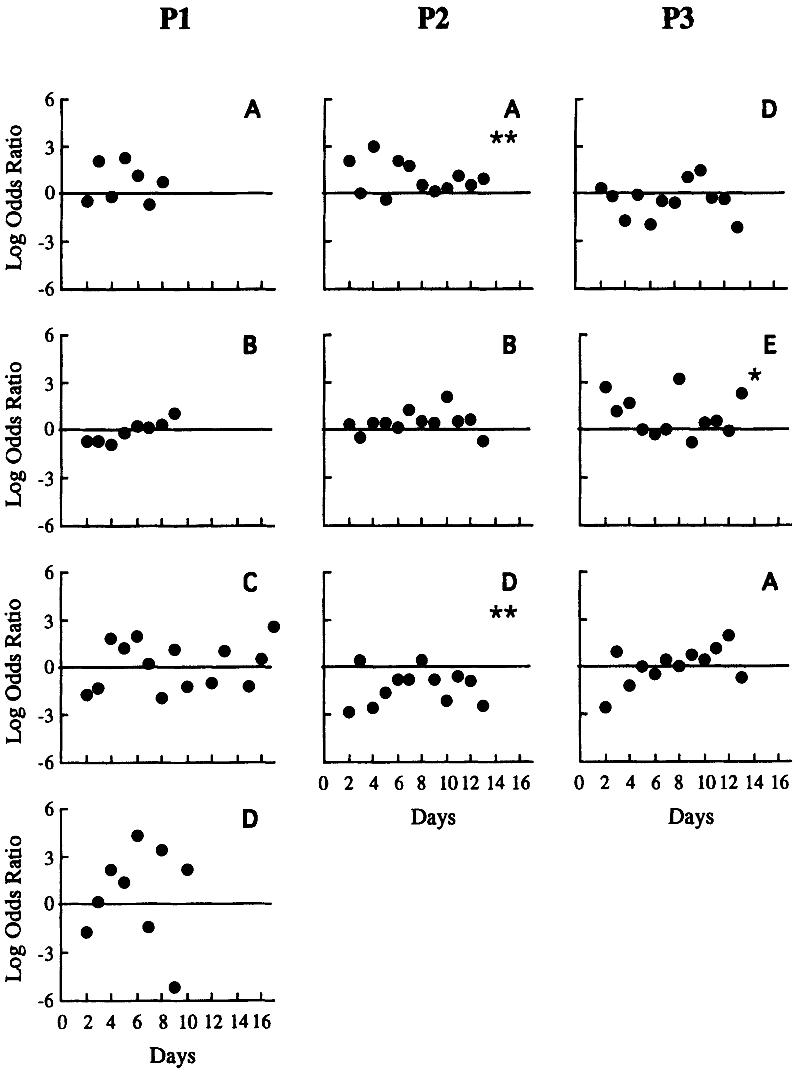

Fig. 2. The log odds ratio for each day. This is the ratio of observed interactions between experienced home ants (who had already been in an interaction) and visitors to the expected interactions given the proportion of experienced home ants in the arena. Values above zero indicate that ants that had previously interacted with non-nestmates tended to interact again. Values below zero indicate that they tended not to interact again. Each data point shows the log odds ratio for one day's visits. Each graph shows the distribution of the log odds ratio statistic for one home/visitor experiment. Each column shows the data for one home colony replicate (P1, P2 and P3). Results from seven of the 10 experiments are not significantly different from the null distribution, indicating that there are no specialised detectives. Wilcoxon signed-rank test; $^*p < 0.05$; $^{**}p < 0.01$.

tion, all $p > 0.15$); the remaining experiment showed a positive trend in the preference of marked ants to interact with visitor-colony ants (Spearman's rank correlation, P1-B, $N = 8$, $r = 0.91$, $p = 0.016$).

Fighting was rarely seen during the study; 68 out of 2621 interactions were fights and fights occurred in just six of the 10 experiments, on 37 of the 120 days on which visits occurred. Most fights were initiated by home-colony ants, and most of these were initiated by ants from P1 (Table 1). The proportion of interactions that were fights varied amongst experiments (range 0-0.2; Table 1). There was no effect of the time that colonies had been in the laboratory on the amount of fighting in an experiment. Experiments with P1 and experiments with P3 were identical with respect to the amount of time that home and visitor colonies had been kept in the laboratory, but there were many more fights during experiments with P1 than with P3. A small number of ants were responsible for all the fights; of the 46 home-colony ants that fought, 15 fought with more than one visitor-colony ant. In addition, fighting did not seem to be a product of previous interaction experience; 31 of the 46 fighters fought on their first interaction. No mortality occurred during fights.

There was individual specialisation for fighting behaviour. Ants that fought had a more combative history than ants that met and separated. For each day that a fight occurred, we calculated the Mann-Whitney U-statistic (the probability that a home-colony ant involved in a fight had a more combative history than a home-colony ant that did not fight). All U-values were greater than or equal to 0.5, indicating the presence of specialised fighters (Fig. 3). The distribution of U-values for P1 was significantly different from the distribution expected if there were no fighters (2-tailed sign test, $N = 11$, $p < 0.001$; Fig. 3), with most values being greater than 0.5, indicating that the ants that fought had experienced more fights than ants that met and separated. Neither P2 nor P3 produced sufficient data for conclusive statistical analysis (2-tailed sign test, P2, $N = 4$, $p = 0.063$; P3, $N = 2$, $p = 0.25$; Fig. 3). However, the non-significant p-values appear to be a product of the small sample size, as there were no U-statistic values less than 0.5 in either of these data sets. In fact, four home-colony ants were responsible for eight of the nine fights seen in the P2 replicate, whilst one home-colony ant was responsible for three of the four fights seen in the P3 replicate. These results are consistent with the existence of specialised

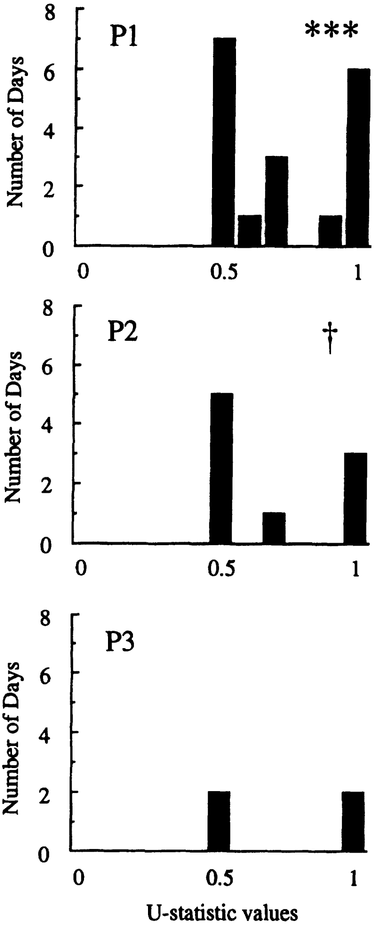

Fig. 3. The distribution of the Mann-Whitney U-statistic values for each home colony replicate (P1, P2 and P3). The statistic was calculated for each day on which fighting occurred. The abscissa shows the probability that, on a given day, the ants that fight have a more combative history than the ants that meet and separate. The bars show the number of days for which a given value was obtained. If there was no specialisation for fighting, the values would be distributed symmetrically around 0.5. The observed distributions (with all values equal to or greater than 0.5) show that ants that fight generally have a more combative history than the ants that meet and separate (2-tailed sign test; $^{\dagger}p = 0.063$, $^{***}p < 0.001$).

fighters, rather than a random distribution of fighting behaviour amongst all foragers.

There was no effect of encounters on the day to day location of foragers. The home colonies did not respond consistently to encounters by changing the number of ants in the arena from one day to the next (Runs test, nine of the 10 experiments $p > 0.05$; P1-B, $N = 13$, $r = 5$, $p < 0.05$; Spearman's rank correlation coefficient, nine of the 10 experiments $p > 0.06$; P1-C, $N = 17$, $r = -0.82$, $p = 0.001$).

Discussion

Our results show that in *P. barbatus* colonies there are no individuals that specialise in interacting with non-nestmates. In the absence of detectives, how might a colony distinguish neighbours from strangers?

One possibility is that the neighbour-stranger discrimination expressed by a colony is a consequence of each individual ant's interaction experience. If every ant must learn for herself what a neighbour ant smells like, then at least two interactions with neighbour ants are required for neighbor-stranger discrimination to be expressed (one in which to learn, and one in which to discriminate). However, the number of interactions a forager experiences with ants from neighbouring colonies is probably very low. The mean probability that an individual forager will meet an ant from a neighbouring colony on a given day is 0.06, with a range of 0.01-0.23 (Gordon & Kulig, 1996). An ant is a forager for about 30 days, after which she probably dies (Gordon & Hölldobler, 1987). Thus, on average, a forager will interact with only 1.8 ants (0.06×30) from a particular neighbour colony during the time she forages. Though this average interaction rate is low, if enough ants interact with two or more neighbour ants in their lifetime, there may still be enough foragers that recognise neighbours to enable the colony to respond differently to neighbours and strangers. A second possibility is that ants communicate information to their nestmates about the colony-specific odour of non-nestmates with whom they have interacted. In this case, only a few ants would have to meet neighbours twice, and most ants would recognize a neighbour at their first interaction with one, having already learned from their nestmates the colony-specific odour of the neighbour colony. Further work is needed to test these hypotheses.

Colony size can affect the degree of task specialisation (Gordon, 1989b). The experiments reported here were performed with relatively small colonies (a 5-year-old colony in the field contains about 12000 ants; Gordon, 1992). However, it is the foragers that encounter neighbours, and task fidelity of foragers does not vary with colony size in *P. barbatus* (Gordon, 1989b). This suggests that the lack of specialisation for interaction found in this study is not related to colony size.

A *P. barbatus* colony does have specialised fighters. In all three home colonies, a small number of ants consistently fought when they met invaders, whilst the majority of interacting ants simply met invaders and then both ants went their separate ways. The test for effects of our marking protocol provides further evidence that fighting is performed by a few individuals. If all ants were equally likely to fight, then in the test experiments less than three of the 23 ants that fought in the first trial should have fought in the second trial (overall probability of a fight = 23 fighters/108 trials), but 17 of the ants fought again. In the field, interactions between ants from neighbouring *P. barbatus* colonies rarely involve fighting (Gordon & Kulig, 1996). Our results help to explain this. Fighting may occur only when a specialized fighter happens to interact with a non-nestmate. Since the proportion of fighters in a colony is low, most interactions between non-nestmates will not involve fighters. In addition, we found that fighting did not occur on every experimental day. In the field, the proportion of encounters in which fights occur varies considerably from day to day, from 20 to 60% (Gordon & Kulig, 1996). Our results suggest this may be due to fluctuation in the number of fighters in the foraging pool.

There was no evidence that laboratory conditions strongly affected the frequency of fighting during experiments. In the field, 5% of interactions between ants of different colonies were fights (Gordon & Kulig, 1996); here 3% of all interactions were fights. The frequency of fighting we observed varied with the identities of the participating colonies. For example, P1 fought with three out of four visitor colonies, whilst P2 and P3 fought with only two and one, respectively, of the three visitor colonies they encountered. There were fights when visitor colony A encountered all three home colonies; there were never fights when colony D encountered any of the three home colonies. One explanation for this variation is that some colonies are more similar in colony-specific odour than others, and the likelihood of fighting depends on the magnitude of the difference in colony odour. There was no relation between the amount of fighting during any home/visitor pairing and the length of time that either colony had been kept in the laboratory. This suggests that variation in fighting was not an artifact of laboratory conditions. It seems unlikely that differences among colonies in the level of fighting are related to colony size, either of the home colony or the visitor colony. All home colonies were of equal size, and there was no apparent relation between visitor-colony size and the extent of fighting. Another possible and non-exclusive explanation is that the home colonies differed in their proportion of specialised fighters, contributing to variation in the frequency of fighting.

Further work is needed to relate our results on fighting behaviour to that of *P. barbatus* colonies in the field. Our study did not measure effects of colony size or of laboratory conditions. Colonies in the field compete for space within which to search for food (Gordon, 1993), but we do not know whether laboratory colonies are similarly competing for space in their foraging areas.

Since only a few ants fight, only a few ants will incur the costs of fighting (20% of all fights end in injury or death; Gordon & Kulig, 1996). Porter & Jorgensen (1981) found that ants of *P. owyheei* forage only about 14 days before they die, and suggested that the allocation of old and worn-out ants to foraging minimised the cost of this loss to the colony. *P. barbatus* foragers, on average, have a longer lifespan of about 30 days (Gordon & Hölldobler, 1987). If some ants specialise in fighting over many days, as they did in this study, and the risk of death through fighting is higher than the risk of death during other foraging activity, then, by taking on the risks of fighting, fighters may increase the longevity of other foragers. This increased longevity may allow foragers to experience more interactions with non-nestmates. Thus, the existence of specialised fighters may enable more foragers to learn the odour of neighbouring colonies.

Individual variability in aggressive behaviour occurs in many social insects, including some ants (*Rhytidoponera confusa,* Crosland, 1990; *Formica sanguinea*, Dobrzanska, 1959), and the honey bee (*Apis mellifera,* Moore *et al.*, 1987), in which the tendency to fight depends on individual age. In *P. barbatus* we observed no obvious behavioural or morphological characteristics that predicted whether an ant would fight on its first interaction with a non-nestmate. The relationship between individual age and fighting specialisation remains to be investigated. Adult *P. barbatus* workers in the laboratory get darker over time (pers. obs.), and fighters were neither noticeably darker nor lighter than ants that did not fight. Some ants may always be more aggressive than others. An alternative is that an ant might choose what to do in its first interaction and then be more likely to behave similarly in all future interactions. In this case, if the initial probability of fighting is low for all ants, only a small number of ants will ever become fighters. In addition, the initial probability of fighting could be affected by the behaviour of the other ant in an interaction. Ants from different colonies may behave in ways that are more or less likely to elicit attacks from non-nestmates; this would explain the variation we observed in fighting during experiments with different visitor colonies. Further work is needed to test these hypotheses.

The colonies we observed did not respond to encounters with non-nestmates on one day by reducing or increasing the number of ants that went to the encounter site on the following day. This may be a consequence of the small size of the experimental colony. In the field, small colonies are more likely to return to the site of previous encounters than larger colonies (Gordon, 1991, 1992).

The results of this and other studies (Lenoir, 1987; Jeanne, 1988) demonstrate the need to understand the contribution of individual specialisation to colony-level behaviour in social insects. Individual specialisation in fighting behaviour may determine the outcome of encounters, and so variation in individual behaviour may help to determine variation amongst colonies in their competitive ability. The lack of individual specialisation to interact with non-nestmates raises intriguing questions about how colonies discriminate neighbours and strangers.

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