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journal homepage: www.elsevier.com/locate/anbehavBehavioural syndromes at multiple scales in *Myrmica* antsBen B. Chapman^{a,b,*}, Harry Thain^{a,1}, Jennifer Coughlin^{a,1}, William O. H. Hughes^{a,1}^a Institute of Integrative and Comparative Biology, University of Leeds^b Division of Aquatic Ecology, Department of Biology, Lund University

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Behavioural syndromes (correlations between suites of behavioural traits) have been documented in a wide range of animals and are important for the understanding of evolution and ecology. Previous research has focused primarily on behavioural syndromes composed of individual animals: we investigated behavioural syndromes at the individual, caste and colony levels in *Myrmica* ants. We first related an individual's position on a behavioural syndrome (i.e. its behavioural phenotype) to the role it took within the colony (i.e. its caste). At an individual level, behavioural phenotype was strongly related to task allocation: individuals from the patroller caste were bolder, more aggressive and more active than individuals from both the foraging–recruit and brood–carer castes, which did not differ from each other. Second, the patroller caste exhibited a boldness–aggression syndrome that was not present in brood carers. Finally, at a colony level, sociability was correlated with boldness. Colonies containing individuals that spent more time interacting with one another were also composed of individuals that responded boldly to an introduced alarm stimulus. Furthermore, the mean behavioural scores of the patroller and brood–carer castes were positively correlated in many key behaviours, including activity level, aggression, sociability and response to an alarm, which suggests that colonies were internally concordant (behaviourally consistent across castes). Our results show conclusively that ants exhibit behavioural syndromes not only at the individual level but also at the caste and colony levels. This raises the intriguing possibility that other highly social animal groups may similarly exhibit group-level behavioural syndromes.

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A great deal of recent work in behavioural ecology has shown that the existence of animal personality (consistent individual differences in behaviour) is widespread and can be found in both behaviourally complex animals (e.g. humans, Buckholtz et al. 2008; fish, Dingemanse et al. 2007; birds, Kurvers et al. 2010) and relatively simple animals (e.g. spiders, Riechert & Hedrick 1993; crustaceans, Briffa et al. 2008). Animal personality studies often show that behaviours are consistent across both time and/or context (Bell 2007; Reale et al. 2007). A diverse array of personality traits have been studied, including boldness, activity, sociability, reactivity, exploration and aggressiveness (Koolhaas et al. 1999; Reale et al. 2007). In addition to consistency across context and over time, personality studies have also documented suites of correlated behaviours in a wide range of taxa; for example, many species have individuals that are both risk-takers and aggressive, or individuals that are risk-averse and nonaggressive (Bell 2007). These suites of

correlated behaviours at the population level have been referred to as 'behavioural syndromes' (Sih et al. 2004), whereas an individual's combination of the behaviours that form a behavioural syndrome (i.e. its position on a behavioural syndrome) is referred to as a behavioural phenotype (Bell 2007). The positive correlations between aggression and activity in *Gryllus integer* field crickets (Kortet & Hedrick 2007) and territory defence and foraging behaviour in *Agelenopsis aperta* spiders (Riechert & Hedrick 1993) are examples of behavioural syndromes. Recent work has highlighted that behavioural syndromes are also evident in social insect species at a collective level, with bee colonies showing correlations between a number of fitness-related behaviours (Wray et al. 2011). This field has received significant attention in the past few years, primarily because the existence of behavioural syndromes is widely thought to have profound implications for ecology and evolutionary biology (Sih et al. 2004).

The expression of behavioural syndromes often has a social context (Magnhagen & Bunnefeld 2009; Piyapong et al. 2010), as group living is a widespread strategy (Krause & Ruxton 2002). A great many animals, from bacteria to whales, live in groups at some stage in their life, and depending on the species, social groupings can be temporally ephemeral, such as midge mating swarms (Allee

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1931), or stable, as in matrifocal pods of killer whales, *Orcinus orca* (Baird & Whitehead 2000). Within a given population, social groups differ from one another, for example in group size, phenotypic composition and social structure (Hölldobler & Wilson 1990; Krause & Ruxton 2002). Different groups have also been documented to differ in their behaviour; for example, collective motion became increasingly coordinated with increasing density in swarms of desert locusts, *Schistocerca gregaria* (Buhl et al. 2006). Furthermore, colonies of red harvester ants, *Pogonomyrmex barbatus*, were recently shown to differ in their collective foraging behaviour (Gordon et al. 2011). What has been studied to a far lesser extent is whether groups of animals differ consistently in behaviour, or whether it is possible to characterize certain groups across a suite of correlated behaviours. Collective behaviour has been documented in many animal groups, from shoals of fish to flocks of birds (Sumpter 2006). Where groups collectively and cohesively behave as a single unit with emergent properties and behaviours, it may be possible to ascribe behavioural types to such groups, and indeed assess the existence of behavioural syndromes at higher levels of organization than the individual. Selection can also act at the group level (e.g. in social insects), which means that in some animals the evolutionary potential for group-level behavioural syndromes exists.

Here we tested the idea that multilevel behavioural syndromes exist in eusocial insects, using two biologically similar species of red ants (*Myrmica* spp.) as the model system. Ants are well suited to address this question experimentally, as they live in stable societies that have different levels of organization (individual, caste, colony). Ant societies are also highly structured and are characterized by having a division of labour, whereby different tasks are performed by different individuals within the group. In cases of such division of labour it is likely that individuals of a certain personality will be best suited to a specific task, and that patterns of task allocation might be related to an individual's position on a behavioural syndrome. Here, as part of our broader investigation into behavioural syndromes at multiple levels, we also asked whether an individual's position on a behavioural syndrome is related to the role an individual takes within the colony (i.e. its caste). To answer these questions we first classified personality for individual *Myrmica* ants that engaged in three distinct tasks: patrollers, foraging recruits and brood carers (Weir 1958). We refer to these as castes. We predicted that patrollers would be more active, aggressive and bold than other castes. Second, we assayed individuals from 14 colonies across a suite of behaviours, and present evidence to suggest that behavioural syndromes exist at a colony and caste level, in addition to at an individual level.

METHODS

Colonies of *Myrmica ruginodis* and *Myrmica rubra* (used in experiments 1 and 2, respectively) were maintained in plastic boxes (24.5 × 18.5 cm and 7.5 cm high) under identical laboratory conditions for 2–4 months before the beginning of behavioural assays. Within each housing box the colony nested in a 90 mm petri dish with a plaster base and red acetate lid. Colonies were maintained at 21 ± 3 °C on a diet of 20% sucrose solution and *Tenebrio molitor* mealworm larvae, with ad libitum water. Each colony was monogynous, containing just a single queen, but genetic analyses suggested that two of the 14 colonies assayed in experiment 2 had polygynous origins (J. Slaa, personal communication).

Experiment 1: Individual-level Behavioural Syndromes

For four colonies of *M. ruginodis*, we identified by observation over 5 days individuals that were patrollers, foraging recruits or

brood carers, and marked them with a task-specific colour of paint ($N = 23, 10, 9$ and 8 individuals per colony). Individuals were marked immediately after engaging in a task. Brood carers were individuals that actively tended the larvae and eggs within the nest; patrollers were individuals that made forays into the foraging arena when no food was present and without collecting water; and foraging recruits were individuals that entered the arena to forage following the discovery of food by a patroller. Ants were chilled on ice, given a task-specific paint spot on the thorax and an individual-specific paint spot on the abdomen, and then kept in isolation until the paint had dried before being returned to their colony. This procedure had no observable effect upon individual behaviour, with individuals continuing to engage in their task over the following days. The few individuals that we observed engaging in multiple tasks (e.g. both patrolling and foraging) were not assayed for behavioural traits, as we were interested in caste-specific differences in behaviour. We then tested the 50 marked individuals in four behavioural assays on consecutive days. All trials were recorded using a SONY DCR-HC62 camcorder, except the heterospecific encounter trial, which was scored directly by observation. We changed the paper base of assay arenas before the beginning of each trial to eliminate pheromone trials left by previous focal individuals. Following the completion of each assay we returned focal individuals to their home colony. Assays were not conducted blind, as individuals were visibly marked according to caste and individual ID.

Novel environment assay

Individual boldness and activity were determined by quantifying exploration of a novel environment. Assays were conducted in plastic containers (24.5 × 18.5 cm and 7.5 cm high) with a sheet of gridded (1 cm²) paper fixed to the floor and a refuge (cotton wool ball: 3 × 2 cm) in one corner. At the beginning of the trial, the focal ant was carefully placed beneath the refuge. We measured the time taken to emerge from the refuge ('emergence'), and then the number of squares entered ('activity1') and the time spent in the refuge ('refuge') over the following 300 s.

Heterospecific encounter assay

We quantified individual aggression by staging encounters with ants from a closely related species (*M. rubra*). We staged three encounters per focal ant in a 6.6 cm petri dish. The focal ant was placed first into the arena, and then a single heterospecific ant was introduced immediately after. The initial encounter between the ants was scored as: Flee = 0; Ignore = 1; Antennate then attack = 2; Instant aggression = 3. The heterospecific ant was then removed and the assay repeated for two further encounters, with approximately 60 s between encounters. The sum of the scores for the three encounters gave a score of individual aggression ('aggression') for each focal ant of between 0 ('nonaggressive') and 9 ('highly aggressive').

Response to alarm pheromone assay

We assessed the response of individual ants to an alarm stimulus in plastic boxes (12.2 × 8 cm and 2 cm high) with 1 cm² gridded paper on the base. The alarm stimulus was an *M. rubra* worker with a crushed head. As with most ants, *Myrmica* produce alarm pheromones in the mandibular glands that differ little in composition between species and can be released experimentally by crushing the head (Blum 1969). The focal ant was placed in the arena first, allowed to acclimatize for 120 s, and the number of squares the ant entered then counted for the next 120 s as a second measure of activity ('activity2'). The alarm stimulus was then placed in the arena within 2 cm of the focal ant and the time spent in close proximity (within 1 cm) of the alarm stimulus recorded over the next 120 s as an index of boldness in response to an alarm stimulus ('alarm').

Social tendency assay

To measure social tendency, the focal individual was placed in a plastic box (12.2 × 8 cm and 2 cm high) with 1 cm² gridded paper on the base, together with a stimulus ant from the same colony. Following a 120 s acclimatization period, we quantified the time the ants were within 2 cm of one another over a 120 s period ('social').

Following the completion of the final trial we measured the size of each ant by photographing the head and measuring the head width in ImageJ software (<http://rsbweb.nih.gov/ij/>).

Experiment 2: Colony-level Behavioural Syndromes

We assayed ants from 14 colonies of *M. rubra* for activity, aggression, boldness and social behaviour. For each colony, we counted the individuals in each colony as a measure of colony size (size range: 50–160 individuals, mean ± SD = 79 ± 37), and assayed 12 brood carers and 12 patrollers, which we identified following the same procedure as for experiment 1. All individuals were collected simultaneously from a colony and returned to their original colony following the trial. Ants were not individually marked, as we were interested here in colony- and caste-level behaviour; hence we did not carry out repeated measurements upon individuals in this experiment. We determined 'aggression' and 'social' behaviour using the same protocols as in experiment 1. We quantified individual 'activity' in a novel environment using a similar protocol to before, except the trial began immediately and lasted 180 s. We calculated the number of squares an individual entered as an index of activity: individuals that did not emerge from the refuge in this time were excluded from further analysis, as effectively activity could not be measured here (brood carer $N = 35$; patroller $N = 7$; total $N = 42$). We quantified an individual's response to an alarm cue by measuring the distance of the focal ant from the alarm stimulus (crushed cadaver) every 20 s of a 3 min trial ('alarm'), and used the mean individual distance (MID) from stimulus to calculate an index of boldness as 1/MID ('boldness'). For analysis we used the mean of individual behavioural scores to assess whether colonies or castes within colonies exhibited behavioural syndromes. We did not assess collective behavioural syndromes, that is, we did not quantify the collective behaviours of the colony. Rather we investigated whether based on the mean behaviour of individuals within the colony we found behavioural correlations. In addition to looking for correlations between different mean behaviours at the caste and colony level, we also tested for between-caste, within-colony correlations in all behaviours to assess internal concordance (i.e. do colonies with bold patrollers also have bold brood carers?).

Statistical methodology

All statistics were carried out using R (R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.). We used Spearman rank correlation tests to assess whether behaviours were correlated with one another (i.e. to investigate behavioural concordance and the existence of behavioural syndromes) across individuals in experiment 1, or castes and colonies in experiment 2. For experiment 1 we used principal components analysis to reduce the complex inter-correlated data into important axes of variation and then examined the relationship between caste and an individual's behavioural phenotype score (PC1) with general linear modelling (GLM). In experiment 2 to compare mean behaviours for different castes (patroller and brood carer) we carried out paired t tests where behaviour scores did not violate parametric assumptions (i.e. for between-caste comparisons of mean individual activity and boldness) and Wilcoxon signed-ranks tests when they did (for between-caste comparisons of mean aggression and sociability). Throughout

we used q values to control the false discovery rate for the analysis of correlated behaviours (Storey 2002). The q value of a test measures the proportion of false positives incurred (false discovery rate) when that particular test is statistically significant.

RESULTS

Experiment 1: Individual Behavioural Phenotype and Task Allocation

Many of the seven behaviours assayed were correlated with one another (Fig. 1), suggesting the existence of a complex behavioural syndrome in *M. ruginodis*. We also found a marginally significant negative relationship between boldness to an alarm and sociability at an individual level ($P = 0.07$, $q = 0.086$). Furthermore, certain behaviours were consistent within and across contexts, with the two independent measures of activity correlating strongly with one another (Spearman rank correlation: 'activity1' and 'activity2': $r_s = 0.51$, $N = 50$, $P < 0.001$, $q = 0.001$), as did within-trial measures of boldness (Spearman rank correlation: 'refuge' and 'emergence': $r_s = 0.34$, $N = 50$, $P = 0.01$, $q = 0.03$).

Principal components were extracted from the correlated behaviours: PC1 explained 47.1% of the variance in the data. We analysed data from the first three principal components but only report the results from PC1, which was the only component with significant effects, and furthermore explained the highest proportion of the variance of the data. From herein we refer to PC1 as 'behavioural phenotype score', as it encapsulates the multivariate components of the correlated behaviours that constitute the behavioural syndrome we describe in this species. High behavioural phenotype scores indicate aggressive, active, bold individuals, and low behavioural phenotype scores indicate inactive, shy, low-aggression individuals (Fig. 2). Analysis showed that worker caste had a strongly significant relationship with behavioural phenotype (GLM: $F_{2,47} = 13.5$, $P < 0.0001$; Fig. 3). Individuals from the patroller caste had a significantly higher behavioural phenotype score (first principal component) than brood-carer ants ($P < 0.0001$) and foraging recruits ($P = 0.0004$), signifying that they

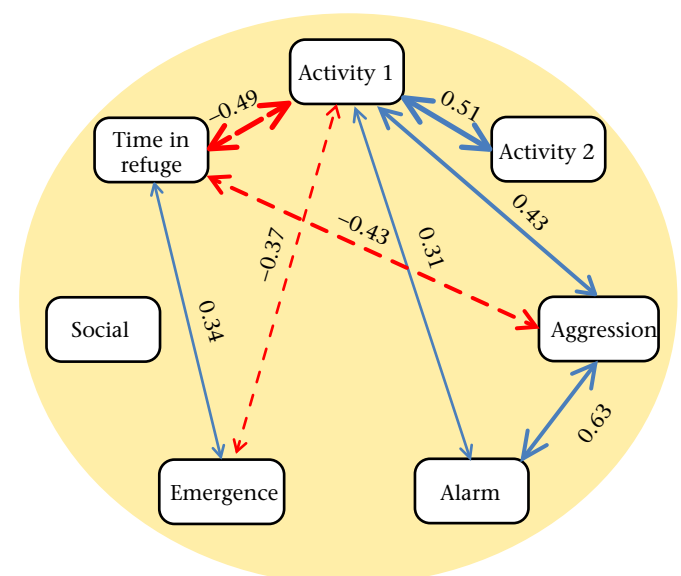


Figure 1. Within-individual correlations in behaviour from experiment 1. Arrows indicate significant relationships ($P < 0.05$; $q \leq 0.05$), with solid blue lines for positive relationships and dotted red lines for negative relationships. The thickness of the line indicates the strength of the correlation coefficient, which is also shown.

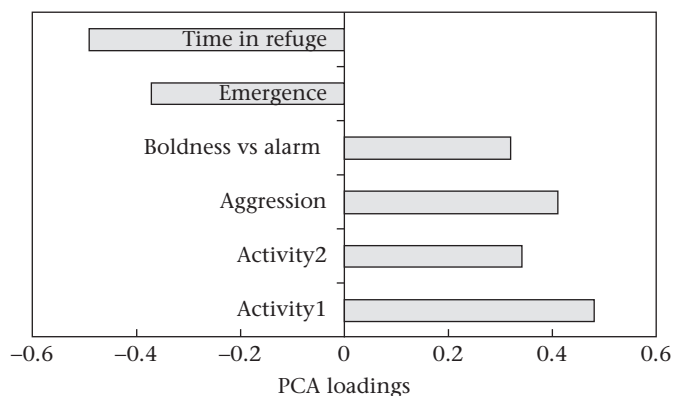


Figure 2. Loadings of variables for the first principal component axis (PC1) for different individual behaviours in experiment 1. Positive PC1 scores indicate that an individual has a bold, aggressive and active behavioural phenotype, with low refuge use and emergence scores. Conversely, a negative PC1 score indicates that an individual spends a long time in a refuge, emerges slowly, and has low aggression, boldness and activity. PCA = principal component analysis.

were more aggressive, active and bold. Foraging recruits and brood carers did not differ in behavioural phenotype score ($P = 0.26$). Castes did not differ in head width (GLM: $F_{2,52} = 1.26$, $P = 0.26$).

Experiment 2: Behavioural Correlations at Multiple Scales

Behavioural syndromes at a caste level

We found evidence of a boldness–aggression syndrome within the patroller caste of *M. rubra* (Spearman rank correlation: $r_s = 0.59$, $N = 14$, $P = 0.026$, $q = 0.046$); hence, colonies whose patrollers were bold in response to an alarm stimulus were also highly active, whereas colonies with relatively less bold patrollers were also less active. This syndrome was not evident for the brood-carer caste ($P > 0.1$). There was a nonsignificant trend for a sociability–boldness syndrome at a caste-level (patrollers: $r_s = 0.48$, $N = 14$, $P = 0.06$, $q = 0.078$; brood carers: $r_s = 0.47$, $N = 14$, $P = 0.05$, $q = 0.068$). Hence, colonies whose individuals were bold in response to an alarm stimulus also tended to contain individuals that were highly sociable. No other behavioural correlations were evident at a caste level ($P > 0.1$).

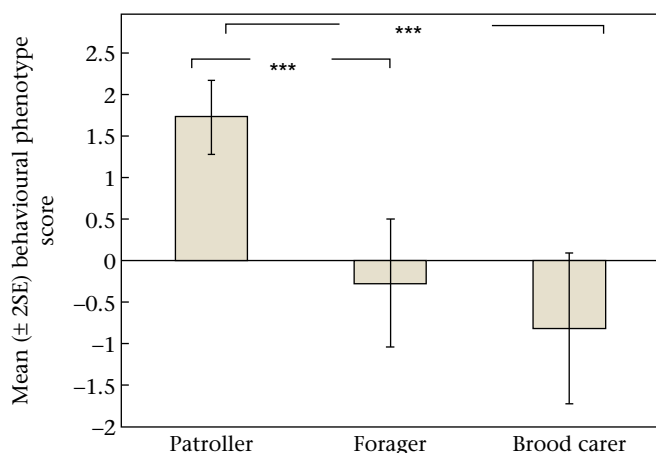


Figure 3. Behavioural phenotype score (PC1) differs, depending on worker task allocation in ants in experiment 1. High behavioural phenotype score values indicate aggressive, active, bold individuals. Conversely, low scores indicate low activity, nonaggressive, shy individuals. *** $P < 0.0001$.

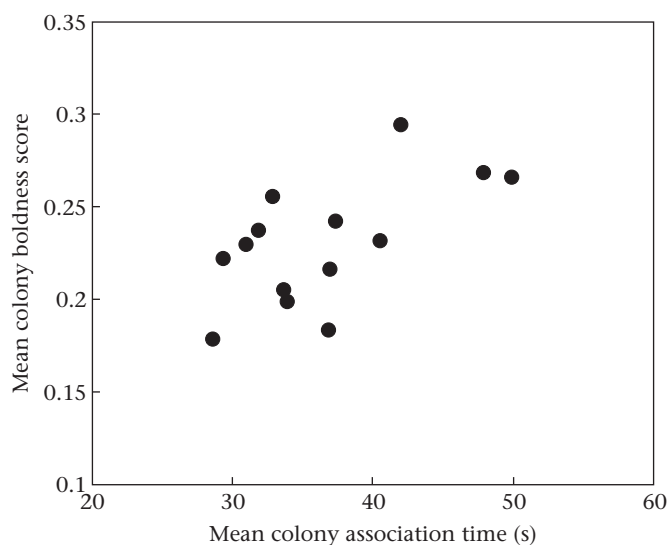


Figure 4. The correlation between mean colony boldness and association time (sociability) in experiment 2.

Behavioural syndromes at a colony level

We found evidence of a significant sociability–boldness syndrome at a colony level (Spearman rank correlation: $r_s = 0.60$, $N = 14$, $P = 0.02$, $q = 0.038$; Fig. 4). Hence colonies that contained individuals that were bold in response to an alarm stimulus also tended to contain individuals that were highly sociable. No other behavioural correlations were evident at the colony level ($P > 0.1$). There was no effect of colony size upon any of the four behaviours ($P > 0.1$).

Within-colony behavioural concordance between castes

Colonies showed strong internal concordance in mean behaviour (i.e. positive correlations) between the patroller and brood-carer castes for activity, aggression, boldness and sociability (Spearman rank: ‘activity’: $r_s = 0.73$, $N = 14$, $P = 0.004$, $q = 0.01$; ‘aggression’: $r_s = 0.61$, $N = 14$, $P = 0.02$, $q = 0.038$; ‘boldness’: $r_s = 0.74$ (Fig. 5), $N = 14$, $P = 0.002$, $q = 0.007$; ‘sociability’:

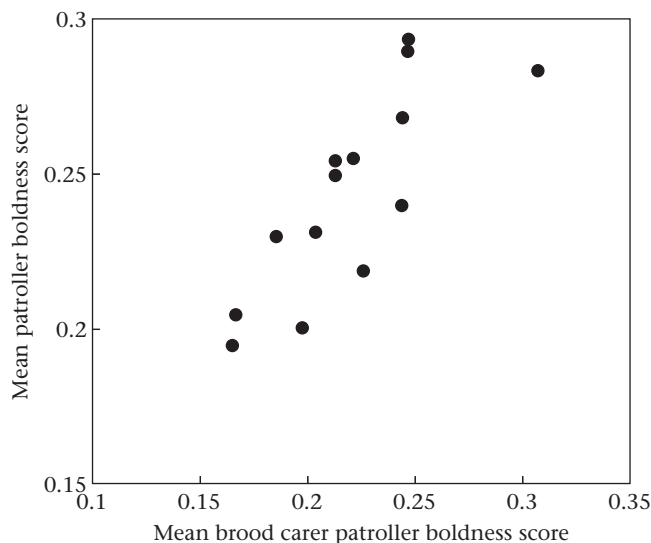


Figure 5. Within-colony concordance in behaviour in experiment 2: correlation between castes across colonies for mean individual boldness.

$r_s = 0.56$, $N = 14$, $P = 0.036$, $q = 0.05$). Furthermore, castes differed in all behaviours. Patrollers were significantly more active (paired t test: $t_{13} = -5.33$, $P < 0.001$), bolder ($t_{13} = 4.18$, $P = 0.001$) and more aggressive (Wilcoxon signed-ranks exact test: $Z = -1.93$, $N = 14$, $P = 0.05$) than brood carers. Brood carers were more sociable than patrollers, spending significantly longer associating with conspecifics ($Z = -3.11$, $N = 14$, $P = 0.002$). The degree of behavioural variability was also internally concordant for two behaviours. We found a significant positive correlation within colonies between castes for the variance of activity (Spearman rank correlation: $r_s = 0.72$, $N = 14$, $P = 0.005$, $q = 0.01$) and aggression ($r_s = 0.86$, $N = 14$, $P < 0.0001$, $q = 0.001$). No such relationship was evident for sociability ($r_s = 0.25$, $N = 14$, $P = 0.39$) or boldness ($r_s = -0.15$, $N = 14$, $P = 0.6$).

DISCUSSION

Our results show that behavioural syndromes exist at multiple scales in *Myrmica* ants. At an individual level, behavioural phenotype correlated with task allocation within a colony. We also make the novel extension that behavioural syndromes exist at caste and colony levels, with correlations between mean colony and caste behaviours, which suggests that concepts of behavioural syndromes can be applied to social groups as well as individual animals.

In our first experiment we showed that task allocation was related to an individual's behavioural phenotype score in *Myrmica* ants. Different roles within the colony require different behaviours, and an optimal evolutionary solution to task allocation would be the formation of behavioural specialists for which there is a cost to switching roles. The evolution of behavioural specialism would also necessarily lead to the existence of correlated behaviours where multiple behaviours were important for the tasks in question. In our study we showed that ants from the patroller caste had active, aggressive and bold personalities. These traits are probably important for individuals of this caste, as their function is to explore the surrounding landscape, searching for food items, and they may also encounter aggressive predators or patrollers from other colonies of ants (Hölldobler & Wilson 1990). Conversely, brood carers had a shy, passive and inactive behavioural phenotype. This caste remains within the colony, and hence high levels of activity are unlikely to be useful; their role in the case of an attack against the colony may be to protect the young and move the eggs to a new and safe location; hence a fleeing response to an alarm cue and a low aggression score. Our experiments did not investigate causality in the relationship between task allocation and individual behavioural phenotype, so we can only speculate on which trait underlies the other. Future work, such as removal experiments to force task switching, would be an important next step in understanding the relationship between caste and behavioural phenotypes. What drives the differences in behavioural phenotype at the individual level we document here in *Myrmica* ants is not known. As we measured each individual ant only once, we cannot preclude the hypothesis that differences in behavioural phenotype are ephemeral, and could be related to a transient state such as hunger level. However, the strong relationship we document between caste and behavioural phenotype score is strongly suggestive that social role is an important factor in behavioural differences. A recent study showed that experience of aggressive encounters made Argentine ants, *Linepithema humile*, more consistently aggressive (Van Wilgenburg et al. 2010). It is plausible that as individuals from each caste share similar experiences, if these experiences act to canalize different behaviours related to task specialization, this could produce a behavioural syndrome. This idea is supported by recent work that demonstrated the critical role of experience in shaping individual patterns of task allocation in the Japanese ant

Cerapachys biroi (Ravary et al. 2007). The mechanistic underpinning of role specialization in many social insects has also been shown to have a physiological basis (Robinson 2009). For example, in honeybees, *Apis mellifera*, behavioural shifts between castes are mediated by chemical signals exchanged between workers, which stimulates juvenile hormone production (Huang et al. 1998). Therefore social insects may provide a useful model system to develop questions about the relationship between physiology and behavioural syndromes, an area of significant interest in this field (Careau et al. 2008).

Our results show that, in *Myrmica* ants, the existence of behavioural syndromes is linked to an individual's social role within the colony. The role of social structure in driving and maintaining the existence of behavioural syndromes in nature has recently been a focus of debate (Bergmüller & Taborsky 2010). Behavioural niches can be shaped by social conflict, whereby individuals reduce overt conflict by taking different roles from one another, as shown by numerous examples from evolutionary game theory (Maynard Smith 1982). Here we show that a behavioural syndrome is evident in a cooperative system, and that an individual's position on the syndrome is closely related to task allocation within the social group. As the division of labour in eusocial societies increases colony efficiency and has contributed to the ecological success of social insects (Bourke & Franks 1995), the behavioural phenotypic variation we document is likely to be a crucial component in the functioning and success of the social group.

Whether behavioural syndromes predict task allocation in other animals is an interesting, and untested, question. The Lake Tanganyika cichlid *Neolamprologus pulcher* cooperatively rears its young, with some nonbreeding adults remaining in the territory to assist in offspring rearing (helpers) and essentially queuing for the breeding position, while other individuals leave their natal territory to acquire a breeding position (dispersers). Recent work showed that individuals with these different life history strategies differed in behavioural phenotype (Bergmüller & Taborsky 2007). However, to our knowledge studies placing task allocation within a social group in the context of behavioural syndromes are scarce, and future work might investigate the generality of our finding across a range of taxa that also exhibit division of labour.

Our second major finding in this work is that behavioural syndromes exist at multiple levels in *Myrmica* ants. We described behavioural syndromes at the caste and colony levels, and also showed internal concordance in many key behaviours within colonies, with positive correlations between the mean caste behavioural scores for all behaviours. We also showed that the patterns of behavioural correlations differ at different levels: ants from the patroller caste exhibited an aggression–boldness syndrome at the caste level that was not evident at a colony level or for brood carers. The aggression–boldness syndrome has been documented in many taxa: for example, in fish (Huntingford 1976; Bell & Sih 2007), birds (Groothuis & Carere 2005) and rodents (Koolhaas et al. 1999). The underlying basis for this syndrome may be individual variation in physiology via a specific hormone that acts on both aggression and boldness in this caste. Alternatively, this may be owing to variation in the age or experience of patrollers: older individuals are of less value to the colony and may be more aggressive (Van Wilgenburg et al. 2010).

At a colony level, we found a behavioural correlation between sociability and response to an alarm stimulus, with colonies composed of highly social individuals also being composed of individuals that responded boldly to the experience of an alarm cue. One intriguing (and untested) explanation for this correlation is that, for colonies with strong social networks (i.e. colonies with high 'sociability' scores), information about potential danger such as alarm cues transmits rapidly through the colony, allowing

individuals to respond more boldly to a simulated threat (Krause et al. 2007). In other words, maintaining a strong social network may remediate some of the costs to boldness to the colony. Alternatively, both behaviours in the syndrome may reflect defensive behaviours, with ants from bold colonies also staying in close proximity with other individuals from their colony in order to defend one another in a novel and potentially risky environment. Data from other studies shows that boldness–sociability syndromes exist in some species (e.g. European wrasse, *Symphodus ocellatus*; Budaev 1997) but are absent in others (e.g. zebrafish *Danio rerio*; Moretz et al. 2007). The direction of the boldness–sociability syndrome varies between species that exhibit this syndrome: our colony results showed a positive correlation, whereas results on many other species show the opposite pattern (i.e. a negative correlation between boldness and sociability, e.g. European wrasse: Budaev 1997; three-spined sticklebacks, *Gasterosteus aculeatus*; Ward et al. 2004). In group-living, noneusocial animals there are costs involved in associating with conspecifics (for example, increased competition), as well as benefits that include risk reduction in a predator encounter (Krause & Ruxton 2002). In eusocial insects, within-group competition is reduced compared with other group-living species, and this may explain the differences between the structure of the colony-level behavioural syndrome we report here and the boldness–sociability syndromes documented in noneusocial species. We found only a marginally significant trend for a relationship between boldness in response to an alarm stimulus and sociability at an individual level in red ants, and the direction of this relationship is the opposite to that we found at a colony level (i.e. there is a negative relationship between sociability and boldness), which suggests that different factors determine boldness at individual and colony levels. At the individual level, we showed that response to an alarm and sociability are connected to task allocation, with patroller ants being bolder and less social than brood-carer ants, while at the colony level our results support the idea that boldness may be influenced primarily by the strength of the social group. We note that our measure of sociability was a free-ranging trial, which means that the score of the focal individual is also dependent upon the behaviour of the stimulus ant. This may have increased the noise in these data, especially in experiment 1, which may potentially explain why sociability is not a significant component of the behavioural syndrome at an individual level.

We also showed very strong internal concordance in mean behaviour for colonies across all behaviours assayed; in other words, the mean behaviour of ants from the patroller caste was positively correlated with the mean behaviour of brood-carer ants. Hence colonies can be accurately characterized as being relatively bold or shy in response to an alarm, active or inactive, social or unsocial, and aggressive or passive. Behavioural concordance at a colony level could have a genetic basis (as all the colony workers are offspring of the queen) if behavioural traits are heritable in *Myrmica* ants, as they are in a number of other species (e.g. Brown et al. 2007). Evidence that genotype influences behaviour in social insects is abundant; for example, recent work has related task allocation to genotype in a species of leafcutter ant, *Acromyrmex echinatior* (Waddington et al. 2010). If behaviour is strongly heritable in our study species, the concordance in behavioural variability that we document in activity and aggression could be related to the amount of genetic diversity within a colony (i.e. via the queen multiple mating). This is speculative, however, and controlled experiments would be required to test this intriguing hypothesis.

Alternatively, within-colony behavioural concordance could derive from individual workers experiencing a common environment (the colony) during development. A number of studies have shown that behaviours that are often components of behavioural

syndromes are responsive to experience: for example, related to simulated predator encounters (Brown et al. 2007), environmental consistency (Chapman et al. 2010) and social environment (Chapman et al. 2008; Piyapong et al. 2010), as is individual behaviour in ants (Ravary et al. 2007; Van Wilgenburg et al. 2010). A final explanation is that the queen of the colony can actively shape the behavioural phenotypes of the colony workers via pheromonal control of worker behaviour. This has been widely documented in relation to the pheromonal regulation of the production of sexual workers by queens (e.g. Vargo & Fletcher 1986).

The question of whether the higher-order behavioural concordance and correlations represent an adaptive strategy, whereby behavioural phenotypes are a form of behavioural strategy with different phenotypes ultimately having equivalent fitness payoffs over time (Bell 2007; Reale et al. 2007; Smith & Blumstein 2008), or are simply the product of the constraining effects of physiology/pleiotropy that create nonadaptive linkage between behaviours (Bergmüller & Taborsky 2007), is crucial to our understanding of the causes and consequences of behavioural syndromes. We suggest that social insects may provide fertile systems to address these kinds of questions, as they are amenable to both experimental manipulations and studies in field conditions. Irrespective of what drives differences in behavioural phenotype between colonies, the potential consequences are numerous. Highly sociable colonies may be more susceptible to parasites and pathogens, and more exploratory and active colonies will contain individuals more likely to encounter such dangers. Behavioural syndromes have also been implicated in species' invasions (Cote et al. 2010). Furthermore, they may have important implications for population and community dynamics, landscape ecology and potential speciation (Reale et al. 2007).

Whether we might expect to find evidence of group-level behavioural syndromes in other social species is an intriguing question. Recent evidence from honeybees shows that collective behavioural syndromes are also exhibited by colonies of bees (Wray et al. 2011), and that colony behaviours are also linked to fitness measures such as colony productivity and winter survival. Groups of noneusocial animals could also potentially exhibit collective behavioural syndromes. This could occur if assortment by individual behavioural phenotype occurs, either actively through shoal choice (Krause & Ruxton 2002), or passively via differences in habitat use, activity patterns (Pike et al. 2008) or provenance (if kin groups are formed and personality is heritable). Work in this fascinating area is in its infancy, although the recent surge of research into collective behaviour that focuses on the emergent behaviour of social groups of individuals (Sumpter 2006) may act as a conduit for assessment of the existence and importance of group-level behavioural syndromes.

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References

- Allee, W. C. 1931. *Animal Aggregations*. Chicago, Illinois: University of Chicago Press.
- Baird, R. W. & Whitehead, H. 2000. Social organisation of mammal eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, **78**, 2096–2105.
- Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B*, **274**, 755–761.
- Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in three-spined sticklebacks *Gasterosteus aculeatus*. *Ecology Letters*, **10**, 828–834.
- Bergmüller, R. & Taborsky, M. 2007. Adaptive behavioural syndromes due to strategic niche specialization. *BMC Ecology*, **7**, 10–15.

- Bergmüller, R. & Taborsky, M. 2010. Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, **25**, 504–511.
- Blum, M. S. 1969. Alarm pheromones. *Annual Review of Entomology*, **14**, 57–80.
- Bourke, A. F. G. & Franks, N. R. 1995. *Social Evolution in Ants*. Princeton, New Jersey: Princeton University Press.
- Briffa, M., Rundle, S. D. & Fryer, A. 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B*, **275**, 1305–1311.
- Brown, C., Burgess, F. & Braithwaite, V. A. 2007. Experiential and heritable effects of boldness on a tropical poeciliid. *Behavioral Ecology and Sociobiology*, **62**, 237–243.
- Buckholtz, J. W., Callicott, J. H., Kolachana, B., Hariri, A. R., Goldberg, T. E., Genderson, M., Egan, M. F., Mattay, V. F., Weinberger, D. R. & Meyer-Lindenberg, A. 2008. Genetic variation in MAOA modulates ventromedial prefrontal circuitry mediating individual differences in human personality. *Molecular Psychiatry*, **13**, 313–324.
- Budaev, S. V. 1997. Alternative styles in the European wrasse, *Symphodus ocellatus*: boldness-related schooling tendency. *Environmental Biology of Fishes*, **49**, 71–78.
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Miller, E. R. & Simpson, S. J. 2006. From disorder to order in marching locusts. *Science*, **312**, 1402–1406.
- Careau, V., Thomas, D., Humphries, M. M. & Réale, D. 2008. Energy metabolism and animal personality. *Oikos*, **117**, 641–653.
- Chapman, B. B., Ward, A. J. W. & Krause, J. 2008. Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, **76**, 923–929.
- Chapman, B. B., Morrell, L. J. & Krause, J. 2010. Unpredictability in food supply during early life influences boldness in fish. *Behavioral Ecology*, **21**, 501–506.
- Cote, J., Fogarty, S., Weinersmith, K., Brodin, T. & Sih, A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B*, **277**, 1571–1579.
- Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, **76**, 1128–1138.
- Gordon, D. M., Guetz, A., Greene, M. J. & Holmes, S. 2011. Colony variation in the collective regulation of foraging by harvester ants. *Behavioral Ecology*, **22**, 429–435.
- Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.
- Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Harvard University Press.
- Huang, Z. Y., Plettner, E. & Robinson, G. 1998. Effects of social environment and worker mandibular glands on endocrine-mediated behavioural development in honey bees. *Journal of Comparative Physiology A*, **183**, 143–152.
- Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, **24**, 245–260.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruijs, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behaviour and stress physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.
- Kortet, R. & Hedrick, A. 2007. A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment. *Biological Journal of the Linnean Society*, **91**, 475–482.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.
- Krause, J., Croft, D. P. & James, R. 2007. Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology*, **62**, 15–27.
- Kurvers, R. H. J. M., Oers, K. V., Nolet, B. A., Jonker, R. M., Van Wieren, S. E., Prins, H. T. H. & Ydenberg, R. C. 2010. Personality predicts the use of social information. *Ecology Letters*, **13**, 829–883.
- Magnhagen, C. & Bunnefeld, N. 2009. Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proceedings of the Royal Society B*, **276**, 3369–3375.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Moretz, J. A., Martins, E. P. & Robison, B. 2007. Behavioral syndromes and the evolution of correlated behavior in zebrafish. *Behavioral Ecology*, **18**, 556–562.
- Pike, T. W., Samanta, M., Lindström, J. & Royle, N. J. 2008. Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B*, **7**, 2515–2520.
- Piyapong, C. P., Krause, J., Chapman, B. B., Ramnarine, I. W., Louca, V. & Croft, D. P. 2010. Sex matters: a social context to boldness in guppies (*Poecilia reticulata*). *Behavioral Ecology*, **21**, 3–8.
- Ravary, F., Lecoutey, E., Kaminski, G., Châline, N. & Jaisou, P. 2007. Individual experience alone can generate lasting division of labor in ants. *Current Biology*, **17**, 1308–1312.
- Reale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour*, **46**, 669–675.
- Robinson, E. J. H. 2009. Physiology as a caste-defining feature. *Insectes Sociaux*, **56**, 1–6.
- Sih, A., Bell, A. & Johnson, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Smith, B. R. & Blumstein, D. T. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, **19**, 448–455.
- Storey, J. D. 2002. A direct approach to false discovery rates. *Journal of the Royal Statistical Society, Series B*, **64**, 479–498.
- Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B*, **361**, 5–22.
- Van Wilgenburg, E., Clémencet, J. & Tsutsui, N. D. 2010. Experience influences aggressive behaviour in the Argentine ant. *Biology Letters*, **6**, 152–155.
- Vargo, E. L. & Fletcher, D. J. C. 1986. Evidence of pheromonal queen control over the production of male and female sexuals in the fire ant, *Solenopsis invicta*. *Journal of Comparative Physiology A*, **159**, 741–749.
- Waddington, S. J., Santorelli, L. A., Ryan, F. R. & Hughes, W. O. H. 2010. Genetic polyethism in leaf-cutting ants. *Behavioral Ecology*, **21**, 1165–1169.
- Ward, A. J. W., Thomas, P., Hart, P. J. B. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **55**, 561–568.
- Weir, J. S. 1958. Polyethism in workers of the ant *Myrmica*. *Insectes Sociaux*, **5**, 97–128.
- Wray, M. K., Mattila, H. R. & Seeley, T. D. 2011. Collective personalities in honeybee colonies are linked to colony fitness. *Animal Behaviour*, **81**, 559–568.