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ORIGINAL PAPER

Colony genetic diversity affects task performance in the red ant *Myrmica rubra*

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Abstract High relatedness and low genetic diversity among individuals in a group is generally considered crucial to the evolution of cooperative behaviour. However, in about a third of social insect species, intracolonial genetic diversity is increased because of derived polyandry (multiple mating by queens) and/or polygyny (multiple reproductive queens). Several studies have shown that increased intracolonial genetic diversity can enhance task performance in honey bees, but evidence of such effect in other social insects is still lacking. Why increased genetic diversity has evolved in some, but not all species, is a fundamental question in sociobiology. In this study, we investigated the effect of intracolonial genetic diversity on the task of nest migration, using the facultatively polyandrous and polygynous red ant *Myrmica rubra*. Genetic diversity significantly affected migration speed, but its effects were context dependent. Migration speed correlated positively with genetic diversity in one experiment in which migrations were into a known nest site, due to quicker transfer of brood into the new nest once consensus was reached. However, in a another experiment in which migration included scouting for new nest sites, migration speed correlated negatively with genetic diversity, due to slower discovery of new nest sites and slower transfer of brood into the new nest. Our results show for the first time that genetic diversity affects task performance in a social insect other than the honeybee, but that it can produce contrasting effects under different conditions.

Keywords Colony migration · Genetic diversity · *Myrmica rubra* · Polyandry · Polygyny · Task performance

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Introduction

In organisms as diverse as mammals, birds, insects and microbes, high genetic relatedness between group members appears to have been crucial to many of the evolutions of highly cooperative societies (Hamilton 1964a, b; Hughes et al. 2008a; Cornwallis et al. 2010; Kuzdzal-Fick et al. 2011; Lukas and Clutton-Brock 2012). Individuals can gain indirect fitness by helping to rear their relatives, and these benefits are highest when individuals are closely related, i.e. share a single mother and father (Hamilton 1964a, b). In the eusocial Hymenoptera (ants, some bees and some wasps), monandry (queens being inseminated by a single male) and monogyny (colonies headed by a single functional queen) are indeed ancestral, but reduced genetic relatedness among colony members due to polyandry or polygyny has evolved in about a third of species (Hughes et al. 2008a, b). Despite the increased potential for reproductive conflict among less related individuals, several studies have shown that colonies with more genetically diverse individuals can perform better. There is convincing evidence that genetic diversity improves disease resistance in ants and bees (Tarpy 2003; Hughes and Boomsma 2004; Seeley and Tarpy 2007; Reber et al. 2008; Ugelvig et al. 2010), even in the obligately monandrous and

monogynous bumble bee *Bombus terrestris* (Baer and Schmid-Hempel 1999, 2001). In addition, there is strong evidence that genetic diversity improves social organisation and task performance in the extremely polyandrous honeybee *Apis mellifera*. Genetically diverse honeybee colonies show better intranidal temperature homeostasis, increased foraging rates and increased colony growth (Jones et al. 2004; Mattila and Seeley 2007). Genetic effects on individual task propensity or performance are well documented (e.g. Constant et al. 2012; Jones et al. 2004; Robinson and Page 1988; Waddington et al. 2010) and underlie the link between genetic diversity and social performance, potentially through enhanced division of labour in genetically diverse groups (e.g. Robinson and Page 1989; Bonabeau et al. 1996; Beshers and Fewell 2001; Myerscough and Oldroyd 2004; Tarapore et al. 2010).

Several studies have looked at the correlation between genetic diversity and colony growth or colony fitness in species other than honeybees. In the monogynous and monandrous bumble bee *B. terrestris*, the effect of experimentally increased genetic diversity on colony fitness followed a U-shaped function, with small increases in genetic diversity being costly and higher levels resulting in similar fitness to the natural monandrous state (Baer and Schmid-Hempel 1999, 2001). In the monogynous harvester ant *Pogonomyrmex occidentalis*, genetic diversity was positively correlated with colony growth rate, and consequently with colony survival and achievement of a sufficient size to reproduce (Cole and Wiernasz 1999). In two other ant species, no correlation between genetic diversity and colony growth or number of sexuals was found (Sundström and Ratnieks 1998; Fjerdingstadt et al. 2003). In the above-mentioned studies where genetic diversity did affect colony growth, it is unknown whether this correlation was caused by improved disease resistance or improved colony organisation, or both. In the only experimental study to date on colony organisation in social insects other than the honeybee, Rosset et al. (2005) found no effect of genetic diversity on short-term task efficiency in the monandrous but polygynous ant *Linepithema humile*. A better understanding of the effect of genetic diversity on social organisation across species is therefore needed to explain why some, but not all, social insects evolved polyandry and/or polygyny.

Colony migration is a highly social event, involving movement of all colony members. It first requires the discovery of a new nest site, followed by assessment of nest site quality (through a collective decision-making process) and, if consensus has been reached, transfer of nestmates and brood into the new site (reviewed in Visscher 2007). During nest migration, the colony's queen(s) and brood are exposed to potential predators, making migration a vulnerable step in the colony's life cycle. Migration speed is therefore likely to affect colony fitness. Migration patterns and decision-making rules have been studied in a variety of social insects (*A. mellifera*: see Visscher 2007; *Myrmica rubra*: Abraham and Pasteels 1980; *Temnothorax* ants: Franks et al. 2002; Dornhaus et al. 2004; Pratt 2005; Pratt and Sumpter 2006; *Pachycondyla obscuricornis*: Pezon et al. 2005; *Aphaenogaster senilis*: Avargues-Weber and Monnin 2009; *L. humile* and *Tapinoma sessile*: Scholes and Suarez 2009; *Monomorium pharaonis*: Evison et al. 2012a, b). For example, ants and bees assess the number of workers present in a potential nest site, a process referred to as "quorum-sensing" (see Visscher 2007). Initially, some nest mates might be recruited to a new nest site, e.g. through tandem running (*Temnothorax* species) or waggle dancing (honeybees). However, the final stage of emigration, through fast recruitment of nest mates and carrying of brood in ants (e.g. Pratt et al. 2002; Seeley and Visscher 2003, 2004), only takes place when numbers of nestmates in the new nest are sufficiently high, i.e. a quorum threshold has been met. Several social and ecological parameters have been tested for their effect on colony migration and it has been found that both colony size and environmental conditions affect migration patterns, including total migration time (Rosset et al. 2005), nest site discovery time and quorum threshold (Franks et al. 2003; Dornhaus et al. 2004; Dornhaus and Franks 2006). However, effects of genetic diversity on migration speed have not yet been investigated. Natural nest migrations can be triggered by various factors including nest disturbance, nest microclimate change, predation, competition, and improvement of foraging efficiency (Hölldobler and Wilson 1990). When the old nest is still intact (unforced migrations), accuracy of selecting the best available new home is more important than decision speed. When the resident nest is destroyed (forced migrations), there is a critical need for immediate shelter, and migration speed becomes more important than accuracy (Pratt and Sumpter 2006).

Here, we investigate whether genetic diversity affects task performance in a social insect other than the honeybee, using the social task of nest migration. We used the facultatively polyandrous and polygynous red ant *M. rubra* as our study species because this common European species shows a wide natural range of intracolonial genetic diversity (e.g. Pearson 1983), and nest migration occurs frequently under natural conditions, especially when colonies are small (Dobrzanska and Dobrzanski 1976 cited in Abraham and Pasteels 1980). In two migration experiments, we tested for effects of genetic diversity on migration speed and nest site selection under different conditions.

Materials and methods

Study species

Seventeen *M. rubra* colonies were obtained from two populations in Germany during summer 2009, one near Berlin

(Population 1, N=13) and one near Boppard (Population 2, N=4). Colonies were housed in the lab in plastic boxes (22×16×7 cm) with a dark brood chamber (Ø=9 cm), and kept at room temperature (20 °C) and natural light conditions. Colonies were provided with fresh mealworms and 10 % sucrose solution at least three times a week, and water ad libitum. Colonies were hibernated from 1 December 2009 until 13 April 2010, at 7 °C. The migration experiments started after hibernation (summer 2010), so that during the experiments the colonies were at the same point in their yearly colony cycle. All colonies contained only a single queen at the time of the experiments. For both migration experiments, colonies contained at least 20 workers and 7 brood items (larvae+pupae). The number of workers (20–180) and brood (7–130) were not significantly different between Experiments 1 and 2 (paired t test, t_{13}=1.01, P=0.33 and t_{13}=0.66, P=0.52, respectively). Our colonies were small with regard to natural colony size, which ranges from several hundred to thousands of workers (e.g. Elmes 1991; Seppä and Walin 1996). Neither the amount of brood nor the number of workers was correlated with genetic diversity (Pearson's correlation, Experiment 1 brood: r=−0.24, N=17, P=0.36, workers: r=−0.06, N=17, P=0.83, Experiment 2 brood: r=−0.08, N=14, P=0.78, workers: r=0.03, N=14, P=0.93). The amount of brood was positively correlated with the number of workers (Pearson's correlation, Experiment 1: r=0.60, N=17, P=0.01; Experiment 2: r=0.73, N=14, P=0.003). See Online Resource Table S1 for additional information on colony size during Experiments 1 and 2.

During both experiments, two nest types were offered that differed in internal cavity size, entrance size, and/or the amount of light that entered the cavity, to test for potential effects of genetic diversity on nest site choice. Experience can improve migration speed (e.g. Langridge et al. 2004, 2008), but none of the colonies had been forced to migrate in the year prior to the experiments.

Experiment 1

The first migration experiment was conducted with 17 colonies over 3 days (July 21, 22, 23, five to six colonies per day). Colonies were forced to migrate out of their existing nest site and select one of two new sites to test for the effect of genetic diversity on migration speed and nest site selection (see Online Resource Figure S1 for a scheme of the experimental set-up). Colonies were installed in larger transparent migration boxes (35×55×15 cm) the preceding afternoon by carefully transferring the nest box and all exploring workers, all food and the water tube. Fluon was applied to the top edges of the boxes to prevent ants from escaping. Under the box, a 1-cm-grid paper numbered along the length was used to divide the box into two areas: around the old nest and around the new nests (with the cut-off line along the 37 cm mark). The old nest was centred on the 5 cm line. The following morning, all dead ants and food were removed, and two new potential nest sites (a small box and a tube) were placed in the migration box, at 35 cm from the old nest and 16 cm apart. The nest tube consisted of a 15-ml test tube (Ø 17 mm), filled half with water blocked with cotton wool, leaving the top 5 cm empty for nesting, wrapped in a layer of red foil. The nest box consisted of a closed plastic box covered in red foil, about 1 ant height (4.5×3.2×0.2 cm), with a small entrance hole (Ø 2 mm) and moist cotton wool in the back. Therefore, both nest types were dark and humid, as preferred by *Myrmica* ants (Abraham and Pasteels 1980), but differed in entrance size (small in box and large in tube), height (low in box and high in tube), and volume (ca. 2 cm^3 in box and 11 cm^3 in tube). *Myrmica* ants prefer confined spaces (Abraham and Pasteels 1980), and we therefore hypothesized that the box would be preferred over the tube. Immediately after placement of the two new nests, migrations were forced by removing the top lid of the resident nest and shining a hot bright light on it (100 W clear bulb, after Abraham and Pasteels 1980). The number of workers and brood inside and outside of the nest was counted immediately after opening, and the presence of the queen was verified. Hereafter, every 10 min (every 5 min during the first half hour), the number of ants and brood in the old nest, in each of the new nests, and outside of the nests (around the old nest and around the new nests) was counted. The experiment ended when 95 % of the brood was moved into one of the new nests, or, in the cases where colonies split, when brood was located at two locations for more than 2 h.

Experiment 2

The second experiment was very similar in set-up to the first experiment with two important exceptions: first, the new nest sites consisted of two tubes, instead of one box and one tube, because most colonies chose to migrate into the tube during Experiment 1. Both tubes contained moist cotton wool as in the first experiment, but one was transparent and the other wrapped in red foil as in the first experiment. *Myrmica* ants prefer dark nest sites over light ones (Abraham and Pasteels 1980), so that the ants could choose between one "good quality" nest site (i.e. dark tube) and one "poor quality" nest site (i.e. light tube). Second, and most importantly, the new nest sites were already available when the colonies were moved into the migration boxes, the afternoon before the experiment. Colonies were free to explore the new nest sites before start of the experiment, which can make subsequent migrations quicker (Stroeymeyt et al. 2010). The experiment was conducted with 16 colonies (in the 17th colony worker population had decreased to less than 20 workers) over 3 days (August 4, 5, 6). However, one colony had already migrated into the dark tube before the start of the migration experiment, and in another colony the queen had disappeared. These two

colonies were excluded from further analyses resulting in N= 14 colonies for Experiment 2.

Microsatellite analysis

To establish the intracolonial genetic diversity, 16–32 workers per colony were genotyped before the experiments at six polymorphic microsatellite loci (*MP-67*, *Msca7*, *Msca50*, *MS26*, *MS86*, *MS3.62*; Steiner et al. 2006; Vepsäläinen et al. 2009), or, for four colonies, all 68–96 workers in the colonies were genotyped afterwards. A middle leg was removed and legs were stored individually in 100 % ethanol and at −20 °C until extraction. DNA was isolated from the legs using Chelex resin (35 μl 5 % Chelex solution, boiled for 15 min). DNA was amplified by PCR using fluorescent-dye labelled primers (Applied Biosystems) and GoTaq® Flexi DNA polymerase (Promega) in a Veriti thermal cycler (ABI). Amplification conditions and annealing temperatures (Ta) differed between primers (see Online Resource Table S2). Amplified fragments were detected on a 3130*xl* capillary sequencer (ABI) and analysed using GeneMapper v3.7 (Applied Biosystems). See Online Resource Table S2 for additional information on heterozygosity of the loci. Average genetic relatedness of the workers within a colony (r) was estimated using the Relatedness 5.0.8 software (Queller and Goodnight 1989). The colonies from near Berlin and Boppard in Germany were considered as having come from two populations (Populations 1 and 2, respectively). Population allele frequencies were calculated in the programme for each population, weighing nests equally, and using a frequency bias correction by nest. The precise association between genes and migration behaviour is unknown so, similar to previous studies (e.g. Cole and Wiernasz 1999; Fjerdingstad et al. 2003), we used 1−r as a proxy for genetic diversity because this estimates the whole-genome within-colony genetic diversity resulting from polyandry and/or polygyny (Queller and Goodnight 1989), and overall correlated positively with other diversity measures (Nei's diversity index: r=0.84, P<0.001; standardized allelic richness: ρ=0.39, P=0.12; Shannon's diversity index: r=0.66, P=0.004; Online Resource Table S1). Calculations were performed at the end of the observation period so that observations were performed blind with respect to the genetic diversity of colonies.

Statistical analyses

Total migration time was taken as the time from destruction of the old nest until at least 95 % of all brood was moved into one of the new nests. However, two colonies split their brood over two sites and remained split at the end of the day in both experiments. When the amount of brood at either site did not change by more than 5 % over a 2-h time period, we considered splitting to be the final stage of the emigration process. In these cases, we defined total migration time as the time from destruction of the old nest until there was no more visible movement of brood to and between the sites. During Experiment 1, in the two colonies that split, there was still some movement of brood into the box until the end of the experiment so that we had no clear measure of total migration time. For these two colonies, we used truncated data in the analysis of total migration time. In Experiment 2, there was no more visible movement of brood to and between the sites for the two colonies that split, and thus we had a clear measure of total migration time. No truncated data were used in the linear models.

Nest site discovery time was taken as the time from destruction of the old nest until an ant entered one of the two new nest sites. Clear recruitment of workers to a new nest was not observed, but a sudden increase in workers in a new nest coincided with or was quickly followed by transportation of brood into the new nest. Therefore, we defined the quorum threshold as the number of workers present in the potential nest site when transportation of brood into this nest started. The quorum threshold was calculated by taking the average of the number of workers present in the new nest during the observation (i) just before brood was moved in and (ii) when the first brood was observed in the new nest. The difference between these two numbers was generally low, with a median difference of 4 workers for Experiment 1, and 3.5 workers for Experiment 2.

In Experiment 1, nest type preference was tested for significance using a Binomial test. To test for loyalty to their first finding, a Fisher Exact test was used. A GLM with binary response variable was used to test for effects of genetic diversity, colony size, population and day of experiment on nest preference. Differences between colonies that chose to migrate into the box and those that migrated into the tube in total migration time, quorum threshold and time to reach quorum were tested for significance using t tests. To test for effects of genetic diversity and colony size on total migration time and scouting intensity we used parametric (Pearson's correlation coefficient r) and non-parametric (Spearman rank correlation r_s) correlation tests. Colonies that moved into the box were different from those moving into the tube in many aspects (see "Results") and could therefore not be pooled for analyses. Colonies that moved into the tube were tested for effects of genetic diversity on different migration steps (N=11). Too few colonies moved into the box for statistical analysis (N=4). Colonies were pooled for the analysis of discovery time of the new nest, before nest site selection had taken place.

In both Experiments, we used general linear models (LM), or generalized linear models (GLM) with a negative binomial error structure and log link function, to test for effects of genetic diversity and colony size (number of workers and/or amount of brood) on various migration steps (i.e. total migration time, discovery time of a new nest, ant minutes exploring

before a new nest was found (sum of number of ants present around the new nest sites at 5–10 min intervals multiplied by the preceding time interval (min), until a worker entered a new nest), quorum threshold, time to achieve quorum from first discovery of the nest, and migration time after achieving quorum). We included population or day of the experiment as a factor, to reduce variance in response due to differences between populations or between experiment days. In all cases, the minimal adequate model was obtained by stepwise deletion tests (likelihood ratio tests for change in deviance; Crawley 2007). *P* values reported for the significance of a variable in the model give results of these deletion tests. Migration steps were tested for correlation with total migration time using a Pearson's correlation test (discovery time, time to reach quorum, and time needed to move brood into the new nest). All statistical tests were conducted in R version 2.10.1 (R Development Core Team 2009). The "MASS" package was used for the negative binomial regression models (Venables and Ripley 2002). All tests were two-tailed with a significance level of α=0.05, unless stated otherwise.

Results

During both experiments, most colonies started moving their brood immediately after opening of the nest. Over time, brood was usually brought out of the old nest and piled in a darker spot against the old nest. Some colonies moved their brood to under the tube(s) before moving it into a new nest, i.e. into a tube or box. The effects of genetic diversity on migration speed are summarized in Table 1 for each Experiment.

Experiment 1

During the first migration experiment, new nest sites only became available at the time of destruction of the old nest. Seventeen colonies were used.

Table 1 Main effects of genetic diversity on colony migration

	Experiment 1	Experiment 2[a]	Experiment 2[b]
Total migration time	Positive	Negative	–
Discovery time new nest	Positive	N.A.	–
Nest site selection	–	–	–
Quorum threshold	–	–	
Time to achieve quorum	–	–	
Migration time after quorum	Positive	Negative	–

[a] Colonies which had already discovered the new nest site before destruction of the old nest (*N*=9)

[b] Colonies which had NOT already discovered the new nest site before destruction of the old nest (*N*=5)

Nest site selection

Two colonies migrated to under the tube, and two colonies split their brood and workers between under the tube and the box, slowly migrating part of their brood from under the tube into the box. This movement was still ongoing at the end of the experiment. Of the remaining colonies, significantly more colonies migrated to the tube than the box (11 vs. 2, binomial test P=0.022) despite approximately equal discovery of the two nest types (10 colonies first discovered the tube, 7 colonies first discovered the box, binomial test P=0.63). Colonies that found the tube first were significantly more loyal to their first finding (nine out of ten migrated into the tube) than colonies that found the box first (two out of seven moved into the box; Fisher exact test: P=0.018). So although migrations were forced, colonies did show nest site selection, preferring the tube over the box. Colonies selecting the box had significantly more brood than colonies selecting the tube. Genetic diversity did not affect nest site selection (GLM brood: X^2_1=7.45, P=0.006, genetic diversity: X^2_1=0.10, P=0.75, Online Resource Table S3).

Total migration time

Total migration time varied widely between colonies, from 1.5 to 7 h (average+SE=207+20 min, N=17). Genetic diversity did not seem to affect total migration time (Spearman rank correlation r_s=0.02, P=0.94, N=17). However, a significant part of the variation in total migration time was explained by differences in nest site selection. Colonies that chose to migrate (partly) into the box had significantly longer migration times than colonies that chose to migrate into the tube (*t* test: t_{13}=2.5, P=0.027; two colonies that migrated to under the tube were excluded). For the colonies that migrated into the tube, total time to migrate was significantly correlated with genetic diversity (GLM with negative binomial errors: X^2_2=7.64, P=0.02, Online Resource Table S4). Only two out of the four colonies from Population 2 migrated into the tube, but in the colonies from Population 1, migration time significantly increased with diversity (GLM, X^2_1=5.01, P=0.025; Fig 1a), and was not affected by colony size (brood or workers, Online Resource Table S5).

Discovery time of new nest

On average, approximately half of the total migration time (49 %) was used to discover a new nest site, with large differences between colonies (range=14–93 %, N=17). Time to discover and enter a new nest (range=5 min to 5 h) was positively correlated with genetic diversity (GLM, X^2_1=5.41, P=0.02; Fig. 2a), but not affected by colony size or population (Online Resource Table S6). The positive relationship between genetic diversity and discovery time was not explained

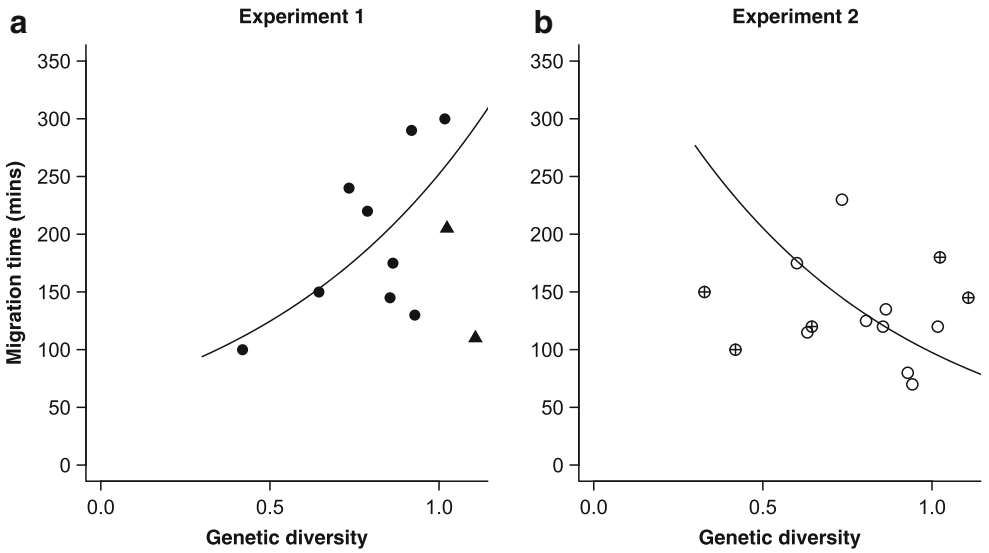

Fig. 1 Relationship between genetic diversity and total migration time (min) during Experiment 1 (**a**), where a new nest site had to be discovered after destruction of the old nest and Experiment 2 (**b**) where new nest sites were present before destruction of the old nest. **a** Because total migration time differed between the two nest types (box versus tube) in Experiment 1 (see text), only colonies that migrated into the tube are included. Both genetic diversity and population had a significant effect on migration time (Table S4). *Circles* represent colonies from Population 1, *triangles* represent colonies from Population 2. The *line* gives the expected relationship for colonies from population 1 (y=exp(4.12+1.41×diversity)). **b** The effect of genetic diversity on migration time depended on whether a new nest site was already discovered before the old nest was destroyed. *Open circles* represent colonies that had already discovered a new nest site before destruction of the old nest, *crossed circles* represent colonies that had not already discovered a new nest before destruction of the old nest. The *line* gives the expected relationship for colonies that had already discovered the new nest before destruction of the old nest (y=exp(6.07−1.49×diversity)). The correlation was not significant for colonies that had not discovered the new nest before destruction of the old nest (*crossed circles*)

by lower scouting intensity, because scouting intensity around the new nests 5–30 min after onset of the experiment was not correlated with genetic diversity (absolute number of scouts: $P \geq 0.48$ at 5, 10, 15 and 30 min; relative number of scouts (scouts/workers): $P > 0.38$ at all 4 time points). Rather, the number of scouts was strongly correlated with colony size (5 min: r_s=0.55, N=17, P=0.023; 10 min: r=0.71, N=14, P=0.004; 15 min: r_s=0.68, N=13, P=0.004; 30 min: r_s=0.68, N=13, P=0.005). Interestingly, more diverse colonies spent significantly more ant scouting minutes around the new nest

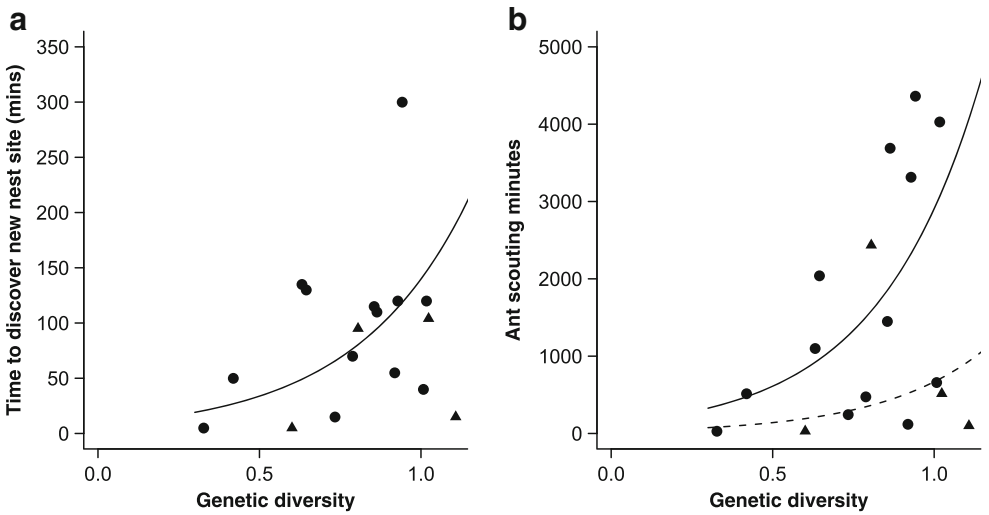

Fig. 2 Positive relationship between genetic diversity and (**a**) discovery time of a new nest site and (**b**) the amount of scouting time needed (ant scouting minutes $\sum_{t=0}^{t=\text{found new}}$(#ants×5 min) before a new nest site is discovered and entered, after the old nest is destroyed (Experiment 1). *Circles* Population 1, *triangles* Population 2. The *curves* give the expected relations based on the models. Discovery time=exp(0.82+2.84×diversity+0.64×day), see online resource Table S6, line given for the second experimental day. Scouting time $_{\text{(population 1, solid line)}}$=exp(1.96+3.12×diversity+0.015×workers+1.47), scouting time $_{\text{(population 2, hashed line)}}$=exp(1.96+3.12×diversity+0.015×workers, see online resource Table S7, lines given for average number of workers (95)

sites before entering them than less diverse colonies (GLM, X^2_1=3.92, P=0.048; Online Resource Table S7; only colonies from Population 1: X^2_1=5.15, P=0.023; Fig. 2b). This suggests that genetic diversity affects the readiness of workers to enter a new nest site, and thus their exploratory behaviour. Colonies that needed more time to discover a new nest subsequently completed migration (i.e. migration time after discovery of new nest) quicker than colonies that needed less time to discover a new nest site (Spearman rank correlation: r_s=−0.64, N=15, P=0.01; the two colonies that moved under the tube were excluded from this analysis). This indicates that the time needed to find a new nest site affects subsequent migration time.

Quorum threshold

Colonies that migrated into the box had a higher quorum threshold, and tended to take longer to reach this quorum after discovery, compared to colonies that migrated into the tube (average+SE quorum threshold=27+6 and 11+2 workers respectively, t test: t_{13}=3.2, P=0.007; average+SE time to reach quorum=149+23 and 66+22 min respectively, t test: t_{13}=2.11, P=0.054). For colonies that migrated into the tube (N=11), quorum threshold significantly differed between the two populations, but was not correlated with genetic diversity (Online Resource Table S8, Fig. 3b). However, quorum threshold tended to increase with discovery time of the tube (LM, $F_{1,9}$=5.09, P=0.054, Online Resource Table S8). Time to achieve quorum threshold after discovery was not significantly correlated with quorum size, colony size or genetic diversity for colonies that moved into the tube (Fig. 4a), but was negatively correlated with discovery time of the new nest site (GLM, X^2_1=4.34, P=0.037; Online Resource Table S9). This suggests that discovery time can affect subsequent migration time.

Migration time after reaching quorum

For colonies that migrated into the tube (N=11), migration time after reaching quorum (range=10–95 min, mean ± SE= 37±14 min) increased with genetic diversity, the amount of brood and time to reach quorum (Online Resource Table S10; Fig. 4b). Time to reach quorum after discovery (Fig. 4a) was not significantly different from time to subsequently migrate 95 % of the brood into the new nest (Fig. 4b; Wilcoxon test, W=66, P=0.74), and both variables explained part of the variance in total migration time (Fig. 1a; time to reach quorum: Spearman rank correlation r_s=0.67, P=0.022; time needed to move brood into the new nest: Pearson's correlation r=0.57, P=0.065). Time to discover a new nest did not explain total migration time (Pearson's correlation r=0.008, P=0.98).

Experiment 2

During the second migration experiment, new nest sites had been available ca. 17 h before destruction of the old nest. Only one of the colonies had already moved into the new nest site before destruction of the old nest. In one colony, the queen had disappeared and in another colony population size had decreased to less than 20 workers, resulting in a sample size of 14 colonies.

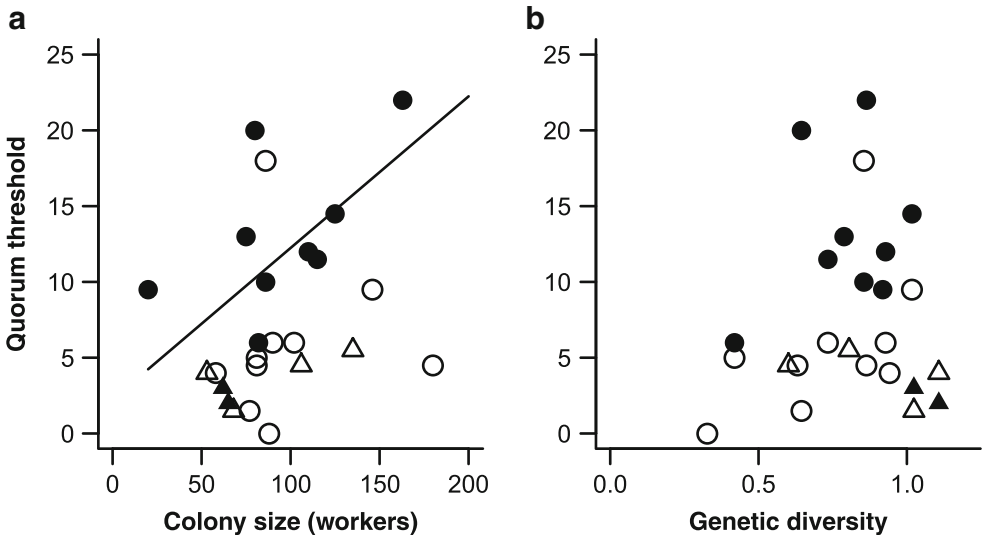

Fig. 3 The relationship between quorum threshold and **(a)** colony size and **(b)** genetic diversity during Experiment 1 (*filled symbols*, only colonies that moved into the tube) and Experiment 2 (*open symbols*). *Circles* represent colonies from Population 1, *triangles* represent colonies from Population 2. The line in **a** gives the expected linear relation between colony size and quorum threshold during experiment 1 (y=0.10×+2.24, Pearson's correlation test, r^2=0.37, P=0.048). Data from Experiment 2 were non-normally distributed, but also showed a positive correlation between colony size and quorum threshold (Spearman rank correlation test, ρ=0.53, P= 0.05). Quorum threshold was not significantly correlated with genetic diversity (see online resource tables S8 and S13)

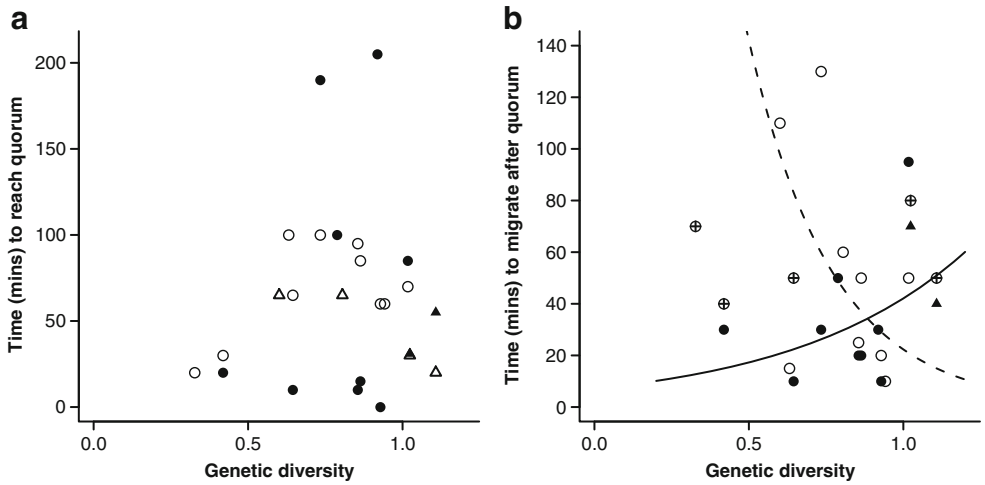

Fig. 4 Relationship between genetic diversity and (**a**) time to reach quorum after discovery and (**b**) time to move brood into the new nest after reaching quorum. *Closed symbols* represent data from Experiment 1, *open symbols* represent data from Experiment 2. *Circles* represent colonies from Population 1, *triangles* represent colonies from Population 2. **a** Time to reach quorum was not significantly correlated with genetic diversity (see online resource tables S9 and S14). **b** Time to move brood after quorum increased with genetic diversity during Experiment 1 (*solid line* for average amount of brood (40) and average time to reach quorum (66 min): $y=\exp(1.96+1.78\times\text{diversity})$, see online resource table S10). During Experiment 2, the effect of genetic diversity on time to move brood after quorum depended on whether a new nest site was already discovered before destruction of the old nest (online resource Table S15). *Open circles* represent colonies that had already discovered a new nest site before destruction of the old nest, *crossed circles* represent colonies that had not already discovered a new nest before destruction of the old nest. Time to move brood decreased for colonies that had already discovered the new nest (*open circles*, *hashed line* for average number of workers (109): $y=\exp(6.81-3.70\times\text{diversity})$, see Online Resource Table S16)

Nest site selection

All colonies moved most of their brood into the dark tube, except for one colony which moved its brood and 26 workers into the light tube while the queen and 30 workers moved into the dark tube. This was the only colony that had already discovered both nest sites by the start of the experiment.

Total migration time

Total migration time into a known nest site ranged from 1 to 4 h (average + SE=134+11 min, $N=14$). Out of the 14 colonies, at least 9 had discovered their new nest site before destruction of the old nest, i.e. at least one ant was seen in the tube during the 30 min preceding destruction of the old nest. Genetic diversity did not differ between the colonies that had discovered a new nest before destruction of the resident nest, and those that had not (Welch two sample *t* test, $t=-0.70$, $df=4.74$, $P=0.51$). Colonies that had already discovered the new nest did not migrate significantly quicker than colonies that had not already discovered the new nest (Welch two sample *t* test, $t=0.43$, $df=11.6$, $P=0.68$). The effect of genetic diversity on total migration time was significantly different for colonies that had already discovered the new nest site compared to colonies that had not already discovered the new nest site (GLM with a significant interaction between "new nest already discovered" (yes/no) and genetic diversity: $X^2_1=9.02$, $P=0.003$, Online Resource Table S11, Fig 1b). For colonies that had not already discovered the new nest site, genetic diversity had no significant effect on total migration time (GLM, $X^2_1=1.71$, $P=0.19$). For colonies that had already discovered the new nest site, migration time decreased with genetic diversity (GLM, $X^2_1=6.14$, $P=0.054$; Online Resource Table S12).

Discovery time of new nest

For the five colonies that had not already discovered a new nest before onset of the experiment, discovery time of the new nest ranged from 5 to 75 min. Discovery time of a new nest was not significantly correlated with genetic diversity or colony size (Pearson's correlations *workers*: $r=-0.49$, $N=5$, $P=0.40$; *brood*: $r=0.38$, $N=5$, $P=0.53$; *genetic diversity* $r=0.51$, $N=5$, $P=0.38$). However, discovery time was negatively correlated with day of experiment ($r=-0.93$, $N=5$, $P=0.02$), which, together with the low sample size, may have obscured any potential effects of genetic diversity on discovery time. Scouting intensity around the new nest sites ranged from 30 to 495 ant minutes and was not significantly correlated with genetic diversity, colony size or day of experiment (Pearson's correlations *genetic diversity:* $r=0.15$, $N=5$, $P=0.81$; *workers*: $r=0.05$, $N=5$, $P=0.94$; *brood*: $r=0.61$, $N=5$, $P=0.27$; *day of experiment:* $r=-0.66$, $N=5$, $P=0.22$).

Quorum threshold

The number of workers present in the tube when the first brood arrived ranged from 1 to 18 workers (average+SE= 5+1 workers, N=14 colonies). Quorum threshold significantly decreased with time to discover a new nest site (GLM, X^2_1= 4.38, P=0.036), and tended to increase with genetic diversity (X^2_1=4.38, P=0.062, Fig. 3b), but was not significantly correlated with colony size (Fig. 3a) or Population (Online Resource Table S13).

As in Experiment 1, time to achieve quorum after discovery was not correlated with quorum size, colony size, population or genetic diversity (Fig. 4a), but was negatively correlated with time to discover the dark tube (GLM, X^2_1=23.0, P<0.001; Online Resource Table S14).

Migration time after reaching quorum

Migration time after reaching quorum (range=10–130 min, N=14, mean ± SE=54±9 min) was significantly correlated with the amount of brood and genetic diversity, but the effect of genetic diversity depended on whether or not the new nest site was discovered before destruction of the old nest (GLM genetic diversity×discovery: X^2_1=3.9, P=0.048; Fig. 4b; Online Resource Table S15). When the dark tube was discovered before the colony was forced to migrate (N=9), genetically more diverse colonies were quicker in moving their brood into the new nest once migration had started (GLM, X^2_1=4.98, P=0.026; Fig. 4b, Online Resource Table S16). When the dark tube was not discovered before being forced to migrate (N=5), the time to migrate 95 % of all brood once migration had started was not correlated with genetic diversity (Pearson's correlation r=0.21, P=0.73; Fig. 4b) or with day of experiment (r=−0.40, N=5, P=0.50).

When the dark tube was already discovered before onset of the experiment (N=9), time to reach quorum was not significantly different from time to subsequently migrate the brood into the new nest (Welch corrected t test: $t_{10.5}$=−1.67, P= 0.12). However, total migration time was mostly explained by variance in time to move brood into the new nest (Pearson's correlation: r=0.94, P=0.0002), and not by time needed to reach quorum (Pearson's correlation: r=0.49, P=0.18; Fig. 4). This shows that the positive effect of genetic diversity on migration speed into a known nest site is mediated through its effect on moving brood.

Discussion

The study shows that the genetic diversity of colonies affects the performance of the social task of nest migration in the red ant *M. rubra*. However, the effect of genetic diversity depended on the conditions. In Experiment 1, greater genetic diversity resulted in longer migration times, with more genetically diverse colonies being slower to discover a new nest site and to move brood into the new nest once a quorum threshold was reached. In Experiment 2, genetic diversity had no effect on the migrations of colonies which had not yet discovered a new nest by the start of the experiment. However, greater genetic diversity resulted in shorter migration times for those colonies which had already discovered a new nest, due primarily to a faster completion of the migration once a quorum threshold had been reached. Conditions therefore affected not just the strength of the effect of genetic diversity on migrations, but also the direction of the effect.

The positive effect of genetic diversity on the migration of colonies in Experiment 2 that were migrating to nests that they had already discovered, is in keeping with the positive effects of genetic diversity on task performance in honeybees (Jones et al. 2004; Mattila and Seeley 2007). This effect is generally considered to be due to a more optimum division of labour because of genotypic differences in response thresholds to engage in particular tasks (Robinson and Page 1989; Bonabeau et al. 1996; Beshers and Fewell 2001; Myerscough and Oldroyd 2004; Tarapore et al. 2010), although it could also be due to genotypic differences in the performance of the tasks (Constant et al. 2012). The positive effect of genetic diversity on migration speed in the experiment here appeared to be primarily due to a more rapid completion of the migration once a quorum threshold had been reached. Assuming that ants in the colony had to complete multiple tasks at this point, such as brood transport, trail marking and nest organisation, it may be that a greater diversity of genotypes results in a more optimum number of ants being allocated to each task (Myerscough and Oldroyd 2004), with the result that the migration is completed quicker.

In contrast to the above, there was a negative effect of genetic diversity on the migrations in Experiment 1. This appeared to be primarily due to more genetically diverse colonies taking longer, in terms of ant minutes scouting, to discover a new nest, and also longer to enter it. The vast majority of studies consider effects of genetic diversity on division of labour to be positive (Oldroyd and Fewell 2007), so the finding that they can also be negative is potentially important. Interestingly, many ants were observed in the immediate vicinity of the new nest before a worker finally entered it. *Myrmica* and other ants engaged in exploration often do so tentatively, with each ant travelling over, and a little beyond, substrate that has previously been marked with pheromone before turning around (Aron et al. 1986; Cammaerts and Cammaerts 1987, 1996; Gordon 1988; pers. obs. EJS). One possible explanation for the negative effect of genetic diversity could be that if the exploratory pheromones deposited vary genotypically, as other cuticular hydrocarbons can (Nehring et al. 2011), then perhaps more variable cues cause ants to hesitate more on the pheromonally marked area

before advancing into an unexplored area. However, there is little theoretical basis for predicting negative effects of genetic diversity on division of labour, and clearly far more work on the precise effects of genotypic variation on specific behaviours and cues is needed.

The strongest conclusion from the results is that the effect of genetic diversity on migration can vary depending on the conditions. In Experiment 1, the effect appeared to be negative, while in Experiment 2, it appeared to be positive for colonies that had already found a new nest site prior to migration. The two experiments differed in multiple aspects which may explain this, such as the alternative new nest type (dark box versus light tube), previous migration experience (first versus second forced migration) and potentially environmental conditions (experiments were carried out on different dates). However, the most obvious aspect that may explain the conditional effect of genetic diversity on migration is that the ants in Experiment 1 had to discover the new nest site as part of the experiment, whereas those in Experiment 2 did not. Importantly, there was also a similar difference within Experiment 2 between the colonies which already discovered the new nest by the start of the experiment and the colonies which had not. Only in the former colonies did genetic diversity appear to be beneficial. In addition, for colonies which had not discovered a new nest by the start of the experiment, the effect of genetic diversity on migration differed between Experiments 1 and 2. Only in the first experiment did genetic diversity appear to be a disadvantage. This difference in results might have been caused by the low sample size in Experiment 2 (N=5), but factors such as previous experience might also have played a role. Possibly, the benefits of genetic diversity are less when colonies are under more stressful conditions, such as when they have no previous migration experience (Exp 1), or when they have to urgently discover a new nest before they can migrate (Exp 1, some colonies in Exp 2). This hypothesis could explain the differences in genetic effects both between and within the experiments, under the assumption that the perceived amount of stress was highest in Experiment 1 (genetic diversity disadvantageous), intermediate in Experiment 2 for colonies that had not already discovered a new nest site prior to emigration (genetic diversity no effect), and lowest in Experiment 2 for colonies that had already discovered a new nest site prior to emigration (genetic diversity beneficial). Regardless of the mechanism, the condition-dependent nature of the effects we found may in part explain why previous studies have produced mixed results (Jones et al. 2004; Rosset et al. 2005; Mattila and Seeley 2007).

The colonies used in our study were small with regard to natural colony sizes, and it remains unknown whether the effects of genetic diversity on migration, as found in this study, compare to those in larger natural colonies. Nevertheless, migrations especially occur in small colonies (Dobrzanska and Dobrzanski 1976 cited in Abraham and Pasteels 1980), so that our results seem relevant for at least part of the natural colony migrations.

Our study shows for the first time that intracolonial genetic diversity can affect task performance in a social insect other than the honeybee, but that the effects are condition-dependent. It has recently been argued that species-specific differences in the genetic architecture underlying division of labour, including non-additive as well as additive effects, may explain interspecific differences in the effect of genetic diversity on colony performance (Libbrecht and Keller 2013). This certainly seems likely, but, independent of such interspecific differences in the genetic architecture, our study suggests that differences in environment or context can also impact upon the strength and direction of the effect. The benefits of genetic diversity may therefore differ between species experiencing different environmental conditions, which may in part explain why more social insect species have not evolved polyandry or polygyny.

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