The effect of experience on collective decision-making

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A B S T R A C T

Social groups repeatedly solving a complex task can improve their collective performance. To study the mechanisms of collective improvement, we tested the effect of experience on collective decision-making using acorn ants (*Temnothorax ambiguus*). During a six-emigration training phase, colonies in the choice treatment gained experience choosing to move into one of two nests varying in quality, while colonies in the no-choice treatment had only a single available nest. Both treatments were tested in a subsequent test with two nests of varying quality. We found that experience improved decision-making speed, regardless of treatment. We also found that colonies of the choice treatment were more proficient by carrying a larger proportion of individuals directly into the better-quality nest. However, there was no steady improvement in proficiency throughout their training. Using social network analysis, we quantified changes in group performance over successive emigrations. We found that network density, our measure for social connectedness, and the coefficient of variation of out-strength distribution, our measure for workload distribution, did not differ between treatments and remained stable over successive emigrations. We conclude that collective experience with decision-making may improve subsequent group performance, but the mechanisms of improvement remain unclear. Further research on decision-making in house-hunting ants will advance our understanding of the mechanisms underpinning collective improvement.

1. Introduction

Collective behaviour, the coordination of individuals within a social group, is a fundamental pillar of social behaviour in both human and non-human animals. Frequently, social groups must collectively navigate through landscapes (Aikens et al., 2022; Kashetsky et al., 2021), coordinate protection against predators (Doran et al., 2022; Jandt et al., 2020), or share important foraging information (Palacios-Romo et al., 2019; von Frisch, 1993). Collective behaviour requires communication and decision-making. For example, Biro et al. (2006) released pairs of pigeons (*Columba livia domestica*) to navigate home together after they received experience navigating individually. When the distance between each pigeon's preferred path was small, the pair averaged their homing route. However, when the distance between the preferred paths reached a certain threshold, the pair would adopt a leader and follow that individual's path closely. Further, some pods of humpback whales (*Megaptera novaeangliae*) feed via bubble-netting which involves considerable coordination. Pods will blow bubbles while circling and closing in on prey, densely packing the small fish together before the whales

simultaneously swim through the fish with their mouths open to feed (Jurasz and Jurasz, 1979). These examples illustrate how social groups must share information and coordinate their behaviour to successfully problem-solve.

Social groups must collectively solve complex tasks repeatedly throughout their lives. This repetitive problem solving creates the potential for groups to develop exceptional skills and knowledge resulting in superior performance compared to groups with less problem-solving experience. For example, with age and experience, wolf packs increase hunting success (Sand et al., 2006). Collective improvement is the result of both individual-level learning and group-level learning (Argote, 2013), in which social interactions facilitate information transfer (Collet et al., 2023). Despite its potential, little research has critically quantified the progression of collective learning or how decision-making changes with experience in humans or non-human animals.

Here, we provide ant colonies with extensive experience on a natural decision-making task to measure collective improvement. Most ants live in colonies that consist of familiar individuals whose tasks are allocated according to division of labour (Hölldobler and Wilson, 1990). This
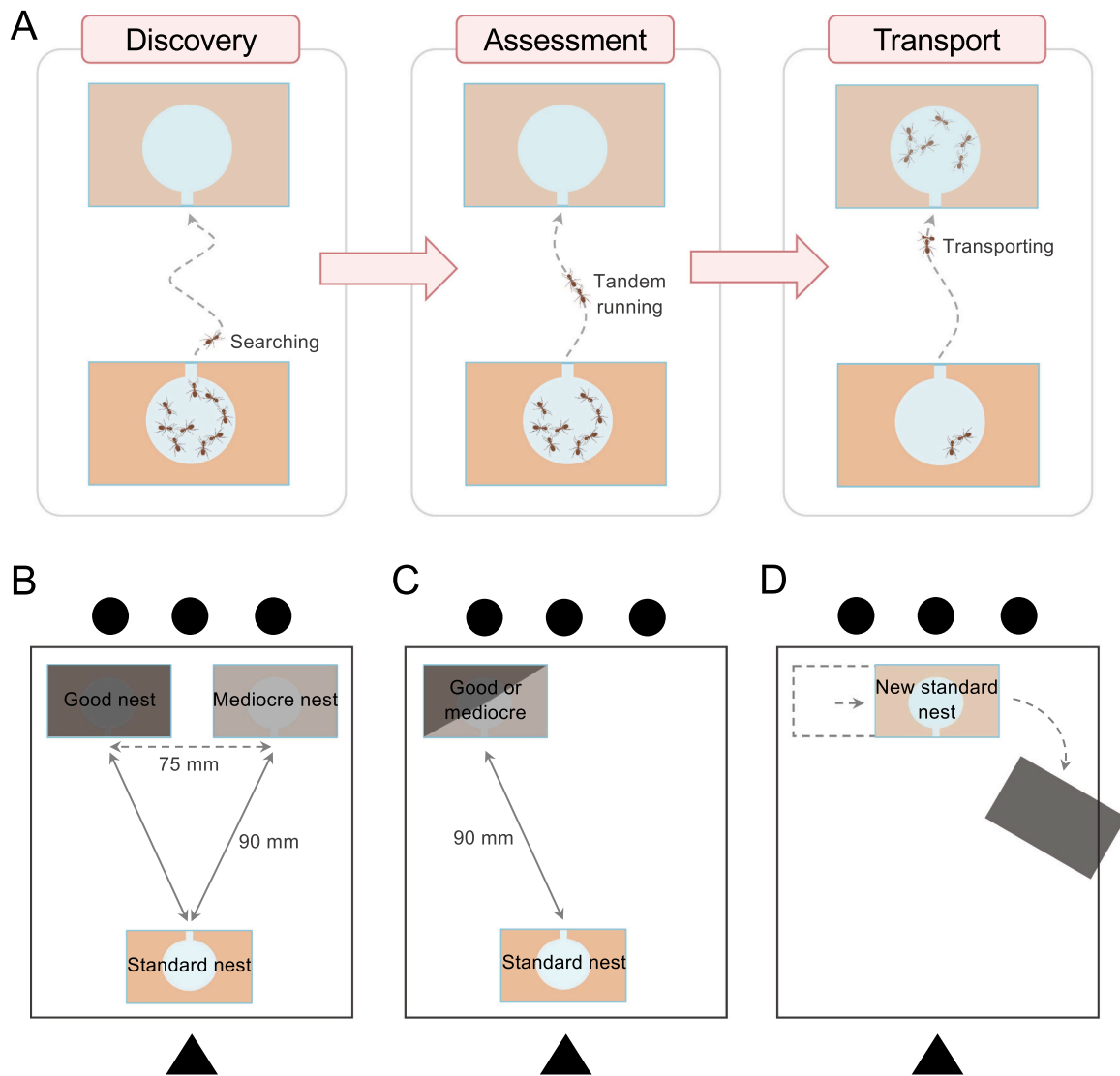
Fig. 1. A) The first of three emigration phases begins when the glass cover slide is removed from the old nest. During the discovery phase, workers search for a new nest. Workers then assess the quality of prospective nests and recruit nestmates to these nests via tandem running. After choosing a nest, workers transport the remaining colony members into the chosen nest. B) The experimental arena set up for the training session of the choice treatment, and the test for both the choice and no-choice treatment, C) the training session for the no-choice treatment, D) after the 40-hour rest interval. we removed the filter and positioned the nest in the center to convert the occupied nest into the new standard nest. The black circles and triangles were landmarks glued to the walls of the arenas to enhance ant spatial orientation.

colony structure provides the necessary timescale and task organization for superior collective performance to develop, making ant colonies a good model system. House-hunting is a well-studied behavioural system of collective decision-making in social insects (Franks et al., 2003a; Sasaki and Pratt, 2018; Seeley and Buhrman, 1999; Visscher, 2007), and the genus *Temnothorax* is an especially tractable system for studying collective-decision making in laboratory conditions. *Temnothorax* ant colonies (acorn or rock ants) often consist of tens to a few hundreds of individuals that nest in pre-formed cavities such as in rotting acorns or under rocks, which are subject to frequent disturbances (Möglich, 1978; Wheeler, 1903). When their current nest becomes inadequate, individual *Temnothorax* scouts will search for a new nest (Möglich, 1978). Scouts assess nest quality based on characteristics such as darkness, cavity height, and entrance size—ranked respectively in order of importance (Franks et al., 2003b). *Temnothorax* ants discover nests either individually or through a recruiting behaviour called tandem running (Wilson, 1971), in which a knowledgeable leader shows a naïve

follower the route to a new nest or food source (Franks and Richardson, 2006; Pratt, 2008; Sasaki et al., 2020). Once enough scouts have accepted the new nest, they begin transporting brood and nest mates into that nest (Fig. 1a; Pratt, 2005a, 2005b; Pratt et al., 2002). Only a minority of colony members actively partake in emigration—most workers get carried to the nest or may walk there themselves (Pratt et al., 2002).

Surprisingly, few studies have explored how prior experience affects collective decision-making during emigration (Biro et al., 2016; Sasaki and Pratt, 2018), and those that do focus on the speed of emigration. Emigrating to a single nest option naturally involves collective behavior (Pinter-Wollman et al., 2012). Repeated experience emigrating increases the overall speed of emigration when one nest option is available (Langridge et al., 2004, 2008; Mitrus, 2016). However, these studies involve no element of choice between more than one nest option. Deciding between numerous nest options is a fundamental part of emigration, as natural environments typically have multiple prospective

nests available. Previous experience assessing nests can also affect subsequent decision-making. For example, individual scouts that assessed nests in descending order of quality (excellent-, good-, then poor-quality) treated the good- and poor-quality nests similarly. Contrarily, scouts that assessed three nests in ascending order of quality (poor-, good-, then excellent-quality) spent increasingly more time assessing each nest of increasing quality (O'shea-Wheller et al., 2017). Colonies learn to focus their efforts assessing specific nest qualities that have been informative of better-quality nests in the past (Sasaki and Pratt, 2013). Further, colonies that had explored a good- and mediocre-quality nest a week prior to emigration—thus possessing the knowledge of both nests—relocated more quickly to one of the nests compared to colonies that were naïve to both nests (Stroeymeyt et al., 2010). Taken together, these studies illustrate how prior experience can influence the speed of house-hunting in acorn ants. However, it remains unclear if the other aspects involved in the process of collective decision-making itself, as opposed to just the overall speed of emigration, improve with collective experience.

In this study, we tested if repeated experience with collectively deciding between two nest options can improve a group's decision-making performance. We first provided acorn ant colonies (*Temnothorax ambiguus* Emery 1895) with experience emigrating by providing a binary choice between two nests of varying quality (choice treatment) or a single nest of either quality (no-choice treatment) (Fig. 1b, c). We then tested both treatments on a final binary decision-making task (Fig. 1b). We predicted that colonies from the choice treatment would be faster and more proficient at collective decision-making than colonies from the no-choice treatment because they would have gained experience deciding between two nest options, fostering improvement. We defined proficiency as the proportion of ants transported directly from the old nest to the better of the two nests (see 'Measures' for details). In addition to our key predictions for the test phase, we also made two secondary predictions regarding colony performance during the training phase. First, we predicted that colonies from both treatments would increase their decision-making speed over the six emigrations of the training phase, similar to previous studies studying overall emigration speed (Langridge et al., 2004, 2008; Mitrus, 2016). Second, we predicted that colonies from the choice treatment would improve in proficiency throughout training. Using social network analysis (SNA), we quantified how social interactions changed as colonies gained experience emigrating (Croft et al., 2008; Krause et al., 2015). We measured two metrics: network density and the coefficient of variation (CV) of the network's out-strength distribution. Network density, which is the proportion of realized connections among all possible connections, allowed us to assess how interconnected the colonies were. An increase in network density over time would indicate that colonies relied more heavily on interactions between individuals to complete an emigration as they gained experience. On the other hand, a decrease in network density would indicate that more ants located and moved to the new nests on their own. Second, we measured the CV of the network's out-strength distribution to capture the extent to which labour associated with that emigration was evenly divided amongst workers. If the CV of out-strength distribution increased over successive emigrations, it would indicate that the workload was increasingly being centralized to a few individuals. Alternatively, a decrease in the CV of out-strength distribution with experience would indicate that the workload was spreading out more evenly amongst colony members over time.

2. Methods

2.1. Ethical note

Our research adhered to all applicable laws and did not require approval from an ethics committee. However, we treated the ants according to high ethical standards with the assumption that they experience emotion and pain.

2.2. Collection and maintenance of colonies

We collected more than 60 acorns containing *T. ambiguus* from the Heartland Forest in Niagara Falls, Ontario during July 2020 and May 2021. We used the largest 40 of these colonies for our main experiment. These 40 colonies were tested within nine months of collection and contained between 12 and 107 adults (mean = 47.75) and zero to five queens (mean = 1.75). We emigrated colonies into standard lab nests made of balsa wood sheets 1.6 mm thick with a circular cavity 38 mm in diameter, and an entrance two mm wide and four mm long (modified from Franks et al., 2003b). We sandwiched the balsa wood between two glass slides (75 ×50×1 mm). We placed nests individually into plastic containers (110 ×110×38 mm) with dead *Drosophila melanogaster*, honey, and water provided ad libitum except during emigrations. We kept colonies in 12 hr:12 hr light, dark cycle at 22 °C ± 2 °C. All colonies used in the main experiment were eventually released back into Heartland Forest.

2.3. Experimental design

Throughout the experiment, colonies lived in their experimental arenas (290 ×160×112 mm) lined with Fluon (Formica Ant Products) at a stable brightness of approximately 333 lux. Two dissimilar landmarks (three black circles, one black triangle) remained in the same location throughout the experiment to aid in navigation (Hunt et al., 2018; Mcleman et al., 2002). We tested a total of 40 colonies over four replicates. Each replicate included 10 colonies, five in the choice treatment and five in the no-choice treatment. We randomly assigned colonies into treatments while matching similar number of workers between the treatments (mean ± SD, choice treatment = 49.7 ± 25.58, no-choice treatment = 45.7 ± 26.75). We confirmed through preliminary experiments that *T. ambiguus* colonies prefer darker nests and deemed the darker nest as the good-quality nest, and the dim nest was the mediocre-quality nest. For more details, see 'Preliminary Trials' in the supplementary material.

2.3.1. Training emigrations

In the training phase, each colony emigrated six times. In each emigration, colonies of the choice treatment had a choice between one good-quality nest and one mediocre-quality nest, while colonies of the no-choice treatment encountered only a single nest (Fig. 1b, c). For the no-choice treatment, colonies were provided with a good-quality nest in three emigrations and a mediocre-quality nest in the other three emigrations. While colonies in both treatments experienced the two nest qualities during the training phase, only colonies from the choice treatment were ever presented with both nests simultaneously, thus gaining experience with collective decision-making between two nest options. We randomized and counterbalanced the order and placement of the nests in the arenas throughout all emigrations.

Prior to the first training emigration, we placed each colony into a clean experimental arena to acclimate overnight. We placed new nests 90 mm away from and facing the occupied standard nest (new entrance to old entrance; Fig. 1b, c). For the choice treatment, the two nests were side by side, 75 mm apart (new entrance to new entrance; Fig. 1b). To initiate emigration, we removed the roof and balsa wood walls of the occupied standard nest to simulate natural, irreparable nest damage. We allowed ants to emigrate, and video recorded each emigration for up to five hours. If colonies remained split between two nests after five hours, we ceased recording, and briefly removed the light filters of each nest to take a photo to record the number of workers, queens and estimated brood count in each nest. Then we removed the roof of the nest occupied with the least number of queens and brood to force reunification. We removed the light filter for roughly the same time it would take to take a photo for colonies that did not split to ensure the same amount of disturbance. In a few instances, colonies had brood remaining in the old nest past five hours, so we continued recording until all brood items

were moved into a new nest. In one emigration of a no-choice colony, all brood items had not been moved by eight hours, so we ceased recording and manually added brood to the new nest. After each emigration, we removed the old nest and unused nest, and added food and water to the arena.

After colonies lived in their chosen experimental nest for 24 h, we removed the filter from the nest and shifted it to the center of the arena while maintaining it close to the landmark they had emigrated towards, converting it into a standard nest on the opposite side of the arena as their previous standard nest (Fig. 1d). This resulted in colonies alternating between emigrating towards and away from the triangle landmark. Colonies remained in the standard nest for approximately 40 h. We then moved colonies to clean arenas, allowing acclimation for 15 min prior to initiating emigration. Moving colonies to clean arenas did not appear to stress the colonies as they did not react in an alarming manner (e.g., increased movement or walking speed). Mortality was tracked for the 8 colonies marked for SNA, ranging from 0 to 4 dead ants throughout the three-week experiment, with an average of 1.25 dead ants per colony. Because of the stress of opening the nests and remarking these 8 colonies (see 'Painting Individuals' in the supplementary material for details), it is reasonable to assume that the remaining 32 colonies experienced less stress, and thus less mortality, which is in line with our anecdotal observations. We reused arenas, light filters, and glass slides after cleaning them with 70 % ethanol to remove pheromones. Balsa wood is too absorbent to clean, so we discarded each piece after a single use, even if a colony did not choose that nest. We scored videos using Behavioural Observation Research Interactive Software (BORIS) (Friard and Gamba, 2016). For details, see 'Scoring Videos' in the supplementary material.

2.3.2. Test emigration

The test emigration allowed us to examine how the distinct experiences of colonies from the choice and no-choice treatments affected their decision-making ability. We used an identical protocol to that of the training phase and initiated the test 40 h after the sixth training emigration of each colony. We placed one good and one mediocre nest in each arena (Fig. 1b) for colonies in both treatments, and initiated emigration by removing the roof and balsa wood walls from the standard nests.

2.3.3. Measures

We used two parameters to quantify performance throughout the three emigration phases (Fig. 1a). Decision latency was the duration between discovering a nest until the first transport. Previous studies (e. g., Sasaki et al., 2018, 2019) measured decision latency as the duration between the discovery and last transport. However, the last transport could be an outlier, and the speed of which the ants perform the action of transporting would confound this definition of decision latency. Thus, we chose to measure decision latency as the time between nest discovery and the first transport because it isolates the decision-making process by including the assessment of the new nest(s) once they have been discovered and the choice to accept the nest, which occurs when transports begin. We measured decision latencies for all test and training emigrations. Transport proficiency was the proportion of transports into the good nest directly from the old nest, i.e., the number of transports directly to the good nest divided by the number of direct transports to either new nest. We chose this measure because the most proficient emigration should consist of assessment of the alternative nests, choice of the best nest, followed by transports exclusively to the best nest. Because our proficiency measure requires a choice between two nests, we measured this during the test, and for only the choice treatment throughout training.

2.4. Statistical analyses

We analyzed the data using R version 4.1.2 (R Core Team 2020), and

used the *tidyverse* package version 1.3.0 (Wickham et al., 2019) to organize the data. For the test emigration, we used the *lmer* function from the *lme4* package version 1.1–26 (Bates et al., 2015). We used generalized linear models (GLM) to compare the performance of the choice and no-choice treatments during the test emigration. To model decision latency, the duration between the first discovery and first transport was the dependent variable and treatment, replicate and colony size were the fixed factors. We used replicate as a fixed factor because it had too few levels to be a random factor. To model transport proficiency, the arcsine square root of the proportion of transports directly to the better nest was the dependent variable and treatment, replicate and colony size were the fixed factors. The sample size for both GLMs was 20 colonies for both the choice and no-choice. We tested the significance of the effects using the *Anova* function from the car package version 3.0.10 (Fox and Weisberg, 2019), reporting the Wald χ^2 test statistic and p-value.

We used three generalized linear mixed models (GLMM) to analyse the changes in performance over the course of the six training emigrations within each treatment. We analysed decision latency during the training phase for both treatments separately because the choice treatment had two nest options while the no-choice had one, thus we thought directly comparing decision latency between treatments is inapt. We modelled decision latency for each treatment using the *glmmTMB* function from the *glmmTMB* package version 1.0.2.2 (Brooks et al., 2017). Duration between the first discovery and first transport was the dependent variable, and trial, replicate and colony size were the fixed factors, with colony ID as a random factor. With the *lmer* function, we modelled transport proficiency for the choice treatment using the arcsine square root transformation of the proportion of transports directly to the better nest as the dependent variable, with trial, replicate and colony size as fixed factors, and colony ID as a random factor. We did not model transport proficiency for the no-choice treatment over the training phase as there was only one nest option. For all three training phase models, we inspected diagnostic plots for the models using the *DHARMa* package, then, tested the significance of the fixed effects using the *Anova* function from the *car* package. Contrary to our prediction, visual inspection comparing the decision latencies between treatments (Fig. 3) suggested that there was little difference in decision latency between the treatments. We confirmed this observation by running a posteriori GLMM using the *glmmTMB* function with decision latency as the dependent variable, with trial, treatment, trial by treatment interaction, replicate, and colony size as fixed factors, and colony ID as a random factor. The lack of difference between treatments could arise from both nest qualities meeting the acceptance threshold of the scouts. If indeed the ants perceived both nest qualities as sufficiently high, we would expect no differences in decision latencies in trials of the no-choice treatment with either the good- or mediocre-quality nests. We tested this prediction via the *glmmTMB* function with decision latency as the dependent variable, trial, nest quality, trial by nest quality interaction, replicate, and colony size as fixed factors, and colony ID as a random factor.

There are several emigrations missing from these training phase GLMMs. First, a no-choice treatment colony performed no transports during their first emigration; thus, we could not record decision latency for this emigration. Secondly, we excluded one emigration of a choice treatment colony for both performance measures for trial two, owing to a lost video. With these exclusions, the sample size for all models was 20 colonies for the choice-treatment and 20 colonies for the no-choice treatment throughout each emigration, with these exceptions: one colony was missing for the sixth emigration of the GLMMs analyzing decision latency and the GLMM analysing changes in proficiency for the choice treatment, and one colony was missing for the first emigration in the GLMM analysing changes in the decision latency of the no-choice treatment.

2.5. Social network construction and analyses

To use social network analysis, we marked workers and queens from eight colonies (four colonies in each treatment) in the fourth replicate for individual identification within their colony. Each of these colonies contained between 26 and 45 workers. For details, see 'Painting Individuals' in the supplementary material. We constructed social networks based on the eight painted colonies (containing 26–45 workers, mean = 34, and zero to three queens, mean = 1.5). We created network visualizations and ran our analyses with R version 4.1.1 (R Core Team, 2021), using the *igraph* package (Csardi and Nepusz, 2006) to build the networks. Due to a hard drive failure, we could not construct the first emigration for colony 47, or the test emigration for any colony. Nonetheless, applying SNA to the first, third, and fifth emigration still provided us with substantial data to quantify how experience affects social interactions over time.

The social networks depict all direct interaction events that occurred between individuals over the course of a single emigration. Interaction events included all transports, and successful forward and reverse tandem runs, originating from the standard nest, new nest, or arena floor, and finishing at the front wall of the target nest. The number of interaction events that a dyad engaged in are represented by weighted and directed edges that originate from the recruiting individual (tandem run leader or transporter) to the receiver (tandem run follower or transportee). Individual nodes represent all ants that were present during the emigration excluding males, unpainted new workers who rarely participated in recruitment behaviours, and individuals that could not be identified in video recordings. Ants that died during the experiment were included in the networks until they died and were excluded onwards. In total, we were able to identify both ants in a dyad for 631/639 recruitment events.

We analyzed changes in colony-level network metrics with linear mixed-effects models (LMMs) in R using the package *lme4* version 1.1–27.1 (Bates et al., 2015) and report Wald χ^2 values generated with the *Anova* function from the *car* package version 3.0–11 (Fox and Weisberg, 2019). We verified model fits by visually inspecting plots of model residuals using the *DHARMa* package (Hartig, 2019). We constructed two LMMs: the first with network density as the dependent factor, and the second with the coefficient of variation (CV) of a network's out-strength distribution as the dependent factor. Despite the multitude of existing social network metrics, we decided a priori to focus only on our two measures because SNA metrics are often not independent of one another and represent the same underlying biological phenomena (Croft et al., 2011; Farine and Whitehead, 2015). We chose density, the most commonly used group-level SNA metric (Webber and Vander Wal, 2019), as it directly corresponds to the extent to which colony members relied on social interactions to complete an emigration. It is therefore a highly intuitive and biologically relevant measure. In addition to changes in number of interactions, we wanted a metric that captured task allocation since previous studies have highlighted the importance of division of labour in *Temnothorax* ants during emigration (Pinter-Wollman et al., 2012; Sendova-Franks and Franks, 1995). We therefore decided to use the CV of a network's out-strength distribution as we believe it captures workload distribution much more directly than other network-level metrics such as modularity or clustering coefficient.

To obtain the CV of a network's out-strength distribution, we first calculated out-strength for each ant in a colony, which directly translates to the number of interactions where an individual initiated an interaction with another ant. By plotting the distribution of out-strength values for all ants of a colony in each emigration and then calculating each out-strength distribution's CV, we measured how spread out the emigration workload was amongst individuals. Large CV values therefore correspond to networks where very few individuals led most tandem runs and transports while small CV values correspond to networks where most individuals generally led the same number of recruitment events. To assess changes in these two colony-level metrics over

successive emigrations and the effect of decision-making experience, both models included colony treatment, emigration number, and their interaction as fixed factors and colony ID as a random factor.

3. Results

3.1. Colony performance

During the test emigration, we did not observe a significant effect of treatment on decision latency during the test emigration ($\chi^2_1 = 0.19$, p = 0.66, Fig. 2a). However, the choice treatment had significantly higher transport proficiency than the no-choice treatment ($\chi^2_1 = 3.92$, p < 0.05, Fig. 2b).

Colonies of the choice treatment significantly decreased their decision latency throughout the training phase ($\chi^2_1 = 37.21$, p < 0.0005, Fig. 3a). Likewise, colonies of the no-choice treatment significantly decreased their decision latency throughout the training phase ($\chi^2_1 = 54.72$, p < 0.0005, Fig. 3b). We constructed two separate models for the decision latency in the training phase because we expected colonies of the choice treatment to have overall longer decision-latencies than colonies of the no-choice treatment owing to having to choose between two nests. However, we observed no significant difference in decision latencies between the treatments throughout training ($\chi^2_1 = 0.90$, p = 0.34, Fig. 3). The similar decision latencies between treatments could be the result of both nest qualities being acceptable quality to the scouts. To confirm, we tested decision latency in no-choice colonies emigrating to either nest type and observed no significant difference ($\chi^2_1 = 1.11$, p = 0.29, mean in seconds $\pm$ SD, 2046.33 $\pm$ 1192.25, and 2026.27 $\pm$ 1523.57, for the good-quality and mediocre-quality nests respectively). As for proficiency, we did not detect a significant change throughout the training phase for the choice treatment ($\chi^2_1 = 0.67$, p = 0.41, Fig. 4).

3.2. Social network analysis

For exemplification, the interaction events are illustrated for the first, third, and fifth emigration of one choice and one no-choice colony in Fig. 5. Through visual inspection of the networks (Fig. 5, Figs S1-S2) we observed that most individuals had participated in an interaction (as the leader or follower of a tandem run, transporter, or transportee) at least once throughout the three networks. Meanwhile, in most colonies and emigrations, only a handful of individuals emigrated to the new nest without an interaction event.

We did not detect a change in network density over the three successive emigrations ($\chi^2_1 = 0.47$, p = 0.49, Fig. 6a). That is, the average number of social interactions remained stable throughout the three successive emigrations. There was no significant difference between treatments ($\chi^2_1 = 0.26$, p = 0.60), and the interaction between emigration and treatment was also not significant ($\chi^2_1 = 0.24$, p = 0.62). Additionally, we did not detect a change in the CV of the networks' out-strength distribution throughout the three emigrations ($\chi^2_1 = 1.38$, p = 0.24, Fig. 6b). This indicates no change in relative workload distribution over successive immigrations. Finally, the effects of both treatments ($\chi^2_1 = 0.37$, p = 0.54) and emigration by treatment interaction ($\chi^2_1 = 2.61$, p = 0.11) were non-significant.

4. Discussion

There is growing interest in how collective behaviour changes over time (Collet et al., 2023; Hansen et al., 2021; Ioannou and Laskowski, 2023), but the effect of experience on collective decision-making still remains poorly researched (Biro et al., 2016; Sasaki and Pratt, 2018). So far, research has quantified collective decision-making in pigeons navigating home (Sasaki et al., 2022) and shoaling fish avoiding predators (Hansen et al., 2021). In house-hunting ants, research has tested how exposure to nests can affect subsequent choices (O'shea-Wheller
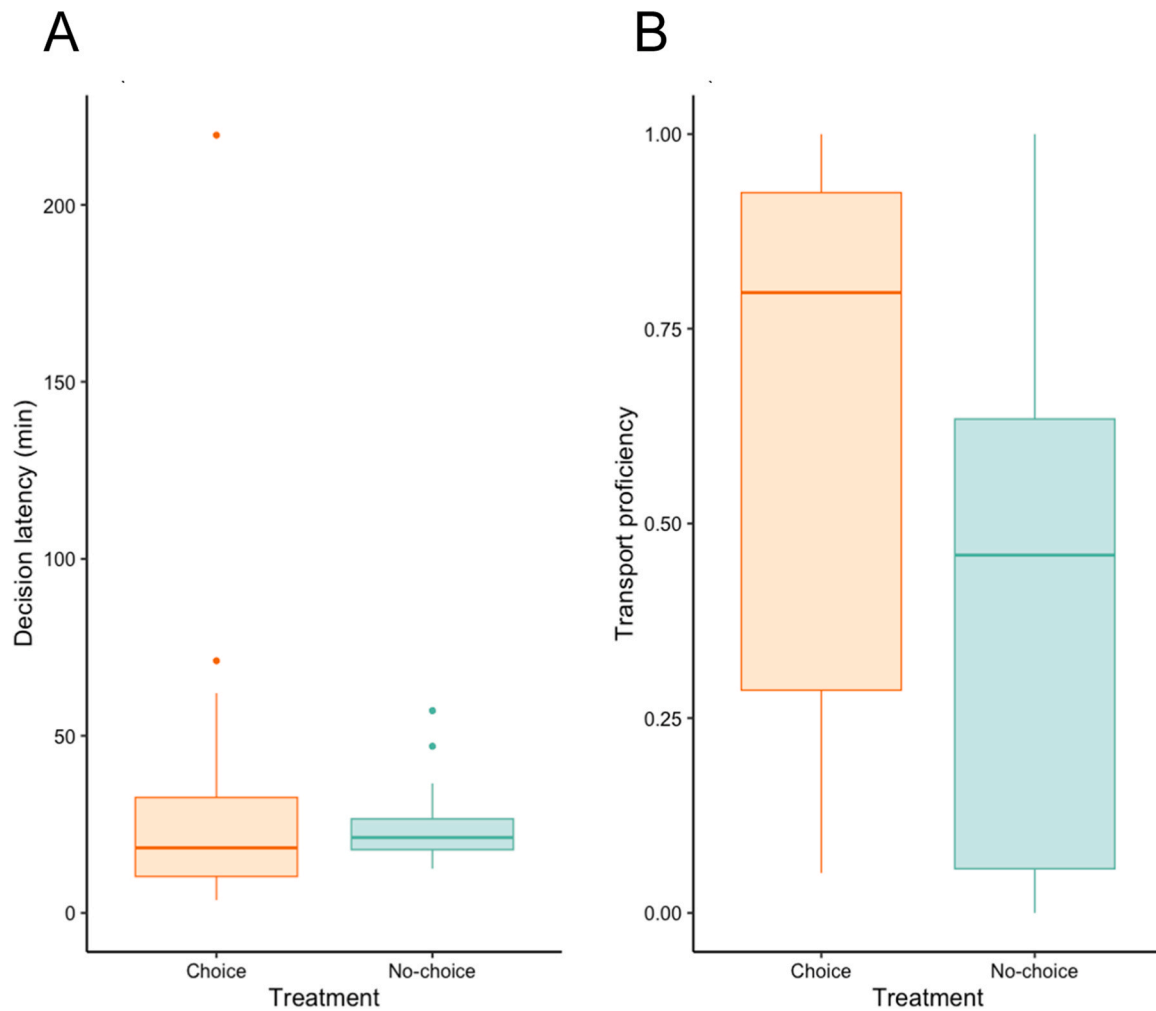
Fig. 2. Performance during the test emigration. Boxplots show the 25th, 50th (median) and 75th percentiles, central vertical lines depict the range, and dots show outliers. A) Decision latency of the choice (n = 20) and no-choice (n = 20) treatments. B) Transport proficiency of the choice (n = 20) and no-choice (n = 20) treatments.

et al., 2017; Sasaki and Pratt, 2013; Stroeymeyt et al., 2010) and how experience with successive emigrations increases overall emigration speed (Langridge et al., 2004, 2008; Mitrus, 2016). Here, we asked if repeated experience emigrating to one of two possible new nests varying in quality improved collective decision-making in house-hunting ants. Our key findings were that we found no difference between the treatments in decision latency during the test emigration (Fig. 2a), but we found that transport proficiency during the test emigration was significantly higher in the choice treatment than no-choice treatment (Fig. 2b).

Throughout the training phase, colonies in both the choice and no-choice treatments increased their speed of reaching decisions with experience emigrating (Fig. 3). This improvement in decision-making speed with experience is consistent with previous studies, which reported that the total emigration speed increases when a single nest option is available (Langridge et al., 2004, 2008; Mitrus, 2016). Contrary to our expectation, the decision latency throughout the training phase did not differ between treatments. In other words, the time it took colonies to choose a nest did not differ when there was more than one option available. Perhaps colonies were favouring speed of emigration over choosing the better option. If the colonies had considered the better-quality nest to be superior, we would expect them to accept it faster than the mediocre-quality nest (Mallon et al., 2001). After investigating this idea, we found no difference in decision latencies of the no-choice treatment when moving into a good- or mediocre quality nest. Thus, our results suggest that both nest qualities were acceptable.

Although we confirmed with preliminary experiments that colonies preferred the good-quality nests, the mediocre-quality nests were also better quality than the standard nest. Unlike the standard nest, both new nests had reduced visible light in the nest cavity, which is the most important consideration when choosing a nest (Franks et al., 2003b). This suggests that when the ants were given a choice between these two nest qualities, they had a lower tendency to reject the mediocre nests than we had initially thought. Additionally, we removed the roof and walls of their old nest, which likely created a sense of urgency. Hence, it is possible that the ants favoured speed of emigrating over precise quality assessment between two good options. Similarly, *T. albipennis* ants favour speed over accuracy when environmental conditions are harsh (Franks et al., 2003a). In an experiment performed by Sasaki et al. (2018), colonies were faster at emigrating during a binary choice compared to no choice. Our results were not consistent with Sasaki et al. (2018) perhaps because their standard nest was an intermediate nest quality between the better- and lesser-quality nests. Accordingly, colonies may decide whether to emigrate faster when given a binary choice if the lesser-quality nest is inferior to the standard nest, promoting the decision to emigrate to the best-quality nest, compared to when given a single option. In comparison, our standard nest was the lowest-quality nest, meaning that colonies always improved the quality of their nest by emigrating regardless of their nest choice. These possibilities might explain why there was no difference in decision-latency between the choice and no-choice treatments during the test, and a high variation in
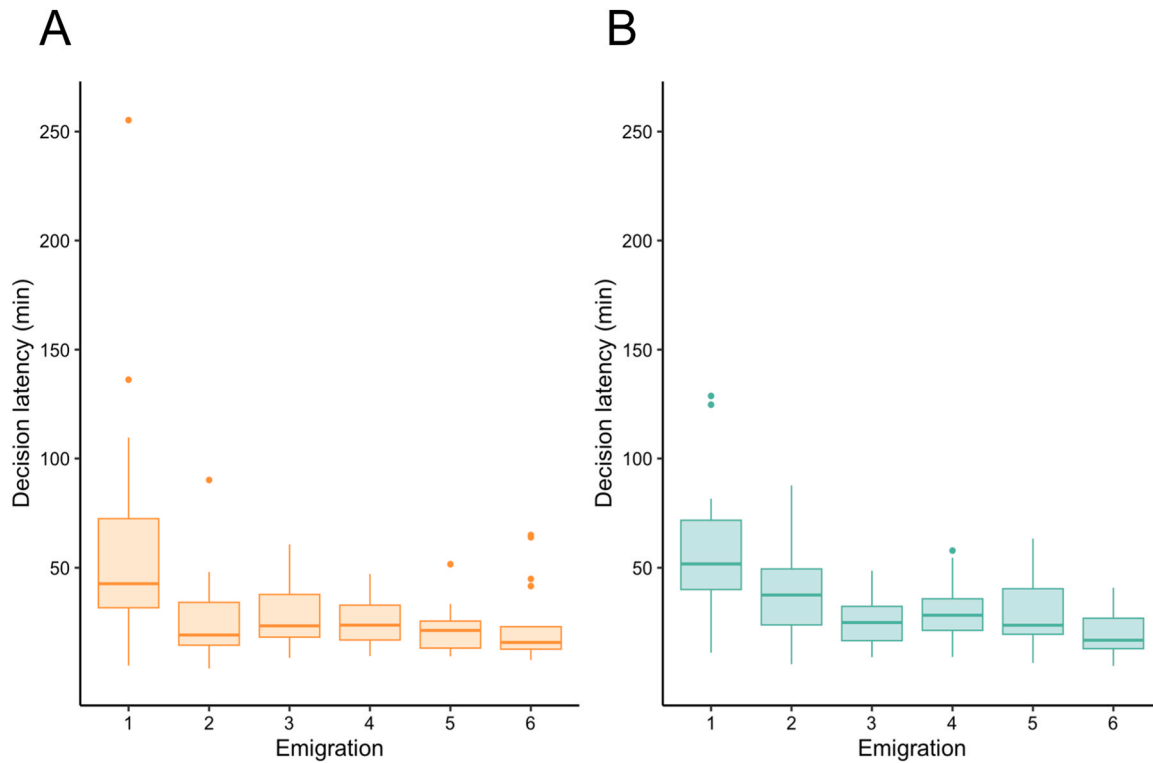
Fig. 3. Decision latencies of the choice (A) and no-choice (B) treatments throughout the six training emigrations. For the choice treatment, the sample size was 20 colonies in each emigration, except for emigration 6 where one data point is missing in each due to a missing video, respectively. For the no-choice treatment, the sample size was 20 colonies in each emigration, except for emigration 1 where one colony did not perform any transports and thus did not have a decision latency measure.
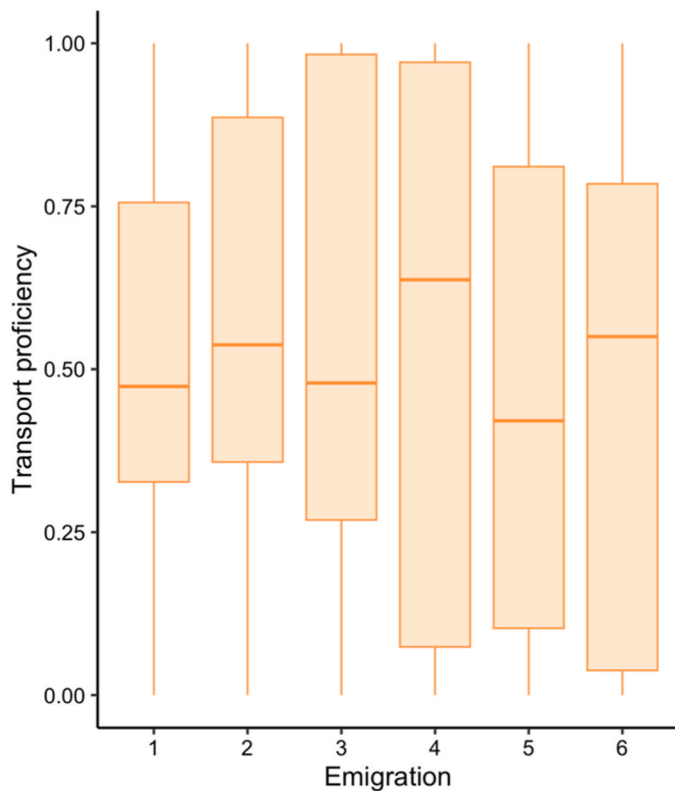

Fig. 4. Transport proficiency of the choice treatment during the training emigrations. The sample size was 20 colonies in each emigration, except for the 6th emigration where one data point is missing due to a missing video.

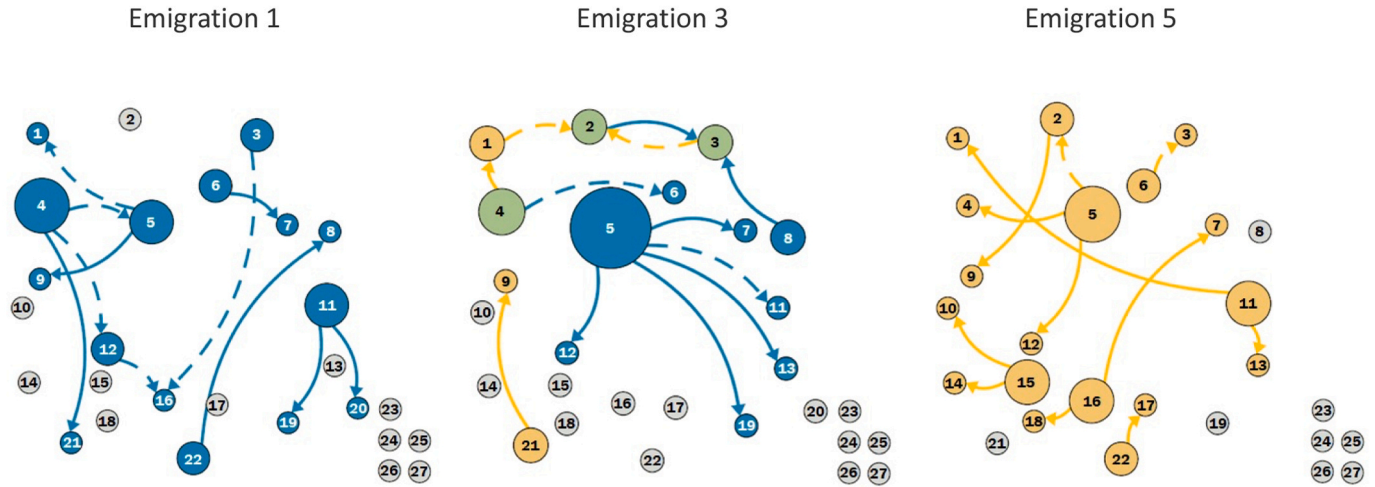transport proficiency throughout the training emigrations of the choice treatment.

While the difference between treatments in transport proficiency during the test phase is consistent with our prediction, we did not see an increase in proficiency throughout the training phase for the choice treatment suggesting that choice colonies did not gradually improve in transport proficiency with increasing experience in decision-making (Fig. 4). Therefore, a possible explanation for the between-treatment difference in proficiency during the test emigration is that rather than experience improving collective decision-making in choice treatment colonies, the lack of nest choices decreased group decision-making performance in no-choice colonies. Essentially, the no-choice treatment may have reduced transport proficiency due to lack of experience in deciding between more than one nest option. In nature, it is likely that ants searching for a new nest have a few options varying in quality. Perhaps the experimental setting of deciding upon a single nest repeatedly caused colonies of the no-choice treatment to lose their collective decision-making ability to choose among multiple nests. An alternative explanation for the difference in proficiency between treatments during the test could have been random variation that our sample size did not account for. Further data are necessary to clarify this issue.

Our social network analyses helped us quantify changes in patterns of interactions over successive emigrations. Unexpectedly, both parameters we measured, network density and the CV of out-strength distribution, showed no difference either over successive emigrations or between treatments. The network density measure indicated that the number of social interactions (transports and tandem runs) required to complete the emigration did not change as the colonies gained experience emigrating, nor did it vary between treatments (Fig. 6a). Second, the CV of out-strength distribution parameter indicated that the distribution of workload of the ant colonies did not change either over time or differ between treatments (Fig. 6b).

Our data about the social dynamics during emigration are different

A

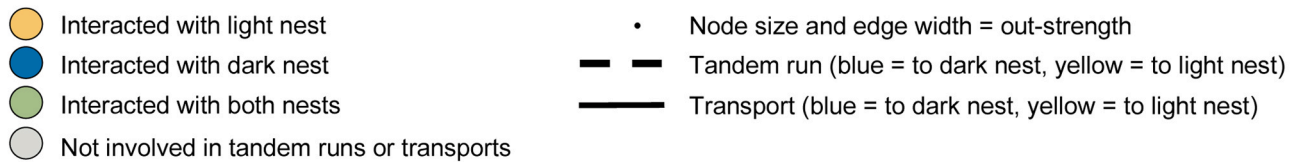## Colony 55 (choice)

B

Colony 60 (no-choice)

○ Interacted with light nest

● Interacted with dark nest

● Interacted with both nests

○ Not involved in tandem runs or transports

• Node size and edge width = out-strength

― ― Tandem run (blue = to dark nest, yellow = to light nest)

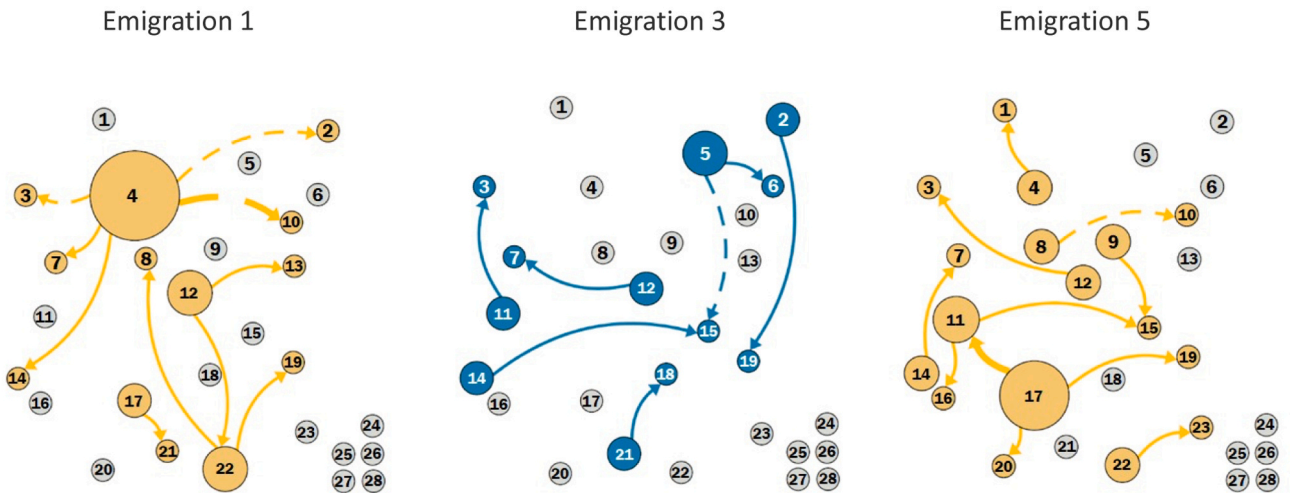―― Transport (blue = to dark nest, yellow = to light nest)

Fig. 5. Examples of social networks for training emigrations 1, 3 and 5 of a choice (A) and a no-choice colony (B). See legend at the bottom of the figure. Individual ants are represented by nodes that remain in the same position for each network. Each number represents a unique ID code for an individual within a colony. Nodes that disappear in later emigrations represent individuals that died throughout the experiment. Social networks for the other colonies are depicted in Figs. S1 and S2.

from those reported for other *Temnothorax* species. We found that emigration workload was relatively spread out amongst workers (Fig. 5, Figs S1-S2). Previous studies reported that a stable minority of workers—an "oligarchy"—are responsible for a majority of the decision-making process during emigration (Pinter-Wollman et al., 2012; Richardson et al., 2018, 2021; Valentini et al., 2020). Individuals within

this minority typically performed the same tasks each emigration and reached consensus on a nest for the entire colony. If we had found evidence of an oligarchy in our experiment, collective improvement in decision-making speed could have been the result of the stable group of individuals improving. However, we found that the workload was relatively spread out amongst workers, and by visually inspecting the
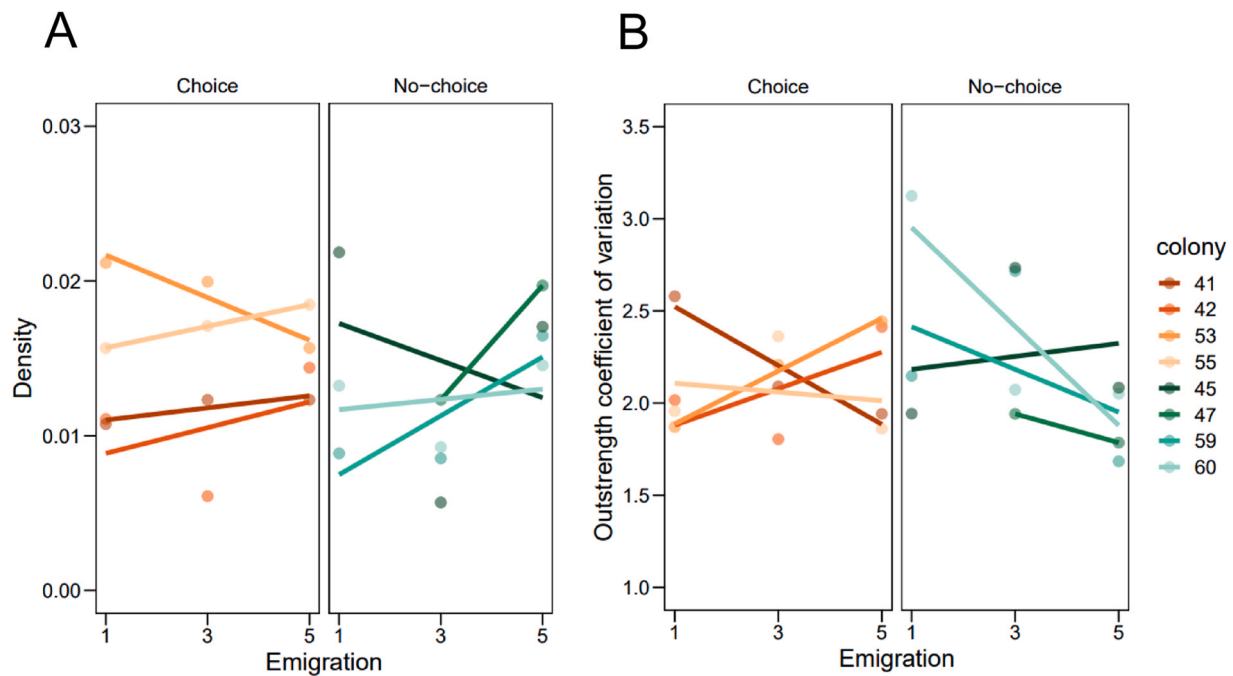
Fig. 6. The two social network metrics for 4 colonies of the choice and 4 colonies of the no-choice treatments during the first, third, and fifth training emigrations. A) Network densities. B) the CV of network out-strength values. The first emigration for colony 47 is missing due to a hard drive storage failure.

networks (Fig. 5, Figs S1-S2), the workload was executed by different individuals each emigration. Possibly, the smaller colony sizes of *T. ambiguus* benefit from a higher degree of behavioural plasticity of workers compared to other *Temnothorax* species, which typically have larger colonies. Because *T. ambiguus* colonies have fewer workers, individuals may do whatever task needs to be done, regardless of their experience. Although some research has explored the relation between task allocation and colony size (e.g., Dornhaus et al., 2008), further research should expand on individual consistency in performing tasks over time and effects of colony size on task allegation.

The fact that the social network parameters we measured did not change over successive emigrations (Fig. 5, Figs S1-S2) is surprising given that the colonies in both treatments improved their decision-making speed. Because colonies in both treatments became faster at decision-making, we expected to find changes in their social organization throughout the training emigrations. Our social network analyses failed to capture how colonies collectively became faster with their decision-making abilities over successive emigrations. It is thus possible that the acorn ants we have studied use a group decision system that we still do not entirely understand. We should note that even for other ant model systems, previous research has provided mixed evidence regarding individual-level improvement on task efficiency with experience. Richardson et al. (2021) found that the experience of a leader was the most important predictor of successful tandem running in *Temnothorax nylanderi*. However, O'Shea-Wheller et al. (2016) reported that experience did not increase tandem running performance in *T. albipennis*. That is, despite the reasonable research effort devoted to deciphering the social decisions underlying emigration decisions in general and in the genus *Temnothorax* in particular (Franks et al., 2002; Sasaki and Pratt, 2018; Seeley and Buhrman, 1999; Visscher, 2007), we lack a complete understanding of that process. Of course, it is possible that different species, even within a single genus, rely on distinct social decision rules, which might limit our ability to generalize. Even closely related species of *Temnothorax* and its sister genus *Leptothorax* are known to differ in multiple aspects of their collective behaviour (Doering et al., 2022; Pratt, 2005a, 2005b), nest type preferences (Prebus, 2017; Rizo, 2000), and social organization (Guénard et al., 2016; Prebus, 2021). Alternatively, the lack of pattern from our social network

metrics could be the result of noise, as these colonies contained 26–45 workers, and our sample size was four colonies per treatment. Nonetheless, our results highlight the importance of exploring how consistent *Temnothorax* species are in their task allocation and leadership strategies.

Our study is a step towards understanding how collective behaviour changes over time and is the first to explicitly test the effects of repeated experience in collective decision-making. We found that colonies increased their speed of collective decision-making with experience emigrating, regardless of whether their prior emigration experiences involved a choice between nests. In fact, decision latency in our final test emigration did not differ between colonies from choice vs. no-choice treatments between. Although we detected a difference between treatments for transport proficiency, further research is required to pinpoint the mechanisms driving this difference in performance. Through SNA, we found that interaction network density and distributed workload remained stable over time and did not differ between colonies presented with no choice compared to a binary choice in nests. Lastly, our study demonstrates how house-hunting ant colonies can serve as an insightful animal model system for examining the developmental mechanisms of collective improvement. By expanding our knowledge of collective learning and decision-making, we can better understand how successful group living is achieved.

Data availability

Data is available at https://github.com/TovahKashetsky/collective _decision_experience.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2023.104962.

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