

Colony size, nestmate density and social history shape behavioural variation in *Formica fusca* colonies

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Funding information

European Union and the European Social Fund, Grant/Award Number: EFOP-3.6.1-16-2016-00022; Hungarian Academy of Sciences (MTA); "AntLab" Marie Curie Career Integration Grant, Grant/Award Number: PCIG11-GA-2012-322110; Higher Education Institutional Excellence Program, Grant/Award Number: NKFIH-1150-6/2019

Abstract

In ants, individuals live in tightly integrated units (colonies) and work collectively for its success. In such groups, stable intraspecific variation in behaviour within or across contexts (personality) can occur at two levels: individuals and colonies. This paper examines how colony size and nestmate density influence the collective exploratory behaviour of *Formica fusca* (Hymenoptera: Formicidae), in the laboratory. The housing conditions of the colonies were manipulated to vary the size of colonies and their densities under a fully factorial design. The results demonstrate the presence of colony behavioural repeatability in this species, and contrary to our expectations, colonies were more explorative on average when they were kept at lower nestmate densities. We also found that experimental colonies created from larger source colonies were more explorative, which conveys that a thorough understanding of the contemporary behaviour of a colony may require knowing its social history and how it was formed. Our results also convey that the colony size and nestmate density can have significant effects on the exploratory behaviour of ant colonies.

KEYWORDS

collective behaviour, colony size, exploration, housing condition, nestmate density

1 | INTRODUCTION

Ants are considered one of the evolutionarily most successful taxa, with more than 13,000 described species (Bolton, 2019) exhibiting diverse social organizations (Hölldobler & Wilson, 1990). Most species of ants form colonies where nestmates permanently live and cooperate with each other without any central leadership (Duarte, Weissing, Pen, & Keller, 2011; Sendova-Franks & Franks, 1999). Workers respond mostly to local cues and tend to specialize on only a few tasks, but can act collectively in several situations, for instance

during nest defence (Detrain, Deneubourg, & Pasteels, 1999; Sakata & Katayama, 2001). The behaviour of colonies can depend on the collective decisions and the behaviour of group members (i.e., workers in ants) (Bengston & Jandt, 2014).

The field of animal personality investigates the within-individual stability of behaviour over time and across situations (Sih, Bell, & Johnson, 2004). Consistent among-individual differences in behaviour are widespread among invertebrates and vertebrates (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). However, in social insects, not only individuals can behave consistently, but also entire

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colonies can show stable characteristic behavioural differences (Bengston & Jandt, 2014; Jandt et al., 2014; Pinter-Wollman, 2012; Wright et al., 2019) and hence can be said to have a collective or colony personality. This colonial level consistency might be important because in highly social organisms like eusocial insects, natural selection acts at the colony level (Blight, Albet Díaz-Mariblanca, Cerdá, & Boulay, 2016; Bockoven, Wilder, & Eubanks, 2015; Hölldobler & Wilson, 1990; Modlmeier, Keiser, Wright, Lichtenstein, & Pruitt, 2015; Pinter-Wollman, 2012; Pruitt & Modlmeier, 2015; Scharf, Modlmeier, Fries, Tirard, & Foitzik, 2012). For example, in *Temnothorax nylanderii* (Foerster, 1850), colonies show consistency in nest reconstruction, relocation after disturbance, removal of corpses and in their aggressive behaviour against the intruders (Scharf et al., 2012). In *Veromessor andrei* (Mayr, 1886), colonies are consistent in both their rate of seed and debris retrieval (Pinter-Wollman, 2012). Such colony phenotypes can be shaped by numerous properties, such as the distribution of the individual level phenotypes that comprise the group (Pruitt, Grinsted, & Settepani, 2013).

In the *Formicidae* group, different species can live in colonies with many different sizes, from a few to 300 million workers (Kaspari & Vargo, 1995). During the development of an ant colony, the number of nestmates usually increases steadily and the rate of colony growth can be influenced by a variety of intrinsic (e.g., number of egg-laying queens) and extrinsic factors (e.g., predation) (Bourke, 1999). In general, larger colonies can produce more complex or impressive collective feats and larger colonies can often organize more efficient foraging networks as well (Merkle & Middendorf, 2004). For instance, in *Messor sanctus* Emery, 1921 collective digging is positively correlated with colony size and the tunnel networks of larger colonies are conspicuously more complex (i.e., contained more edges and vertices) (Buhl, Gautrais, Deneubourg, & Theraulaz, 2004). Similar observations have been made in social bees, wasps and social spiders (Avilés & Tufino, 1998; Donaldson-Matasci, DeGrandi-Hoffman, & Dornhaus, 2013). Larger colonies of honeybees have a more complex dance language, which renders them more efficient at recruiting foragers to novel food patches (Donaldson-Matasci et al., 2013). Empirical evidence suggests that the division of labour and task specialization within social groups increases with group size (Amador-Vargas, Gronenberg, Wcislo, & Mueller, 2015; Anderson & McShea, 2001; Bourke, 1999), though this is not always the case (Dornhaus, Holley, & Franks, 2009). In some species, small colonies invested more in the consensus decision process than the large ones (Cronin & Stumpe, 2014). In aggregate, one can observe that colony size can shape a variety of collective attributes in social insect colonies. It, therefore, stands to reach those changes in colony size that could shape the expression of colony phenotypes that are commonly evaluated in animal personality literature as collective exploration.

Fluctuations in colony size can influence the density of nestmates (number of individuals per nest size) which can be another key parameter affecting within-nest dynamics (Perna & Theraulaz, 2017). However, these aspects are rarely examined in social insects under laboratory circumstances (but see in Cao & Dornhaus, 2008; Gordon, Paul, & Thorpe, 1993; Modlmeier et al., 2019; Pie, Rosengaus, & Traniello,

2004). Changes in colony size and social density, for instance, could alter the way information is transferred between workers, which in turn could shape colony activities (Beshers & Fewell, 2001; O'Donnell & Bulova, 2007) and group behaviour (Pacala, Gordon, & Godfray, 1996). O'Donnell and Bulova's (2007) simulation model indicates that density-mediated changes in social interactions shape the division of labour and the organization of work across colonies. Taken together, the available evidence suggests that social density within nests could be another important factor in determining the phenotypes that colonies express during staged behaviour assays.

A common measure of behavioural repeatability is the rate at which individuals move through a novel space or environment, normally referred to as exploratory behaviour or exploration (Arvidsson, Adriaensen, Dongen, Stobbeleere, & Matthysen, 2017; Dingemanse, Both, Drent, Oers, & Noordwijk, 2002). In this study, we investigated (a) the repeatability of the collective exploratory behaviour in laboratory colonies of *Formica fusca* Linnaeus, 1758 (Hymenoptera: Formicidae) and (b) how colony size and nestmate density influence exploratory behaviour, using a fully factorial experimental design. We examined colony exploration, in particular, because the exploration of the exterior environment is how colonies obtain information about potential food sources, competitors and predators (Clobert, Danchin, Dhondt, & Nichols, 2001; Devigne & Detrain, 2002). For example, Gordon (1996) investigated the exploratory behaviour of colonies of different sizes (*Linepithema humile*, [Mayr, 1868]) and found that the largest number of exploring workers were present in the largest colonies. Similar positive correlation was found between colony size and the number of foragers in the studies with *Pogonomyrmex salinus* Cole 1983 (Porter & Jorgensen, 1981), *Cataglyphis cursor* (Fonscolombe, 1846) (Retana & Cerda, 1991) and *Temnothorax rugatulus* (Emery, 1895) (Charbonneau & Dornhaus, 2015). We therefore predicted that the level of exploratory behaviour would be more intense in large and dense *F. fusca* colonies.

2 | MATERIALS AND METHODS

Formica fusca is a facultative polygynous species (Czechowski, Radchenko, Czechowska, & Vepsäläinen, 2012; Seifert, 2018) being abundant in Central Europe, especially in areas with abundant dead wood. Its nests can be found in dead wood, soil or moss pads. This species relies on the swift discovery of ephemeral food patches and avoiding workers of dominant heterospecifics. *Formica fusca* is thus generally not aggressive, though particularly large colonies can defend some kinds of resources (Seifert, 2018).

Colonies of *F. fusca* were collected from Vámospércs, Hungary (47.524796 N, 21.886494 E) in May 2014, when the workers were active and brood was still not present in nests. These conditions made possible the collection of whole colonies and the accurate counting of workers and queens (workers: 85–635, queens: 1–10). We collected 14 colonies (hereafter: source colony) that were divided into 28 subcolonies (hereafter: experimental colonies). The subcolonies that were considered inappropriate for the observations were removed from the study (dead queen or workers), so finally 22 subcolonies were

retained. Each new experimental colony contained only one fertilized queen (that laid eggs in the laboratory), to diminish the possible effects of queen number in determining colonies' exploratory behaviour. For housing the experimental colonies, we used four different sized artificial nests (made from concrete) with two colony size categories (25 or 135 workers). This produced two experimental densities of 0.25 or 0.5 worker/cm² in a 2 × 2 full factorial design (Table 1). Colonies were fed with Bhatkar diet (Bhatkar & Whitcomb, 1970) and were provided with water ad libitum. They were maintained at room temperature (22–25°C) with a natural light/dark cycle. Colonies were investigated in block design, where every block contained one nest from each of the four treatment combinations, respectively.

2.1 | Behavioural tests: Exploration of novel environment and objects

The exploratory behaviour of *F. fusca* colonies was investigated in circular arenas (diameter: 39.5 cm). Before the assays, we placed two pieces of lead into the arena as novel objects and two drops of sugar solution as a positive signal to instigate scouting. The novel objects

were observable for the ants, but they could not remove them. During the assay, the colony's nest and the arena were connected via a 10-cm-long plastic tube (Figure 1). Thus, workers could freely enter the arena, explore it, and return to the nest. After the acclimatization period (20 min), which permitted the ants to investigate and use the tube connecting the nest with the arena, we opened the tube towards the arena and video recorded the movement of the exploratory workers for 40 min. The camera (Panasonic HC-V510) was focused on the exploratory arena, and the MWrap event recorder (Bán, Földvári, Babits, & Barta, 2017) was used to code the behaviours from the videos. At the time of the analysis, ants entering the arena were not distinguished individually, so every behaviour of workers from the same colony was analysed together.

The following variables were recorded: the latency of first worker entering into the arena (the "entrance," elapsed time between opening the connection and the first worker entering into the arena), the latency of the first return home to the nest ("lat. home," elapsed time from "entrance" to the first return to the colony) and the latency of the first visit to an object ("lat. sugar water" and "lat. object" separately, measured from "entrance"). The number of entries into the arena ("nr. entries") and the number of visits to objects ("nr. objects,"

TABLE 1 Housing conditions (i.e., treatment) with the number of participating colonies in the behavioural tests (i.e., number of colonies tested, per nest types)

Nest type	Nest size (cm ²)	Chamber size (cm ²)	Nr. workers in the nests	Nestmate density (worker/nest size)	Nr. colonies
1	39.25	4.8	20	0.5	6
2	78.5	9.61	20	0.25	3
3	265.5	32.5	135	0.5	7
4	531	65	135	0.25	6

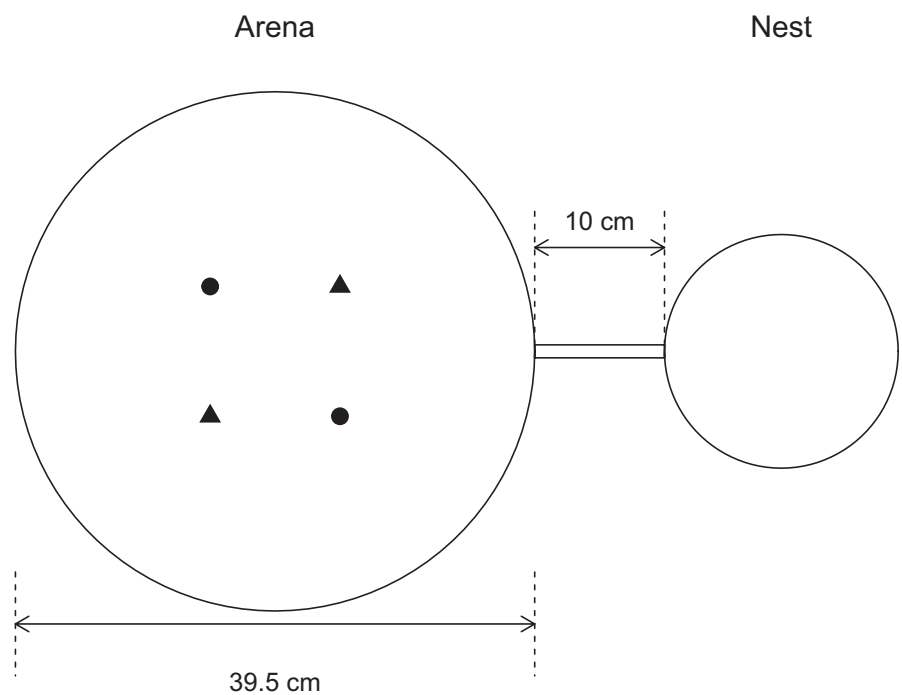


FIGURE 1 Experimental set-up of the foraging arenas and nests to analyse colony level exploration. Different nest sizes were used for the different setups (see Table 1 for details). The sizes of the novel objects are proximate on the figure

"nr. sugar water") were also counted. The number of homecoming workers ("nr. returnings") and the maximum worker number ("max. workers") in the arena were strongly correlated with the "nr. entries" (Spearman correlation: $\rho = 0.978$, $p < .001$, $n = 82$ and $\rho = 0.851$, $p < .001$, $n = 82$, respectively), so we omitted them from subsequent analyses. We also recorded the encounters between the individuals (contact with each other: antennation or trophallaxis; "lat. interactions," "nr. interactions"). The behavioural tests took a month (from 13.06.2014 to 14.07.2014). The behavioural assay was repeated four times per colony, with approximately 8 days (mean = 8.48, median = 8, $SD = 2.52$) separating consecutive assays on the same colony. If the queen of a colony or the colony itself died, no further tests were performed with that colony. We only considered colonies that completed at least two trials ($n = 22$).

2.2 | Statistical analysis

All analyses were performed in the R interactive statistical environment (version 3.3.3, R Core Team 2017). We applied a principal component analysis (PCA) (base "stats" package and "prcomp" function) on the behavioural variables to test for possible correlations among all response variables. The PCA was carried out on the covariance matrix based on the average value of the behavioural variables. We only analysed those principal components (PCs) further that had eigenvalues greater than 1 (Kaiser–Guttman criterion; Jackson, 1993). PCA scores (from first (PC1) and second principal components (PC2)) were analysed using linear mixed-effect models (LMMs). The full models included experimental colony size, treatment density, original queen number and original colony size as fixed effects, and the source colony ID as a random factor. We investigated behavioural repeatability at the colonial level by calculating the repeatability (marked with R) of each variable using the rptR package (Stoffel, Nakagawa, & Schielzeth, 2017) with 1,000 bootstrap steps. p -Values were obtained by likelihood ratio tests, and confidence intervals (95%) were derived by 1,000 permutations. Repeatability values, which are significantly higher than zero, indicate a significant among-colony component to the observed intraspecific variation (Réale et al., 2007). "Nr. entries" and "lat. home" were log-transformed and analysed with Gaussian family, while "entrance," "lat. sugar water," "lat. object" and "lat. interaction" were binomized by the median and analysed with binomial family. "Nr. interactions," "nr. sugar water" and "nr. objects" were analysed with Poisson family and sqrt link. In every case concerning repeatability analysis, experimental colony ID was entered as a random factor. The number of the trials, original queen number, original colony size (recorded at the time of collection), experimental colony size, treatment density, date of the behavioural tests (expressed as Julian date) and time of the behavioural tests (expressed in minutes from midnight) were used as fixed effects. Original colony size was log-transformed prior to our analyses. All models were simplified by removing non-significant terms (backward elimination procedure). Significant effects were assessed based on the t -values (absolute t -value > 2). Tukey's post hoc tests

(lsmeans package; Lenth, 2016) were used to compare the behaviour of the colonies between the four trials.

3 | RESULTS

3.1 | Correlations among the response variables

Principal component analysis is often used to test for the presence of behavioural syndromes (Dingemanse, Dochtermann, & Wright, 2010). In our case, PC1 explained 54.24%, while PC2 explained 21.88% of the total variance (76.12%). The first component was composed of five variables ("entrance," "lat. home," "lat. sugar water," "lat. object" and "nr. entries"), and it can be referred to as "activity in the arena." The higher score indicated that the colony showed a lower level of activity in the arena with higher latency times and fewer entries. The second component was composed of two variables ("nr. sugar water" and "nr. objects"), and it can be referred to as "exploration of the arena" (Table 2).

3.2 | Repeatability of the collective behaviour

We detected temporally consistent among-colony differences in the number of entries into the arena ($R = 0.321$, $SE = 0.121$, $CI = [0.082, 0.562]$, $p = .001$) and in the latency time of the first returning ($R = 0.223$, $SE = 0.116$, $CI = [0.0072, 0.461]$, $p = .039$). The repeatability of other behavioural traits was not significant (Table 3).

3.3 | Effects of the housing conditions

Principal component 1 scores were positively correlated with nest-mate density ($\beta = 1.963$, $SE = 0.878$, $t = 2.236$, $p = .036$) suggesting that colonies from nests with higher densities showed a higher level of activity in the arena during the examination. PC2 was not related to any of the housing condition parameters.

Colonies with high nest density treatment exhibited fewer entries into the arena ($\beta = -0.740$, $SE = 0.261$, $t = -2.781$, $p = .011$), and the first workers returned earlier to the nests ($\beta = -0.856$, $SE = 0.344$, $t = -2.485$, $p = .022$). Larger colonies also exhibited lower latencies for their first workers to return to the nest ($\beta = -0.877$, $SE = 0.346$, $t = -2.531$, $p = .020$). No other significant effects were detected.

3.4 | Effects of the original colony size on behaviour

Experimental colonies spawned from larger source colonies (at collection) initiated exploration earlier ($\beta = -0.952$, $SE = 0.383$, $t = -2.481$, $p = .005$) but were contacting slower with novel objects

TABLE 2 Eigenvector loadings, eigenvalues, and proportion and cumulative proportion of variance for the principal components retained (PCs 1–3)

Variables	PC1	PC2	PC3
"nr. entries"	-0.39455988	-0.06825975	-0.004483957
"nr. sugar water"	-0.04199912	-0.58687140	0.327155226
"nr. objects"	-0.26193725	-0.49338096	0.044376351
"nr. interactions"	-0.21141126	-0.47497473	-0.550507271
"entrance"	0.41837646	-0.17094148	0.095105159
"lat. home"	0.38778244	-0.13636886	0.326969438
"lat. interaction"	0.32538215	0.09696564	-0.671917985
"lat. object"	0.40436364	-0.20548686	-0.142037181
"lat. sugar water"	0.36668127	-0.28714484	-0.017874364
	PC1	PC2	PC3
Eigenvalue	4.88190613	1.96878161	0.71669751
Per cent of variance	54.2434015	21.8753512	7.9633056
Cumulative per cent of variance	54.24340	76.11875	84.08206

TABLE 3 Repeatability (R) of the colony level behaviours. Standard error (SE) and 95% confidence interval (95% CI). *p*-values were calculated by likelihood ratio tests. Repeatability results are in bold

Variables	R	SE	95% CI	<i>p</i>
"nr. entries"	0.301	0.124	0.058, 0.543	.004
"nr. sugar water"	0.00	0.078	0, 0.266	1
"nr. objects"	0.00	0.076	0, 0.253	0.5
"nr. interactions"	0.00	0.092	0, 0.314	0.5
"entrance"	0.00	0.036	0, 0.124	1
"lat. home"	0.223	0.116	0.006, 0.458	.039
"lat. interaction"	0.091	0.086	0, 0.287	.110
"lat. object"	0.00	0.034	0, 0.118	.380
"lat. sugar water"	0.007	0.036	0, 0.120	.260

("lat. object": $\beta = 1.035$, $SE = 0.483$, $z = 2.143$, $p = .032$). We detected no other significant effects of original colony size.

3.5 | Effects of queen number on behaviour

We could not detect any significant association between the number of queens within source colonies and any aspect of the exploratory behaviour of their descendent experimental colonies.

4 | DISCUSSION

The study herein aimed to explore the extent to which *F. fusca* colonies exhibit temporal among-colony repeatability in their collective exploratory tendencies and how these tendencies are affected by the size of the colonies and the densities of workers within the nests. The principal component analysis identified two behavioural axes,

one is related to activity, while the other to exploration. Further analyses suggest that activity is influenced by worker density in the nests. The separate analyses of the behavioural traits also support this effect of colony density.

We detected behavioural repeatability among colonies in the total number of entries and the latency of the first worker to return to the nest. Both of these features are likely to be tied to the successful foraging activity of colonies (according to Gordon, 1983 and Byrne, 1994). Consistent with this prediction, between-colony differences in collective foraging activity have been linked with colony success in several species of ants (e.g. Kühbandner, Modlmeier, & Foitzik, 2014, Modlmeier & Foitzik, 2011, Gordon, 2013, Bengston, Shin, & Dornhaus, 2017, Carere, Audebrand, Rödel, & d'Ettorre, 2018). Carere et al. (2018) found similar associations between worker deployment and return rates in *F. fusca*. We failed to detect consistent among-colony differences in the latency of visitations to staged patches of sugar water or foreign objects. We predicted that worker-worker interactions outside of the nest would be an important determinant of colonies' exploratory tendencies and in the exchange of information about the foraging landscape (Gordon, 1996; Gordon & Mehdiabadi, 1999; Pacala et al., 1996). However, we failed to detect repeatability in any of our metrics of worker-worker interactions (latency to first interaction, total interactions). Moreover, neither of these interaction metrics were associated with colony size, nest density or original queen number. This was at odds with our basic prediction that colonies containing more workers or even denser colonies would be, by default, exhibiting a larger number of worker-worker interactions, as a matter of packing. Recent work on *Camponotus pennsylvanicus* (De Geer, 1773) revealed that colonies of ants can maintain homeostasis in their worker-worker interaction rates in spite of changes to nest density (Modlmeier et al., 2019), which potentially conveys that there is an ambient and optimal level of interaction rates necessary for colony functioning. The fact that worker-worker interactions were also insensitive to colony size and

nest density implies that *F. fusca* can also hone in the level of interactions needed for running the colonies efficiently.

Alterations in group size can have a variety of impacts on the collective phenotypes. However, in colonies of *Temnothorax albipennis* (Curtis, 1854), for instance, collective decision-making was not influenced by experimental alterations in colony size (Dornhaus & Franks, 2006). Similarly, findings from social spiders convey that colony size does not affect the exploratory behaviour in *Stegodyphus dumicola* Pocock, 1898 (Keiser & Pruitt, 2014). Yet, alterations in group size are obviously influential in other systems. The results of Ward, Herbert-Read, Sumpter, and Krause (2011), for example indicate that larger fish groups (eastern mosquitofish, *Gambusia holbrooki* Girard, 1859) are better and faster in decision-making. We found some support that alterations in nest density can impact aspects of colony exploration; this was true for the latency of the first worker to return to the nest and for the total number of the entries. Here, smaller colonies exhibited longer latencies (i.e., later returns) and they showed more entries. Overall the exploration of the *F. fusca* colonies was influenced by the density. Similar density-dependent behavioural differences have been found in colonies of the polydomous *T. rugatulus*, where more intense foraging and scouting activity was observed under high-density conditions (Cao, 2013). Similarly, increasing group size enhances nest construction rates in *Lasius niger* (Linnaeus, 1758) (Toffin, Kindekens, & Deneubourg, 2010), digging rates in some termites (Bardunias & Su, 2010) and the speed of worker returns in *Myrmica punctiventris* Roger, 1863 (Herbers & Choiniere, 1996). In aggregate, it seems that there are cases when group size can strongly influence group behaviour, and in other cases, group phenotypes appear entirely resilient to alteration in group size. For now, the reasons behind such case-by-case outcomes remain elusive.

At odds with the findings from our experimental colonies, we detected an influence of the size of the source colony on the exploratory behaviour of our experimental colonies. Similar effects have been detected before (e.g., *T. albipennis*) (Dornhaus & Franks, 2006). Our manipulations to colony size were performed by randomly removing subsets of workers from the group. Based on the literature, there is a positive relation between the colony size and the rate of individual specialization (see in Anderson & McShea, 2001; Charbonneau & Dornhaus, 2015; Porter & Jorgensen, 1981) with higher efficiency at collective behaviours such as task partitioning (Anderson & Ratnieks, 1999). So, the faster exploration rates of our experimental colonies derived from large source colonies may reflect on an enhanced searching behaviour, since these colonies may contain more foragers who have earlier (before splitting) experience in this scope of duties. The ants' individual experience can influence the exploration activity and by this the successfulness of the foraging (Pasquier & Grüter, 2016).

In summary, we detected significant among-colony differences in the collective foraging behaviour of *F. fusca* colonies, where larger experimental colonies and experimental colonies derived from large source colonies were more efficient. Moreover, the exploration of the colonies was influenced by the density of the nestmates. The results herein convey that a thorough understanding of how a colony behaves at present may require knowing its demographic history and how the descendant colony came to be.

ACKNOWLEDGEMENT

We would like to thank Miklós Bán, Attila Fülöp and Enikő Gyuris for providing technical help and Ferenc Báthori for assistance in the field. We are grateful for the helpful comments of the editor and the referees, which greatly improved the manuscript. The publication was supported by the EFOP-3.6.1-16-2016-00022 project. The project is co-financed by the European Union and the European Social Fund. AT was supported by two "Bolyai János" scholarships of the Hungarian Academy of Sciences (MTA), by the ÚNKP-18-4-DE-452 and by the ÚNKP-19-4-DE-303 New National Excellence Program of the Ministry of Human Capacities and by the "AntLab" Marie Curie Career Integration Grant (PCIG11-GA-2012-322110), part of the 7th European Community Framework Programme. ZB was financed by the Higher Education Institutional Excellence Program (NKFIH-1150-6/2019) of the Ministry of Innovation and Technology in Hungary, within the framework of the FIKP-DE Behavioural Ecology Research Group thematic program of the University of Debrecen.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL NOTES

Ethics approval was not required for the study. We worked with an unprotected species collected from an unprotected site.

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REFERENCES

- Amador-Vargas, S., Gronenberg, W., Wcislo, W. T., & Mueller, U. (2015). Specialization and group size: Brain and behavioural correlates of colony size in ants lacking morphological castes. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142502. <https://doi.org/10.1098/rspb.2014.2502>
- Anderson, C., & McShea, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biological Reviews*, 76(2), 211–237. <https://doi.org/10.1017/S1464793101005656>
- Anderson, C., & Ratnieks, F. L. W. (1999). Task partitioning in insect societies. I. Effect of colony size on queueing delay and colony ergonomic efficiency. *American Naturalist*, 154(5), 521–535. <https://doi.org/10.1086/303255>
- Arvidsson, L. K., Adriaenssen, F., van Dongen, S., De Stobbeleere, N., & Matthysen, E. (2017). Exploration behaviour in a different light: Testing cross-context consistency of a common personality trait. *Animal Behaviour*, 123, 151–158. <https://doi.org/10.1016/j.anbehav.2016.09.005>
- Avilés, L., & Tufiño, P. (1998). Colony size and individual fitness in the social spider *Anelosimus eximius*. *The American Naturalist*, 152(3), 403–418. <https://doi.org/10.1086/286178>
- Bán, M., Földvári, M., Babits, M., & Barta, Z. (2017). Simple command-line open-source software to analyse behavioural observation video recordings. *Acta Zoologica Academiae Scientiarum Hungaricae*, 63(1), 137–142. <https://doi.org/10.17109/AZH.63.1.137.2017>

- Bardunias, P. M., & Su, N. Y. (2010). Queue size determines the width of tunnels in the formosan subterranean termite (Isoptera: Rhinotermitidae). *Journal of Insect Behavior*, 23(3), 189–204. <https://doi.org/10.1007/s10905-010-9206-z>
- Bengston, S. E., & Jandt, J. M. (2014). The development of collective personality: The ontogenetic drivers of behavioral variation across groups. *Frontiers in Ecology and Evolution*, 2, 1–13. <https://doi.org/10.3389/fevo.2014.00081>
- Bengston, S. E., Shin, M., & Dornhaus, A. (2017). Life-history strategy and behavioral type: Risk-tolerance reflects growth rate and energy allocation in ant colonies. *Oikos*, 126(4), 556–564. <https://doi.org/10.1111/oik.03527>
- Beshers, S. N., & Fewell, J. H. (2001). Models of division of labor in social insects. *Annual Review of Entomology*, 46, 413–440. <https://doi.org/10.1146/annurev.ento.46.1.413>
- Bhatkar, A., & Whitcomb, W. (1970). Artificial diet for rearing various species of ants. *Florida Entomologist*, 53(4), 229–232. <https://doi.org/10.2307/3493193>
- Blight, O., Albet Díaz-Mariblanca, G., Cerdá, X., & Boulay, R. (2016). A proactive-reactive syndrome affects group success in an ant species. *Behavioral Ecology*, 27(1), 118–125. <https://doi.org/10.1093/beheco/ arv127>
- Bockoven, A. A., Wilder, S. M., & Eubanks, M. D. (2015). Intraspecific variation among social insect colonies: Persistent regional and colony-level differences in fire ant foraging behavior. *PLoS ONE*, 10(7), <https://doi.org/10.1371/journal.pone.0133868>
- Bolton, B. (2019). An online catalog of the ants of the world. Available from <http://antcat.org> (accessed: 27.05.2019).
- Bourke, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology*, 12(2), 245–257. <https://doi.org/10.1046/j.1420-9101.1999.00028.x>
- Buhl, J., Gautrais, J., Deneubourg, J. L., & Theraulaz, G. (2004). Nest excavation in ants: Group size effects on the size and structure of tunneling networks. *Naturwissenschaften*, 91(12), 602–606. <https://doi.org/10.1007/s00114-004-0577-x>
- Byrne, M. M. (1994). Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica*, 26(1), 61–72. <https://doi.org/10.2307/2389111>
- Cao, T. T. (2013). High social density increases foraging and scouting rates and induces polydomy in *Temnothorax* ants. *Behavioral Ecology and Sociobiology*, 67(11), 1799–1807. <https://doi.org/10.1007/s00265-013-1587-5>
- Cao, T. T., & Dornhaus, A. (2008). Ants under crowded conditions consume more energy. *Biology Letters*, 4(6), 613–615. <https://doi.org/10.1098/rsbl.2008.0381>
- Carere, C., Audebrand, C., Rödel, H. G., & d'Ettorre, P. (2018). Individual behavioural type and group performance in *Formica fusca* ants. *Behavioural Processes*, 157, 402–407. <https://doi.org/10.1016/j.beproc.2018.07.009>
- Charbonneau, D., & Dornhaus, A. (2015). Workers 'specialized' on inactivity: Behavioral consistency of inactive workers and their role in task allocation. *Behavioral Ecology and Sociobiology*, 69(9), 1459–1472. <https://doi.org/10.1007/s00265-015-1958-1>
- Clobert, J., Danchin, E., Dhondt, A. A., & Nichols, J. D. (2001). *Dispersal*. Oxford, UK: Oxford University Press.
- Cronin, A. L., & Stumpe, M. C. (2014). Ants work harder during consensus decision-making in small groups. *Journal of the Royal Society Interface*, 11(98), 20140641. <https://doi.org/10.1098/rsif.2014.0641>
- Czechowski, W., Radchenko, A., Czechowska, W., & Vepsäläinen, K. (2012). *The Ants of Poland with Reference to the Myrmecofauna of Europe*. Warsaw, Poland: Natura optima dux Foundation.
- Detrain, C., Deneubourg, J. L., & Pasteels, J. M. (1999). Information processing in social insects. *Information Processing in Social Insects*, 59(4), 896–897. <https://doi.org/10.1006/anbe.2000.1391>
- Devigne, C., & Detrain, C. (2002). Collective exploration and area marking in the ant *Lasius niger*. *Insectes Sociaux*, 49, 357–362. <https://doi.org/10.1007/PL00012659>
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6), 929–938. <https://doi.org/10.1006/anbe.2002.2006>
- Dingemans, N. J., Dochtermann, N., & Wright, J. (2010). A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. *Animal Behaviour*, 79(2), 439–450. <https://doi.org/10.1016/j.anbehav.2009.11.024>
- Donaldson-Matasci, M. C., DeGrandi-Hoffman, G., & Dornhaus, A. (2013). Bigger is better: Honeybee colonies as distributed information-gathering systems. *Animal Behaviour*, 85(3), 585–592. <https://doi.org/10.1016/j.anbehav.2012.12.020>
- Dornhaus, A., & Franks, N. R. (2006). Colony size affects collective decision-making in the ant *Temnothorax albipennis*. *Insectes Sociaux*, 53(4), 420–427. <https://doi.org/10.1007/s00040-006-0887-4>
- Dornhaus, A., Holley, J.-A., & Franks, N. R. (2009). Larger colonies do not have more specialized workers in the ant *Temnothorax albipennis*. *Behavioral Ecology*, 20(5), 922–929. <https://doi.org/10.1093/beheco/arp070>
- Duarte, A., Weissing, F. J., Pen, I., & Keller, L. (2011). An evolutionary perspective on self-organized division of labor in social insects. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 91–110. <https://doi.org/10.1146/annurev-ecolsys-102710-145017>
- Gordon, D. M. (1983). Daily rhythms in social activities of the harvester ant, *Pogonomyrmex badius*. *Psyche: A Journal of Entomology*, 90, 413–423. <https://doi.org/10.1155/1983/60725>
- Gordon, D. M. (1996). The organization of work in social insect colonies. *Nature*, 380, 121–124. <https://doi.org/10.1002/cplx.10048>
- Gordon, D. M. (2013). The rewards of restraint in the collective regulation of foraging by harvester ant colonies. *Nature*, 498, 91–93. <https://doi.org/10.1038/nature12137>
- Gordon, D. M., & Mehdiabadi, N. J. (1999). Encounter rate and task allocation in harvester ants. *Behavioral Ecology and Sociobiology*, 45(5), 370–377. <https://doi.org/10.1007/s0026500050573>
- Gordon, D. M., Paul, R. E., & Thorpe, K. (1993). What is the function of encounter patterns in ant colonies? *Animal Behaviour*, 45, 1083–1100. <https://doi.org/10.1006/anbe.1993.1134>
- Herbers, J. M., & Choiniere, E. (1996). Foraging behaviour and colony structure in ants. *Animal Behaviour*, 51(1), 141–153. <https://doi.org/10.1006/anbe.1996.0012>
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Harvard University Press.
- Jackson, D. (1993). Stopping rules in principal components analysis: A comparison of heuristic and statistical approaches. *Ecology*, 74(8), 2204–2214.
- Jandt, J. M., Bengston, S., Pinter-Wollman, N., Pruitt, J. N., Raine, N. E., Dornhaus, A., & Sih, A. (2014). Behavioural syndromes and social insects: Personality at multiple levels. *Biological Reviews*, 89(1), 48–67. <https://doi.org/10.1111/brv.12042>
- Kaspari, M., & Vargo, E. L. (1995). Colony size as a buffer against seasonality: Bergmann's rule in social insects. *The American Naturalist*, 145(4), 610–632. <https://doi.org/10.1086/285758>
- Keiser, C. N., & Pruitt, J. N. (2014). Personality composition is more important than group size in determining collective foraging behaviour in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 281(1796), 20141424. <https://doi.org/10.1098/rspb.2014.1424>
- Kühbandner, S., Modlmeier, A. P., & Foitzik, S. (2014). Age and ovarian development are related to worker personality and task allocation in the ant *Leptothorax acervorum*. *Current Zoology*, 60(3), 392–400. <https://doi.org/10.1093/czoolo/60.3.392>
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33. <https://doi.org/10.18637/jss.v069.i01>

- London, K. B., & Jeanne, R. L. (2003). Effects of colony size and stage of development on defense response by the swarm-founding wasp *Polybia occidentalis*. *Behavioral Ecology and Sociobiology*, 54(6), 539–546. <https://doi.org/10.1007/s00265-003-0662-8>
- Merkle, D., & Middendorf, M. (2004). Dynamic polyethism and competition for tasks in threshold reinforcement models of social insects. *Adaptive Behavior*, 12(3–4), 251–262. <https://doi.org/10.1177/105971230401200310>
- Modlmeier, A. P., Colman, E., Hanks, E. M., Bringenberg, R., Bansal, S., & Hughes, D. P. (2019). Ant colonies maintain social homeostasis in the face of decreased density. *eLife*, 8, 1–17. <https://doi.org/10.7554/eLife.38473>
- Modlmeier, A. P., & Foitzik, S. (2011). Productivity increases with variation in aggression among group members in *Temnothorax* ants. *Behavioral Ecology*, 22(5), 1026–1032. <https://doi.org/10.1093/beheco/arr086>
- Modlmeier, A. P., Keiser, C. N., Wright, C. M., Lichtenstein, J. L. L., & Pruitt, J. N. (2015). Integrating animal personality into insect population and community ecology. *Current Opinion in Insect Science*, 9, 77–85. <https://doi.org/10.1016/j.cois.2015.03.008>
- O'Donnell, S., & Bulova, S. J. (2007). Worker connectivity: A simulation model of variation in worker communication and its effects on task performance. *Insectes Sociaux*, 54(3), 211–218. <https://doi.org/10.1007/s00040-007-0946-5>
- Pacala, S. W., Gordon, D. M., & Godfray, H. C. J. (1996). Effects of social group size on information transfer and task allocation. *Evolutionary Ecology*, 10(2), 127–165. <https://doi.org/10.1007/BF01241782>
- Pasquier, G., & Grüter, C. (2016). Individual learning performance and exploratory activity are linked to colony foraging success in a mass-recruiting ant. *Behavioral Ecology*, 27(6), 1702–1709. <https://doi.org/10.1093/beheco/arw079>
- Perna, A., & Theraulaz, G. (2017). When social behaviour is moulded in clay: On growth and form of social insect nests. *The Journal of Experimental Biology*, 220(1), 83–91. <https://doi.org/10.1242/jeb.143347>
- Pie, M. R., Rosengaus, R. B., & Traniello, J. F. A. (2004). Nest architecture, activity pattern, worker density and the dynamics of disease transmission in social insects. *Journal of Theoretical Biology*, 226(1), 45–51. <https://doi.org/10.1016/j.jtbi.2003.08.002>
- Pinter-Wollman, N. (2012). Personality in social insects: How does worker personality determine colony personality? *Current Zoology*, 58(4), 579–587. <https://doi.org/10.1093/czoolo/58.4.580>
- Porter, S. D., & Jorgensen, C. D. (1981). Foragers of the harvester ant, *Pogonomyrmex owyheei*: A disposable caste? *Behavioral Ecology and Sociobiology*, 9(4), 247–256. <https://doi.org/10.1007/BF00299879>
- Pruitt, J. N., Grinsted, L., & Settepani, V. (2013). Linking levels of personality: Personalities of the “average” and “most extreme” group members predict colony-level personality. *Animal Behaviour*, 86(2), 391–399. <https://doi.org/10.1016/j.anbehav.2013.05.030>
- Pruitt, J. N., & Modlmeier, A. P. (2015). Animal personality in a foundation species drives community divergence and collapse in the wild. *Journal of Animal Ecology*, 84, 1461–1468. <https://doi.org/10.1111/1365-2656.12406>
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews of the Cambridge Philosophical Society*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>
- Retana, J., & Cerda, X. (1991). Behavioural variability and development of *Cataclyphis cursor* ant workers (Hymenoptera, Formicidae). *Ethology*, 89, 275–286.
- Sakata, H., & Katayama, N. (2001). Ant defence system: A mechanism organizing individual responses into efficient collective behavior. *Ecological Research*, 16(3), 395–403. <https://doi.org/10.1046/j.1440-1703.2001.00404.x>
- Scharf, I., Modlmeier, A. P., Fries, S., Tirard, C., & Foitzik, S. (2012). Characterizing the collective personality of ant societies: Aggressive colonies do not abandon their home. *PLoS ONE*, 7(3), e33314. <https://doi.org/10.1371/journal.pone.0033314>
- Seifert, B. (2018). *The Ants of Central and Northern Europe*. Tauer, Germany: Lutra, Verlags- und Vertriebsgesellschaft, p 408. ISBN: 9783936412079.
- Sendova-Franks, A., & Franks, N. (1999). Self-assembly, self-organization and division of labour. *Philosophical Transactions: Biological Sciences*, 354(1388), 1395–1405. <https://doi.org/10.1098/rstb.1999.0487>
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- Toffin, E., Kindekens, J., & Deneubourg, J.-L. (2010). Excavated substrate modulates growth instability during nest building in ants. *Proceedings of the Royal Society B: Biological Sciences*, 277(1694), 2617–2625. <https://doi.org/10.1098/rspb.2010.0176>
- Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences*, 108(6), 2312–2315. <https://doi.org/10.1073/pnas.1007102108>
- Wright, C. M., Lichtenstein, J. L. L., Doering, G. N., Pretorius, J., Meunier, J., & Pruitt, J. N. (2019). Collective personalities: Present knowledge and new frontiers. *Behavioral Ecology and Sociobiology*, 73(3), <https://doi.org/10.1007/s00265-019-2639-2>

How to cite this article: Somogyi AÁ, Tartally A, Maák IE, Barta Z. Colony size, nestmate density and social history shape behavioural variation in *Formica fusca* colonies. *Ethology*. 2020;126:727–734. <https://doi.org/10.1111/eth.13022>