Colony structure, population structure, and sharing of foraging trees in the ant *Myrmeceia nigriceps* (Hymenoptera: Formicidae)

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Abstract
Foraging ants face many dangers in search of food and often need to defend their prey to ensure the colony’s survival, although ants may also follow a peaceful foraging strategy. A non-aggressive approach is seen in the Australian bull ant *Myrmeceia nigriceps*, in that workers of neighboring nests sometimes share foraging trees. In this study, we observed 31 nests at Mount Majura Nature Reserve in Canberra (Australia), 12 of which shared a foraging tree with at least one other nest in at least one of three nights. We genotyped 360 individuals at five published microsatellite loci and further established a set of nine polymorphic loci for *M. nigriceps*. Our results revealed a significant correlation between tree sharing and geographical distance between nests. We found no correlation between internest relatedness and tree sharing, geographical distance between nests and internest relatedness, and intranest relatedness and tree sharing. We further investigated the colony structure of *M. nigriceps*. All colonies were monodomous; the number of queens per colony ranged from one to two, and the number of fathers from one to three. No instances of worker drifting were found in this study.

Keywords Foraging behavior · Tree-sharing · Microsatellites · Dispersal

Introduction
Foraging is one of the most vital parts of survival in the life of an ant colony. However, it is also one of the costliest activities as workers spend great amounts of energy and face many risks in search of food (Dornhaus and Powell 2009). Different species of ants employ different strategies for the discovery, retrieval, and defense of food. For example, workers may forage individually or in groups and use morphological, chemical, and behavioral defenses to ensure survival and safety of resources (Hölldobler and Wilson 1990; Dornhaus and Powell 2009). As an alternative to a defensive approach, ants may also avoid aggressive behavior or share food sources (d’Ettorre and Lenoir 2009).

The ant genus *Myrmeceia* consists of 93 described species (Hasegawa and Crozier 2006; Taylor 2015) which are endemic to Australia or, in one instance, New Caledonia. Although rejected as among the most basal formicids, ants of this genus have retained many biological traits that are considered to be archaic (Ogata and Taylor 1991; Ward and Brady 2003; Hasegawa and Crozier 2006). Commonly known as “bulldog ants” or “bull ants”, these ants are characterized by relatively large bodies, little morphological difference between queens and workers, strongly toothed, long mandibles, and aggressive behavior, which is accompanied by a painful stinger (Eriksson 1985; Ogata and Taylor 1991; Ward and Brady 2003). They forage individually, have unusually large eyes and rely extensively on vision for navigation and capture of prey. Several species operate in discrete temporal niches, ranging from strictly diurnal to crepuscular to strictly nocturnal. During these species-specific timespans, workers leave the nest individually to forage on near-standing trees (Narendra et al. 2017). On the trees, the ants hunt for a wide variety of arthropods, feed on sap produced by trees, and tend to aphids, coccids and mealybugs for honeydew (Reid et al. 2013). Evolutionary adaptations of the
visual system of species to the specific light environments in which they operate show how well these ants are adapted to their temporal niches (Narendra et al. 2011, 2016, 2017). Their visual navigation and foraging ecology set bull ants up as attractive model organisms in ecological neurobiology (Narendra et al. 2016; Kamhi et al. 2020).

One such study system is *Myrmecia nigriceps* Mayr, 1862, which represents a crepuscular–nocturnal foraging schedule (Narendra et al. 2016). It belongs to the *gulosa* species group, one of nine recognized species groups within the genus *Myrmecia* (Ogata 1991; Ogata and Taylor 1991). Studies have focused on the species’ brains and their visual systems (Greiner et al. 2007; Narendra et al. 2011, 2016; Narendra and Ribi 2017; Sheehan et al. 2019), and little is known about its general biology, including its social structure, which is a key aspect of ant ecology. Attributes influencing a colony’s social structure include the number of queens (monogyny versus polygyny), number of fathers (monandry versus polyandry), and number of nests (monodomy versus polydomy; Steiner et al. 2009). *Myrmecia nigriceps* can be found in underground earth nests, indicated by characteristic gravel mounds surrounding the nest entrance. The colony comprises a few hundred workers (Shattuck 1999; van Wilgenburg et al. 2007) and can be found in habitats where colonies have access to lone standing *Eucalyptus* trees to forage on, such as tall grassy woodland and dry sclerophyll open forest (Baines et al. 2013). Even though workers of *M. nigriceps* are extremely aggressive towards hetero-specific intruders, van Wilgenburg et al. (2007) found a general absence of aggression towards conspecific nest-intruders in a series of bioassays introducing non-nestmates to foreign colonies of *M. nigriceps*. This peaceful behavior can sometimes also be seen when ants of adjoining colonies encounter each other while foraging. In juxtaposition, Readhead (2014), who investigated aggression and cuticular hydrocarbon profiles in a subpopulation of *M. nigriceps* also used in this work, found no absence of aggression but rather noted instances of avoidance.

Here, we aim to investigate the social structure of one population of *M. nigriceps* which has been subject to previous neurobiological studies. We try to find out whether (i) geographical distance between nests correlates with sharing of foraging trees, (ii) internest relatedness correlates with sharing of foraging trees, and (iii) geographical distance between nests correlates with internest relatedness. Further, we test for correlation of (iv) intranest relatedness with sharing of foraging trees and lastly investigate whether nests that share foraging trees represent separate colonies or if they rather belong to the same polydomous colony.

**Materials and methods**

**Field work and DNA extraction**

Field work was conducted in Canberra, Australia, from 6–19 November 2017 and 11–17 December 2017. A total of 36 nests of *Myrmecia nigriceps*, from three main locations, (i) Mount Majura Nature Reserve (31 nests; henceforth Majura North), (ii) a second site at Mount Majura Nature Reserve (two nests; Majura South), and (iii) the Australian National University campus (three nests; ANU; Fig. 1ab), were marked and recorded by GPS (Garmin, eTrex 10, Olathe, Kansas). We used ants from all the nests to investigate colony and population structure. Only at Majura North did we identify the trees on which ants from each nest forage. Foraging behavior was observed for three nights per nest (partially split between the two field work periods) by following individual ants from the nest entrance to their respective foraging trees, which were defined as such by workers.

![Fig. 1](nearmap.com.au)
ascending the stem for 0.5 m. To keep track of the workers without disturbing them, a headlamp with red light was used. As foraging onset regularly occurs during evening twilight and does not exhibit seasonal changes, reflected in the activity patterns of the related species *Myrmecia pyriformis* (Narendra et al. 2010, 2011), all observations started 30 min before sunset and ended when no more workers could be seen foraging. After completion of all foraging observations, workers were collected and stored in absolute ethanol p.a. Genomic DNA was extracted using DNeasy Blood and Tissue Kit (Qiagen, Hilden; Germany) according to the manufacturer’s instructions, except that proteinase K digestion was prolonged to overnight incubation.

**Primer characterization and microsatellite genotyping**

Five published microsatellite loci (Mbre11(HEX), Mbre16 (FAM), Mbre17 (PET), Mbre67 (NED), Nmac18 (PET)) were selected from a set of 16 loci (Qian et al. 2011a) after testing on 24 individuals for amplification success, scorability, and allele count. A total of 360 workers, 10 ants per nest, were genotyped at these five loci. Additionally, a set of nine species-specific loci was newly developed for *Myrmecia nigriceps* (Table 1). For this, genomic DNA of two degased individuals was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). DNA was quantified with ribogreen (Thermo Fisher, Waltham, USA) and tested for human contamination by AluJ real-time PCR (Kaneko et al. 2011) in triplicates; human positive controls were run as standard in a dilution series 1:1, 1:10, and 1:100. Illumina PE250 libraries were prepared by a commercial sequencing facility (IGA, Udine, Italy), and sequenced on the Illumina NextSeq 500 system. Low-quality reads were discarded and SciRoKo (Kofler et al. 2007) was used to identify di- and trinucleotide repeat units. To obtain reads with at least eight microsatellite repeat units, a 100 bp flanking region at both sides, and a balanced GC content in the flanking region, custom Python scripts were used. Microsatellite primers were designed using FastPCR v6.71 (Kalander et al. 2017) and Primer3web v4.1 (Untergasser et al. 2012). All 14 loci (five published and nine novel ones mentioned above) were labeled with a fluorescent dye via M13-tailed PCR (Boutin-Ganache et al. 2001), using the following thermal profile: 95 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 45 s, followed by a final extension at 72 °C for 10 min. Amplifications were carried out in a 5 μl reaction volume containing 1× Rotorgene Probe-PCR Kit Mastermix (Qiagen, Hilden, Germany), 0.02 μM forward primer, 0.2 μM M13-tailed primer, 0.2 μM reverse primer, and 0.5 μl DNA extract on a UnoCycler 1200 (VWR, Radnor, USA). Amplification success was checked by agarose gel electrophoresis. Capillary electrophoresis was performed using an ABI 3130 instrument (Applied Biosystems, Foster City, USA) at a commercial sequencing facility (CRC Sequencing Facility, Chicago, USA). Alleles were scored

| Locus ID | Fluorophore | Locus-specific primer sequences (5′–3′) | Repeat motif | Size range (bp) | TA (°C) |
|----------|-------------|----------------------------------------|--------------|----------------|---------|
| Mnig41   | FAM         | F: cgatgacagacgagaaaatt R: aatattggtgcccccaa | CT           | 204–218        | 55.0–61.0|
| Mnig43   | FAM         | F: aaggcaagacagtctctct R: cgatattgcaaaaaagca | CTG          | 204–228        | 54.9–60.9|
| Mnig45   | PET         | F: caggccccctccacctct R: agatccttgacgattgtgg | GA           | 240–262        | 55.0–61.0|
| Mnig48   | HEX         | F: caattgtagcagatacg R: tcacgagctgctctctg | CT           | 214–256        | 54.2–60.2|
| Mnig49   | HEX         | F: aaatcgaagctcaacggaga R: gctggagatctggctctg | GA           | 196–212        | 54.5–60.5|
| Mnig52   | HEX         | F: tcgatatggttctctgt R: cagcaacatgctgtcttct | AT           | 175–213        | 53.9–59.9|
| Mnig54   | NED         | F: aacggctcttgctcttct R: gacgctgtctgtctgttct | CT           | 234–255        | 55.0–61.0|
| Mnig66   | PET         | F: aaatgactgcagacag R: agaagcctctgtctctcg | TC           | 219–231        | 52.5–62.2|
| Mnig58   | NED         | F: ccccgctctgctctctct R: ttgagcagctgccaaacg | CT           | 207–249        | 54.8–60.8|

Fluorophore (FAM, HEX, NED, PET); Size range (basepairs); TA, annealing temperature (°C). Note that we appended M13-tails to the 5′ end of the locus-specific forward primers leading to an increase of allele length of 19 bp.
Population genetic analysis

Linkage Disequilibrium (LD) was calculated using GenePop on the Web (Raymond and Rousset 1995). Deviations from Hardy–Weinberg equilibrium (HWE), F-statistics, and pairwise relatedness following Queller and Goodnight (1989) were calculated using GenAlEx v6.41 (Peakall and Smouse 2012). The mean relatedness within nests (intranest relatedness) and the mean relatedness between nests (internest relatedness) were calculated based on pairwise relatedness in GenAlEx v6.41. The possible presence of null alleles was tested using MicroChecker v2.2.3 (van Oosterhout et al. 2004). Both HWE and LD were tested on a subset of the original dataset using single worker genotypes randomly sampled from each nest. Bonferroni–Holm corrections for multiple comparisons were performed at significance level 0.05 (Armstrong 2014). After adjusting coordinates with help of orthophotos from 2014 (source: services.ga.gov.au, retrieved 26 Jun 2016) and noted position of trees, geographic distance between nests was calculated using ArcGIS v10.5.1 (www.esri.com).

Logistic regressions of (i) tree sharing against geographical distance and (ii) tree sharing against internest relatedness were performed in R v4.0.2 (R Core Team 2020) using RStudio v1.4.1103 (RStudio Team 2020). For this, only nest pairs with the potential for tree sharing were included in the analyses, meaning there was at least one tree visited by the workers of at least one nest during at least one night within a radius of 20 m for both nests; tree sharing was defined as the number of trees shared per night, averaged over three nights. A Mantel test for (iii) correlation between geographical distance and internest relatedness was performed. For the Mantel test, the function “mantel.rtest” in the package “ade4” was applied using 4999 permutations (Dray and Dufour 2007). Additionally, (iv) a logistic regression of tree sharing index \( T_s \), defined as the number of trees shared with at least one other nest out of the number of trees visited per night, averaged over three nights, against intranest relatedness was also performed using R. All logistic regressions were fit using a general linear model (GLM) with binomial error structure using the function “glm” in the R base package. Model fits were checked using the package DHARMa (Hartig 2020). All regression and Mantel test plots were created using the packages ggplot (Wickham 2016) and ggpubr (Kassambara 2020).

Parentage and sibship alignments

Parentage and sibship alignments (v) for all nests were estimated using COLONY v2.0.6.5 (Jones and Wang 2010). COLONY runs were performed using full likelihood (FL) Method, high precision, and long runtime. A test set of runs with both allelic dropout rates and other possible errors set to 0.0001, 0.0005, 0.001, 0.005, 0.01, and 0.05 was used to determine suitable error rates. For this, the error rates suggested by the program as well as improbable sibship relations (e.g., shared mothers between nests from Majura North, Majura South, and ANU) were taken into consideration. The final error rates were set to 0.0005 for all loci except Mnig 52, which was set to 0.05 and 0.0025 for allelic dropout rates and other errors, respectively. Additionally, individuals with many missing data were excluded from runs to correct for patterns created by missing values. We performed five parallel runs with different randomized seed number using the above-mentioned error rates to assure reproducibility. Assignment probability had to be at least 0.95 for all individuals of a nest for its results to be interpreted.

Results

Nest sites and foraging observations

We found an average distance of 159.90 m ± 111.88 m (mean ± standard deviation; \( n = 31 \), min 3.12 m, max 477.84 m; Fig. 1ab) between nests at Majura North. Of these 31 nests, 12 were observed sharing a foraging tree with at least one other nest in at least one of three nights (Supplement 1, Fig. 2). We observed that tree-sharing frequencies between nests ranged from 0.00 (no sharing) to 0.33 (one of three nights), 0.67 (two of three nights), and 1.00 (all three nights). We found that average tree sharing \( (T_s) \) was 0.31 ± 0.43 (min 0.00, max 1.00; Supplement 1).

Basic population genetics and relatedness

We detected linkage between microsatellite loci Mnig49 and Mnig66 and deviations from HWE and the presence of null alleles at loci Mbre11, Mbre16, Mbre67, and Mnig48, leading us to exclude the latter five loci. For the remaining nine loci, no linkage and no deviation from HWE were observed; they yielded a total of 106 alleles, with an average of 11.8 alleles per locus ± 5.7 (mean ± standard deviation; min 6, max 23). We found that the average expected heterozygosity \( H_e \) for each locus was 0.55 ± 0.15 (min 0.29, max 0.74). Additionally, we found that the average internest relatedness was −0.01 ± 0.09 (min −0.24, max 0.32), while the average intranest relatedness was 0.39 ± 0.15 (min 0.17, max 0.73; Supplement 1).
Mantel test and regressions

We found that as the geographical distance between nests decreased, tree sharing significantly increased (GLM with binomial error structure, \( z = -2.089, p = 0.037 \), residual deviance 15.41 on 28 degrees of freedom (df), Fig. 3a). We found no effect between tree sharing and internest relatedness (GLM with binomial error structure, \( z = 1.367, p = 0.172 \), residual deviance 19.65 on 28 df, Fig. 3b), nor between geographical distance between nests and internest relatedness (Mantel test with 4999 permutations, \( r = -0.20, p = 0.998 \), Fig. 3c). Lastly, we found no correlation between tree-sharing index \( T_s \) and intranest relatedness (GLM with binomial error structure, \( z = 0.688, p = 0.491 \), residual deviance 29.82 on 24 df, Fig. 3d).

Parentage and sibship determinations

We produced identical results for four out of five runs (COLONY), with the fifth deviating in three out of 14 nests (which remained from the original 36 nests after failing to meet the required probability). We identified no worker that shared a parent with a worker from another nest, that is, all nests sampled represented separate colonies (Supplement 2). We were able to identify both monogynous and oligogynous colonies, as well as monandrous and polyandrous colonies (Supplement 2). Out of 31 colonies at Majura North one was monogynous-monandrous. We found an average number of 1.10 ± 0.32 (min 1, max 2) queens per colony and an average number of 2.20 ± 0.63 (min 1, max 3) fathers. We detected all fullsibs (sharing both mother and father) as well as all halfsibs (sharing either mother or father) within their respective colonies.

Discussion

Tree sharing

Of 31 nests of *Myrmecia nigriceps* at Majura North, 12 were observed to share a foraging tree with at least one other nest. However, no relation between foraging and genetic relatedness and no worker drifting were found. Van Wilgenburg et al. (2007) tested worker behavior of *M. nigriceps* towards non-nestmate intruders and found that workers generally respond passively towards non-nestmate conspecifics that approach the nest entrance and that some intruders even remain in the nest for several minutes before re-emerging. In a different population of *M. nigriceps*, it was clear that non-nestmates tend to respond aggressively to each other and that aggressiveness increases with chemical distance (Readhead 2014), which suggests that *M. nigriceps* uses cuticular hydrocarbons for nestmate recognition and aligns with the fact that related *Myrmecia* species effectively do so as well (Dietemann et al. 2002). The correlation between tree sharing and geographical distance could purely reflect convenience for foraging, meaning that neighboring trees are more easily accessible. Possibly, though, it could also indicate that nests in close proximity may avoid aggression if necessary. It could mean a neutral situation, as some nests shared foraging trees in all nights although other trees without conspecifics from other nests were available, but tree sharing was not obligatory between all nests. As only a few individuals of a colony are tasked with foraging, ants can benefit by sharing resources and thus avoiding the high costs of aggression (Ellis and Robinson 2015). This might be even more relevant for *M. nigriceps*, where all individuals of a colony must forage. In a colony as small as that of *M. nigriceps*, the loss of individual workers might be non-trivial, which could explain non-aggressiveness between non-nestmates (van Wilgenburg et al. 2007). In this case, specifically, it could mean that foragers employ avoidance behavior as a strategy to reduce the cost of fighting as observed by Readhead (2014). Furthermore, the small
nest size and the corresponding number of foragers might be low enough for the ants not to encounter one another on the trees. In the trap-jawed ant *Daceton armigerum*, which also forages singly and hunts on sight, sharing of trees (and even foraging trails) was also observed with colonies of other arboreal ants; those encounters are not always peaceful as *D. armigerum* often kills these other ants and steals their prey (Dejean et al. 2012). As no such behavior is recorded for *M. nigriceps*, it seems that if trees offer a great amount of space, food resources are not limiting within a particular foraging tree for these ants (Reid et al. 2013).

**Colony structure**

We found that all colonies were monodomous. The average intracolony relatedness of *Myrmecest nigriceps* was $0.39 \pm 0.15$, the number of queens ranged from one to two per colony, and the number of fathers from two to three. Generally, our findings match those of studies performed with species closely related with *M. nigriceps*. When
BayesNet: Using Bayesian Networks for Predicting Financial Risk

Bayesian networks are graphical models that represent probabilistic relationships among random variables. In the context of financial risk prediction, these networks can be used to model the dependencies between various financial indicators and predict outcomes such asdefault risk. The network structure is defined by a directed acyclic graph (DAG), where nodes represent variables and directed edges indicate causal relationships.

BayesNet can be constructed through various methods, including parameter estimation and structure learning. Parameter estimation involves estimating the conditional probability distributions of the nodes given their parents in the network. Structure learning involves determining the optimal graph structure that best represents the data. Once the network is constructed, it can be used for prediction, diagnosis, and sensitivity analysis.

In financial applications, BayesNet can help risk managers to identify key drivers of default risk, understand the impact of individual factors, and evaluate the effectiveness of different mitigation strategies. By incorporating expert knowledge and historical data, BayesNet models can provide a comprehensive view of the complex interplay between various financial indicators and default outcomes.
Lastly, an analysis of diet could provide insight in whether different colonies have specialized on different food sources, which might explain the non-aggressive behavior when non-nestmates encounter each other on foraging trees due to non-overlapping trophic niches.

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Author contributions AN, WA, FMS, and BCS-S designed the research; VA and AN did the fieldwork; VA and WA did the molecular-genetic analyses in the laboratory; VA, WA, PK, FMS, and BCS-S analyzed the data; VA wrote the manuscript, with contributions from AN, WA, PK, FMS, and BCS-S.

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Code availability Not applicable.

Declarations

Conflict of interests Not applicable.

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