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A Review of Jaw Morphology and Foraging Behaviour in the Bulldog Ant (*Myrmecia Gulosa*) Group

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ABSTRACT

Formicidae are one of the most diverse groups that, along with termites, make up one third of the total animal biomass on Earth. Contributing to their success is the large variety of foraging behaviours and morphologies ants have evolved in response to various food supplies. On the world continent Gondwana, *Myrmeciinae*, were the dominant group with many characters considered primitive or ancestral within Formicidae. The *Myrmecia gulosa* group retains ancestral traits of the *Myrmeciinae*, now found only in Australia. This research aims to a review the facial morphologies and foraging behaviours of the *M. gulosa* group to better understand their unique success in Australia, compared to their demise elsewhere. Evaluation of jaw morphology, foraging behaviour, and geographical distribution revealed a narrow range of morphologies and consistent foraging behaviour across 41 of 42 studied species all over Australia. Based on similar morphologies of 41 species and behaviours of eleven, eight of which were considered well researched, it is possible that understudied *M. gulosa* species will demonstrate traits similar to well-researched species. It appears that *M. gulosa* species maintained ancestral traits that failed to allow the present-day success of *Myrmeciinae* elsewhere, and likely allowed the diversification of other ant genera. The following collated results suggests, members of the *M. gulosa* species group appear not to face the same food resource selective pressures that led to diversification in other ant genera and further supports food resources as an important selective pressure for other ant genera that *M. gulosa* possibly failed to adapt to.

Introduction

Every animal needs nutrients to survive, and therefore must acquire food that contains the appropriate nutrients. Food acquisition requires animals forage or hunt; however, the specific nature of these activities can differ between various species, or even within species in different geographical areas, depending on the available resources and the organism's required nutrients. It is assumed that as resources change, a change in foraging and hunting behaviours will also occur if the animal is to survive. This is perhaps demonstrated best by Darwin's finches of the Galapagos islands, where selection pressures caused changes in foraging behaviour and beak morphology (Grant, 1981; Petren et al., 2005; Rundell & Price, 2009). However, this kind of diversification may stall if the necessary selective pressures are not present in a given ecosystem where a lack of unique selective pressures may cause retention of ancestral traits (Ward & Brady, 2003). By studying foraging and hunting behaviours alongside morphology and distribution, we can potentially reveal selective pressures that drive the diversification of species or maintain traits among species in the absence of changing selective pressures.

Ants, members of Order Hymenoptera, Family Formicidae, are an extremely diverse group. They are cosmopolitan in distribution, with indigenous species found everywhere except areas of extreme cold (Greenland, Iceland, and the Antarctic), physically outnumber every other terrestrial animal, and have social communication comparable to humans (Keller & Elizabeth, 2009; Wheeler, 1990). Ants are usually one of the dominant terrestrial insects in the areas where they occur, but their dominance has been documented most in tropical rainforests where they and termites account for almost one third of the entire animal biomass (Fittkau & Klinge, 2016).

Ant species exhibit myriad methods of hunting and foraging, from farming fungi, and herbivory, to stalking, and coordinated group hunting (Hölldobler & Wilson, 1990). Thus, food resources were one of many factors that drove the vast diversification of the Formicidae family (Grant, 1981). Depending on the needs of a particular species, ants forage and hunt for solid and liquid nutrients both on the ground and higher up in surrounding vegetation (Hölldobler & Wilson, 1990). Foraging success may also be dictated by nest size, where larger colonies require more resources, but also have increased potential for success arising from larger numbers of individuals (Wheeler, 1990). Mating systems may also affect foraging habits, as motivations to provide for the colony may be dependent on the degree of relatedness from one individual to another (Hölldobler & Wilson, 1990).

To help perform their diverse hunting and foraging behaviours, ants have myriad, distinct morphologies. Leaf-cutter ants have characteristic mandibles they use to cut fresh vegetation that is composted to grow the ants' true food source, a symbiotic fungus (Rytter & Shik, 2016), with different species showing different pincer morphology (Rytter and Shik's 2016). Ponerine ants (Leptogenys nitida) show cooperative hunting behaviour, where hunting groups, whose members have razor-like mandibles, fan out and forage for prey arthropods. When prey is found, recruitment signals are communicated and prey is cooperatively stung, poisoned and carried back to the nest by the hunting group (Duncan & Crewe, 1994). These behaviours, while distinct, rely on individuals with their unique morphologies to acquire nutrients: leaf cutters to a patch of vegetation and ponerines to a struggling prey item. In contrast, another ponerine ant (Dinoponera gigantea) showed more opportunistic foraging as a generalist species with a more serrated-gripping mandible type for collecting seeds, fruits, carrion, and hunt live prey (Fourcassié & Oliveira, 2002); they showed more randomness in foraging, and were limited to foraging during dawn and dusk.

The foraging behaviours and morphologies can also arise as a product of the various ecosystems and climate zones in which various ants occur, another form of adaptive radiation (Petren et al., 2005). In this situation, leaf cutter ants of tropical climates have the razor like mandibles to harvest plant, ponerine ants have hooked mandibles that can target the larger variety of prey items found in North and South America (Erik T. Frank & Linsenmair, 2017; Shepherd, 1982). This interconnectedness of foraging behaviour, morphology, and habitat in ants is particularly interesting when considering the continent of Australia.

Australia is the largest island in the world and has unique collection of climate properties compared to other continents (Westoby, 1994). With a large portion of central desert region surrounded by grassland, temperate, tropical, subtropical, and equatorial climate regions, Australia potentially has the largest habitat diversity within a relatively small geographical area (Floren & Linsenmair, 2005). Because Australia is a large island, endemic island species further increase the diversity of vertebrates, invertebrates, and plants alike (Chisholm et al., 2016). However, the biodiversity of Australia is declining and indicates that biodiversity is not progressing forward and changing quickly enough to compete with feral invasive species (Dickman, 2019). Australia is the only native range of extant species of the *M. gulosa* group of ants. Commonly known as Bulldog ants, these ants are known for their painful sting and large mandibles.

M. gulosa ants are a species group with 42 members that belong to the subfamily *Myrmeciinae,* which contains 89 species divided across nine species groups (Ogata & Taylor, 1991). Because this research was limited to seven months during the Covid 19 pandemic, the *M. gulosa* group offered a reasonable research load while being still being large enough to find trends in the chosen variables and allow for in depth research into each species of the group. These ants exhibit morphological and behavioural features that are considered ancestral traits and distinct from other Formicidae families (V. Dietemann et al., 2002; Quian, 2012; Robertson, 1971). They were thought to be one of the most ancestral ant groups; however, recent studies suggest *Myrmecia* originated on Gondwana, were distributed across different southern continents after isolation by tectonic plates, dispersed outside of Gondwana across Europe, and went extinct everywhere except Australia after global break-up of the continents (Ward & Brady, 2003). One species outside the *M. gulosa* group is observed to survive on New Caledonia, but as a smaller island off the East coast of Australia, New Caledonia likely exhibits similar trends as the larger island Australia (Ward & Brady, 2003). Because

Australia has the sole occurrence of this group, study of *M. gulosa* morphologies and behaviours can provide evidence for the kinds of selective pressures these ants faced in the past, pressures faced currently, and how quickly the pressures are changing (Norberg, 2004).

By examining information of mandible characteristics, location, and foraging habits, a more complete understanding of the success of the *M. gulosa* group in Australia can be achieved. Factors of colony size, mating systems, and foraging motivations were also considered, as they relate to the foraging behavior of study species but were not the focus of my research. By studying this group, we can better understand how niche groups of ants are interacting with their specific environments. Thus, I hypothesize due to the success of the *M. gulosa* group that there is a retention of ancestral characteristics that subtly adapted to different climate zones based on the selective pressures of food, where different forms of the same morphology exist in different climate zones and show tendencies of adaptive radiation similar to that of Darwin's Finches. This research, furthermore, provides a review of the *M. gulosa* group, focusing on foraging morphologies and behaviours related to their foraging, described in the literature, as a potential means of understanding their distribution and success in Australia – why they retained ancestral traits and other ants did not.

Methods

Literature Search

I conducted an extensive search of the primary literature for behavioural analyses of *M. gulosa* group as the *M. gulosa* species was too specific. These papers often had descriptions of the various study species. I particularly looked for physiological descriptions of the head and mandible regions and notes on foraging. The morphologies studied include mandible length, mandible tooth number, and tooth pattern; however, surrounding morphologies of the eyes and brain were also looked at as they relate to the navigation efficiency used in the foraging behaviour.

Using keywords such as *Myrmecia gulosa*, foraging, feeding, behaviour, hunting, navigation, and ecology, I searched the primary literature through Web of Science, Google scholar, journal of Entomology, Myrmecological News, *Insectes Sociaux*, and other databases. The preliminary search returned only 62 papers that consistently researched eight of all 42 potential species. Some papers were excluded because of their explicit focus on venom glands or venom biochemistry. These papers featured little of the foraging behavior and head morphology of ant species; however, stinging behaviour was included where appropriate as it relates to the incapacitation of prey items and defense of the nest.

Additional papers, useful monographs, and theses were found by mining the references of the primary literature. Correspondence with experts yielded antwed.org as a key web resource.

Tooth and Mandible Measurements

Photographed of each species were found through the Australia Museum and National Insect Collection in Canberra, who directed me to antweb.org, stating it a highly reputable source. Photographs of 36 of the 42 species were posted as single specimens and all 36 of these photographs were used; another 5 species were measured from Clark's (1951) drawings. Only photos that included scales were used, so measurements could be accurate to the nearest 0.1 cm. Teeth were counted from the apex to the base, with the apex being considered a tooth, and thus included in the count (Figure 1). Tooth size was examined for repeating patterns of small and large teeth, where small was considered half the height of the largest tooth.

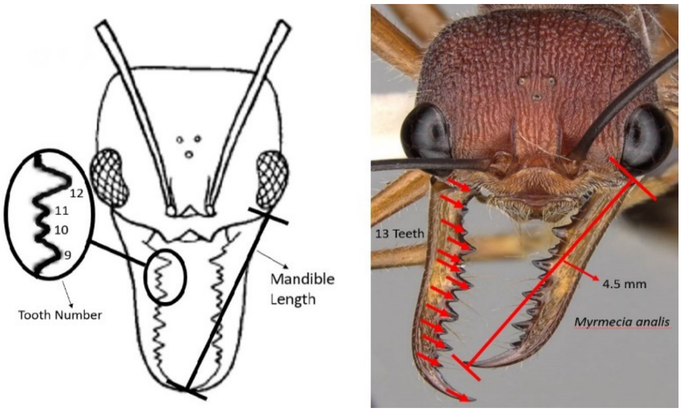


Figure 1. Schematic drawing of head measurement methodology and associated example of one of the study species with accurate values. Schematic image taken from (Clark, 1951). *M. analis* image taken from (*Ant Web*, n.d.). Both images were modified to include additional schematic lines and text. Image created by Jacob Ulrich, 2021.

Behaviour

Notes on the behavior and ecology of each species were compiled with physical measurements into a table to allow ease of comparison between species, and to reveal potential connections between behaviours and morphological features.

Geographical Location

Using the accumulated data, I grouped species into recognized climate zones, numbering regions of the same climate zone that did not touch as different regions. I established the locations of each species on the climate zone map by referring to collection databases/map recordings of each species from antweb.org. Climate zones were established and mapped with meteorological data by the Bureau of Meteorology from the Australian Government (*Climate Classification Maps*, 2016)

Statistical Analyses

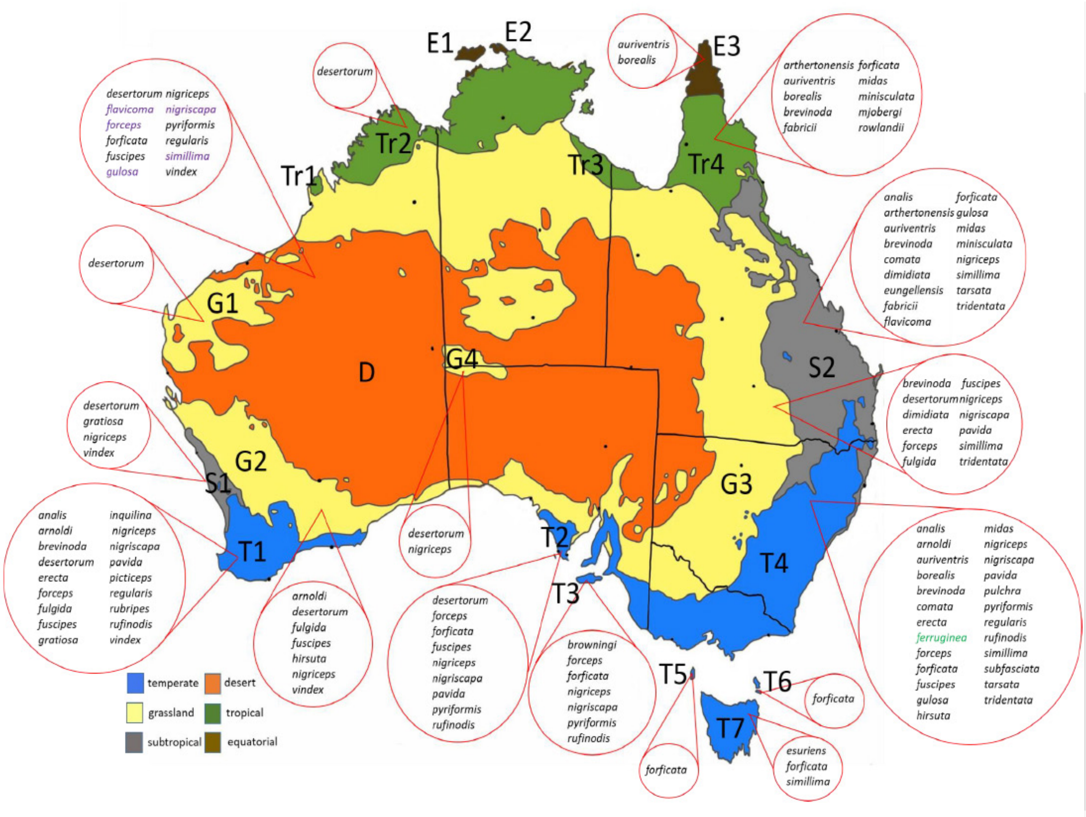
Because the data were non-parametric and consisted of one measurement for each species, no formal statistical tests could be run. However, due to the close relatedness of the ants, spatial analysis could be done using a descriptive approach of boxplots. Thus, boxplots of these features were created, allowing examination of data spread, and identification of outliers.

Results

The compiled information presented here comes from 68 sources for 42 species, spanning Clark (1951) to Kamhi et al. (2020). Most behavioural comparisons come from a compilation of the primary peer-reviewed literature, while most of the quantitative morphological and geographical measurements are from antweb.org and antmaps.org. Morphological measurements were taken from photographs of single museum specimens while geographical data was compiled and mapped from ≥ 5 collection records. Only primary sources that gave ecological and behavioural descriptions of their study species were included. From the literature, species that were covered in five or more many articles were considered well-studied. Based on this, eight species were in this category: *M. brevinoda*, *M. desertorum*, *M. gulosa*, *M. midas*, *M. nicriceps*, *M. pavida*, *M. pyriformis*, and *M. simillima*. The remaining 34 species were covered in additional papers, but not as extensively. All papers discussing species of the *M. gulosa* group used to generate the results below are given in appendix 1 and specific measurements of each species can be found in appendix 2 as digital supplementary material attached to this article.

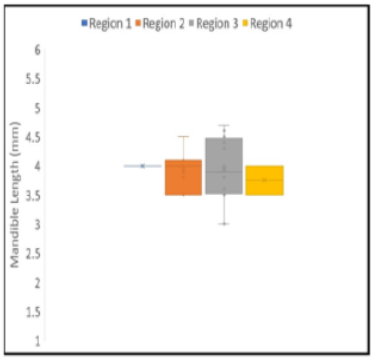
Geographical Location

In the six climate zones recognized and mapped by the Australian government, the largest, the Desert, has one region, whereas the Temperate zone is the most fragmented with seven regions. Figure 2 shows the various climate regions with associated species of *M. gulosa* collected, observed, and/or location mapped included in the region, but does not show where species occurred in each region. One distinct pattern is a larger abundance of species situated near the west, south, and east coasts. Another interesting observation is that *M. desertorum*, a well-studied species, is widespread across five climate zones. Ten species are observed only in one climate region: *M. inquilina* and *M.* rubripes in T1; M. rowningi in T3; M. ferruginea, M. pulchra, and M. subfasciata in T4; M. esuriens in T7; M. mjobergi and M. rowlandi in Tr4; and M. eungellensis in S2.

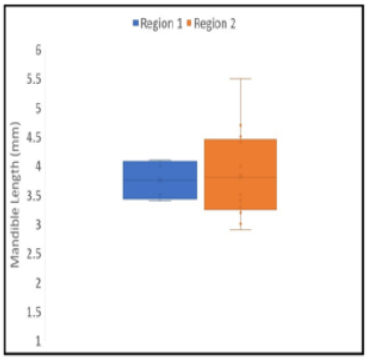


Mandible and Tooth Measurements

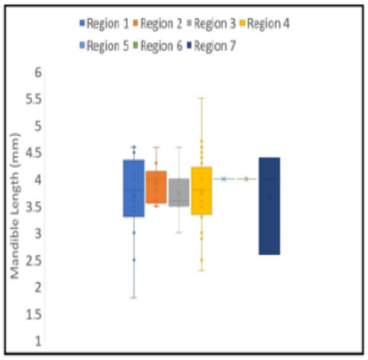
The mandible lengths showed a small spread of data across climate zones, but the Desert zone had a distinct outlier: *M. regularis*. A total of 41 of 42 species were measured; no picture could be found for the one, unmeasured species *M. ferruginea*. The measured species had a mean mandible length of 3.7 ± 0.8mm and median of 3.6mm. From the box plots of mandible lengths in each climate zone and associated regions (Figure 3), *M. regularis* in the Desert zone is noteworthy with its uncharacteristically small mandible length of 2.5mm. Multiple species: *M. flavicoma*, *M. forceps*, *M. gulosa*, *M. nigriscapa*, and *M. simillima* were sampled at the exact same geographic location by the same researcher, a trend that did not occur in other zones, but little variance was detected between the complete and trimmed groups. Grassland, Subtropical and Tropical regions all featured small spreads of the data, with means between regions within ± 0.4mm of each other. The mean and median, respectively, of each climate zone was: Grasslands 3.9 ± 0.5mm, 4mm; Subtropical 3.8 ± 0.7mm, 3.8mm; Tropical 3.8 ± 1.0mm, 3.8mm. The regions showed an expected trend of higher species number in the southern and eastern coastal regions. Subtropical, Temperate, and Tropical zones all show a maximum of 5.5 and 5.6mm mandible lengths arising from different species. The Temperate zone is particularly interesting because it had the highest numbers of species across all climate zones. Despite having the largest variety of species, the mean mandible length for each region remained relatively consistent, with a small spread of the data with most species falling within ±0.75mm of the mean of the Temperate zone 3.8 ± 0.7mm and median 3.8mm.



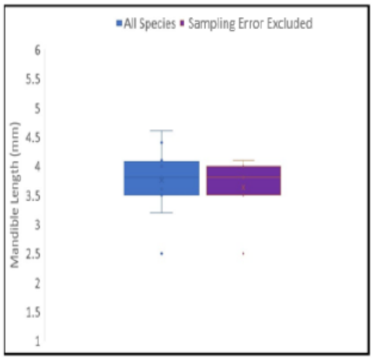
A. Grasslands



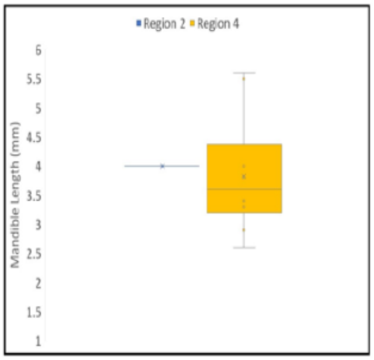
B. Subtropical



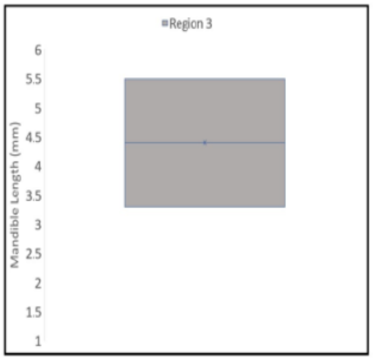
C. Temperate



D. Desert



E. Tropical



F. Equatorial

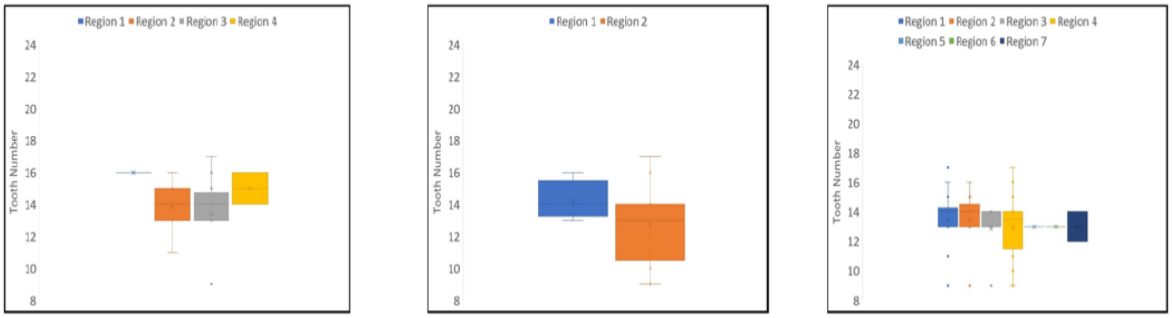
The tooth measurements also showed a relatively small spread of data across the climate zones and associate regions (Figure 4), but four of the six climate zones (Grasslands, Subtropical, Temperate, and Tropical) had many outliers. Five species had a low tooth number (nine) and became outliers in most regions where they occurred. In contrast, *M. mjobergi,* in the Tropical zone, was an outlier with 22 teeth. The overall data had a relatively small spread, with 29 species within one standard deviation from the mean of 13.1 ± 2.6 teeth and median of 13 teeth. Some skewness occurred where uniquely large and small phenotypes were located but was not uncharacteristic of the small sample size. This is evident in the Desert region (mean 13.8 ± 2.0 teeth, median 14 teeth), where the "All Species" group included a low outlier. However, if that outlier is removed, the rest of the data has a spread similar too the other zones. This pattern is also observed in the T1-T4 regions of the Temperate zone that showed an overall mean of 13.1 ± 1.9 teeth and median 14 teeth. In regions where only a single species occurred, the box plots appear as single lines and indicate where individual species fall in comparison to other regions. Interestingly, *M. desertorum* in Tr2 is an outlier compared to the box plot for the tropical region, possibly because of the upward skewing of the *M. mjobergi* outlier where the tropical zone showed a mean of 13 ± 3.6 teeth and median 12 teeth. A similar pattern also exists in the Grassland zone where *M. desertorum* was the only species observed in the G1 region and is outside the interquartile range of the other regions where the Grassland zone showed a mean of 13.8 ± 2.1 teeth and median 14 teeth. Finally,it is interesting that in regions T7 and E3 the spread of mandible measurements is reduced when considering tooth number.

Behaviour

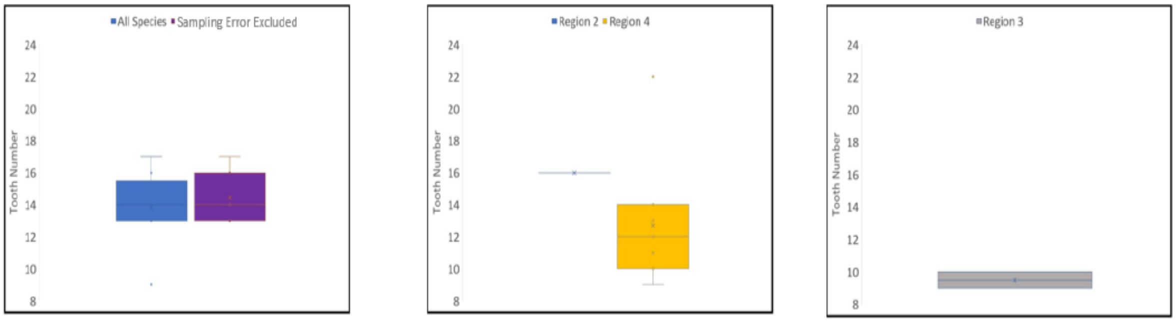
All members of the *M. gulosa* group had general similarities in foraging behaviour. Most species were documented as retaining the ancestral trait of foraging solitarily for nectar from neighbouring trees or from other plants at the base

Figure 3. Mandible length (mm) of *M. gulosa* study species across six climates zones, and respective regions in Australia. Note a consistent mean mandible length of *3.7 ± 0.8mm* across the six climate zones. Where species abundance is lower, larger interquartile ranges occur such as in Temperate zone region 7. The distinct low-lying outlier in desert regions occur in both"All Species"and "Sampling Error Excluded"groups that excludes purple font species in Figure2.

of trees. Eucalyptus trees were specifically mentioned in many articles, but it is unclear if the *M. gulosa* group rely



A. Grasslands B. Subtropical C. Temperate



D. Desert E. Tropical F. Equatorial

Figure 4. Tooth number of *M. gulosa* study species across six climates zones, and respective regions in Australia. Note the less consistent mean tooth number of *13.1 ± 2.6 teeth*. Each region shows a narrow interquartile range, indicative of lower variance in the morphologies. Note the distinct outliers in subtropical, temperate, desert, and tropical regions where the tropical region has the only high-lying outlier. The low-lying outlier of the desert region was only found in the "All Species" group, where the "Sampling Error Excluded" group excludes the purple font species in Figure 2.

on eucalyptus exclusively or if eucalyptus is simply the dominant tree species in the areas observed. It was also common for species to forage independently for insect prey; many researchers noted a large variety of prey items, from termites to butterflies. Eleven of the 42 species are generalist predators, where individuals retrieved prey items for carnivorous larvae, but adults fed on nectar. Twenty-nine of 42 species, however, had no behavioural observations of their foraging, either because the focus of the research was on another aspect, or, as in the case of *M. ferruginea,* was lacking entirely. *M. inquilina,* was noted unique, as a socially parasitic species within the *M. gulosa* group; as such, it was not considered a generalist predator. Eleven species exhibited unique behaviours associated with foraging (Table 1). Of interest, *M. gulosa* and *M. simillima*, two larger species, consume and share trophic eggs (unfertilized eggs) in addition to foraging, a behaviour not commonly observed in Formicidae. One third of the listed species, including *M. gulosa* and *M. simillima*, also exhibit some degree of polyandry between workers and drones within the colony, a mating strategy not commonly seen in ants. The trophic egg laying appeared connected with polyandry; the production of trophic eggs and polyandry has been found in four species; additionally, the trophic egg laying is also observed in species who secrete antibiotic compounds (Table 1).

Differences in the visual systems of the species are also noteworthy as they may affect foraging. While all the species were reported as using visual cues, *M. midas* and *M. pyriformis* were noted as having specialized light reception and analysis systems connected to their highly visual hunting, *M. nigriceps* supplements visual cues with aural cues, and *M. tarsata*, a diurnal hunter, has different eye structure than nocturnal species (Table 1).

The use of stinging and/or aggressive behaviours toward prey compared to nestmates or other *Myrmecia* species revealed some interesting details. Prey items and interspecific intruders to the nest were stung immediately by *M. brevinoda*, *M. gulosa*, and *M. simillima*. Of note, researchers found that the Dufour's gland, which synthesizes venom, in *M. gulosa* produces eight fractions of proteins, notably less than other Formicidae groups. Intraspecific intruders were rarely killed if at all. Intraspecific invasion was successful in species with larger colony sizes where larger colonies require more foraging resources but benefit from increased numbers of individuals. *M. nigriceps* was one species noted to accept interspecific intruders to the benefit of the colony (Table 1).

An examination of the active times of observed species, when they would be foraging, revealed twenty-eight species are noctidiurnal and six are nocturnal (Table 2). Activity times are consistent with temperature and light requirements of the given species, where one diurnal species was specifically noted because of specialized light facets of the eye that are distinct from nocturnal spec

Table 1. Unique foraging behaviours of well-studied and understudied *M. gulosa* species.

Species	**Unique Characteristics, Strategies, and Findings**
M. brevinoda	- Complex nest architecture with colonies in the thousands (Quian, 2012); has polygyny with reduced polyandry. - Older workers evenly disperse through the large and small worker groups (Higashi & Peeters, 1990). - Smaller intermandibular gap compared to *M. gulosa* and *M. simillima* species that is better adapted to regurgitating food to be shared amongst nestmates (Crosland et al., 1988).
M. desertorum	- Forages in the day. Ambushes flying insects by jumping and tackling them from nearby trees. Similar ambush behaviour is noted for *M. comata* (Gray, 1974b, 1974a; Sjögren, 1991).
M. eungellensis	- Hunts bees and hunts near water (Ogata & Taylor, 1991).
M. gulosa	- Produces trophic eggs in addition to foraging (V. Dietemann et al., 2002). - Prevents colony bacterial infection by topical secretions of workers spread sharing of forage and trophic eggs (J. A. Mackintosh et al., 1999). - Stinging directly correlated to temperature: no stinging below 20°C (Cavill et al., 1964). - The Dufour gland only contains 8 fractions of proteins for their venom (Cavill & Williams, 1967).
M. inquilina	- Parasitic species that targets *M. vindex* nests. The queen produces no workers and is thought to feed exclusively on the colony's eggs (Douglas & Brown, 1959).
M. midas	- Some of the first in the *M. gulosa* group to demonstrate visual acuity and learning ability. Appear to have a learned memory of their immediate environment and navigational abilities stemming from visual cues and use of an internal celestial compass (Freas et al., 2018; Freas, Narendra, & Cheng, 2017; Freas, Narendra, Lemesle, et al., 2017; Freas & Cheng, 2019). - Workers have higher numbers of specialized facets in the middle-frontal part of each eye that is more sensitive to light and transmits informative signals faster than other ant species that forage in the daylight (Ogawa et al., 2019).
M. nigriceps	- Detects prey visually and aurally (Eriksson, 1985). - Individuals show no aggression to alternate nest individuals, and sometimes accept new individuals into the colony (Van Wilgenburg et al., 2007).
M. pavida	- Queens have polyandrous mating where ~3.8 males mate with a single female (Chappell et al., 2013).
M. pyriformis	- Foraging changes with moon illumination. Foraging negatively affected by low light (Islam et al., 2020; Narendra et al., 2013; Reid et al., 2013). - Head rolls in accordance with body movements. Rolling appears in sync with the step pattern, but also relies on visual and nonvisual cues to "anticipate" how to move its head (Raderschall et al., 2016). - Exhibits breeding behavior like *M. pavida* and *M. gulosa*: protandrous with ~ 4 males (Sanetra, 2011).
M. simillima	- No behavioural research. Similar trends in prey, trophic egg specialization and intermandibular gap as in *M. gulosa* and *M. desertorum* (Crosland et al., 1988; Gray, 1974a).
M. tarsata	- Primarily active during the day into twilight and have different eye morphologies than primarily nocturnal species (Narendra et al., 2011). - Evidence of differential morphological investment in the different functional brain regions of daytime active *M. tarsata* vs. nighttime active *Myrmecia* species (Sheehan et al., 2019).

Table 2. Subspecies of *M. gulosa* and noted activity levels.

Species	**Active time**
M. analis	Noctidiurnal
M. arnoldi	Noctidiurnal
M. arthertonensis	Noctidiurnal (Taylor, 1985)(Taylor, 1985)
M. auriventris	Noctidiurnal
M. borealis	Unknown
M. brevinoda	Nocturnal around twilight (Lester & Keall, 2005)
M. browningi	Unknown
M. comata	Noctidiurnal
M. desertorum	Diurnal 11am-6pm in winter; 6-7am and 6-8pm in the summer (Ogata & Taylor, 1991)
M. dimidiata	Noctidiurnal
M. erecta	Nocturnal (Ogata & Taylor, 1991)
M. esuriens	Noctidiurnal
M. eungellensis	Unknown
M. fabricii	Unknown
M. ferruginea	Noctidiurnal (Taylor, 1985)(Taylor, 1985)
M. flavicoma	Noctidiurnal
M. forceps	Noctidiurnal
M. forficata	Noctidiurnal
M. fulgida	Noctidiurnal
M. fuscipes	Unknown
M. gratiosa	Noctidiurnal
M. gulosa	Nocturnal (Lieke, 1981)
M. hirsuta	Noctidiurnal
M. inquilina	Noctidiurnal
M. midas	Noctidiurnal
M. minuscula	Unknown
M. mjobergi	Nocturnal
M. nigriceps	Nocturnal (Narendra et al., 2011)
M. nigriscapa	Noctidiurnal
M. pavida	Noctidiurnal
M. picticeps	Unknown
M. pulchra	Noctidiurnal
M. pyriformis	Nocturnal, between 10-15°C ground temperatures (Gray, 1974a; Jayatilaka et al., 2014)
M. regularis	Noctidiurnal
M. rowlandi	Noctidiurnal
M. rubripes	Noctidiurnal
M. rufinodis	Noctidiurnal
M. simillima	Noctidiurnal (Taylor, 1985)(Taylor, 1985)
M. subfasciata	Noctidiurnal
M. tarsata	Noctidiurnal (Narendra et al., 2011)
M. tridentata	Unknown
M. vindex	Noctidiurnal

Discussion

Geographical Location

One trend evident from the geographic analysis was a larger number of species located along the west, south and east coasts of Australia. It has been suggested that *Myrmecia gulosa* are outcompeted in the northern climates by other ant species, or that *Myrmecia gulosa* has not evolved to survive in these tropical climates (Brown, 1953). However, because ant species have various tolerances to temperature and humidity (Hölldobler & Wilson, 1990), it is expected that different climate zones will support various diversities of ants, and organisms in general, based on the species' ability to survive in that particular environment, with tropical zones usually showing the highest diversity (Macarthur, 1965). Thus, another explanation of the low number of species reported from the north may be related to ease of sampling. As little research has been done on these ants, abundance of species may be reflecting a bias toward areas closer to civilization that provide easier access for research. The map of species' locations shows relatively few species found in the tropical and equatorial regions along the northern coastline, where human habitation is low (*Regional Population Growth, Australia, 2017-18*, 2019). I expect that more species than those listed occur in northern regions; and, due to biases in research location, I suspect the recorded instances may not be fully representative of the true distribution of all *M. gulosa* species. Indeed, because ants and termites make up one third of the total animal biomass and are documented most often in tropical rainforests (Fittkau & Klinge, 2016), I expect more *M. gulosa* will be found in the tropical and equatorial regions. The distribution of *M. desertorum* supports this, as it appears to be a generalist, occurring in five of the six climate zones, with no observations in the north equatorial regions. Considering this species has a broad range of ecological tolerances (Gray, 1974a; Rtorum & Gray, 1971); I predict that *M. desertorum* likely occurs in at least one of the northern equatorial regions and has simply not been observed there yet. Following this reasoning, it is possible that other species occur in other climate zones than currently observed, as it is unlikely that *M. desertorum* is unique in this aspect, because it shares many similarities with most of the studied species.

Although more research is needed to confirm they do not occur elsewhere, ten species of *M. gulosa* are currently only found in one region of the various climate zones. If they are found unique to one region, they may exhibit niche adaptations specific to the environment of the zone in which they are found, similar to endemic island species having features unique to their environment (Borges et al., 2006). While *M. browningi* and *M. esuriens* are only found on southern islands, the other eight species are located on the main island of Australia and showed some deviation from the mandible length and tooth number of the mainland species, with a large difference found in *M. mjobergi* in the Tr4 region. *M. mjobergi* is the only species that nests off the ground, in epiphytes (Taylor, 1985) and may have adapted a larger jaw morphology in response to unique selective pressures associated with nesting in trees. The specific habitats in which the ants are found, *M. mjobergi* and the 41 ground dwelling species, may be separated enough that conditions between them cannot be traversed by these species (Kadmon & Allouche, 2007). Four of these endemic region species increased the range of phenotypes in the climate zones in which they occurred; considering these ten species are not well studied, the four may have evolved subtly unique phenotypes in response to unique selection pressures incurred from inhabiting isolated regions where the other six retained the ancestral physiologies. Similarities in jaw morphology and foraging behaviour among the 42 described species also suggest that other *M. gulosa* species may be more widely distributed, like *M. desertorum*, than currently described and supports the need for focused research in the northern regions of Australia and into specific species.

Mandible and Tooth Measurements

Across the various climate regions, mandible length and tooth number showed no drastic differences when comparing the various box plots. However, regions with higher species counts had the whiskers of their box plots extending to account for notably unique phenotypes of the island-like species and unique mainland morphologies. The temperate zone had the most endemic species and showed a larger range of data where unique morphologies like the 5.5mm mandible of *M. auriventris* stick out. Overall, the data feature a tight grouping of mandible length and tighter grouping of tooth morphologies across the various regions that suggests species may have retained similar ancestral jaw morphologies on account of having no difference in their foraging behaviours, diets, and activity times. Despite 10 species appearing as endemics, they maintained similar mandible lengths and tooth numbers to exploit similar food resources. With 42 distinct species (Ogata & Taylor, 1991), the potential selective pressures for speciation events to occur do not appear to have been related to acquiring food resources; thus, this could explain why an ancestral jaw form is retained in the extant populations (Ward & Brady, 2003). These morphologies are also accompanied by relatively similar foraging behaviours that are considered. Although some species exhibit more derived behaviors that are tangentially related to their foraging, it is unclear if these unique behaviours are truly unique or simply have not been observed in understudied species.

Behaviour

Foraging

Eleven of the 42 species are confirmed generalist predators, with a twelfth species, M. inquilina, exhibiting social parasitism (DOUGLAS & BROWN 1959, GRAY 1974a, LIEKE 1981, TAYLOR 1985, OGATA & TAYLOR 1991, LESTER & KEALL 2005, Anon, Antweb); the eight well-studied species exhibited more specific characteristics to their generalist predation and solitary nectar foraging behaviour that occurs nocturnally or noctidiurnally.

The tendency for M. gulosa to forage on eucalyptus trees is further discussed. The observations that most foraging of nectar takes place in eucalyptus trees (Freas & Cheng, 2019), did not speak to the trees as a necessity or a coincidental presence. Given that the majority of eucalyptus species are found in Australia (Sellers, 1910), this may be a crucial element in the M. gulosa group surviving only in Australia. The role of eucalyptus should be investigated for possible coevolution with the M. gulosa group where nectar variety and foraging tactic on trees are compared between eucalyptus and other tree varieties to see if the ants have higher survival on a particular tree species.

Vision was noted as important in the foraging of M. gulosa species observed to forage nocturnally. Individuals do not use pheromone trails to forage because the larger, forward-facing eyes of this species group are excellent at capturing varying intensities of light and committing received visual signals to memory (Kamhi et al., 2020b; Robertson, 1971), during the active time of the species. The fact that most species forage nocturnally, or noctidiurnally, suggests that similar activity times will appear in species with unknown activity times that have similar morphologies and foraging behaviors. Foraging nocturnally or noctidiurnally could allow avoidance of daytime predators and allow the ants to forage in comfortable temperatures.

Nocturnal foraging is facilitated by specialized light facets in the frontal part of each eye that receive more light and transmit faster nerve cycles to the ant's brain, first observed in M. midas (Ogawa et al., 2019). This could suggest that M. midas, specifically, and possibly all M. gulosa adapted to nighttime hunting and foraging to cope with possible hotter daytime temperatures of Gondwana (Scotese et al., 1999) and then retained these traits in the hotter climates of Australia, as seen in other desert dwelling animals (Levy et al., 2016; Shillington, 2002), but now may be exclusively foraging nocturnally because of a physical inability to see key navigational landmarks because of a higher light sensitivity leading to blinding by light. The noctidiurnal species, M. tarsata and M. pyriformis, having different facets that are negatively affected by lower light levels of sun and moonlight suggests a minimum level of light is required to forage effectively, and demonstrates the group's reliance on visual perception, another possible retention of ancestral traits while other ant genera evolved to their unique environments (Duncan & Crewe, 1994; Fourcassié & Oliveira, 2002; Kenne et al., 2000; Narendra et al., 2011; Schatz et al., 1997). Despite varying light sensitivities with their vision, all observed species of M. gulosa exhibit some form of memorization of their immediate landscape associated with sight, where altering key landmarks causes temporary disorientation (Czaczkes et al., 2013; Freas, Narendra, & Cheng, 2017; Freas, Narendra, Lemesle, et al., 2017).

Navigation

The process of memorization implies a process where younger individuals learn the landscape to be effective, contributing members of the colony. Because *M. gulosa* relies on vision instead of pheromones to navigate (Jackson et al., 2006; Shepherd, 1982), their movement through their environment needs to be consistent to improve the efficiency in learning and allow them to be more effective foragers; repeated exposure to the same stimuli will quicken the learning process (Morand-Ferron, 2017). This predictable landmark learning method is supported by the characteristic head rolls observed in *M. pyriformis* where head rolling is in rhythm with step and direction of the individual to help reduce error in the image of surrounding landmarks and anticipate head rolling on uneven terrain (Raderschall et al., 2016). Comparison of the current environmental image to past memory must be consistent to not introduce excess error to the image and can be expected to be done along the same general route to and from foraging sites of eucalyptus trees. *M. brevinoda* exhibits a possible mentoring method of older individuals to younger individuals distinguished by brighter sharper mandibles. Mentoring may further expedite the learning process that individuals undergo (Higashi & Peeters, 1990; Rtorum & Gray, 1971). Memorizing the environment may help the ants maximize their use of a rich foraging site, as they can return to a food-rich location time and again.

The tendency for multiple species to make numerous trips for nectar or prey items could depend on the time of success where earlier successes may be followed by second and possibly third trips (Gray, 1974a). Trips may also be affected by environmental temperatures, where stinging behaviour was not observed below 20°C in *M. gulosa* (Cavill et al., 1964) and *M. pyriformis* specifically foraged between 10-15°C ground temperature (Jayatilaka et al., 2011) where detection of temperature was observed to occur through specialized structures of the antennae of *M. pyriformis* (Ramirez-Esquivel et al., 2014); structures that may be present in other species of *M. gulosa*. Particular species, however, were observed to have unique hunting behaviors.

Prey Handling

The strategy *M. desertorum* and *M. comata* have of jumping from trees onto flying prey items has only been described for these two species, which are noted as aggressive defenders of their nests (Gray, 1974a; Rtorum & Gray, 1971; Sjögren, 1991). It is possible that this increased aggression in nest defense translates into increased aggression in hunting as seen in other ant species (Duncan & Crewe, 1994; Erik Thomas Frank et al., 2017; Kenne et al., 2000; Schatz et al., 1997), and may be present in other aggressive species for whom foraging has not been observed (Gray, 1973). Helping these ants be aggressive hunters and defenders is their venom, used when stinging.

Stinging prey items is a common tactic for predatory ants, where venoms are synthesized in the Dufour's gland of the ant (Hölldobler & Wilson, 1990; Ogata & Taylor, 1991; Wheeler, 1990). However, many ant genera feature unique venom compositions that contain, on average, 15 fractions of proteins (Billen, 1990b, 1990a; Matuszek et al., 1994) compared to the eight fractions found in *M. gulosa* (Cavill & Williams, 1967). A gain of seven fractions in other ant genera may have evolved from alternative selective pressures faced in different environments where new venomous compounds may be more painful and provide better defence or adapted to new prey items (Brand et al., 1973). Thus, the fact that no increase in fraction number occurred in *M. gulosa* may indicate a need for more fractions is lacking (Ewen & Ilse, 1970; Robinson et al., 2018; Street et al., 1994); if eight fractions suffice, there may have been no selective pressures to evolve more.

Upon returning to the nest, adults of the various species do not consume the prey items. Instead, they are given to the carnivorous larvae, whereas the adults feed on nectar and, in some species, share food droplets among individuals to supplement external nest foraging of nectar further (Crosland et al., 1988). Sharing of food droplets thus indicates a type of altruistic behaviour between individuals that may be motivated by colonial kin relationships (Hölldobler & Wilson, 1990). While not measured in this project, other studies have observed smaller mandible gaps in species such as *M. brevinoda* that share food drops or otherwise hold droplets on their mandibles (Crosland et al., 1988). A smaller intermandibular gap showed easier handling and passing of food droplets between individuals and may provide evidence of motivations to sharing regurgitated food droplets. It may also suggest possible pressures for other species to evolve smaller intermandibular gaps such as seen in leafcutter ants handling regurgitated droplets during foraging to extend foraging trips, term "lunch box" droplets (Rytter & Shik, 2016). The food sharing is only one form of supplemental nutrition though.

Intracolonial Behaviour

To date, three species; *M. desertorum*, *M. gulosa*, and *M. simillima,* feature additional methods of nutrient acquisition by consuming trophic eggs laid by conspecific workers in the colonies. These three species are distinctly larger, so consump tion may be needed to sustain larger body sizes. Energy costs to lay these eggs may be high; however, workers were observed to lay eggs intermittently as individuals, thus no one individual would incur a higher cost to benefit ratio where costs were possibly distributed across a colony (Crosland et al., 1988; V. Dietemann et al., 2002). The trophic eggs may be contributing in another way to the success of the species that produce them.

The *M. gulosa* group is one of the only groups of ants where the colony is capable of continuation after the founding queen has died or been removed (Vincent Dietemann et al., 2003; Vincent Dietemann, Liebig, et al., 2005; Vincent Dietemann, Peeters, et al., 2005). This is done, in part, by the larger worker continuously laying trophic eggs, then smaller workers shifting to reproductive egg laying after removal of the queen (V. Dietemann et al., 2002). Research into the larger mandible gap of *M. gulosa* suggest it makes for easier handling of these trophic eggs (Crosland et al., 1988), where trophic eggs are shared amongst other adults along with antibacterial compounds secreted by the metapleural glands (J. A. Mackintosh et al., 1999). It is unclear if the sharing of these antibacterial compounds, also being researched for pharmaceutical application (James A. Mackintosh et al., 1998), is intentional or a by-product of the trophic egg sharing; however, the result is a reduction of colony infections connected to their foraging habits. With the added cost of laying trophic eggs there must be motivation for individuals to lay them; thus, *M. gulosa*, as a colonial group like other ants and bees, is driven by kin selection, (Hölldobler & Wilson, 1990; Wheeler, 1990) but is reproductively different from typical Formicidae. Where the source of fertile eggs in other Formicidae is generally the queen, *M. gulosa* species are observed to produce fertile eggs from queens as well as the colony's workers.

While trophic eggs are unfertilized, for workers to lay reproductive eggs requires mating. Polygamous mating among workers will reduce kin selection, as genetic diversity of the colony increases; thus, motivations to forage may be affected if genetic lineages stray too far from a majority. However, the tendency for polygamous mating to occur between workers may be the key to *M. gulosa* remaining colonized after losing their colony queen; polygamous mating systems are not commonly observed in Formicidae, and could improve a species' overall success after the founding queen is removed or killed compared to other Formicidae who experience colony collapse shortly after losing their queen (Chappell et al., 2013; V. Dietemann et al., 2002; Qian et al., 2011; Ward & Brady, 2003). Analysis of the intercolonial genetic diversity of *M. pyriformis*, polyandrous with ~4 males, showed four distinct genetic lineages (Sanetra, 2011). It is, therefore, possible that *M. brevinoda*, *M. gulosa*, and *M. pavida* show similar trends of multiple genetic lineages. This could suggest that after a colony is orphaned and opts for a polygamous mating system, parental roles are spread across the colony. While true paternity is unknown, the entire colony continues to have alloparental and cooperative breeding motivations to remain colonized and assist non-related individuals despite polyandry reducing kin-selection motivations (Chappell et al., 2013). The focus then shifts from the queen to the colony in the queen's absence, supported by reproducing individuals being killed in the *M. gulosa* species if laying reproductive eggs when a queen is present (Vincent Dietemann et al., 2003). However, this is only one possible explanation, as strictly monogamous species like *M. vindex* can persist as long as two years after the founding queen's absence (Haskins & Haskins, 1980).

The *M. gulosa* group is observed to accept new members into their colonies; these members may assist in foraging efforts or add additional costs to the minimum amount foraged by the rest of the colony and act as parasites. However, it is unclear if the detection of new individuals is physically possible, or if the cost of accepting new individuals is lower than trying to dispose of them. *M. nigriceps* is one such species that is observed to accept new individuals into the colony occasionally, but often shows no aggression even if individuals are not accepted (Van Wilgenburg et al., 2007). This is in stark contrast to aggressive behaviors exhibited by *M. brevinoda*, *M. gulosa*, and *M. simillima* that are observed to kill interspecific intruders almost immediately, but intraspecific members integrate easily (Crosland, 1989). This suggests that the ability to detect new individuals is present in this species group; if it were absent, I would expect interspecific intruders to invade nests of any *Myrmecia* species successfully. However, the success of intraspecific individuals may indicate that detecting senses can be tricked or relatedness between species is closer for some species than others as noted in *M. pilosula*; a member of the larger Myrmeciinae group that has been observed to perform successful crossbreeding with closer related species (Meyne et al., 1995). Thus, the genetic lineages that separate species and possibly trigger aggression in *M. gulosa* may be less clear than originally thought.

Social Parasitism

M. inquilina is an exception in the *M. gulosa* group; it is one of the only known socially parasitic ant species that does not kill the founding queen. This species is only known from identification of a workerless queen that invades the colonies of *M. vindex* and appears to feed exclusively on the eggs of *M. vindex*. It is, however, unclear how the workerless queen both invades and maintains her presence in the parasitized colony as the colonies are often not lacking a founding queen (Douglas & Brown, 1959). Because detection of other individuals is visual and auditory, it is possible that *M. inquilina*, which does not appear distinctly different from the *M. vindex* species, may be mimicking the founding queen to maintain invasion (Akino et al., 1999; Barbero et al., 2009; Fischer et al., 2020; Hojo et al., 2009). It is also possible that *M. inquilina* remains undetected by the invaded colony by emitting sense-dulling signals (Fischer et al., 2020; Lenoir et al., 2001) or masking traits. The presence of this parasitic species further supports the ancestral nature of the *M. gulosa* group; no other ant genera contain and sustain an ant parasite like *M. inquilina*. Because the presence of *M. inquilina* may rely on the inability of *M. vindex* to detect it, the *gulosa* group may be less derived than other ant species where parasites like *M. inquilina* do not occur. However, while *M. gulosa* may model possible ancestral traits and behaviors, evolution of a social parasite may also suggest future evolution of social parasites in more recent genera of Formicidae if the ability to detect *M. inquilina* is, in fact, present; more focused research will be required to answer this question.

Conclusion

Considering the similarities of foraging behavior, jaw morphology, and geographical distribution among species, food availability is unlikely to be a major selective pressure on the *M. gulosa* group that is further supported by their relatively unchanged jaw morphology and unique, ancestral solitary foraging behavior. Moving forward, understudied species should be the focus of future research projects, and attention given to the tropical zones of Australia, as species richness is expected to be higher than currently documented. Further studying the genetic relatedness of individual species may also corroborate my claims of similar behaviors and morphologies being exhibited across understudied species and understudied regions of Australia. Despite the *M. gulosa* group being previously considered ancestral with a primitive morphology (Hasegawa & Crozier, 2006; Rabeling et al., 2008) however, there is now evidence of their more recent evolution and retention of ancestral morphologies compared to other Formicidae (Moreau, 2009; Rabeling et al., 2008) that suggests there may be something unique to Australia that supports the survival of these relatively unchanged ants. It may be that food was not lacking, predation was not a threat, or competition was not an issue as much as it was in the rest of the world; thus, where they went extinct everywhere else, the *M. gulosa* group had ideal conditions for their success in Australia. From the many questions that remain, there is clearly much research yet to be done on the *M. gulosa* group.

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