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Does the Evolution of Mobility or Storage Behaviours in Ants Preclude the Other?

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ABSTRACT

All organisms require adaptations to deal with uncertainty in their environments. In Formicidae, the hugely diverse family of ants, several strategies are evidently in play. The aim of this study was to characterize the occurrence of two of these coping strategies, mobility and storage, to uncover whether the evolution of one of these behaviours precludes the other. A meta-analysis of current published literature regarding mobility and food storage behaviours was conducted across the ant phylogenetic tree. Searches were carried out on multiple databases and results were eliminated, reducing the dataset from 1483 search results to 177 papers. Binary occurrence data and categorical group identity was collected for colony mobility and resource storage. A significant negative relationship was found between the occurrence of colony mobility behaviours and food storage behaviours, suggesting a species showing one trait is likely to not show the other. Although a negative correlation was found, this was only identified with the inclusion of statistically inferred negative results created to fill in gaps in the dataset, in calculations based solely on the real data no relationship was found. A categorical scale within each strategy was also compared between subfamilies with the results showing significant differences, suggesting evolutionary differences in the acquisition of phenotypes. Biases were found in the data collected in the meta-analysis, based on the geographic sources of data and the subfamily identities of species, which can be used to inform further research as to which facets of the field are less explored.

Abstract Word Count = 246

INTRODUCTION

The Formicidae family is diverse and has evolved to occupy ecological niches across the globe, the family is now made of over 12,000 described species spread across 17 extant subfamilies (Ward 2007). This huge diversity has allowed for the wide range of physiological and behavioural adaptations to emerge, although similarities can be found across all species.

Ants make an interesting behavioural model, especially due to their eusocial population structure. Eusociality is defined by four main characteristics - communal living,

cooperative care of young, generational overlap, and division of reproductive labour (Wilson & Hölldobler 2005, Nowak & al. 2010) - and is contingent on high levels of cooperation and altruism between individuals (Robinson & Barker 2017). This leads to the existence of huge city-sized societies of ants, with colonies sometimes spanning across several component nest parts - known as polydomy (Robinson 2014). A wide range of behaviours can thereby be observed on multiple scales - from viewing colonies as superorganisms, to differentiating between different behavioural groups (often referred to as castes), and on an individual level (Queller & Strassmann 2002, Korb & Heinze 2004, O'Shea-Wheller & al. 2016). The complex social organisation behaviours of ant colonies have been well studied and allowed the field of ant-algorithms to emerge. These algorithms have a wide range of computational applications which provide solutions through the application of many small parts contributing to a collective whole (Dorigo & al. 2000).

Ants are one of the few organisms which carry out all of the behaviours of diversification, mobility, storage, and exchange in response to resource shortage (Deslippe & Savolainen 1994, McGlynn 2012, Ellis & al. 2014, Shik & al. 2014). Each of these behaviours appears widely across the Formicidae family, likely from multiple evolutions. This is due, at least in part, to their large and highly social communities and ability to cooperate.

This study focussed on the occurrence of two of these behavioural coping strategies: mobility and storage. In species other than ants, these behaviours are not commonly observed to co-occur. Humans in particular, whose behaviour is by far the most well characterised, historically made the switch from being highly mobile hunter gatherers to geographically stable agricultural communities which increased the capability for long-term storing of food (Kelly 1992, Rowley-Conwy 2001). Modern-day human hunter-gatherer societies are likely still weighing up this cost-benefit analysis today. It stands to reason that ants would similarly invest in one of these strategies to the detriment of the other.

Resource storage within ants can occur in multiple forms, with some species and subspecies showing far more extreme phenotypes than others. One of the most extreme examples of internal storage of food resources can be found in species of honeypot ants, whose replete workers make up a morphologically distinct class in

84 which the crops of these individuals are hugely distended (Duncan & Lighton 1994).
85 The stored water, sugars, and lipids can then be regurgitated to other members of the
86 colony providing food (Rissing 1984). Extreme examples of external resource storage
87 also exist, one of the most famous examples being the leaf-cutting ants who farm their
88 fungal food source in specialised chambers of the nest (Suen & al. 2011, Jesovnik & al.
89 2013). Seed harvesting ants are another common example of external storage where
90 specialist granary chambers can be located within the nest (Reyes-Lopez &
91 Fernandez-Haeger 2002).

92
93 Mobility, the second trait studied here, is similarly diverse. Behaviours range from the
94 highly nomadic lifestyle of the army ants, where near constant relocation is used to
95 locate resources, to relocation of a 'permanent' nest in response to damage or spoiling
96 (McGlynn 2012, Burns 2020). Propensity to relocate could theoretically be ranked on a
97 scale, although no consensus methodology currently exists between papers. The
98 decision to relocate a nest is often based on a cost-benefit trade off when comparing
99 the qualities of the current nest site to the proposed new site, with a colony collectively
100 making the decision to move or not based on the benefits (Gibb & Hochuli 2003, Pratt
101 2008, Doran & al. 2015). Nest relocations are a costly process that requires the
102 excavation of a new nest and the transport of the larval and egg brood via social
103 carrying (Leal & Oliveira 1995). It has previously been suggested that differing colony
104 relocation strategies interplay with the foraging and resource consumption strategies
105 used by ant species (McGlynn & al. 2004). Food availability also correlates with
106 relocations, which often occur when local resources are depleted, under high
107 competition, or when otherwise no longer deemed suitable by the colony (Topoff &
108 Mirenda 1980, Brown 1999, McGlynn 2006).

109
110 Among the proposed costs of these relocations is the loss of stored food resources or
111 the energy required to transport these to the new nest site (Nickele & al. 2012). The
112 evolution of a replete caste, who internally store liquid food to distribute among the
113 colony, may reduce the propensity to relocate due to reduced speed and mobility in
114 these workers (Duncan & Lighton 1994, Blanchard & al. 2000). This morphological
115 caste often has to be carried by workers when relocating, as they are unable to quickly
116 transport themselves over long distances, creating an additional burden on the colony
117 (Børgesen 2000). Leaf-cutting ants, who are completely reliant on their fungus farms,
118 appear to be more likely to relocate chambers within the nest in response to stress

rather than abandoning the site (Römer & Roces 2015). In contrast to these examples highly mobile nomadic species typically consume food on the spot rather than carrying it back to a central nest, evidencing the other extreme of the trade-off (Djiéto-Lordon & al. 2001).

Despite assumptions made by many myrmecologists over the years that the mobility and storage behavioural phenotypes are at odds with each other, to my knowledge no previous review has occurred across the Formicidae family. A statistical analysis based on data collected from a large quantity of species could be valuable in further characterizing the food storage and colony relocation behaviours. The hypothesis explored here is that the evolution of one of these strategies would preclude the evolution of the other, and thus the two traits would not co-occur in any one species. This hypothesis was made on the basis that the costs of relocating stored materials, or conversely storing materials in a highly mobile colony, would outweigh any benefits to the colony.

METHODS

Search Protocol

Two databases were used in the process of the meta-analysis, Web of Science and Scopus. Databases were selected on their likelihood to include papers in the relevant field. All searches were conducted by searching for terms at the title, key words, and abstract levels; this allowed for a relatively high rate of relevant results while limiting the number of hits to a manageable number.

All searches were conducted in the google chrome browser in incognito mode, this was to ensure maximum reproducibility by avoiding personalised search results. Searches were carried out between 27/01/2021 and 15/02/2021, search results were explored in full for the papers available at that time.

Search terms were decided in advance based on keywords found in papers relevant to mobility and food storage. A record of the search terms used and which database they were carried out in can be seen in table 1. In the data collection phase of the meta-analysis, gaps were often left where data for one of the behaviours, storage or mobility, was located but not the other. To fill in these gaps, the names of each species

155 identified in the study were searched alongside key words for both strategies. A
 156 complete account breaking down each search including the reasons behind
 157 eliminations and an expanded version of the combined 'species' searches highlighted
 158 in table 1 is shown in table S1.

159

Table 1. A record of searches carried out in the meta-analysis. Included is which database was searched, the search terms used, the number of results from each search, and the number of final papers used from each search. The two searches flagged with '**SPECIES**' represent combined data for 108 searches, each of which used the scientific names of species previously found in the meta-analysis as a search term - in the format of genus species.

Database	Key Words	Search Results	Papers used for Data Collection
Web of Science	Ant AND Relocat*	265	78
Web of Science	Ant AND Nomad*	60	16
Web of Science	Ant AND Internal Stor*	34	2
Web of Science	Ant AND Food AND Stor*	203	23
Web of Science	Ant AND Stockpil*	3	0
Web of Science	Ant AND Honeypot	9	3
Web of Science	Ant AND Transport AND Resource*	99	4
Scopus	Ant AND Storage AND Food	108	3
Scopus	Ant AND Relocat*	219	9
Web of Science	Ant AND Replete	21	4
Scopus	Ant AND Replete	22	2
Web of Science	SPECIES AND Stor*	248	7
Web of Science	SPECIES AND *migrat*	192	26

160

161 Papers were eliminated based on their appropriateness to the hypothesis at three
 162 different levels; based on the title, abstract, and finally the full text. Several papers were
 163 also eliminated from the study due to the full text being inaccessible behind a paywall.
 164 All papers found to be inaccessible were requested on researchgate if the author was
 165 available. Papers were also limited to those written in English. The total number of

search hits can be seen in figure 1 along with the number of papers removed by each level of elimination and the final number of papers included in the study.



Figure 1. Flow chart representing the reduction in the dataset from the initial number of search results to the number of papers from which data was extracted. The reason for each elimination and its corresponding effect size can be seen on each step. The final 177 papers represent a success rate of 11.9% of data extracted from the search results.

A table containing the complete list of the 347 papers identified in the meta-analysis as references, alongside the point of elimination if applicable, can be found in the supplementary materials table S2.

Data Collection

Taxonomy data was collected at subfamily, genus, and species levels. Species names from older papers were updated to the most recent taxonomic name identified as valid on the hymenoptera name server.

Mobility phenotype data was obtained on two scales. The first was a binary yes/no for occurrence of mobility behaviours. The second categorised the type of mobility into four

groups based on the definitions discussed by McGlynn in 2012. Categories were Nomadism, Intrinsic Relocators, Adventitious, and Unstable Nesters. Nomadism was defined as near constant relocations with only transient nest-sites. Intrinsic relocators were made up of serial monodomy, seasonal polydomy, seasonal migration, and itinerant relocation behaviours. Adventitious nest relocation is emigration in response to nest spoiling. Finally, Unstable Nesters were those moving by necessity due to ephemeral conditions.

Resource storage data was also collected on a binary yes/no scale alongside a categorical definition. The categories chosen were Internal, External, and Larval storage. Internal storage was defined by a stockpile of food kept inside of ant bodies that is capable of being distributed to other members of the colony. External storage was the stockpiling of raw materials, typically within specialised chambers of the nest. Larval storage, the smallest category, was used in the event a species is known to keep a specialised buffer of larval brood for consumption under resource shortage conditions. When resource storage occurred, the reported resource type was also recorded.

In addition to taxonomy, storage, and mobility data, several other relevant details were collected from papers. For each study it was recorded whether it was lab or field based. The location of each field study or the location from where lab populations were collected was abstracted for each study. Geographical data was primarily collected as longitude and latitude, if this was not available an approximate estimate based on the qualitative location was recorded. From this geographical data it was inferred whether the study species was native or invasive. The type of habitat was also recorded, although this information was rarely available.

Statistical analysis

All data was imported into R for statistical analysis and graphical representation. Version control and backup of data was carried out using github in a repository which can be viewed and downloaded at <https://github.com/JessamyA/AntMetaAnalysis>. The R script files and datafiles are also available in the supplementary materials.

217 A phylogenetic consensus tree for subfamily evolutionary relationships was made
218 based on those created for several previous studies (Brady & al. 2006, Ward 2007,
219 Borowiec & al. 2019), this was used to control for phylogeny.
220

221 A one-way chi squared analysis was used to compare the proportions of species
222 subfamily identity uncovered in the meta-analysis to the real-world proportions, where
223 the real world proportions were the expected results. The calculations were automated
224 using spreadsheet functionality. 95% confidence intervals were used as the threshold
225 for significance.
226

227 To further generate data for species for which information was only available for one of
228 the traits, negative results were statistically inferred by estimating the level to which
229 each species is studied. This was done by recording the number of results when each
230 species name was searched on both Web of Science and Scopus, then averaging the
231 values. These values allowed the allocation of each species into one of three
232 categories; low-studied (mean results < 50), medium-studied ($50 \leq \text{mean results} <$
233 100), and high-studied ($100 \leq \text{mean results}$). The thresholds were selected by plotting
234 the mean results data on a histogram (figure S1) which visually showed two troughs in
235 the distribution at the values of 50 and 100. The premise behind this approach is that
236 well-studied species are more likely to have behaviours reported if they are present.
237

238 Contingency tables were used to perform Fisher's exact analyses to statistically test
239 both the co-occurrence of storage and mobility behaviours and the differences between
240 subfamily behavioural type proportions. These analyses were performed in R and can
241 be seen in the script included in the supplementary materials. Pairwise post-hoc
242 analysis was performed using the rcompanion package to compute p-values for each
243 individual categorical paring within the contingency table. A 95% confidence interval
244 was used as the significance level.
245

246 Pearson's product moment correlation coefficient was used as a second statistical
247 measure for the co-occurrence of storage and mobility behaviours, this analysis was
248 performed in R. Here, a value of 1 was assigned for a positive result, 0 for a negative
249 result, and 0.5 for conflicting data. The significance of p-values was deduced using a
250 95% confidence interval. To test the assumption that the data is normally distributed a

Shapiro test was performed, the assumption that the data was linear was tested visually.

RESULTS

Bias

Bias in the methodology of the meta-analysis was explored, starting with the ratio of subfamilies found in the meta-analysis compared to their prevalence in the real world. One-way chi-squared analysis was used to compare the observed proportions of subfamilies (Figure 2(a)) to the expected real world ratios (Figure 2(b)). A significant difference, to a 95% confidence limit, was found between the subfamily proportions indicating there was a bias in the study ($df = 7$, $p\text{-value} = 8.390e-7$). The subfamily Dorylinae was particularly overrepresented in the study, this was to be expected due to the high mobility in its army ant constituent species. Only 7 of the 17 Formicidae subfamilies with extant species were identified within the meta-analysis. The remaining 10 subfamilies only contain 3.94% of species, a relatively low proportion.

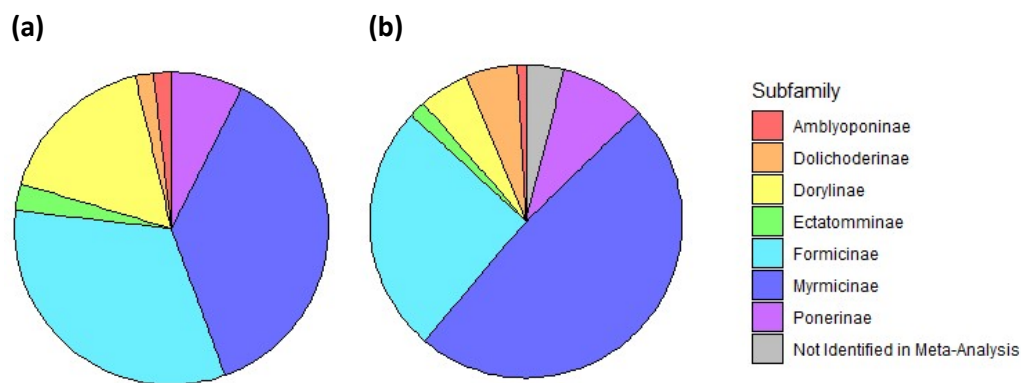


Figure 2. (a) Pie chart representing the relative proportions of species belonging to each subfamily found in the meta-analysis. Each of the 7 subfamilies identified are coloured for identification. (b) Pie chart representing relative proportions of species belonging to each subfamily in the real world. Subfamilies identified in the meta-analysis are named and represented in colour, as visible in the key. Subfamilies not identified in the meta-analysis, a total of 10 subfamilies, are grouped into one category coloured grey.

271 A global heat map of the field locations or the location from which lab based
 272 populations were collected was plotted (Figure 3). The region of highest density was
 273 located in southern central America, with a large number of datapoints located in
 274 Panama and Costa Rica. The regions with the least data include Africa and Oceania,
 275 likely due to an intrinsic bias in the field regarding where research takes place. Of the
 276 studies included in this analysis only 6%, for which location data was available, were
 277 studying species within their invasive ranges.
 278

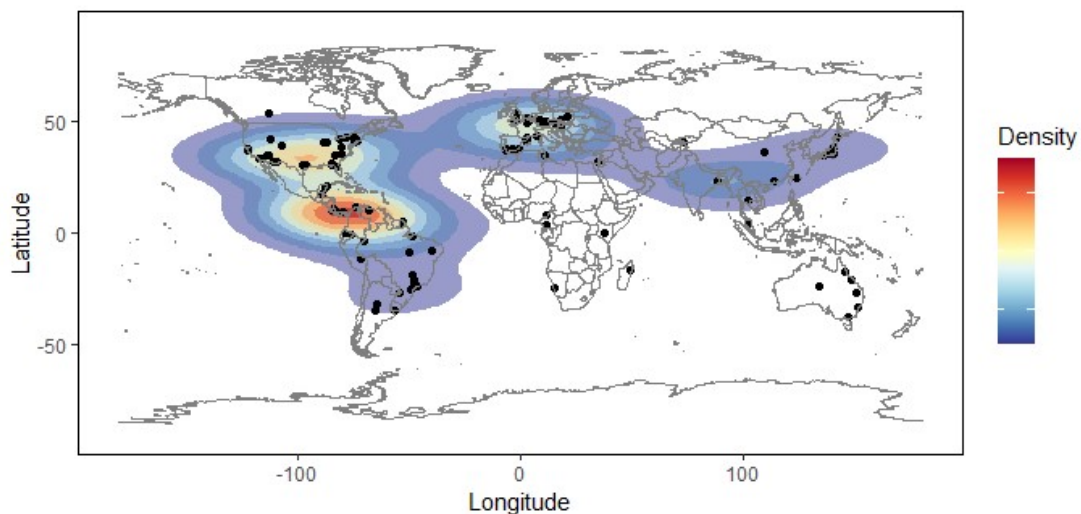


Figure 3. Locations of field studies or sites of ant collection found in the meta-analysis on a global scale. Each black point represents a study location, with a density heat map overlaid.

279
 280 The meta-analysis protocol flagged a larger number of papers relating to mobility and
 281 nest relocations as opposed to storage. Mobility data was collected for a total of 76
 282 species, but in comparison storage data was only available for 46. The artificially
 283 generated negative results increased these values but did not correct this disparity.
 284 Increases are to 84 and 52 respectively when including the high-studied group, and
 285 further to 87 and 59 when also adding in the medium-studied group.

286

287 A slight majority of studies included within this meta-analysis took place in the field at
 288 53.39% as opposed to in the lab. Although field results are arguably more powerful due
 289 to being more representative of behavioural systems in the wild, the lab based results
 290 were also included in this study due to the relatively small number of species for which
 291 there are data-points for both mobility and storage.

292

293 ***Co-occurrence of Mobility and Storage Behaviours***

294

295 A relatively small number of species with data for both storage and mobility was
296 uncovered in the meta-analysis. Of the 108 species in the meta-analysis only 14 had
297 real data for both behaviours. The high-studied statistically inferred results added 14
298 species and the medium-studied group added a further 10 species to the available
299 data-set - although these are of a progressively lower level of reliability. This brought
300 the total number of species with data for both storage and mobility to 38. A list of these
301 species, alongside the behaviours found for them in the analysis, are shown in table 2.
302 A complete list of all 108 species can be found in the supplementary materials.

303

Table 2. Table showing the 38 species for which data on the behavioural phenotypes for both storage and mobility are known. Species are organised into three categories based on the expected reliability of the data; category 1 contains only real data, category 2 is the species added to the dataset when including the high-studied group, category 3 is the species added to the dataset when including the medium-studied group. Data highlighted in **bold** is the real data found in the meta-analysis, non-bolded data is the statistically inferred negative results. If the species data contains 'BOTH' there was evidence that a species both did and did not perform a behaviour. Within the three categories species are grouped by subfamily then alphabetised at the genus level.

	Taxonomy			Reason for inclusion	Data	
	Subfamily	Genus	Species		Storage	Mobility
1	Dorylinae	Neivamyrmex	nigrescens	Real data	BOTH	Y
	Formicinae	Camponotus	detritus	Real data	N	Y
	Formicinae	Euprenolepis	procera	Real data	Y	Y
	Formicinae	Formica	fusca	Real data	Y	Y
	Formicinae	Formica	podzolica	Real data	N	N
	Formicinae	Melophorus	bagoti	Real data	Y	Y
	Myrmicinae	Acromyrmex	heyeri	Real data	Y	Y
	Myrmicinae	Atta	sexdens	Real data	Y	BOTH
	Myrmicinae	Carebara	urichi	Real data	Y	Y
	Myrmicinae	Monomorium	pharaonis	Real data	Y	Y
	Myrmicinae	Pogonomyrmex	badius	Real data	Y	Y
	Myrmicinae	Pogonomyrmex	mayri	Real data	N	Y
	Myrmicinae	Temnothorax	albipennis	Real data	Y	Y
	Ponerinae	Platythyrea	modesta	Real data	N	Y
2	Dolichoderinae	Linepithema	humile	High-studied	N	Y
	Formicinae	Camponotus	floridanus	High-studied	Y	N
	Formicinae	Cataglyphis	bicolor	High-studied	N	N
	Formicinae	Cataglyphis	fortis	High-studied	N	Y
	Formicinae	Formica	lugubris	High-studied	Y	N
	Formicinae	Formica	polystena	High-studied	N	Y
	Formicinae	Formica	rufa	High-studied	Y	N
	Formicinae	Lasius	flavus	High-studied	Y	N
	Formicinae	Oecophylla	smaragdina	High-studied	N	Y
	Myrmicinae	Acromyrmex	octospinosus	High-studied	Y	N
	Myrmicinae	Atta	colombica	High-studied	Y	N
	Myrmicinae	Messor	barbarus	High-studied	Y	N
	Myrmicinae	Pogonomyrmex	barbatus	High-studied	N	Y
	Myrmicinae	Solenopsis	invicta	High-studied	BOTH	N
3	Dolichoderinae	Tapinoma	sessile	Medium-studied	N	Y
	Dorylinae	Eciton	burchellii	Medium-studied	N	Y
	Ectatomminae	Ectatomma	rudum	Medium-studied	N	Y
	Formicinae	Camponotus	japonicus	Medium-studied	N	Y
	Formicinae	Camponotus	pennsylvanicus	Medium-studied	N	Y
	Formicinae	Camponotus	rufipes	Medium-studied	Y	N
	Formicinae	Cataglyphis	cursor	Medium-studied	Y	N
	Myrmicinae	Acromyrmex	echinator	Medium-studied	Y	N
	Myrmicinae	Aphaenogaster	rudis	Medium-studied	N	Y
	Myrmicinae	Aphaenogaster	senilis	Medium-studied	N	Y

305 Co-occurrence of resource storing and colony mobility behaviours was statistically
306 analysed. These tests were performed across all species and subfamilies in order to
307 look at overall evolution of the two traits. Fisher's exact analyses were performed, due
308 to the small sample sizes of the groups, to look for significant divergence from the null
309 hypothesis that mobility and storage behaviours occur independently of the other.
310 When conflicting evidence was uncovered, where there was proof of both the existence
311 and the absence of a behaviour in a species, a half weighting was given to both
312 groups. The species with real data showed no significant difference from the expected
313 ($p = 0.3571$, Figure 4(a)), this is similarly the case when the statistically inferred
314 negative results from the high-studied group were included in the analysis ($p = 0.2305$,
315 Figure 4(b)). However, with the additional inclusion of the statistically inferred negative
316 results in the medium-studied group a significant result to the 95% confidence interval
317 is seen ($p = 0.006366$, Figure 4(c)). This suggests that the knowledge of a species'
318 phenotype for either storage or mobility can allow for a prediction to be made as to their
319 phenotype for the other trait.
320

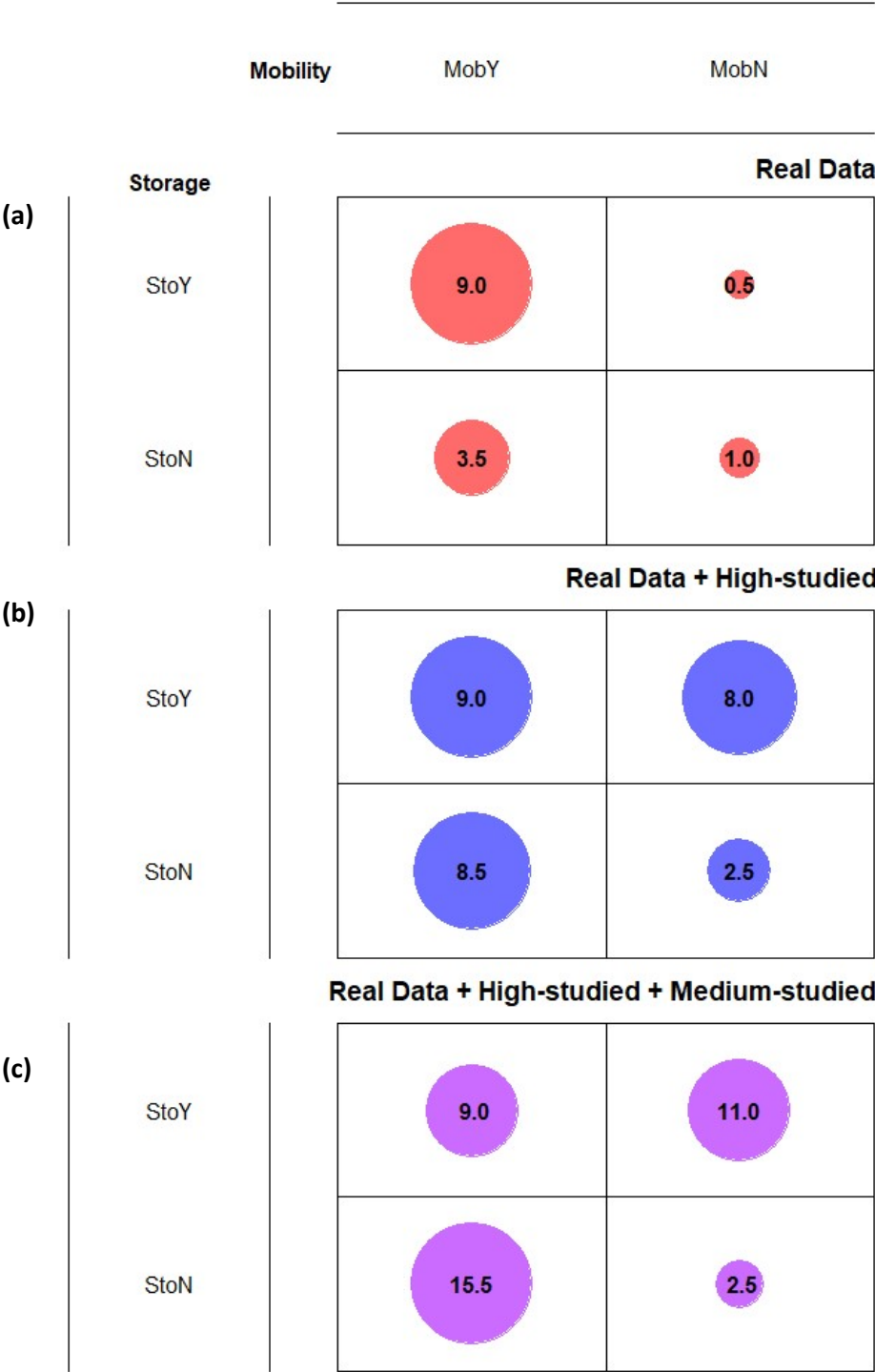


Figure 4. Balloon plots representing the co-occurrence of binary storage and mobility in the three statistically tested groups. (a) Real data only. (b) Read data plus the species in the high-studied statistically inferred group. (c) Real data plus the species with negative results statistically inferred from both the high-studied and medium-studied groups.

322 A second statistical measure of the co-occurrence of mobility and storage was
323 performed using a Pearson's product moment correlation coefficient. The correlation
324 analysis was then run between storage and mobility with a negative correlation
325 predicted if the evolution of one trait does preclude the evolution of the other. The
326 results of this analysis were similar to the prior Fisher's exact test, where the real data
327 ($p = 0.3036$, $cor = 0.2963$) and the inclusion of only the high-studied negative results (p
328 $= 0.1811$, $cor = -0.2602$) showed no significant relationship. However, once again the
329 additional inclusion of the medium-studied showed a significant negative correlation to
330 a 95% confidence level ($p = 0.004883$, $cor = -0.4471$). Pearson's correlation tests
331 assume normality and linear data. Although the data studied here is linear, when a
332 shapiro test was performed it showed the data is not normally distributed. This was to
333 be expected given the manner in which the binary count data was converted into a
334 linear correlation appropriate format and is thus considered acceptable. A figure
335 showing the three observed correlation lines alongside the predicted correlation line
336 can be seen in Figure 5.
337

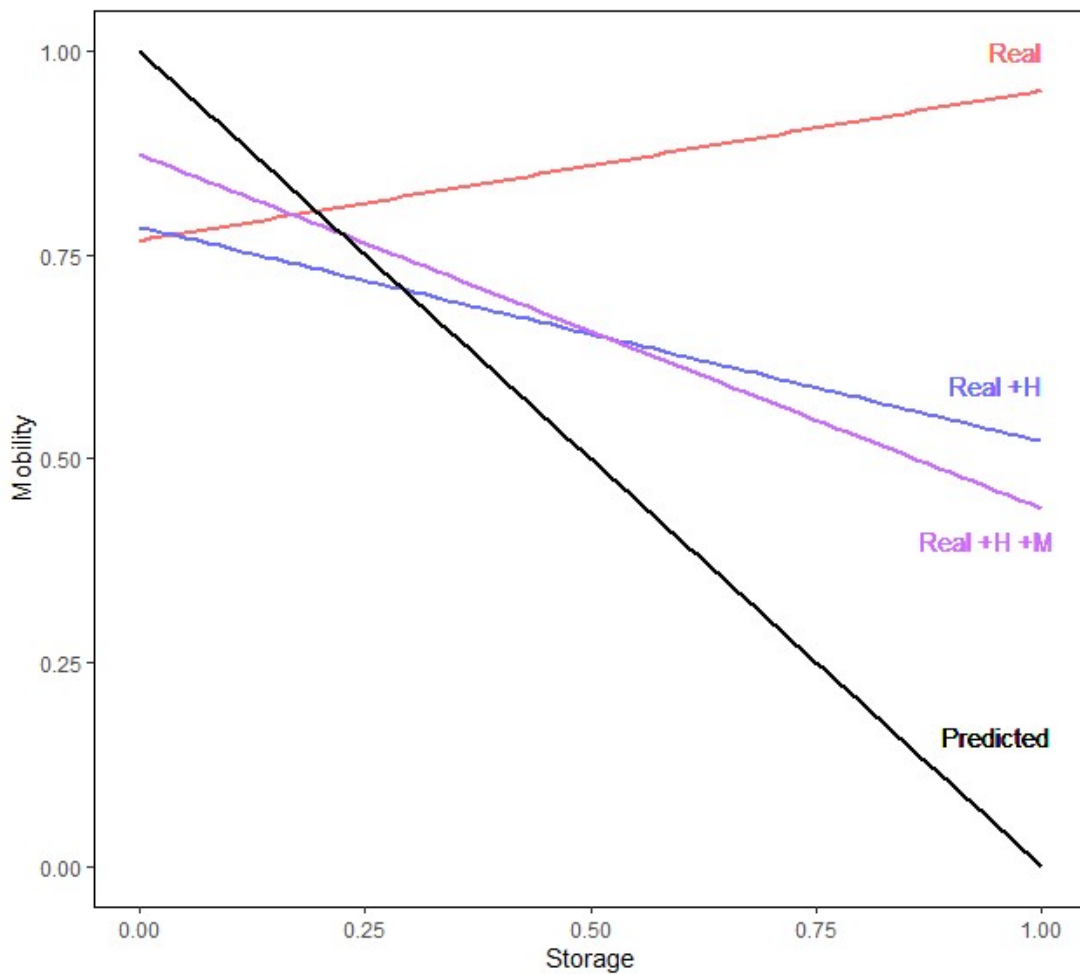


Figure 5. Graph showing the correlation between storage and mobility behaviours under the three statistical analyses compared to the predicted correlation. All lines are colour-coded and labelled within the figure. +H signifies the inclusion of the high-studied species and +M the inclusion of the medium-studied species.

338

339 Although the two aforementioned statistical analyses show that there appears to be a
 340 significant inverse correlation between storage and mobility behaviours it is important
 341 to note that this is not a perfect relationship. In the real data group (shown in table 2)
 342 there is evidence that 10 of the 14 species exhibit both storage and mobility
 343 behaviours. This is direct evidence that the evolution of one trait does not completely
 344 preclude the evolution of the other.

345

346

347 ***Diversity of Behaviours Across Phylogeny***

348

349 Counts for the occurrence of each categorical behaviour type group, for both storage
350 (ie. Internal, External, and Larval) and mobility (ie. Nomadism, Intrinsic Relocators,
351 Adventitious, and Unstable Nesters), were created per subfamily. When conflicting
352 evidence was uncovered, where there was proof of behaviour in multiple categories in
353 a species, a partial weighting was given to each relevant group.

354

355 Mobility behaviours were spread across all seven subfamilies identified in the meta-
356 analysis, although clear differences in the distribution of the types were evident (Figure
357 6). These differences were statistically analysed in R using fisher's exact test showing
358 a significant relationship between the subfamily and mobility types to a 95% level of
359 confidence ($p = 0.0004998$). A post-hoc pairwise analysis showed each subfamily's
360 proportion of mobility types was statistically distinct from all the others, similarly each
361 mobility type had a significant difference in distribution to all others. When subfamilies
362 were organized by the phylogenetic consensus tree, the points at which each
363 categorical type evolved can be visually estimated.

364

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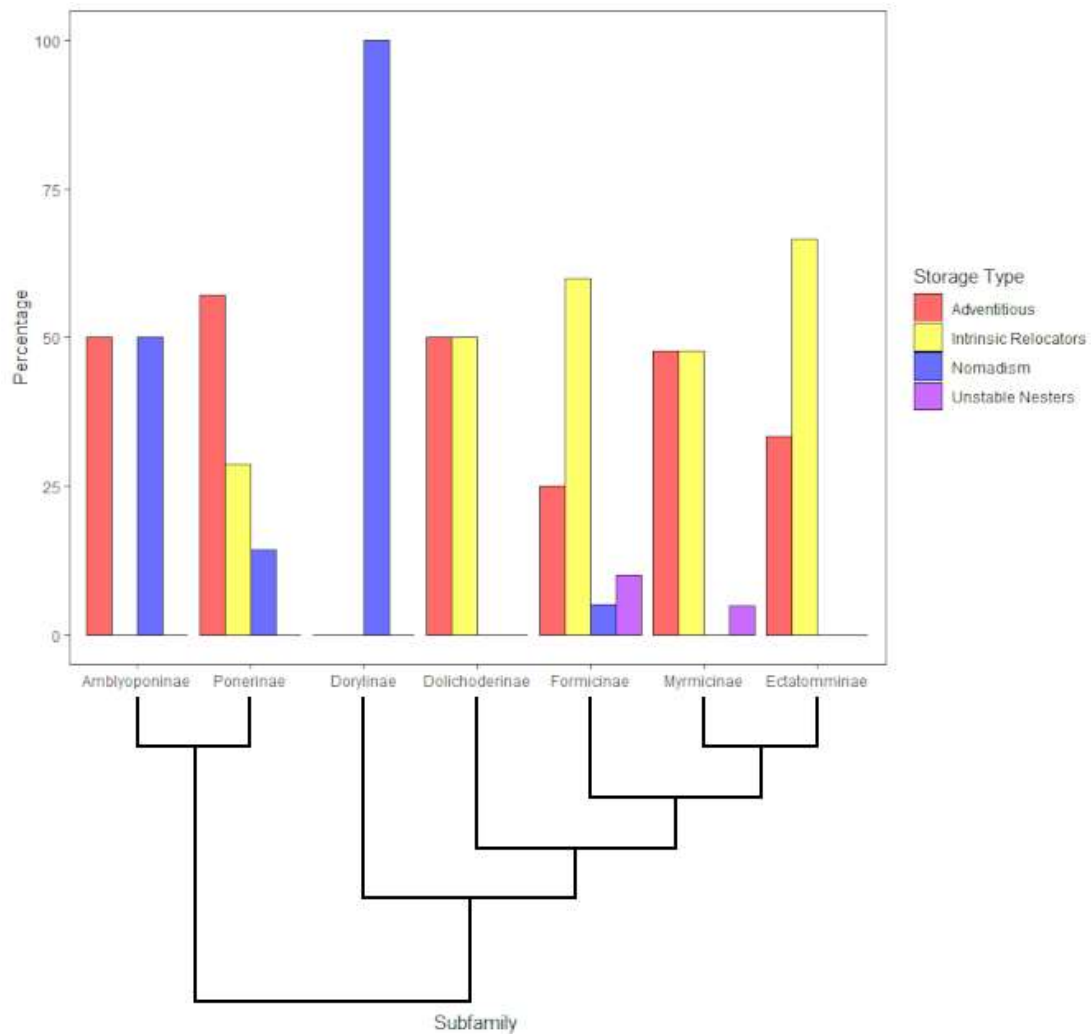


Figure 6. Bar graph representing proportions of each of the four categorical mobility types found within each subfamily. Species identified in the meta-analysis were not equally distributed across the subfamilies so values are presented as percentage within subfamilies. Beneath the bar graph the relatedness between subfamilies is denoted by the phylogenetic tree.

366

367 Conversely to mobility, storage behaviours were only identified in three of the
 368 subfamilies; Ponerinae, Formicinae, and Myrmicinae (Figure 7). It is unclear whether
 369 the lack of data for the remaining subfamilies is due to storage behaviours not
 370 occurring within them or due to a lack of published results. Three negative results,
 371 within the Dolichoderinae and Ectatomminae subfamilies, were inferred statistically.
 372 When the proportion of the different storage types was explored with a Fisher's exact
 373 test a significant relationship between subfamily and storage types was shown to a
 374 95% level of confidence ($p = 2.2e-16$). Post-hoc pairwise analysis showed all

subfamilies were statistically different from one another, this was also the case when comparing between storage types.

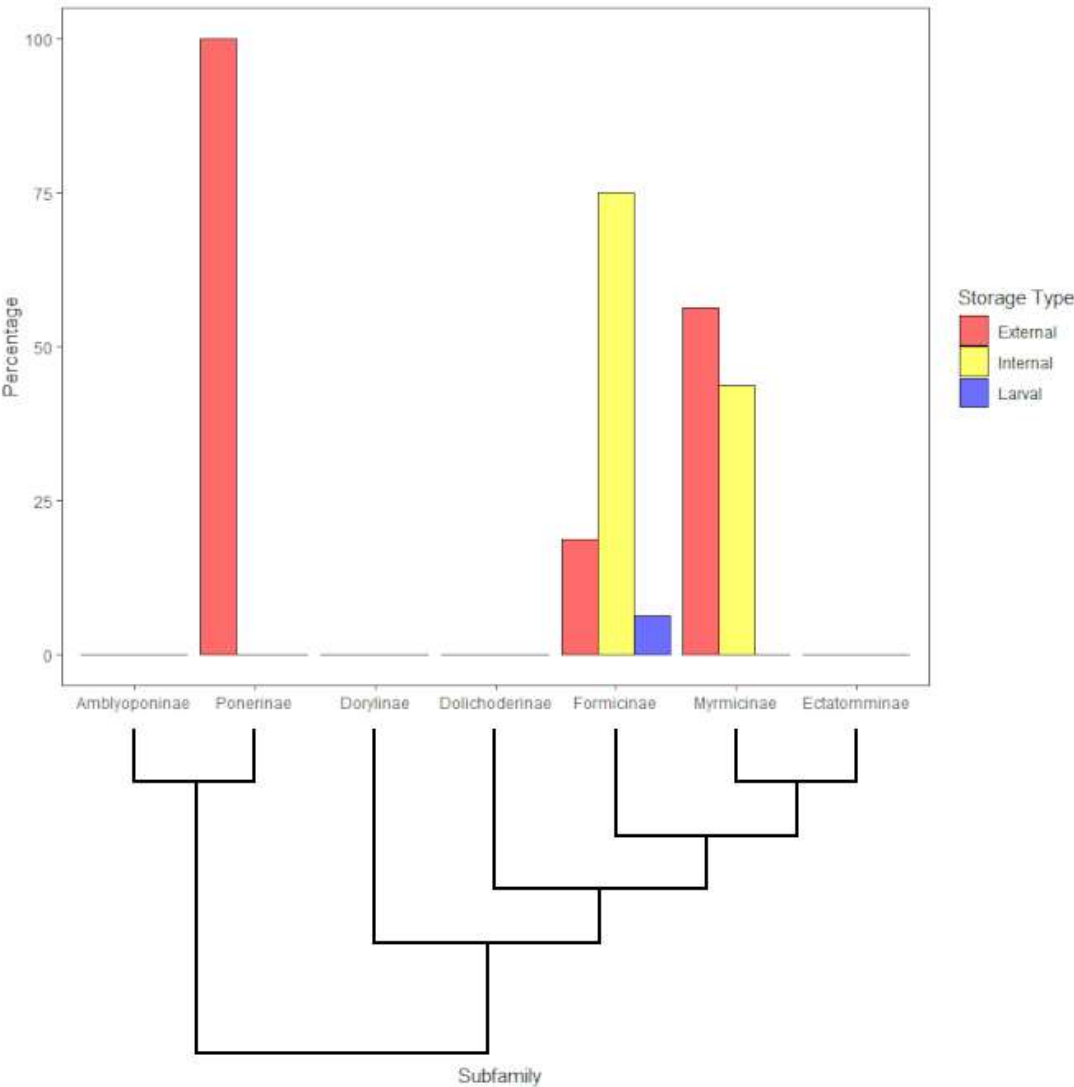


Figure 7. Bar graph representing proportions of each of the three categorical storage types found within each subfamily. Species identified in the meta-analysis were not equally distributed across the subfamilies so values are presented as percentage within subfamilies. Beneath the bar graph the relatedness between subfamilies is denoted by the phylogenetic tree.

382 **DISCUSSION**

383

384 This study has, through its exploitation of current published literature regarding ant
385 behaviour, answered the question of whether the evolution of food storage or colony
386 mobility precludes the evolution of the other. From the data analysed within this study
387 there appears to be a significant interplay between the occurrence of colony relocation
388 and food storage behaviours, whereby the evolution of one does reduce the chance
389 that a species will perform the other. Both the Fisher's exact tests and Pearson's
390 correlation tests discussed above statistically confirmed this conclusion. This
391 correlation was, however, only seen with the inclusion of both the high and medium-
392 studied statistically inferred negative results - not in the analysis of the real data
393 collected from the meta-analysis. This statistical correlation is clearly not evidence of a
394 complete inability for an ant species to evolve both of these behavioural types - in the
395 real data collected from the meta-analysis there are several instances where species
396 performed both behaviours. In these cases, it is possible that the behavioural
397 phenotypes may have been less extreme, allowing for the co-occurrence. This is
398 suggested by the fact two of these 10 species showed conflicting evidence for the
399 occurrence of a behaviour.

400

401 This study gives evidence that ant species do undergo the predicted cost-benefit trade
402 off in their evolution and primarily invest in one of the two strategies for coping with
403 resource shortage. This agrees with the long-standing unverified assumptions made by
404 myrmecologists that these two behavioural strategies are at odds with each other. As
405 this appears to be a novel study across the Formicidae family there is currently no
406 peer-reviewed literature either in agreement or contradicting this conclusion.

407

408 The trend discussed here, whereby ant species appear to invest primarily in one of two
409 strategies, mirrors the trends previously reported in human behaviour (Kelly 1992,
410 Rowley-Conwy 2001). This increases the validity of ant colonies as a behavioural
411 model organism for human social behaviour (Smith & al. 2009, Robinson & Barker
412 2017). There may be benefits in comparing the results shown here in Formicidae to
413 other species, particularly to other eusocial insects, to discover whether the trade-off
414 shown here is further replicated.

415

An additional facet of the data collected within this study allowed for an exploration of the evolution of the defined categorical behavioural types, within storage and mobility. Comparisons of proportions between subfamilies showed significant differences in the proportion of both storage and mobility behavioural types between each subfamily. This suggests there have been evolutionary differences in the acquisition of these behaviours. This study is in agreement with the prior suggestion that these traits have evolved multiple times over the natural history of the Formicidae family (Borowiec 2019). Based on the data and statistical analyses compiled in this study, knowledge of the subfamily membership of a species could be used to create a prediction of the behavioural phenotypes it will exhibit. In the obvious case of Dorylinae, where the component species only appear to exhibit nomadic relocation and extremely limited storage, behavioural predictions have long been made (Wilson 1958). The categorical group analysis also showed the evolution of these different behaviours across the Formicidae phylogenetic tree.

A significant bias to specific subfamilies was found within this study, when compared to the real world proportions within the Formicidae family. This bias was considered to be within acceptable bounds and the project was continued due to the assumption that the behaviours explored may be more prevalent in certain subfamilies than others. The Dorylinae subfamily, for example, is known for its overabundance of nomadic species - it stands to reason that similar trends may exist within other subfamilies (Borowiec 2019). The difference may also be due to an intrinsic bias in the subfamily study ratio within the field, certain subfamilies are likely more attractive for research purposes. This would only be able to be counteracted by the collection of more raw data from the under-represented subfamilies.

Geographical data similarly showed a bias based on location of ant origin, with particular information gaps in the continents of Oceania and Africa. This bias did not appear to align with global species density data, viewed via antmaps.org, where these continents appeared to have a high level of species diversity (Janicki & al. 2016, Guénard & al. 2017). The bias uncovered in this study was likely due to a general bias in ecological scientific research towards Europe and the Americas, although it may also have been accentuated by the limiting of papers to those published in English (Lach & al. 2010). Although this suggests a bias in the dataset, I would predict this is representative of a larger issue where this same bias would be mirrored across all

451 myrmecological research. The bias evidenced here should be considered by
452 myrmecologists, and those allocating grants to them, as to where future research
453 should take place - in order to fill gaps in our knowledge of ant behaviour.

454

455 Due to the general propensity of academic writing not to publish negative results, the
456 dataset collected in the meta-analysis is primarily made up of confirmed cases of a
457 behaviour and relatively few negative results (Borenstein & al. 2009, Russell 2012,
458 Song & al. 2013). Each species identified in the process tended to have data for one of
459 the two key behaviours, mobility and storage, but not the other. This was a recurring
460 issue throughout the study where statistically inferred negative results, based on the
461 level of study for each species, were created and used in the statistical analysis.
462 Conclusions can be drawn using these artificial negatives but a certain level of
463 scepticism is required as the trend only occurs when including these results - there is a
464 risk that this result is the product of confirmation bias. Real-world research, preferably
465 from field observations, confirming these negative results would have more power. It is
466 therefore suggested that increased observation and reporting of these negative results
467 be conducted by behavioural myrmecologists.

468

469 Time constraints impacted this study, further searches across a larger variety of
470 databases may uncover additional studies relevant to the hypothesis. In the case of
471 further data collection occurring, particular attention should be given to older ant life-
472 history literature which typically were not identified in the digital databases used in this
473 study.

474

475 In this study levels of storage and relocation behaviours are assigned to categories as
476 this was considered to be the most appropriate way to collect data from papers of
477 varying quality, age, and style. This is, however, a simplification of the real world
478 diversity of these traits (McGlynn 2012). In an ideal world, mobility data would be
479 collected and analysed on a linear 'propensity to relocate' scale; this would allow for a
480 more complex statistical analysis to take place. This could theoretically be recorded as
481 mean time between colony relocations in the field or level of disturbance required
482 before relocation occurs under controlled conditions. Similarly, storage data would
483 ideally be collected on a scale measuring 'percentage of food resources consumed
484 from stored materials'. This could potentially be studied using radioisotope tracking of
485 food sources, which has been successfully used to study the flow of food through ant

colonies in the past (Buffin & al. 2009, Buffin & al. 2012). Scales such as these representing the extremeness of the phenotype were not possible for this study. For future research into this topic it is suggested that either a method for converting prior research into this format or future data is produced with standardized measurements.

The results of this study have implications for the field of behavioural myrmecology, showing that knowledge of the behavioural phenotype for one of the traits studied here may allow a prediction of the other for a given species. A greater understanding of the patterns by which species behave could allow for improved conservation and predicting their many roles in an ecosystem. One of the potential uses for this research is fine tuning the management of invasive pest species. A species-specific approach to pest management is intrinsic to any strategy employed in order to conserve the natural diversity of native insect species (Kogan & Lattin 1993). Being able to better predict the behaviours of an ant species could allow for a more targeted application of the appropriate pest management strategy. A greater behavioural understanding could have knock on benefits for the field of ant-algorithms which have been created based on the foraging and movement behaviours of ants (Dorigo & al. 2000, Lanan 2014).

It is the intention of the author that, through the findings of this study, behavioural ecologists will take note of the areas of myrmecology which require further research in order to enhance our knowledge of ant behaviour. Furthermore, this study provides support for the assumption that ant species primarily evolve either mobility or storage strategies to the detriment of the other - a previously untested hypothesis across the Formicidae family as a whole.

Main Text Word Count = 4893

ACKNOWLEDGEMENTS

Many thanks to the University of York biology department for providing me with the resources to complete this study. Special thanks to my supervisor Elva Robinson for sharing her knowledge and giving advice over the last year.

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