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Colony size evolution in ants: macroevolutionary trends

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Abstract Colony size is an incredibly important factor in social insect ecology: it affects everything from foraging strategies to colony defense to mating systems to the degree of polymorphism. However, colony sizes vary dramatically among ant species (Formicidae): sizes range from several workers living together to super-colonies that stretch for hundreds of kilometers. Although the origins of eusociality and colonial life have been extensively theorized, little work has been done describing the evolution of colony size that followed after. Our study provides the first large-scale investigation into such issues, incorporating colony size data from 118 genera and recently published, nearly complete genus-level molecular phylogenies. We find that colony size change exhibits a bifurcation pattern similar to the feedback loop theory posited by Bourke 1999. Once colony sizes become sufficiently large, they rarely undergo radical decreases in size on a macroevolutionary scale. Additionally, the magnitude of colony size changes seem relatively small: rarely do colony sizes jump from small to large sizes without first transitioning through an intermediate size. Lastly, we echo many previous authors in advocating for the release of unpublished sociometric data and a push toward its further acquisition.

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Introduction

The theoretical origin of eusociality in insects is a well-discussed topic in biology (Wilson 1971; Oster and Wilson 1978; Crozier and Pamilo 1996). There are multiple possible theoretical routes to eusociality in Hymenoptera (bees, wasps, and ants), and the specific models continue to be debated (Wilson 2008; Hughes et al. 2008; Abbot et al. 2011; Nowak et al. 2010).

However, little work has been dedicated to describing the evolution of the developing complex social characteristics that followed; the macroevolutionary trends in social characteristics such as colony size, division of labor, and foraging strategies remain understudied in ants (Anderson and McShea 2001). Although several myrmecologists have posited that ants (Hymenoptera: Formicidae) originally evolved from a solitary wasp-like species—first living in small family units, then increasing in colony size and complexity over time (Hölldobler and Wilson 1990; Bourke and Franks 1995)—the specifics of this progression are often only implied in the literature and not explicitly stated or tested (Dew et al. 2012).

Perhaps the most fundamental social characteristic of the social insect colony is simply its size. In ants, colony sizes range from a just few individuals living together under a leaf or stone to decentralized nests with hundreds of millions of workers. In fact, recent research has suggested that many of the largest Argentine ant supercolonies across the globe—each spanning hundreds or thousands of kilometers—together comprise an intercontinental supercolony that

represents the most populous recorded animal society (Van Wilgenburg et al. 2010). Clearly studying the evolution of colony size across ants can reveal many new insights into their biology: it is an important factor in ant ecology, affecting traits such as foraging strategies, lifespan differential between queen and workers, colony defense, reproductive output, and colony-wide social immune responses (Beckers et al. 1989; Anderson and McShea 2001). Dornhaus et al. (2012) argue that as body size is often considered the most important factor in shaping the life-history, physiology, and ecology of a unitary organism, so too might colony size be most important in shaping the life and collective organization of colonial organisms.

New, reliable molecular phylogenies for the ants, incorporating fossil evidence (Brady et al. 2006; Moreau et al. 2006; Moreau and Bell 2013), provide the framework to address questions of the evolution of ecological characters in a phylogenetically controlled framework. Unfortunately at this time, as Oliver et al. (2008) mention, it is impossible to conduct a large-scale, species-level analysis controlling for phylogeny when considering all 13,000+ species of living ants. Although ideally a phylogenetic analysis using comparative methods is done on the species-level, several studies (Oliver et al. 2008; Koh et al. 2004; Lucky et al. 2013; Moreau and Bell 2013) have already conducted successful genus-level phylogenetic analysis on insects.

As of yet, evolutionary patterns in colony size across the ant radiation remain understudied, and theories have never been tested in a phylogenetic framework (Anderson and McShea 2001). To address this we will leverage the nearly complete, genus-level ant phylogenies to test various hypotheses and models of colony size evolution (Dew et al. 2012). Specifically, we will test whether average colony sizes change slowly across a continuum or in leaps and bounds, whether there is a bias towards increasing in colony size, or if certain islands of stability exist from which there is little change.

Materials and methods

Colony size estimates

As noted by Kramer and Schaible (2013), published colony size data for eusocial insects is generally scarce. Although several comparative studies on colony size exist, often correlating size with various factors such as foraging strategies, physiology, and life history (Beckers et al. 1989; Hou et al. 2010), much of our data was gathered from the primary literature to include as many species and data points as possible. In our literature search, we compiled data for 476 records from controlled experiments, field measurements, and anecdotal observations (see Table S1 for a list of all data used in this study). Especially for rare species with

small colony sizes, rough estimates were often the only informed measures available.

We searched for average mature colony sizes—when available—and when multiple size estimates for a species were reported, the mean colony size was calculated and recorded. Yet as Dornhaus et al. (2012) point out, calculating a mean can be misleading via the inclusion of immature colonies. Thus when ranges were given, the maximum value was recorded. When the only information on colony size was present in graphs averages were calculated via estimating values.

Average colony size estimates were then calculated for each particular species: each independently derived estimate was used as an individual data point within the species-level calculation. In addition, several colony size estimates were reported without species-level identification; in an effort to include as much genus-level information as possible, these data were included in our study but not incorporated into any species-level mean calculations.

The distribution of species' colony sizes within a genus often exhibited a slight to extreme right skew in our data, as demonstrated in Fig. 1a, d with the example genera *Strumigenys* and *Pheidole*. In most genera with an adequate number of species-level estimates, log-transforming the average species sizes produced a roughly normal distribution, demonstrated in Fig. 1b, c. However, even after being log-transformed, several genera remained skewed with deviations from normality occurring at the extreme values, Fig. 1e, f. Thus, to produce a representative size for each genus, average species sizes were logged and then a trimmed mean—an estimate of central tendency for small samples that is less sensitive to outliers than the geometric mean (Tukey and McLaughlin 1963)—of 15 % was calculated for each genus.

Phylogenetic comparative methods

To control for shared evolutionary history, we used a modified version of the recent ant phylogeny of Moreau and Bell (2013), as this tree represents the largest molecular phylogeny currently available for Formicidae (incorporating over 295 ant specimens and all 21 extant subfamilies) and is well supported with 45 fossils as minimum constraints for divergence dating. Several instances of paraphyly in the ultrametric tree were resolved by examining recently published phylogenies for specific clades where taxonomic revisions elevated these taxa to genus level. In addition 16 genera, which were not previously included, were added according to recent molecular phylogenies (Ward et al. 2015; Schmidt 2013). The tree was pruned using Mesquite ver 2.75 (Maddison and Maddison 2011) to include only the genera for which colony size information was available. Taxonomic classification follows that available at the beginning of the study (Bolton 2013).

Fig. 1 Colony size distributions and normality assessment for the log-transformed colony size distributions of typical genera. A smoothing bandwidth of 35 was used in the density plots of the untransformed colony sizes, and a bandwidth of 0.5 was used in the logged distributions. Colony size is on the *x*-axis in (**a** and **d**) and the logged colony size is on the *x*-axis in (**b** and **e**). *Strumigenys* (*n* = 22 species-level estimates) in **a**–**c** is typical of most genera: the recorded colony size distribution in the genus is right-skewed (**a**). When the colony size estimates are log-transformed, the distribution approaches normality (**b**, **c**). However, several genera such as *Pheidole* (*n* = 36 species estimates) shown in **d**–**f** exhibit an extreme right skew (**d**) that persists even after being log-transformed (**e**, **f**). Note that the extreme values highly deviate from normality in (**f**)
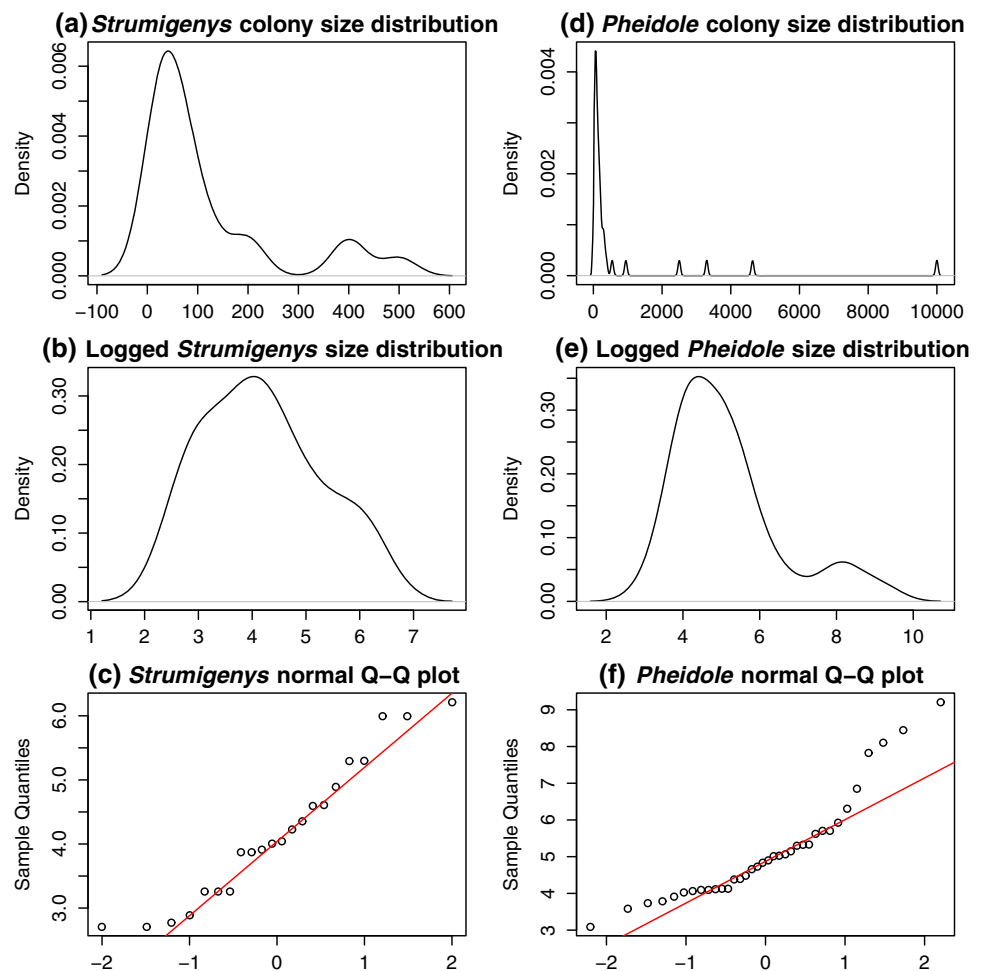
To evaluate various models of colony size evolution, we used the multistate speciation and extinction analysis (MuSSE) in FitzJohn's (2012) software package '*diversitree*' for *R* (Fitzjohn et al. 2009; R Core Development Team 2015). MuSSE simultaneously analyzes rates of speciation, extinction, and transition between several phenotypic trait categories. To minimize the number of parameters and estimate change between several broad size ranges, genera were binned into one of three categories according to the average colony size estimate for each genus: small (<100 individuals per average colony), medium (between 100 and 10,000), and large (over 10,000). These particular divisions represent Kaspari and Vargo's (1995) classifications. In the models below, small colony sizes are represented by "S", medium by "M", and large by "L".

We consider five possible models of colony size evolution (Table 1). First, the labile model assumes colony size transitions have very few constraints and allows for transitions to occur between any and all size categories ($L \rightleftarrows S \rightleftarrows M \rightleftarrows L$). The irreversible growth model posits that colony size has a tendency to increase, with sizes rarely decreasing ($L \leftarrow S \rightarrow M \rightarrow L$). The step-wise evolution model states that colony size increases or decreases in small steps, and that it must transition through intermediate sizes instead of jumping from small to large or vice versa ($S \rightleftarrows M \rightleftarrows L$). Lastly, we examine two threshold models that have a critical 'point of no return.' The standard threshold model posits that once colony size becomes significantly large, crossing some specific critical point, it rarely transitions back to smaller sizes ($L \leftarrow S \rightleftarrows M \rightarrow L$). Bourke's bifurcation model is a variation of the standard threshold model: it merely adds the requirement that changes are small in magnitude ($S \rightleftarrows M \rightarrow L$). Inspired by hypotheses purposed in Bourke (1999), it can be thought of as a combination of the step-wise model and the standard threshold model.

In addition, symmetric versions of each model were tested when applicable, so as to lower the number of parameters. In the symmetric models, transition rates between two categories were set to be equal in both directions: for example, the transition rate from the small colony size category to the medium size category would be the same as from the medium category to the small. Symmetric transitions are represented here with double-headed arrows

Table 1 Comparison of macroevolutionary models and fitted parameters, ranked from the lowest AIC values to the highest

Model name	Diagram	Df	lnLik	AIC	ΔAIC	Lambda1	Lambda2	Lambda3	$q12$	$q13$	$q21$	$q23$	$q31$	$q32$
Bourke's bifurcation (symm)	S ↔ M → L	5	−661.42	1332.84	0	0.003	0.034	0.009	0.031	–	0.031	0.004	–	–
Standard threshold (symm)	L ← S ↔ M → L	6	−661.43	1334.86	2.02	0.003	0.034	0.009	0.031	2.73E-5	0.031	0.004	–	–
Labile (symm)	L ↔ S ↔ M ↔ L	6	−662.16	1336.31	3.47	0.035	0.004	0.010	0.033	0.005	0.033	1.24E-6	0.005	1.24E-6
Standard threshold	L ← S ⇄ M → L	7	−661.4	1336.81	3.97	0.004	0.034	0.009	0.028	8.34E-8	0.030	0.004	–	–
Step-wise (symm)	S ↔ M ↔ L	5	−664.14	1338.28	5.44	0.035	0.002	0.013	0.043	–	0.043	0.008	–	0.008
Bourke's bifurcation	S ⇄ M → L	6	−663.51	1339.02	6.18	0.029	0.013	0.009	0.017	–	0.006	0.007	–	–
Labile	L ⇄ S ⇄ M ⇄ L	9	−660.66	1339.32	6.47	0.034	0.005	0.017	0.026	0.005	0.020	1.01E-9	2.63E-6	0.009
Step-wise	S ⇄ M ⇄ L	7	−662.72	1339.43	6.59	0.019	0.009	0.034	0.016	–	0.021	4.01E-8	–	0.025
Irreversible growth	L ← S → M → L	6	−665.02	1342.05	9.2	0.028	0.012	0.009	0.014	9.67E-8	–	0.008	–	–
Minimal	NA	4	−672.11	1352.23	19.38	0.007	0.033	0.002	0.014	0.014	0.014	0.014	0.014	0.014

Symmetric versions of the models (symm) include symmetric transitions between two categories represented with double-headed arrows (↔). Such transition rates set to be equal in both directions: for example, the transition rate from the small colony size category to the medium size category would be the same as from the medium category to the small
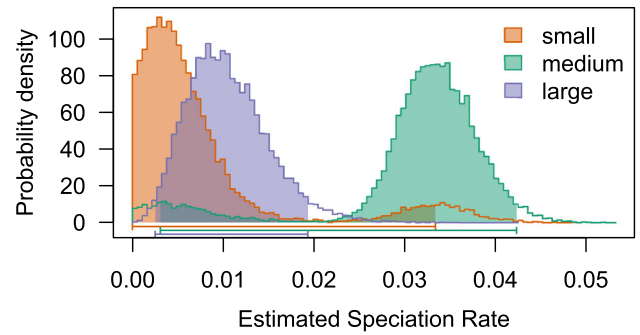

Fig. 2 The posterior probability distribution of speciation rates in Bourke's symmetric bifurcation model. Speciation rates for the small colony size category are the lowest, with medium-size colonies speciating more frequently than even the large colony size category

(↔) between categories. The additional symmetric versions are as follows: the symmetric labile model (L ↔ S ↔ M ↔ L), the symmetric step-wise model (S ↔ M ↔ L), the symmetric standard threshold model (L ← S ↔ M → L), and the symmetric version of Bourke's bifurcation model (S ↔ M → L). Lastly, a final "minimal model" was added as a benchmark. In this model, all transition rates between every category are set to be identical in magnitude (no representation is available).

Speciation rates were unconstrained in all of our models, but extinction rates were set to zero, because of their difficulty in being estimated in MuSSE-like models (Maliska et al. 2013). These models were analyzed with MuSSE, and the resulting AIC scores were used to evaluate the various models and their fits to the phylogeny. Additionally, *diversitree's* default maximum likelihood-based ancestral state reconstruction (ASR) function was used to estimate the probabilities of average colony size categories on the internal nodes of the phylogeny.

To visualize inferred transition and speciation rates, posterior probability distributions were calculated for the most successful model using Markov chain Monte Carlo (MCMC) Bayesian analysis in the *diversitree* package. The chains were run for 20,000 iterations discarding the first 10 % of samples as burn-in. Distributions for the speciation and transitions rates of all three size categories are presented for the best fit model in Figs. 2 and 3.

Results

Colony size estimates

Through our review of the published scientific literature, we were able to include over 400 species from 118 ant genera (Table S1). Average colony size estimates for species ranged from 2.5 (in *Thaumatomyrmex contumax*) to
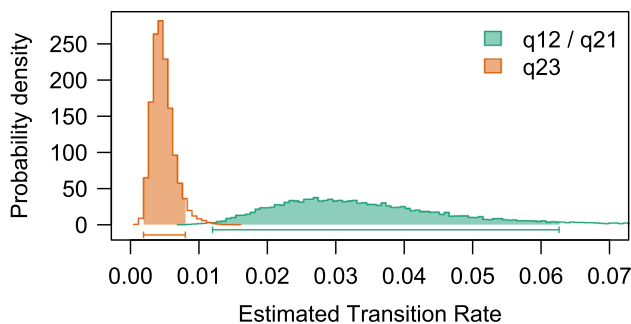
Fig. 3 The posterior probability distribution of transition rates in Bourke's symmetric bifurcation model. The transition rate from the medium size category to the large category (q_{23}) is significantly smaller than the transition rate between the small size category and the medium bin (q_{12}/q_{21}). Note that the transition rate constrained to be symmetric (q_{12}/q_{21}) has a wide spread, indicating that the actual rates might not be exactly equal

3.06×10^8 (in *Formica yessensis*). Average genus estimates ranged from 4.5 (in *Protomognathus*) to 3.0×10^6 (in *Dorylus*). After binning our average colony size estimate for each genus into small (<100 individuals per average colony), medium (between 100 and 10,000), and large (over 10,000) categories, the bins contained 46, 51, and 19 genera for analysis, respectively.

Phylogenetic comparative methods

The phylogeny we used representing 118 ant genera, along with genus-based average colony sizes and ancestral state reconstructions, is shown in Fig. 4. Our ASR from the most successful model infers a medium-sized average colony at the root of the ant phylogeny. Likewise, internal nodes were dominated by high probabilities of the medium size category. We interpret this as a result of our inability to sample the extinct, basal genera that would presumably reveal a small ancestral colony size. Additionally, it is likely that sociometric data on small ant societies is under-represented in the literature (Dornhaus et al. 2012).

Considering the various evolutionary hypotheses, the symmetric versions of each model, when such versions were applicable, consistently produced lower AIC scores than their higher-parameter counterparts. This is not unexpected, given that previous studies have found the number of estimated parameters to strongly affect the reliability of model fitting (de Vos et al. 2014). Results are shown in Table 1, including an additional "minimal model" in which all transition rates are constrained to be equal. Noticeably, of the top four models, three are threshold-based.

Bourke's symmetric bifurcation model (S ↔ M → L) had the lowest AIC score at 1332.84, closely followed by the symmetric version of the standard threshold model (L ← S ↔ M → L) at 1334.86 (ΔAIC = 2.02). As
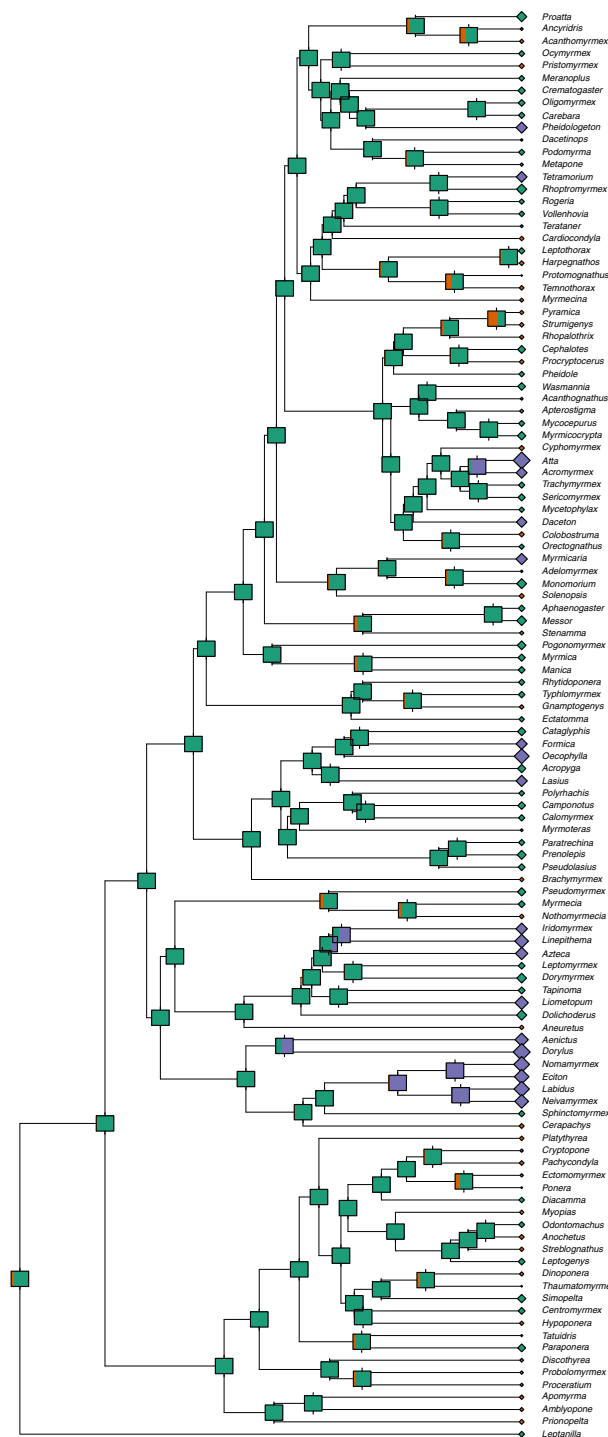

Fig. 4 Ant phylogeny including colony size data and ancestral state reconstruction. Tip decorations are proportional to the logged average genus colony *size*, and *colors* indicate binned size category. *Brown* marks the small size category, *green* the medium, and *purple* the largest

Burnham and Anderson (2004) suggest, ΔAIC values of approximately two or less indicate substantial support. It is also worthy to note that these two highest-ranking models

very closely resemble one another in terms of parameter values. The additional transition rate constrained to zero in Bourke's bifurcation model—the transition from small colonies directly to large—is also incredibly low in the standard threshold model when it is allowed to vary freely. Even the asymmetric version of the standard model exhibits the same pattern.

The posterior probability distributions estimating rates for Bourke's symmetric bifurcation model are shown in Figs. 2 and 3. The medium size category has the highest speciation rate, followed by the large and small categories, respectively, although the 95 % confidence intervals of the distributions overlap. However, the symmetric transition rate between small and medium colony sizes (S ↔ M) is clearly significantly larger than the rate going from medium to large sizes (M → L). The spread of these two distributions is also noticeably different: we suspect the demanded symmetry may consolidate two rates that are deviate slightly in magnitude.

Discussion

To investigate the evolution of colony size across the ants, we leveraged data on colony size from the scientific literature and a nearly complete genus-level ant phylogeny. We then tested several models for the evolution of colony size across the ants in a phylogenetically controlled analysis. The similarity between the two best-fit models—Bourke's symmetric bifurcation model (S ↔ M → L) and the standard symmetric threshold model (L ← S ↔ M → L)—tells a particular story: on a macroevolutionary scale, average colony size rarely jumps from a small to large size without first transitioning through an intermediate size. This suggests that multiple traits of smaller effect contribute to the overall colony size, or that large, punctuated colony size shifts rarely occurred. This kind of pattern has also been observed in allodapine bees, where changes in colony sizes are the result of small, incremental "tinkerings" (Dew et al. 2012).

More obviously, the low AIC scores for the threshold models suggest that there is some sort of critical point in terms of colony size for ants; on an evolutionary scale, once the colony becomes large enough, it rarely decreases in size. This theory was first proposed by Bourke (1999). Along with the many correlates of colony size in ants—such as hunting strategies, degrees of polyethism, etc.—Bourke (1999) noted several social features, which can form an evolutionary feedback loop. Specifically, a large colony size decreases workers' relative reproductive potential, which enables the queen to further specialize as a purely reproductive individual, allowing the colony size to grow further. Lower worker reproductive competition also relaxes the

selective constraints on permissible worker morphologies, increasing the degree of polymorphism and specialization. The newly increased efficiency resulting from this specialization can lead to an increase in colony size as well. Bourke (1999) claims that two islands of stability exist, the first in which ecological pressures—such as limited nesting resources, short growing seasons, or the competitive advantage of reproducing earlier at the expense of colony size—promote the evolution of small colonies composed of monomorphic workers with higher individual reproductive potential. The second island consists of the mutually stable, coevolved "socially complex" traits detailed above. The mathematics developed by Gautrais et al. (2002) for social insects corroborate this theory, describing a bifurcation phenomenon in their models that generates similar patterns: specializations only occur after the colony size passes some critical threshold. Our analysis further confirms such patterns across ant genera.

These theories also explain the evolutionary patterns in the previously mentioned allodapine bees. Dew et al. (2012) notes that most of the allodapine species have very small, monomorphic colonies with reproductive workers. One species, however, *Exoneurella tridentata*, seems to have left the island of stability associated with small colonies—presumably after escaping certain nesting constraints by inhabiting long-lasting substrates—and landed squarely in the second island, with exceptionally large colony sizes and discrete morphological worker and queen castes (Dew et al. 2012). Our results suggest such theories reflect biological reality on a larger scale: these ideas now have a firmer foundation when tested in a phylogenetic framework.

However, another prediction by Bourke (1999) could partly explain the possible upward trend in colony size: when colonies grow to sizes not previously seen in that lineage, the ecological niche for such a size is always vacant. Once these species find themselves without competitors, they stay there. Bourke adapted this argument from Bonner (1988), who presented it regarding body size in unitary organisms. Although this theory may apply to medium colony sizes and larger, the dismal fit of the irreversible growth model (L ← S → M → L) suggests that such a bias may be marginal, especially concerning transitions between small and medium sizes.

It should be noted that our results from such a large-scale analysis represent broad brush strokes: huge amounts of variance exist on almost every level of our analysis due to data that is both missing and naturally variable. First, our study suffers from the lack of a species-level phylogeny for the ants and the limited number of detailed colony size studies that have been conducted for most species. We would like to echo Anderson and McShea (2001), as well as Beckers et al. (1989) and others, in their plea for the release of more sociometric data for ants (and other organisms).

Although molecular phylogenies are progressing rapidly—gaining finer detail and greater reliability—hypotheses regarding the evolution of social complexity cannot be tested unless sociometric data for these genera or species is also published (Tschinkel 1991; Dornhaus et al. 2012). Already we have much more data on evolutionary relationships between ants than we do about their social ecology. Such sociometrics, even if unassociated with a formal publication, should be made public to aid comparative studies. In addition, there is a high degree of natural variation in the data gathered, which serves to highlight the fact that studies across geographic distributions and seasons are critical. For example, within a single ant colony, seasonal variation in colony size can span an order of magnitude (Laskis and Tschinkel 2009). Compounded by differences between colonies and environments, size can span even greater degrees of variation within a species. Even within a genus, the differences can be staggering: *F. yessensis* has reported colony sizes approximately 5.8 orders of magnitude larger than *Formica fusca* colonies. However, such natural variation does not preclude the study of macroevolutionary patterns in colony size; if anything, it further highlights the necessity of such work.

The mechanisms that exert selection pressure on colony size are still not completely understood. Although larger colonies have been found to outperform smaller colonies in difficult tasks such as nest choice (Sasaki et al. 2013), recent theoretical studies suggest that small groups are better decision-makers in complex environments (Kao and Couzin 2014). However, this situation is complicated further by the large number of traits that are correlated with colony size in ants and other social insects. Future studies—in addition to acquiring more data on colony size—should incorporate and analyze these traits, such as degree of polygyny, morphological skew, polydomy, polymorphism, individual worker reproductive potential, and division of labor, in a phylogenetic context to control for shared evolutionary history. Such efforts could tease apart the causal factors associated with colony size change and shine light on the optimal group size debate.

Although our analysis represents an initial investigation into colony size evolution across the ants, such work is already proving informative. Our best models reflect and bolster theories already present in studies of eusociality. Andrew Bourke's theorized islands of stability in colony size evolution (1999) seem to be upheld: colony sizes often change slowly along a continuum, yet after crossing a certain threshold in size, a feedback loop forms and decreases seem no longer feasible.

References

Abbot P, Abe J, Alcock J et al (2011) Inclusive fitness theory and eusociality. Nature 471:E1–E4. doi:10.1038/nature09831

Anderson C, McShea DW (2001) Individual versus social complexity, with particular reference to ant colonies. Biol Rev Camb Philos Soc 76:S1464793101005656. doi:10.1017/S1464793101005656

Beckers R, Goss S, Deneubourg JL, Pasteels JM (1989) Colony Size, communication and ant foraging strategy. Psyche A J Entomol 96:239–256. doi:10.1155/1989/94279

Bolton B (2013) An online catalog of the ants of the world. http://antcat.org. Accessed 1 Jan 2013

Bonner JT (1988) The evolution of complexity by means of natural selection. Princeton University Press, Princeton

Bourke AFG (1999) Colony size, social complexity and reproductive conflict in social insects. J Evolut Biol 12:245–257. doi:10.1046/j.1420-9101.1999.00028.x

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Brady SG, Schultz TR, Fisher BL, Ward PS (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. Proc Natl Acad Sci 103:18172–18177. doi:10.1073/pnas.0605858103

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304. doi:10.1177/0049124104268644

Crozier RH, Pamilo P (1996) Evolution of social insect colonies: sex allocation and kin selection. Oxford University Press, Oxford

de Vos JM, Hughes CE, Schneeweiss GM et al (2014) Heterostyly accelerates diversification via reduced extinction in primroses. Proc Biol Sci 281:20140075. doi:10.1098/rspb.2014.0075

Dew RM, Rehan SM, Tierney SM et al (2012) A single origin of large colony size in allodapine bees suggests a threshold event among 50 million years of evolutionary tinkering. Insectes Soc 59:207–214. doi:10.1007/s00040-011-0206-6

Dornhaus A, Powell S, Bengston S (2012) Group size and its effects on collective organization. Annu Rev Entomol 57:123–141. doi:10.1146/annurev-ento-120710-100604

FitzJohn RG (2012) Diversitree: comparative phylogenetic analyses of diversification in R. Methods Ecol Evol 3:1084–1092. doi:10.1111/j.2041-210X.2012.00234.x

FitzJohn RG, Maddison WP, Otto SP (2009) Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. Syst Biol 58:595–611. doi:10.1093/sysbio/syp067

Gautrais J, Theraulaz G, Deneubourg J-L, Anderson C (2002) Emergent polyethism as a consequence of increased colony size in insect societies. J Theor Biol 215:363–373. doi:10.1006/jtbi.2001.2506

Hölldobler B, Wilson EO (1990) The ants. Belknap Press of Harvard University Press, Cambridge

Hou C, Kaspari M, Vander Zanden HB, Gillooly JF (2010) Energetic basis of colonial living in social insects. Proc Natl Acad Sci USA 107:3634–3638. doi:10.1073/pnas.0908071107

Hughes WOH, Oldroyd BP, Beekman M, Ratnieks FLW (2008) Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science 320:1213–1216. doi:10.1126/science.1156108

Kao AB, Couzin ID (2014) Decision accuracy in complex environments is often maximized by small group sizes. Proc Biol Sci 281:20133305. doi:10.1098/rspb.2013.3305

Kaspari M, Vargo EL (1995) Colony size as a buffer against seasonality: Bergmann's rule in social insects. Am Nat 145:610. doi:10.1086/285758

Koh LP, Sodhi NS, Brook BW (2004) Ecological correlates of extinction proneness in tropical butterflies. Conserv Biol 18:1571–1578. doi:10.1111/j.1523-1739.2004.00468.x

Kramer BH, Schaible R (2013) Colony size explains the lifespan differences between queens and workers in eusocial Hymenoptera. Biol J Linn Soc 109:710–724. doi:10.1111/bij.12072

Laskis KO, Tschinkel WR (2009) The seasonal natural history of the ant, *Dolichoderus mariaes*, in northern Florida. J Insect Sci 9:1–26. doi:10.1673/031.009.0201

Lucky A, Trautwein MD, Guénard BS et al (2013) Tracing the rise of ants-out of the ground. PLoS ONE 8:e84012. doi:10.1371/journal.pone.0084012

Maddison WP, Maddison DR (2011) Mesquite 2.75: a modular system for evolutionary analysis. http://www.mesquiteproject.org

Maliska ME, Pennell MW, Swalla BJ (2013) Developmental mode influences diversification in ascidians. Biol Lett 9:20130068. doi:10.1098/rsbl.2013.0068

Moreau CS, Bell CD (2013) Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. Evolution (N Y) 67:2240–2257. doi:10.1111/evo.12105

Moreau CS, Bell CD, Vila R et al (2006) Phylogeny of the ants: diversification in the age of angiosperms. Science 312:101–104. doi:10.1126/science.1124891

Nowak MA, Tarnita CE, Wilson EO (2010) The evolution of eusociality. Nature 466:1057–1062. doi:10.1038/nature09205

Oliver TH, Leather SR, Cook JM (2008) Macroevolutionary patterns in the origin of mutualisms involving ants. J Evolut Biol 21:1597–1608. doi:10.1111/j.1420-9101.2008.01600.x

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Sasaki T, Granovskiy B, Mann RP et al (2013) Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. Proc Natl Acad Sci 110:13769–13773. doi:10.1073/pnas.1304917110

Schmidt C (2013) Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). Zootaxa 3647:201–250. doi:10.11646/zootaxa.3647.2.1

R Core Development Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Tschinkel WR (1991) Insect sociometry, a field in search of data. Insectes Soc 38:77–82. doi:10.1007/BF01242715

Tukey JW, McLaughlin DH (1963) Less vulnerable confidence and significance procedures for location based on a single sample: trimming/winsorization 1. Indian J Stat 25:331–352

van Wilgenburg E, Torres CW, Tsutsui ND (2010) The global expansion of a single ant supercolony. Evolut Appl 3:136–143. doi:10.1111/j.1752-4571.2009.00114.x

Ward PS, Brady SG, Fisher BL, Schultz TR (2015) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Syst Entomol 40:61–81. doi:10.1111/syen.12090

Wilson EO (1971) The insect societies. Belknap Press of Harvard University Press, Cambridge, Massachusetts

Wilson EO (2008) One giant leap: how insects achieved altruism and colonial life. Bioscience 58:17–25. doi:10.1641/B580106