

SYMPOSIUM

“Simple” Biomechanical Model for Ants Reveals How Correlated Evolution among Body Segments Minimizes Variation in Center of Mass as Heads Get Larger

Philip S. L. Anderson ^{1,1,2,3} Michael D. Rivera,² and Andrew V. Suarez^{1,2,3,4}

¹Department of Evolution, Ecology and Behavior, University of Illinois, Urbana-Champaign, IL, USA; ²Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana-Champaign, IL, USA; ³Beckman Institute for Science and Technology, University of Illinois, Urbana-Champaign, IL, USA; ⁴Department of Entomology, University of Illinois, Urbana-Champaign, IL, USA

From the symposium “Melding Modeling and Morphology: Integrating Approaches To Understand The Evolution Of Form And Function” presented at the annual meeting of the Society for Integrative and Comparative Biology January 3–7, 2020 at Austin, Texas.

¹E-mail: andersps@illinois.edu

Synopsis The field of comparative biomechanics strives to understand the diversity of the biological world through the lens of physics. To accomplish this, researchers apply a variety of modeling approaches to explore the evolution of form and function ranging from basic lever models to intricate computer simulations. While advances in technology have allowed for increasing model complexity, insight can still be gained through the use of low-parameter “simple” models. All models, regardless of complexity, are simplifications of reality and must make assumptions; “simple” models just make more assumptions than complex ones. However, “simple” models have several advantages. They allow individual parameters to be isolated and tested systematically, can be made applicable to a wide range of organisms and make good starting points for comparative studies, allowing for complexity to be added as needed. To illustrate these ideas, we perform a case study on body form and center of mass stability in ants. Ants show a wide diversity of body forms, particularly in terms of the relative size of the head, petiole(s), and gaster (the latter two make-up the segments of the abdomen not fused to thorax in hymenopterans). We use a “simple” model to explore whether balance issues pertaining to the center of mass influence patterns of segment expansion across major ant clades. Results from phylogenetic comparative methods imply that the location of the center of mass in an ant’s body is under stabilizing selection, constraining the center of mass to the middle segment (thorax) over the legs. This is potentially maintained by correlated rates of evolution between the head and gaster on either end. While these patterns arise from a model that makes several assumptions/simplifications relating to shape and materials, they still offer intriguing insights into the body plan of ants across ~68% of their diversity. The results from our case study illustrate how “simple,” low-parameter models both highlight fundamental biomechanical trends and aid in crystalizing specific questions and hypotheses for more complex models to address.

Introduction

Biological systems, be they genetic, organismal, ecological, or evolutionary, are inherently complex, comprised of multiple interdependent variables with nonlinear relationships to each other (Anderson et al. 2011b). The “complex” nature of these systems makes them prohibitively difficult to analyze in their entirety, that is, taking all potential

variables into account. Herein lies the power of biological models. As virtual reproductions of natural systems, models allow for complex systems to be compartmentalized and analyzed more easily. Models are employed at all levels of biology including such diverse areas as gene transfer (Suchard 2005; Nazarian et al. 2018), animal locomotion (Miller et al. 2012), and character evolution across

lineages (Butler and King 2004). The one uniting aspect of these models is that they are not literal replications of reality, but simplifications of the systems being studied. Since all models are simplifications, they must make assumptions to reduce the number of variables accounted for. Therein lies a fundamental trade-off in model construction: more assumptions result in fewer variables and reduced model complexity, making analyses easier. However, additional assumptions also result in models moving further away from the biological reality under study. While it would seem advantageous to always construct models that are as realistic as possible, even “simple” models can be extremely valuable for exploring biological systems.

The Melding Modeling and Morphology symposium at SICB 2020 and associated manuscripts collected in this volume focus on models exploring the relationship between morphology and function. These are primarily biomechanical models, which aim to understand biology through the lens of physics and mechanics. The field of biomechanics has a long history of modeling biological processes based on physical principles ranging in complexity from simple lever models (Barel 1983; Westneat 1995; Davis et al. 2010) to complex multi-body dynamic models (Curtis et al. 2008; Shi et al. 2012; Watson et al. 2014). For our contribution to this symposium, we start with a brief description of “simple” models and their advantages to biological study. We then apply a “simple” model of the center of mass to ants (Hymenoptera: Formicidae) to explore functional consequences of the evolution of head expansion across the clade.

“Simple” models

The term simple has a lot of connotations and is often used to denote something that is lacking or shallow. To avoid this bias, we use a very specific definition of simple for our purposes—to reduce complexity for clarity and for ease of understanding (e.g., to simplify). Models are comprised of parameters, aspects of the system that are directly accounted for in the model as variables/constants. All aspects of the biology of a system that are not accounted for are either assumed to remain at some unspecified constant, or are removed entirely. For example, the vertebrate jaw can be modeled as a simple third-order lever. Levers, mechanisms that transfer force using a stiff beam rotating around a fulcrum, have long been used to model the transfer of force and motion around biological joints (Archimedes, Third Century BC). Parameters in the

jaw model include the length from the muscle attachment to the joint (inlever) and the joint to the teeth (outlever). The ratio of these values gives a measure of force transmission along the jaw called mechanical advantage (Barel 1983; Westneat 1995). Other aspects of jaw shape such as its thickness or curvature are assumed to be constant/nonexistent and removed from the model. In effect, the more parameters that are accounted for in the model, the more “complex” the model is. Alternatively, a “simple” model is one in which few parameters are included and the system is highly abstracted through the reduction of parameters. The lever model for a jaw is fairly simple as it excludes shape outside of basic length measures. The model can be made more complex by adding more aspects of the biological system, such as including muscle angles to allow for a more biologically accurate measure of mechanical advantage (Westneat 2003), but requires more knowledge of the system. We will use “simple” and “complex” as shorthand throughout the article for the relative number of parameters accounted for by a model.

Advantages of “simple” models

While the advantages for adding complexity to a biomechanical model are intuitive (e.g., closer approximation of the natural world, accounting for more variation), the advantages to simplifying a model may be less clear. One common use for a model is to isolate the effects of different parameters. Often, these involve sensitivity analyses, where the effects of varying parameters on output variables are tested and compared (e.g., Baumgart and Anderson 2018; Ilton et al. 2018; Hamlet et al. 2020). This is a strength of modeling, as parameters not being tested directly can be held constant, so that the effects of variation in those parameters are effectively negated. Many parameters that can be modeled are often not of interest to the researcher, so removing them from the model is the most efficient way to keep them constant across analyses. This idea is ubiquitous in engineering, where a common principle of design is Keep It Simple, Stupid (KISS). Originally attributed to aircraft engineer Kelly Johnson of Lockheed Skunk Works (Rich 1995, 13), KISS postulates that mechanical designs should exclude unnecessary/extraneous elements. This carries over into building models: focus on parameters that matter and simplify/remove parameters that are not of interest.

Simplifying a biological system to isolate variables of interest is a common feature of finite element

analyses (FEA; Clough 1960; Zienkiewicz et al. 2005, 733; Rayfield 2007). FEA is a technique where virtual loads are applied to a digital model of a real-world structure to estimate how that structure may react under stress. These “digital models” can be derived from X-ray/surface scans of the real structure, or created virtually within the program. FEA is often used to model complex morphologies (such as entire vertebrate skulls; e.g., Dumont et al. 2005, 2011), however, simpler models can be applied to a single morphological parameter of interest while the rest of the structure is left generalized. For example, Anderson et al. (2011a) created basic cone models to stand in for mammal teeth in an FEA to describe the specific effects on adding a cingulum to the base without worrying about changes to the rest of the tooth. Similarly, durophagous teeth have been modeled as modified cones, varying a couple parameters to create a range of tooth shapes for both experimental and theoretical analyses (Crofts and Summers 2014; Crofts 2015). These studies both simplify a morphological model in order to isolate one parameter of interest to be examined within a relatively complex structure.

Another advantage of simple biomechanical models is that they can be broadly applied to a variety of organisms, while complex models often reflect specific systems. Ilton et al. (2018) recently developed a broad biomechanical model simulating the basic components of a latch mediated spring system. This “toy model” as the authors call it contains the basic components of a system that can store and release mechanical energy: a spring, a muscle to load the spring, a latch that holds the spring in place, and a projectile that is launched by the spring during release. These few parameters allow this model to potentially simulate any number of latch and spring biological systems, from jumping in frogs and grasshoppers, the power amplified strikes of mantis shrimp and trap jaw ants, and the mechanisms driving suction feeding in pipefishes and bladderworts (Longo et al. 2019). Furthermore, this model allows researchers to investigate the effects of particular parameters (such as spring mass and latch shape) on output variables including launch speed and force (Ilton et al. 2018). Simple models such as this offer opportunities for examining fundamental physical rules governing a diverse array of mechanical systems.

Broadly applicable models also allow researchers to explore the interaction of biomechanical principles with evolution. One such example is the four-bar linkage mechanism that has been used to model function in systems as varied as the jaws of both

extant and extinct fishes (Westneat 1990; Anderson and Westneat 2007), and the raptorial strikes in crustaceans (Patek et al. 2007). The wide applicability of these four-bar models has allowed the evolution of these systems to be explored to identify major trends within groups (Wainwright 2007; Anderson and Patek 2015) as well as comparing evolutionary patterns between them (Hu et al. 2017; Muñoz et al. 2018).

Finally, simple models generally require fewer computational resources and less time to develop and analyze. Ideally, such logistical issues would not be a concern. However, it is often not efficient to spend time and resources on a model that may not work or produce meaningful results. Simple models, in this case, can generate preliminary data or provide good approximations for a new system, allowing a test of whether the system is appropriate for the questions of interest. Once this has been established, additional time and resources can be devoted to constructing more complex models that are tailored to test specific hypotheses.

To further illustrate these advantages, we devote the rest of this article to a case study on determining the center of mass in ants. The specific model used has few parameters, reducing the body of an ant to a linear series of connected ellipsoids. Although this removes a great deal of morphological detail, this simplification allows us to include measurements of interest for over 68% of ant generic diversity. The results of this case study give insight into evolutionary trends in ant body proportions that could be expanded upon with more sophisticated models in the future.

Case study: Center of mass in ants

Ant species exhibit remarkable variation in head shape and size, reflecting their varied ecology and evolutionary histories (Fig. 1). In addition, many species exhibit pronounced intraspecific variation where worker variation exceeds worker-queen dimorphism. Across roughly 14,000 described species of ants, 13% have evolved a morphologically variable worker caste (Wills et al. 2018). In species where worker morphology varies allometrically, the head is often exaggerated in size resulting in castes often referred to as majors and minors (Wilson 1953, see discussion in Peeters 2019; Fig. 1). The additional head volume is primarily filled with muscle allowing big-headed ants to perform specialized tasks like seed-milling, resource processing, and nest defense (Powell 2008; Tschinkel and Kwapich 2016). While variation in head to body size ratio among workers

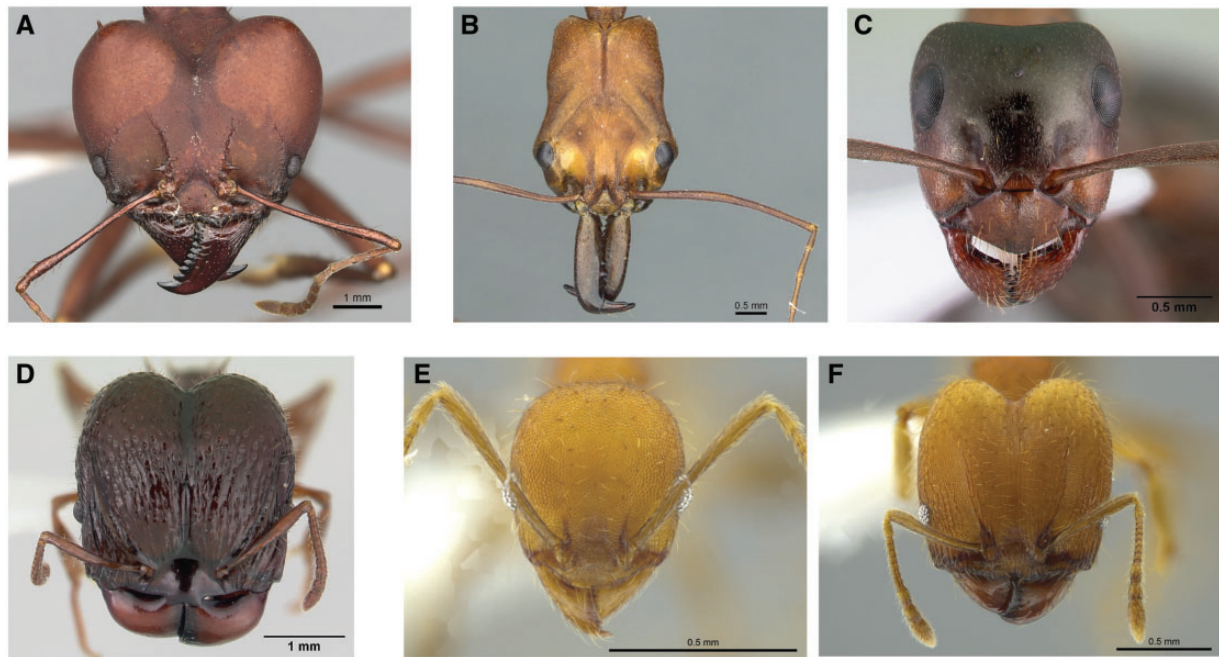


Fig. 1 Diversity of ant heads. (A) *Atta robusta*, ID # CASENT028178 (photo by Shannon Hartman). Scale bar = 1 mm. (B) *Odontomachus schoedli*, ID# CASENT0915898 (Photo by Anna Pal). Scale bar = 0.5 mm. (C) *Formica ulkei*, ID #CASENT0179860 (Photo by Erin Prado). Scale bar = 0.5 mm. (D) *Acanthomyrmex ferox*, ID#CASENT0178570 (Photo by April Nobile). Scale bar = 1 mm. Some species have variation in head size and shape between castes, such as *Pheidole anastasio*. (E) *Pheidole anastasio* minor (ID# CASENT0619900, Photo by Jeremy Pillow). Scale bar = 0.5 mm. (F) *Pheidole anastasio* major (ID# CASENT0613680, Photo by Jeremy Pillow). Scale bar = 0.5 mm. All photos are from antweb.org.

within a colony can be significant, affecting a number of functions (Burd 2000; Powell 2008), body size and shape are evolutionarily labile traits (Pie and Tschá 2013; Blanchard and Moreau 2016; Wills et al. 2018).

The variation in head size relative to body size across ant lineages raises two related questions: How do big-headed ants keep from tipping forward? How much variation is there in ants' center of mass (the point around which a body is balanced)? An ant's legs are attached to the thorax, subsequently ants with larger heads risk shifting the center of mass anterior to these supports (Fig. 2A). An increase in head mass is offset, in part, by an enlarged prothorax segment housing neck muscles that allow ants to support their head even when carrying prey items many times their weight (Keller et al. 2014). However, larger heads still pull the overall center of mass of the ant forward. This may pose a constraint on relative head size; a large enough head could result in the center of mass being in the head itself, anterior to the supporting legs, leading to instability. While some groups may circumvent this, for example, by having large-headed castes act as relatively sedentary seed mills (Wilson 1984; Tschinkel and

Kwapich 2016), most ant species need to maintain balance over the legs restricting relative head size.

The hypothesis of center of mass causing constraint on head size assumes that head size is all that influences the position of the center of mass. However, there is a great deal of variation among ant abdomen size and shape as well. In Hymenoptera (ants, bees, wasps, etc.), the first abdominal segment is fused to the thorax and are collectively called the mesosoma. The second, and in some taxa third, abdominal segments are constricted into scale-like petiole(s). The remaining segments are referred to as the "gaster" (Fig. 3; Hölldobler and Wilson 1990). Here, we refer to the petiole and gaster separately as we treat them separately in our analyses. The gaster, if expanded, will pull the center of mass in the posterior direction, potentially counterbalancing head expansion and allowing for greater expansion of each. All of this is purely hypothetical mechanics of a segmented body. As biologists and biomechanists, we are interested in how the relationship between body segments plays out across the evolution of ants.

In order to begin to explore these questions, we apply a simple (i.e., relatively low-parameter) model

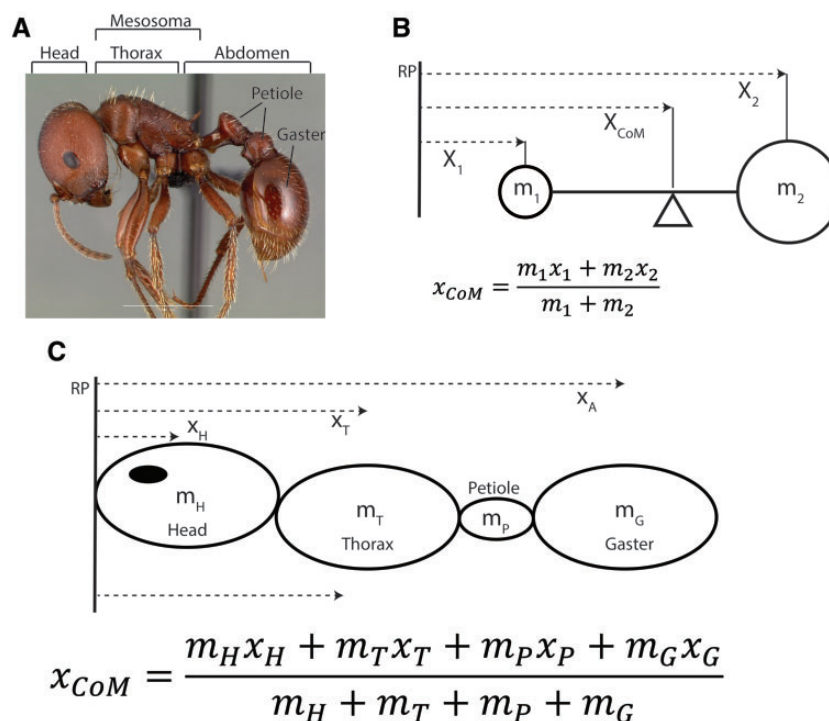


Fig. 2 Model for locating the anterior-posterior position of the CoM in a segmented morphology. **(A)** Image of *P. barbatus*, ID# CASENT0006306 (Photo by April Nobile, taken from antweb.org). Scale bar = 2 mm. **(B)** Basic model for position of the CoM between two distinct masses. Variables are: X = distance from some reference point; m = mass of a segment. **(C)** The CoM model applied to a simplified version of an ant body (same variables as in A). The segments are reduced to regular ellipsoids based on maximum length, depth, and width measures from the photographs.

for calculating the anterior-posterior location of the center of mass (CoM hereafter) to a diverse set of ant genera. Our goal is to examine how the location of the CoM varies across the clade in relation to relative segment sizes. We use the parameters of our CoM model in a series of phylogenetic comparative methods to test the following: (1) Is the evolution of CoM correlated to the evolution of head expansion alone or the relative size of multiple segments? (2) What is the rate of evolution of CoM and how does it compare to the rate of evolution of head, petiole, and gaster size? We predict that CoM is under stabilizing selection, and therefore will show lower rates of evolution. (3) Finally, are there correlated shifts between CoM and head expansion? We address these questions both across ant genera and across a selection of species within the genus *Pheidole*. We chose this genus as nearly all *Pheidole* species have two discrete worker castes (majors/minors) that vary in head size.

Methods

Simple model of the center of mass for an ant body

The first step for our modeling study is to identify the main biomechanical parameters(s) we are

interested in. The CoM of an object represents the point at which a linear force acting upon the object will result in a linear acceleration without rotation. This is also the point upon which an object is balanced (center of balance). We expect that in a segmented body, like that of an ant, the anterior-posterior location of the CoM should be above the legs (e.g., the support structures). This position helps the body stay balanced. Next, we identify how we can measure this parameter in our system. There is a simple equation that dictates the CoM for a series of connected masses in a line (Fig. 2B). This equation deals with location in a single dimension, but illustrates how the arrangement of masses along this vector will influence the location of the CoM. We use this equation to estimate the anterior-posterior location of the CoM across ant taxa.

To apply the CoM equation to our ants, we must make several assumptions (Fig. 2C). We treat the segments of the ant body—head, thorax, petiole, and gaster—as discrete segments along a single vector, ignoring variation in the dorso-ventral or lateral placement of the segments relative to each other. To estimate mass for each segment, we assumed a density of 1 kg/m^3 so that we can equate volume to mass (but see below). We then estimated the volume of

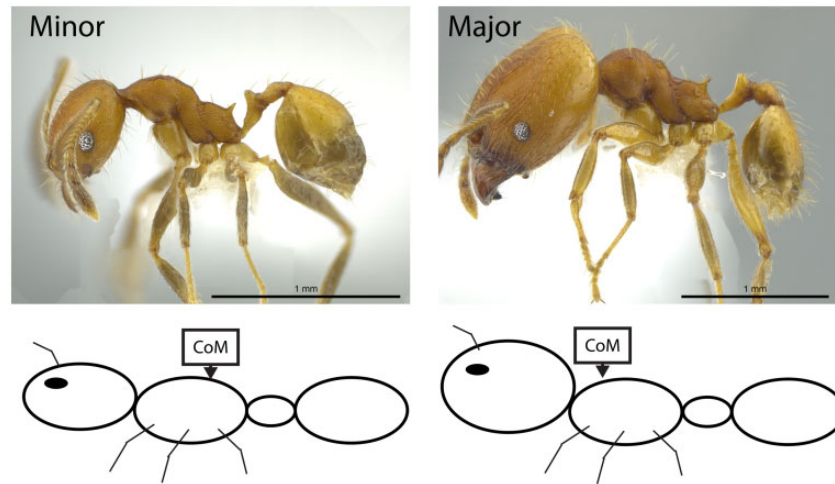


Fig. 3 Simplification of the minor and major caste workers of *P. anastasioi*. Images show the difference in relative head size between minor (ID# CASENT0619900, Photo by Jeremy Pillow) and major (ID# CASENT0613680, Photo by Jeremy Pillow) castes. Both scale bars = 1 mm. The schematic drawings illustrate the hypothesis that an expansion of the head should result in an anterior shift in the position of the CoM as calculated in our model. All photos are from antweb.org.

each segment by measuring its length, height, and width from photographs. As the relative orientation of the various segments will vary between specimens, we measured each segment individually. For the head, we measured the maximum length from the clypeus (excluding the mandibles) to the occipital margin, the maximum width including eyes and the maximum depth. For the remaining segments, we measured the maximum anterior-posterior length between attachment points and then the maximum width and depth along those lengths. Note that these length measures may not be homologous across taxa as the goal was not to identify homologous measures, but estimate overall volume of each segment for each taxon.

These measurements were used to calculate the volume of an ellipsoid which is used as a proxy for mass. To measure the length between segments, we assumed the segments would be lined up end to end along the anterior-posterior axis of the segments with no spaces between them and a reference point placed at the front end of the head. The length to each segment is treated as the sum of lengths of the segments (assuming no space between segments). [Figure 2](#) shows these simplifications, illustrating how we are modeling the ants for this case study. All measurements were taken in ImageJ ([Schneider et al. 2012](#)).

Using the equation in [Fig. 2C](#), we calculated the CoM along the ant body. As the ant taxa examined here span multiple orders of magnitude in body size, we normalized the distance from the reference point to the CoM by overall body length. This gives us a measure of relative CoM which is reported as a

percentage of body length. Note that with this relative measure, the lower the number, the closer the CoM is to the head. Similarly, to capture relative expansion of the head and abdomen, the estimated mass of the head, petiole, and gaster was divided by overall mass. These numbers capture how expanded these segments are relative to the rest of the body. Finally, we compare our various parameters (relative segment mass and CoM) in a phylogenetic context to understand how CoM evolves in relation to variation in segment size across the body.

To examine the effects of our density assumption, we collected density data from one ant species to convert our volumes into actual mass estimates. We measured the mass of heads, thoraxes, and abdomens of nine dried specimens of *Pogonomyrmex rugosus* using a UMX2 microbalance (Mettler-Toledo, Leicester, UK). The segments were then imaged and measured using a Leica M205 C stereomicroscope. Volume was estimated using linear measurements; the head and abdomen assumed to be spheres and the thorax an ellipsoid.

Taxa selection

All ant images used for the project were sourced from AntWeb (antweb.org), an online repository of photographs of museum specimens maintained by Brian Fisher at the California Academy of Sciences. All specimens had at least three images available: front view of the head, lateral view of the whole body, and dorsal view of the whole body. These three views allowed for length, width, and height measurements to be taken of the head, thorax,

petiole, and gaster. We collected measurements for two distinct datasets. The first is a genus level dataset consisting of 231 genera (68% of all ant genera). One representative species was used for each genus with one individual used per species. The selection for species was based on both availability as well as size (the largest species available was generally used). For the phylogenetic analyses, we used the genus-level phylogeny of [Blanchard and Moreau \(2016\)](#). The second is a species level analysis of the genus *Pheidole*. *Pheidole* is known for having multiple worker castes including majors with greatly expanded heads ([Fig. 3](#)). For this latter analysis, we chose 98 *Pheidole* species that were included in the phylogeny of [Moreau \(2008\)](#), and selected one minor and one major specimen per species. Specimens were selected for both analyses based on relative lack of deformation, which is particularly key for the gaster which can be highly extended/variable in shape even within a colony based on age or other factors ([Tschinkel 2013](#)). A full list of specimens used and associated metadata can be found in Appendix ([Supplementary Table S1](#)).

Phylogenetic analyses

To assess evolutionary relationships among the parameters of our CoM model, we performed phylogenetic least-squares regression (PGLS) using the R package CAPER v. 0.2 ([Orme et al. 2012](#)). PGLS is a common method for comparing evolutionary covariation between traits ([Pagel 1997](#)). For these analyses, delta (change in rate of evolution) and kappa (gradual vs. punctuated evolution) were fixed at one whereas lambda (phylogenetic signal) was estimated using maximum-likelihood methods. Estimating lambda allows the model to deviate from a strict Brownian motion (random-walk) model of evolution. The PGLS models were used to measure strength of correlation between CoM and the relative sizes of the head, petiole, and gaster segments. As PGLS is a linear regression analysis, it assumes normal distributions for variables tested. We tested all variables for normality using Shapiro tests and log-transformed any variables that deviated from normality. The Akaike Information Criterion (AIC) was used to assess which independent parameters (head, petiole, and gaster masses) or combination of parameters had the strongest correlation with the evolution of CoM.

To assess the relative rate of evolution of the CoM and segment masses, we estimated and compared their Brownian Motion (BM) rate parameter (s^2) using a likelihood ratio test. Specifically, we

compared the likelihood of a model in which s^2 varied among parameters to one in which the rates were constrained to be equal ([Adams 2013](#)). Because all of the parameters are treated as percentages (either percent length or percent of overall mass), they have the same scale of variation (0–1). Therefore, differences in evolutionary rates represent the amount of relative change in proportion to the mean and can be statistically compared ([O'Meara et al. 2006](#); [Ackerly 2009](#); [Adams 2013](#)). We bounded our estimates of s^2 using a 95% confidence interval derived from the standard errors of evolutionary rate. We calculated standard errors from the square root diagonals of the inverse Hessian matrix, using code provided by M. Munoz originally written by D. Adams. To determine whether evolutionary rates were distinct between parameters, we fitted two models to our data: 1) where evolutionary rates of CoM and masses were constrained to be equal and 2) where evolutionary rates were free to vary among the parameters. These models were compared using likelihood ratio tests ([Adams 2013](#)). We also performed the same rate comparisons on every pairwise combination of parameters. As higher variance in a trait can artificially inflate its estimated evolutionary rate ([Ives et al. 2007](#); [Adams 2013](#)), and we expected there to be differences in variance between the traits, our evolutionary rate comparisons explicitly incorporate within-species measurement error using the `ms.err` option with the `compare rates` function ([Adams 2013](#)).

The above analyses were applied to both the genus-level and *Pheidole* datasets with one exception. For the *Pheidole* data, all analyses are done using parameters from the major and minor castes separately to see if there are differences in evolutionary patterns between castes ([Fig. 3](#)).

Results

Genus level analysis

Across all genera, plotting head length versus the CoM reveals the CoM for any given ant genus is located posterior to the head consistent with our stabilization assumption ([Fig. 4A](#)). Notably, all 231 ant genera fall above the line defined by the CoM being equal to head length (e.g., $y = x$); any ant below that line would have a CoM located in the head. [Figure 4B](#) shows the relationship between total body length and CoM. Here, the trend line drawn indicates the CoM laying at the anterior-posterior midpoint of the body (e.g., $y = 0.5x$). Most ants cluster fairly tightly around this line, indicating that most of

the CoM measured fall between 0.4 and 0.6 of total body length (Supplementary data).

The results of the PGLS analyses revealed that both head and gaster mass show significant evolutionary correlations with CoM (Table 1). However, the model that included both head and gaster masses was the best predictor of CoM position overall, illustrating that both of these segments show an evolutionary relationship with CoM. A slightly higher

likelihood is found if you also add petiole mass to this model. However, the amount of extra variance explained is minimal, and notably the petiole mass by itself does not correlate with CoM. PGLS based on a model that incorporates the density data shows essentially the same patterns of correlation except that the head by itself is a much better predictor of CoM than the gaster by itself (Table 2).

Figure 5 shows the estimated BM rate parameters for our variables from both the original model (open circles) and the model that incorporates density variation (filled circles). CoM shows an order of magnitude lower rate parameter than either the head or gaster expansion (as calculated from relative masses) in the initial model. When density is added, the gaster shows a reduced rate of evolution, but it is still higher for the CoM. The relative mass of the petiole shows a significantly lower rate parameter than the CoM in both models.

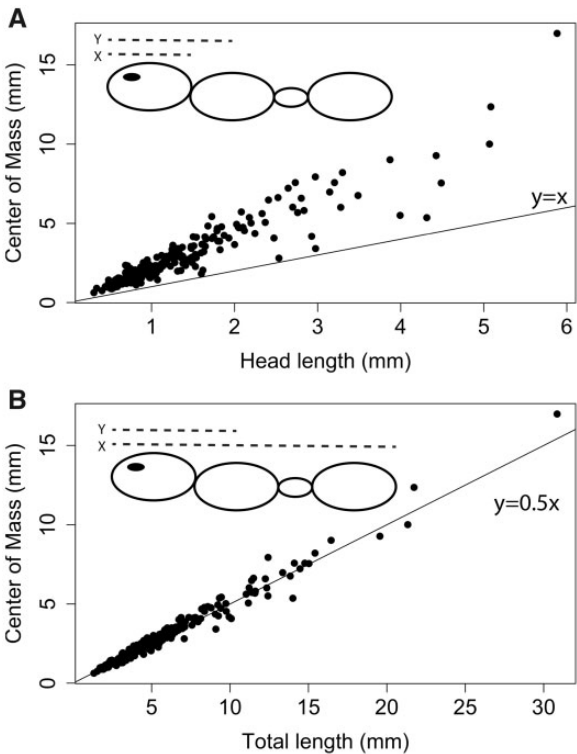


Fig. 4 Scatterplots of head length and body length versus the location of the CoM across ant genera. (A) Head length versus CoM. The line represents the boundary where any points below the line have the CoM located in the head segments. Notably, none of the ant genera falls below this line. (B) Total body length versus CoM with a line at $y=0.5x$. The ants cluster around the line representing the midpoint of the body, showing that CoM is fairly constrained to the middle of the body.

Pheidole

Similar to the genus level data, the vast majority of *Pheidole* species lie above the $x = y$ line in the head length versus CoM plot (Fig. 6). There is a distinct difference between the major and minor castes, with the minor castes lying much further from the line than the majors, indicating a general trend of majors having more anteriorly positioned CoM. Majors also show more scatter across the plot than the minors. A few majors also fall under the $x = y$ line, indicating a CoM located in the head. The body length versus CoM plot again shows a relatively tight clustering around the $y = 0.5x$ line, although primarily for the minors. The majors are almost entirely below that line, illustrating the apparent anterior shift in CoM from minor to major caste.

PGLS results for both majors and minors (Table 3) show the same pattern as in the genus level analysis. One difference is a significant evolutionary correlation between the petiole and CoM for the majors as well. The same patterns are seen in the

Table 1 Results from PGLS comparing relative segment masses versus the position of the CoM for the model that does not include density

| Model I | Lambda | Sig | R ² | Log lik | AIC | AICc |
|--------------------|--------|--------|----------------|---------|-----------|-----------|
| Log head size | 0.632 | <0.001 | 0.816 | 590.989 | −1177.977 | −1177.924 |
| Log petiole size | 0.316 | 0.394 | 0 | 399.305 | −794.609 | −794.557 |
| Log gaster size | 0.434 | <0.001 | 0.829 | 602.805 | −1201.61 | −1201.558 |
| Head + Petiole | 0.587 | <0.001 | 0.819 | 595.218 | −1182.437 | −1182.26 |
| Head + Gaster | 0.751 | <0.001 | 0.929 | 699.215 | −1390.43 | −1390.253 |
| Petiole + Gaster | 0.690 | <0.001 | 0.867 | 628.38 | −1248.761 | −1248.584 |
| All three segments | 0.857 | <0.001 | 0.935 | 705.62 | −1395.24 | −1394.592 |

AICc is AIC with a correction for small sample sizes.

Table 2 Results from PGLS comparing relative segment masses versus the position of the CoM for the model that includes density

| Model II | Lambda | Sig | R ² | Log lik | AIC | AICc |
|--------------------|--------|--------|----------------|---------|-----------|-----------|
| Log head size | 0.731 | <0.001 | 0.621 | 642.907 | -1281.814 | -1281.762 |
| Log petiole size | 0.480 | 0.11 | 0.007 | 535.767 | -1067.533 | -1067.48 |
| Log gaster size | 0.573 | <0.001 | 0.34 | 582.244 | -1160.489 | -1160.436 |
| Head + Petiole | 0.586 | <0.001 | 0.625 | 648.125 | -1288.249 | -1288.072 |
| Head + Gaster | 0.806 | <0.001 | 0.712 | 672.998 | -1337.996 | -1337.819 |
| Petiole + Gaster | 0.655 | <0.001 | 0.356 | 584.616 | -1161.233 | -1161.056 |
| All three segments | 0.705 | <0.001 | 0.71 | 677.442 | -1338.883 | -1338.234 |

AICc is AIC with a correction for small sample sizes.

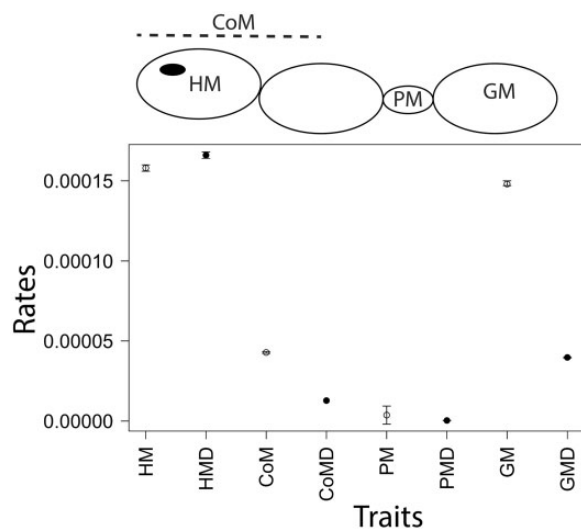


Fig. 5 Evolutionary rates for the genus level analysis of relative segment size and CoM traits (CoM, CoMD). For both the original model (open circles) and the model which incorporates density data (closed circles), CoM rates are much lower than either the relative mass of the head (HM, HMD) or gaster (GM, GMD) while higher than the relative mass of the petiole (PM, PMD). A “D” on the end of a trait name denotes that trait for the model that includes density. Error bars represent 95% confidence intervals.

model that incorporates density, with a strong correlation between the head and CoM relative to the other segments individually (Table 4).

Estimated rate parameters for the variables in both *Pheidole* castes are similar to the genus level analyses in that CoM has a significantly lower rate parameter than either head or gaster mass, while petiole mass is lower than CoM (Fig. 7). Unlike the genus-level analysis, there was a larger disparity between head and gaster rates, but the direction differed in majors and minors. Minors show a higher rate parameter in the gaster compared to the head, while this is reversed in majors. More striking is the difference in rates between the majors and minors: majors have rate parameters that are an order of magnitude higher than minors across all variables, illustrating

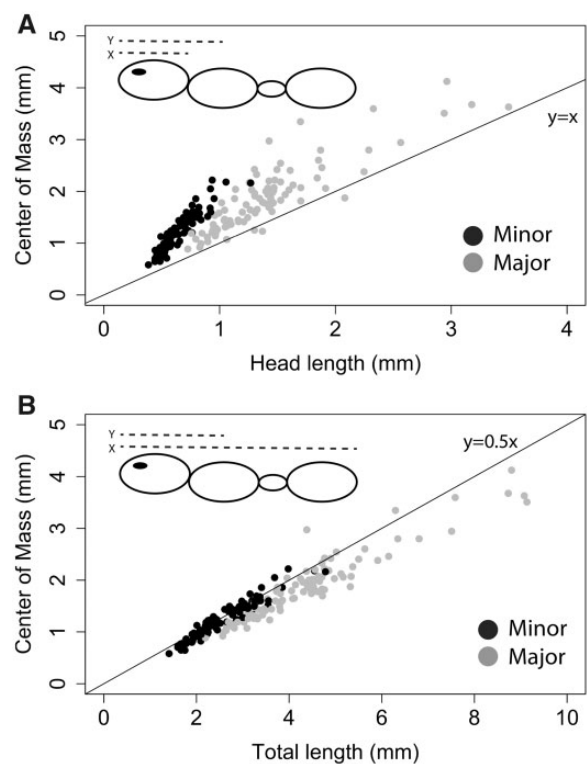


Fig. 6 Scatterplots of *Pheidole* head length and body length versus CoM for both minor (black) and major (gray) castes. (A) Head length versus CoM shows a few taxa crossing the $y = x$ line, meaning that the CoM is in the head in a few species for the majors. (B) Body length versus CoM shows that the CoM is still clustering around the midpoint of the body in minors, while majors generally have CoM further anterior.

much higher evolutionary rates in our model parameters for majors versus minors. We can also see the effects of including the uneven density data clearly. In the model that includes density, the gaster expansion and CoM show similar rates, both well lower than the rate of head expansion.

Discussion

We use a “simple,” low-parameter model of CoM in ants to illustrate patterns of body-segment evolution

Table 3 Results from PGLS comparing relative segment mass to the relative position of the CoM in both minor and major *Pheidole* workers

| | Lambda | Sig | R ² | Log lik | AIC | AICc |
|--------------------|--------|--------|----------------|---------|----------|----------|
| Model I: Minors | | | | | | |
| Log head size | 0.801 | <0.001 | 0.9 | 187.915 | -371.83 | -371.691 |
| Log petiole size | 0.199 | 0.012 | 0.06 | 93.433 | -182.867 | -182.728 |
| Log gaster size | 0.215 | <0.001 | 0.928 | 207.51 | -411.02 | -410.88 |
| Head + Petiole | 0.828 | <0.001 | 0.903 | 189.529 | -371.057 | -370.581 |
| Head + Gaster | 0.000 | <0.001 | 0.974 | 253.199 | -498.399 | -497.923 |
| Petiole + Gaster | 0.146 | <0.001 | 0.933 | 211.543 | -415.085 | -414.609 |
| All three segments | 0.000 | <0.001 | 0.977 | 260.769 | -505.538 | -503.738 |
| Model I: Majors | | | | | | |
| Log head size | 0.383 | <0.001 | 0.81 | 144.074 | -284.147 | -284.01 |
| Log petiole size | 0.000 | <0.001 | 0.113 | 78.306 | -152.613 | -152.473 |
| Log gaster size | 0.448 | <0.001 | 0.92 | 181.886 | -359.772 | -359.633 |
| Head + Petiole | 0.955 | <0.001 | 0.961 | 179.415 | -350.829 | -350.353 |
| Head + Gaster | 1.000 | <0.001 | 0.995 | 225.207 | -442.414 | -441.938 |
| Petiole + Gaster | 1.000 | <0.001 | 0.993 | 204.623 | -401.245 | -400.769 |
| All three segments | 1.000 | <0.001 | 0.996 | 236.67 | -457.338 | -455.538 |

AICc is AIC with a correction for small sample sizes.

Table 4 Results from PGLS comparing relative segment mass to the relative position of the CoM in both minor and major *Pheidole* workers

| | Lambda | Sig | R ² | Log lik | AIC | AICc |
|--------------------|--------|--------|----------------|---------|----------|----------|
| Model II: Minors | | | | | | |
| Log head size | 0.444 | <0.001 | 0.663 | 183.98 | -363.961 | -363.821 |
| Log petiole size | 0.164 | 0.84 | 0 | 136.966 | -269.931 | -269.792 |
| Log gaster size | 0.154 | <0.001 | 0.432 | 162.584 | -321.168 | -321.029 |
| Head + Petiole | 0.489 | <0.001 | 0.663 | 184.387 | -360.774 | -360.3 |
| Head + Gaster | 0.000 | <0.001 | 0.789 | 205.947 | -403.893 | -403.417 |
| Petiole + Gaster | 0.157 | <0.001 | 0.418 | 162.602 | -317.204 | -316.727 |
| All three segments | 0.000 | <0.001 | 0.811 | 213.019 | -410.039 | -408.239 |
| MODEL II: Majors | | | | | | |
| Log head size | 0.679 | <0.001 | 0.828 | 178.114 | -352.228 | -352.088 |
| Log petiole size | 0.000 | <0.001 | 0.235 | 121.371 | -238.742 | -238.603 |
| Log gaster size | 0.349 | <0.001 | 0.397 | 129.52 | -255.04 | -254.9 |
| Head + Petiole | 1.000 | <0.001 | 0.98 | 181.212 | -354.424 | -353.948 |
| Head + Gaster | 0.800 | <0.001 | 0.871 | 184.886 | -361.773 | -361.297 |
| Petiole + Gaster | 0.688 | <0.001 | 0.702 | 154.298 | -300.595 | -300.119 |
| All three segments | 1.000 | <0.001 | 0.985 | 194.789 | -373.578 | -371.778 |

These results are based on the model that incorporates density.

AICc is AIC with a correction for small sample sizes.

within and across genera related to head expansion. These results show the location of the CoM is correlated across phylogeny with both head and gaster size, implying that head expansion in certain lineages is not constrained merely by CoM, but is counterbalanced by

gaster expansion. Evolutionary rates analyses also imply that CoM may be under stabilizing selection relative to the size of the various segments. Together, these results illustrate the utility of low-parameter models in exploring the evolution of functional characters.

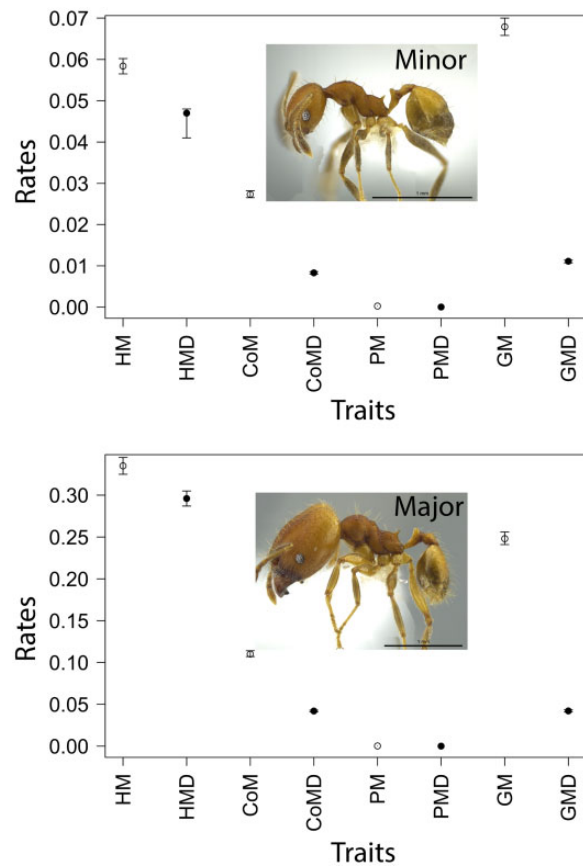


Fig. 7 Evolutionary rates for the *Pheidole* species level analysis of relative segment size and CoM traits (CoM, CoMD). Rates are shown for both minor and major castes. Similar to the genus level analysis, both the original model (open circles) and the model which incorporates density data (closed circles), show CoM rates much lower than the relative mass of the head (HM, HMD), but higher than the relative mass of the petiole (PM, PMD). Unlike the genus level analysis, relative gaster mass (GM, GMD) shows similar rates to CoM. These results are the same for both minor and major castes. A “D” on the end of a trait name denotes that trait for the model that includes density. Error bars represent 95% confidence intervals. Photo credits as in Fig. 3.

CoM in ants

The relative size of the head is highly variable across ant genera. Many species (such as those within the genus *Pheidole*) have worker castes with variable head sizes (e.g., minors and majors). In these groups, majors often fill specialized roles including nest defense and seed milling (Wilson 1984, Wills et al. 2018), and increasing muscle volume allows for greater bite forces with their mandibles. Our results illustrate that this increase in relative head size is often correlated with an increase in the relative size of the gaster as well. This pattern holds across genera as well as between major and minor worker castes in the genus *Pheidole* and implies that head expansion

in ants is not limited solely by CoM. Head expansion can be offset with concomitant gaster expansion and may prevent the CoM from moving into the head and throwing off balance.

There are a couple of important caveats to consider. First, in ants where majors have particularly large heads, and the CoM moves too far anteriorly, mobility will be limited. Our *Pheidole* analysis suggests that the CoM is in fact located in the head for the majors of some species. These species should have a hard time moving, although majors whose role is seed milling may have relatively sedentary lifestyles anyway (Wilson 1984; Tschinkel and Kwapich 2016). A second, potentially more significant caveat, is that it is unlikely that the gaster has evolved to be larger merely as a counter-balance to head expansion. Attempting to assign direction to the evolution of these traits is not feasible from simple evolutionary correlations and there are several potential selection pressures that may result in an increase in gaster size relative to body size. For example, majors of some species lay trophic eggs (e.g., Peeters et al. 2013) or haploid eggs that develop into males (e.g., Smith et al. 2007). The reproductive condition of the majors in these species may necessitate a larger abdomen irrespective of head size. Regardless, the coupled expansion of the head and gaster allows for both to likely achieve relative sizes beyond what could evolve separately while maintaining balance.

The evolutionary rates analyses show another intriguing trend, that the CoM evolves at an order of magnitude slower rate than either the head or the abdomen expansion. Given the close correlation between these three traits seen in the PGLS, the rate results imply that CoM may be under stabilizing selection. While head and gaster expansion undergo higher rates of evolution, the CoM remains at a relatively stable value, around the midpoint of the animal (e.g., Fig. 4B). The maintenance of CoM around this average value matches the pattern of stabilizing selection: natural selection favors non-extreme values for a trait, resulting in stabilization around a particular trait values and a reduction in genetic variance (Haldane 1954; Robertson 1956). While the basic morphological model here cannot offer any insights into the population genetics or specific selection processes occurring, it does present a fairly clear pattern that is worth further examination.

CoM is a derived functional trait partly determined by the head and gaster sizes, which are not necessarily under any sort of stabilizing selection and may even be under distinct patterns of directional selection. We could, therefore, ask what mechanism constrains morphology such that CoM can maintain

a stable position? Is there some developmental or genetic mechanism that links head and gaster size? As noted above, there is little reason to believe that either head or gaster size evolve as simple counter-balances to each other, and yet they both evolve at higher rates than CoM to help maintain a stable position. Teasing apart these aspects of ant morphology will take much more than a “simple” functional model of CoM, but this model has presented some ideas worth pursuing with more complex analyses.

One general trend that arises across these analyses occurs when we make our model slightly more complex by accounting for potential differences in density between the segments. These differences alter how mass is calculated from volume and result specifically in the head being heavier per cubic millimeter of volume than the gaster, likely reflecting the proportion of the head dedicated to muscle. The head shows a stronger direct correlation with CoM based on the pGLS tests. This not surprising, given that overall the heavier head will now exert a larger influence on the equation for CoM than the comparatively lighter gaster. The head expansion also shows a much higher rate of evolution than either the CoM or gaster expansion, the latter two having almost the same evolutionary rates in the *Pheidole* analysis. This is mostly due to a large drop in evolutionary rate of relative gaster size when the density data are included. Why this occurs is unclear, but further suggests that differences in material properties across segments are an important factor to the center of mass.

One final note on the petiole: prior to analyses, one hypothesis we had concerning the position of the CoM in big-headed ants was not just a counter-balancing with the gaster but a potential lengthening of the petiole as well, to help shift the gaster mass further back. Our results suggest the petiole has very little correlation with CoM either across genera or *Pheidole* species. Furthermore, the petiole has a lower rate of evolution than even the CoM in all analyses. Whether this is due to strong directional or stabilizing selection for a specific petiole length (relative to body length) is unclear. It does, however, indicate that petiole size as measured here is a relatively conserved trait, an interesting observation considering the large range of petiole shapes seen across genera.

Assumptions

We would be remiss not to address some of the assumptions of our CoM model, and their potential

effect on the results. The CoM model is essentially one dimensional, neither taking the dorso-ventral or lateral distributions of mass into account. In terms of the latter, we can likely assume lateral symmetry within ants. Previous work has been done on the lateral location of the CoM, particularly in terms of locomotion of hexapodal insects (Hughes 1952; Zollikofer 1994; Ting et al. 1994). These studies illustrate the potential issue with shifting CoM during locomotion. Less has been done looking at the dorso-ventral distribution of mass, although this has been looked at in foraging ants that need to carry oversized food back to the nest (Moll et al. 2013). A model which attempts to incorporate full 3D CoM calculations would be exponentially more complex, but would allow for a more complete exploration of shifting CoM with both morphology and behavior.

Another major assumption/simplification in our model is reducing the complex segment shape into simple ellipsoids. Just a brief look at Fig. 1 illustrates how much variation there is in ant head shape as well as size. In particular, certain taxa such as *Microdaceton tibialis* (Fig. 1) have “horns” that protrude from the back of the head and likely overlap with the thorax. This may act to also lessen anterior shifts in CoM as part of the head is now further posterior than our model assumes. Similarly, gasters tend to have much of their mass shifted toward the anterior end as opposed to the regular ellipsoid shapes used here. Furthermore, there can be a great deal of variation in gaster size and shape even within colonies depending on the age of an individual, its nutritional or reproductive state, and how it was collected (Tschinkel 2013). A potential future direction for research could involve examining the variability in gaster shape across phylogeny in comparison with head size or CoM.

Notably, the thorax is often very irregularly shaped in ants, big headed ants in particular appear to have thorax segments which are enlarged near the anterior end, giving the look of “shoulders.” This is generally to house the muscles used to support their oversized heads (Keller et al. 2014). The need for such muscles highlights another issue beyond simple head shape: how the ant holds these segments. Big-headed ants tend to hold their heads up and may do so in a way that further reduces the anterior shift in CoM. Such behaviors are seen in leaf and grass cutter ants while carrying food items (Moll et al. 2013). Estimating segment CoM in such complex shapes in varying positions is, again, much more complex than what we have done here. However, increase in is

accessibility of computed tomography (CT) technology makes collecting such data for future models more feasible (Davies et al. 2017).

The CoM model also simplifies how mass is calculated for each segment by assuming a density of 1 kg/m^3 , allowing us to assume that the volume of the segment has a one-to-one relationship with mass. This assumption both neglects variation between segments and variation of density within a segment, which may alter the position of the CoM for each segment in the same way shape is described above. We specifically tested for these effects by testing a second model that incorporated limited density data from one species. The results suggest that the overall patterns remained even as some of the details change. Big-headed ants, if the head expansion is driven by mandibular action for defense of food reduction, will likely show even greater differences in materials in the head including expanded muscles and potentially denser materials in the mandibles. Both of these could result in greater shifts the CoM anteriorly. As with shape, advances in the availability of CT scan technology potentially make it easier to identify variation in material density across segments, allowing for more detailed modeling (Waugh et al. 2006; Adams et al. 2018).

There are other assumptions made by the model as well, such as the nature of the connection between segments and aspects of the animals' stance. All of these could, with greater or lesser levels of ease, be incorporated into future models to gain a more complete picture of the center of balance in ants and how it relates to expansion of the particular segments. However, the low-parameter model used here does highlight specific avenues of future inquiry for minimal investment of time and resources.

The utility of “simple” models

Our instinct in the biological sciences is often to try and make our models conform to biological reality as closely as possible. Hopefully in this short discussion and case study, we have illustrated the potential power and utility of simple, low-parameter models. The CoM model for ants makes several fundamental assumptions and simplifications, modeling ants as little more than a series of homogenous ellipsoids in a straight line. However, this simplicity allowed for a focused study of CoM across 68% of known ant genera for minimal cost in both time and resources. The results from this model also gave valuable insights into the arrangement of mass across the ant body as well as potential evidence of stabilizing selection and correlated evolution of multiple

segments. We have also shown that incremental increases in complexity can also reveal new insights into the system. By incorporating limited density data, we verified that differences in materials can exert strong influences on the CoM measure, even as overall patterns of evolution held. All of these trends need to be further tested with more complex models, but this work illustrates that there is a pattern to be testing to begin with.

The utility of “simple” models extends outside of research to the teaching realm as well. Modeling is a key concept in both the physical and life sciences. In their Framework for K-12 Science Education, the National Research Council lists modeling as one of the key science and engineering practices to be taught at all age levels (NRC 2012). Low-parameter models allow for even elementary students in the sciences to not just use models, but potentially develop their own within a classroom setting. By instilling these skills early, students are able to gain experience with this fundamental aspect of research and develop the skills required to determine for themselves what level of “simplicity” or “complexity” their given biological problem requires.

Acknowledgments

We would like to thank L. Waldrop and J. Rader for inviting us to take part in the Melding Morphology and Modeling Symposium at the SICB 2020. M. Muñoz and D. Adams provided R code and advice on evolutionary rates analyses. S. Crofts offered vital discussion on the implementation of the CoM Model. We also thank two anonymous reviewers for their insightful comments which helped improve the manuscript tremendously.

Funding

Funding provided by NSF (IOS 17-55336 to P.S.L.A. and A.V.S.). M.D.R. was funded via the NSF Graduate Research Fellowship Program (NSF GRFP 2015196745).

Supplementary data

Supplementary data available at *ICB* online.

References

- Ackerly D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proc Natl Acad Sci U S A* 106:19699–706.
- Adams DC. 2013. Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Syst Biol* 62:181–92.

- Adams GJ, Cook RB, Hutchinson JR, Zioupos P. 2018. Bone apparent and material densities examined by cone beam computed tomography and the Archimedes technique: comparison of the two methods and their results. *Front Mech Eng* 3:23.
- Anderson PSL, Patek SN. 2015. Mechanical sensitivity reveals evolutionary dynamics of mechanical systems. *Proc Biol Sci* 282:20143088.
- Anderson PSL, Westneat MW. 2007. Feeding mechanics and bite force modeling of the skull of *Dunkleosteus terrelli*, an ancient apex predator. *Biol Lett* 3:77–9.
- Anderson PSL, Gill PG, Rayfield EJ. 2011a. Modeling the effects of cingula structure on strain patterns and potential fracture in tooth enamel. *J Morph* 272:50–65.
- Anderson PSL, Bright JA, Gill PG, Palmer C, Rayfield EJ. 2011b. Models in palaeontological functional analysis. *Biol Lett* 8:119–22.
- Barel C. 1983. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Neth J Zool* 33:357–424.
- Baumgart A, Anderson P. 2018. Finding the weakest link: mechanical sensitivity in a fish cranial linkage system. *R Soc Open Sci* 5:181003.
- Blanchard B, Moreau CS. 2016. Defensive traits exhibit an evolutionary trade-off and drive diversification in ants. *Evolution* 71:315–28.
- Burd M. 2000. Body size effects on locomotion and load carriage in the highly polymorphic leaf-cutting ants *Atta colombica* and *Atta cephalotes*. *Behav Ecol* 11:125–31.
- Butler MA, King AA. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am Nat* 164:683–95.
- Clough RW. 1960. The finite element in plane stress analysis. *Proceedings of ASCE Conference Electronic Computation*, 2nd, Pittsburgh, PA.
- Crofts SB. 2015. Finite element modeling of occlusal variation in durophagous tooth systems. *J Exp Biol* 218:2705–11.
- Crofts SB, Summers AP. 2014. How to best smash a snail: the effect of tooth shape on crushing load. *J R Soc Interface* 11:20131053.
- Curtis N, Kupczik K, O'higgins P, Moazen M, Fagan M. 2008. Predicting skull loading: applying multibody dynamics analysis to a macaque skull. *Anat Rec* 291:491–501.
- Davies TGD, Rahman I, Lautenschlager S, Cunningham J, Asher R, Barrett P, Bates K, Bengtson S, Benson R, Boyer D, et al. 2017. Open data and digital morphology. *Proc Biol Sci* 284:20170194.
- Davis JL, Santana SE, Dumont ER, Grosse IR. 2010. Predicting bite force in mammals: two-dimensional versus three-dimensional lever models. *J Exp Biol* 213:1844–51.
- Dumont ER, Davis JL, Grosse IR, Burrows AM. 2011. Finite element analysis of performance in the skulls of marmosets and tamarins. *J Anat* 218:151–62.
- Dumont ER, Piccirillo J, Grosse IR. 2005. Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats. *Anat Rec* 293:319–30.
- Haldane J. 1954. The measurement of natural selection. *Proc. 9th Int Congr Genet* 1:480–7.
- Hamlet C, Strychalski W, Miller L. 2020. Fluid dynamics of ballistic strategies in nematocyst firing. *Fluids* 5:20.
- Hölldobler B, Wilson EO. 1990. *The ants*. Cambridge (MA): Harvard University Press.
- Hu Y, Nelson-Maney N, Anderson P. 2017. Common evolutionary trends underlie the four-bar linkage systems of sunfish and mantis shrimp. *Evolution* 71:1397–405.
- Hughes GM. 1952. The co-ordination of insect movements. *J Exp Biol* 29:267–85.
- Ilton M, Bhamla MS, Ma X, Cox SM, Fitchett LL, Kim Y, Koh J, Krishnamurthy D, Kuo C-Y, Temel FZ, et al. 2018. The principles of cascading power limits in small, fast biological and engineered systems. *Science* 360:eaao1082.
- Ives AR, Midford PE, Garland T. 2007. Within-species variation and measurement error in phylogenetic comparative methods. *Syst Biol* 56:252–70.
- Keller RA, Peeters C, Beldade P. 2014. Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. *Elife* 3:e01539.
- Longo SJ, Cox SM, Azizi E, Ilton M, Olberding JP, St. Pierre R, Patek SN. 2019. Beyond power amplification: latch-mediated spring actuation is an emerging framework for the study of diverse elastic systems. *J Exp Biol* 222:jeb197889.
- Miller LA, Goldman DI, Hedrick TL, Tytell ED, Wang ZJ, Yen J, Alben S. 2012. Using computational and mechanical models to study animal locomotion. *Integr Comp Biol* 52:553–75.
- Moll K, Roces F, Federle W. 2013. How load-carrying ants avoid falling over: mechanical stability during foraging in *Atta vollenweideri* grass-cutting ants. *PLoS One* 8:e52816.
- Moreau CS. 2008. Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). *Mol Phylogenet Evol* 48:224–39.
- Muñoz MM, Hu Y, Anderson PSL, Patek SN. 2018. Strong biomechanical relationships bias the tempo and mode of morphological evolution. *Elife* 7:e37621.
- National Research Council. 2012. *A framework for K-12 science education: practices, crosscutting concepts, and core ideas*. Washington (DC): The National Academies Press.
- Nazarian P, Tran F, Boedicker JQ. 2018. Modeling multispecies gene flow dynamics reveals the unique roles of different horizontal gene transfer mechanisms. *Front Microbiol* 9:1–11.
- O'Meara BC, Ané CM, Sanderson MJ, Wainwright PC. 2006. Testing for different rates of continuous trait evolution in different groups using likelihood. *Evolution* 60:922–33.
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2012. Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5 (<http://cran.r-project.org/web/packages/caper/index.html>).
- Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zool Scr* 26: 331–48.
- Patek SN, Nowroozi BN, Baio JE, Caldwell RL, Summers AP. 2007. Linkage mechanics and power amplification of the mantis shrimp's strike. *J Exp Biol* 210:3677–88.
- Peeters C. 2019. Castas: homología y analogía en la forma y función. In: Fernández F, Guerrero R, Delsinne T, editors.

- Hormigas de Colombia, Universidad Nacional Colombia. p.159–64. 978-958-783-766-7.hal-02324626
- Peeters C, Lin C-C, Quinet Y, Segundo GM, Billen J. 2013. Evolution of a soldier caste specialized to lay unfertilized eggs in the ant genus *Crematogaster* (subgenus *Orthocrema*). *Arthropod Struct Dev* 42:257–64.
- Pie M, Tschá MK. 2013. Size and shape in the evolution of ant worker morphology. *PeerJ* 1:e205.DOI10.7717/peerj.205
- Powell S. 2008. Ecological specialization and the evolution of a specialized caste in *Cephalotes* ants. *Funct Ecol* 22:902–11.
- Rayfield EJ. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annu Rev Earth Planet Sci* 35:541–76.
- Rich BR. 1995. Clarence Leonard (Kelly) Johnson 1910–1990: a biographical memoir. Washington (DC): National Academies Press.
- Robertson A. 1956. The effect of selection against extreme deviants based on deviation or on homozygosity. *J Genet* 54:236–48.
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671–5.
- Shi J, Curtis N, Fitton LC, O'Higgins P, Fagan MJ. 2012. Developing a musculoskeletal model of the primate skull: predicting muscle activations, bite force, and joint reaction forces using multi-body dynamics analysis and advanced optimization methods. *J Theor Biol* 310:21–30.
- Smith CR, Schoenick C, Anderson KE, Gadau J, Suarez AV. 2007. Potential and realized reproduction by different worker castes in queen-less and queen-right colonies of *Pogonomyrmex badius*. *Insectes Soc* 54:260–7.
- Suchard MA. 2005. Stochastic models for horizontal gene transfer: taking a random walk through tree space. *Genetics* 170:419–31.
- Tschinkel WR, Kwapich CL. 2016. The Florida harvester ant, *Pogonomyrmex badius*, relies on germination to consume large seeds. *PLoS One* 11:e0166907.
- Ting LH, Blickhan R, Full RJ. 1994. Dynamic and static stability in hexapedal runners. *J Exp Biol* 197:251–69.
- Tschinkel WR. 2013. The morphometry of *Solenopsis* fire ants. *PLoS One* 8:e79559.
- Wainwright PC. 2007. Functional versus morphological diversity in macroevolution. *Annu Rev Ecol Evol Syst* 38:381–401.
- Watson PJ, Groning F, Curtis N, Fitton LC, Herrel A, McCormack SW, Fagan MJ. 2014. Masticatory biomechanics in the rabbit: a multi-body dynamics analysis. *J R Soc Interface* 11:20140564.
- Waugh DA, Feldmann RM, Schroeder AM, Mutel M. 2006. Differential cuticle architecture and its preservation in fossil and extant *Callinectes* and *Scylla* claws. *J Crustacean Biol* 26:271–82.
- Westneat MW. 1990. Feeding mechanics of teleost fishes (Labridae; Perciformes): a test of four-bar linkage models. *J Morph* 205:269–95.
- Westneat MW. 1995. Feeding, function and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst Biol* 44:361–83.
- Westneat MW. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. *J Theor Biol* 223:269–81.
- Wills BD, Powell S, Rivera MD, Suarez AV. 2018. Correlates and consequences of worker polymorphism in ants. *Annu Rev Entomol* 63:575–98.
- Wilson EO. 1953. The origin and evolution of polymorphism in ants. *Q Rev Biol* 28:136–56.
- Wilson EO. 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 16:89–98.
- Zienkiewicz OC, Taylor RL, Zhu JZ. 2005. The finite element method: its basis and fundamentals. Amsterdam: Elsevier Butterworth-Heinemann.
- Zollikofer CE. 1994. Stepping patterns in ants: III. Influence of load. *J Exp Biol* 192:119–27.