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9-16-2020

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Lindsay D. Waldrop

Chapman University, waldrop@chapman.edu

Jonathan Rader

University of North Carolina at Chapel Hill, jrader@live.unc.edu

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Recommended Citation

Lindsay D Waldrop, Jonathan A Rader, Melding Modeling and Morphology: A call for collaboration to address difficult questions about the evolution of form and function, *Integrative and Comparative Biology*, Volume 60, Issue 5, November 2020, Pages 1188–1192, <https://doi.org/10.1093/icb/icaa132>

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The authors

Melding Modeling and Morphology: A call for collaboration to address difficult questions about the evolution of form and function

Lindsay D. Waldrop
Schmid College of Science and Technology,
Chapman University, Orange, CA 92866 USA
Tel: +1 (714) 516-5615, Fax: +1 (714) 532-6048
waldrop@chapman.edu

Jonathan A. Rader
Dept. of Biology,
University of North Carolina, Chapel Hill, NC, USA
jrader@live.unc.edu

July 27, 2020

Abstract

The nascent field of evolutionary biomechanics seeks to understand how form begets function, and researchers have taken two tacks towards this goal: inferring form based on function (comparative biomechanics) or inferring function based on form (functional morphology). Each tack has strengths and weaknesses, which the other could improve. The symposium, “Melding Modeling and Morphology – Integrating approaches to understand the evolution of form and function” sought to highlight research stitching together the two tacks. In this introduction to the symposium’s issue, we highlight these works, discuss the challenges of interdisciplinary collaborations, and suggest possible avenues available to create new collaborations to create a unifying framework for evolutionary biomechanics.

Keywords: evolutionary biomechanics; comparative biomechanics; functional morphology; computational modeling

Two Paths...

Evolutionary biomechanics seeks to understand how form begets function. Researchers have largely taken two tacks toward this goal: 1) observing and modeling representative organisms (inferring form based on function), and 2) quantifying trait diversification and evolutionary constraint (inferring function based on form). The latter is primarily focused on exploration of large data sets of morphometric measurements, while the former most often evaluates specific hypotheses of function with a focus on a narrow range of taxa.

These approaches have led to the development of sophisticated, but disparate toolsets, including mathematical and computational models, geometric morphometrics, and phylogenetics. These are powerful approaches, yet each tack has limitations that would benefit from the strengths of the other. We organized a symposium at the 2020 meeting of the Society for Integrative and Comparative Biology to identify barriers that may be maintaining the gulf between modelers and morphologists and to chart a path toward fruitful collaborations that can tackle seemingly intractable problems in biology.

The Challenge of Big Data

The availability of large comparative data sets presents an exciting frontier for comparative biomechanics (Muñoz and Price, 2019). However, it also presents newfound challenges. Curating and analyzing big data sets is computationally demanding, and complex multivariate data can be statistically unwieldy (Walker, 2010). When faced with large sets of autocorrelated data, many researchers have turned to dimensional-reduction techniques like principal component analysis (PCA) to study evolutionary diversification of morphology among clades (Jolliffe and Cadima, 2016). By reducing the dimensionality of a set of morphological measurements, PCA is a powerful tool for exploring very large data sets. Changes in morphology are mapped onto phylogenies and can be linked with observations of ecology or behavior to illuminate the functional pressures that drive adaptive evolution in morphology (e.g. Lockwood et al., 2002; McCoy et al., 2006). However, this approach is inherently correlational, and therefore lacks the mechanistic explanation of the functional consequences of specific changes in morphology.

Modeling approaches can provide this explanatory power, enriching the description of form and function. Furthermore, the relationship between principal-component axes and specific morphological features is frequently murky and subjective, so the results of PCA and similar *post-hoc* dimensional reduction techniques can be difficult to evaluate as functional hypotheses. Again, modeling a simplified version of a complex form-function system can provide valuable insight into the sensitivity of biomechanical performance to changes in individual morphological parameters and interactions of suites of traits. By stripping away traits that are irrelevant to the performance outputs of interest, this strategy of *a-priori* dimensional reduction fosters hypothesis development by highlighting traits (Waldrop et al., 2020), rather than further muddying already turbid waters.

Limitations of Narrow Focus

In comparative biomechanics, sophisticated computational and mathematical models are used to study the mechanisms of action of a system (e.g. Tytell et al., 2016; Battista et al., 2015). These models can be simple, which can direct attention to important features of a system quickly (Anderson et al., 2020). With the rapid increase in computational power, models have increasingly incorporated fine details of morphology, kinematics, and behavior to produce accurate results of function (Battista, 2020a,b). The models can lead to insights of function that are impossible to obtain from morphological studies or biomechanical experiments (Koehl, 2003; Waldrop and Miller, 2015a). These results can be used to interrogate the interplay between selection pressures and resulting morphological change (Schwenk et al., 2009; Padilla et al., 2014).

Modeling is often limited to only a handful of species because of the complexity and costliness of developing and running the models, so broad phylogenetic comparisons are

difficult. Understanding the widespread patterns of morphology is not possible with a modeling approach alone. However, evolution represents a long running performance and sensitivity test, with many multi-dimensional engineering and biomedical problems that researchers struggle with already solved (Patek, 2014). Natural systems are also fraught with tradeoffs and constraints that, without phylogenetic comparative analyses are difficult to disentangle to yield useful principles from biological function (Patek, 2014; Wolff et al., 2017).

Collaborations in Focus

Both approaches have much to offer each other toward understanding evolution and biodiversity of form and function. Morphometrics can take advantage of increasingly large data sets of morphological measurements and other aspects of biology to produce functional hypotheses. Modeling can then provide a test of these functional hypotheses with accurate reproduction of function. However, a unified framework is needed to bring these two approaches together.

A few researchers have begun to bridge phylogenetic analyses and modeling to study functional evolution. Taylor and Thomas (2014) presented the first work that attempts to test functional relationships identified by morphometric data through dimensional analysis and linear regression. Anderson and Patek (2015) and Muñoz et al. (2017) present estimates of trait evolution based on a simple model of mechanical sensitivity of the four-bar linkage system in stomatopod appendages. Polly et al. (2016) provides the first full framework for generating and testing functional hypotheses using finite element analysis on mammal skulls and a simple model of evolution. Waldrop et al. (2018, 2020) extend parameter analysis tools of uncertainty quantification to generate hypotheses of function based on a computational model which can then be compared to morphometric data. Each of these studies uses novel analysis techniques in an attempt to bridge the gap between the two methodologies, yet none provide a common and flexible solution to integrating the two approaches.

The purpose of this symposium was to examine the idea of studying the evolution of functional structures using mixed methods of classic biomechanics, together with computational and mathematical modeling, all in a phylogenetic framework. The symposium meant to bring together speakers with backgrounds in both approaches, to promote ideas by speakers who have worked to develop methods, and to offer a forum to foment conversation between both camps.

In the symposium, we heard from a diverse set of researchers focused on a host of functional problems from ammonites to frogs:

- Molly Womack explored the morphology and locomotion of frogs (Buttimer et al., 2020). Rosyln Dakin discussed the morphological and physiological underpinnings of maneuvering flight in hummingbirds (Dakin et al., 2018), and Mary Salcedo presented novel tools to quantify the intricate geometries of insect wing venation (Salcedo et al., 2019; Salcedo, 2020). Each of these complex biological systems represent the types of questions that are ripe for modeling advances.
- Philip Anderson reminded us that sometimes “simple” models are what’s best for initial testing of functional questions (Anderson et al., 2020).
- The authors (Rader and Waldrop) presented a unified model of functional morphology of gliding flight in birds; first using uncertainty quantification of a model

of gliding flight to generate hypotheses (Waldrop et al., 2020), and then using morphological measurements of bird wings to test these predictions (Rader et al., 2020).

- Nicholas Battista presented an immersed boundary method (IBM) tool that makes fluid dynamics modeling accessible to a wider range of researchers and trainees (Battista, 2020a).
- Nicholas Battista and Nicholas Hebdon presented sophisticated modeling of biological problems that strike at the heart of function-morphology relationships. (Battista, 2020b) uses his formulation of IBM to explore the sensitivity of parameter change in simple swimmers. Hebdon (2020) analyzed the hydrodynamic performance changes in altering morphology with computational fluid dynamics modeling of ammonite shells.
- Roi Holzman and David Polly presented modeling of performance landscapes. Polly (2020) examines the effects of functional trade-offs on traversing performance valleys. Olsson et al. (2020) describes different functional constraints for prey type in suction-feeding fish.
- Martha Muñoz described the exciting frontier of evolutionary biomechanics in the era of big data where it is finally possible to bring large, taxonomically broad data sets to test predictions about the evolution of functional traits. She illustrated her point with vignettes on her work with four-bar linkage systems in multiple organismal lineages, and the evolution of feeding and locomotory traits in wrasses (labridae; Camarillo and Muñoz, 2020).

Future Opportunities for Collaboration

After many calls for biologists and mathematicians to come together to solve big problems (i.e. Halanych and Goertzen, 2009; Schwenk et al., 2009; Padilla et al., 2014), why are there not more collaborations between morphologists and modelers?

- Biological problems are messy and do not fit neatly into mathematical frameworks. Biological problems are often intractably complex, and models that are simple enough to be tractable for modelers often lose the biological realism and nuance that satisfy biologists.
- Biology and mathematics have created disparate toolsets and languages for describing the world. This separation has led to the development of different academic cultures (Waldrop and Miller, 2015b).
- Even the problems themselves point to major differences in research interests. Biologists are focused on answers to applied questions (i.e. how systems work) using applications of mathematics tools, while mathematicians are interested in developing new mathematics. This division is often reflected in priorities of funding organizations such as the National Science Foundation, making funding for interdisciplinary projects difficult to secure.
- Furthermore, each set is pressured to publish in their discipline's specialty journals. This is particularly pressing for early career researchers, which limits the opportunity for cross-collaboration during the formative career stage.

When forming new collaborations, we see two main challenges. First, a group must find a project that can satisfy the intellectual desires of both sides: include new tool development for modelers and the application of those tools to elucidate central processes in biological problems. Second, a group must find a balance between representing the biological target systems by capturing the essence of each system while creating a tractable problem that can return results with reasonable amounts of time and effort.

Despite the struggle in creating and sustaining collaborations, we see a rich set of opportunities for collaboration between functional morphology and comparative biomechanics to solve some of biology's grand challenges. To this end, the areas to watch are:

- *Joining morphologists, phylogeneticists, and modelers already working on similar problems.* There are a host of problems for which modelers have already developed sophisticated models, morphologists have rich data sets, and phylogenetics have appropriate tools. All that is needed is for these groups to find each other and work together.
- *Applications of existing mathematics and engineering to current problems in biology.* There is more to math than calculus, and many areas of mathematics have already developed tools to describe and explain patterns that exist in biology. Current tools are rich with examples: Kendall's shape space and Riemann geometry form the basis for PCA (e.g. Mitteroecker and Huttegger, 2009); network analysis has been applied to community assemblages and genomic analyses (Dunne, 2006); Markov processes clarify many problems in systems biology (e.g. Ullah and Wolkenhauer, 2007); and game theory led to the description of evolutionary strategies (Taylor and Jonker, 1978).
- *Development of new mathematics through collaborations.* Biological problems, although complex, present the type of challenges that mathematicians often find fascinating. These complex problems are ripe for the development of new mathematics, examples such as development of the immersed boundary method for flexible structure-fluid interactions (Peskin, 2002), stokeslets for modeling flagella- and cilia-driven fluid flows (Smith, 2009), and genetic algorithms based on natural selection (Mirjalili et al., 2020), among others.

As the rapid progress in computational power continues to make more complex biological problems accessible to modeling, we anticipate a boom in interdisciplinary research developing the nascent field of evolutionary biomechanics.

Funding

We would like to thank the Company of Biologists, the Divisions of Comparative Biomechanics and Vertebrate Morphology, and the Society for Integrative and Comparative Biology for providing funding to run the symposium and travel for students in the complementary sessions.

Acknowledgements

We would like to thank all of our participants, in both regular and complementary sessions, for making the symposium a success. Additionally, we would like to thank the

audience of the symposium for showing up at 7:45 am to help us brainstorm the problems of collaborating and the solutions to successful collaborations.

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