

Collective Animal Behavior

Author: Karsai, Istvan

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causally account for select observations of organismal properties. Contrary to what Rieppel suggests, the term *species* is not just a “theoretical term,” wherein “a theory gives relevant meaning to a theoretical term by conveying substantial (and reversible) empirical knowledge about the causal relations in which entities to which the term refers take part. The theory that tells us about the causal roles species engage in is evolutionary theory” (p. 161). Individual organisms, not taxa, have causal relations. We invoke a variety of theories under the rubric of evolutionary biology to infer such relations as the means to causally account for what we observe of those individuals. Those hypotheses are what we refer to as *taxa*. Recognizing the reality that all of systematics is about acquiring (usually vague) causal understanding diminishes the effectiveness of Rieppel’s arguments.

Systematics cannot be reduced to mere classification. It is a field of science concerned with systematization—the act of pursuing causal relationships per the goal of science, which is to pursue causal understanding.

The essay “Beyond belief: The steady resurrection of phenetics” by David M. Williams, Malte C. Ebach, and Quentin D. Wheeler is one of the more peculiar installments. The authors are fearful that systematics is being distorted into phenetics. Their solution? Stave off the “artificial” relationships of phenetics by looking to eighteenth-century French botanist Augustin Pyramus de Candolle’s “real” relationships. But of course, this raises the question of what one means by the term *relationship* in the contexts of science and systematics. Williams and his colleagues want to reduce relationships to instances of sameness: “Classification is meant to make sense of relationships by looking for sameness, which is observable, rather than an

event, which is only partially observable. In this sense, relative relationships, in the sense of sameness..., are better ways to classify and summarize overall taxic relationships than inferring genealogies or phylogenies. An inference is purely abstract, whereas relationships are real” (p. 187). This position fails for several fundamental reasons. Relationships, whether they are based on similarity or causality, are by their very nature hypothetical constructs, because they are our inferential reactions to sensory data. Systematics cannot be reduced to mere classification. It is a field of science concerned with *systematization*—the act of pursuing causal relationships in accordance with the goal of science, which is to pursue causal understanding. It is when systematics is accurately framed in the milieu of that causal objective that phenetics, like pattern cladistics, is reduced to the arcane. The last two essays, “Monographic effects on the stratigraphic distribution of brachiopods” by Gordon B. Curry and “The eukaryote Tree of Life” by Diana Lipscomb, offer nothing germane to either this section of the book or to the topic of cladistics.

The final installment, part 4, “Biogeography,” contains three essays. In “Tethys and teleosts,” Peter L. Forey examines three issues regarding the utility of phylogenetic hypotheses for Cretaceous teleost fishes: filling out causal conditions implied by those trees with actual data on geological events (e.g., vicariance), determining rates of taxon evolution, and determining rates of teleost morphological evolution. Although the first issue is a reasonable action in accordance with systematics’ goal of pursuing causal understanding, the remaining two are, at best, dubious. The essay “East–West continental vicariance in *Eucalyptus* subgenus *Eucalyptus*” by Pauline Y. Ladiges, Michael, J. Bayley, and Gareth J. Nelson is a study in methodological folly. Ladiges and her colleagues compiled morphological and DNA (ITS; external transcribed spacer, ETS) sequence data. Phylogenetic analyses were performed with just sequence data sets, both separate and combined. From the ITS + ETS strict consensus

tree, nodes with high bootstrap support were converted to binary characters, *sensu* the supertree approach. These “characters” were added to the morphological data matrix to infer cladograms that the authors claim “contributes to the discovery of the biogeographic history of subgenus *Eucalyptus*” (p. 282). Such a claim does not hold. By their very inference (using the term loosely), supertrees are empirically vacuous constructs. Assigning any significance to them for phylogenetic or biogeographic purposes is unacceptable. In “Wallacea deconstructed,” Lynne R. Parenti and Malte C. Ebach provide a solid analysis of the empirical validity of the Indo-Australian region known as Wallacea. Relying on areas of endemism, phylogenetic analyses, and area cladograms, Parenti and Ebach show that Wallacea does not form a single, natural unit, but rather spans two biogeographic areas.

Does *Beyond Cladistics* fulfill the editors’ intent of documenting the nature and future of cladistics? For the most part, it falls short as a useful systematics reference. As for indicating the future, the book demonstrates that a tremendous amount of work is still required to raise systematics—phylogenetic or otherwise—to the status of a unified, scientific paradigm.

KIRK FITZHUGH

Kirk Fitzhugh (kfitzhugh@nhm.org) is curator of polychaetes at the Natural History Museum of Los Angeles County in California.

LIVING TOGETHER: UNITING THE HOW AND THE WHY

Collective Animal Behavior. David J. T. Sumpter. Princeton University Press, 2010. 312 pp., illus. \$39.50 (ISBN 9780691148434 paper).

We are social organisms, and we are always fascinated by other social creatures. Yet understanding how and why collective and social

behaviors emerge proves to be a remarkable challenge. From H. G. Wells's concept of a "world brain" to William Morton Wheeler's "super-organism," many theories have surfaced and tried to answer these questions. Successful investigation of collective systems can be achieved through two major steps: (1) linking different levels of organization and (2) applying a set of techniques suitable for the analysis of systems at many different physical scales. If we want to understand how an ant colony is able to find and exploit transient food resources, we need to understand ants' individual behavior, feedback mechanisms, individual- and colony-level decisions, cues, and signals and then to connect the different levels of organization together. *Collective Animal Behavior* is an excellent guide in showing us how this is possible.

What makes David Sumpter's book unique and worthwhile reading? Namely, the target audience is the scientist interested in social and collective phenomena. The book assumes that the reader has a sound, fundamental knowledge of science. Therefore, the subject matter reaches the current state of progress in the field immediately. Yet although *Collective Animal Behavior* is scholarly and insightful, it is also a very accessible and easy read. This accessibility largely stems from the honest, personal approach with which the author starts his book: "...anyone who works with me can confirm that I can be slightly single minded about how I do things" (p. ix). Sumpter has studied many interesting facets of collective behavior, and he is currently a professor at the Mathematics Institute of Uppsala University in Sweden. He, along with two collaborators, also has a blog on collective behavior to disseminate this field of research to the public.

The focus of the book is on how interactions between organisms produce group-level patterns, such as fish schools or spiders' social webs. Why do these interactions evolve? What

mechanisms ensure that these patterns can be formed and maintained? Sumpter skillfully builds bridges between mechanistic and functional approaches. In his own words, "Mechanisms should not simply be considered as a way of obtaining parameters for the cost-benefit curves of functional models. Rather, we should aim to form functional explanations that fully account for the underlying mechanisms" (p. 11). Filled with examples of how considering both mechanism and functional explanations can lead to a much deeper understanding of biological phenomena, the book takes a refreshing view that piqued my interest and made reading an intellectual delight.



The tool that Sumpter uses to present, analyze, and make us understand collective behavior is mathematical modeling. Models are excellent tools for deciphering fundamental dependencies between individual interactions and group-level patterns. Beyond demystifying biological phenomena, mathematical modeling also helps us search common cores of different biological systems, such as human applause and the synchronized flashing of fireflies. Models give us predictions that can be compared to field data or that can allow us to generate "what-if" scenarios that promote further research. The models presented in *Collective Animal Behavior* are simple and easy to understand—not solemn appendices or boxed texts that are tempting to pass over, but integrated parts of the biological story.

The content is well organized and covers nearly every aspect of collective behavior, starting with the questions of why and how animals form groups. A key advantage of living in a group is the ease of information transfer. How will this information transfer affect individual decisions? How will these individual decisions lead to adaptive colony-level patterns? How will these simple rules of thumb and individual decisions result in the spectacular movements of swarms and fish schools or make synchronization of behavior possible? We learn how ants and termites can build complex and intricate structures or form trail networks that are much larger than the individuals themselves. Later chapters present interesting generalizations on how social systems can self-regulate to avoid pitfalls such as congestion, and how complexity at the individual level affects the collective complexity. The book concludes by integrating two main themes: how different mechanisms of collective behavior evolved through natural selection and how, through mechanistic understanding, we gain insight into the function of biological systems.

Collective Animal Behavior provides an excellent synthesis of mathematical modeling and biology with experimental and theoretical studies. A few introductory chapters to the book could have captured more readers from the student population, but this volume does come with a homepage (www.collective-behavior.com/Site/Home.html), and the author has generously made many of the models he constructed available to those who want to run their own simulations. If the author keeps this portal up to date and his blog active, I am confident that readers interested in collective behavior, modeling, artificial intelligence, behavioral ecology, and evolution will enjoy not just the book but the complete interactive package.

ISTVAN KARSAI

Istvan Karsai (karsai@etsu.edu) is a theoretical biologist and an associate professor in the Department of Biology at East Tennessee State University in Johnson City, Tennessee.