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The strategy concept and John Maynard Smith's influence on theoretical biology

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Abstract. Here we argue that the concept of strategies, as it was introduced into biology by John Maynard Smith, is a prime illustration of the four dimensions of theoretical biology in the post-genomic era. These four dimensions are: data analysis and management, mathematical and computational model building and simulation, concept formation and analysis, and theory integration. We argue that all four dimensions of theoretical biology are crucial to future interactions between theoretical and empirical biologists as well as with philosophers of biology.

Introduction

No-one could dispute that John Maynard Smith was one of the towering figures in theoretical biology during the second half of the 20th century. His influence has been far reaching, both because of his own contributions to the field and his encouragement of many younger theoretical biologists, mathematicians, economists, and philosophers of biology. His many students and protégées have recently discussed what the field owes to John in eulogies and commentaries, so we can refer readers to these accounts (Charlesworth 2004a, b; Spratt 2004; Szathmáry and Hammerstein 2004; Karlin 2005; Michod 2005; Sigmund 2005). Here, as a way of honoring John's memory, we want to discuss just one of his numerous contributions that is now solidly entrenched within the framework of theoretical biology, namely the notion of strategies. Rather than giving a detailed historical account of the development of his ideas about strategies, which would require more space than we have, we will discuss how the strategy concept, as used by John Maynard Smith, reflects a specific style of scientific argumentation. This style is characteristic of a highly inclusive conception of theoretical biology, one that spans experimental, mathematical, conceptual, and integrative approaches and is thus an important model for current efforts to re-position theoretical biology in the post-genomic age.

Before we can begin our discussion of the role of the concept of strategies, we have to briefly define what we mean by theoretical biology. The history of theoretical biology in the 20th century is complex, as it lacks the coherence of a well-defined experimental research program or even the disciplinary identity that comes with a specific methodological approach (such as functional biology), a shared set of objects and techniques (as in molecular biology), or the study of a particular process (e.g. evolution). Theoretical biology can best be understood as a set of somewhat diverse questions, approaches and research agendas that nevertheless share a family resemblance. Quantification and mathematical modeling have clearly been important, but there have also been several more conceptually oriented contributions that have led to valuable insights. In recent years questions of data analysis and computational methods have risen in prominence, but so have collaborations between theorists and experimental biologists. In short, and in agreement with Maynard Smith, we submit that any attempt to define a core or an essence of theoretical biology, or to limit its scope to just one or a few methodological approaches (such as mathematical modeling), is a futile exercise. We also argue, again following Maynard Smith, that conceptual analysis, theoretical integration, and even well-founded speculation, are all legitimate aspects of theoretical biology (Maynard Smith and Szathmáry 1995).

The four dimensions of theoretical biology

There are at least four different, yet interrelated, aspects of theoretical biology in the post-genomic age that are important to the future of the field. Firstly there is the need to analyze, organize, and manage large amounts of data. This is the domain of bioinformatics and of certain areas of computational biology. The challenges of data analysis and representation are substantial; not only are we currently in a phase of exponential growth in the amount of data available, there are also different data types that need to be connected (for example, integrating sequence information and medical histories). Data mining is nowadays a desired skill for theoretical and experimental biologists alike; in many ways the computational and mathematical tools developed in bioinformatics have become the microscope of the 21st century, allowing us to "see" new connections and structures. But, as the notion of data mining already suggests, it is impossible to separate bioinformatics from the more conceptual and theory-driven dimensions of theoretical biology that provide insights into what counts as a desirable research objective.

The second area of theoretical biology that we would like to distinguish involves mathematical and computational model building and analysis. The last decades have seen a substantial expansion in available simulation and modeling approaches (ranging from standard systems of differential equations to agent-based models and models in spatial ecology), not to speak of the substantial increase in computational capacity. Model building and simulation have thus become an integral part of many areas of biology. They are also a legitimate part of theoretical biology proper, where the emphasis is not so much on creating an accurate mathematical representation of particular processes, but on gaining insights of a more general nature by means of abstract representations of these processes. Examples of this kind of analysis are the Price equation or the fundamental replicator equation (Price 1970; Hofbauer and Sigmund 1988, 1998; Grafen 2000; Page and Nowak 2002; Komarova 2004; van Veelen 2005). In both cases an abstract formulation of fundamental properties of evolutionary dynamics has led to major insights, and is applicable to a variety of different cases. Maynard Smith used mathematical modeling and analysis in a similar vein both in his research and his pedagogical endeavors (Maynard Smith 1958, 1968, 1974, 1978, 1982, 1989; Maynard Smith and Szathmáry 1995). One important goal of this kind of theoretical biology is to inquire to what extent different phenomena can be understood as instances of similar underlying processes or dynamics. As we will discuss below, the concept of strategies and the game theoretical framework of which it is a part have revealed fundamental similarities between diverse biological phenomena, from mating to developmental plasticity.

In our view, concept formation and conceptual analysis constitutes the third area of theoretical biology, one that is also related to many ongoing efforts within philosophy of biology. Conceptual analysis is often closely linked to mathematical analysis, as many theoretical ideas in biology are expressed in formal terms, but in our opinion it deserves to be identified as a distinct part of theoretical biology. As the examples below show, it is precisely through the application of a *concept*, such as strategy, to a wide range of phenomena that new insights often emerge. Darwin’s own analogy between artificial selection, which he knew from first-hand experience, and inferred processes in natural populations is the best known example of the power of this approach. As more data and more powerful computational tools become available, the importance of concept formation and conceptual analysis to aid in the discovery of similarities between different systems and processes is likely to increase.

The fourth area of theoretical biology involves theory integration. This is especially important today as the life sciences are in a phase of rapid expansion and ever increasing specialization; while at the same time biological concepts are increasingly being applied outside the traditional boundaries of the life sciences, e.g. in artificial life. Such interactions can be extremely fruitful, as has been the case with economics and biology where there have been multiple waves of mutual influence (Hammerstein and Hagen 2005).

Summarizing our conception of theoretical biology, we see it as both foundational and practical, mathematical and conceptual, and in close partnership with empirical research. Theoretical biologists are engaged in all areas of biology, managing and analyzing data, developing new methods for representing and visualizing data, building mathematical models and developing simulations, formulating concepts that adequately represent the underlying biological phenomena, and contributing to the theoretical integration of the life sciences. A theoretical biology that honors the memory of John Maynard Smith is one that accomplishes these goals while avoiding baroque mathematics detached from reality.

The strategy concept

In classical game theory, a strategy is conceived as a plan of how one would behave in all the different decision situations that might occur during the game (Von Neumann and Morgenstern 1953; Selten 1991; Gintis 2000; Gigerenzer and Selten 2001). Mathematically speaking, a strategy maps a player's possible decision situations to actions (or probability distributions over actions). Instead of deterministically assigning a definite action to a situation, a strategy may also contain the instruction to randomize action, e.g. by flipping a coin. This is important because unpredictability can be of great relevance in strategic interactions.

An example of a decision is 'whether or not to take an umbrella when leaving the house', and the concrete situation may be 'overcast sky'. In a game of chess, the list of decision situations contains all possible configurations of figures on the board that may arise during a game. Correspondingly, a chess player's strategy would be an incredibly long list of instructions – the game of chess was indeed designed for its complexity. In a typical card game, such as poker, we see another aspect that needs to be captured by the notion of a strategy. It is not sufficient to characterize a decision situation by all the aspects of the real world that a player can perceive at the moment of choosing between different actions. A poker player is well advised to keep track of what cards the players used on previous moves, i.e. to keep track of the history of the play.

This means that the appropriate game-theoretic notion of 'decision situation' includes all the information about the past and present that is available to the player. Therefore, in principle, even learning processes can be interpreted as strategies. Having in mind human individuals who are planning their future decisions, classical game theory thought of strategies as being generated by rational reasoning. Examples are the general preparing a battle or the husband planning to persuade his spouse to join in with an activity that he prefers – the so called battle of the sexes.

John Maynard Smith's adoption of the concept of strategy

John Maynard Smith introduced the notion of strategy to biology but gave it an ingenious new interpretation. While he agreed with game theorists in considering the strategy as a list of "how to act in different situations", he introduced a radically different view of how strategies are generated. In the field of evolutionary game theory, pioneered by Maynard Smith, it is the process of natural selection and not an individual organism that exerts the choice between strategies. Strategies are inherited traits that control an individual's actions like a computer program governing a robot (Maynard Smith 1982, 1988). Economists were so excited about this new way of conceptualizing their own theory that they adopted it from Maynard Smith, replacing natural selection by appropriate social learning processes, where individuals, for example, have a tendency to imitate the more successful members of their society. Under appropriate assumptions, the same 'replicator equation' can be interpreted as natural selection or population learning.

In the field of animal behavior, strategic analysis has greatly improved our functional understanding of why animals do what they do. For example, the following simple strategy captures in many cases the essence of animal ownership: 'be ready to engage in a physical fight for a resource when you are in possession of it before the opponent arrives; avoid escalated fighting when the opponent had it first'. This strategy is similar to a car driver's strategy that tells him how to behave when two cars approach an intersection from two different directions: 'accelerate if the other car comes from the left side, hit the break if it comes from the right'. In both the animal ownership and human driver examples, it pays under a wide range of assumptions to play the respective strategy if the other members of the population play it as well. Switching to another strategy involves a crash (or escalated physical combat) that may not be worth it. In this sense, animal ownership as well as the driver's behavior at an intersection is maintained by the logic of deterrence.

In our short discussion of owners and car drivers, we did not refer to classical game theory but used the powerful analytical principle introduced by Maynard Smith. This principle is to search for strategies with the following property: if all members of a population play this strategy, it is best for an individual to also play this strategy. In the context of natural selection such a strategy is called 'evolutionarily stable' or an ESS.

In the car driver example it is obvious that if all other members of a population follow the conventional rules for priority of access at an intersection, it would indeed be best for an individual to follow these rules too. Not all traffic rules are self-enforcing in this sense – hence the role of police in enforcing traffic codes. In the evolutionary games analyzed by Maynard Smith, the conditions for evolutionary stability are very similar to those that characterize a Nash equilibrium (the central solution concept of classical game theory). In this sense the parallel between the choice of strategy made by natural selection and that by a rational decision process is more than a metaphor (Hammerstein 1996).

The analogy between natural selection and strategic analysis helps us understand animal behavior, but it can also be used to address important issues in the evolution of development and ontogeny. Phenotypes can be interpreted as expressions of a developmental strategy. The strategic view of ontogeny (e.g. Hagen and Hammerstein 2005) implies that individuals within a species will not necessarily develop along the same path. Just as moves in a game depend on the state of play, development is sensitive to particular environmental conditions, taking one path in some circumstances and another path in others. Although members of a species develop the 'standard equipment' of morphological structures, such as the heart, lung, etc., they may differ in important respects. Male fig-wasps, for example, may either develop wings or forego wing production to instead develop giant mandibles and heavy armaments that would have been difficult to integrate into the design of a 'flying machine'.

A well-studied empirical example of 'strategic ontogeny' is that of water fleas (*Daphnia*). Sometimes but not always a water flea populations occasionally experience high predation pressure. Water fleas are capable of developing a helmet-like morphological structure that protects them from predators (Brooks 1965). The helmet's construction requires substantial investment of resources, however, that could be used for reproduction instead.

If water fleas can sense the presence of predators far enough in advance of an attack, the strategic view of ontogeny would suggest that they should build the helmet only when needed. Can they sense their predation risk? Predators of *Daphnia* leave chemical traces in the water that *Daphnia* use as an environmental cue. In experiments, the relative helmet length of *Daphnia* almost doubles in the presence of caged predators (Agrawal et al. 1999). Helmet development is thus conditional on information about the environment that is acquired during ontogeny. The data show that when predators are present, the helmets lower mortality risks from predation dramatically. Like a good chess player, water fleas are making developmental 'moves' that reveal evolved 'strategic expertise'.

The strategy concept as an example of a more inclusive theoretical biology

The concept of strategies, as it was introduced by Maynard Smith and subsequently applied to many different areas within biology, serves as a perfect illustration of the multiple dimensions of theoretical biology advocated in this paper. The idea that strategies are not confined to choices of individuals, but can also include inherited traits that are products of natural selection, transformed the way evolutionary biologists looked at social behavior as well as other aspects of organismal biology (Noë et al. 2001; Hammerstein 2003; Hagen and Hammerstein 2005). The introduction of a theoretical concept – strategy – thus profoundly changed the interpretation of already existing data and inspired novel patterns of data collection. In this sense the concept of strategy can be said to be part of the bioinformatics or data analysis dimension of theoretical biology.

The game theoretical origin and the subsequent refinement of the strategy concept to include such novel ideas as evolutionary stable strategies have been reflected in a whole new family of mathematical models within evolutionary biology (Maynard Smith 1982, 1988; Hammerstein 1996; Hofbauer and Sigmund 1998; Sigmund 2005). Even the most cursory review of current mathematical approaches within the behavioral sciences reveals how much game theoretical methods have contributed, but also how much the further development of mathematical game theory and its applications in economics have been influenced by biological considerations (Axelrod 1990, 1997; Skyrms 1996, 2004; Bicchieri et al. 1999; Gintis 2000; Bowles 2004). While nobody would question the claim that the mathematical analysis of behavior based on game theoretical ideas is part of theoretical biology, we also emphasize its connections to the other dimensions of theoretical biology described above, in particular concept formation and theoretical integration.

In many ways the idea of strategies is a prime example of conceptual innovation within theoretical biology. As with most innovations, it did not emerge de novo, but was co-opted from economics (not unlike Darwin's own intuitions, which also owed a lot to economic theory). But in the transfer between different theoretical disciplines the concept itself was transformed; strategies were no longer confined to human actors (and rational ones at that), they were now seen as products of natural selection, as an adaptation to certain types of environment. The evolutionary focus brought about new perspectives in so far as questions about the evolutionary stability of strategies became a major concern. This in turn led to new types of mathematical analysis, focusing, for instance, on population-level dynamics and repeated games (Hofbauer and Sigmund 1998). In the case of the strategy notion in biology, conceptual and mathematical analysis have thus always been closely linked.

But the concept of strategy and the mathematical framework that emerged around that concept have also led to increased theoretical integration of a variety of traditionally distinct domains of biology. While the idea of strategies was first applied to simple cases of animal (including human) behavior, its range would soon be expanded to include different forms of learning. Especially in cases of repeated games, so characteristic of interactions within social groups, learning from previous interactions with the same individual would be a crucial component of the decision making process. Ideas such as the notion of reciprocal altruism depend on this ability of organisms to learn from previous experiences. But learning is not just a property of brains and neural memory. Other systems of the body, such as the immune system, also "learn", i.e. they extract information from the environment and store this information in their own memory system. "Learning" can then be seen as a strategy of organisms to deal with different types and degrees of unpredictability in their environment. And different learning systems, including the genetic, immunological, neural and cultural, operate on different timescales and with different degrees of complexity.

In light of current attempts to integrate developmental with evolutionary biology in the form of the proposed 'Evo Devo' synthesis, it is worth considering developmental plasticity as a form of strategy that has both a genetic and an epigenetic basis (e.g. Hagen and Hammerstein 2005). Phenotypes can then be considered as developmental strategies. Such a strategic view of development can have far reaching consequences, as it can help to address one of the biggest obstacles for the Evo Devo synthesis, namely the difficulty of merging population-based evolutionary approaches with the more typological concepts of developmental biology. As we currently do not possess significant amounts of data on population-level genetic variation within developmental systems, the theoretical concept of phenotypes as strategies should allow us to at least study the potential evolutionary dynamics of such variants. This might well be the first step towards a mathematical foundation for Evo Devo, one of Maynard Smith's interests during his later years (Raff 1996; Hall 1998; Maynard Smith 1999; Bonner 2000; Wagner 2000, 2001; Wagner and Larsson 2003; Amundson 2005; Laubichler 2005).

These few examples already demonstrate how the idea of strategies, when employed in a variety of different contexts, contributes to theoretical integration, one of the aspects of theoretical biology described above. Emphasizing theoretical integration, which often receives less attention than other dimensions of theoretical biology, allows us to ask a whole new set of biological questions. What is the range of application of a concept such as strategies? What are the similarities and differences between different models that are based on strategy as a central concept? Can we transfer insights gained from the analysis of one particular system to another domain? Is there a more general notion of strategy that captures something fundamental about biological systems? These questions are in part philosophical, but they also have a practical significance for theoretical biology. The goal of any theory is to accomplish at least some level of generality, but it is not always clear how this can be achieved. Biological systems are characteristically complex, hierarchical, and composed of many different elements. This makes reduction to the properties of a small set of shared building blocks more or less impossible. Unification, then, means identifying shared processes and dynamics that are characteristic of a wide range of different phenomena. Capturing these processes with the right kinds of concepts and associated mathematical representations is thus the prime challenge for theoretical biology in the post-genomic age.

Conclusion

To anyone who surveys the range of contributions to current theoretical biology, for instance by analyzing the table of contents of the *Journal of Theoretical Biology*, the field must look healthy and vigorous and at the same time lacking a clear focus. The multitude of mathematical models and the range of phenomena to which these are applied is certainly impressive, but any innocent observer will have a difficult time seeing the forest among all those massive trees. As he did so often, John Maynard Smith pointed us in another direction, away from getting caught in details and towards the project of conceptual and theoretical integration. In this paper we have only used one of his ideas – the concept of strategies in biology – to briefly sketch how theoretical biology can encompass much more than just mathematical modeling.

Applied to theoretical biology as a whole, Maynard Smith's contributions highlight the importance of conceptual analysis and theoretical integration. And this can also be the beginning of a renewed friendship between theoretical biologists and philosophers of biology.

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