Concept

The Strategic View of Biological Agents

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What is a strategy? The term *strategy* has been used by many disciplines in a variety of contexts ranging, for example, from the game of chess and the Cuban missile crisis to markets, computer networks, political systems, cooperation, mating, parasitism, intragenomic conflict, and growth patterns. Despite this wide use of the term, only one discipline—game theory— has carefully examined the concept. In game theory, a *pure strategy* is a complete plan for a player's choices in the game under consideration. A chess player's pure strategy would thus have to specify all moves in all the situations that might arise on the chessboard during a match.

Whereas in chess the pieces on the board are visible to both players, in many games players have only limited information about the objective state of affairs. In a number of card games, for example, a player's one hand is not known to the other. Thus, players' strategies must make use of the subjective state of affairs. This state is often referred to as the information situation or information set. Strategies can therefore be viewed as a map of information states to actions (adding the term "conditional" to "strategy" is thus redundant). For agents with memory, the information situation often includes knowledge about the course of play. This is of great importance to many applications and it demonstrates the richness of the strategy concept.

A lot can be gained from widening the concept's scope beyond that of pure strategies. What game theorists call a *behavior strategy* is a plan that assigns to each situation a probability distribution over the choices in that situation. This distribution may or may not place all weight on one choice.

In a behavior strategy, the choices for different situations are stochastically independent.

Another concept is that of a *mixed strategy* which differs from that of a behavior strategy as follows. In a mixed strategy, the player chooses among a number of pure strategies according to a probability distribution over these pure strategies—as opposed to choices during the game. To illustrate the difference, let us compare a behavior strategy with a cooking recipe. The recipe may at some stage contain the instruction to flip a coin in order to decide about mild or hot spicing. In contrast, a mixed strategy would flip a coin to decide between Italian and Mexican recipes. The concept of a mixed strategy can be extended to mixtures of behavior strategies.

Subtleties of the strategy concept It can be shown for *extensive games* with *perfect recall* that every mixed behavior strategy is *realization-equivalent* to a behavior strategy (Kuhn 1953; Selten 1975). The description of strategic behavior by mixed strategies introduces a spurious multiplicity, however (Hammerstein and Selten 1994). To illustrate this, consider the biological Hawk-Dove game played between an owner and an intruder. This game has two situations (owner, intruder) and two possible actions (escalate, display) for each situation. The behavior strategy "in each situation flip a coin in order to choose an action" can be realized by two distinct mixtures of pure strategies, namely "play all four pure strategies with probability $1/4$" or "play Hawk or Dove, each with probability $1/2$." The example shows that the description of behavior by mixed strategies introduces a spurious multiplicity of strategies. For biological purposes it therefore makes more sense to use the behavior strategy concept than the mixed strategy concept.

Insights about realization equivalence have to be taken with a grain of salt when game theory meets systems biology. The randomized switching between strategic modules is different from a randomized switch within a module when robustness to errors is important. Confusing entire recipes is different from inaccurate action during one step of realizing a single recipe.

How strategies are generated   The mathematical depiction of a strategy does not reflect the process that generated it. By itself the strategy concept does not even contain the idea of "doing well" in a game. What a strategy is good for thus depends on the process that generated it. The strategy-generating process may be genetic or cultural evolution, learning, reasoning, or soliciting the advice of an astrologer. With the exception of the latter, these processes often, but not always, generate similar strategies.

Conventional game theory mainly invokes *rational decision making* as the process that chooses a strategy with the aim of maximizing some utility. Assuming that all players in a game know that all players know that all are rational, it is possible to analyze games without being hampered by facts. Any discrepancies between human behavior and theoretical results can be disregarded by saying that humans are not fully rational and thus do not fall within the scope of this theory, which only deals with fictitious rational players. From this perspective, game theory looks like a rather philosophical endeavor, as was recognized by Harsanyi and Selten (1988). In a herculean effort, they explored what the concept of economic rationality "really means." Roughly speaking, a baby would have to make a lifetime consumption plan, taking into account its retirement options at age 65 and the mathematical intricacies of Harsanyi and Selten's equilibrium selection theory. Compared to game-theoretic views on rationality, human rationality is obviously quite bounded. On the positive side, as Harsanyi and Selten would say, it is of course possible to use the discrepancies between economic rationality and the facts as an interesting starting point for investigating the patterns of real decision making in humans and other organisms. In this sense, the conventional research program in game theory is more fruitful than it might appear to a biologist.

Nonetheless, if choosing a strategy always required rational decision making, the relevance of the strategy concept to biology would be quite limited. Fortunately, biologically plausible processes like evolution and learning can generate strategies that satisfy important rationality criteria.

Under the heading *method of fictitious play* (Brown 1951) game theorists long ago started to study the strategies generated by learning in games. The original motivation was not an interest in learning as such, however, but an interest in using learning algorithms to compute Nash equilibria (Nash 1951), the "candidates" for rational solutions (in a two-player game a *Nash equilibrium* is a pair of strategies, each of which is a *best response* to the other). A strategic solution, once found, could then be taught to business managers. Given this motivation, it was still not clear how game theory could explain the unschooled behavior of real organisms.

A major breakthrough linking game theory with the real world was achieved when Maynard Smith and Price (1973) initiated the field of *evolutionary game theory*. In the body of theory that originated from their seminal paper, strategies have at least some heritability and are generated by genetic evolution through mutation and selection. Thus strategies are part of organismic design. The key idea uniting this "blind" biological process with the choice process of rational agents is the evolutionarily stable strategy (ESS). An ESS is a strategy that, when played by the vast majority of individuals, cannot be replaced by mutant strategies. For a large class of models, an ESS satisfies the Nash equilibrium conditions. This means that the highly developed strategy concept of rational decision theory can be applied to all organisms, including viruses, bacteria and plants. Conversely, economists now often try to interpret observed examples of optimal strategic behavior in humans as generated by a learning process similar to natural selection.

Strategic perspectives on key biological issues   Natural selection is a process that "learns" about survival and reproduction of a particular organism in a particular environment and stores the learned strategy in that organism's genome. When particular caterpillars eat wild radish plants, for instance, the plants produce 10-fold higher concentrations of mustard oil (an "expensive" toxin) on newly formed leaves. Although the plants cannot avoid the initial attack, they deter subsequent feeding by the caterpillars and other herbivores (Agrawal 1999). Wild radish thus follows a simple evolved strategy: invest more in the production of chemical defense if sensing an attack. The strategic view of biological agents directs our attention to this *conditionality*, i.e., to the translation of information into action.

Realized ontogeny is not to be confused with the developmental strategy that gave rise to it. If we look at a chess player performing in a game, we see only what this player does under the specific circumstances of that game. It would take observations of many different games to infer the underlying strategy of the player if it exists. Similarly, one has to study the development of wild radish plants under different circumstances to identify their *developmental strategy*. Although the variation in concentrations of mustard oil seems to be largely environmental (i.e., caused by the presence or absence of a caterpillar attack), the underlying strategy is genetic. This gives us a new perspective on the *nature-nurture problem* and shows that the observed environmentally determined variation is fully compatible with the view that genes play a central role in determining this variation (e.g., Hagen and Hammerstein 2005).

Whether genetically evolved strategies are best conceived as pure, mixed, or behavior strategies, or as genetic polymorphisms, depends in particular on the nature of switching mechanisms. In Pacific Salmon, there are two distinct male phenotypes that differ in size and fighting ability (Gross 1985). The

larger male with superior fighting abilities is called *hooknose*; the smaller, weaker male is called *jack*. Jacks mature early and hooknoses mature late. There are several qualitatively different ways in which morphological type can be determined. First, there could be a genetic difference among the types that plays the role of a switch (genetic polymorphism). Second, there could be a mechanism that flips a coin (mixed strategy). Third, the males could use a cue that indicates which type would have more success given their current state (pure strategy or behavior strategy). Behavioral geneticists would typically emphasize that in the first case the phenotypic variation is largely explained by genetic variation, whereas phenotypic variation is largely explained by environmental variation in the other two cases (reality would be more complicated, of course). This standard analysis conceals the underlying similarity in strategy of all three cases. In all three cases, the hooknoses would have hooked jaws and canine-like teeth for fighting and a cartilage back shield for protection (these features are less pronounced in jacks). Both hooknoses and jacks would possess most, if not all, of the genes for both types. The main difference would be only in the nature of the *switch*.

Biologists first thought that the switch used by Pacific Salmon was genetic. Breeding experiments seemed to support this view. Theoreticians emphasized both the genetic and coin flipping possibilities. However, further studies strengthened the case for a state-dependent switch (Gross 1991). The facts are that if males have sufficient fat reserves (their state) at an early age, they tend to become jacks. The switch is important because it would be dangerous to try and swim to the spawning site without enough fuel, i.e., fat. If a male has not accumulated enough fat by spawning season, it must feed in the ocean an additional year. This affords it the opportunity to become much larger and paves the way for the specialized fighting adaptation of the hooknose.

In view of this strategic analysis, the behavioral observation that hooknoses are better competitors than jacks at the spawning site might hide the possibility that the strong hooknoses—facing high mortality in the ocean—have lower fitness than the weak jacks. The "winners" then would be the "losers." We also learn from this biological example that the identification of strategies requires a look at the entire lifespan of individuals. It therefore seems quite natural that the strategy concept has received considerable attention in *life history theory* where it is often termed *norm of reaction* (Stearns 1992).

Does the mixed strategy concept make sense? Few economists believe that when it comes to important decisions, managers flip coins, as in a mixed strategy. The intuitive distaste for mixed strategies has led to interesting theoretical investigations. If an individual has two or more behavioral options, but also some "private" information about the relative value of the options, one might always expect a strategy to evolve where the individual chooses the option with highest value. In light of this idea one might expect mixed strategies to always disappear as solutions of games when there is sufficient private information. In classical game theory, this idea has been expressed by Harsanyi in his famous *purification theorem* (Harsanyi 1973; Binmore 1992). A basic assumption of the theorem is that the private variables of different players of the game are statistically independent.

A recent analysis by Leimar et al. (2004) suggests that the applicability of the idea may be limited to this case of statistical independence. When the private variables of interacting individuals are correlated, randomized strategies might instead be the typical outcome. For example, if it is better to produce females when it is warm, then without randomization all offspring will be female in warm weather. This creates an incentive, however, to produce males, the otherwise less beneficial sex.

Biological reality seems to support the arguments of Leimar et al. (2004). Studies of the European kestrel (Pen et al. 1999) revealed that males would gain more benefits than females from being produced early in the season. The reason is that male breeding opportunities in their second year depend strongly on getting an early start in the first year. Simple models suggest that mothers should play a "bang-bang" strategy where they produce only one sex early in the season and only the other at a later stage. Real kestrels, however, seem to randomize at all stages, shifting probabilities as the season progresses.

Genetic polymorphism and extended phenotypic plasticity
So far we have seen that the strategy concept is valuable for analyzing development, life history, and phenotypic plasticity. If some genes "program" a decision mechanism that uses environmental information (e.g., season) or internal physiological states (e.g., fat reserves), this decision mechanism might in principle also gather relevant information by "looking" into the organism's own genome. Consider a population living in a patchy environment with small migration. Imagine a focal gene with two alleles A and B that are both maintained in the population (genetic polymorphism) because some patches favor allele A and others favor B. If it is important for an organism to know whether it lives in one or the other patch type, one way to figure this out would be to investigate which of the two alleles of the focal gene are present in the organism. This would allow the organism to make use of information "collected" by the last few generations via the effects of selection acting on the gene under consideration (Leimar et al. in press). Without thinking in strategic terms, a geneticist would have a hard time recognizing this kind of extended phenotypic plasticity, and would instead use the same example as a case for nonplasticity because the genetic polymorphism determines the observed variation. We see here once again that

although the basic strategy concept does not involve genes, it is important for understanding genetic roles that do not emerge from the standard genetics framework.

Final remarks Biology is polarized in its attitudes toward the strategy concept. In one camp are the mainstream systems biologists, molecular biologists, and physiologists who have been extraordinarily successful at elucidating fundamental biological mechanisms and their dynamics, such as the circadian clock, cell division, and cardiovascular regulation. This camp studies internal mechanisms whose functions are generally intuitively obvious. The big question is not why we have a circadian clock but how it works. Because strategic analysis typically ignores implementation details, to date it has offered relatively little to these biologists.

The other camp includes behavioral and evolutionary ecologists, functional morphologists, and some social scientists interested in functional properties that are often not intuitively obvious and can only be understood through strategic analysis. This camp has found strategic analysis so useful that it tries to apply it to domains where most biologists fail to see agents that could execute strategies. The most famous such example is Dawkins' selfish gene. Here, simple molecules are seen as strategic agents although they seemingly have no computational capabilities that would allow them to translate information into action, as the strategy concept requires. This criticism fails to appreciate that molecules can have context-dependent interactions with other molecules that are regulated by particular chemical domains. Burt and Trivers' (2006) review of the literature on selfish genetic elements reveals numerous examples of context- and timing-specific molecular "actions" which are difficult to understand without a strategic framework. At the other extreme of biological organization, some biologists in this camp (e.g., Richerson and Boyd 1999; Wilson 2002) argue that conceptualizing social groups as strategic agents explains important phenomena, such as large-scale cooperation and religion (for one critique, see Hagen and Hammerstein 2006).

The future of biology, we believe, will see much closer cooperation between these two camps of biologists. On the one hand, systems and molecular biologists will increasingly encounter mechanisms whose functions are not obvious so that strategic analysis is needed. On the other hand, behavioral and evolutionary ecologists will discover that strategic analysis depends critically on details of the implementation. Such analysis usually requires an understanding of errors, for example, but the nature of errors frequently depends on mechanistic detail.

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