Evolutionary Simulation Models and its Application to The Handicap Principle

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Simulations have been used in the field of Artificial Life as well as in biology, physics or engineering for many different purposes. One of them is modeling systems of interacting units. However the use of simulations as models is a rather new tool and there are still some doubts about the scientific value of their results. Some of the issues about using simulations as models in science are going to be discussed. Evolutionary simulation models are of interest in the field of adaptive behavior since one of its main concerns is the evolution of biological systems. In order to study the adaptive behavior of a system you have to model its dynamics (behavior) and a good way to do it is by implementing an evolutionary simulation model of the system.

Evolutionary simulation modeling can be a very useful tool; however it has to be handled carefully. First it is going to be explained what is meant by evolutionary simulation models using the same definition used by Bullock (1997) and trying to carefully establish a distinction between commonly used evolutionary techniques and evolutionary simulation models. Simulations have proved good in modeling systems of interacting agents such as those biologists are interested in. With a particular example—proving the validity of Zahavi's (1975) handicap principle on the stability of honest signaling—it is going to be shown how an evolutionary simulation modeling approach can be a much better way of dealing with this type of problems than previous attempts using action-response games. At the end it should be clear some of the pros, the contras and the limits of using simulations as models.

The use of simulations has become very popular in the field of artificial life as well in many other sciences and engineering. Bullock (1997) uses the term evolutionary simulation models as "the use of computer simulations as evolutionary models of adaptive systems", highlighting that "I do not wish to refer to just any use of computer modeling within evolutionary biology, nor any evolutionary simulation design within artificial life". The use of computers in evolutionary biology usually lacks modeling the very important small details that determine the completeness of a model with respect to the problem being studied; there is also lack of interest in the dynamics, focusing only on stability of the final states. On the other hand evolutionary simulation design in artificial life usually lacks applicability to real world problems. For Bullock the most important aspect is the evolution of the simulation is how it unfolds in time—the dynamics of the system more than its final state—a characteristic similar to that of evolutionary or dynamical systems. This style of modeling can be of much interest to theoretical biologist or anyone interested in the adaptive behavior of a system, however it is not being used much maybe because of its novelty and controversy. It can also appear interesting to an artificial life enthusiast, however most of what has been done so far lacks the scientific rigour needed to classify as an evolutionary simulation model.

As it is going to be explained along this essay, evolutionary simulation models are to be used as a modeling tool of a scientific theory—that is, it is indispensable for the simulation to have a hypothesis to prove coherent—and that evolutionary simulation models are not meant to reproduce reality nor to replace experimental data.

Individual-based evolutionary models are strong for modeling systems of interacting agents such as those concerning biologists (i.e. Social behavior, communication, etc) since many hypotheses about these kind of systems are not easily obtained with mathematical models. In order to study a system using evolutionary simulation modeling the system must consist of interacting agents competing for a certain resource. The system will evolve over time, agents must reproduce in a way that the average fitness of the whole population increases and information about the parents must be inherit by their offspring with a certain degree of variability.

Simulations are used for several different purposes, they can contribute with conceptual as well as methodological approaches in whatever field they are being used. However, since this a new technique there is still some controversy about how simulations can be used as models. This issue is presented by Di Paolo, et al. (2000). Who also presents 2 extreme perspectives about the use of simulations as models; the first one sees simulations as 'emergent computational experiments', where simulations are as unrealistic and simple as possible and its outcome has to relate in some way to an existing system. On the other hand some people treat simulations as realistic experiments. For them the outcome of the simulation has to be an exact representation of reality, that is, simulations have to behave exactly in the same way as the real world does—that is, from the same initial condition a simulation has to exactly replicate the behavior of the system being modelled —in order to be able to generate new hypothesis or predict new behaviors. For a further discussion and some references of this 2 opposing perspectives see Di Paolo, et al, (2000). The two perspectives differ in the way of approaching the problem, one wants to model exactly what is going on (life-as-it-is), the other wants with very simple rules emerge some pattern that relates to a particular system (life-as-it-could-be). As Braitenberg (1984) points in his law of "up-hill analysis and downhill invention" the second can be a lot easier, but it is less likely that you can use it to prove some hypothesis. The first approach can be useful for some purposes but when you are concerned about systems of interacting agents it can be impossible to create such a realistic simulation. Evolutionary simulation models lay somewhere in between this 2 perspectives, they have to include lots of detail and relations—or as much as is needed to investigate the coherence of a hypothesis—but they don't have to exactly replicate reality.

Using simulation to make science can raise the question of what new information can be obtained from it, if you know how the simulation works (because you made it) and you know the initial condition. A simulation can help you visualize the dynamics of the system in a simpler way than how equations do. Equations can sometimes be difficult to solve, or problems difficult to visualize from the equations. Simulations can be useful to realize the existence of previously ignored relations, or can even be useful to discard a hypothesis if the outcome of the simulation does not turn out as expected. However, simulations can also be dangerous tools. The scientist has to be aware of the relations being modeled and that simulations are not obvious at all, they have to include as much detail as it is necessary and the result has to be analyzed thoroughly with respect to the model. Di Paolo, et al, (2000) describes simulations as 'computer experiments' and compares them with 'thought experiments' in the way they are used to make science. Simulation results are not substitutes for empirical evidence, they can help you demonstrate the logical coherence (or incoherence) of a hypothesis, also the result of a simulation establishes the plausibility of the hypothesis, and that does not mean that the model is absolutely true. Noble, et al. (2001).

To illustrate some of the problems about using simulations as models, I'm going to refer to the particular example of modeling communication. It is a theme that has caused some controversy (on this issue) and can point to some of the important aspects that a simulation must have and the limits of using simulations as a tool in science. Rather than mentioning all the different attempts to model communication, I'm going to point some of the problems raised on some of the attempts dealing with simulations.

If the simulation is going to be used as a model it has to be made so as to prove a hypothesis or collaborate with some new knowledge, relation, or theory. One of the common problems that arise when using simulation is that they lack a scientific inspiration, some simulations can show very interesting results, but they contribute nothing at all to science. Noble (1998) claims that "those simulations that build on models and theories from theoretical biology will be much more likely to result in useful findings", which doesn't mean that those who are not are 'hopeless', they can still lead into some novel direction that we hadn't thought before. Werner and Dyer (1991) evolved a signaling protocol that aloud female stationary agents to guide male blind agents moving on a 2-dimensional grid world toward them. Their results are nice but they don't tell us much about the world or how the communication channel could have evolved. There is no applicability of their work.

The purpose of the simulation—proving a particular hypothesis—is not the only point that has to be taken into account. There have been several attempts to contribute to biological theories without success. Enquist and Arak (1993) used evolutionary simulation modeling to show that symmetrical signals were preferred by perceptual mechanisms. They used an artificial neural network which interacted with a genetic algorithm to model a natural visual system. At first sight their work seems to have great value, but upon repetition, analysis and complementation, Bullock (1997) and Bullock & Cliff (1997) show that the results obtained were biased by the methodology used. There were problems with the implementation of the genetic algorithm and of the artificial neural network which favored the results obtained. For further detail on these problems you can refer to the reference above. The example above show there are still problems with the understanding of the tools used for simulations. Unlike calculus, the tools used in simulations (such as dynamical systems, genetic algorithms, statistics, cellular automata, artificial neural networks, etc) are currently being developed. Most simulation users are not being taught this tools and the theory about them is still under-developed. Special attention has to be taken in small details such as time steps, grid-size, mutation rates or even the form of encoding the information feed into the simulation. Many models of real-world systems behave in a non-linear way which means they can be very sensitive to their implementation. What is going to be modeled has to be clear, and a right choice of parameters that better fit the phenomena being model has to be made, as well as some experimentation of how these parameters influence the evolution (including convergence, trajectories, basins of attraction, etc.) of the system. Some more work is still needed to establish a good methodology, as well as the might-go-wrong's-for the use of these tools in evolutionary simulation models.

Evolutionary simulation modeling has been successfully applied to clarifying the theory of the evolution of honest signaling. There had been some problems justifying honest signals being evolutionary stable—since there wasn't any known 'force' preventing 'cheaters' from displaying signals about some quality level they don't posses—and signaling systems are inherently honest and stable. Evolution is also supposed to find cheap and efficient solutions, which raises the question, why those extravagant wasteful signals evolve? There are lots of examples from biology of animals (even plants) that advertise their quality (or their need) by means of displaying a particular signal. A very good review can be found in Johnstone (1997). Zahavi (1975,1977) suggests in what he calls "The Handicap Principle" that the cost involved in displaying an advertising signal about the quality or the need of the carrier stabilizes its honesty. If there is a cost involved in wearing an advertising signal about the quality of the bearer, individuals that are healthier or wealthier can more easily afford to display the signal than those who are not. See Bullock (1999) for a review of Zahavi's latest book. Johnstone (1997) separates handicap models in 2 kinds. The first kind deals with the evolutionary stability of honest signals advertising quality, while the second one with the ones advertising need. A peacock with a very big and colorful tail can more easily attract a mate but at the same time it attracts predators, and probably a big tail reduces its escaping speed. There is a cost— being an easy prey—in wearing the colorful tail but there is also a benefit—being more attracted to females or controling more territory—and only the fittest individuals that can afford that cost—being fast enough to avoid predators—are going to be able to wear it. Another way to see the handicap principle can be explained in terms of begging chicks. Chicks beg louder—to their parents for food—according to their size and hunger, yet the more you beg the more food you get. Begging at the same time wastes energy, so the cost of begging—if you are not hungry enough—can be more than the benefit of getting food. High need signalers gain more benefit from a resource than low need signalers (food means more to you when you are really hungry!). Some attempts to prove the validity of the handicap principle had focused either on one or the other. Enquist (1985), Grafen (1990) and Hurd (1995) are examples of the first kind, assuming that the signaler quality affect the cost of signal production, while Godfray (1991) of the second kind, assuming that signaler quality affects the benefit of an observer's response.

Bullock (1998) expands Grafen (1990) game-theoretic model of the evolutionary stability of honest signaling increasing its generality and implementing it as an evolutionary simulation model. He concludes that Zahavi's handicap condition ceases to be either necessary or sufficient for the stability of honest signaling, and that stability of honest signals can be obtained from non-handicap conditions, as well as non-stability of honest signals can be obtained from Zahavi's handicap conditions.

Bullock changed Grafen's fitness function which "cannot accommodate the possibility that the fitness consequences of receiver responses might vary with signaler quality independently from the manner in which the negative fitness consequences of advertising vary with signaler quality" (Bullock (1998)), the new function implemented by Bullock was more general and could accommodate all the possibilities left by the other models. These models previous to Bullock tried to prove particular cases of The Handicap Principle, they all successfully showed that some handicap conditions reach stable honest signaling, but failed to conclude appropriately. Their models weren't general enough to become a prove of The Handicap Principle, they only showed that for special cases honest signaling is an evolutionary stable strategy and failed by overestimating their result.

If you are concerned about the adaptive behavior of a system your main interest involves the dynamics (i.e. behavior, evolution) of the system. Conventional action-response games focus on the stability of a final state of the system rather than on the trajectory taken by the system towards this final state. They are not interested in the dynamics, and therefore it is complicated to see how the system evolves in time. When dealing with problems concerning an individual-based system, such as those found in theoretical biology or economics, there are many small scale factors that influence the dynamics of the system and are very difficult to model as conventional action-response game. Game theoretic models cannot capture low level details of space, time and interactions among the individuals. Bullock (1998) made a grid-world implementation of Grafen's (1990) game with a population of signalers and a population of receivers and ran an evolutionary simulation to see the evolution of the playing strategies used by the players. It is important to note that Bullock is studying the *attainability* of honest signals which involves the dynamics of the playing strategies. The previous attempts only worried about the stability of honest signals and not how this could have evolved. Bullock's approach can tell us more about the dynamic-world (and our world is dynamic). The evolutionary scale is very big compared to a human life-time, and it can be given the case that an honest signaling case that appears to be stable by us is not stable. On the other hand there is still some importance in the way this equilibrium state is obtained and on its basins of attraction. Evolutionary simulation models can help us in this matter while the conventional action-response games used in evolutionary biology can't.

Noble (1998) comment:

"Bullock tells us that if signalers and receivers are in a situation in which signalers always want positive responses and receivers want to respond positively only to high-quality signalers, then a handicap signaling equilibrium can be achieved if certain relationships regarding the cost and the benefit functions for signalers. Other, non-costly signaling equilibria may also be possible under certain circumstances. The application of Bullock's result to sexual signaling in a real species would be far from easy, because of the general problem of assessing fitness costs and benefits in complex real-world ecologies, but it is clearly telling us something about the world." (pp. 74).

As he points out the application of his result is difficult to visualize in a real species, but his results make us realize that handicap conditions are not the only way to achieve stable honest signaling, and that some handicap conditions might be an stable honest signaling strategy. The function used by Bullock (1997) was a general function with 2 parameters that could contemplate many more relations between cost, need, and benefit in both receiver and signaler than the one used in previous models (e.g. Grafen (1990)).

Evolutionary simulation modeling has many properties that are of interest in biology, mainly because it models the dynamics of the system, but also because small-scale details such as space, time or spatially distributed phenotypes can be included. These simulations should be as general as possible when trying to prove some hypothesis and should include as much detail as it is necessary. Special attention has to be made in the construction of the model and in interpreting the outcome of a simulation with respect to what was feed into it. Evolutionary simulation models use tools that are still being developed and can be tricky to use. There is still much to be learned about the use of these tools in order to produce safe simulations. However, evolutionary simulation models can contribute to proving the coherency of a hypothesis and to establish new relations that were previously very difficult to observe from equations or experimental data. Evolutionary simulation models are not meant to exactly reproduce the world, they are meant to study the dynamics of a system.

References

[1] Arak, A.,& Enquist, M. (1993). Hidden Preferences and the evolution of signals. Phil. Trans. R. Soc. Lond., Series B, 340, 207-213.

[2] Braitenberg, V. (1984). Vehicles: Experiments in Synthetic Psychology. MIT Press, Cambridge, MA.

[3] Bullock, S. (1997). Evolutionary simulation models: On their Character, and Application to Problems Concerning the Evolution of Natural Signaling Systems. Ph.D. Thesis, School of Cognitive and Computing Sciences, University of Sussex, Brighton, UK.

[4] Bullock, S. (1997b). An exploration of signaling behavior by both analytic and simulation means for both discrete and continuous models. In Husbands, P., & Harvey, I. (Eds.), Proceedings of the Fourth European Conference on Artificial Life (ECAL'97), pp. 454-463 Cambridge, MA. MIT Press / Bradford Books.

[5] Bullock, S. (1998). A continuous evolutionary simulation model of the attainability of honest signaling equilibria. In Adami, C., Belew, R., Kitano, H., & Taylor, C. (Eds.), Artificial Life VI, pp.339-348. MIT Press, Cambridge, MA.

Bullock, S. (2000). Jumping to Bold Conclusions, A Review of The Handicap Principle: A Missing Piece of Darwin's Puzzle by Zahavi, A. Zahavi, A. Adaptive Behavior, 7(1),129-134.

[6] Bullock S., Cliff, D. (1997). The role of 'hidden preferences' in the artificial co-evolution of symmetrical signals. Proc. R. Soc. Lond., Series B. 264, 505-511.

[7] Di Paolo, E. A., Noble, J., & Bullock, J. (2000). Simulations as Opaque Thought Experiments. In Bedau, M. A., McCaskill, J. S., Packard, N. H., & Rasmussen, S. (Eds), Artificial Life VII: Proceedings on the Seventh International Conference on Artificial Life, pp. 497-506. MIT Press, Cambridge, MA.

[8] Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behavior. Animal Behavior, 33, 1152-1161.

[9] Enquist, M., & Arak, A. (1993) Selection of exaggerated traits by female aesthetic senses. Nature, 361, 446-448.

[10] Godfray, H. C. J. (1991). Signalling of need by offspring to their parents. Nature, 352, 328-330.

[11] Grafen, A. (1990). Biological Signals as handicaps. Journal of Theoretical Biology, 144, 517-546.

[12] Hurd, P. L. (1995). Communicationin discrete action-response games. Journal of Theoretical Biology, 174, 217-222.

[13] Johnstone, R. A. (1997). The evolution of animal signals. In Krebs, J. R.,& Davies, N. B. Behavioral Ecology: An Evolutionary Approach (Fourth Edition)., pp.155-178.

[14] Noble, J.(1998) The Evolution of Animal Communication Systems: Questions of Function Examined through Simulation. Ph.D. Thesis, School of Cognitive and Computing Sciences, University of Sussex, Brighton, UK.

[15] Noble, J., Di Paolo, E. A., & Bullock, S. (2001) Adaptive Factors in the Evolution of Signalling Systems. In A. Cangelosi and D. Parisi (Eds.), Simulating the Evolution of Language. Pp. 53-78. Springer Verlag, Heidelberg.

[16] Werner, G. M., & Dyer, M. G. (1991). Evolution of Communication in Artificial Organisms. In Langton, C, G., Taylor, C., Farmer, J. D., & Rasmussen, S. (Eds.), Artificial Life II-SFI Studies in the Sciences of Complexity, Vol. X, pp. 659-687 Redwood City, California, Addison-Wesley.

[17] Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). Journal of Theoretical Biology, 67, 603-605.

[18] Zahavi, A. (1975). Mate selection - A selection for a handicap. Journal of Theoretical Biology, 53, 205-214.