



UvA-DARE (Digital Academic Repository)

Evolution of altruism: Exploring adaptive landscapes

Spichtig, M.

Publication date
2013

[Link to publication](#)

Citation for published version (APA):

Spichtig, M. (2013). *Evolution of altruism: Exploring adaptive landscapes*. [Thesis, fully internal, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

Discussion

Based on my excursions through adaptive landscapes in the chapters of this Thesis, I will first summarize the main conclusions per chapter and then attempt to discuss a wider perspective.

In Chapter 1, I explored how altruism can evolve as a sexually selected handicap. This excursion is interesting in that altruism affects the fitness variation that the handicap is supposed to signal. The idea behind altruism as a handicap signal is that altruists tend to have higher fitness than non-altruists, but when altruists are mating partners with higher fitness they incur the cost of altruism by promoting the fitness of others! The result is a process of shifting fitness between individuals that can affect the fitness superiority that the altruistic handicap aims to signal. I found that evolution of altruism is promoted when altruism maintains fitness superiority (or even accentuates it), but hampered otherwise.

In Chapter 2, I explore the validity of an earlier proposition that opting out of repeated Prisoner's Dilemma games (i.e., the option to suspend repetitions) promotes the evolution of cooperation. The reason to explore this critically is that the supposed advantage of certain conditional cooperators (referred to as Out for Tat strategies) as invaders of defector-dominated populations is reduced if loners (i.e., strategies which consistently opt out) are the alternative invaders. Moreover, I consider strategies that exploit these conditional cooperators because opting out can open the opportunity to cheaply (and falsely) signal remorse. However, I found that the evolution of cooperation is promoted as long as the payoff from opting out exceeds the payoff from mutual defection and is also not high enough to constitute a tempting alternative to opting in and playing repeated games.

In Chapter 3, I explore the effects of mutation-generated variation on frequency dependent selection on strategies spanning the range from cooperation to defection. The unrestricted emergence of mutants enables strategies to benefit from (1) interacting with mutants and from (2) interacting with the faithfully reproduced descendants of mutants. My excursions through this adaptive landscape show that mutation-generated variation does not always promote cooperation – in contrast to what McNamara et al. (2004, 2008) found earlier and thought was due to the first benefit. I discovered evolution can result in periodic fluctuations in the level of cooperation, which I show to be due to the second benefit.

In Chapter 4, I use Levene's concept of evolution under spatial or temporal heterogeneity from biology and apply this to the evolution of social norms in an economic context. Compliance to a social norm can be heterogeneous in that the fraction of compliers differs between societies (spatial heterogeneity) or varies within a society over time (temporal heterogeneity). I show that complying with a social norm can evolve to be a conditional behavior in societies where overall compliance with the social norm fluctuates over time.

In the introduction to this Thesis, I question the view of evolutionary biologists on evolution as a straightforward optimization process. I think genetic evolution is actually a special form of an optimization process which is best explained by contrasting it with cultural evolution: Humans confronted with selecting a strategy to deal with a social situation can discard strategies that evidently do not yield a benefit. This is a form of pre-selection as it takes place before the strategies are used and exposed to selection in the social situation. Genetic evolution stands out by the lack of the option to preselect strategies: Mutation can be expected to generate strategies independent from their expected yield potential and, hence, independent from their fitness. I characterize these two forms of optimization processes as follows:

Genetic evolution: mutation \rightarrow selection
Cultural evolution: innovation with pre-selection \rightarrow selection.

Thus, innovation can be seen as ‘a mutation’ in cultural evolution. The arrow in the diagram expresses in which direction new genotypes/innovations are generated by mutation after which they become exposed to selection. The bacterial mutator strains that were taken as an example in the introduction, show that the mutation rate itself can be subject to selection. A user of a genetic algorithm can usually tune the parameters to enhance adaptability and thus, the search for the optimum. This is a good approach when the interest is to find optima. The task of an evolutionary biologist, however, goes beyond finding optima. That optima need not be attained in the course of evolution is a well-known phenomenon, e.g., in the context of gene flow preventing local adaptation (Kirkpatrick and Barton 1997). Gene flow and mutation share the characteristic that they change gene pools. I propose that the (periodic in)direct effects discussed in Chapter 3 represent (periodical) prevention of adaptation caused by mutation. In line with the arrow-direction in the diagram, mutation influences selection and these processes together may prevent that the expected optimum is attained (i.e., the evolutionarily stable state defined by Cressman 1996). For much the same reasons I found in Chapter 2 that the evolutionary trajectories proposed by Batali and Kitcher (1996) can be undermined under (or even by) the mutation regime chosen in the model.

Since mutations can prevent evolving populations from reaching specific optima and are arbitrary with respect to optima, it renders evolution as an ‘optimization process’ rather suboptimal. The optimization process would proceed more efficiently only if mutation would pre-select new genotypes with higher fitness than the parental type. As outlined in the previous paragraph, cultural evolution can constitute such an optimization process. However, the empirical data on strategy selection in cultural evolutionary settings (see, e.g., Kurzban and Houser 2005; Traulsen et al. 2010) seem not yet sufficient to validate this hypothesis. Although pre-selection is an attribute of cultural evolution, I think it is also an attribute of many models in evolutionary theory. Famous is the example of Axelrod and Hamilton (1981) who asked peers to submit strategies for a computer tournament of the iterated Prisoner’s Dilemma game. The ambition to win the tournament suggests careful (pre-)selection of the strategy over submitting an arbitrary strategy. We, evolutionary biologists, should caution against the interpretation of such results because, in my opinion, our primary task is to study selection rather than performing selection ourselves.

In my view, any form of pre-selection can bias the underlying optimization process. Thus, if not backed up by empirical data, I advocate avoiding pre-selection by defining the modeled set of genotypes as general and as comprehensive as possible. I consider the studies by Lindgren (1992) and van Veelen et al. (2012) as genuine examples of generally and comprehensively defined sets, but also the rX sets used in Chapter 3 (to be honest, they were defined by Cressman 1996). The definition of the sets used in Chapter 2 is also general, but I consider the implemented restriction to condition game behavior only on the previous action of the opponent also as a form of pre-selection (see also discussion section in Chapter 2).

A problem with comprehensive definitions of genotype sets is that analysis of such sets readily becomes intractable with increasing size of the set. Admittedly, my endeavors to model genotype sets as comprehensive as possible are rather idealistic. Even more so, the modeled genome need not be general and comprehensive if the modeler aims to reflect constraints imposed by nature (i.e., a comprehensive model of a genotype can be an invalid representation of genotype with known constraints). For example, the preference locus x in Chapter 1 codes for a preference for senders or a preference for non-senders. My motivation to model it in this way is to define the genome in a general and comprehensive manner, but biological reality may be different, e.g., locus x may code only one of the two preferences. This problem can only be solved by empirical studies that investigate how mutation and innovation generate new phenotypes (see Traulsen et al. 2010 for a good example). If mutation is understood as a factor influencing selection, then it is crucial to understand which types of mutants are generated and which types are not. Whenever this information is lacking, I propose that genotypes are modeled as comprehensive as possible. Constraining the modeled genotypes can still become another research paradigm, once evolution of comprehensive genotypes is understood.

References

- Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 221:1390-1396.
- Batali J, Kitcher P (1995) Evolution of altruism in optional and compulsory games. *J Theor Biol* 175:161-171.
- Cressman R (1996) Evolutionary stability in the finitely repeated prisoner's dilemma game. *J Econ Theor* 68:234-248.
- Kirkpartick M, Barton NH (1997) Evolution of a species' range. *Am Nat* 150:1-23.
- Kurzban R, Houser D (2005) Experiments investigating cooperative types in humans: A complement to evolutionary theory and simulations. *PNAS* 102:1803-1807.
- Lindgren K (1992) Evolutionary phenomena in simple dynamics. In: *Artificial Life II*, C Langton et al. (eds.), pp. 295-312. Addison-Wesley, Redwood City.
- Traulsen A, Semmann D, Sommerfeld RD, Krambeck H, Milinski M (2010) Human strategy updating in evolutionary games. *PNAS* 107:2962-2966.
- van Veelen M, Garcia J, Rand DG, Nowak MA (2012) Direct reciprocity in structured populations. *PNAS* 109:9929-9934.