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COMMENTARY

Useful ways of being wrong

H. KOKKO

Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Science, University of Helsinki, Helsinki, Finland

The statistician George Box once remarked: ‘All models are wrong, but some models are useful’. It is a common, albeit understandable, mistake by empiricists to think that a model is flawed if it does not incorporate all the features known to influence an evolutionary or ecological process. When such an argument is taken to the extreme, it is easy to see why it becomes untenable. My own favourite example is a map of a countryside. Maps are models that are designed to help us grasp certain features of the landscape. For example, a map might consist of contour lines which help us predict which way a river will flow once we stumble across it. But a map would become completely useless if it had every tuft of grass marked on it. Including every detail would mean that we ended up carrying a paper or plastic version of the whole landscape with us on a hiking trip. In other words, staring at a too detailed model teaches us nothing more than staring at the original ecosystem, with its complete mess of evolutionary and ecological detail.

So, we must simplify, to make the essentials of the process understandable to our poorly equipped brains. The rule: Boil the system down to the essential features – the equivalent of contour lines and location of rivers and roads; this is the level where true understanding can be gained. But which features are essential, and which ones can be ignored, in a natural population where everything interacts with everything? This question is no less grand than what science is all about: trying to distinguish the important causal factors from the unimportant ones. An empiricist is trying to answer this question with long datasets of field observations, or clever experiments, or perhaps both. He might also have to make compromises: study one species in greater detail than another, because experiments are so much easier with a fish that is easy to catch. A modeller faces similar problems: she has to rely on a combination of intuition and empirically derived knowledge when making decisions on what to include in a model – and often her choices will be based on mathematical convenience. It is far easier, for example, to build a theory where we assume that mutations obey a particular ‘nice’ (say, normal) distribution, than to take into account the possibility of much more freakish options.

Adaptive dynamics is a set of modelling rules where certain features of ecology and genetic change are put in the limelight. In particular, adaptive dynamics always makes it explicit that populations are regulated, and infinite growth is not permitted. Other features, such as the details of how sexual reproduction and diploidy can alter the dynamics of gene frequencies, are seen as less important, and consequently ignored. Waxman & Gavrilets (2004) provide a very clear presentation on the inherent assumptions, and the general impression remains: the simplifying choices that produce adaptive dynamics models are quite different from standard population genetic models, even if they reflect aspects of the same evolutionary process (Page & Nowak, 2002).

Does this matter? I can think of at least three important ways in which it does. First, different assumptions automatically bring about different sorts of mathematical convenience. As noted by Waxman & Gavrilets (2004, p. 26), standard population genetics often becomes very difficult when tackling frequency-dependent selection. Getting an answer to a question can then be so much easier with an adaptive dynamics framework. Secondly, certain questions cannot be answered at all unless a particular mechanism is included in a model. Take, for example, the question whether evolutionary processes can decrease the carrying capacity of an environment (Kokko & Sutherland, 1998; Adams, 2001), change the type of population dynamics (Ferrière & Gatto, 1993; Abrams & Matsuda, 1997), make a population more vulnerable to extinction (Kokko & Brooks, 2003; Poethke *et al.*, 2003) or even cause evolutionary suicide (Matsuda & Abrams, 1994; Gyllenberg & Parvinen, 2001; Webb, 2003). Because understanding density dependence is central to these questions, models designed to answer them simply cannot be built without explicitly incorporating a density regulating mechanism (e.g. Kozlowski & Janczur, 1994; Mylius & Diekmann, 1995). It is then not surprising that the above models have many features in common with the adaptive dynamics framework, although they do not always stick to exactly the same terminology.

The third reason why it is important to be aware of the underlying assumptions is the conceptual understanding itself that we gain from modelling. Perhaps the most striking example is the somewhat different view that adaptive dynamics offers on population fitness from traditional population genetic theory. Fisher (1930) showed that natural selection will increase population fitness, given that there is additive genetic variation in fitness. Fitter types replace unfit ones, leading to a steady uphill progress. However, in adaptive dynamics the process is viewed differently. Consider an ‘unfit’ ancestral population. Whatever the flaw the individuals have in their design, it cannot be so severe that the population could not persist (otherwise, extinction will terminate

Correspondence: Hanna Kokko, Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Science, University of Helsinki, PO Box 65 (Viikinkaari 1), FIN–00014 Helsinki, Finland.
Tel.: +358 9 1915 7702; fax +358 9 1915 7694;
e-mail: hanna.kokko@helsinki.fi

any further evolution). Consequently, the population of unfit individuals grows up to its carrying capacity, where every individual on average reproduces just enough to replace itself. Hence average fitness in the population equals unity. If the fit genotype now arises through mutation and spreads, it will replace the unfit one, but at equilibrium the fit population again becomes regulated – and individuals will, again, have mean fitness of unity.

So, does natural selection increase population fitness, or not – in other words, do the results of adaptive dynamics violate Fisher's fundamental theorem or even prove it wrong? The key issue here is what is understood by fitness. In the standard population genetic formulation, density dependence is typically not in the limelight, although density- and frequency-dependent forms of selection can be constructed too (e.g. Charlesworth, 1994). Frank & Slatkin (1992) provide a very clear description of how population regulation is included in the Fisherian population genetic world. The total change in fitness can be partitioned in two components: if fitness changes from w_0 to w_1, while the environment changes from e_0 to e_1, the total change is $\Delta w = (w_1|e_0 - w_0|e_0) + (w_1|e_1 - w_1|e_0)$. The first term refers to the change in 'fitness' due to natural selection, while the second term describes the deterioration of the environment as the fitter type takes over the population. The increasing fitness is much emphasized in the literature, but it reflects only the first half of the equation: it is a quantity that reflects a genotype's capacity to fill an unlimited world with copies of itself. If we were to make an experiment where the fit and the unfit populations exist separately in a competition-free environment, we might well find that the fitness difference could be reflected in their intrinsic rates of growth. In a real world where resources do become limiting, however, this fitness measure does not convey the whole truth, which is instead captured by Δw. This quantity can remain zero despite a fitness change described by $(w_1|e_0 - w_0|e_0)$, so there is full agreement with the adaptive dynamics world. The difference is truly one of emphasis: in adaptive dynamics, processes that lead from e_0 to e_1 are always studied explicitly.

The lesson? It is not easy to keep track of developments in the theory of ecology and evolutionary biology. Nature is diverse, and so are the problems it offers to the inquiring mind. This is also reflected in the diversity of modelling frameworks that we use to study ecological and evolutionary questions. There is, unfortunately, no single correct answer to the level of simplification that is most useful, or to the kinds of assumptions to make. A particularly regrettable side consequence is that researcher's brains easily become overloaded with the plethora of methods and terminology: if 'fitness' becomes jargon so that its usual meaning varies between modelling approaches, little wonder that a student new to the field can feel perplexed!

The problem is particularly severe when most researchers only apply their own favourite method in their model building. Waxman & Gavrilets (2004) point out repeatedly how the adaptive dynamics school appears to have ignored earlier relevant work. Similar reflections of ignorance, or downright dismissals of 'alternative' approaches, undoubtedly exist in the opposite direction too. It is all too easy to claim, say, that the asexual nature of adaptive dynamics means its applicability is severely limited, when in truth the omission only becomes a flaw if some particular feature of sexual reproduction (say, genetic dominance) really turns out to matter.

Sadly, there is no easy remedy: there is no other way to know whether dominance would have made a difference to a result, than to investigate the alternative model where its effects are incorporated – unless the effects are likely to be so straightforward that a verbal argument is sufficient to convince everyone of the outcome. The fact that natural processes are rarely straightforward is, of course, the justification why modellers still have work to do, and can justify their requests for a salary. In the meanwhile, one must simply try to make sure that every researcher, whether an empiricist or theoretician, is aware of the simplifications and assumptions inherent in each model, and to encourage work that scrutinizes the ways the different approaches relate to each other. No doubt, this is an extremely tall order. But the fact that Waxman & Gavrilets (2004) have produced a review on a methodology that is not their 'own' is a superb illustration that steps towards such understanding can be made.

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References

Abrams, P.A. & Matsuda, H. 1997. Prey adaptation as a cause of predator-prey cycles. *Evolution* **51**: 1742–1750.

Adams, E.S. 2001. Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* **32**: 277–303.

Charlesworth, B. 1994. *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge.

Ferrière, R. & Gatto, M. 1993. Chaotic population dynamics can result from natural selection. *Proc. R. Soc. Lond. B* **251**: 33–38.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.

Frank, S.A. & Slatkin, M. 1992. Fisher's fundamental theorem of natural selection. *Trends Ecol. Evol.* **7**: 92–95.

Gyllenberg, M. & Parvinen, K. 2001. Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.* **63**: 981–993.

Kokko, H. & Brooks, R. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Ann. Zool. Fennici* **40**: 207–219.

Kokko, H. & Sutherland, W.J. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *Am. Nat.* **152**: 354–366.

Kozlowski, J. & Janczur, M. 1994. Density-dependent regulation of population number and life-history evolution: optimization of age at maturity in a simple allocation model for annuals and biennials. *Ecol. Model.* **73**: 81–96.

Matsuda, H. & Abrams, P.A. 1994. Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**: 1764–1772.

Mylius, S.D. & Diekmann, O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* **74**: 218–224.

Page, K.M. & Nowak, M.A. 2002. Empathy leads to fairness. *Bull. Math. Biol.* **64**: 1101–1116.

Poethke, H.J., Hovestadt, T. & Mitesser, O. 2003. Local extinction and the evolution of dispersal rates: causes and correlations. *Am. Nat.* **161**: 631–640.

Waxman, D. & Gavrilets, S. 2005. 20 Questions on adaptive dynamics. *J. Evol. Biol.* **18**: 1139–1154.

Webb, C. 2003. A complete classification of Darwinian extinction in ecological interactions. *Am. Nat.* **161**: 181–205.

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