



Evolution of learning strategies in temporally and spatially variable environments: A review of theory



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ABSTRACT

The theoretical literature from 1985 to the present on the evolution of learning strategies in variable environments is reviewed, with the focus on deterministic dynamical models that are amenable to local stability analysis, and on deterministic models yielding evolutionarily stable strategies. Individual learning, unbiased and biased social learning, mixed learning, and learning schedules are considered. A rapidly changing environment or frequent migration in a spatially heterogeneous environment favors individual learning over unbiased social learning. However, results are not so straightforward in the context of learning schedules or when biases in social learning are introduced. The three major methods of modeling temporal environmental change – coevolutionary, two-timescale, and information decay – are compared and shown to sometimes yield contradictory results. The so-called Rogers' paradox is inherent in the two-timescale method as originally applied to the evolution of pure strategies, but is often eliminated when the other methods are used. Moreover, Rogers' paradox is not observed for the mixed learning strategies and learning schedules that we review. We believe that further theoretical work is necessary on learning schedules and biased social learning, based on models that are logically consistent and empirically pertinent.

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1. Introduction

Learning is a means of acquiring information about the environment and of expressing a phenotype (behavior) appropriate to that environment. Two forms of learning may be distinguished by the source of the information acquired. Individual learning (IL) occurs when an organism depends on its personal experience to gather the information directly from the environment, e.g., by trial-and-error. The second form of learning is social learning (SL), which occurs when an organism obtains the information indirectly by copying other organisms, e.g., by imitation.

A learning strategy is the way in which an organism combines IL and SL, either simultaneously or sequentially, and its relative dependence on each. Biases associated with SL in the choice of whom to copy are also an integral part of a learning strategy. The simplest strategies involve the use of IL or SL but not both. Each learning strategy can be regarded as a genetic adaptation to a specific kind of environmental variability. A learning strategy supports culture, to the extent that an innovation produced by IL is propagated through the population by SL. The learning strategy available to a

species will – in conjunction with other factors such as its demography – determine the nature and properties of its culture.

Evolutionary models of learning, the subject of this review, are to be distinguished from classical learning models in psychology, which were constructed as mathematical formulations for how to assess the probabilities of alternative behaviors upon presentation of stimuli to a subject. These probabilities changed dynamically so that the subject's behavior over time would also change. The focus was on modifications of individual behavior over the course of such trials (Bush and Mosteller, 1955; Hanania, 1959). Extensions of such models have been made to competitive situations where the members of a set of players adopt behaviors at each time step that depend on the history of decisions made by all the players (e.g., Izquierdo and Izquierdo, 2008). Common applications allow players to choose one of two behaviors, and the time-dependent and asymptotic probabilities of adopting each behavior are computed.

Our focus is on the evolution of learning strategies in a population. Each learning strategy is assumed to be genetically determined and – in the models that we consider in this review – not modifiable by learning. The fitness of a learning strategy in a given environment depends on whether the behavior(s) it dictates is (are) adaptive or maladaptive in that environment. The environment may change in time or vary spatially, and a behavior that

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may have been the best, in terms of natural selection, in one environment may not be the best in another. The fitness of a learning strategy also depends in a frequency-dependent manner on what the competing strategies are doing. Earlier studies (e.g., Boyd and Richerson, 1985; Rogers, 1988; Feldman et al., 1996) emphasized SL, as this form of learning is essential for culture. More recently, learning strategies combining IL and SL that support cumulative culture are receiving attention (e.g., Enquist et al., 2007; Borenstein et al., 2008; Aoki, 2010; Lehmann et al., 2010; Aoki et al., 2012).

In ecology, the evolution of learning has been widely studied in the context of foraging (e.g., Barnard and Sibly, 1981; Stephens, 1991; Rodriguez-Gironés and Vásquez, 1997; Giraldeau and Caraco, 2000; Eliassen et al., 2009; Dubois et al., 2010; Katsnelson et al., 2011; Arbilly et al., 2011). The models in this area often address complex situations and posit specific targets of learning, such as where to forage or whether to produce or to scrounge. As such, these models are usually not amenable to a formal mathematical treatment. The evolutionary models of learning that we consider in this review are more “abstract”, in the sense that the behavioral alternatives are distinguished only by whether they are adaptive or maladaptive, or by the degree of adaptedness. Some models are phrased in terms of the number of adaptive cultural traits carried by an organism (Lehmann and Feldman, 2009; Nakahashi, 2010), but they will not be addressed in this review. In the simplest situations, we can write down the dynamical equations describing the changes in the frequencies of the competing learning strategies in terms of their variable fitnesses in the different environments to which they are exposed. More complicated situations involving strategies that differ in the probabilities of using IL or SL can sometimes be modeled by the evolutionarily stable strategy (ESS) approach (Maynard Smith, 1982).

The models reviewed in detail in this paper are numbered sequentially from 1 to 11. We seek the stable equilibria of the dynamical equations or alternatively the ES learning strategy. In addition, we briefly discuss several interesting but complex models, some of which have been investigated using Monte Carlo/agent-based simulations. It will be seen that the results obtained from the simpler models can usefully be applied to interpreting the observations on the more complex models. Finally, we ask whether the presence of SL will improve the (geometric) mean fitness of a population relative to when it is absent—i.e., we address the so-called Rogers’ paradox (Rogers, 1988; Boyd and Richerson, 1995). Table 1 summarizes the provenance of models 1–11 and indicates for each model whether or not Rogers’ paradox occurs.

2. Dynamical models in temporally variable environments

The basic models of this section assume the simplest learning strategies, namely those that involve the use of IL or SL but not both. They also assume dichotomous variation in the phenotype (behavior) that can be acquired by learning. It is then possible to write down the difference equations governing the frequency dynamics of the learning strategies and phenotypes, which is done here for three of the four models.

2.1. Model 1: infinite-states l -cycle coevolutionary model

This model, which was first described by Feldman et al. (1996) in a slightly less general form, is coevolutionary in the sense that the learning strategies and behaviors can coevolve. Consider an infinite population of haploid organisms in which a genetic locus with two alleles determines whether an organism is an obligate individual learner or an obligate social learner. Among the adults of each generation, we distinguish two behaviors, correct or wrong, which are adaptive or maladaptive, respectively, in the environment faced by that generation. Behaviors are defined

Table 1
Provenance of Models 1–11 and possibility of Rogers’ paradox.

Model	Provenance	Comments ^a	Rogers’ paradox
1	Feldman et al. (1996)	Generalization	Always observed
2	Feldman et al. (1996)	Parameter range extended	Sometimes resolved
3	Rogers (1988)	Modified formulation	Always observed
4	Kendal et al. (2009)	Simplification	Sometimes resolved
5	Feldman et al. (1996)	Detailed analysis	Resolved
6	Boyd and Richerson (1988, 1995)	Modified formulation	Not considered
7	Aoki and Nakahashi (2008)	Unmodified	Sometimes resolved
8	Enquist et al. (2007)	Reworded	Sometimes resolved
9	Aoki et al. (2012)	Unmodified	Resolved
10	Nakahashi et al. (2012)	Unmodified	Not addressed
11	Wakano and Aoki (2006)	Unmodified	Not addressed

^a Comments refer to the present analysis and discussion of the models in the corresponding references.

relative to the environment, so that when the environment changes, so do the behaviors that are correct or wrong. These adults reproduce asexually without fertility differences.

A newborn individual learner gathers information directly from the environment and achieves the correct behavior on its own before becoming an adult. However, it suffers a cost, c , which can be interpreted as the probability of making a fatal mistake. Hence, a fraction $1 - c$ of individual learners survive to adulthood, and they all show the correct behavior.

A newborn social learner, on the other hand, acquires its behavior by faithfully copying (i.e., imitating) a random member of the parental generation. Its behavior will be correct only if the behavior that it copies from its exemplar (i.e., cultural parent) is correct in the environment into which it is born. We assume that the environment changes every l generations, with that change occurring just prior to birth. Moreover, an environmental change results in a previously unknown state, which entails that neither of the two preexisting behaviors (correct or wrong) can be correct after the environmental change. Hence, only the individual learners can acquire the correct behavior immediately after an environmental change; this is known as the infinite environmental states assumption. A social learner with correct behavior has fitness (relative viability) 1, whereas the fitness associated with wrong behavior is $1 - s$. We assume $0 < c < s < 1$; otherwise, the individual learners will be selected out unconditionally.

Hence, among the surviving adults of any generation, there can be three phenogenotypes (i.e., genotype–phenotype combinations, Feldman and Cavalli-Sforza, 1984): individual learner, social learner with correct behavior (SLC), and social learner with wrong behavior (SLW). Let us denote their respective frequencies in the parental generation by z , x , and y , and the corresponding frequencies in the offspring generation by z' , x' , and y' . Then, the difference equations governing the dynamics of these variables can be written as follows. When there is an intervening environmental change, which occurs once every l generations, we have

$$Vx' = 0, \quad (1.1a)$$

$$Vy' = (1 - s)(x + y), \quad (1.1b)$$

$$Vz' = (1 - c)z, \quad (1.1c)$$

where

$$V = (1 - c)z + (1 - s)(1 - z). \quad (1.1d)$$

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