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Trade-off between learning and exploitation: The Pareto-optimal versus evolutionarily stable learning schedule in cumulative cultural evolution

Joe Yuichiro Wakano *, Chiaki Miura

Meiji Institute for Advanced Study of Mathematical Sciences, Meiji University, 164-8525 Tokyo, Japan

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ABSTRACT

Inheritance of culture is achieved by social learning and improvement is achieved by individual learning. To realize cumulative cultural evolution, social and individual learning should be performed in this order in one's life. However, it is not clear whether such a learning schedule can evolve by the maximization of individual fitness. Here we study optimal allocation of lifetime to learning and exploitation in a two-stage life history model under a constant environment. We show that the learning schedule by which high cultural level is achieved through cumulative cultural evolution is unlikely to evolve as a result of the maximization of individual fitness, if there exists a trade-off between the time spent in learning and the time spent in exploiting the knowledge that has been learned in earlier stages of one's life. Collapse of a fully developed culture is predicted by a game-theoretical analysis where individuals behave selfishly, e.g., less learning and more exploiting. The present study suggests that such factors as group selection, the ability of learning-while-working ("on the job training"), or environmental fluctuation might be important in the realization of rapid and cumulative cultural evolution that is observed in humans.

1. Introduction

In the evolution of modern humans, innovative stone tools might have played an important role. Advanced and complex lithic industries could never have been invented by a single individual without building on knowledge acquired from others. They are the results of cumulative cultural evolution in which knowledge is inherited from parental generations and passed on to descendant generations. However, if all individuals simply copied what was already known, there would be no advancement in technology. Contribution to culture by improving on the preceding knowledge, such as a discovery of a new adaptive use or form of stone tools, is also crucial for cultural evolution. Thus, it is an important problem to determine what learning strategy can support the cumulative culture that develops the fastest: when and how should an individual perform learning during one's life?

The balance between the time allocated to learning and the time allocated to the exploitation of the learned knowledge is then the next question. To maximize the accumulation rate of culture, one should spend sufficient time to absorb the existing knowledge in the parental generation and then spend all the rest of the lifetime to improve the knowledge by individual learning. However, such a learning schedule does not necessarily maximize the fitness of an individual, i.e., the expected number of biological offspring.

Although many modeling studies have been performed (e.g., Feldman and Cavalli-Sforza, 1984, Boyd and Richerson, 1985, Rogers, 1988, Wakano et al., 2004, Aoki et al., 2005, Rendell et al., 2010), researchers have started surveying the evolution of leaning as life-history strategies only recently (Aoki, 2010; Aoki et al., 2012; Lehmann et al., 2013). A learning schedule considered in this paper is a broad developmental pattern over a single individual's lifetime in the differential use of IL and SL with regard to behaviors that may take a long time to be acquired. It differs from the ordered application of IL and SL in skill acquisition at any one time, which may occur repeatedly during one's lifetime (e.g., Boyd and Richerson, 1985, Borenstein et al., 2008). One of the well-known studies on a leaning schedule is the Social Learning Tournament (Rendell et al., 2010). However, the Tournament included so many factors and the analytic treatment is impossible. Enquist et al. (2007) compared the performances of pure SL strategy, pure IL strategy, and "critical social learner" who performs individual learning (IL) only if social learning (SL) had failed to achieve an OK solution. They showed that critical social learner outperforms the pure strategies and thus evolves. Aoki et al. (2012) performed a more exhaustive study of a two-stage model in which any mixture of SL and IL is allowed in each stage and the environment may fluctuate. They showed that in a constant environment pure SL followed by pure IL is an evolutionarily stable strategy when the efficiency of SL is not too low.

* Correspondence to: 4-21-1 Nakano, Nakano-ku, 164-8525 Tokyo, Japan.
E-mail address: joe@meiji.ac.jp (J.Y. Wakano).

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Table 1
Parameters and variables.

Variable	Classification	Meaning	Range
z	Dynamical variable	Cultural level	$0 \le z$
α	Parameter	Gain of cultural level per unit effort of IL	$0 < \alpha < 1$
β	Parameter	Efficiency of SL	$0 < \beta < 1$
u_0	Life history strategy	Allocation of learning effort to IL in 1st stage	$0 \le u_0 \le 1$
u_1	Life history strategy	Allocation of learning effort to IL in 2nd stage	$0 \le u_1 \le 1$
v	Life history strategy	Allocation of time to learning efforts (IL+SL) in 2nd stage	$0 \le v \le 1$

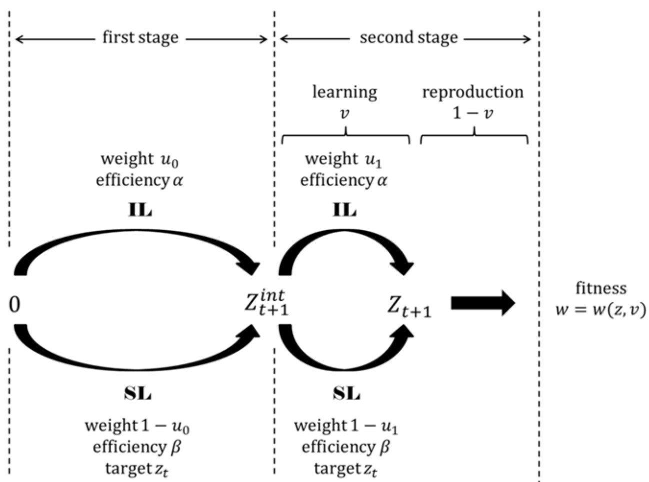

Fig. 1. Schematic illustration of staged life learning schedule in this model.

In a series of studies on the evolutionarily stable learning schedule, Lehmann et al. (2013) studied a case when trade-off between learning and exploiting exists. This model is far more complex as it includes many factors (i.e., continuous time axis, horizontal transmission, and environmental changes). One of their results is that, when environmental change is negligibly rare, the equilibrium of the cultural level realized by the evolutionarily stable learning schedule is not very high compared to the level realized by the pure IL strategy. This result is counter-intuitive because improvement achieved by IL should accumulate over generations when environmental change is rare (a sufficiently small decay rate of information), and thus we naturally expect the cultural level to increase to reach the maximum level that is transmittable to the next generation (limited only by the efficiency of SL). However, the predicted cultural level was far below this level.

The goal of the present study is to clarify the factors that facilitate or suppress the cumulative cultural evolution over generations. When and how does the maximization of individual fitness (natural selection) also maximize the cultural level of the society after a sufficient number of generations? For this purpose, we first propose a relatively simple model with a two-stage life history. Second, we perform a full mathematical analysis of the Pareto-optimal strategy and the evolutionarily stable strategy (ESS) when there is no trade-off between learning and exploiting. Third, an analysis of the case with the trade-off follows. We also show an analysis of a case when the fitness function is an exponential function of the cultural level. Finally we discuss the similarity of our model to models of public goods game.

2. Model and results

2.1. Model

Our model is a modification and extension of Aoki et al. (2012). Here we assume a constant environment. Let z denote the cultural level, e.g., complexity of stone tool or the industry. We assume that the cultural level is represented by a one-dimensional variable. For example, the Acheulean lithic culture might be represented by $z = 10$, while the Aurignacian lithic culture might be represented by $z = 20$. We use the terminologies 'culture', 'cultural level', and 'information (level)', interchangeably. For simplicity, we assume that all individuals with the same cultural level carry the same information. Thus, social learning from another person with the same z value brings no new information.

Life history assumptions are summarized in Fig. 1. Every individual is born with no information ($z = 0$). For simplicity, we assume two learning stages in one's life. In each stage, an individual can perform IL, SL, or any mixture of IL and SL. What is learned in the first stage and in the second stage are added and become the mature phenotype, that is the cultural level of an adult. Adults reproduce offspring, act as exemplars for the next generation, and die.

When an individual performs IL, she gains information α per unit effort. For SL, we only consider oblique transmission across generations. When performing SL, a young individual tries to copy the mature phenotype in the parental generation. The increase of cultural level per unit effort of SL is proportional to the difference in the cultural level of the social learner and that of a randomly chosen exemplar in the previous generation. The coefficient is β. See Table 1 for a summary of parameters and variables.

Allocation of effort is the evolving strategy in this study. In the first stage, an individual performs IL with effort u_0 and SL with effort $1 - u_0$. In the second stage, the individual allocates the learning effort to IL and SL with a ratio $u_1 : 1 - u_1$. During this second stage, the individual can reproduce offspring. Reproductive success is determined by two factors; cultural level and the effort put into reproduction. Most animals including human can learn something before the body sexually matures. It also seems adaptive to allocate more learning effort in the earlier stage of life than allocating learning effort equally in all life stages. Thus, we assume that an individual does not reproduce in the first stage. In the second stage, the fraction v of time is dedicated to learning, and the fraction $1-v$ to exploiting the knowledge for reproduction. Thus in the second stage, efforts $u_1 v$, $(1 - u_1)v$, and $1 - v$ are allocated to IL, SL, and exploitation, respectively. The life history strategy is represented by the triplet (u_0, u_1, v).

The model assumptions above are denoted by the following recursion that describes the dynamics of cultural level z_t in generation t;

$$\begin{aligned} z_{t+1^{\mathrm{INT}}} &= u_0\alpha + (1 - u_0)\beta z_t \\ z_{t+1} &= z_{t+1^{\mathrm{INT}}} + v\left[u_1\alpha + (1 - u_1)\beta(z_t - z_{t+1^{\mathrm{INT}}})\right], \end{aligned} \quad (1)$$

where all individuals adopt the same life-history strategy (Aoki et al., 2012). Our model slightly differs from the previous study (Aoki et al., 2012) as we assume a constant rate of improvement by IL while the previous study assumes that the improvement by IL is proportional to the difference between the current z value and the target value.