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Specialized hybrid learners resolve Rogers' paradox about the adaptive value of social learning

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ABSTRACT

Culture is considered an evolutionary adaptation that enhances reproductive fitness. A common explanation is that social learning, the learning mechanism underlying cultural transmission, enhances mean fitness by avoiding the costs of individual learning. This explanation was famously contradicted by Rogers (1988), who used a simple mathematical model to show that cheap social learning can invade a population without raising its mean fitness. He concluded that some crucial factor remained unaccounted for, which would reverse this surprising result. Here we extend this model to include a more complex environment and limited resources, where individuals cannot reliably learn everything about the environment on their own. Under such conditions, cheap social learning evolves and enhances mean fitness, via hybrid learners capable of specializing their individual learning. We then show that while spatial or social constraints hinder the evolution of hybrid learners, a novel social learning strategy, complementary copying, can mitigate these effects.

1. Introduction

For many years, a common assumption was that social learning enhances a population's fitness by reducing costs—such as metabolic, opportunity or predation costs—below those incurred by individual learning (Boyd and Richerson, 1985). However, in a seminal model, Rogers showed that costs cannot be the only factor (Rogers, 1988). In his model, a population of individual learners track a temporally varying environment. Because social learners acquire information more cheaply than individual learners, social learning is selected for. However, this eventually leads to there being too few individual learners tracking the environment for up-to-date information to be learned and spread. The fitness of social learning thus declines until an evolutionary equilibrium is reached, and the population becomes a mix of both types of learners. Rogers' key observation was that social learners' fitness at this point equals that of individual learners. In other words, while lower costs give social learners an initial fitness advantage that allows them to invade, social learning does not increase the population's mean fitness. These results contradict the notion that, just because social learning can increase individual fitness by reducing costs, it must increase the population's fitness in doing so. Though not strictly paradoxical, this finding was considered so striking that it came to be known as Rogers' paradox (Enquist and Ghirlanda, 2007; Rendell et al., 2010).

Rogers did not dispute the notion that social learning enhances population fitness. Rather, his model was intended to show that costs cannot be the sole reason why. A number of extensions have been made to the model in an effort to resolve his paradox. These include adding flexible learning (Boyd and Richerson, 1995; Enquist and Ghirlanda, 2007; Kameda and Nakanishi, 2002, 2003), cumulative improvement across generations (Boyd and Richerson, 1995; Tomasello, 1999; Ehn and Laland, 2012), adaptive filtering (Enquist and Ghirlanda, 2007), spatial structure (Kobayashi and Ohtsuki, 2014; Rendell et al., 2009), and risk avoidance (Arbilly et al., 2011).

Here, we present a novel approach, inspired by the social foraging literature. We propose that cheap social learning increases mean fitness when environments are complex and resources are limited, by enabling the formation of a skill pool. A skill pool is a group of foragers in which different individuals specialize in searching for different resources (Giraldeau, 1984; Giraldeau and Caraco, 2000; Giraldeau and Lefebvre, 1986). For instance, individual birds in foraging groups may have different foraging repertoires, often characterized by specializations in finding and extracting food from particular sources. When individuals join the food discoveries of others with different specializations, this can be mutually beneficial and efficient for the group. Individuals can then increase the efficiency of their particular searches

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while benefitting from the increased diversity and quantity of the foods available to everyone (Giraldeau, 1984; Giraldeau and Caraco, 2000). There is evidence for intraspecific foraging specialization, not only in many species of birds (e.g., Beauchamp et al., 1997; Brown, 1969; Davis, 1975; Grant, 1981), but also in insects (Heinrich, 2004), fish (Bryan and Larkin, 1972), and mammals (Partridge, 1976; Schaller, 2009). Although much of this work did not focus on skill pools per se, such specialization establishes an important foundation for the formation of skill pools in the context of foraging.

We consider individuals who specialize their learning across multiple problems, which may include foraging. By devoting attention to solving a particular problem, individuals learn better solutions. At the same time, they may use social learning to copy peers who specialize in solving other problems. We show that, in complex environments, this complementary use of social learning resolves Rogers' paradox by enhancing mean fitness. Like other proposed resolutions (Boyd and Richerson, 1995; Enquist and Ghirlanda, 2007; Ehn and Laland, 2012; Kameda and Nakanishi, 2002, 2003), we focus on a behavioral strategy that combines social and individual learning in a flexible manner. However, our resolution reflects the likely ecological reality that many environments are too complex for a single individual to learn perfectly with any reliability. Our extension of Rogers' model is also psychologically plausible in that it implements realistic limitations on attention and time (Dukas, 2004).

We extend Rogers' model by (a) adding a second environmental dimension and set of actions, (b) adding an attention parameter that determines the effectiveness of individual learning, and (c) creating hybrid learners that learn one environmental dimension individually and the other socially. We also explore how a novel social-learning strategy, complementary copying, facilitates evolution of these hybrids when there are social or spatial constraints in the environment.

Extension (a): the second environmental dimension. Rogers' model specifies an environment that exists in one of two possible states (0 or 1). Individuals can adapt to the environment by matching their behavior (also coded 0 or 1) to the environment. We allow the environment to vary across n states, each of which is paired with a behavior that maximizes the payoff when used in the proper context. We also add a second environmental dimension that is in one of n states, but changes independently of the first dimension. The environment may therefore be in any of n^2 states, taking both dimensions into account. This scheme enables specialization by allowing an individual to learn individually on one dimension and socially on the other.

Extension (b): the attention parameter. By introducing an attention parameter, we constrain individual learning by limiting its available resources. We assume that the problems individuals face are sufficiently challenging that finite resources must be allocated between them. This parameter ranges from 0 to 1 and indicates the extent to which one environmental dimension is attended to over the other. When no attention is paid to a particular dimension, an individual learner randomly guesses which action to take for that dimension, whereas the full attention guarantees successful learning. The total amount of attention across the two dimensions sums to 1, such that paying more attention to one dimension necessitates paying less attention to the other.

The attention parameter can be interpreted in two ways. If viewed as a summary of the total amount of resources available to a learner, it represents how these resources are divided between the two dimensions. It can also be regarded as the total finite amount of time that an agent can spend on learning; agents have limited time, and the attention parameter indicates the proportion of time spent on each dimension. These are realistic constraints that are present in many real-world learning tasks, and we will see that they can play a critical role in resolving Rogers' paradox.

Extension (c): hybrid learning. Because we consider environments that vary across two dimensions, two new behavioral strategies are possible: learning individually on the first dimension and socially on the second, and the reverse. Because these strategies involve using both social and individual learning, we refer to them as "hybrid learning." We include both hybrid learning strategies, as well as purely social and purely individual learners. Note that a group consisting of both types of hybrid learners is analogous to a skill pool, because each type can use social learning to exploit the other type's specialized individual learning. However, instead of taking hybrid learning for granted (Boyd and Richerson, 1995; Tomasello, 1999; Rendell et al., 2010; Kobayashi and Ohtsuki, 2014), we examine how social learning and hybrid learners could evolve.

We analytically compute the fitness of different learners under the three proposed extensions, and with an invasion analysis, we examine conditions under which the hybrid learners can evolve and resist invasion. We then show that social learning can improve mean fitness by enabling the formation of a skill pool of hybrid learners. Because our model builds on that of Rogers, we first describe his model.

2. Rogers' analytical model

Rogers' model assumes a large population of haploid individuals undergoing weak selection, where generations do not overlap. We denote the fitness of individual learners by w_i, the benefit of accurate learning by b, and the cost of individual learning by c. In Rogers' model, we have:

$$w_i = b(1 - c), \tag{1}$$

where $1 - c$ represents the cost efficiency of individual learning. For simplification, we omit base fitness w, which was in Rogers' original model.

Assuming no significant cost of social learning, the average fitness of social learners, w_s, is a function of two factors: (i) the proportion of agents adopting social learning, p and (ii) the probability of environmental change, u. Because a social learner copies behavior that was originally acquired by individual learning, the rate of environmental change (i.e., whether or not the environment has changed since the original, individual learning) is a critical factor.

A social learner chooses an individual learner to copy uniformly at random. Given that the proportion of individual learners is $1 - p$, the probability that an action was initially discovered by an individual learner τ generations ago, and has been copied ever since by social learners is $p^{\tau-1}(1 - p)$. Taking into account the fact that the environment changes at each step with probability u, the probability that the copied action is still accurate, P_s, can be computed as $p^{\tau-1}(1 - p)(1 - u)^{\tau}$. Since in social learning, τ can take any integer values, we need to sum all the probabilities:

$$P_s = \sum_{\tau=1}^{\infty} p^{\tau-1}(1 - p)(1 - u)^{\tau} = \frac{(1 - p)(1 - u)}{1 - p(1 - u)} \tag{2}$$

Thus, the average fitness of social learners in Rogers' model, w_s, can be computed as:

$$w_s = b \cdot P_s = \frac{b(1 - p)(1 - u)}{1 - p(1 - u)} \tag{3}$$

At evolutionary equilibrium, when w_i=w_s, we get:

$$b(1 - c) = \frac{b(1 - \hat{p})(1 - u)}{1 - \hat{p}(1 - u)} \Rightarrow \hat{p} = 1 - \frac{(1 - c)u}{(1 - u)c} \tag{4}$$

Replacing $\hat{p}$ in (3) gives the same fitness as (1) for individual learners. Thus, in Rogers' model, social learning does not enhance population fitness at equilibrium (Fig. 1).

3. Our extension of Rogers' model

In our model, we add another environmental dimension. Both dimensions have n states. Subscript notation refers to the type of learning, with i for individual learning and s for social learning: ii refers