

Resolving Rogers' Paradox with Specialized Hybrid Learners

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Abstract

Culture is considered an evolutionary adaptation that enhances human reproductive fitness. A common explanation is that social learning, the learning mechanism underlying cultural transmission, enhances fitness by avoiding the extra costs of individual learning. This explanation was disproved by a mathematical model of individual and social learning, showing that social learners can invade a population but do not enhance its fitness. We extend this model to include a more complex environment, limited cognitive resources, and hybrid learners that combine social and individual learning. In this extended model, we show that social learning evolves and enhances population fitness via hybrid learners capable of specializing their individual learning.

Keywords: Rogers' Paradox, Social Learning, Evolution of Learning, Skill Pools, Specialization

Introduction

In cognitive science, explanations often view evolution in opposition to learning and development (e.g., Elman et al., 1996; Pinker, 2002). Such an oppositional stance misses the point that all three processes are concerned with change, albeit on different time scales. We see learning cycles as nested within developmental cycles, and developmental cycles nested within evolutionary cycles. This permits consideration of possible interactions between these three mechanisms of adaptation. Here we study interactions between learning and evolution with an agent-based simulation. We are particularly interested in the evolution of social learning.

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 & Richerson, 1985). However, in a seminal model, Rogers (1988) showed that costs cannot be the only factor. In this model, a population of individual learners track a temporally varying environment. Because social learners acquire information more cheaply than individual learners, they are 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. Social learners' fitness 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 stage must equal that of individual learners. In other words, while lower costs gave social learners an initial fitness advantage that allowed them to invade, social learning did 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 as well. Though not strictly paradoxical, this finding was considered so striking that it came to be known as Rogers' paradox (Enquist & Ghirlanda, 2007; Rendell et al., 2010a).

It is worth noting that humanity's extreme population growth, which is indicative of an increase in absolute fitness, is commonly attributed to social learning (Ehn & Laland, 2012). Accordingly, Rogers (1988) 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 & Richerson, 1995; Enquist & Ghirlanda, 2007; Kameda & Nakanishi, 2002, 2003), cumulative improvement across generations (Boyd & Richerson, 1995; Tomasello, 1999; Ehn & Laland, 2012), adaptive filtering (Enquist & Ghirlanda, 2007), spatial structure (Kobayashi & Ohtsuki, 2014; Rendell et al., 2010a), and risk avoidance (Arbilly, Motro, Feldman, & Lotem, 2011).

Here, we present a novel approach, inspired by the social foraging literature. We propose that social learning increases mean fitness 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 & Caraco, 2000). Rather than focusing exclusively on foraging, we consider individuals who specialize their learning across multiple problems, which may—but need not—include foraging. By devoting attention to solving a particular problem, individuals learn better solutions. Coincidentally, they may use social learning to copy peers who specialize in solving other problems. We show that this complementary use of social learning resolves Rogers' paradox by enhancing mean fitness. Like other proposed resolutions (Boyd & Richerson, 1995; Enquist & Ghirlanda, 2007; Ehn & Laland, 2012; Kameda & Nakanishi, 2002, 2003), we focus on a behavioral strategy that combines social and individual learning in a flexible manner. However, our resolution is both ecologically and psychology plausible, and provides a particularly robust resolution to Rogers' paradox.

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.

Extension (a): the second environmental dimension. Rogers’ model specifies an environment that exists in one of two possible states (0 or 1). Individuals match their behavior to the environment by choosing between two behaviors (also 0 and 1). 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, when both dimensions are taken 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 limit the accuracy of 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 must randomly guess which action to take for that dimension. 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.

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, or 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 & Richerson, 1995; Tomasello, 1999; Rendell et al., 2010a, 2010b; Kobayashi & Ohtsuki, 2014), we examine how social learning and hybrid learners evolve.

We argue that these extensions lead to a more ecologically and psychologically plausible model. First, complicating the environment to include more problems reflects the reality that learners must often cope with multiple problems, where solutions do not necessarily generalize. Second, we use an attention parameter to capture the notion that engaging with multiple problems requires distributing resources between them. Though social and individual learning are often treated as alternative processes, they are typically complementary (Laland, 2004). Moreover, there is strong evidence for skill pool-based hybrid learning. For instance, birds are known to form skill pools (Giraldeau & Caraco, 2000).

By creating an agent-based simulation, we show that social learning can improve mean fitness by enabling the formation

of a skill pool of specialized hybrid learners. Because our model builds on that of Rogers (1988), we turn next to describing his model.

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:

$$w_i = b(1 - c), \quad (1)$$

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 . Since 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_k , 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:

$$P_{ks} = \sum_{\tau=1}^{\infty} p^{\tau-1}(1 - p)(1 - u)^\tau = \frac{(1 - p)(1 - u)}{1 - p(1 - u)} \quad (2)$$

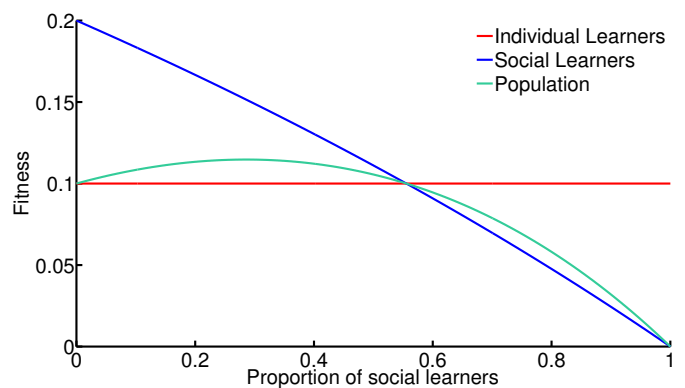


Figure 1: Fitness of social and individual learners and average fitness (mean) as the proportion of social learners increases in Rogers’ (1988) analytical model.

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

$$w_s = b \cdot P_{ks} = \frac{b(1-p)(1-u)}{1-p(1-u)} \quad (3)$$

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

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

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 (Figure 1).

Our Extension of Rogers' Model

We modify Rogers' model in a few ways. First, we add another environmental dimension with the same benefit, b , for selecting the correct action. In computing the fitness of pure individual learners, w_{ii} , we define the cost as a separate constant instead of as a proportion of benefit as in Equation (1). We also assume that attention is divided between the two dimensions; a is the attention paid to one dimension, and $1-a$ is the attention paid to the other dimension. In this section, we develop some intuitions regarding our simulation results by extending Rogers' analytical work.

We denote the type of learning by subscripts: i for individual learning and s for social learning; ii refers to pure individual learners, ss refers to pure social learners, is refers to hybrid learners who learn individually on only the first dimension, and si refers to hybrid learners who learn individually on only the second dimension.

Taking into account the attention parameter, the probability of choosing the correct behavior by individual learning is $P_{ki1} = 1/n + a(n-1)/n$ for the first dimension, and $P_{ki2} = 1/n + (1-a)(n-1)/n$ for the second dimension. Therefore, paying full attention to one dimension guarantees accurate learning, and paying no attention is equivalent to selecting an action uniformly at random.

For individual learners, the average fitness is computed as the sum of average benefit on each dimension minus the cost of individual learning on both dimensions:

$$\begin{aligned} w_{ii} &= b \left(\frac{1}{n} + \frac{n-1}{n}a \right) + b \left(\frac{1}{n} + \frac{n-1}{n}(1-a) \right) - 2c \\ &= \frac{b(n+1)}{n} - 2c. \end{aligned} \quad (5)$$

Note that this average payoff does not depend on a .

We modify Equation (2) to account for our extensions to Rogers' model. The proportion of all social learners, p , is replaced by the proportion of all agents learning socially on a dimension ($p_{ss} + p_{si}$ for the first dimension and $p_{ss} + p_{is}$ for the second dimension). Similarly, the proportion of all individual learners, $1-p$, is replaced by p_{ii} and p_{is} for the first dimension and p_{ii} and p_{si} for the second dimension, each multiplied by the probability of choosing the correct action,

P_{ki} , on the corresponding dimension. Putting this together, we modify Equation (2) to get:

$$P_{ks1} = \frac{(P_{ki1}^{ii} \cdot p_{ii} + P_{ki1}^{is} \cdot p_{is})(1-u)}{1 - (p_{ss} + p_{si})(1-u)}, \quad (6a)$$

$$P_{ks2} = \frac{(P_{ki2}^{ii} \cdot p_{ii} + P_{ki2}^{si} \cdot p_{si})(1-u)}{1 - (p_{ss} + p_{is})(1-u)}, \quad (6b)$$

where the third subscript shows the dimension and the superscript shows the type of learner.

Since the average fitness of pure individual learners does not depend on a , there should be no evolutionary preference for how attention is divided. Assuming a uniform random distribution for a , we can say that on average there is a $E[1/n + a(n-1)/n] = (n+1)/2n$ probability that copying an individual learner on an environmental dimension yields the correct action (where $E[\cdot]$ represents the expected value). As for hybrid learners, they do not need to pay any attention to the dimension for which they are doing social learning. Thus, hybrid learners can fully specialize on the individual learning dimension. With this, we can represent the fitness of hybrid and social learners as follows:

$$w_{ss} = b \left(\frac{(\frac{n+1}{2n} p_{ii} + p_{is})(1-u)}{1 - (p_{ss} + p_{si})(1-u)} \right) + b \left(\frac{(\frac{n+1}{2n} p_{ii} + p_{si})(1-u)}{1 - (p_{ss} + p_{is})(1-u)} \right)$$

$$w_{is} = b \left(\frac{1}{n} + \frac{n-1}{n}a \right) + b \left(\frac{(\frac{n+1}{2n} p_{ii} + p_{si})(1-u)}{1 - (p_{ss} + p_{is})(1-u)} \right) - c$$

$$w_{si} = b \left(\frac{(\frac{n+1}{2n} p_{ii} + p_{is})(1-u)}{1 - (p_{ss} + p_{si})(1-u)} \right) + b \left(\frac{1}{n} + \frac{n-1}{n}(1-a) \right) - c$$

Our goal here is to identify the situations where hybrid learning is a more adaptive strategy than individual learning (i.e., $w_{is}, w_{si} > w_{ii}$). The fitness of hybrid learners is maximized when $p_{is} = p_{si} = 0.5$. Thus, under relatively favorable conditions, we can roughly predict that hybrid learners will be selected for when:

$$\frac{b}{c} < \frac{nu + n}{(n+1)u - (n-1)} \quad (7)$$

Even when the cost of individual learning is $c = 0$, hybrid learners should be selected for when $u < (n-1)/(n+1)$. Similarly, we can identify likely parameter settings where pure social learning is favored (i.e., $w_{ss} > w_{is}, w_{si}$):

$$\frac{0.5(1+u)}{u} > \frac{b}{c} \quad (8)$$

Note that this does not depend on n .

The curves in Figure 2 mark the predicted boundaries between regions where evolution favors particular learners (the boundary between social and hybrid regions does not depend on n). For values of u below $(n-1)/(n+1)$, the b/c ratio would be negative which does not make conceptual sense. Thus, we allow b/c to asymptote at $u = (n-1)/(n+1)$, by letting u vary only above $(n-1)/(n+1)$ up to 1.

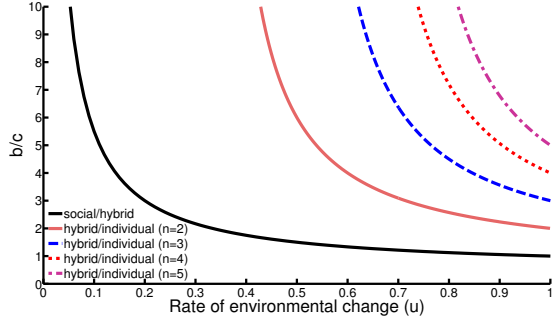


Figure 2: Boundaries of regions where evolution favors particular learners.

Simulations

Although our analytical predictions give a rough indication of expected evolutionary outcomes, we also test these predictions using agent-based computer simulations. Each agent has three genes: (i) learning strategy (social or individual) on the first environmental dimension, (ii) learning strategy on the second environmental dimension, and (iii) attention to the first environmental dimension (ranging from 0 to 1). Each of these three genes are initialized randomly. States of the two environmental dimensions are also randomly chosen.

Each evolutionary cycle has four phases: reproduction/death, environmental change, learning, and recording. Reproduction is asexual, and an agent's probability of reproduction is equal to its fitness. The population consists of up to 300 agents, where an agent can reproduce only if there is space for its offspring. A child inherits its genes from its parent, with a mutation (changing the genes to another random value) probability of 0.0001 per gene. After reproduction, each agent dies with probability 0.1. Following that, each environmental dimension can change with probability u .

The next phase of every evolutionary cycle is learning. If an agent has the social learning allele on a dimension, it selects another agent uniformly at random and imitates its behavior on that dimension. A pure social learner can copy different agents for each dimension.

Individual learning follows social learning. Agents with the individual learning allele on one or both dimensions observe the corresponding environmental dimension(s) with their inherent attention parameters.

Following the learning cycle, the fitness and frequency of each of the genotypes are recorded. Fitness is determined by the total benefit (b times the number of the agent's correct actions) minus the total cost (c times the number of dimensions for which the agent uses individual learning).

Each run or simulated world has 1000 evolutionary cycles. The rate of environmental change is varied from 0 to 0.8 in steps of 0.2 and b/c ratio is varied from 1 to 6 (30 different pairs of parameters in total). We ran 20 worlds in each of these 30 cells. Benefit of learning is held at a constant value of 0.2. Results are robust across other variations of b/c ratio, rate of environmental change, and mutation rates.

Figure 3 shows proportions of genotypes, in the form of pie-chart results for $n = 2, 3, 4,$ and 5 levels on each environmental dimension along with the predicted evolutionary boundaries. Each pie chart is derived by averaging proportions of the three genotypes across 20 simulated worlds, where each world is initially populated by 300 agents. As number of levels of environment and behaviors increase from 2 to 5, hybrid genotypes become more prevalent at the expense of the pure individual genotype. This is indicated by a decrease in red and increase in lime as number of levels increases, from Figure 3(a) to 3(d). All boundaries agree with the analytical predictions (Fig. 2).

Table 1 presents the relative adaptive advantage of social learning across the parameter space of our simulations for $n = 2$ and $n = 5$ (results are similar for other n and get stronger as n increases). Each entry in the table represents the percent difference between the average fitness values obtained from simulations (averaged over 20 runs) and the predicted average fitness for a population of individual learners as computed in Equation (5). Each percent advantage of social learning is computed as:

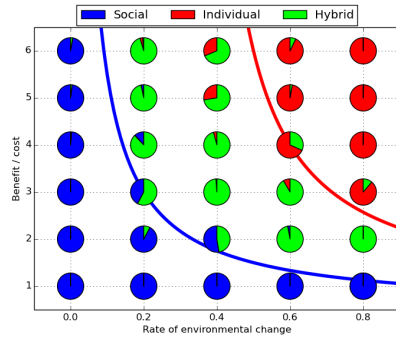
$$100 \times \frac{\bar{w} - w_{ii}}{w_{ii}}, \quad (9)$$

where \bar{w} is the mean fitness averaged across 20 runs and w_{ii} is the theoretical fitness of a population of individual learners as computed in Equation (5).

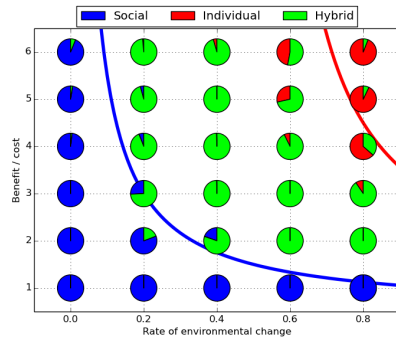
Results are shown for each combination of b/c ratio (from 2 to 6) and each rate of environmental change (from 0 to 0.8). Results for the b/c ratio of 1 are omitted because individual learner fitness is negative at that b/c value. The results show that social learning strongly enhances population fitness everywhere else in this parameter space. Fitness enhancement due to social learning is strongest at lower levels of these two key parameters (i.e. low b/c ratios in a relatively stable environment), and weakest at the highest levels of these two parameters (i.e. high b/c ratios in an unstable environment). The tri-color background groups similar values in a heat map to better illustrate the trend for greater fitness enhancement of social learning with decreases in rate of environmental change and b/c ratio. The fitness advantage provided by social learning increases with problem complexity, defined as n , the number of possible behaviors.

Discussion

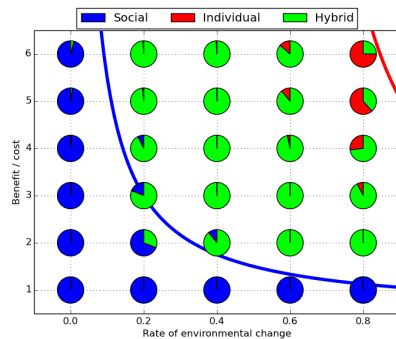
Our simulation results support the hypothesis that the inclusion of hybrid learners enhances fitness by fostering specialization, similar to skill pools in foraging bird populations (Giraldeau & Caraco, 2000). We find that individual learning is favored at high rates of environmental change and moderate to high benefit/cost ratios, while social learning is favored in more stable environments with low benefit/cost ratios. Between these two extremes, we find that hybrid learning is favored where one or both of these two key parameters



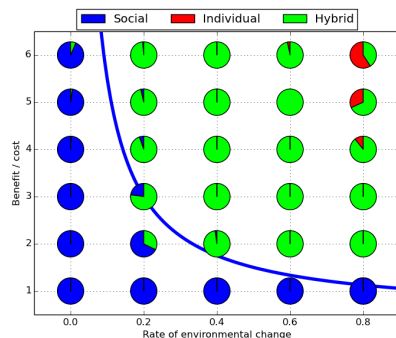
(a) 2 levels



(b) 3 levels



(c) 4 levels



(d) 5 levels

Figure 3: Proportions of genotypes as a function of environmental and behavioral variation.

Table 1: Percent fitness advantage provided by social learning in 20 simulations (5 b/c ratios \times 4 levels of problem complexity), each averaged over 20 runs for (a) $n = 2$ and (b) $n = 5$. Results are similar for other n and get stronger as the number of states increases.

(a) $n = 2$

		Rate of Environmental change				
		0	0.2	0.4	0.6	0.8
b/c ratio	6	69	43	28	23	22
	5	70	58	34	24	23
	4	92	65	50	28	25
	3	135	73	61	51	30
	2	324	120	159	137	146

(b) $n = 5$

		Rate of Environmental change				
		0	0.2	0.4	0.6	0.8
b/c ratio	6	142	88	63	43	33
	5	143	108	92	72	38
	4	199	130	103	80	48
	3	256	192	145	114	85
	2	885	487	477	419	347

are at a moderate level. We also show that, as environments become more complex, hybrid social learning becomes increasingly favored, at the expense of individual learners. This invasion of hybrids in a parameter space that otherwise favors pure individual learners (in simpler environments) is due to the hybrids' unique combination of cost-saving social learning with individual exploration of a rapidly changing, complex environment. In these circumstances, the inherent flexibility provided by hybrid learners is more adaptive than the rigidity of pure social and pure individual learners.

These genotypic trends are driven by underlying differences in individuals' fitness. When individual learning has a cost, the presence of social learning, whether pure or hybrid, strongly enhances reproductive success. Mirroring this pattern, the population's mean fitness increases with stability of the environment and decreasing benefit/cost ratio, providing a robust resolution to Rogers' paradox.

Rogers showed that pure social learning ultimately does not raise mean population fitness, because as social learners become more prevalent they increasingly risk acquiring outdated behaviors (Rogers, 1988). This problem is particularly severe as environments become less stable. Hybrid learners can resolve this problem because they are flexible enough to maintain both individual and social learning within a population over a wide range of environments.

In contrast to previous proposed resolutions of Rogers' paradox, by allowing for hybrid learners, our model makes

fewer complicating assumptions and exhibits adaptive social learning in a broader range of circumstances. Notably, we find that social learning strongly enhances fitness in every sector of the large parameter space we explore. Other proposed resolutions of Rogers' paradox find that social learning enhances fitness by relatively small amounts and often in restricted parametric conditions, whether using conditional social learning (Kameda & Nakanishi, 2002, 2003; Rendell, Fogarty, & Laland, 2009), critical social learning (Boyd & Richerson, 1995; Enquist & Ghirlanda, 2007; Rendell et al., 2009), individual refiner learning (Ehn & Laland, 2012), adaptive filtering of maladaptive behaviors (Enquist & Ghirlanda, 2007), cumulative cultural transmission across generations (Boyd & Richerson, 1995; Ehn & Laland, 2012; Tomasello, 1999), strategic social learning strategies (Laland, 2004), risk avoidance (Arbilly et al., 2011), or spatial characteristics of the environment (Kobayashi & Ohtsuki, 2014). Although none of these other techniques operate in the simulations described here, it is likely that many of them could further enhance the adaptive advantage of social learning within the context of our hybrid learning scheme. While postulating a novel resolution of Rogers' paradox, our model is also simple enough to be applicable to a wide range of species and is supported by evidence from foraging birds (Giraldeau & Caraco, 2000). Many of the previously proposed techniques require more complex cognition, and are in some cases likely restricted to humans.

In conclusion, we find that Rogers' paradox can be robustly resolved by the inclusion of hybrid learners who can specialize in learning one problem individually and another socially. With hybrid learning and an extra cost for individual learning, social learning becomes particularly adaptive. The extra cost of learning individually is not the whole story, as it is not necessary for the evolution of social learning. Thus, we identify several important factors involved in the evolution of social learning: hybrid genotypes enabling complementary specialization, relative environmental stability, a relatively low ratio of benefit to cost, and extra costs for individual learning. In our framework, only hybrid genotypes are essential for the emergence of social learning, but the other three factors can increase the payoffs of social learning.

The role of specialization in driving cooperation, productivity, and social organization in humans has been widely recognized by scholars from Plato and Ibn Khaldun to Adam Smith, Emile Durkheim, and many others. Work discussed and presented here suggests that such specialization of agents could have deep evolutionary roots well beyond the human species.

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