

Adaptive challenges for cognition underlying cultural learning

Cristina Moya^{*±} and Patricio Cruz y Celis Peniche^{*}

Cite as: Moya, C. & Cruz y Celis Peniche, P. (Sept, 2024). Adaptive challenges for cognition underlying cultural learning. In M. L. Fisher (Editor-in-chief). *APA Handbook of Evolutionary Psychology*, Volume 1, Section 2.

Cultural evolution minimally relies on social learning. As our knowledge of the range of taxa that engage in social learning has expanded (e.g., to include bees, asocial lizards, cephalopods), our understanding of the cognition underlying these adaptations has sharpened. This comparative work additionally clarifies the possible nature of the additional cognitive mechanisms that evolved in the human lineage that differentiate the extensive role of cultural transmission in our species compared to that in other animals. In no other species are social learning capacities leveraged to produce such different ways of living. While the cognitive mechanisms for cultural capacities are shared across all humans, they must be capable of preparing any individual for a multitude of possible lives—e.g., that of a trans-Saharan pastoralist trader, an arctic forager, an urban factory worker, or a sedentary office worker. While the range of cultural niches may have expanded recently, Paleolithic foragers too would have needed cognitive mechanisms to prepare them for multiple possible lives as they faced diverse ecologies across time and space even before migrating out of Africa 50,000 years ago (d’Errico et al., 2017; Scerri & Will, 2023). These landscapes of cultural clusters produce a series of adaptive challenges for our species.

Most of the cultural evolution literature treats learners and models from whom they learn, in an undifferentiated way. This leaves unanswered several questions about the nature of cognitive mechanisms commonly proposed as engines of cultural change. How do learners know that a particular cultural variant is more adaptive, or that a particular social model is relatively fitter? How evident must the benefits of cultural variants be to encourage their adoption? How similar to a model does a learner need to be for them to reap these fitness benefits? If people disproportionately copy the majority, how do they ascertain what the majority behavior is? Does the relevant set of models vary according to the domain of information? Does it include outgroup members? If people disproportionately copy successful or prestigious others, how do they identify and acquire the traits responsible for such a model’s success or prestige? To what degree do learners rely on domain-specific or domain-general cues of success or prestige? What happens when different success or prestige hierarchies conflict, as they often do in cases of

^{*} Anthropology Department, University of California - Davis

[±] Author correspondence: moya@ucdavis.edu

culture contact? Addressing such questions requires paying close attention to the cognitive mechanisms used for social learning.

In this chapter we review accumulating research on the social learning mechanisms that power cultural evolution. We begin by outlining some adaptive challenges that learners face, emphasizing cases of individual learning. Many of these challenges are shared with social learning, but it also helps highlight the circumstances under which social learning is particularly valuable. We then turn to the specific inferential challenges that must be addressed by cognitive mechanisms for social learning. We review several proposed heuristics that humans and other animals use to extract information from conspecifics, while considering how they deal with each inferential challenge. We finish by describing some of the big debates regarding the cognition underlying cultural capacities in humans and how they provide avenues for future research.

General challenges to learning

The ubiquity of spatial and temporal variation in environments presents a challenge that often favors adaptations for learning. If an environment is predictable or stable enough, natural selection may favor canalized responses as a more reliable way of ensuring the adaptive outcome. Otherwise learning on one's own or learning from other organisms who themselves learn—i.e. individual and social learning respectively—will likely evolve. In other words, learning mechanisms should have evolved through natural selection by helping organisms make adaptive (i.e., fitness-enhancing) decisions in variable environments (Richerson & Boyd, 2008). Learning is a minimal precondition for a species, such as our own, to be a cultural one. This means that to understand human cognitive mechanisms for culture, we must understand the nature of both individual, and particularly social, learning mechanisms in our species.

Because we are such adept learners, and perhaps because of the taxonomic ubiquity of the capacity to learn (it apparently does not even require a central nervous system; Bielecki et. al., 2023), it may be easy to overlook the entailments of learning cognition. Box 1 breaks down several of the challenges that learners face when determining which of several actions to take. While the Box focuses on social learning, many of the challenges are parallel for individual learners. For one, determining the payoffs (i.e., potential fitness-consequences) of a behavior is difficult (leftmost arrow in Box 1 figure). Just as individual learners may wish to ascertain the optimal amount of wine to drink for their health, the medical community has been trying to predict the health consequences of wine-drinking since at least ancient Mesopotamian and Egyptian times (Norrie, 2002). Today legions of researchers continue debating whether wine improves cardiac health, despite having the latest scientific and statistical techniques, and large longitudinal datasets at their disposal. This is testament to the difficulty of learning anything important in the world.

To make matters more difficult, long-term fitness consequences of behaviors are by definition unobservable (fitness payoffs in Box 1). To address this problem, learning animals like ourselves have evolved reinforcement mechanisms that rely on finding several primary rewards (e.g., food, mild temperatures) satisfying. For example, we can individually learn which foods are safe to eat in part because we have evolved taste receptors that make us find toxic foods unpalatable and ensuing stomach aches painful. However, primary rewards can be more closely (e.g., quenching thirst) or distantly (e.g., hugging a friend) related to fitness outcomes. Such proxies for fitness can be substituted for success cues in the Box 1 figure, reflecting their imperfect causal relationship with long-term fitness payoffs—e.g., sometimes sweet-tasting foods, like deadly nightshade berries, are quite toxic. Furthermore, prioritizing across rewards can be a challenge. For example, even if we did figure out the optimal number of glasses of wine to drink per hour to minimize the risk of a heart attack, this might come with tradeoffs to one's social life that have even larger fitness consequences.

Humans are able to learn associations well beyond those that natural selection would have favored, leading to more questions about learning cognition and the role of secondary rewards in reinforcing beliefs. For some reliably recurring features of the environment with important fitness consequences, natural selection has bootstrapped the learning process with some prior expectations (i.e., genetically-evolved intuitions) regarding traits that will be associated. For example, in humans and other primates learning to fear snakes is easier than learning to fear flowers (Ohman & Mineka, 2003), and learning to avoid food after nausea is easier than learning to avoid a bright and noisy stimuli after the same physiological experience (Garcia & Koelling, 1966). However, we have also figured out that light is both a particle and a wave, though surely there are no prepared-learning mechanisms that directly bootstrap that intuition, and in fact several evolved intuitions that may work against such discovery (indeed one of us, along with the majority of humans, is still not sure how this is possible). Such knowledge would not have been possible without a form of social learning that allows for the intergenerational cultural accumulation of knowledge – i.e., cumulative culture (Mesoudi & Thornton, 2018). However, individual learners within that intergenerational process would also have had to confront their evolved intuitions about the properties of matter.

In addition to these challenges, individual trial and error learning can be particularly difficult in circumstances where experimenting is risky, costly, or impossible (Richerson & Boyd, 2005). For example, trying new foods can entail poisoning risks for an omnivorous animal. Even if an activity is fairly safe, learning curves can be steep, as would be the case if one tried to teach oneself computer programming without teachers or textbooks. Furthermore, there are important behaviors that are often learned, despite limited opportunities to choose adaptively. For example, the age at which people start to reproduce varies widely within and across cultures, in part because humans learn when is the best time to do so. Trial-and-error learning (i.e., trying out several ages to have a first child) would be impossible for this life history decision,

suggesting that social learning is more useful than individual learning for this trait. Furthermore, behaviors like reproductive onset have payoffs that depend on what others do. If one starts looking for mates well before or after others do, one is likely going to have a limited or suboptimal selection of potential mates. It is therefore beneficial in this case to coordinate with others in one's group. This means it would be foolish to try to learn the optimal strategy on one's own as if it were independent of others' actions.

Under the circumstances outlined in the last paragraph, learning would be particularly useful if one could additionally rely on the experiences of others—that is, if one could incorporate social learning. It is therefore not surprising that social learning is pervasive across animal taxa (Galef, 2009). This ability to learn from conspecifics even extends to solitary species that do not engage in parenting, such as the red-footed tortoise, suggesting that it may rely on associative learning mechanisms in common with individual learning (Wilkinson, 2010). Furthermore, both individual experiences and social information can be integrated to capitalize on the benefits of each kind of information. The relative reliance on each kind of learning should vary adaptively, depending on factors such as the quality of each information source (Perreault et al., 2012) and the extent to which learners are motivated by instrumental versus conventional concerns (Legare & Nielsen, 2015). While individual learning is not necessary for cultural learning to produce adaptive outcomes (Muthukrishna & Henrich 2016), some empirical work on online programming competitions suggests that it is precisely a mix of social and individual learning strategies that is responsible for much accumulation of cultural innovations (Miu et al., 2020). Parallels in bird song suggest that both social influence and individual introduction of species-typical variants are necessary to stabilize complex songs (Feher et al., 2009). Indeed the value of social information often depends on high quality individually-learned information being incorporated into the pool of available ideas. This suggests the need for cognitive mechanisms that discern when it is best to use socially versus individually learned information.

Challenges specific to social learning

Figuring out the causal links between *others'* actions and adaptive outcomes is likely even harder than discerning the payoffs of one's own actions. This is partly because there is no direct physiological feedback when others take actions. For example, if one is assessing toxicity risks of a new food, we have adaptive disgust systems that respond directly to the foods we have eaten (Curtis, 2007), but not an equivalently direct system that responds to the food that others have eaten. This means a social learner must figure out which cues to use to assess the model's payoffs. If a model immediately makes a disgusted face after eating something, determining the causal relations may be relatively straightforward (although even the association between a disgusted face and food edibility takes time to develop in childhood; Shutts et al., 2013). On the other hand, if the model falls ill after leaving a learner's proximity, learning that the food is toxic will be more difficult, if not impossible.

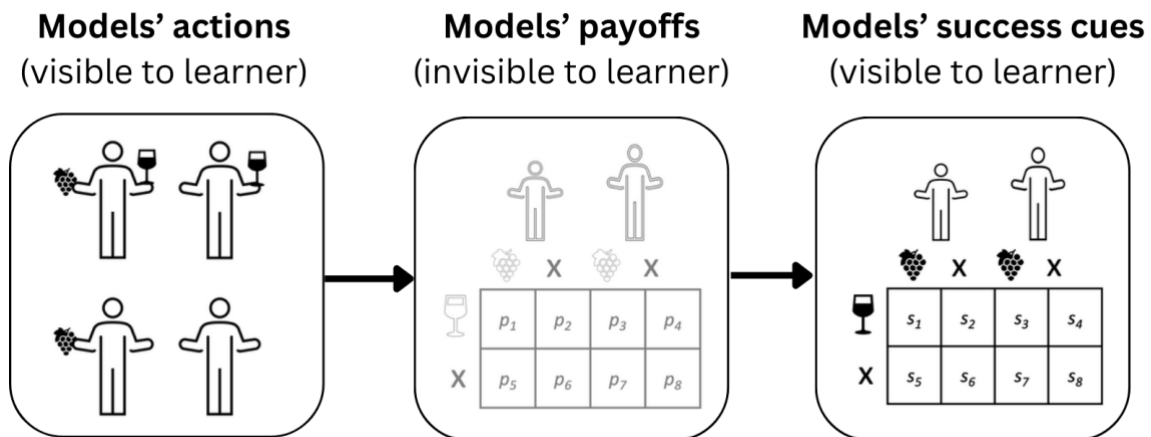
An additional challenge specific to social learning is that the same action can have different fitness consequences for different people (illustrated as different payoffs to wine drinking for short and tall models in Box 1; e.g. perhaps the short people require less wine). One model may make a disgusted face upon eating a durian, while another may find it perfectly edible, nutritious, and perhaps even a delicacy. Minimally, this introduces noise into the information available across different models. Even more problematically, evidence that an action leads to a models' success is an imperfect indicator that the same action will work well for oneself. For example, a nut that is safe for a model to eat, may cause a lethal allergy in the learner. A similar inferential problem exists in the case of individual learning, although to a much lesser extent. That is, in many ways a learner is not the same person at age eight and 80. Indeed, people can develop lethal food allergies within their lifetime, meaning that maintaining an individually-learned food preference can also be dangerous. This means a learner, and especially a social learner, must have ways of assessing the likelihood that what has worked for someone else (or themselves in the past) will also work for them (now).

Ideally, to take advantage of social learning one would have access to many genetic and cultural clones of oneself and a time machine. Consider a learner deciding between multiple actions. The clones would be assured to be good models, meaning they would have the same fitness functions as the learner (i.e., a behavior that is optimal for one clone would be so for all). The clones would have identical fitness functions in no small part because they would have lived in the same environment as the learner up to this point in time. From this point on, the clones would have to take the different actions the learner is considering, (perhaps a difficult ask of clones). A quick trip to the future in the time machine would allow one to measure each clone's long-term fitness outcomes as a function of the actions they had taken. Having a fairly large sample of clones taking each possible decision would guard against stochastic consequences of each action. In summary, a social learner would do well to make use of information from a large sample of models similar to herself and about the future fitness consequences of their actions.

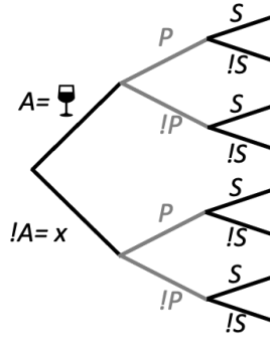
Barring this science fictional paradise for the social learner, different forms of social information are varying degrees removed from this ideal. For example: (a) the number of models may be limited, (b) the models may be dissimilar to oneself in various ways that either affect the payoffs to the same action or one's ability to imitate the action faithfully, (c) information about the models' actions or payoffs may be hard to access, or (d) the success cues (i.e., potential proxies of said payoffs) may be quite distantly related to fitness outcomes. To make the tradeoffs more severe, if a learner spends too much time getting close to this ideal (i.e., considering many models who are very similar to them, finding hidden information about actions and outcomes, looking for the success cues that are best indicators of long-term fitness) the benefits of social- relative to individual-learning will be reduced, if not obviated. In the next section we consider each of these deviations from the ideal and consider the kinds of heuristics people use to make decisions under such limitations.

Box 1. The challenge of adaptive decision-making for social learners.

The figure below illustrates the relationship between actions, fitness payoffs, and success cues. Social learners have access only to information in black (not to the grayed out fitness payoffs, p). That is, they can see multiple models taking each of the four possible actions (e.g., consuming grapes, wine, both, or none). Models can also vary in ways relevant to their payoffs, here illustrated as tall and short models perhaps benefiting differently from drinking a large glass of wine. However, this kind of variation between models may or may not be observable to learners. Learners can also see proxies for fitness such as success cues, labeled s . These are causally related to the fitness payoffs, but to varying degrees. For example, these may include cues to their health or social status. Fitness payoffs, p , and success cues, s , may be different as a function of having taken either of the four actions, features of the models, and their interaction. In the case of individual learning, success cues can be substituted with primary or secondary reinforcers, and model variation collapses to within-person variation (e.g., the age or time of day at which the learner took each action).



To illustrate the inferential challenge for a learner, let's simplify this problem to a categorical one with only two options available; drinking or not drinking wine. In this simpler world drinking wine, action A , has an equivalently higher payoff, P , regardless of an individual's grape consumption or height (i.e., in the above figure, $p_1 = p_2 = p_3 = p_4$ are high payoffs and all other payoffs are equivalently low), and where this in turn leads to some higher probability of a success cue, S , (i.e., $s_1 = s_2 = s_3 = s_4$ and are higher probability than all other equivalently low success cues). Let's further assume the learner knows that there are essentially only two relevant actions (drinking wine or not, while grape consumption is irrelevant) and correspondingly two payoffs. Note, all of these assumptions require a cognition capable of assessing their plausibility. The structure of all possible outcomes is laid out below, where $!P$ represents not getting the high fitness payoff, and $!S$ represents not exhibiting the success cue.



$$Pr(P/A) / Pr(P/!A)$$

While the above values are not visible to the learner, the probability of exhibiting a success cue given an action, $Pr(S/A)$, is visible, as is the probability of exhibiting a success cue given one does not take an action, $Pr(S/!A)$. These can be written out as:

$$Pr(S/A) = Pr(P/A) Pr(S/P) + Pr(!P/A) Pr(S/!P)$$

$$Pr(S/!A) = Pr(P/!A) Pr(S/P) + Pr(!P/!A) Pr(S/!P)$$

Rearranging these we get the following target risk ratio:

$$Pr(P/A) / Pr(P/!A) = \frac{Pr(S/A) - Pr(!P/A) Pr(S/!P)}{Pr(S/!A) - Pr(!P/!A) Pr(S/!P)}$$

Only the terms in black represent information accessible to the learner, while those in gray are opaque to the learner. Not surprisingly, the higher the probability of exhibiting a success cue given an action, relative to when an action is not taken, the higher the target risk ratio. This means, all else equal, a social learner would do well to copy those exhibiting success cues so long as these are indeed correlated with higher payoffs. However, several opaque factors can mitigate the value of this information. The higher the probability of the success cue given one did not get the fitness payoff, $Pr(S/!P)$, the lower the target risk ratio. This makes sense as the success cue is relatively less informative if even people who do not get the fitness payoffs exhibit it (e.g., people who do not have higher fitness payoffs might nonetheless look healthy). However, it is quite a challenge to assess the reliability of a success cue in the absence of information about the associated fitness payoffs. Similarly, if there is a

high probability of getting a low payoff when the action is taken, – $Pr(!P/A)$ is high – or a low probability of getting the low payoff if an action is *not* taken – $Pr(!P!/A)$ is low – then the target risk ratio will also be lower, though perhaps unbeknownst to the learner. Again the learner would have to make some guesses about the likelihood of getting the low payoff given one does or does not take an action to make the best use of the directly observable information. Even this simplified scenario suggests quite a few cognitive demands to make the best use of available social information. This does not even consider the multiple possible actions, their interactions, or the features of the models that are illustrated at the top of this box which would further weaken the value of the available information $Pr(S/A)$ and $Pr(S!/A)$.

197

198 **Possible heuristics that address social learning tradeoffs**

199 **Limited models: When one does not have infinite clones**

200 People should be attuned to how many demonstrators they are able to learn from, both for
 201 informational and normative reasons. Having more demonstrators increases the quality of social
 202 information, all things being equal. Several evolutionary models focused on informational
 203 motivations for learning show that larger model sets favor a reliance on social relative to
 204 individual learning (King & Cowlishaw, 2007, Perreault et. al., 2012). Notably, the latter model
 205 also shows there are quickly diminishing returns to the information provided by each additional
 206 demonstrator, suggesting it is adaptive to incorporate social information even in circumstances
 207 with few models. In a larger model set, however, consensus can also provide stronger evidence
 208 that a norm is being enforced, giving learners an additional motivation to conform.

209

210 Some experimental evidence bears out these predictions. In lab studies of social learning the
 211 larger the number of demonstrators, the more likely participants are to use this information
 212 (Morgan et. al., 2012; Bond, 2005), at least for some tasks with few behavioral options
 213 (Muthukrishna et. al., 2016; see Mercier & Morin, 2019 for a recent review). The converse of
 214 this is that when people have few demonstrators to learn from they are more likely to rely on
 215 individual observations. However, these theoretical and empirical studies overwhelmingly
 216 assume that the other demonstrators represent independent decisions, have no conflicts of
 217 interests with the learner, and have no particular expertise or disadvantage regarding the target
 218 cultural traits. People do indeed copy even single demonstrators, though for more complex or
 219 sensitive tasks these are often carefully chosen on the basis of their success, prestige,
 220 trustworthiness, or willingness to act as teachers. We will return to these cases in later sections.
 221 In addition to integrating asocial and social sources of information, a learner must have ways
 222 of aggregating information learned from multiple demonstrators. One of the largest debates in
 223 this respect is the extent to which people exhibit a conformist bias. While the common use of
 224 conformism simply connotes copying the majority, a more specific form that the learning

heuristic can take is to disproportionately copy the majority trait (Henrich & Boyd, 1998; Wakano & Aoki 2007). In other words, the strict form of conformism is a frequency-dependent form of social learning. For example, if 55% of demonstrators drink wine, the more inclusive form of conformism would mean that learners should have a 55% chance of adopting wine-drinking, whereas the narrower form of conformism would require learners to show a greater than 55% chance of adopting wine-drinking. There is widespread evidence of the former (also known as unbiased transmission) across species, and more recently a couple case studies in monkeys and birds that suggest the stricter form of conformism as well (Smaldino et. al., 2018; Aplin, 2015; Van de Waal et al., 2013). Even within humans, some experiments gave rise to skepticism that strict conformism was common (Eriksson & Coultas, 2009). However, later studies that incentivized people's behavior and considered participants' prior expectations also demonstrated strict conformism in humans (Muthukrishna et. al., 2016). A recent review suggests that the possibility of conflicts of interests between demonstrators and learners may help explain some of the variation in this literature (Mercier & Morin, 2019). Furthermore, formal models suggest that when learners integrate individual and social information from multiple demonstrators in a Bayesian manner it gives rise to a psychology that weighs information in a conformist-like way—i.e., people are expected to disproportionately adopt the behavior that the majority uses, particularly when the adaptive behavior is in the majority (Perreault et. al., 2012).

While the difference between these two meanings of conformism may seem small, it has important implications for patterns of cultural variation. Strict conformism (but not unbiased social learning) reduces cultural diversity within groups by making the majority trait even more common. This may help explain why cultural group boundaries sometimes show abrupt differences rather than gradual spatial variation (i.e., cultural clines). The resulting cultural landscapes of relatively low within-group variation, and higher between-group variation can facilitate culturally-structured group selection (Handley & Mathew, 2020).

Inaccessible information: When one cannot clearly observe the demonstrators' actions

Getting full information about a models' actions and/or visible payoffs (i.e., success cues in Box 1) may be difficult, even when one has few demonstrators to learn from. This makes it more difficult for learners to assess how successful a model is (discussed more in next section) and to identify which traits are causally responsible for this success.

Even if a learner is able to determine which model is most successful, it would behoove them to also identify which of their many traits contribute to their apparent higher fitness. In Box 1 we have simplified this task to ascertaining whether grape eating, wine drinking, or perhaps some interaction of these behaviors, is responsible for greater success. While such causal inferences are often useful for individual learning as well, in the case of social learning the learner cannot as readily rely on primary reward systems (e.g., feeling satiated or ill) to assess

the value of an action. This challenge may be particularly acute in humans given the extent of our social learning and the many environmental conditions that affect our phenotypes (i.e., our plasticity). This is because multiple traits likely interact to affect outcomes under such circumstances. As Henrich and Henrich (2007, p. 14) put it, “are people successful in farming because of what they plant, when they plant, how they plant, or how they make sacrifices to the spirits—or all four?”. One or many intermediate, sometimes non-observable, traits may also be necessary for the observable traits to effectively lead to the observed success cues. For example, the technique used by the Tukanoans to remove cyanide from the staple crop bitter-manioc is a causally opaque, multi-step, multi-day process (Henrich, 2016). Scraping, grating, washing, boiling, and—importantly—waiting several days are necessary for manioc consumption to be safe. While the first steps are more easily observable, the last one is both crucial and often harder to observe. A naive observer would have a hard time deciding which one to copy (i.e., which technique produces higher payoffs).

One possible strategy for overcoming the challenges entailed by establishing causal relevance is overimitating; that is, copying many, even causally unnecessary, traits (Lyons et. al. 2007) from successful or prestigious others (Boyd & Richerson, 1985; Henrich & Gil-White, 2001). For example, among the Yasawa islanders, being considered a successful yam-grower increases the chances that someone is chosen as a good model for learning about fishing and medicinal plants (Henrich & Broesch, 2011). Similarly, children often reproduce the irrelevant actions of other high-status (i.e., a school principal; McGuigan, 2013) or prestigious models (i.e., those who receive more bystanders’ attention; Chudek et al., 2016). Children are prone to copy with precision the general behavior of an adult demonstrator, misinterpreting their many actions as causally meaningful, even when many of these are evidently irrelevant to achieving an observable end-result (Lyons et. al., 2007), or when the same end-result could be achieved by simpler or more efficient means (Melzoff, 1988). Human adults also seem to overimitate, sometimes with even greater fidelity than children (McGuigan et. al., 2011; Kline et. al. 2020).

This type of ‘wholesale’ copying seems to be unique to humans (Whiten et. al., 2009), and may be a side-effect of cognitive adaptations for high-fidelity social learning that ensure complex cultural traits and procedures are inherited as a package (Legare & Nielsen, 2015). In contrast, neither chimpanzees (Horner & Whiten, 2005), bonobos (Clay & Tennie, 2018), nor orangutans (Nielsen & Susianto, 2010) seem disposed to imitate a model’s actions beyond those evidently required to obtain an end-result (e.g., a reward or payoff). Such emulation of outcomes, rather than faithful copying of models’ actions, in non-human apes may reflect the fact that their cultural repertoires do not incorporate complex sequences of actions or sets of traits that have to be copied in tandem. Faithful copying of action sequences has been suggested as one possible way that human social learning is more likely to lead to cumulative culture than that of other animals (Shipton & Nielsen, 2015).

Learning from models who are willing to teach or provide observers closer access to their behavioral repertoire can also facilitate copying only the traits that are causally relevant. Such direct instruction or ability to observe models closely would be particularly important for skills that are difficult to learn from distant observation or from only seeing the end results (e.g., cooking, flintknapping, computer programming). Because of the potentially altruistic nature of teaching (Hoppit et. al. 2008), close kin often play important roles as teachers (Kline et. al. 2013). However, not all adults may be equally adept at specialized skills. Under such circumstances, specialists with valuable skills or information will be in high demand, particularly from learners seeking quality time with them. It has been suggested that markets for these valuable models represent the origin of prestige hierarchies in humans (Henrich & Gil-White 2001).

Faithful imitation mechanisms may interact with these ‘prestige biases’ in social learning, motivating learners to copy a prestigious model even in domains beyond those in which the model is successful (e.g., professional athletes are still influential marketers of cereal brands). Nonetheless, it would behoove learners to be strategic in seeking high-quality demonstrators when it matters most. For example, it is more important to learn how to make shoes than how to tie shoelaces from an expert. This could be both because of the larger costs of getting it wrong or, more relevant to our current discussion, because of the difficulty of getting all the details of a complex causal sequence right. Indeed, interviews with fisher-horticulturalists in Yasawa, Fiji, suggest that the more difficult a skill is to acquire the more likely it is to be learned through oblique transmission (i.e., from an older non-parent), suggesting a selective search for skilled demonstrators or teachers (Kline et. al., 2013).

While our discussion so far has focused on cognitive mechanisms that would be useful for social learners, the prevalence of intentional teaching in humans (Kline, 2015), and functionally similar behaviors in other species (Thornton & Raihani, 2008) suggests an important parallel line of inquiry into the cognition of those who act as models. For example, assuming interests are aligned between models and learners, how do teachers assess the mental states of their pupils? How do they devise useful interventions that facilitate the transmission of relevant knowledge? Some developmental evidence suggests these capacities arise in early childhood (Ronfard & Corriveau, 2016; Qiu & Moll, 2022), perhaps in tandem with theory of mind capacities (Strauss et. al., 2002). However, there is active debate regarding the nature of cognitive mechanisms for teaching and the extent to which they can be accounted for by more general learning processes that allow for the cultural evolution of effective pedagogical practices (Brandl et. al., 2023). Nonetheless, this recognition that much cultural transmission results jointly from learners’ and teachers’ interactions highlights new questions, including regarding the learner’s psychology (Gweon, 2021). For example, learners will also need to discern between intentional actions that serve pedagogical purposes and those that should be

copied to achieve the desired outcome. Again, similar skills that start developing in early childhood (Ziv et. al., 2008), and the mechanisms underlying these, remain under investigation.

Unknowable fitness consequences: When one does not have a time machine

While action sequences may be difficult to observe, long-term fitness consequences (i.e., grayed out elements in Box 1) are never directly observable, at least without a time machine. However, there are many visible proxies for fitness payoffs. These proxies can vary in how detectable they are and how strongly they correlate with fitness.

When the fitness proxies are observable and predictive of fitness one would do well to imitate higher actions associated with these cues of success. Indeed, mathematical models that assume learners can directly assess models' fitness-relevant payoffs and preferentially, or more faithfully, imitate them accordingly (i.e., payoff bias, or directly biased social learning) show this to be an adaptive strategy under a wide range of circumstances (e.g., Boyd & Richerson, 1985: chapter 5; Schlag, 1998, 1999; Henrich & Boyd, 2002; Kendal et. al., 2009). These models presume individual variation in the quality (i.e., adaptive value) of information, either due to chance events, or because some individuals engaged in more costly, but more reliably accurate, individual learning.

A wide range of animals imitate conspecifics' behaviors that evidently lead to greater rewards, or to avoid those that lead to worst outcomes. That is, they pursue a 'copy-if-better' strategy. This has been shown both in the wild and in the lab, and in diverse taxa such as birds (Mason & Reidinger 1982, Zentall, Sutton & Sherburne 1996), fish (Pike et. al., 2010), insects (Leadbeater & Chittka, 2009), and non-human primates (Van Leeuwen et al., 2013, van Leeuwen & Call, 2017; Vale et al. 2017; Barrett et. al., 2017; Bono et al. 2018). Notably, when researchers assess the extent to which humans engage in payoff-biased copying, the payoffs on the task are usually directly reported to participants in lab settings and, despite the social information being freely available, it is often underused (Mesoudi, 2011).

The value, or even the possibility, of payoff-biased imitation may be lower in our species because observing good proxies for fitness (i.e., fitness-relevant payoffs) is much harder for many human behaviors. Not only are complex sequences of actions often necessary for arriving at a payoff, these payouts often involve delayed returns in a long-lived species like humans. Furthermore, the payoffs can vary considerably across ecological or cultural contexts. This can make the direct assessment of a model's payoffs a difficult, costly, or impossible task. For example, in the manioc-processing example described previously, boiling alone reduces the bitter taste—potentially overcoming an evolved cognitive bias guiding our food preferences—and prevents the most immediate symptoms of poisoning. Cognitive mechanisms for discerning fitness-relevant payoffs may easily be satisfied by such a useful proxy. However, the long-term negative health consequences of consuming improperly processed manioc may take years to

develop. Assessing these long-term payoffs, let alone linking them back to the different manioc processing techniques, presents a difficult inferential challenge. Such opaque payoffs may be the norm rather than the exception. A learner attempting to copy the best hunting techniques could find themselves in a similar situation. Even if assessing payoffs for a given hunt is fairly transparent, hunting success can be highly unpredictable, and even the best hunters often return empty-handed (Hill & Kintigh 2009; Gurven & Hill 2009).[†] Precise information on potential models' returns would require sampling multiple hunting trials for each individual[‡]—increasing the costs of social- relative to individual learning. Reiterating the challenges described in the previous section, accurately assessing which behaviors are associated with a known hunting payoff (e.g., a model's tools, walking style, or supernatural beliefs) may be downright impossible.

Though payoffs of actions may not always be observable, characteristics of potential models can serve as proxies of fitness-relevant outcomes and guide social learning. Such strategies are known as indirectly biased social learning, since copying is conditioned on features of the model rather than features of the action itself. Recalling previous examples, one could look at the relative height or body size of different hunters to decide which one to copy, or adopt the manioc-processing style of the oldest or most respected model. Not only are these strategies useful when payoffs are opaque, but knowing whether a model is generally successful can reflect information integrated over a longer timespan. For example, in the case of stochastic hunting returns, any one hunt using a specific tool may be unsuccessful, but if a model using that tool looks well-fed and healthy this may be a good indication that their toolkit is worth copying. Verbal and mathematical models argue such a 'success bias' could be a highly adaptive learning heuristic. Flinn and Alexander (1982) were among the first to argue learners could benefit from imitating models that appear more successful. Boyd and Richerson (1985) mathematically illustrate how copying successful models based on easily observable traits—such as wealth or good health—could be potentially more adaptive than a direct bias, so long as these secondary traits are highly correlated to those responsible for a model's higher fitness.

In addition to looking directly at models for fitness-relevant success cues, learners can also use third-parties' stances towards models as information about the models' success. In cases where people are trying to acquire specialized skills, learners may compete with each other for access to successful models, offering costly gifts, aid, or public praise in exchange for learning opportunities (Henrich & Gil-White, 2001). Henrich and Gil-White further hypothesize that once this becomes a stable dynamic, natural selection would have favored learners who used

[†] “Big game hunters like the Hadza make large game kills only 4% of the time (Hawkes et al. 1991), whereas the !Kung, Ache, and Hiwi, targeting smaller game, make kills 27%, 50%, and 44% of the time, respectively” (Gurven & Hill, 2009: 53).

[‡] “Among Aché hunters, who bring home game on 48% of days, Hill and Kintigh (2009) calculated that a sample of 260 days is required to estimate a hunter's true mean daily acquisition rate with $\pm 20\%$ accuracy” (Stibbard-Hawkes et. al., 2018: p. 640).

other peoples' deferential behavior to ascertain who is a successful model. They suggest both success- and prestige-biased learning strategies may be uniquely human given their value derives from picking out skilled models in social systems where such information is unequally distributed.

While indirectly biased transmission may be particularly important to our species, the animal social learning literature suggests a wide range of taxa are capable of using these mechanisms (reviewed in Cruz y Celis Peniche, in press), presumably because there are many circumstances when an actions' payoffs are unobservable. For example, fruit flies and flycatchers copy the egg-laying behavior of more reproductively successful females (i.e., those that lay the most eggs; Pasqualone & Davis, 2011; Seppänen et al., 2011), evening bats follow more successful conspecifics to foraging patches using body size as an indicator of prior success (Wilkinson, 1992), and house mice (Choleris et al. 1997) and female guppies (Dugatkin & Godin, 1993) preferentially copy the diet- or mate-choices of older models, respectively, likely using body size as a correlate of age.

Ethnographic and experimental evidence (reviewed in Henrich & Henrich, 2007: chapter 2; Jimenez & Mesoudi, 2019) support the hypothesis that humans use indirect cues of competence, success, and prestige as correlates of a model's fitness to guide their social learning. For example, among the Yasawa islanders of Fiji (Henrich & Broesch, 2011), community members who were ranked as more successful were also more likely to be listed as models learners would go to for advice, both within and across domains of expertise. Experiments with infants, children, college students, or adult participants recruited online reveal learners preferentially copy models who appear more competent or skillful (Zmyj et. al., 2010), obtain higher scores or tokens in a task (i.e., success; McElreath et al., 2008; Mesoudi, 2011; Vale et al., 2014), are looked at by more bystanders (Chudek et. al., 2012), or who are imitated the most by other learners (Atkisson et. al., 2012; Brand et. al., 2020; Brand et. al., 2021).

The observability of prestige and success cues may lower the costs[§] of indirectly biased social learning relative to both directly biased and asocial learning strategies (Boyd & Richerson, 1985: chapter 8). However, because imitation is conditioned on correlated traits—rather than the adaptive trait itself—indirectly biased transmission is potentially less accurate than both directly biased social learning and individual learning (Henrich & Henrich 2007). The extent to which these learning strategies are adaptive therefore depends on the extent to which prestige or success cues are causally related to a model's higher fitness across a range of contexts (Boyd & Richerson 1985: chapter 8; Cruz y Celis Peniche, 2024). In the Box 1 scenario the strength

[§] “Essentially, with indirect bias the individual uses the lives of others as experiments to evaluate different cultural variants. Because of this, indirect bias may be much cheaper than direct bias, particularly for traits which have multiple effects over an individual's lifetime. It also means that indirect bias will increase the probability of an individual acquiring a favored cultural variant in many different environments” (Boyd & Richerson 1985: 258).

of this association would be represented by the unobservable odds ratio; $[Pr(S/P) / Pr(!S/P)] / [Pr(S!/P) / Pr(!S!/P)]$, reflecting the odds of expressing a success (or prestige) cue, S , to not expressing it conditioned on having received a fitness payoff, P , compared to when the fitness payoff was not achieved. Estimating this association is mathematically parallel to the challenge presented by directly biased transmission, but requires the additional challenge of learning associations with diverse cues to success, while payoffs are often more directly linked to primary reward systems. For example, it might be easier to form positive associations between actions and greater food rewards than actions and a model's larger body size.

At least in some hunter-gatherer groups and in some domains, people do accurately assess models' success, and their prestige is correlated with fitness proxies. However, nearly all these results focus on men's status. For example, among the Tsimane of Bolivia (von Rueden et al. 2008), men who are thought to be more skilled food producers are also more respected. Among the Yasawa islanders previously described, individuals ranked as better fishermen were indeed more skillful when measuring their actual fishing returns over a span of six years (Henrich & Broesch, 2011). Among the Hadza of Tanzania (Stibbard Hawkes et al., 2018), men's reputations for skillful hunting were also correlated with performance in various hunting-related tasks. Perhaps most clearly, across dozens of non-industrial societies (e.g., hunter-gatherers, pastoralists, horticulturalists, agriculturalists, fishing groups) different metrics of male status—including material wealth (such as land and cattle), hunting skill, and social or political influence—are positively correlated with male reproductive success (Irons 1979; Hill 1984; Von Rueden et. al., 2011; Von Rueden & Jaeggi, 2016).

Ethnographic and experimental studies suggest human learners are sensitive to the domain-specificity of a model's apparent success or prestige. For example, among the people from Yasawa islands, being educated is prestigious, but *negatively* associated with being chosen as a model to learn about fishing, growing yams, or medicinal plants (Henrich & Broesch, 2011). Similarly, being perceived as a good fisher might spillover into being chosen as a model for learning about yam growing, but not for learning about medicinal plants (perhaps because the latter is a female domain). This pattern has been replicated more cleanly in an online experiment showing that when information is available on the domain in which a model is prestigious, learners preferentially copy models from a similar domain over models that are either generally prestigious, or are so in different domains (Brand et. al., 2021). However, when this information is not available, learners will preferentially copy those who are generally prestigious, over those who are not prestigious, and over those who are prestigious in an irrelevant domain. This raises the question of what generally-successful or -prestigious people would look like outside the laboratory, across cultural boundaries, and which cues a cognitive system could use to assess this.

On the other hand, overactive use of success and prestige-biased transmission is often faulted for the spread of behaviors that have negative fitness consequences. For example, the imitation of prestigious teachers with low-fertility norms and the associated valuation of education-based status has been implicated in the spread of maladaptively low reproductive behaviors (Richerson & Boyd, 2005; Colleran, 2016). Many common indicators of high status such as education and wealth are often negatively correlated with fitness correlates, particularly for women, in contemporary societies (Colleran & Snopkowski, 2018). This highlights the risks of indirectly biased social learning when the cues being used to choose models are divorced from fitness proxies.

Several mechanisms can weaken the relationship between status or prestige cues and fitness proxies. For one, success cues such as height or body size are partly heritable, meaning variation in these is partly accounted for by genetic variation. Wagner and Danchin (2010) would refer to these as "genetically determined social information" as opposed to "performance information." Models experiencing higher payoffs may do so because they have better-quality information (i.e., the trait is indeed something learnable) or because they are fitter in ways that cannot be copied (e.g., they have a genotype well-suited to a given environment). In the latter cases, the relationship between actions and success outcomes will be weak and not worth learning about. Second, in humans, success cues can also be inherited culturally (e.g., material wealth), without them necessarily being the result of a model's competence, skill, or ability to reap greater payoffs in a given environment. Such intergenerational inheritance of wealth and other indicators of success again divorce the cues to social success from fitness proxies. Finally, the more non-kin social influences in a society, the more likely non-fitness enhancing practices are to spread. When social information is exclusively transmitted vertically (from parents to offspring), the information will only survive across generations if the individuals reproduce enough. In other words, in such situations ideas are transmitted along the same pathway as genes ensuring that the path for cultural success requires genetic success. The addition of non-kin cultural transmission pathways opens up the possibility that ideas (e.g., ways of ascribing status) that are not useful for reproducing can still spread in a population (Newson et. al. 2005). The importance of these last two processes may indeed be accelerating over the last couple centuries with the breaking of kin-ties and increasing intergenerationally inherited inequality in many societies. Cross-cultural comparative research could test whether cognitive mechanisms for indirectly biased transmission are particularly maladaptive in societies with high rates of wealth inheritance and little kinship structure.

Dissimilar others: When one does not have clones

There are several reasons why learners should be inclined to learn from others who are similar to them. Indeed, ideally one would learn from others who were genetic and cultural clones living in the same environment. A learner should want to ensure that (1) they can copy the relevant behavior, and that (2) they would see the same fitness benefits as the demonstrator from copying

the action. Deviations from this ideal can result from the learner and demonstrator having different underlying traits or their living in functionally different environments. For example, it may not be profitable, or perhaps even possible, for a short basketball player to learn dunking strategies from a tall basketball player. Similarly, environmental circumstances can change the payoffs of dunking, as when the National Collegiate Athletic Association in the United States banned college players from dunking the ball, even though professional basketball players at the same time were scoring highly with such moves (Houck 2000). Both kinds of scenarios can make a certain action either impossible to imitate or low payoff for the learner even if the model had successfully used it. We consider each challenge in turn.

Learners need to be capable of imitating the traits that are causally responsible for a model's higher payoffs (i.e., they must have access to grapes or wine in the Box 1 example). This presumes first understanding which trait is causally relevant for the visible success cues (i.e., is it eating grapes, drinking wine or their interaction that increased a model's longevity). Even once a trait has been identified as causally relevant, how do we know we can acquire it? Slam dunking a basketball may be a very effective way of scoring points in a game, but may be near impossible for people under 5 feet playing on a standard court.

Even if learners can imitate a given trait, they may not be able to reap similar fitness benefits from adopting it. While an evidently successful or prestigious model may have access to better information, learners need to ensure such information is useful to them, or compatible with their own phenotype. For example, one may recognize Olympic athletes as successful and prestigious, but fail to achieve similar results after imitating them if one is not particularly talented in those disciplines. Similarly, younger people may be more inclined to imitate slightly—rather than considerably—older models, particularly for traits that require mastering progressive stages of complexity (Henrich & Broesch, 2011). Despite older models generally exhibiting greater skill or success, slightly older peers could help scaffold the learning process. Given the behaviors that maximize payoffs often vary considerably across cultural or ecological contexts, it is reasonable to assume that payoff-biased learners will prioritize models that are either more similar to themselves (i.e., are more likely to have compatible fitness functions), or whose skills or payoffs result from specific domains that are relevant to their own behavioral strategies. Formal models confirm that learning from similar others can be an adaptive strategy so long as the markers used to ascertain similarity are sufficiently predictive of the learner and model sharing fitness functions (Smaldino & Velilla, 2024).

Much more research has been done on the affiliative consequences of similarity (Cialdini 2001) and affiliative motivations for imitating others (Over & Carpenter 2012) than on the effects of similarity on the likelihood of learning from someone. These results leave unclear the extent to which learning from similar others is motivated by learners and models experiencing different fitness consequences if they are dissimilar. This possibility, however, may help explain the

generally more robust evidence for same-gender biased imitation than for same-ethnicity or same-race biased learning (reviewed in Saunders in press). Social conventions are often gendered, and deviations from gender-appropriate behavior policed. This means that learning from different gender individuals may come with more reliable social costs. Indeed, young US children exhibit preferences for novel playthings that are chosen by others of their same gender and age (Shutts et. al. 2010). On the other hand, the cultural repertoires of people with different racial identities are not as regularly policed in contemporary multi-ethnic states. Perhaps it is not surprising then that US children do not show as reliable a bias with respect to learning from same-race (African or European descended) demonstrators as they do with respect to learning from same-gender others (Shutts et. al. 2010). Other research suggests children preferentially learn from same accented models (Kinzler et. al. 2011), perhaps highlighting cognitive mechanisms for assessing another evolutionarily relevant form of cultural similarity that may guide social learning (Moya, 2013, 2023).

However, similarity-biased learning is not universally advantageous. For example, people who are dissimilar on some important dimensions may nonetheless have useful information. Short basketball players might not profit from copying tall player's dunking strategies, but the latter may still know which shoes help them fly. Furthermore, underlying fitness functions or environmental circumstances are not always fixed (e.g., people can learn skills, which in turn changes which actions are most profitable for them). If these can evolve, there are conditions under which copying the majority is more likely to evolve than copying similar others (Saunders, in press). This suggests even further adaptive challenges. Humans need cognitive mechanisms for assessing the relevant form of similarity to base their learning on, which traits to learn from similar others, and the likelihood that the circumstances affecting payoffs change.

Future Directions

Throughout this article we have touched on the many challenges that cultural learners face when learning from others. Each of these represents an avenue of further research into the cognition that solves these problems. For the remainder of the article, we turn to some of the big debates in the field that are further fodder for future research.

First, it is worth noting that debate persists about the extent to which the cognitive mechanisms that people use for cultural learning evolved due to specific selective pressures for more sophisticated cultural capacities (Henrich, 2016; Muthukrishna et. al., 2018) as opposed to as byproducts of other adaptations. There are several alternative perspectives. For example, one posits that many of the cognitive capacities that seem to aid with cultural learning (e.g., selective social learning, high fidelity imitation, language), are themselves products of cultural evolution rather than innate cognitive precursors to the process (Heyes, 2019). By this account, reinforcement learning and social learning mechanisms shared with other species can provide many of the cognitive precursors necessary to make humans a cultural species. Another

proposal is similarly skeptical that humans have cognitive adaptations specific to cultural learning, but places greater emphasis on social cognitive adaptations like moral emotions and ones for reputation management (Scott-Phillips, 2022). The fact that culture and genes can co-evolve (Moya & Henrich, 2016) and that both cultural and genetic evolution can produce adaptations that shape cognition, makes it more difficult— though perhaps not impossible—to differentiate these proposals (Wertz & Moya, 2019). Research that combines lines of evidence that compares across species, across cultures within humans, and across the lifespan can help shed light on the form and function of the cognitive mechanisms that allow for cultural learning.

The debates about the selective pressures that shaped cultural learning cognition dovetail with questions about what makes social learning in humans different from that in other species. In other words, what is it about the ways we learn from each other that make us a cultural species? Paralleling the debates above, some scholars believe the uniquely human aspects of cognition are orthogonal to cognition that evolved for social learning per se (Scott-Phillips, 2022), while others emphasize the fundamental role of the cognition underlying intergenerational cumulative cultural learning (Tennie et. al., 2009; Boyd, 2018). Many proposals, particularly those under the latter umbrella, not only highlight the importance of social learning mechanisms like high-fidelity copying, but also of cognitive capacities and motivations for cooperating with others. Given that at least six million years separates our species from our common ancestor with chimpanzees and bonobos, it is unlikely that we will find a single cognitive adaptation that clearly separates our cultural capacities from those of other species. A growing paleoanthropological literature is attempting to infer when certain cognitive capacities developed based on the artifact evidence of our ancestors and close hominin relatives (Paige & Perreault, 2024). Furthermore, ongoing research across living species is slowly narrowing the possible mechanisms that seem to be uniquely human, even challenging the idea that our species alone engages in cumulative culture (Sinclair et. al., 2022). Such complementary lines of evidence can help us think through the sequence through which a suite of adaptations could have built a cognition capable of the cultural competences we see in humans today.

The tendency to teach others is one candidate practice that may differentiate human from non-human culture (Csibra & Gergely, 2011). This perspective sets up a fruitful research area for further research regarding the co-evolution of teacher and learner psychology (Gweon 2021). A disproportionate amount of research thus far has focused on learner cognition, and much is yet to be explored about the cognitive mechanisms that underlie effective teaching. For example, how do adults know the best age at which to introduce children to different skills? How do they change the presentation of material to make it more accessible or digestible for the developing child? These questions have been most commonly addressed with respect to language learning and the possibility that caretakers change their speech patterns for the benefit of infant learners (Hilton et. al., 2022). However, socialization in other domains and later in development merit more attention.

A focus on teaching among non-parents generates theoretically interesting research avenues given the greater possibility of conflicts of interests between teachers and learners when they are unrelated. In addition to the risks of unintentional errors in communication, learners must be wary of intentional misdirection. This is particularly a challenge for our species given how much we socially learn using cheap and symbolic language. This sets up a need for cognitive mechanisms that discern which information is reliable (Sperber et. al., 2010). However, too much epistemic vigilance obviates some of the benefits of social learning. That is, if one spends too much effort figuring out who is lying or providing inaccurate information then social learning may become as costly as individual learning. Some have proposed that third-party monitoring of information quality reduces this risk of deception, thus facilitating the evolution of language (Boyd & Mathew, 2015). Nonetheless, learners must manage the tradeoffs between spending time verifying the quality of socially learned information and making the most efficient use of other's information. A full accounting of the cognitive mechanisms underlying epistemic vigilance requires further research.

There are many ways that recent historical social changes likely shaped the dynamics of cultural learning, but little empirical work examining the consequences of these transitions. Most of us likely live in larger, more anonymous, more diverse, more unequal, and less kin-based societies than would have been typical for most of our evolutionary history. This means that genetically-evolved cognitive adaptations for cultural learning might be producing more maladaptive behaviors today than they would have done in the environments in which they were favored by natural selection. For example, the fact that we live in a more anonymous and less kin-based society may encourage individuals to engage in more epistemic vigilance, thus increasing the cost of social, compared to individual, learning. Lower fertility rates and formal schooling may have reduced children's opportunities to learn from other children (Boyette & Hewlett, 2017). Such demographic shifts can fundamentally alter cultural transmission dynamics (Kandler et. al., 2023). Occupational specialization, multi-ethnic states, and greater intergroup interaction rates have magnified the ways that models and learners can differ from each other and the importance of sophisticated cognitive rules for similarity-based social learning (Smaldino & Velilla, 2025). Specialization also offers new pathways to success that are often at odds with reproductive goals more closely associated with fitness, particularly for women (Colleran & Snopkowski, 2018). This suggests another way that indirectly-biased transmission can increasingly lead to maladaptive outcomes. These examples of theoretically relevant historical changes highlight the need to understand cultural learning as it happens in diverse populations. There is no way we can understand how a cultural learning cognition evolved to work if we do not understand the kinds of population structures across which it is designed to operate. Each of these demographic and structural sources of cultural variation open up more avenues for future research into the cognition of cultural learning. For example, it becomes necessary not only to explore the cognition for ascertaining who is trustworthy, who is the right age to learn

from, who is similar enough to copy, and who is a successful model; but also to understand how these cognitive rules develop and function across a the full range of cultural environments.

Conclusion

We have outlined several challenges that social learning adaptations face to safeguard against adopting cultural traits with low payoffs. Humans rarely have the opportunity to aggregate across large samples of demonstrators (as social scientists do when learning about the world) before deciding whether to learn from someone. They will rarely have the opportunity to measure all the relevant actions that models took to discern which ones mattered. Learners can never observe fitness payoffs of their models, and have to carefully assess which cues to success might be useful indicators of long-term fitness. Finally, no two people are identical, and learners face the challenge of assessing which models are similar enough to be worth learning from.

It is important to recognize that cultural evolutionary processes do provide several mechanisms for sifting between traits that can have better or worse outcomes for their users, even if the users are not particularly smart or strategic users of that information. However, it is equally important to consider ways a social learning cognition can be well-built to deal with the many situations where humans have to make decisions with limited information and considerable uncertainty. We have further highlighted several areas of current debate where we believe future research can be particularly profitable. Not only do many details of social learning cognition remain unresolved, but the cognitive changes that make humans a cultural species are disputed. Investigating the design of human cultural cognition would benefit from cross-cultural comparative efforts that recognize the important ways that our learning environments have changed across time and space.

References

- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538-541. <https://doi.org/10.1038/nature13998>
- Atkisson, C., O'Brien, M. J., & Mesoudi, A. (2012). Adult Learners in a Novel Environment Use Prestige-Biased Social Learning. *Evolutionary Psychology*, 10(3). <https://doi.org/10.1177/147470491201000309>
- Barrett, B.J., McElreath, R.L., & Perry, S.E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B*, Vol. 284(1856). <https://doi.org/10.1098/rspb.2017.0358>
- Barrett, J. L.
- (2000). Exploring the natural foundations of religion. *Trends in Cognitive Sciences*, 4(1), 29-34.

- (2008). Coding and quantifying counterintuitiveness in religious concepts: Theoretical and methodological reflections. *Method & Theory in the Study of Religion*, 20(4), 308-338.
- Becker, G. S., & Lewis, H. G. (1973). On the interaction between the quantity and quality of children. *Journal of political Economy*, 81(2, Part 2), S279-S288.
- Bielecki, J., Nielsen, S. K. D., Nachman, G., & Garm, A. (2023). Associative learning in the box jellyfish *Tripedalia cystophora*. *Current Biology*, 33(19), 4150-4159.
- Bond, R. (2005). Group size and conformity. *Group Processes & Intergroup Relations*, 8(4), 331-354.
- Bono, A. E., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schneider, A., & van de Waal, E. (2018). Payoff-and sex-biased social learning interact in a wild primate population. *Current Biology*, 28(17), 2800-2805. <https://doi.org/10.1016/j.cub.2018.06.015>
- Borgerhoff-Mulder, M. (1998). The demographic transition: are we any closer to an evolutionary explanation?. *Trends in Ecology & Evolution*, 13(7), 266-270. [https://doi.org/10.1016/s0169-5347\(98\)01357-3](https://doi.org/10.1016/s0169-5347(98)01357-3)
- Boone, J. L., & Kessler, K. L. (1999). More status or more children? Social status, fertility reduction, and long-term fitness. *Evolution and Human Behavior*, 20(4), 257-277.
- Boyd, R. (2018). *A different kind of animal: How culture transformed our species*. Princeton University Press.
- Boyd, R., & Mathew, S. (2015). Third-party monitoring and sanctions aid the evolution of language. *Evolution and Human Behavior*, 36(6), 475-479.
- Boyd, R., & Richerson, P.J.
- (1985). *Culture and the Evolutionary Process*. Chicago: The University of Chicago Press.
- (1987). The evolution of ethnic markers. *Cultural Anthropology*, 2(1), 65-79.
- Boyer, P. (1994). *The naturalness of religious ideas: A cognitive theory of religion*. University of California Press.
- Boyette, A. H., & Hewlett, B. S. (2017). Autonomy, equality, and teaching among Aka foragers and Ngandu farmers of the Congo Basin. *Human Nature*, 28, 289-322.
- Brand, C.O., Heap, S., Morgan, T.J.H. & Mesoudi, A. (2020). The emergence and adaptive use of prestige in an online social learning task. *Nature Scientific Reports* 10, 12095. <https://doi.org/10.1038/s41598-020-68982-4>
- Brand, C. O., Mesoudi, A., & Morgan, T. J. (2021). Trusting the experts: The domain-specificity of prestige-biased social learning. *Plos one*, 16(8), e0255346. <https://doi.org/10.1371/journal.pone.0255346>
- Brandl, E., Mace, R., & Heyes, C. (2023). The cultural evolution of teaching. *Evolutionary Human Sciences*, 5, e14.
- Chudek, M., Baron, A.S., & Birch, S. (2016). Unselective Overimitators: The evolutionary implications of children's indiscriminate copying of successful and prestigious models. *Child Development*, Vol. 87 (3): 782-794. <https://doi.org/10.1111/cdev.12529>
- Chudek, M., Heller, S., Birch, S., & Henrich, J. (2012). Prestige-biased cultural learning: Bystander's differential attention to potential models influences children's learning. *Evolution and Human Behavior*, 33(1), 46-56.
- Cialdini, R. B. (2001). The science of persuasion. *Scientific American*, 284(2), 76-81. <https://www.jstor.org/stable/26059056>
- Clay, Z., & Tennie, C. (2018). Is overimitation a uniquely human phenomenon? Insights from human children as compared to bonobos. *Child development*, 89(5), 1535-1544.
- Choleris, E., Guo, C., Liu, H., Mainardi, M., & Valsecchi, P. (1997). The effect of demonstrator age and number on duration of socially-induced food preferences in house mouse (*Mus domesticus*). *Behavioural Processes*, 41(1), 69-77. [https://doi.org/10.1016/S0376-6357\(97\)00029-6](https://doi.org/10.1016/S0376-6357(97)00029-6)

- Colleran, H. (2016). The cultural evolution of fertility decline. *Philosophical Transactions of the Royal Society B*, Vol. 371: 20150152. <https://doi.org/10.1098/rstb.2015.0152>
- Colleran, H., & Snopkowski, K. (2018). Variation in wealth and educational drivers of fertility decline across 45 countries. *Population Ecology*, 60, 155-169.
- Cruz y Celis Peniche, P. (In press). Do non-human animals copy successful and prestigious models? Disentangling payoff-biased transmission across taxa. *SocArXiv*. <https://doi.org/10.31235/osf.io/prkn8>
- Cruz y Celis Peniche, P. (2024). Are there any true formal models of success- and prestige-biased social learning. *Journal of Cognition and Culture*, 24, 465-491. <https://doi.org/10.1163/15685373-12340196>
- Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1149-1157.
- Curtis, V. A. (2007). Dirt, disgust and disease: A natural history of hygiene. *Journal of Epidemiology & Community Health*, 61(8), 660-664.
- d'Errico, F., Banks, W. E., Warren, D. L., Sgubin, G., van Niekerk, K., Henshilwood, C., Daniau, A. & Sánchez Goñi, M. F. (2017). Identifying early modern human ecological niche expansions and associated cultural dynamics in the South African Middle Stone Age. *Proceedings of the National Academy of Sciences*, 114(30), 7869-7876.
- Derex, M., & Boyd, R. (2016). Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences*, 113(11), 2982-2987.
- Dugatkin, L. A., & Godin, J. G. J. (1993). Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behavioral Ecology*, 4(4), 289-292.
- Ensminger, J. (1994). The political economy of religion: An economic anthropologist's perspective. *Journal of Institutional and Theoretical Economics*, 150(4), 745-754.
- Eriksson, K., & Coultas, J. C. (2009). Are people really conformist-biased? An empirical test and a new mathematical model. *Journal of Evolutionary Psychology*, 7(1), 5-21.
- Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, 459(7246), 564-568.
- Flinn, M. V., & Alexander, R. D. (1982). Culture theory: The developing synthesis from biology. *Human Ecology*, 10, 383-400.
- Galef, B. G. (2009). Culture in animals? In K. N. Laland & B. G. Galef (Eds.), *The Question of Animal Culture* (pp. 222-246). Harvard University Press.
- Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, 4, 123-124.
- Gervais, W. M., & Henrich, J. (2010). The Zeus problem: Why representational content biases cannot explain faith in gods. *Journal of Cognition and Culture*, 10(3-4), 383-389.
- Gervais, W. M., Willard, A. K., Norenzayan, A. & Henrich, J. (2011). The cultural transmission of faith: why innate intuitions are necessary, but insufficient, to explain religious belief. *Religion*, 41(3), 389-410
- Gigerenzer, G. (2008). Why heuristics work. *Perspectives on Psychological Science*, 3(1), 20-29.
- Goodman, A., Koupil, I., & Lawson, D. W. (2012). Low fertility increases descendant socioeconomic position but reduces long-term fitness in a modern post-industrial society. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4342-4351.

- Gruber, J. H. (2005). Religious market structure, religious participation, and outcomes: Is religion good for you? *The BE Journal of Economic Analysis & Policy*, 5(1), 0000101515153806371454.
- Gurven, M., & Hill, K. (2009). Why do men hunt? A reevaluation of “man the hunter” and the sexual division of labor. *Current Anthropology*, 50(1), 51-74.
- Handley, C., & Mathew, S. (2020). Human large-scale cooperation as a product of competition between cultural groups. *Nature Communications*, 11(1), 702.
- Henrich, J., & Boyd, R.
- (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19(4), 215-241.
 - (2002). On modeling cognition and culture. *Journal of Cognition and Culture*, 2(2), 87-112. <https://doi.org/10.1163/156853702320281836>
- Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences*, 366(1567), 1139–1148. <https://doi.org/10.1098/rstb.2010.0323>
- Henrich, J., & Henrich, N. (2007). *Why Humans Cooperate? A Cultural and Evolutionary Explanation*. Oxford: Oxford University Press.
- Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165-196.
- Henrich, J.
- (2009). The evolution of costly displays, cooperation and religion: credibility enhancing displays and their implications for cultural evolution. *Evolution and Human Behavior*, 30, 244-260.
 - (2016). *The secret of our success: How culture is driving human evolution, domesticating our species, and making us smarter*. Princeton University press.
- Heyes, C. (2019). Précis of cognitive gadgets: The cultural evolution of thinking. *Behavioral and Brain Sciences*, 42, e169.
- Hill K., Kintigh K. (2009). Can anthropologists distinguish good from poor hunters: implications for hunting hypotheses, sharing conventions, and cultural transmission. *Current Anthropology* 50, 369–377.
- Hill, J. (1984). Prestige and the Reproductive Success in Man. *Ethology and Sociobiology*, 5, 77-95.
- Hilton, C. B., Moser, C. J., Bertolo, M., Lee-Rubin, H., Amir, D., Bainbridge, C. M., ... & Mehr, S. A. (2022). Acoustic regularities in infant-directed speech and song across cultures. *Nature Human Behaviour*, 6(11), 1545-1556.
- Hoppitt, W. J., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., & Laland, K. N. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution*, 23(9), 486-493.
- Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, 8, 164-181.
- Houck, D. W. (2000). Attacking the rim: The cultural politics of dunking. In T. Boyd & K.L. Shropshire (Eds.) *Basketball Jones: America above the rim*. (pp. 151-169). NYU Press.
- Irons, J. (1979). Cultural and biological success. In N. Chagnon & W. Irons (eds.). *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, pp. 257-272. Massachusetts: Duxbury.
- Jiménez, Á.V., & Mesoudi, A. (2019). Prestige-biased social learning: current evidence and outstanding questions. *Palgrave Communications* Vol. 5: 20. <https://doi.org/10.1057/s41599-019-0228-7>

- Kandler, A., Fogarty, L., & Karsdorp, F. (2023). The interplay between age structure and cultural transmission. *PLOS Computational Biology*, 19(7), e1011297.
- Kaplan, H. S., Lancaster, J. B., Johnson, S. E., & Bock, J. A. (1995). Does observed fertility maximize fitness among New Mexican men? A test of an optimality model and a new theory of parental investment in the embodied capital of offspring. *Human Nature*, 6, 325-360.
- Kendal, J. R., Ihara, Y., & Feldman, M. W. (2005). Cultural niche construction with application to fertility control: a model for education and social transmission of contraceptive use. *Morrison Institute for Population and Resource Studies. Working Paper*, 102.
- Kendal, J., Giraldeau, L. A., & Laland, K. (2009). The evolution of social learning rules: payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical Biology*, 260(2), 210-219.
- King, A. J., & Cowlshaw, G. (2007). When to use social information: the advantage of large group size in individual decision making. *Biology letters*, 3(2), 137-139.
- Kinzler, K. D., Corriveau, K. H., & Harris, P. L. (2011). Children's selective trust in native-accented speakers. *Developmental Science*, 14(1), pp.106-111.
- Kline, M. A. (2015). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, 38, e31.
- Kline, M. A., Boyd, R., & Henrich, J. (2013). Teaching and the life history of cultural transmission in Fijian villages. *Human Nature*, 24, 351-374.
- Kline, M. A., Gervais, M. M., Moya, C., & Boyd, R. T. (2020). Irrelevant-action imitation is short-term and contextual: Evidence from two under-studied populations. *Developmental Science*, 23(3), e12903. <https://doi.org/10.1111/desc.12903>
- Kramer, K. L., Hackman, J., Schacht, R., & Davis, H. E. (2021). Effects of family planning on fertility behaviour across the demographic transition. *Scientific reports*, 11(1), 8835.
- Laland, K. N., & Brown, G. R. (2006). Niche construction, human behavior, and the adaptive-lag hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 15(3), 95-104.
- Laland, K., Matthews, B., & Feldman, M. W. (2016). An introduction to niche construction theory. *Evolutionary ecology*, 30, 191-202.
- Lang, M., Purzycki, B. G., Apicella, C. L., Atkinson, Q. D., Bolyanatz, A., Cohen, E., Handley, C., Kundtová Klocová, E., Lesorogol, C., Mathew, S., McNamara, R. A., Moya, C., Placek, C. D., Soler, M., Vardy, T., Weigel, J. L., Willard, A. K., Xygalatas, D., Norenzayan, A., & Henrich, J. (2019). Moralizing gods, impartiality and religious parochialism across 15 societies. *Proceedings of the Royal Society B*, 286: 20190202.
- Lawson, D. W., & Borgerhoff Mulder, M. (2016). The offspring quantity-quality trade-off and human fertility variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1692), 20150145. <https://doi.org/10.1098/rstb.2015.0145>
- Leadbeater, E., & Chittka, L. (2009). Bumble-bees learn the value of social cues through experience. *Biology Letters*, 5(3), 310-312.
- Legare, C. H., & Nielsen, M. (2015). Imitation and innovation: The dual engines of cultural learning. *Trends in cognitive sciences*, 19(11), 688-699.
- Lu, Y., & Colleran, H. (In press). Fertility transitions. In *The Oxford Handbook of Cultural Evolution*, edited by J. Tehrani, J. Kendal, and R. Kendal. Oxford University Press.
- Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, 104(50), 19751-19756.

- Mace, R. (1998). The co-evolution of human fertility and wealth inheritance strategies. *Philosophical Transactions of the Royal Society*, 353, 389–397.
- Mason, J. R., & Reidinger, R. F. (1982). Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *The Auk*, 99(3), 548–554.
- McElreath, R., Bell, A.B., Efferson, C., Lubell, M., Richerson, P.J. & Waring, T. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off biased social learning strategies. *Philosophical Transactions of the Royal Society B*, 363: 3515–3528. <https://doi.org/10.1098/rstb.2008.0131>
- McElreath, R., Boyd, R., & Richerson, P. (2003). Shared norms and the evolution of ethnic markers. *Current anthropology*, 44(1), 122–130.
- McGuigan, N. (2013). The influence of model status on the tendency of young children to over-imitate. *Journal of Experimental Child Psychology*, Vol. 116(4): 962–969. <https://doi.org/10.1016/j.jecp.2013.05.004>
- McGuigan, N., Makinson, J., & Whiten, A. (2011). From over-imitation to super-copying: Adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology*, 102(1), 1–18.
- Mercier, H., & Morin, O. (2019). Majority rules: how good are we at aggregating convergent opinions?. *Evolutionary Human Sciences*, 1, e6.
- Mesoudi, A. (2011). An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior*, Vol. 32(5):334–342. <https://doi.org/10.1016/j.evolhumbehav.2010.12.001>
- Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution?. *Proceedings of the Royal Society B*, 285(1880), 20180712.
- Miu, E., Gulley, N., Laland, K. N., & Rendell, L. (2020). Flexible learning, rather than inveterate innovation or copying, drives cumulative knowledge gain. *Science Advances*, 6(23), eaaz0286.
- Monstad, K., Propper, C., & Salvanes, K. G. (2008). Education and fertility: Evidence from a natural experiment. *The Scandinavian Journal of Economics*, 110(4), 827–852.
- Morgan, T. J., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2012). The evolutionary basis of human social learning. *Proceedings of the Royal Society B: Biological Sciences*, 279(1729), 653–662.
- Moya, C.
- (2013). Evolved priors for ethnolinguistic categorization: a case study from the Quechua–Aymara boundary in the Peruvian Altiplano. *Evolution and Human Behavior*, 34(4), 265–272.
 - (2023). What does it mean for humans to be groupish?. *Philosophy Compass*, 18(2), e12893.
- Moya, C., & Henrich, J. (2016). Culture–gene coevolutionary psychology: Cultural learning, language, and ethnic psychology. *Current Opinion in Psychology*, 8, 112–118.
- Muthukrishna, M., Doebeli, M., Chudek, M., & Henrich, J. (2018). The Cultural Brain Hypothesis: How culture drives brain expansion, sociality, and life history. *PLoS Computational Biology*, 14(11), e1006504.
- Muthukrishna, M., & Henrich, J. (2016). Innovation in the collective brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1690), 20150192.
- Muthukrishna, M., Morgan, T. J., & Henrich, J. (2016). The when and who of social learning and conformist transmission. *Evolution and Human Behavior*, 37(1), 10–20.
- Newson, L., & Richerson, P. J. (2009). Why do people become modern? A Darwinian explanation. *Population and Development Review*, 35(1), 117–158.

- Newson, L., Postmes, T., Lea, S. E., Webley, P., Richerson, P. J., & McElreath, R. (2007). Influences on communication about reproduction: the cultural evolution of low fertility. *Evolution and Human Behavior*, 28(3), 199-210. <https://doi.org/10.1016/j.evolhumbehav.2007.01.003>
- Newson, L., Postmes, T., Lea, S. G., & Webley, P. (2005). Why are modern families small? Toward an evolutionary and cultural explanation for the demographic transition. *Personality and Social Psychology Review*, 9(4), 360-375.
- Nielsen, M., & Susianto, E.W.E. (2010). Failure to find over-imitation in captive orangutans (*Pongo pygmaeus*): Implications for our understanding of cross-generation information transfer. In J. Håkansson (ed.). *Developmental Psychology*, pp. 153-167. New York. NY, U.S.A.: Nova Science Publishers.
- Norenzayan, A., Shariff, A. F., Gervais, W. M., Willard, A. K., McNamara, R. A., Slingerland, E. & Henrich, J. (2016). The cultural evolution of prosocial religions. *Behavioral and Brain Sciences*, Vol. 39, E1.
- Norrie, P. A. (2002). The history of wine as a medicine. In *Wine*, pp. 21-55. CRC Press.
- Öhman, A., & Mineka, S. (2003). The malicious serpent: Snakes as a prototypical stimulus for an evolved module of fear. *Current Directions in Psychological Science*, 12(1), 5-9.
- Over, H., & Carpenter, M. (2012). Putting the social into social learning: explaining both selectivity and fidelity in children's copying behavior. *Journal of Comparative Psychology*, 126(2), 182. <https://doi.org/10.1037/a0024555>
- Paige, J., & Perreault, C. (2024). 3.3 million years of stone tool complexity suggests that cumulative culture began during the Middle Pleistocene. *Proceedings of the National Academy of Sciences*, 121(26), e2319175121. doi: 10.1073/pnas.2319175121
- Pasqualone, A. A., & Davis, J. M. (2011). The use of conspecific phenotypic states as information during reproductive decisions. *Animal Behaviour*, 82(2), 281-284.
- Perreault, C., Moya, C., & Boyd, R. (2012). A Bayesian approach to the evolution of social learning. *Evolution and Human Behavior*, 33(5), 449-459.
- Pew Research Center. (2014). Religion in Latin America: Widespread change in a historically Catholic region. *Pew Research Center (web page)*. *Religion and Public Life*. <https://www.pewresearch.org/religion/2014/11/13/religion-in-latin-america/>
- Pike, T. W., Kendal, J. R., Rendell, L. E., & Laland, K. N. (2010). Learning by proportional observation in a species of fish. *Behavioral Ecology*, 21(3), 570-575.
- Purzycki, B. G., Apicella, C., Atkinson, Q. D., Cohen, E., McNamara, R. A., Willard, A. K., ... & Henrich, J. (2016). Moralistic gods, supernatural punishment and the expansion of human sociality. *Nature*, 530(7590), 327-330.
- Purzycki, B. G., Henrich, J., Apicella, C., Atkinson, Q. D., Baimel, A., Cohen, E., McNamara, R. A., Willard, A. K., Xygalatas, D., & Norenzayan, A. (2018). The evolution of religion and morality: a synthesis of ethnographic and experimental evidence from eight societies. *Religion, Brain and Behavior*, Vol. 8(2), 101-132.
- Purzycki, B. G., & Willard, A. K. (2016). MCI theory: A critical discussion. *Religion, Brain & Behavior*, 6(3), 207-248.
- Qiu, F. W., & Moll, H. (2022). Children's pedagogical competence and child-to-child knowledge transmission: Forgotten factors in theories of cultural evolution. *Journal of Cognition and Culture*, 22(5), 421-435.
- Richerson, P.J. & Boyd, R.
- (1984). Natural selection and culture. *BioScience*, Vol. 34(7): 430-434. <https://doi.org/10.2307/1309632>

- (2005). *Not by Genes Alone: How culture transformed human evolution*. Chicago: The University of Chicago Press.
- Ronfard, S., & Corriveau, K. H. (2016). Teaching and preschoolers' ability to infer knowledge from mistakes. *Journal of Experimental Child Psychology*, 150, 87-98.
- Saunders, D. (in press). When is Similarity-biased Social Learning Adaptively Advantageous?. *The British Journal for the Philosophy of Science. Journal for the Philosophy of Science*.
<https://doi.org/10.1086/724448>.
- Scott-Phillips, T. (2022). Biological adaptations for cultural transmission?. *Biology Letters*, 18(11), 20220439.
- Scerri, E. M., & Will, M. (2023). The revolution that still isn't: The origins of behavioral complexity in Homo sapiens. *Journal of Human Evolution*, 179, 103358.
- Schlag, K.H.
- (1998). Why imitate, and if so, how? *Journal of Economic Theory*, 78 (1), 130-156.
<https://EconPapers.repec.org/RePEc:eee:jetheo:v:78:y:1998:i:1:p:130-156>
- (1999). Which one should I imitate?. *Journal of Mathematical Economics*, 31(4), 493-522.
[https://doi.org/10.1016/S0304-4068\(97\)00068-2](https://doi.org/10.1016/S0304-4068(97)00068-2)
- Seppänen, J. T., Forsman, J. T., Mönkkönen, M., Krams, I., & Salmi, T. (2011). New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), 1736-1741. <https://doi.org/10.1098/rspb.2010.1610>
- Shipton, C., & Nielsen, M. (2015). Before cumulative culture: The evolutionary origins of overimitation and shared intentionality. *Human Nature*, 26, 331-345.
- Shutts, K., Kinzler, K. D., & DeJesus, J. M. (2013). Understanding infants' and children's social learning about foods: previous research and new prospects. *Developmental Psychology*, 49(3), 419.
- Shutts, K., Banaji, M. R., & Spelke, E. S. (2010). Social categories guide young children's preferences for novel objects. *Developmental Science*, 13(4), 599-610.
- Sinclair, N. C., Ursell, J., South, A., & Rendell, L. (2022). From Beethoven to Beyoncé: Do changing aesthetic cultures amount to “cumulative cultural evolution?”. *Frontiers in Psychology*, 12, 663397.
- Smaldino, P. E., Aplin, L. M., & Farine, D. R. (2018). Sigmoidal acquisition curves are good indicators of conformist transmission. *Scientific Reports*, 8(1), 14015.
- Smaldino, P. E., & Velilla, A. P. (2024). The Evolution of Similarity-Biased Social Learning. *SocArxiv*.
<https://doi.org/10.31235/osf.io/j7yas>
- Soler, M. (2012). Costly signaling, ritual and cooperation: evidence from Candomblé, an Afro-Brazilian religion. *Evolution and Human Behavior*, 33(4), 346-356.
- Sperber, D. (1996). *Explaining culture: A naturalistic approach* (p. 97). Blackwell: Oxford.
- Sperber, D., Clément, F., Heintz, C., Mascaro, O., Mercier, H., Origgi, G., & Wilson, D. (2010). Epistemic vigilance. *Mind & Language*, 25(4), 359-393.
- Stibbard-Hawkes, D.N.E., Attenborough, R.D., Marlowe, F.W. (2018). A noisy signal: To what extent are Hadza hunting reputations predictive of actual hunting skills? *Evolution and Human Behavior*, Vol. 39 (6): 639-651. <https://doi.org/10.1016/j.evolhumbehav.2018.06.005>
- Strauss, S., Ziv, M., & Stein, A. (2002). Teaching as a natural cognition and its relations to preschoolers' developing theory of mind. *Cognitive Development*, 17(3-4), 1473-1487.
- Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2405-2415.

- Thornton, A., & Raihani, N. J. (2008). The evolution of teaching. *Animal Behaviour*, 75(6), 1823-1836.
- Vale, G. L., Flynn, E. G., Lambeth, S. P., Schapiro, S. J., & Kendal, R. L. (2014). Public information use in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Journal of Comparative Psychology*, 128(2), 215–223. <https://doi.org/10.1037/a0034420>
- Vale, G.L., Flynn, E.G., Kendal, J., Rawlins, B., Hopper, L.M., Schapiro, S.J., Lambeth, S.P., and Kendal, R.L. (2017). Testing differential use of payoff-biased social learning strategies in children and chimpanzees. *Proceedings of the Royal Society B*, 284: 20171751. <http://dx.doi.org/10.1098/rspb.2017.1751>
- Van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340(6131), 483-485. <https://doi.org/10.1126/science.1232769>
- Van Leeuwen, E. J., & Call, J. (2017). Conservatism and “copy-if-better” in chimpanzees (*Pan troglodytes*). *Animal Cognition*, 20(3), 575-579.
- Van Leeuwen, E. J., Cronin, K. A., Schütte, S., Call, J., & Haun, D. B. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PLoS One*, 8(11), e80945.
- Von Rueden, C., Gurven, M., & Kaplan, H. (2008). The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior*, Vol. 29(6):402-415. <https://doi.org/10.1016/j.evolhumbehav.2008.05.001>
- Von Rueden, C., Gurven, M., & Kaplan, H. (2011). Why do men seek status? Fitness payoffs to dominance and prestige. *Proceedings of the Royal Society B*, Vol. 278(1715): 2223-2232. <https://doi.org/10.1098/rspb.2010.2145>
- Von Rueden, C. R., & Jaeggi, A. V. (2016). Men's status and reproductive success in 33 nonindustrial societies: Effects of subsistence, marriage system, and reproductive strategy. *Proceedings of the National Academy of Sciences*, 113(39), 10824-10829. <https://doi.org/10.1073/pnas.1606800113>
- Wakano, J. Y., & Aoki, K. (2007). Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theoretical Population Biology*, 72(4), 504-512.
- Wertz, A. E., & Moya, C. (2019). Pathways to cognitive design. *Behavioural Processes*, 161, 73-86.
- Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1528), 2417-2428.
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6(5), 614-616.
- Wilkinson, G. S. (1992). Information transfer at evening bat colonies. *Animal Behaviour*, 44, 501-518.
- Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, 7(6), 343-346.
- Ziv, M., Solomon, A., & Frye, D. (2008). Young children's recognition of the intentionality of teaching. *Child Development*, 79(5), 1237-1256.
- Zmyj, N., Buttelmann, D., Carpenter, M., & Daum, M. M. (2010). The reliability of a model influences 14-month-olds' imitation. *Journal of Experimental Child Psychology*, 106(4), 208-220.