THE CULTURAL TRANSMISSION OF GREAT BASIN PROJECTILE-POINT TECHNOLOGY II: AN AGENT-BASED COMPUTER SIMULATION

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We present an agent-based computer simulation that extends a previous experimental simulation (Mesoudi and O'Brien 2008) of the cultural transmission of projectile-point technology in the prehistoric Great Basin, with participants replaced with computer-generated agents. As in the experiment, individual learning is found to generate low correlations between artifact attributes, whereas indirectly biased cultural transmission (copying the point design of the most successful hunter) generates high correlations between artifact attributes. These results support the hypothesis that low attribute correlations in prehistoric California resulted from individual learning, and high attribute correlations in prehistoric Nevada resulted from indirectly biased cultural transmission. However, alternative modes of cultural transmission, including conformist transmission and random copying, generated similarly high attribute correlations as indirect bias, suggesting that it may be difficult to infer which transmission rule generated this archaeological pattern. On the other hand, indirect bias outperformed all other cultural-transmission rules, lending plausibility to the original hypothesis. Importantly, this advantage depends on the assumption of a multimodal adaptive landscape in which there are multiple locally optimal artifact designs. Indeed, in unimodal fitness environments no cultural transmission rule outperformed individual learning, highlighting how the shape of the adaptive landscape within which cultural evolution occurs can strongly influence the dynamics of cultural transmission. Generally, experimental and computer simulations can be useful in answering questions that are difficult to address with archaeological data, such as identifying the consequences of different modes of cultural transmission or exploring the effect of different selective environments.

Presentamos una simulación por computadora basada en agentes que es una extensión del anterior experimento de simulación (Mesoudi y O'Brien 2008) de transmisión cultural de la tecnología prehistórica de puntas de proyectil en la Gran Cuenca. En esta simulación los participantes son reemplazados por agentes generados por computadora. Como en el experimento, el aprendizaje individual genera bajas correlaciones entre los atributos de los artefactos, mientras que en una transmisión cultural sesgada indirecta (copiar el diseño de la punta del cazador más exitoso) genera altas correlaciones entre los atributos de los artefactos. Esto apoya la hipótesis de que bajas correlaciones en los atributos en la California prehistórica resultan del aprendizaje individual, y que las altas correlaciones en los atributos en la Nevada prehistórica son consecuencia de la transmisión cultural sesgada indirecta. Sin embargo, modos alternativos de transmisión cultural como la transmisión conformista y la imitación aleatoria generan correlaciones altas, en forma similar a las del sesgo indirecto, lo cual sugiere que tal vez sea difícil inferir cuál regla de transmisión generó este patrón arqueológico. Por otro lado, el sesgo indirecto supera todas las otras reglas de transmisión cultural, lo cual da verosimilitud a la hipótesis original. Es importante subrayar que esta ventaja depende de suponer un entorno multimodal adaptativo, en el cual haya múltiples diseños de artefactos localmente óptimos. En efecto, en un entorno de ajuste unimodal, ninguna regla de transmisión cultural superó al aprendizaje individual, destacando así cómo la forma del entorno adaptativo dentro del cual la evolución cultural ocurre, puede influir fuertemente en la dinámica de transmisión cultural. Por lo general, simulaciones experimentales y por computadora pueden ser útiles para contestar preguntas que son difíciles de abordar con información arqueológica, como identificación de las consecuencias de los diferentes modos de transmisión cultural o de exploración de los efectos de los diferentes ambientes de selección.

A major problem archaeologists often face is how to explain spatial and temporal patterns observed in the archaeological record. Why is a particular artifact found in one region but not in another region? Why does an artifact type differ in shape or size between two sites? Why do some artifacts change rapidly, whereas others remain stable over long periods of time? In

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recent years, there has been a growing realization that such patterns can be explained in terms of *cultural transmission* (Bettinger and Eerkens 1999; Eerkens and Lipo 2005, 2007; O'Brien and Lyman 2003a, 2003b; O'Brien et al. 2008; Shennan 2002), which describes the details of how technological skills, knowledge, and practices were passed from individual to individual and from group to group in prehistoric populations. For example, technological knowledge that is transmitted strictly from father to son or mother to daughter will result in artifact distributions and rates of change that are different than those for which the associated technological knowledge is transmitted within a single generation irrespective of kin relations.

In many cases, this increased interest in using cultural transmission to explain patterns in the archaeological record has been associated with, or directly facilitated by, the application of Darwinian evolutionary theory to past cultural change (e.g., Barton and Clark 1997; Eerkens and Lipo 2005, 2007; Lipo et al. 1997, 2006; Lyman and O'Brien 1998; Neiman 1995; O'Brien 1996; O'Brien and Lyman 2000, 2002; Shennan 2002; Shennan and Wilkinson 2001). Archaeologists have found evolutionary methods to be useful because transmission (or inheritance) is a central and fundamental aspect of Darwinian evolution. Darwin himself noted that "any variation which is not inherited is unimportant for us" (1859:75), and over a century later Mayr affirmed that "a comprehension of the fundamental principles of inheritance is a prerequisite for a full understanding of virtually all phenomena in [all branches of] biology" (1982: 629–630). Just as biological inheritance is of fundamental importance in biological evolution, so too is cultural inheritance (or cultural transmission) of fundamental importance in cultural evolution: "for a complete theory of cultural evolution, rules of cultural transmission are essential" (Cavalli-Sforza and Feldman 1981:54). In short, cultural transmission and cultural evolution are inextricably linked concepts, for without cultural transmission there can be no cultural evolution. Darwinian evolution provides a theoretical framework and set of methodological tools that researchers can use to study and understand cultural transmission.

Other theoretical approaches within archaeology (for example, chaîne opératoire [Bleed 2001]) similarly incorporate transmission or learning into explanations of past cultural change, but only cultural evolutionary theory brings with it an extensive body of rigorous mathematical models of cultural transmission that we believe have significant potential for archaeology. Past theoretical work conducted within a cultural evolution framework has examined the consequences of whether cultural transmission is vertical (from parents), oblique (from unrelated members of the parental generation), or horizontal (from peers) (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). Additional research has explored whether people preferentially copy prestigious individuals (Henrich and Gil White 2001) or conform to a group majority (Henrich and Boyd 1998), and the conditions under which people engage in cultural transmission rather than relying on individual learning (Aoki et al. 2005; Boyd and Richerson 1995). This work has shown through the use of formal mathematical models that the details of cultural transmission at the individual level—who copies what, from whom, and when—can have significant effects at the population level. Given that archaeologists deal primarily with population-level data that span long periods of time and were generated by large numbers of people, evolutionary archaeologists have begun to use theoretical distinctions that are concerned with cultural transmission, such as those noted above, to explain specific archaeological phenomena (Bettinger and Eerkens 1999; O'Brien and Lyman 2003a; see below).

However, one problem that arises when we try to apply these theoretical distinctions to archaeological data is that archaeologists seldom have access to accurate, individual-level data that allow them to identify who has copied which trait, from whom, and when. We can usually only infer such details from messy, large-scale, population-level data. One way of addressing this problem is to use computer models to simulate different cultural-transmission rules and match the resulting cultural dynamics to archaeological data (e.g., Eerkens et al. 2006). However, mathematical models are only as good as their assumptions, in this case assumptions regarding people's propensities to learn culturally rather than individually and to engage in the various forms of cultural transmission listed above. We also need to supplement the mathematical and computer models with experimental data from psychology in order to verify the assumptions and findings of those theoretical models.

In this paper we argue that a combination of computer simulation and psychological experiment can significantly improve our understanding of specific patterns in the archaeological record. We present details of an agent-based computer simulation of a recent experiment (Mesoudi and O'Brien 2008) that simulated the cultural transmission of Great Basin projectile point technology, as explored by Bettinger and Eerkens (1999). We stress that this work is not intended to replace traditional archaeological methods; rather, we suggest that computer and experimental simulations offer two potentially useful tools that archaeologists can use to more fully explain their data. Archaeological methods provide real-world historical validity, experimental simulations provide essential psychological and behavioral data, and computer models allow us to systematically and rigorously explore a wide range of conditions and assumptions. Each method informs and enhances the others, to the mutual benefit of all. In the following section we describe the archaeological study that inspired the experimental and computer simulations; we then turn to the details of those simulations.

The Archaeological Data

One of the best examples of the use of cultural-transmission theory to explain archaeological data is Bettinger and Eerkens' (1997, 1999) study of Great Basin projectile points. These stone points were manufactured around A.D. 300–600 following the replacement of the atlatl with the bow and arrow. Bettinger and Eerkens (1999) observed that points found in two regions of the Great Basin differ in the degree to which their attributes, such as length, width, and weight, correlate with each other, and they attributed these differences to the manner in which prehistoric inhabitants of the two regions acquired and transmitted projectile-point technology. Specifically, the attributes of points found in eastern California exhibited weak correlations with each other, indicating diversity in point designs. Bettinger and Eerkens (1999) argued that this was because projectile technology in the region originally spread by means of *guided variation* (Boyd and Richerson 1985), in which individuals acquire a cultural trait and then modify it through individual trial and error. The latter component of individual trial-and-error experimentation caused the point attributes to vary independently, and thus correlations between the attributes decreased.

In contrast, projectile points of the same material and from around the same period found in central Nevada featured uniform designs with highly correlated attributes. Bettinger and Eerkens (1999) argued that those points originally spread as a result of *indirect bias* (Boyd and Richerson 1985), in which individuals copy wholesale the design of a single successful model with no further modification. With no individual trial and error and a single model, point designs soon converged on the same attributes, generating high correlations between attributes. Bettinger and Eerkens (1999) argued that differences between the regions at the individual level (guided variation in California vs. indirect bias in Nevada) generated differences between regions at the population level (uncorrelated attributes in California vs. correlated attributes in Nevada).

The Experimental Simulation

In a previous study (Mesoudi and O'Brien 2008), we conducted an experimental simulation of the archaeological pattern observed by Bettinger and Eerkens (1999) in order to test whether guided variation and indirect bias really do generate the proposed population-level patterns, and if so, under what conditions. Groups of six participants (college students) played a computer game in which each participant designed his or her own "virtual projectile point" and then tested the design in a "virtual hunting environment." Participants entered the values of five attributes of their projectile points (Length, Width, Thickness, Shape, and Color). The closer their point designs were to a hidden optimal point design, the higher their feedback (given in calories).

Participants had 30 trials, or "hunts," during which to modify their point designs.[1] These 30 hunts were divided into three phases. Following Bettinger and Eerkens' (1999) hypothesis, each of the phases simulated a different transmission rule that supposedly generated their Great Basin data (see Mesoudi and O'Brien 2008:Table 2). During Phase 1, the first hunt, participants could copy the point design of one of six previous participants,

Table 1. Correlation Coefficients for Experimental Point Attributes from Mesoudi and O'Brien (2008).

		Width	Thickness	Shape	Color
Length	Hunt 1 (SL)	.801***	.996***	1.000***	.828***
	Hunt 25 (IL)	.272*	-.004	.248	.187
	Hunt 30 (SL)	-.432	-.280	.730*	.664*
		Hunt 1 (SL)	.752***	.856***	.994***
	Width	Hunt 25 (IL)	-.014	.300	.350*
		Hunt 30 (SL)	-.515*	.763*	.342
			Hunt 1 (SL)	.895***	.706***
		Thickness	Hunt 25 (IL)	.162	.190
			Hunt 30 (SL)	.867**	.489
				Hunt 1 (SL)	.603***
			Shape	Hunt 25 (IL)	.130
				Hunt 30 (SL)	.617*

Note: Correlations are Spearman's r_s. SL = Social Learning; IL = Individual Learning. Sample sizes: Hunts 1 and 25, n = 75; Hunt 30, n = 18.
*$p < .05$
**$p < .01$
***$p < .001$.

given information about those previous participants' relative success in the game. Phase 1 therefore simulated indirectly biased oblique cultural transmission—copying the point design of a successful member of the previous generation. During Phase 2, participants had 24 hunts to improve their point designs through individual trial and error, and were not allowed to view the point design of any other participant. Phase 2 therefore simulated guided variation—modifying a culturally acquired point design according to individual trial-and-error learning. During Phase 3, which consisted of five hunts, participants could choose to view and copy the point design of another member of their group, again given information about the other group members' relative success. Phase 3 therefore simulated indirectly biased horizontal (within-group) cultural transmission—copying the point design of a successful member of the same generation. If Bettinger and Eerkens' (1999) conclusions were correct, and the low attribute correlations observed in central Nevada resulted from indirect bias, while the higher attribute correlations in eastern California were a result of guided variation, then our results should reveal low correlations between point attributes during Phase 2 and higher correlations between point attributes during Phases 1 and 3.

As shown in Table 1, this pattern was indeed found, supporting Bettinger and Eerkens's (1999) hypothesis. Attribute correlations were highest during Phase 1 (indirect bias), dropped during Phase 2 (guided variation), and increased again during Phase 3 (indirect bias). Observing this pattern (indirect bias = high correlations; guided variation = low correlations) in the experiment, where we have definitive records of our participants' copying behavior, increases our confidence that the same pattern in the prehistoric Great Basin was generated by a similar cultural process (indirect bias in Nevada = high correlations; guided variation in California = low correlations).

The Agent-Based Computer Simulation

Although the experimental results of Mesoudi and O'Brien (2008) are consistent with Bettinger and Eerkens's (1999) hypothesis, which increases our confidence in the validity of their hypothesis, we stress that experimental simulations of past cultural change would never be able to provide a definitive test of such a hypothesis. There will always be limitations of experimental methods, such as the many differences between our laboratory and the prehistoric environment, or between our Western college-student participants and prehistoric hunters. We acknowledge that some of these limitations may be unavoidable (Mesoudi 2007, 2008; Mesoudi and O'Brien 2008), but we also stress that experimental simulations can usefully complement archaeological methods by allowing us to, for example, re-run history, randomly assign control and experimental groups, and generate complete, uninterrupted, and unbiased datasets.

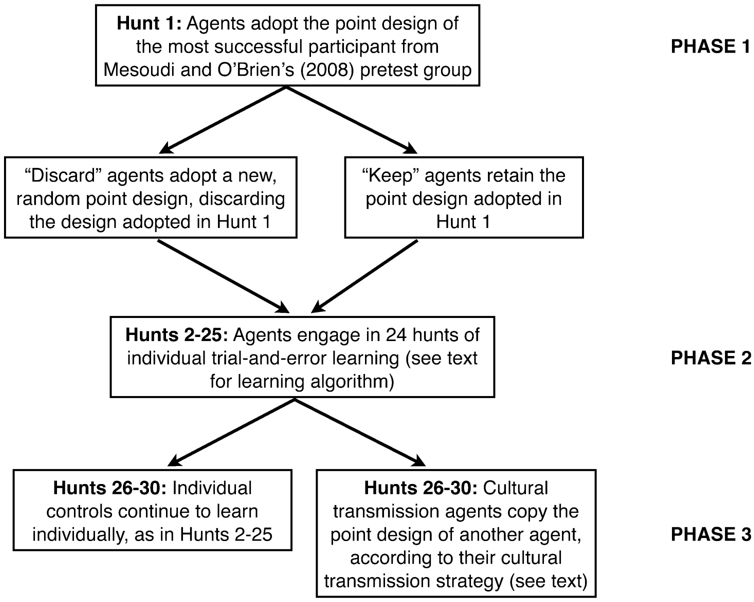

Figure 1. Flow chart showing the design of the agent-based simulation.

In the following section, we hope to demonstrate how the use of agent-based computer simulations can overcome other limitations of experimental simulations. For example, experiments are often limited by the availability of participants and time. This problem is especially prominent when simulating large-scale, population-level archaeological processes, which may have originally involved many hundreds or thousands of people over multiple generations and hundreds of years. These problems can be partially overcome by using agent-based computer models to extend experiments and draw wider conclusions. Agent-based models (Axelrod 1997; Epstein and Axtell 1996; Kohler and Gumerman 2000) involve simulating in a computer program a population of virtual "agents," or "individuals," each with specified characteristics and behaviors, and allowing the agents to interact, learn, and evolve over time. Here we present an agent-based model of the experiment reported in Mesoudi and O'Brien (2008), with agents representing participants and performing the same experimental task as the actual participants.[2] To maximize the validity of the model, we used data from the participants to inform the behavior of the agents. We first verified that the model successfully re-created the data generated by the participants under identical conditions. We then systematically extended parameters such as sample size, group size, and number of trials/generation. Finally, we simulated alternative cultural-transmission strategies and explored the effect of changing the shape of the selective environment.

Model Description

The design of the model was identical in almost every respect to the experiment described in Mesoudi and O'Brien (2008), with computer-generated agents in groups of six designing projectile points. (Indeed, the agent-based model was carried out using exactly the same C++ code that was used to run the experiment, except with input coming from additional code rather than from human participants.) Following the same procedure as the experimental participants, the agents engaged in 30 hunts divided into three phases of learning, each simulating different learning rules. Figure 1 provides a flowchart describing the behavior of the agents. Phase 1 simulated indirectly biased oblique cultural transmission, where agents automatically copied the point attributes of the most successful pretest participant from the experiment, just as most of the experimental participants did during their Phase 1. Phase 2 again lasted 24 hunts and simulated guided variation, during which agents followed the individual-learning strategy defined below. Finally, Phase 3 lasted five hunts and simulated horizontal cultural transmission, where agents copied the point design of another agent in their group according to one of the four cultural-transmission strategies defined below. As in the experiment, we also ran individual-learning control agents who did not copy other agents during Phase 3.

For each of the five types of agents (four cultural-transmission strategies plus one individual-learning group), 50 six-agent groups were simulated. The results discussed in the sections below are the averages from all 50 groups. The different cultural-transmission conditions were independent, meaning that agents interacted only with other agents of the same cultural-transmission strategy, and the results of each group were compared statistically rather than allowing the agent types to compete directly. As in the experiment, we used three different selective environments (three different sets of optimal attribute values). Each group of agents was assigned randomly to one of the three environments. Contrary to the conditions of the experiment, agents modified only the three continuous attributes (Length, Width, and Thickness) and not the two discrete attributes (Shape and Color). This made the individual-learning strategy easier to define and seemed to reflect the participants' behavior given that they modified the continuous attributes more frequently than the discrete attributes. The following sections outline the main research questions that were addressed and our theoretical predictions.

Individual-Learning Strategy

To maximize the validity of the model, we based the individual-learning behavior of our agents as much as possible on the behavior of the participants from the experiment (reported in Mesoudi and O'Brien [2008]). In the experiment, we defined a participant's individual-learning strategy using two parameters. The first, d, was defined as the number of continuous attributes changed during a hunt (where $0 \leq d \leq 5$). The second, c, was defined as the mean magnitude of the change in the three continuous attributes (Length, Width, and Thickness) during a hunt (where $0 \leq c \leq 99$). In the experiment we found that our participants tended to change one attribute at a time ($d = 1$) and by a magnitude of five units ($c = 5$). Following these results, we had the agents in the model use an identical strategy: during each hunt they changed one of the three attributes ($d = 1$) by a magnitude of five units ($c = 5$). (Interestingly, additional simulations not presented here indicated that these values of d and c were in fact optimal, meaning that they gave the highest mean fitness over the 30 hunts.)

On each hunt, an agent selected one of the three attributes at random, and then either increased or decreased the attribute by c. Agents initially selected a direction (increase or decrease) at random for each attribute. If this modification resulted in an increase in score compared to the previous hunt, then the agent continued with that direction for that attribute. If the score decreased, then the agent changed direction. This behavior resembles reinforcement learning or instrumental conditioning (Skinner 1938), or the classic "win-stay, lose-shift" learning strategy (Nowak and Sigmund 1993), and causes the agent to gradually converge on the nearest optimum and oscillate around that optimum (with a radius determined by the magnitude of c). Certainly, more complex and perhaps realistic individual-learning strategies are possible, involving greater modification ($d > 1$, $c > 5$) during early hunts/low scores and less modification ($c < 5$) during later hunts/high scores (as was found for some participants in the experiment). Strategies that use Bayesian learning rules (Oaksford and Chater 2001), or strategies that evolve (Holland 1992), are also viable options. On grounds of parsimony, however, there is no reason to invoke these more complex learning strategies if the simple reinforcement-learning strategy at constant values of d and c successfully re-creates the participants' behavior. First, however, we must evaluate whether this is true.

In Phase 1, all agents started with the same values of Length, Width, and Thickness as the most successful pretest participant, as presented to the experimental participants in their Hunt 1. We then simulated, in Hunt 2, two different learning strategies, "Keep" and "Discard." Agents employing the "Keep" strategy kept the values of Length, Width, and Thickness that they inherited from the most successful pretest participant. Agents employing the "Discard" strategy discarded those inherited values and began their individual learning with randomly generated values of each attribute. We defined these strategies because, in the experiment, participants experienced a different selective environment from the pretest participants (as did agents in the model). The point design that they inherited from the most successful pretest model therefore did not necessarily yield a high score in the participants' environment, so the "Discard" strategy should have been more effective. However, we did not inform the participants that the environment had changed, so some participants may have followed the "Keep" strategy. We were therefore interested in whether the results from the experiment more closely resembled the "Keep" or the "Discard" strategy, and we addressed this using the model.

Cultural-Transmission Strategy

In the final five hunts (Phase 3), agents in cultural-transmission conditions copied the design of other agents in their group according to their cultural-transmission strategy (Laland 2004). The first two strategies we call "model-based strategies" and involve copying the entire point design of a single model. The "copy-the-successful" strategy resembles the behavior of the experimental participants, where agents adopt all of the point-design attributes of the single agent in their group with the highest cumulative score at Hunt 25. As noted above, this strategy resembles Boyd and Richerson's (1985:243) indirect bias, with hunting success as the indicator trait.[3] "Copy-at-random" agents select another agent at random in their group and copy that agent's entire design. This random copying has been explored in an archaeological context by Neiman (1995) and Bentley and Shennan (2003).

The other two strategies we call "trait-based strategies," where agents use information from multiple models when copying each trait. "Copy-the-average" agents adopt the mean Length, mean Width, and mean Thickness of all agents' points in their group, including their own. This strategy resembles Boyd and Richerson's (1985:72) "blending transmission." "Copy-the-majority" agents adopt the modal Length, modal Width, and modal Thickness of all agents' points in their group, including their own, where the 1–100 scale for each dimension is divided into 10 intervals of 10 units and the agents adopt the midpoint of the modal interval. This strategy resembles Boyd and Richerson's (1985:205) "positive frequency-dependent," or "conformist" transmission. Note that the latter two trait-based strategies can be considered (although were not assumed in the model to be) cognitively more complex than the two model-based strategies, given that they require tallying or averaging across the entire group separately for each attribute.

Past theoretical work provides some predictions regarding these cultural-transmission strategies (Boyd and Richerson 1985; Laland 2004). We might predict that *any* form of cultural transmission should reduce within-group variation relative to individual learning (Boyd and Richerson 1985; Eerkens and Lipo 2005), not just the copy-the-successful strategy (indirect bias) as found in the experiment. We might also expect that the conformist copy-the-majority strategy should be particularly effective, given analytical results suggesting that conformity is adaptive under a wide range of conditions (Henrich and Boyd 1998).

Shape of the Adaptive Landscape

In the experiment the participants could modify five different point attributes: three continuous attributes (Length, Width, and Thickness), each ranging from 1–100 arbitrary units, and two discrete attributes (Shape and Color), each taking one of four values. The overall fitness score was the sum of each of these attributes. The continuous attributes had bimodal fitness functions, meaning that each attribute had two optimal values. One was a global optimum, giving the maximum fitness from that attribute, and the other was a local optimum, giving two-thirds the fitness of the global optimum. The farther from each of these fitness "peaks," the lower the fitness feedback (see Mesoudi and O'Brien [2008] for fitness equations). These three bimodal fitness functions, when combined into a single feedback score, yield an adaptive landscape with multiple peaks of varying height, where height in the landscape represents fitness of the design. We argued (Mesoudi and O'Brien 2008) that variation was maintained in the experiment during the Phase 2 guided variation because participants found themselves, purely by chance, at different locally optimal peaks on the fitness landscape. Any slight deviation away from this locally optimal peak decreased the overall feedback, giving the illusion that the participant was at the best possible point design, even though there were other, higher peaks to be found across valleys in the adaptive landscape (participants were not informed of the bimodal fitness functions and thus did not know that there were multiple locally optimal point designs).

Although we argued that the multimodal adaptive landscape was responsible for this maintenance of variation, we did not run an alternative experimental condition in which the adaptive landscape was unimodal, that is, where there was a single peak in the adaptive landscape, with no globally suboptimal peaks on which to get stuck. This was addressed using the model, in an alternative condition assuming a unimodal adaptive landscape. We might expect that a unimodal adaptive landscape will reduce the variation during the guided variation of Phase 2, given that all agents can converge on the single fitness peak. We also predict that this will be more likely to occur with increasing numbers of hunts, allowing for greater convergence on the single peak.

Simulation Results

Individual-Learning Strategy

An important test of the agent-based simulation is whether it can generate the same results using computer-generated agents as did the experiment using real participants, and, by extension, the archaeological data. Recall that we employed two alternative assumptions in the model regarding the starting conditions of the individual learning in Phase 2. In the "Keep" condition, agents kept the point design they inherited from Phase 1. In the "Discard" condition, the agents discarded this point design and started off Phase 2 with random point attributes. By looking at which of these conditions, if either, generates similar results as the experiment, shown in Figure 2a, we can ascertain the degree to which the participants were sticking with the point design that they copied during Phase 1 or whether they discarded this design.

The results of the model simulations supported the latter and showed that the "Discard" strategy successfully re-created the pattern of results observed in the experiment. In the "Keep" condition (Figure 2b), as all agents started at the same place in the point-design space, they tended to converge on the same optima, and thus there was little benefit to the copy-the-successful strategy relative to the individual controls ($F[1,598] = .363$, ns),[4] contradicting the experimental findings. The "Keep" condition also generated low within-group variation during Phase 2, with a within-group coefficient of variation (WGCV) of approximately .15, which does not match the WGCV of around .5 found in Phase 2 of the experiment.

The "Discard" condition (Figure 2c), where agents in the model took random values of Length, Width, and Thickness at the start of Phase 2, more accurately replicated the advantage shown by the participants who engaged in indirectly biased cultural transmission, with significantly higher scores over the last five hunts than individual-learning agents ($F[1,598] = 53.58$, $p < .001$). Within-group variation also matched the experimental results, with within-group variation during Phase 2 matching between-group variation at a magnitude of approximately .5. This suggests that the experimental participants were effectively discarding the low-scoring point designs they inherited and starting from scratch at Hunt 2. This makes sense given that the environment experienced by the agent/participant was different than the environment experienced by the pretest model. We therefore conclude that the reinforcement-learning strategy with the "Discard" assumption accurately captures the behavior of the participants, given the similarity between the results of those agents (Figure 2c) and the experimental participants (Figure 2a). The following results all assume the "Discard" individual-learning strategy.

Cultural-Transmission Strategy

Table 2 shows the correlations among the three continuous attributes at Hunt 25 (following Phase 2) and at Hunt 30 (following Phase 3) for each of the four cultural-transmission strategies plus the individual-learning controls. As expected, no significant correlations occurred at Hunt 25 for any strategy, following individual-learning and before the social-learning strategies were implemented. The individual controls also showed low and nonsignificant correlations at Hunt 30. Hence, individual learning was universally associated with low, nonsignificant correlations between point attributes, just as Bettinger and Eerkens (1999) and the results of the experiment suggested. Additionally, the copy-the-successful agents showed large and significant correlations following cultural transmission at Hunt 30 which were consistent with the results of the experiment. Furthermore, "copy-at-

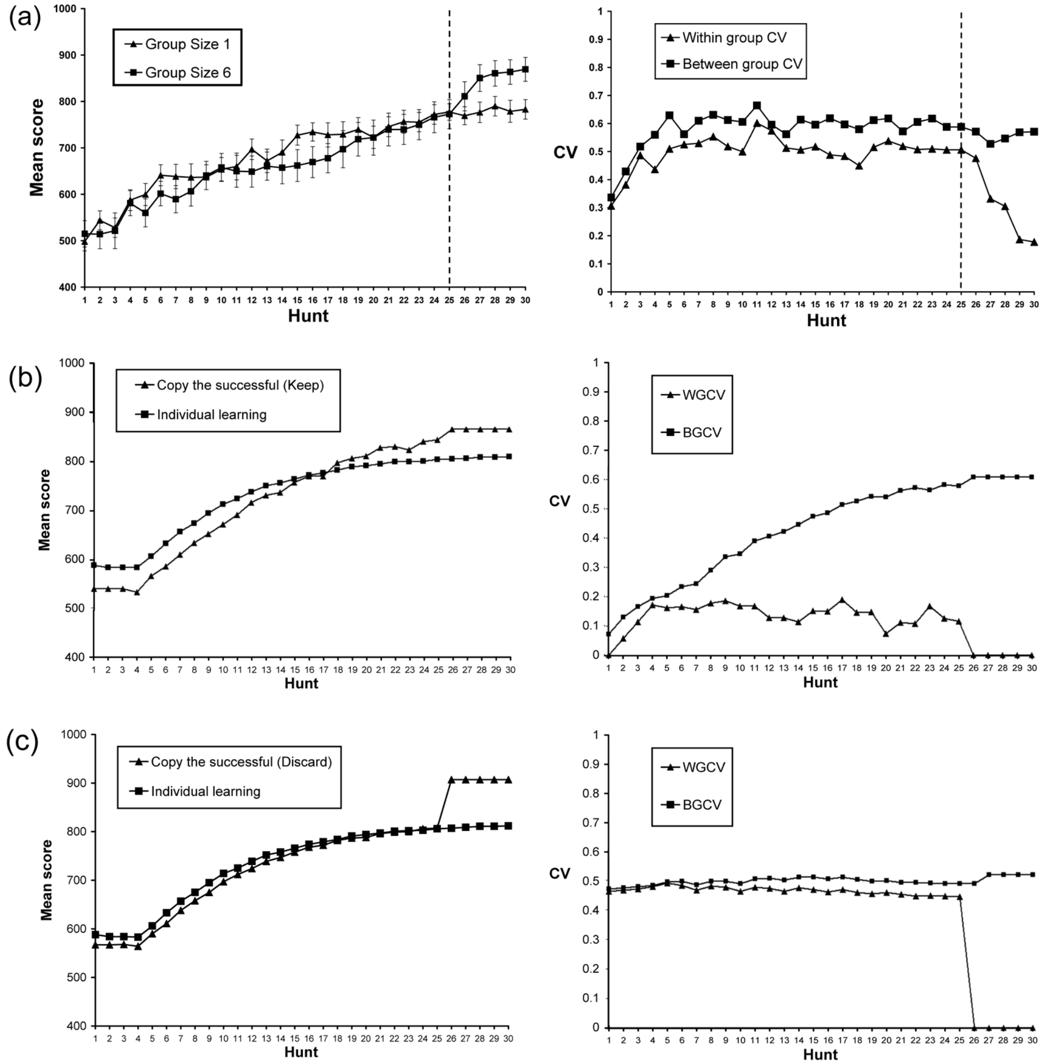

Figure 2. Mean score and coefficients of variation for (a) the experiment (Mesoudi and O'Brien 2008), (b) "copy-the-successful" agents with the "Keep" strategy, and (c) "copy-the-successful" agents with the "Discard" strategy.

random," the other model-based strategy, also demonstrated large and significant correlations at Hunt 30. "Copy-the-average" and "copy-the-majority," the two trait-based strategies, showed a less-marked increase in correlations at Hunt 30, although all but one comparison was significant. The different cultural-transmission strategies also produced similar decreases in within-group variation (Figure 3a), and in each case within-group variation dropped to zero during Phase 3.

From these findings we can conclude that (1) any form of within-group cultural transmission will reduce within-group variation and increase correlations between attributes, and (2) model-based cultural-transmission strategies, where the entire artifact is copied from a single model, generally give higher correlations than trait-based strategies, where multiple models are used for each trait. The first conclusion can be used to distinguish between cultural transmission (of any form) and individual learning in the archaeological record, and further supports the theories and conclusions Bettinger and Eerkens (1999) and Eerkens and Lipo (2005) presented in their research. However, it might be dif-

Table 2. Correlation Coefficients for Model Point Attributes, by Social-Learning Strategy.

	Copy the Successful			Copy at Random			Copy the Average		
	L x W	L x T	W x T	L x W	L x T	W x T	L x W	L x T	W x T
Hunt 25	.026	-.108	-.097	.159	.008	-.114	-.120	-.022	-.198
Hunt 30	.460***	-.564***	-.706***	.482***	-.599***	-.682***	.267*	-.248*	-.498***

	Copy the Majority			Individual Learning		
	L x W	L x T	W x T	L x W	L x T	W x T
Hunt 25	-.125	-.035	.132	-.025	-.203	-.095
Hunt 30	-.489***	-.309*	.069	-.101	-.073	-.037

Note: L = Length; W = Width; T = Thickness. Correlations are Spearman's r_s.
*$p < .05$
**$p < .01$
***$p < .001$.

ficult to use correlations and coefficients of variation to distinguish *between* different cultural-transmission strategies in the archaeological record. We might use the second rule to distinguish between model-based and trait-based cultural-transmission strategies, although given the noise inherent in archaeological data, it may be difficult to detect such small differences in correlation magnitudes.

An indirect way of inferring which cultural-transmission strategy was used in the past might be to compare the relative efficacy of each strategy in terms of the mean fitness payoff to each agent, and infer that the most-successful strategy was more likely to have been employed by prehistoric people. This test is undoubtedly indirect and rests on several large assumptions. Nevertheless, given that we can never directly compare the fitness consequences of different cultural-transmission strategies in prehistoric populations, experimental and computer simulations are probably the only way to address this question.

Figure 3b shows the mean score per agent at each hunt for each cultural-transmission strategy, as well as the individual-learning controls. The different strategies were each compared statistically with the individual-learning control agents. "Copy-the-successful" agents showed significantly higher scores over the last five hunts than individual-learning agents ($F[1,598] = 53.58$, $p < .001$). "Copy-at-random" ($F[1,598] = .31$, ns) and copy-the-majority ($F[1,598] = 3.15$, ns) agents both showed no significant difference from individual learning, whereas "copy-the-average" agents ($F[1,598] = 26.99$, $p < .001$) performed significantly worse than individual learning controls. This striking advantage of the "copy-the-successful" strategy leads us to speculate that although the pattern of correlations observed by Bettinger and Eerkens (1999) could plausibly have been generated by any form of cultural transmission, it was most likely to have been indirectly biased cultural transmission rather than conformist, averaging, or random cultural transmission.

Shape of the Adaptive Landscape

We argued (Mesoudi and O'Brien 2008) that the advantage of indirectly biased cultural transmission in the experiment was due at least in part to the multimodal adaptive landscape, because participants who get stuck on low-fitness peaks can jump to higher peaks in the adaptive landscape by copying fellow group members who happen to have found those higher peaks. One prediction that follows from this is that larger group sizes should yield higher scores because with more agents in a group, it is more likely that one of those group members will arrive at the best possible point design, where all of the point attributes are at global optima. Although the experiment was limited in terms of the number of participants we could plausibly run at any one time, with the agent-based simulation we can simulate what might happen with larger groups. Figure 4a confirms that mean score increases with group size for the "copy-the-successful" cultural-transmission agents. "Copy-the-successful" was the only strategy to exhibit this effect of group size. Figure 4b shows that mean score at Hunt 30 rapidly increases with group size until group size reaches approximately $n = 20$, at which point further increases in group size have little effect.

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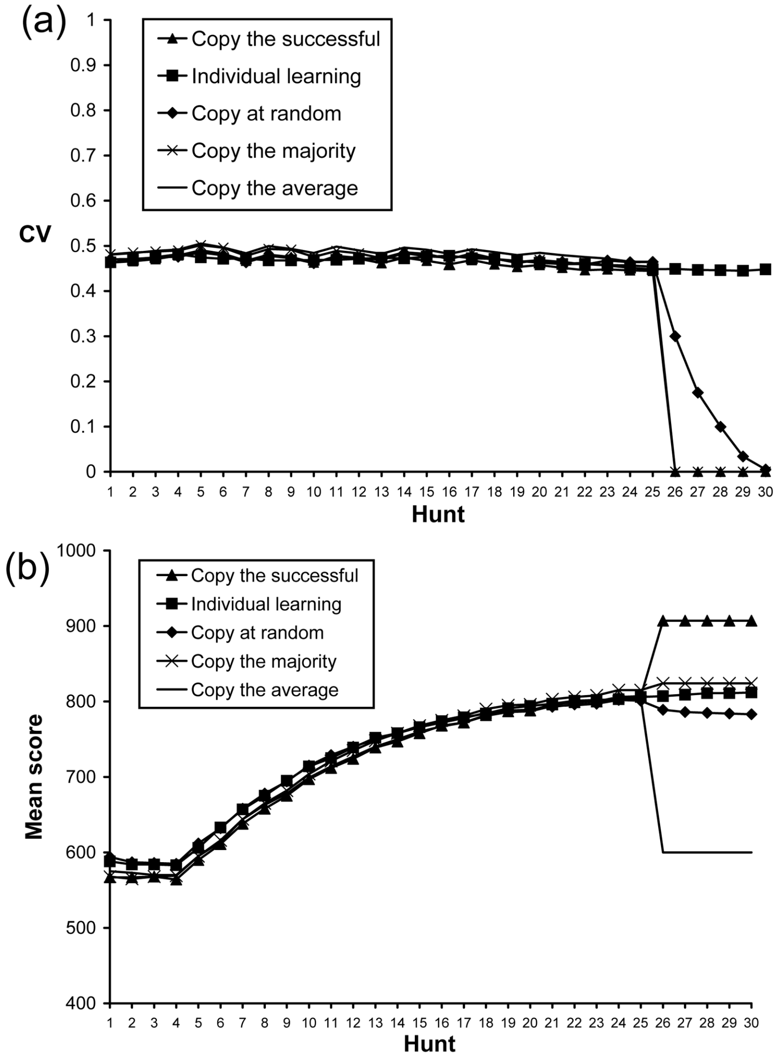

Figure 3. (a) Within-group coefficient of variation (WGCV) and (b) mean score for agents engaged in different cultural-transmission strategies.

As well as manipulating group size, we can also directly simulate learning in a unimodal adaptive landscape, where each attribute has a single normally distributed optimal value. Figure 5a shows that over extended numbers of hunts, individual-learning controls in a unimodal adaptive landscape do better than individual-learning controls in a multimodal adaptive landscape. This is because, given enough time/hunts, individual-learning agents will eventually converge on the single optimal point design, whereas in a multimodal adaptive landscape many will get stuck on globally nonoptimal fitness peaks. Figure 5b shows that individual-learning agents in a unimodal adaptive landscape also exhibit low within-group variation after extended numbers of hunts. The conclusions drawn in the previous section regarding the signatures of different forms of learning in the archaeological record therefore apply only if the selective environment in which that learning takes place is multimodal in shape, that is, there are several stable artifact designs, each with a different fitness. In a unimodal adaptive landscape, individual learners will eventually perform as well as those using indirectly biased cultural transmission (and perhaps outperform them[5]), as well as exhibit similarly low within-group variation.

We can also explain the advantage of the

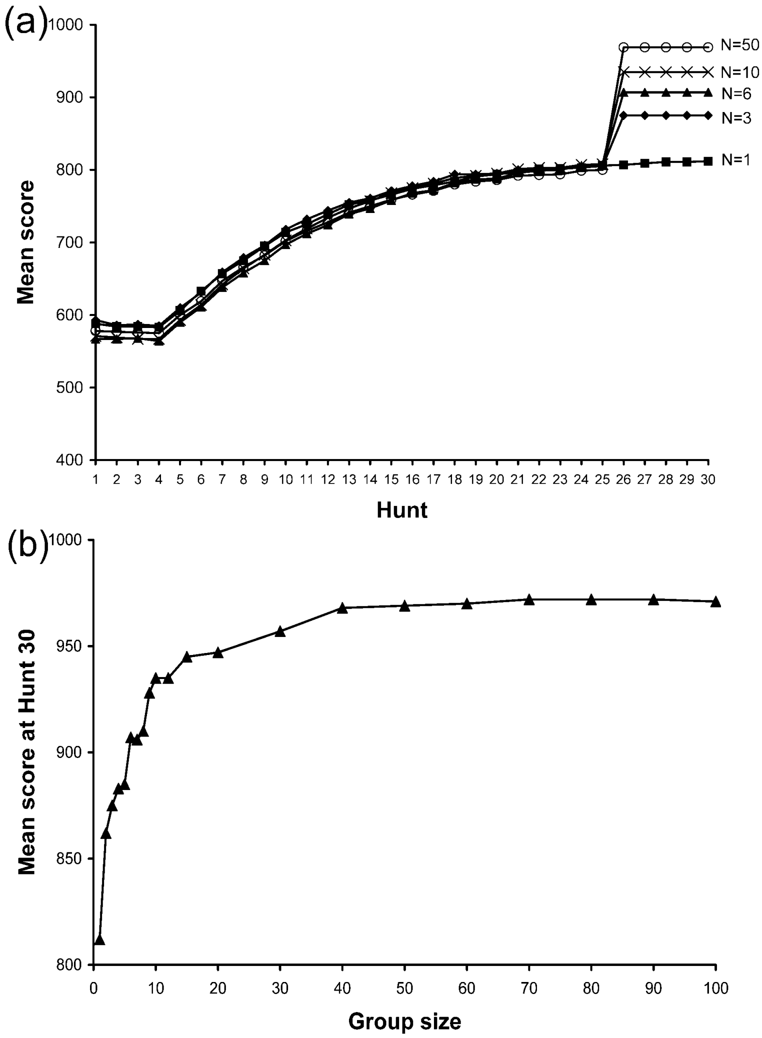

Figure 4. (a) Mean score for "copy-the-successful" agents at different group sizes over all hunts and (b) the relationship between mean score at the last hunt and group size.

"copy-the-successful" agents over the other cultural-transmission strategies (shown in Figure 3b) in terms of the shape of the adaptive landscape. "Copy-the-average" agents did poorly in the multimodal landscape because if half the group is at the global optimum and the other half is at the local optimum, then the average will be in a valley between these two fitness peaks, yielding a low score. "Copy-at-random" and "copy-the-majority" agents effectively choose one peak at random on which to converge, yielding a mean score equivalent to that for individual learning. Changing the selective environment so that each attribute had a unimodal rather than a bimodal fitness function, yielding a single globally optimal peak, improved the "copy-the-majority" strategy, as shown in Figure 5c. In this environment, "copy-the-successful" ($F[1,598] = 54.99$, $p < .001$) and "copy-the-majority" ($F[1,598] = 6.21$, $p < .05$) agents both have significantly greater scores than individual-learning controls, although "copy-the-successful" agents still significantly outperform "copy-the-majority" agents ($F[1,598] = 72.88$, $p < .001$). "Copy-at-random" ($F[1,598] = 4.60$, $p < .05$) and "copy-the-average" ($F[1,598] = 6.90$, $p < .01$) agents both perform worse than individual learners (although individual-learning controls eventually outperform all of these strategies given enough hunts [see note 5]).

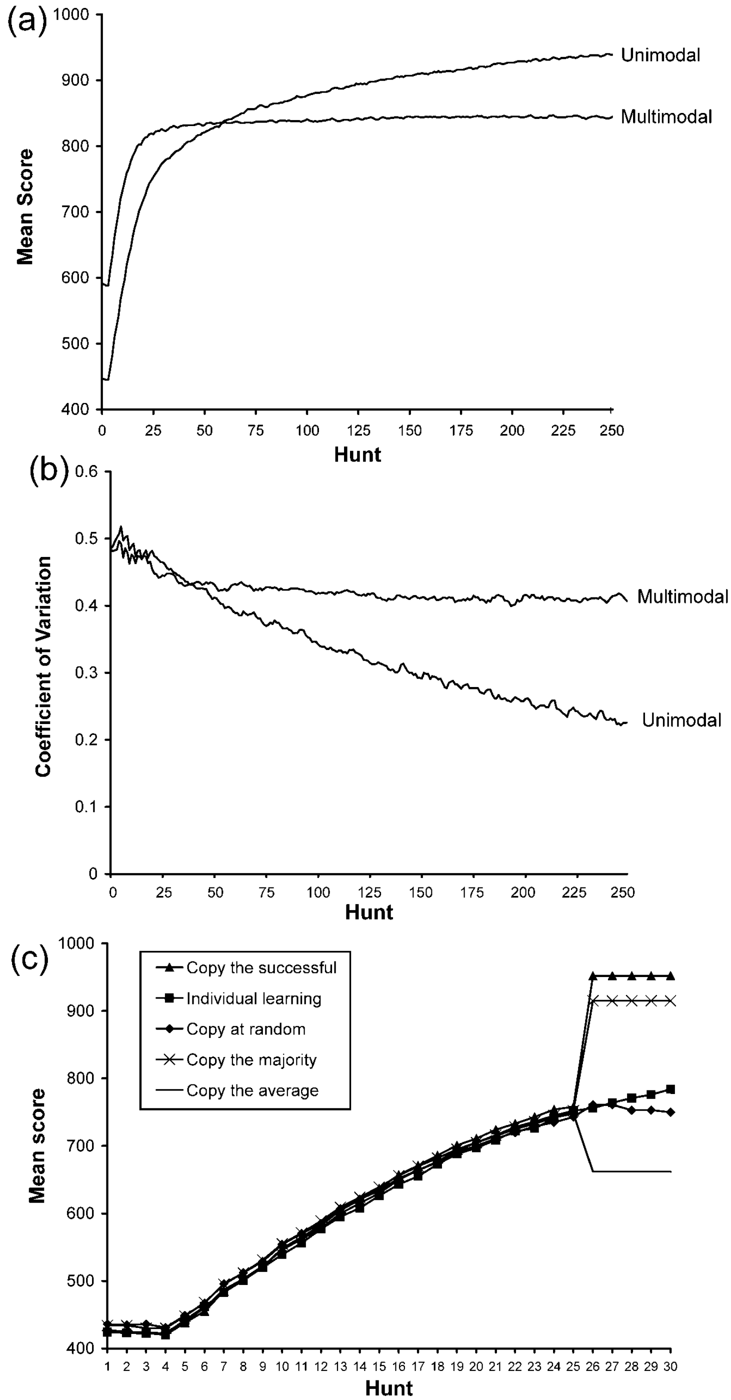

Figure 5. Comparison of a unimodal and a multimodal adaptive landscape on (a) mean score, (b) within-group variation for individual-learning agents over an extended number of hunts, and (c) comparison of different cultural-transmission strategies on a unimodal adaptive landscape.

Discussion

The aim of the present study was to develop an agent-based simulation of a previous experiment (Mesoudi and O'Brien 2008) that had simulated the cultural transmission of prehistoric Great Basin projectile-point technology. In both the experiment and the model, participants/agents designed projectile points and tested them in a virtual hunting environment, with different phases of the experiment simulating different learning rules. Phase 1 simulated indirectly biased cultural transmission from a pretest group of participants, Phase 2 simulated guided variation or individual learning, and Phase 3 simulated indirectly biased horizontal (or within-group) cultural transmission. In the experiment, and under certain conditions of the model, we re-created the patterns of attribute correlations that Bettinger and Eerkens (1999) observed in the Great Basin archaeological record, with indirect bias generating high correlations between attributes and guided variation generating low correlations. The agent-based simulation did more than replicate our findings in the experiment, however. It also permitted us to explore a much wider range of conditions and assumptions than was possible in the experiment, such as increasing the number of participants or trials, comparing alternative cultural-transmission strategies, and changing the shape of the selective environment.

We summarize the findings of the model in the following manner. First, we confirmed that cultural transmission acts to increase correlations between artifact attributes and reduce within-group variation, relative to individual learning. This supports Bettinger and Eerkens' (1999) argument to the same effect with respect to Great Basin projectile point designs, as well as Eerkens and Lipo's (2005) more general model of trait variation. However, whereas Bettinger and Eerkens assumed that this cultural transmission was indirectly biased (that people were copying the most successful group member's point design), here we showed that alternative modes of cultural transmission (copying the majority, copying the group average, and copying at random) generated similarly high correlations between attributes and similarly reduced within-group variation. We did find that "model-based" strategies, where the entire artifact of a single model is copied, generate higher correlations between attributes than "trait-based" strategies, where traits are separately averaged across multiple models. It thus might be possible to use these signatures to distinguish between these two strategies in the archaeological record. Generally, however, given the noise inherent in most archaeological datasets, we suspect that it will be difficult in practice to distinguish between different forms of cultural transmission in the archaeological record *when relying solely on attribute correlations or measures of variation.*

Second, we found that the "copy-the-successful" cultural-transmission strategy, which is analogous to indirectly biased cultural transmission, significantly outperformed the other cultural-transmission strategies and indeed was the only strategy to outperform individual learning. This advantage was even more pronounced in larger groups of around 50 individuals, which have been typical throughout much of human evolution (Dunbar 1995) and are likely to be more representative of the prehistoric societies that generate archaeological data than the groups of six employed in the experiment. If we are willing to assume that prehistoric people were behaving in an adaptive manner, we might infer that the high inter-attribute correlations and low within-group variation Bettinger and Eerkens (1999) found in the central Nevada region of the prehistoric Great Basin was indeed the result of indirect bias, as they argued. Further, this finding that the indirect-bias / "copy-the-successful" strategy outperforms all other cultural-transmission strategies is important because it qualifies previous mathematical models that suggest conformist cultural transmission is favored under a wide range of conditions (Henrich and Boyd 1998), as well as previous analyses that have found evidence of frequency-dependent (conformist or anti-conformist) cultural transmission in the archaeological record (Kohler et al. 2004; Shennan and Wilkinson 2001).

However, we should note that in reality people probably did not (and do not) engage exclusively in a single cultural-transmission rule as did our agents. It is more likely that people flexibly switch between different learning strategies (individual learning, "copy-the-successful," "copy-the-majority") depending on circumstances or experience. For example, novices or apprentices might preferentially follow a "copy-the-successful" strategy in order to quickly and effectively learn a new technology, whereas experts might adopt individual learning in order to refine their existing skills. Indeed, previous cultural evolutionary models (Boyd and Richerson 1995) and experiments (Kameda and Nakanishi 2003) have found this kind of flexible switching of learning strategies to be highly adaptive. Further experiments and models might explore optimal combinations of learning strategies for different tasks and circumstances.

Third, we found that all of these findings are highly dependent on the assumption of a multimodal adaptive landscape, in which multiple, stable artifact designs coexist, each of which yields a different fitness. In a unimodal adaptive landscape, individual learning eventually performs equally as well as or better than every cultural-transmission strategy, and individual learning generates the same low within-group variation as does cultural transmission. This is because individual learning will eventually converge on the single optimal "peak" in the adaptive landscape. In contrast, in a multimodal adaptive landscape, individual learners get stuck on locally optimal but globally suboptimal peaks, whereas "copy-the-successful" agents can jump to peaks of higher fitness found by other individuals.

This might explain the discrepancy between our findings and the previous analyses noted above (e.g., Henrich and Boyd 1998), given that such analyses commonly assume dichotomous traits and fitness functions—that is, behavior can take one of two discrete values, one of which has a higher fitness than the other. Generally, the findings of the model reinforce our speculation in Mesoudi and O'Brien (2008) that the shape of the adaptive landscape will strongly influence the dynamics of cultural transmission. Although there is little specific empirical evidence in this regard, we can speculate that the actual selective environments of cultural traits are more likely to resemble multimodal than unimodal or discrete adaptive landscapes (Bettinger and Baumhoff 1982; Boyd and Richerson 1992; Mesoudi and O'Brien 2008). For example, Cheshier and Kelly (2006) found experimental evidence for tradeoffs in projectile-point designs with respect to different functions, such as accuracy and killing power. For example, they determined that "thin, narrow points have greater penetrating power, but wide, thick points create a larger wound that bleeds more easily" (Cheshier and Kelly 2006:353). Hence, we might expect a bimodal fitness function, one peak maximizing penetrating power and the other maximizing bleeding, with intermediate forms showing low fitness.

Just as population-genetic models suggest that multimodal adaptive landscapes have been important in biological evolution by guiding historical trajectories of biological lineages (Arnold et al. 2001; Lande 1986; Simpson 1944), multimodal landscapes have also likely affected the historical trajectories of cultural artifact lineages. We might look for evidence of this in the archaeological record, perhaps by looking for artifacts or artifact traits that, across a population, converge on a small number of stable forms, which we can infer is due to individual learning. Then, if the artifact or artifact traits abruptly take on a new form, or one of the previous forms, we can infer that this change results from indirectly biased cultural transmission to a new, higher peak in the adaptive landscape. Indeed, the transition from the atlatl to the bow and arrow in the Great Basin might be one example of this. Evidence of migration or intergroup contact at around the time of the shift to a new peak might also be expected.

However, we do not wish to argue that *all* cultural evolution takes place on multimodal adaptive landscapes. Rather, our point is that only by formally testing assumptions regarding selective environments with experimental and computer simulations, as was done here, can we make quantitative predictions that can then be tested with archaeological data. Given that it is extremely difficult to identify the shape of the adaptive landscape in prehistoric environments, experiments and models may, in many cases, be the only way of testing such assumptions. More specifically, our discussion underscores the utility of agent-based computer simulations by demonstrating how they give researchers the ability to escape the constraints imposed by experimental setups and thoroughly explore a set of assumptions. As we showed, the use of data from our initial experiment helps to maximize the validity of models, preventing them from becoming too abstract. We believe that experimental simulations, when supplemented with agent-based models as described here, can be useful tools for simulating aspects of prehistory that are difficult to observe directly in the archaeological record, such as microevolutionary cultural-transmission rules or the shape of adaptive landscapes on which cultural traits evolve. This interplay among historical data, experimental simulations, theoretical predictions, and computer simulations is facilitated by a multidisciplinary evolutionary framework for the study of culture (Mesoudi et al. 2004, 2006; Richerson and Boyd 2005), which naturally emphasizes the importance of individual-level details of transmission in generating population-level patterns, such as those we observe in the archaeological record.

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Notes

1. In fact, participants in Mesoudi and O'Brien (2008) played three seasons of 30 hunts each. The three seasons had different optimal point designs, and during the last season participants had to pay a cost to modify their points, simulating costly individual learning. The model presented here simulated only a single season of hunting with no cost.

2. Our use of agent-based models is slightly different from their more common use in archaeology, which is to directly simulate prehistoric people or households interacting in an explicit spatial environment (e.g., Kohler et al. 2000). In our model, we instead simulate participants in an experiment that itself was intended to simulate prehistoric cultural change, rather than simulating that prehistoric change directly. We believe this added layer of psychological reality adds a certain degree of validity to our agent-based model, although we fully support the more conventional and direct use. Indeed, the two uses are probably quite complementary.

3. Note that this strategy is copy-the-successful-individual, rather than copy-the-successful-behavior. In other words, agents are selecting successful individuals to copy and not (necessarily) successful behaviors. The latter, copying successful behaviors, would resemble Boyd and Richerson's (1985) direct bias and would involve testing a model's behavior to assess its effectiveness before adoption of that behavior. Neither the participants in Mesoudi and O'Brien's (2008) experiment nor agents here could test point designs before choosing whether to adopt them. In practice, however, these strategies are likely to have very similar consequences: individuals are successful because they exhibit successful behaviors, so copying successful individuals will usually result in copying successful behaviors.

4. All statistical tests are mixed ANOVAs on the scores from the last five hunts, with hunt as a within-group factor and strategy as a between-group factor.

5. Several factors determine whether individual learners will outperform copy-the-successful agents in a unimodal adaptive landscape. Primary among these is the length of the individual learning period (Phase 2). If Phase 2 is too short, then it is unlikely that any agent in a group of "copy-the-successful" agents will have found the optimal design. Given that we assume that "copy-the-successful" agents during Phase 3 no longer engage in individual learning, "copy-the-successful" agents will not be able to improve their points further, whereas individual learners can continue to improve their points. Of course, it is unrealistic to assume that agents go through one relatively short period exclusively engaging in individual learning (Phase 2) and then another period exclusively engaging in cultural transmission (Phase 3). To more accurately explore the relative efficacy of individual learning and social cultural transmission in a unimodal adaptive landscape, we might allow agents to "choose" whether to engage in individual learning or cultural transmission during every hunt. This likely would result in information producers (individual learners) and information scroungers (social learners) coexisting at some fixed frequency (Kameda and Nakanishi 2002, 2003). The general point we draw from our current simulations, however, still holds: "copy-the-successful" always outperforms individual learning in a multimodal adaptive landscape, whereas individual learning may sometimes outperform "copy-the-successful" in a unimodal adaptive landscape.

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