The accumulation of stochastic copying errors causes drift in culturally transmitted technologies: Quantifying Clovis evolutionary dynamics

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ABSTRACT

The archaeological record is the empirical record of human cultural evolution. By measuring rates of change in archaeological data through time and space it is possible to estimate both the various evolutionary mechanisms that contribute to the generation of archaeological variation, and the social learning rules involved in the transmission of cultural information. Here we show that the recently proposed accumulated copying error model [Eerkens, J.W., Lipo, C.P., 2005. Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. Journal of Anthropology archaeology 24, 316–334.] provides a rich, quantitative framework with which to model the cultural transmission of quantitative data. Using analytical arguments, we find that the accumulated copying error model predicts negative drift in quantitative data due to the proportional nature of compounded copying errors (i.e., neutral mutations), and the multiplicative process of cultural transmission. Further, we find that the theoretically predicted rate of drift in long-lived technologies is remarkably close to the observed reduction of Clovis projectile point size through time and space across North America.

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Introduction

One of the major transitions in evolutionary history was the evolution of pathways that allowed the transmission of fitness-related, non-genetic information between individuals (Maynard-Smith and Szathmary, 1998). These transmission pathways and the social networks they form have been central to both human cultural and biological evolutionary history (Boyd and Richerson, 1985; Henrich and McElreath, 2003). Because the archaeological record documents changes in material culture over time and space, it is the only empirical record of past human cultural evolution. A primary goal of archaeology must be then to develop quantitative mechanistic theories derived from fundamental principles that explain the rates of change we observe in empirical data. In this paper we move toward this goal by developing stochastic models that describe the cultural transmission of complex technologies, and show how the key parameters can be measured statistically from archaeological data.

While many cultural, behavioral, and biological mechanisms combine to shape the archaeological record, in general, all mechanisms can be classified either as deterministic or stochastic. Deterministic mechanisms are the selective processes that shape variation in material culture via the rules of social learning, whereas stochastic mechanisms are the inherent, random statistical effects of probability that generate variation. Selective processes reflect the human cognitive ability to evaluate the economics of alternative strategies, such as the ability to evaluate the differential performance of tools at particular tasks, or the likely cost-benefit structure of employing different learning strategies in different environmental conditions. These selective processes are best described by biased transmission rules, where the term "bias" refers to a type of social learning that is constrained to some subset of the overall variation within a population (Boyd and Richerson, 1985). Stochastic mechanisms, on the other hand, include both variation generated by the probabilistic nature of naturally-occurring processes, and the random processes of recovery, preservation, and taphonomy that influence sampling from the archaeological record (i.e., Brantingham et al., 2007; Surovell and Brantingham, 2007). One important evolutionary consequence of sampling variation is drift, which is caused by population fluctuations and subsequent founder effects (Lipo et al., 1997; Shennan, 2000, 2001). A second source of drift is the accumulation of neutral, unbiased, but proportional copying errors through time (see Eerkens and Lipo, 2005), a mechanism we explore in detail below.

The archaeology of cultural transmission: quantitative data and lognormality

Archaeological applications of cultural transmission theory focus either on discrete, categorical forms of variation such as changes in the diversity of pottery styles or tool types over time

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or space (e.g., Bettinger and Eerkens, 1999; Brantingham, 2007; Henrich, 2004; Neiman, 1995) or quantitative, continuous variation in archaeological data, which focus on rates of change within particular artifact types (Buchanan, 2006; Buchanan and Collard, 2007; Buchanan and Hamilton, in press; Lycett, 2007; Lycett and von Cramon-Taubadel, 2008; Lycett et al., 2006). Recently, Eerkens and Lipo (2005) outlined a general yet powerful Markovian approach to modeling quantitative variation in archaeological data. Using a simple mathematical framework they showed that Markov models can be used to capture the essential elements of transmission rules that shape the transfer of quantitative information between individuals, which can then be used to inform the mechanisms that drive variation in archaeological data. Their model, which we term the accumulated copying error (ACE) model, describes how imperceptible copying errors during transmission events accumulate over time to become a significant source of variation in the archaeological record. Here we extend their model to show that this general framework leads to a surprisingly rich body of quantitative theory and some non-intuitive insights into cultural change.

When considering quantitative data we move from analyzing changes in the frequencies of discrete, categorical classes of data within or across populations to considering distributions of continuous variation, and the changes in the shapes of those distributions through time and space as measured by their statistical moments. In particular we are interested in measuring rates of change in the first four moments; the mean, variance, skewness and kurtosis.

Quantitative data, particularly measurement data, often will be right skewed. This skew occurs because measurements are ratio level data where zero is an absolute lower bound. The lower bound means that, by definition, measurements must be greater than zero, so the lower tail of the distribution is bounded while the upper tail is unbounded. While the upper tail is unbounded, in general, large measurements occur with exponentially decreasing frequency such that the distribution becomes skewed to the right, as smaller variants are more common than larger variants. This skew is expected to be especially relevant to archaeological assemblages if variation is the result of an inherently reductive technology, such as stone tool manufacture. Specifically, right-skewed distributions will be lognormal when the underlying generative mechanism is multiplicative (Limpert et al., 2001), due to the mechanics of random walks and the laws of logarithms. Unbiased random walks generate normal distributions over time (Allen, 2003; Taylor and Karlin, 1998). Because a lognormally distributed variable is normally distributed on the logarithmic scale it follows from the laws of logarithms that an arithmetic process on the log scale is a multiplicative process on the linear scale. So, while arithmetic random walks (i.e., simple Brownian motion) produce normal distributions of outcomes over time, multiplicative random walks (i.e., geometric Brownian motion) result in lognormal distributions. Indeed, lognormal frequency distributions are common in nature as growth processes are inherently multiplicative (Limpert et al., 2001). We see this mechanism in anthropological data where hunter-gatherer group sizes at multiple levels of social organization are lognormally distributed (Hamilton et al., 2007b) due to the multiplicative process of reproduction and population growth.

Recognizing that different generating mechanisms lead to different kinds of frequency distributions has important implications for understanding how variation in archaeological data is produced. All archaeological frequency distributions consist of artifacts that were manufactured, used, and discarded over some period of time (from days to centuries) and over some measure of space (from sites to continents). Essentially, frequency distributions of artifacts can be thought of as the solutions of multiple mechanistic functions integrated through time and space. By decomposing these frequency distributions it is then possible to

measure rates of change by analyzing changes in the statistical parameters of the distributions. Therefore, by building mathematical models based on the mechanisms of interest we can then understand the generative mechanisms behind empirically observed frequency distributions and develop statistical methods of estimating the key parameters from empirical data. Using this approach it becomes not only possible to measure rates of change in empirical data, but also to deconstruct the various mechanistic processes that contribute to the variances observed in the empirical frequency distributions.

Accumulated copying error model under vertical and biased transmission

The power of the accumulated copying error (ACE) model lies in its simplicity. In most traditional craft technologies social learning of complex tasks usually occurs as a series of transmission events between an apprentice and a master, where a master attempts to teach an apprentice the skills required to replicate a certain type of artifact. In this paper we use the example of the social learning of knowledge required to manufacture a projectile point within a hunter-gatherer society, though the model is generally applicable to the cultural transmission of complex tasks in a variety of socio-economies. If the apprentice is a novice, each copying attempt is likely to vary widely from the master's example, especially given the complexity of the knowledge and skills required in manufacturing a functional projectile point. However, even as the skills of the apprentice progress to the point of expertise, copying attempts will never produce perfect replicas of the master's example, though such copies might be fully functional, easily falling within the acceptable performance criteria for projectile points. These functional points will then be used, and at some point during their use-life will enter the archaeological record.

This inevitable copying error occurs as a result of the lower threshold of human perception (Eerkens, 2000; Eerkens and Lipo, 2005). Experimental research on human subjects shows that in the absence of measuring devices, where subjects were asked to replicate tasks such as drawing simple objects, typical deviations of a copy from its target example are around 3–5% (Eerkens, 2000). This phenomenon is well recognized in the social sciences, and is termed the Weber Fraction. Thus, over multiple transmission events, the Weber fraction compounds to become a significant source of variation (Eerkens, 2000; Eerkens and Lipo, 2005). So, continuing with our projectile point example, as points are manufactured over time, some proportion of the overall variance in size of the total population of points will be due to the accumulation of copying errors over multiple generations, while other sources of variation may include length of use life, and the quality and size of raw material from which the projectile point was manufactured. In the following sections we examine the implications of the ACE model under both unbiased and biased transmission. We have three objectives in our examination of the ACE model. First, we model the long-term implications of the ACE model by examining the expected statistical distributions of projectile point sizes through time. Next, we look at the implications of the ACE model under biased transmission rules, and develop a biased accumulation of copying error (BACE) model. Lastly, we explore how the different components of the model can be estimated statistically from empirical data, and use these estimates to examine spatiotemporal changes in Clovis projectile point size across late Pleistocene North America.

Unbiased transmission: the ACE model

Following Eerkens and Lipo (2005), we outline the ACE model under the basic assumptions of unbiased vertical transmission

where technological knowledge is transmitted strictly from parent to offspring. For the models we outline below, we interpret the Weber fraction as the standard deviation of the overall distribution of copying errors. This is because, all else being equal, the deviation of any copy, x_i, from its expected value, $E[x] = \bar{x}$ is given by $\Delta x = x_i - \bar{x}$. We can write this deviation in terms of the copying error rate $\varepsilon(t)$ thus, $E[x] = x_i + \varepsilon(t)$, where $\varepsilon(t)$ is a normal distribution with mean $\mu_\varepsilon = 0$ and some variance $\sigma_\varepsilon^2 > 0$. Because $\varepsilon(t)$ is a distribution we can expand this equation to show $E[x] = x_i + \mu_\varepsilon + \sigma_\varepsilon$, which reduces to $E[x] = x_i + \sigma_\varepsilon$ as $\mu_\varepsilon = 0$. So the expected change in x is given by $E[\Delta x] = |x_i - \bar{x}| = \sigma_\varepsilon$. Thus the expected deviation of a copy from its target (i.e., the Weber fraction) is given by the standard deviation of the error term, $\sigma_\varepsilon = \sqrt{1/N\sum_{i=1}^{N}(x_i - \bar{x})^2}$.

Eerkens and Lipo (2005) described the accumulated copying error rate model as a simple Markov process where a single sample path is given by

$$Y(t+1) = Y(t) + Y(t) \cdot c \cdot N(0,\ 1), \qquad (1)$$

where Y is the attribute of interest, t is time, c is half the error rate, and $N(0, 1)$ is a standard normal distribution. Because the error term is normally distributed, Eq. (1) is a discrete-time continuous-state Markov process that describes the evolution of Y over time. It is important to note here that Eq. (1) is a multiplicative process, as opposed to an arithmetic process, and so describes a geometric Brownian motion rather than a simple Brownian motion. The multiplicative nature of Eq. (1) arises because of the structure of the error term, the second term on the right hand side of Eq. (1). Here, the error term, $cN(0, 1)$, is proportional to the attribute of interest, $Y(t)$, and so the error is multiplicative. We redefine terms and rewrite Eq. (1) in more standard notation as

$$s_i(t+1) = s_i(t)[1 + \varepsilon(t)], \qquad (2)$$

where $s_i(t)$ is the attribute of interest time t, and $\varepsilon(t)$ is a normally distributed copying error rate with mean zero, and variance, σ_ε^2; that is $\varepsilon(t) = N(0, \sigma_\varepsilon^2)$. Note that the error term, $\varepsilon(t)$, in effect models a neutral mutation occurring during the transmission event. Because random walks are more straightforwardly analyzed on the linear scale we linearize Eq. (2) by taking the natural logarithm of both sides giving

$$S_i(t+1) = S_i(t) + \ln[1 + \varepsilon(t)], \qquad (3)$$

where $S = \ln s$. In addition to copying error there is also variation in $S_i(t)$ due to other random factors, such as variation in the size of raw material nodules, the quality of different raw materials, and the use-life of the tool. Eerkens and Lipo (2005) term these other sources of error structural error. We include structural error in the model by introducing a second stochastic term, $\kappa(t)$, which is a normally distributed random variable with mean 0 and variance σ_κ^2, yielding

$$S_i(t+1) = S_i(t) + \ln[1 + \varepsilon(t)] + \kappa(t). \qquad (4)$$

Note that $\kappa(t)$ is independent of $S_i(t)$. Eq. (4) describes the sample path of an attribute $S_i(t+1)$ as a function of the artifact in the previous generation plus two sources of stochastic error, the proportional copying error rate, $\ln[1 + \varepsilon(t)]$, and structural error, $\kappa(t)$. To examine the long-term behavior of Eq. (4) we expand it in a Taylor series around $\varepsilon(t)$, yielding

$$S_i(t+1) = S_i(t) + \kappa(t) + \left[\mu_\varepsilon - \frac{1}{2}\sigma_\varepsilon^2\right](t). \qquad (5)$$

The expected value of S at time t is found by averaging over Eq. (5), yielding

$$E[S(t)] = \bar{S}(t) = S_0 - \frac{1}{2}\sigma_\varepsilon^2 t. \qquad (6)$$

Note that the expected value is equivalent to the mean value of $S_i(t)$ over a sample of N random walks. Because the error rate $\varepsilon(t)$ is normally distributed, the distribution of all values of $S(t)$ at time t will also be normally distributed, and so the higher moments of the distribution are simply the parameters of a normal distribution.

$$Var[S(t)] = V_S(t) = (\sigma_\varepsilon^2 + \sigma_\kappa^2)t = \sigma_\phi^2 t, \qquad (7)$$

$$Skew[S(t)] = 0, \qquad (8)$$

$$Kurtosis[S(t)] = 3\sigma_\phi^4. \qquad (9)$$

These moments show that the variance of the distribution of $S_i(t)$ increases linearly with time (Eq. (7)), whereas the skewness is zero (Eq. (8)) as normal distributions are symmetrical by definition, and the kurtosis of the distribution is a constant function of σ_ϕ (Eq. (9)). However, we are interested not only in characterizing the distribution of $S_i(t)$, but also in measuring the rate of change in this distribution over time. The rate of change in these parameters over time (their time derivatives) are given by their infinitesimal moments (Karlin and Taylor, 1981)

$$\lim_{\Delta S, \Delta t \to 0} \frac{1}{\Delta t} E[\Delta S] = \alpha = -\frac{1}{2}\sigma_\varepsilon^2, \qquad (10)$$

$$\lim_{\Delta S, \Delta t \to 0} \frac{1}{\Delta t} E[\Delta S]^2 = \beta = \sigma_\phi^2, \qquad (11)$$

$$\lim_{\Delta S, \Delta t \to 0} \frac{1}{\Delta t} E[\Delta S]^\theta = 0, \theta > 2, \qquad (12)$$

where $\Delta S = S(t + \Delta t) - S(t)$. Eq. (10) gives the rate of change in the mean, termed the drift constant, and Eq. (11) gives the rate of change in the variance, termed the diffusion constant, whereas all higher infinitesimal moments are zero as they remain unchanged through time. We can then rewrite Eq. (4) more straightforwardly in terms of the above diffusion parameters thus,

$$S(t+1) = S(t) + \alpha + \sqrt{\beta}\Phi(t), \qquad (13)$$

where $\Phi(t)$ is a standard normal distribution. Simulations of Eq. (13) are shown in Fig. 1. By taking the continuous time limit of Eq. (13), we can describe the evolution of S over time t under the conditions of the ACE model with the stochastic differential equation
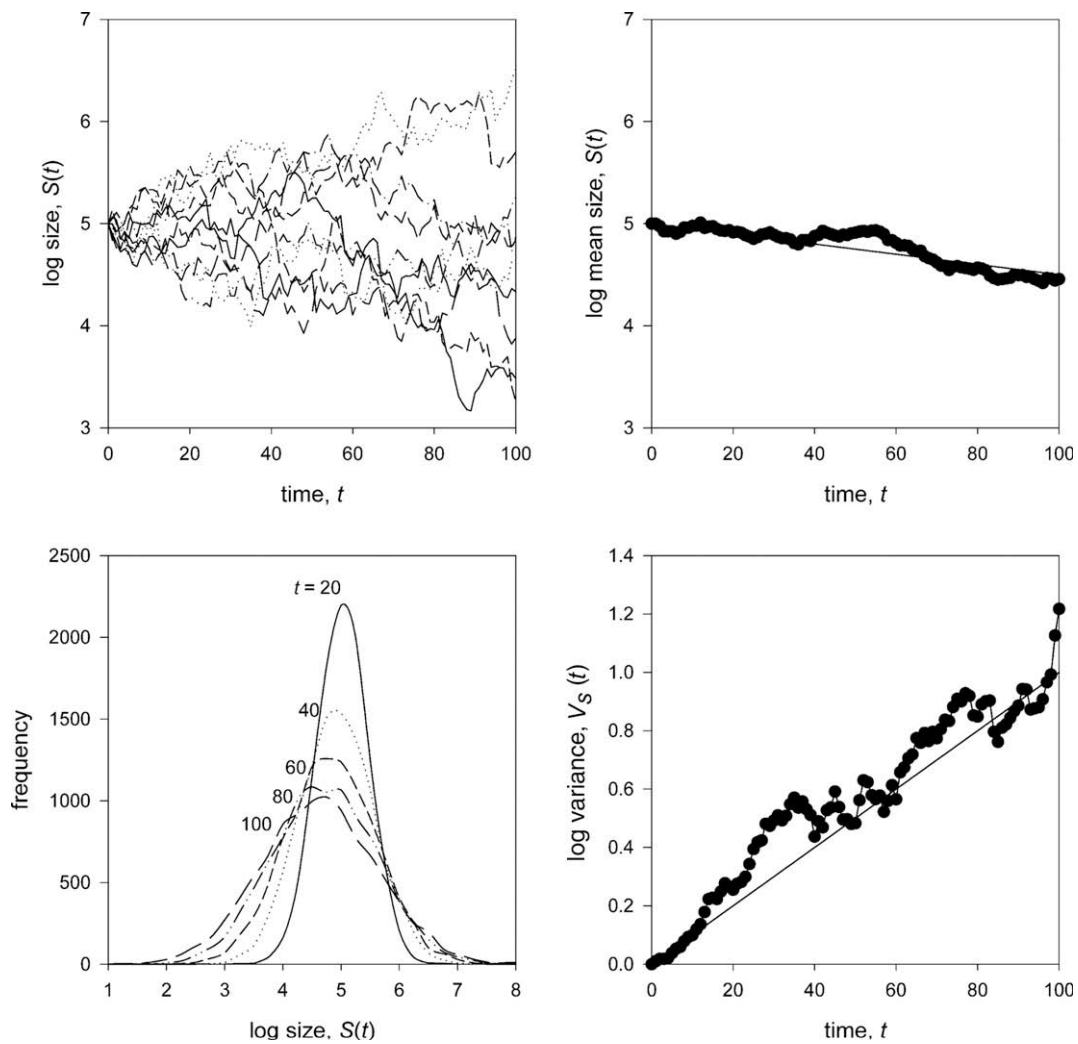
$$dS = -\alpha dt + \sigma dz, \qquad (14)$$

which has the solution,

$$\phi_{ACE}(S|\alpha, \beta, t) = \frac{S_0}{\sqrt{2\pi\beta t}} \exp\left(-\frac{(S - S_0 - \alpha t)^2}{2\beta t}\right), \qquad (15)$$

which is a normal distribution with mean $S_0 - \alpha t$ and variance βt (Fig. 1). In other words, at all times traits subject to transmission described by the ACE model will be normally distributed (on the log scale), but as $\alpha < 0$ the mean of the distribution will drift deterministically to the left, while the variance increases linearly with time at a rate βt. This can be seen clearly in the simulations shown in Fig. 1.

The mean of the distribution drifts negatively over time due to the accumulation of copying errors, which are proportional to the mean value in the previous generation. Thus, the accumulation of unbiased copying errors (i.e., neutral mutations) over multiple transmission events causes drift in the mean over time as those copying errors are proportional to the object being copied even though the probability of creating a copying error is unbiased. While somewhat non-intuitive, this result has a clear empirical interpretation. Because the variance of the distribution governing the copying error is proportional to the object being copied, variants produced in the present generation that are smaller than the mean of the previous generation will be copied with less absolute error in the subsequent transmission event, and so will remain

Fig. 1. Monte Carlo simulations of the unbiased transmission ACE model, Eq. (13) (parameters: $S_0 = 5$, $\sigma_\varepsilon = 0.1$). (A) Ten sample paths of the ACE model (Eq. (13)). (B) Monte Carlo results (10,000 iterations) of point sizes over time, showing that under the conditions of the ACE model the mean decreases through time, while the variance increases. (C) Trend in the mean over time indicating that the average point size decreases through time at a rate of half the variance of the copying error. (D) Trend in the variance over time. The variance increases approximately linearly with time.

small over time. Similarly, variants larger than the mean will be copied with more absolute error in the subsequent transmission event, which increases the probability that eventually they will produce smaller variants over time. So, small variants stay small, and large variants have an increasing probability of eventually producing small variants, with the result that the overall mean of the distribution drifts to the left over time at a rate proportional to the accumulation of copying errors.

Biased transmission: the BACE model

We now build on the simple unbiased vertical transmission model by considering sources of bias in the transmission process and how these processes affect the resulting distributions of traits through time. We are particularly interested in how biasing processes in social learning constrain variance. As above, we start by building a discrete-time, continuous-space Markov model and then use diffusion approximations to describe the long-term statistical properties of the model. We term the model the biased accumulated copying error (BACE) model.

Across human societies a ubiquitous form of bias is conformism where individual social learning is frequency-dependent (Boyd and Richerson, 1985; Henrich and Boyd, 1998), a process akin to stabi-

lizing cultural selection (Cavalli-Sforza and Feldman, 1981). Another common form of bias in human societies is prestige bias, where prestigious individuals influence social learning (Boyd and Richerson, 1985; Henrich and Gil-White, 2001). For this paper we model these two forms of bias identically. We make this simplifying assumption for the following reason. Under conformist bias, each individual within a population chooses either to copy the most frequent variant, often given by the population mean, $\overline{X}(t)$, of the previous generation with probability λ, or to follow the rules of vertical transmission with probability $1 - \lambda$. Similarly, under prestige bias each individual within a population chooses either to copy a prestigious individual, $X_P(t)$, from the previous generation with probability λ, or to follow the rules of vertical transmission with probability $1 - \lambda$. The two models are the same analytically because the population mean $\overline{X}(t)$ is also the expectation of $X(t)$, that is $E[X(t)] = \overline{X}(t)$, so the expected value of any individual chosen at random, such as the prestigious individual, $X_P(t)$, is also given by the population mean, that is $E[X_P(t)] = \overline{X}(t)$. Therefore, if we assume that prestigious individuals produce projectile points of an average size, though perhaps simply of better quality, then mathematically, both conformist and prestige bias are, in the present case, analytically equivalent. However, the model below can be altered straightforwardly to incorporate any biasing scenario.

We think this argument is particularly relevant to the cultural transmission of lithic technology in hunter-gatherer societies. With tasks as complex as projectile point manufacture individual flintknappers are likely to vary considerably in their skill-level. Given the presumed importance of projectile point function to hunting success, highly skilled flintknappers are likely to have been prestigious individuals within any given group. Other prestigious individuals may included successful hunters, for example. In either case it is reasonable to assume such individuals would bias learning strategies as novice flintknappers would likely choose to learn from such experts, rather than learn solely from their parents, who may or may not be skilled flintknappers. However, there is no a priori reason that prestigious flintknappers would produce either particularly small or large projectile points, but likely would produce projectile points of an expected, or average size, presumably with less variance, and of higher overall quality than less skilled flintknappers. As such, we assume that prestigious individuals produce projectile points that are similar in size to the mean, but are copied with greater frequency because they were produced by a master flintknapper, or another type of prestigious individual.

If λ is the strength of bias (i.e., the probability of conforming or copying a prestigious individual during a transmission event), building on the above ACE model, we include the probabilities of bias and non-bias into Eq. (5), thus

$$S_i(t + 1) = [\lambda \bar{S}(t) + (1 - \lambda)S_i(t)] + \kappa(t) + \ln[1 + \varepsilon(t)], \quad (16)$$

and so with probability λ, an individual chooses to copy the mean of the previous generation, and with probability $1 - \lambda$ and individual chooses to copy their parents. We can then rewrite Eq. (16) in terms of the diffusion parameters given above,

$$S_i(t + 1) = S_i(t) + \lambda[\bar{S}(t) - S_i(t)] + \kappa(t) + \alpha + \sqrt{\beta}\varepsilon(t), \quad (17)$$

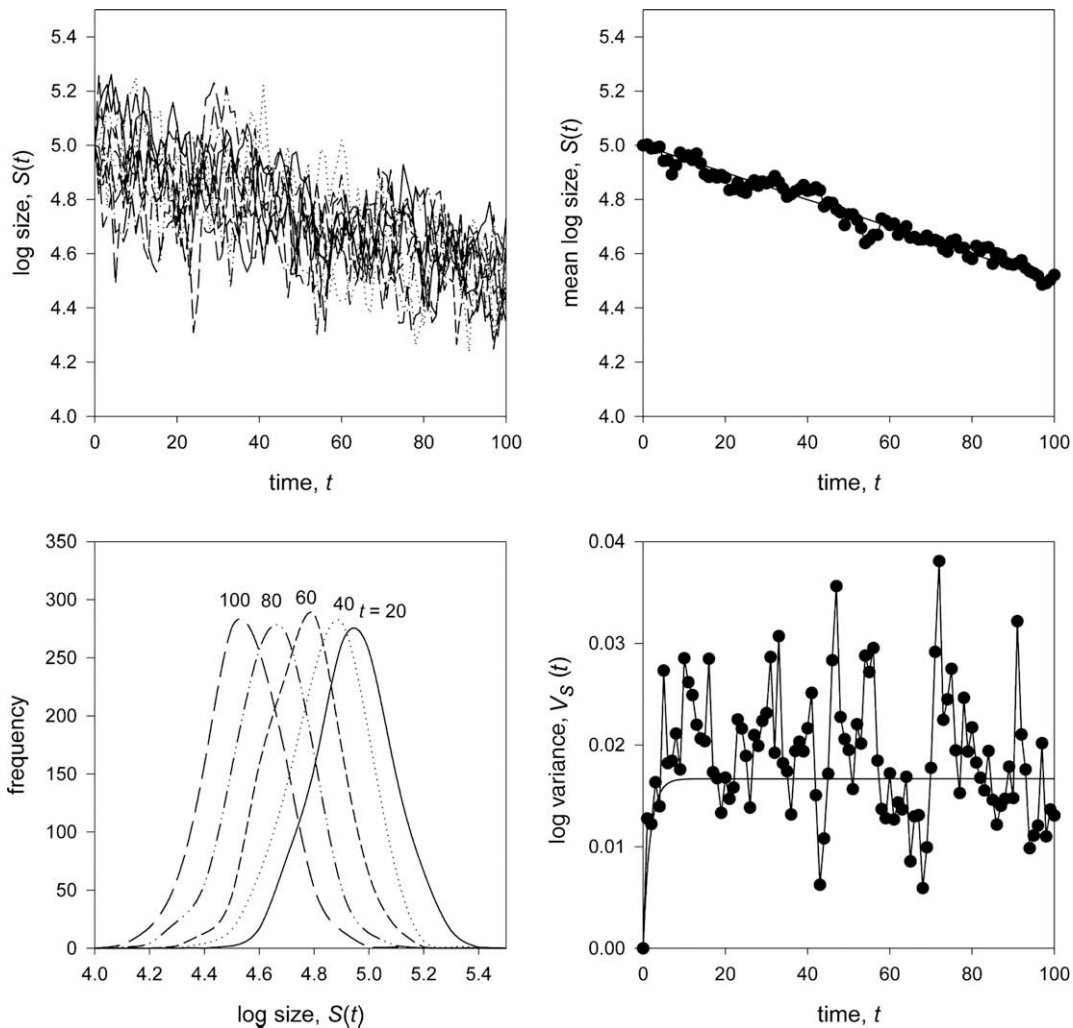simulations of which are shown in Fig. 2. The rate of change in S over time is then

$$\Delta S = \lambda[\bar{S}(t) - S_i(t)] + \kappa(t) + \alpha + \sqrt{\beta}\varepsilon(t), \quad (18)$$

and taking the continuous time limit, we can describe the evolution of S over time t under biased transmission with the following stochastic differential equation

$$dS = \lambda[\bar{S}(t) - S_i(t)]dt + \sigma dz. \quad (19)$$

When the strength of bias is greater than zero ($\lambda > 0$), Eqs. (16)–(18) describe an Ornstein–Uhlenbeck mean-reversion process (Dixit and Pindyck, 1994; Karlin and Taylor, 1981; Taylor and Karlin, 1998), which reduces to Eq. (14) when $\lambda = 0$. As before, the mean value of $S(t)$ is given by the expectation

$$E[S(t)] = \bar{S}(t) = S_0 - \frac{\sigma_\varepsilon^2}{2}t = S_0 - \alpha t, \quad (20)$$

Fig. 2. Monte Carlo simulations of the biased transmission (BACE) model, Eq. (17) (parameters: $S_0 = 5$, $\sigma_\varepsilon = 0.1$, $\lambda = 0.3$). (A) Ten iterations of the BACE model (Eq. (17)). (B) Monte Carlo results (10,000 iterations) of point sizes over time, showing that under the conditions of the biased transmission model the mean decreases through time, while the variance remains approximately constant. (C) Trend in the mean over time indicating that the average point size decreases through time at a rate of half the variance of the copying error, as in the ACE model. (D) Trend in the variance over time. Initially the variance increases rapidly, but quickly reaches equilibrium at $\sigma_\varepsilon^2/2\lambda$.

and the variance

$$\text{var}[S(t)] = \sigma_S^2(t) = \frac{\beta}{2\lambda}(1 - e^{-2\lambda t}). \tag{21}$$

So, while the behavior of the mean is the same as under both biased (BACE) and unbiased (ACE) conditions as the biasing process simply restricts the variance of the distribution, the variance approaches equilibrium at $\beta/2\lambda$, at a rate $1 - \exp(-2\lambda t)$. Therefore, under biased transmission the long-term population variance is bounded by the strength of bias, λ unlike the unbiased vertical transmission model, where the variance increases linearly with time (Fig. 3). The variance reaches equilibrium because the inverse of the strength of bias is the frequency, f at which individuals choose to follow biased learning strategies; that is $\lambda = 1/f$, so if $\lambda = 0.2$, then about 1 in every 5 transmission events an apprentice will choose to conform (copy the mean) rather than learn from their parents. If the strength of bias is greater than zero ($\lambda > 0$) the amount of variation that can accumulate within the population is limited, such that the total amount of variation that can occur at any one time is bounded by the frequency with which individuals choose to conform or copy prestigious individuals. In terms of the infinitesimal moments of the BACE model, the drift coefficient remains the same as the ACE model

$$\lim_{\Delta S, \ \Delta t \to 0} \frac{1}{\Delta t} E[\Delta S] = \alpha = -\frac{1}{2}\sigma_\varepsilon^2, \tag{22}$$

whereas the diffusion coefficient is now

$$\lim_{\Delta S, \ \Delta t \to 0} \frac{1}{\Delta t} E[\Delta S] = \beta = 0 \tag{23}$$

for large t, as the variance is constant with respect to time once it reaches equilibrium. Therefore, over time $S_i(t)$ converges on a stable distribution

$$\phi_{\text{BACE}}(S|\alpha, \beta, t) = \frac{S_0}{\sqrt{2\pi\sigma_s^2}} \exp\left(-\frac{(S - S_0 - \alpha t)^2}{2\sigma_s^2}\right) \tag{24}$$

which is, again, a normal distribution with mean $S_0 - \alpha t$, but with variance σ_s^2 that reaches equilibrium at $\beta/2\lambda$. So, the mean of the distribution drifts negatively at a rate $S_0 - \alpha t$ as in the unbiased case, but the distribution ceases to expand once the variance reaches equilibrium at $\beta/2\lambda$ (Fig. 2). This equilibrium has important consequences for measuring the presence and magnitude of transmission bias in archaeological data.
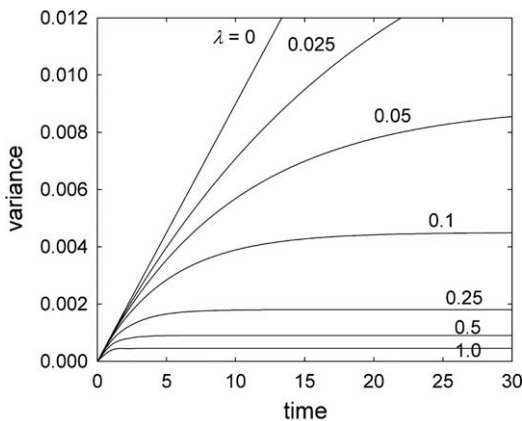

Fig. 3. Plots of Eq. (21) showing variance as a function of both transmission bias, λ, and time, t. When transmission bias is greater than zero (unbiased transmission), variance asymptotically approaches equilibrium at $Var[x] = \sigma_x^2/(2\lambda)$ at a rate $1 - \exp(-2\lambda t)$. This means that transmission bias always constrains long-term variance, whereas variance increases linearly under unbiased transmission ($\lambda = 0$).

Model summary

The arguments above show that regardless of bias in the transmission process, continuous traits passed down across generations through social learning will drift deterministically over time due to the multiplicative nature of the accumulation of copying errors. Indeed, the above analysis demonstrates that biased cultural transmission is best modeled as an Ornstein–Uhlenbeck mean-reversion process, which reduces to geometric Brownian motion (i.e., Brownian motion with drift on the log scale) in the special case when the strength of bias is equal to zero, $\lambda = 0$. This is a particularly important theoretical finding for archaeology because it suggests the relevant null model of cultural transmission, under biased or non-biased processes is negative drift, due to the accumulation of copying errors. In our projectile point example, this model predicts that mean artifact size will decrease steadily through time at a rate of half the variance of the copying error rate. It follows that this trend should be most noticeable in long-lived technologies that are transmitted across multiple generations. It is important to remember that the above analysis is conducted on the log scale. So, while on the log scale the expected change in the mean is $\Delta \bar{S} = \bar{S}(t+1) - \bar{S}(t) = -\alpha$, on the linear scale, $\Delta \bar{s} = \exp(-\alpha)$, so the mean decreases at an exponentially decaying rate, and the expected mean at time t is $E[s(t)] = \bar{s}(t) = s_0 e^{-\alpha t}$.

Further, our analysis shows that biased transmission results in bounded variance, such that the amount of variance within a population should stabilize through time at a level determined by the strength of bias, λ. Because biasing processes are ubiquitous in human social learning (Boyd and Richerson, 1985; Henrich and McElreath, 2003), the null model predicts that population variance in long-lived technologies should be statistically constant through time.

Parameter estimates of the cultural transmission process

We concentrated on defining four sets of parameters: (1) The drift and diffusion constants (and higher infinite moments); (2) the Weber Fraction, or the standard deviation of the copying error rate, σ_ε; (3) the amount of structural error, κ; and 4) the strength of transmission bias, λ. These four parameters allow for a relatively complete description of the mechanisms and sources of variation in archaeological assemblages. As such, we now turn to consider how these parameters can be estimated statistically from empirical data.

Founder effects

As mentioned in the Introduction, one of the key sources of drift is founder effect. All biological populations fluctuate in size through time and space due to naturally occurring variation in reproductive rates caused by a combination of a population's demographic profile (demographic stochasticity) and changes in local environmental and ecological conditions (environmental stochasticity) (Lande et al., 2003). These fluctuations cause the distribution of biological and cultural variation within a population to vary (Henrich, 2004; Shennan, 2000, 2001). Over time, these fluctuations result in sampling bias that has the effect of reducing the overall amount of variation within a population by reducing the (biological and/or cultural) effective population size. Therefore, successive founder effects in human populations are predicted to reduce the within-assemblage variation in archaeological assemblages through time (see Lycett and von Cramon-Taubadel, 2008).

We can use an ordinary least squares regression of the form $V_A = \beta_0 + \beta_1 t + \varepsilon$ to explore intra-assemblage variation, V_A as a function of time, t. If $\beta_1 < 0$, intra-assemblage variation decreases with time, consistent with the hypothesis of drift caused by founder

effects. If $\beta_1 > 0$, then intra-assemblage variation increases with time, perhaps due to increased innovation rates within populations. If $\beta_1 = 0$, then intra-assemblage variation does not vary significantly with time suggesting a relative degree of demographic and cultural stability.

Estimates of statistical moments and copying error

Infinitesimal moments and copying error

We estimate the first four infinitesimal moments using OLS regression. In particular, we use the model $E[S(t)^\theta] = \beta_0 + \beta_1 t + \varepsilon$, where $E[S(t)^\theta]$ is θth moment at time t. As $\beta_1 = dE[S(t)^\theta]/dt$, this is an estimate of the infinitesimal moment. For example, to estimate the drift constant α we use the linear model $\bar{S}(t) = \alpha t + S_0 + \varepsilon$, where the slope of the model is the drift constant, $\alpha = -\sigma_\varepsilon^2/2$. The copying error rate is then found by rearranging the equation for the drift constant thus, $\sigma_\varepsilon = \sqrt{2\alpha}$.

Transmission bias and structural error

The transmission bias model Eq. (17) can be written as the first order autoregressive model $S(t + 1) = \beta_0 + \beta_1 S(t) + \phi$, with the parameters $\beta_0 = \lambda \bar{S}, \beta_1 = 1 - \lambda$, and $\sigma_\phi = \sigma_R \sqrt{1/2\lambda}$, where σ_R is the standard deviation of the residuals. Rearranging these parameters, the transmission bias parameter is then estimated by $\lambda = 1 - \beta_1$, the long-term mean is $\bar{S} = \beta_0/\lambda$ and the structural error term is $\sigma_\kappa = \sigma_\phi - \sigma_\varepsilon = \sigma_R \sqrt{1/2\lambda} - \sqrt{2\alpha}$. It then follows that the proportion of the total error explained by copying error is approximately $\sigma_\varepsilon/\sigma_\phi = \sigma_R^{-1}\sqrt{4\alpha\lambda}$.

Case study: quantifying spatiotemporal gradients in Clovis projectile point size

To illustrate the efficacy of the above model we examine the archaeological example of spatiotemporal gradients in the size of Clovis projectile points across late Pleistocene North America.

The Clovis archaeological record represents the population expansion of the first successful human colonization of North America (Hamilton and Buchanan, 2007; Meltzer, 2004). The initial size of the founder population was likely very small (see Hey, 2005 and references therein), and therefore would have exhibited limited biological and cultural diversity. However, by the end of the Clovis period, a period of no more than a few hundred years (Haynes et al., 1984; Haynes, 2002; Waters and Stafford, 2007), hunter-gatherer populations occurred throughout the North American continent, as well as much of the rest of the Americas (Haynes, 2002). During this period of expansion, Clovis colonists would have encountered novel environments, ecosystems and prey species that varied widely both in space and time as the continent underwent widespread post-glacial ecological changes (Lyons, 2003, 2005; Lyons et al., 2004; Webb et al., 1993; Wright, 1987, 1991). Under these dynamic conditions, the suite of selective pressures on lithic technology would have been complex. On the one hand, in an expanding population undergoing changing ecological conditions, cultural evolutionary theory would predict that there would be both strong frequency-dependent selection and biased social learning toward prestigious individuals (Boyd and Richerson, 1985; Henrich and Boyd, 1998), such as successful hunters or master flintknappers. However, at the same time, population expansion across heterogeneous landscapes would have promoted technological diversification, especially if regional populations adapted to specific local environmental conditions, and became increasingly geographically isolated through time. Furthermore, the most demographically unstable populations would

have been those entering novel environments at the leading edge of the colonizing wave due to small population sizes and the consequent increased stochasticity in growth rates, as well as increased effects of environmental variance caused by the novel ecological conditions.

The effects of cultural evolutionary processes on projectile points are particularly interesting as projectile points presumably played a primary role in hunting technology. Because of their importance it is likely that projectile points, and other aspects of technology, were subject to dynamic, subtle selective pressures as populations expanded into novel ecological niches (see Buchanan and Hamilton, in press). The statistical expectations derived from the ACE/BACE models can be used to quantify rates of change in Clovis projectile point size over time and space and to determine the rules of social learning that characterized Clovis cultural transmission. Clovis projectile points are an ideal case study as they are: (1) technologically complex tools that require significant expertise and investment in learning to reach the generally high level of quality we see in the archaeological record; and (2) because they were manufactured over a period of a few hundred years and therefore were transmitted across several successive generations (Haynes, 2002; Haynes et al., 2007; Meltzer, 1995; Waters and Stafford, 2007).

To examine changes in Clovis projectile point sizes across the Clovis time period we combine expectations of the ACE/BACE model with the spatiotemporal gradient model developed in Hamilton and Buchanan (2007). In Hamilton and Buchanan (2007) we showed that spatial gradients in Clovis-age radiocarbon dates from archaeological sites indicate that the most likely origin of the Clovis colonization of North America was the ice-free corridor, when tested against multiple alternative hypotheses. Our analyses showed that the date of the earliest Clovis occupation across the continent decreased linearly with distance from Edmonton, Alberta, traditionally taken to represent the approximate location of the southern exit of the ice-free corridor (i.e., Martin, 1967; Mosimann and Martin, 1975). Thus spatial gradients in Clovis occupations across the continent also reflect temporal gradients. So, by combining these spatiotemporal gradients with the predictions of the ACE/BACE models we derive four null hypotheses relating to variation in Clovis projectile point size

Hypothesis 1	The overall distribution of point sizes should be lognormal.
Hypothesis 2	The mean size of projectile points should decrease linearly with distance from Edmonton, Alberta.
Hypothesis 3	The expected rate of size decrease over time due to stochastic cultural transmission is predicted by the Weber Fraction, ∼5%. That is to say the drift constant, α, should be negative, and approximately $\sigma_\varepsilon^2/2 = 0.0025/2 = 0.00125$.
Hypothesis 4	Variance in projectile point size should be statistically constant across time, and all higher moments should be non-significant.

Data and methods

Clovis projectile point sample

Our sample consists of 232 Clovis projectile points from 26 assemblages from across the continent (see Table 1 and Fig. 4). Projectile point size was calculated using a morphometric digitizing process that utilizes multiple landmarks to demarcate the outline of points, described in detail elsewhere (Buchanan, 2006; Buchanan and Collard, 2007; Buchanan and Hamilton, in press). An estimate of projectile point surface area is then calculated from the polygon described by the landmarks (Buchanan,

Table 1
Projectile point assemblage metrics from early paleoindian sites included in the analysis (Fig. 4).

Site	Mean size, ln cm^2	Variance, ln cm^2	Distance, km^2	Number of points	Reference(s)
Anzick[a]	3.8797	0.0379	866.3	6	Jones and Bonnichsen (1994), Lahren and Bonnichsen (1974), Owsley and Hunt (2001), Wilke et al. (1991)
Blackwater Draw[b]	3.4158	0.1086	2291.1	24	Boldurian and Cotter (1999), Cotter (1937, 1938), Hester (1972), Howard (1935), Warnica (1966)
Bull Brook[c]	3.5246	0.0195	3326	39	Byers (1954, 1955), Grimes (1979)
Bull Brook II[c]	3.29	0.028	3326	2	Grimes et al. (1984)
Butler[c]	3.434	0.115	2485.5	4	Simons (1997)
Cactus Hill[c]	3.3129	0.0376	3321.8	6	McAvoy and McAvoy (1997)
Colby[b]	3.7414	0.0375	1133.3	4	Frison and Todd (1986)
Debert[c]	3.6737	0.0466	3650.9	6	MacDonald (1966, 1968)
Dent[c]	3.9325	0.0015	1610.8	2	Brunswig and Fisher (1993), Figgins (1933), Haynes et al. (1993)
Domebo[b]	3.5107	0.013	2385.4	4	Leonhardy (1966)
Drake[b]	4.0143	0.0151	1624.1	13	Stanford and Jodry (1988)
East Wenatchee[b]	4.4036	0.0471	832.7	11	Gramly (1993), Lyman et al. (1998)
Fenn[d]	3.9947	0.0401	1298.7	16	Frison (1991), Frison and Bradley (1999)
Gainey[c]	3.3185	0.0804	2484.8	11	Simons (1997), Simons et al. (1984, 1987)
Gault[c]	3.7439	0.0157	2824.3	2	Collins et al. (1992), Collins and Lohse (2004), Hester et al. (1992)
Kimmswick[b]	3.349	0.1	2432.7	3	Graham et al. (1981), Graham and Kay (1988)
Lamb[a]	4.0598	0.0272	2823.1	5	(Gramly, 1999)
Lehner[b]	3.525	0.0929	2475.6	10	Haury et al. (1959)
Miami[b]	3.863	0.034	2257	3	Holliday et al. (1994), Sellards (1938, 1952)
Murray Springs[b]	3.5912	0.0511	2459.3	6	Haynes and Hemmings (1968), Haynes and Huckell (2007), Hemmings (1970)
Naco[b]	3.7568	0.0271	2485.2	8	Haury et al. (1953)
Rummells-Maske[a]	3.9075	0.0231	2120.9	10	Anderson and Tiffany (1972), Morrow and Morrow (2002)
Shoop[c]	3.2661	0.0266	3103.4	14	Cox (1986), Witthoft (1952)
Simon[a]	4.0815	0.0472	1137.6	5	Butler (1963), Butler and Fitzwater (1965), Titmus and Woods (1991), Woods and Titmus (1985)
Vail[c]	3.655	0.0462	3169.6	16	Gramly (1982), Gramly (1984), Gramly and Rutledge (1981)
Whipple[c]	3.463	0.023	3250.7	2	Curran (1984, 1987, 1994)

[a] Indicates projectile point assemblage was identified in the literature as a cache.
[b] Indicates projectile point assemblage was identified in the literature as recovered from a kill.
[c] Indicates projectile point assemblage was identified in the literature as recovered from a camp.
[d] The actual location of the Fenn cache is unknown; however, it was most likely recovered from the three-corners area where Utah, Wyoming, and Idaho meet (Frison and Bradley, 1999).

Fig. 4. Distribution of Early Paleoindian sites with projectile point assemblages examined in the analysis (1, East Wenatchee; 2, Simon; 3, Anzick; 4, Fenn; 5, Colby; 6, Dent; 7, Drake; 8, Murray Springs; 9, Lehner; 10, Naco; 11, Blackwater Draw; 12, Miami; 13, Domebo; 14, Gault; 15, Rummells-Maske; 16, Kimmswick; 17, Butler; 18, Gainey; 19, Lamb; 20, Shoop; 21, Cactus Hill; 22, Bull Brook I; 23, Bull Brook II; 24, Whipple; 25,Vail; 26, Debert).

2006; Buchanan and Collard, 2007). This method is associated with a very low measurement error rate (Buchanan and Hamilton, in press).

The data consist of projectile points from three site types: caches (n = 66), camps (n = 102), and kills (n = 64). Rather than controlling our data set subjectively, by limiting the sample to projectile points from certain site types while excluding others, we control for the potential effects of site type statistically. We feel this approach is particularly important because although points from different site types may reflect different stages of use, all points from all site types must be included in order to analyze the full archaeological range of variation in projectile point form.

Radiocarbon data

To measure time, we use calibrated radiocarbon dates from 23 Clovis-aged sites from across the continent (Table 2). Calibrated dates were calculated using the Intcal04.14 curve (Reimer et al., 2004) in Calib 5.0.

Spatial gradients

To quantify both time and space we followed similar methods to Hamilton and Buchanan (2007). We first calculated the great-circle arc distances (in km) of each assemblage from the point of assumed origin, in this case, Edmonton, Alberta. Projectile point size was then regressed against distance using a General Linear Model (GLM), controlling for both site type and raw material type. We also include an interaction term between site type and distance because of the non-uniform distribution of Clovis site types across the continent. Potential founder effects were analyzed by regressing intra-assemblage variation as a function of distance.

Table 2
Radiocarbon and calibrated dates used in the paper.

Map Number	Site	Mean calibrated date BP	Reference(s)
1	Anzick	12948	Waters and Stafford (2007)
2	Arlington Springs	12901.5	Waters and Stafford (2007)
3	Big Eddy	12842.5	Ray et al. (1998)
4	Bonneville Estates	12922.5	Waters and Stafford (2007)
5	Casper	13106	Frison (2000)
6	Colby	12855.5	Waters and Stafford (2007)
7	Debert	12429	Levine (1990)
8	Dent	12910.5	Waters and Stafford (2007)
9	Domebo	12895	Waters and Stafford (2007)
10	East Wenatchee	13025	Waters and Stafford (2007)
11	Hedden	12437.5	Spiess and Mosher (1994), Spiess et al. (1995)
12	Hiscock	12828.5	Laub (2003)
13	Indian Creek	12925	Waters and Stafford (2007)
14	Jake Bluff	12817.5	Waters and Stafford (2007)
15	Kanorado	12906.5	Waters and Stafford (2007)
16	Lange-Ferguson	12994	Waters and Stafford (2007)
17	Lehner	12891	Waters and Stafford (2007)
18	Lubbock Lake	13010	Waters and Stafford (2007)
19	Murray Springs	12862.5	Waters and Stafford (2007)
20	Paleo Crossing	12912.5	Waters and Stafford (2007)
21	Shawnee-Minisink	12883	Waters and Stafford (2007)
22	Sloth Hole	12969	Waters and Stafford (2007)
23	Vail	12255	Levine (1990)

Temporal gradients

To analyze temporal gradients, radiocarbon dates were organized into bins 450 km wide as measured from the point of origin (see Hamilton and Buchanan, 2007 for details). Projectile point dimensions were also binned into gradient bins of the same width; means, variances, skewness, and kurtosis were measured for the distribution of artifact sizes within each bin. To assess rates of change in the mean, variance, skewness, and kurtosis of projectile point sizes over time the moments per bin were regressed against time, measured by the mean calibrated radiocarbon date per gradient bin, producing estimates of the infinitesimal moments. To estimate transmission bias, following the methods outlined above, we regressed mean point size, $\bar{S}(t+1)$ as a function of $\bar{S}(t)$.
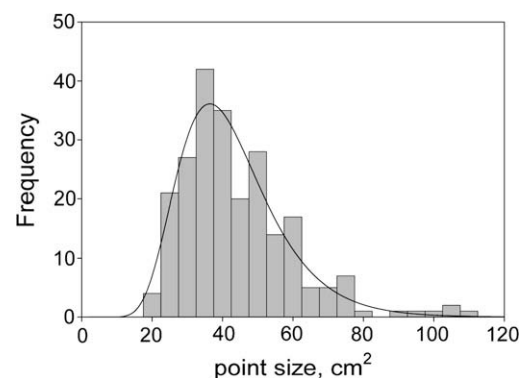
Results

Hypothesis 1

Fig. 5 illustrates that although the sample size is relatively small, the frequency distribution is well fit by a lognormal distribution, indicating that the sample displays the expected distribution of the total population of Clovis points predicted by the ACE/BACE model.
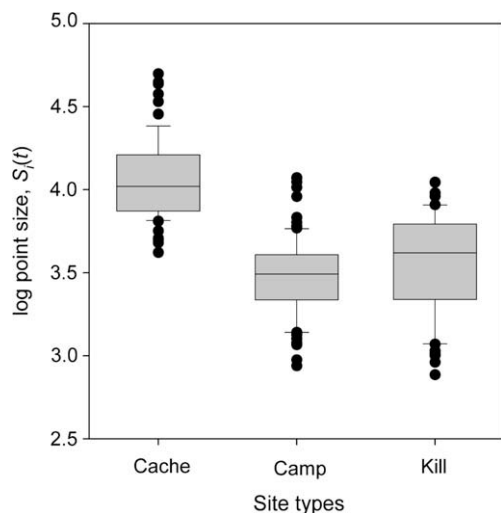
Hypothesis 2

A one-way ANOVA of log point size indicates significant differences between the three site types (ANOVA: $F_{2,231} = 108.65$, $p < 0.001$), and multiple comparisons indicate that cached points are significantly larger than both camp and kill site points, though the variances are similar (Fig. 6). This result is not surprising given that cached projectile points seem to reflect tools near the beginning stages of use-life (Kilby, 2008; Kilby and Huckell, 2003), while camp and kill site points are either discards or hunting losses, generally at the latter stages of their use-life. The projectile point sample also includes tools manufactured from several different raw materials, another potential source of variation. However, a one-way ANOVA of log point size shows no significant difference between raw material types (ANOVA: $F_{8,231} = 1.55$, $p = 0.14$) suggesting that raw material type does not significantly influence this analysis.

A least squares regression of intra-assemblage variance by distance is not significantly different from zero (Linear regression: $F_{25} < 0.01$, $r^2 < 0.01$, $p = 0.97$) and so we find no evidence of founder effects in these assemblages. The regression of projectile point size as a function of linear distance from the point of origin shows that

Fig. 5. Frequency distribution of the projectile point sizes (n = 232). The distribution is skewed to the right and well-fit by a lognormal distribution, as predicted (solid line).

Fig. 6. Boxplots of log point sizes for the three primary site types; caches, camps, and kills. All distributions are approximately normal on the log scale and the variances are similar. Cached points are significantly larger then both camp and kill site points (see text for details), while camp and kill sites points are not significantly different from each other.

projectile point size decreases significantly as a function of distance (Fig. 7). Although there is a significant linear relationship between log point area and distance from origin (Linear Regression: $F_{1,231}$, $p < 0.001$, $r^2 = 0.34$, AIC = 90.19), the amount of variation in point size is better explained by a quadratic model (Quadratic Regression: $F_{2,230}$, $p = < 0.001$, $r^2 = 0.41$, AIC = 67.62). The quadratic model is $y = y_0 + \beta_1 x + \beta_2 x^2 + \varepsilon$, where x is distance, and so the quadratic term $x^2 = (\text{distance})^2$ is straightforwardly interpreted as area. Therefore, point size not only decreases with linear distance from origin, but also as a function of the area that distance encompasses. This may be a result of the internal dynamics of a spatially expanding population. As a population grows in size on a two-dimensional landscape, the leading edge of the colonizing wave advances linearly with time at a velocity determined by the population growth rate and the rate of diffusion. Diffusion is a function of the mean square displacement of an individual over their lifetime, measured as the average distance between birth and first reproduction, or
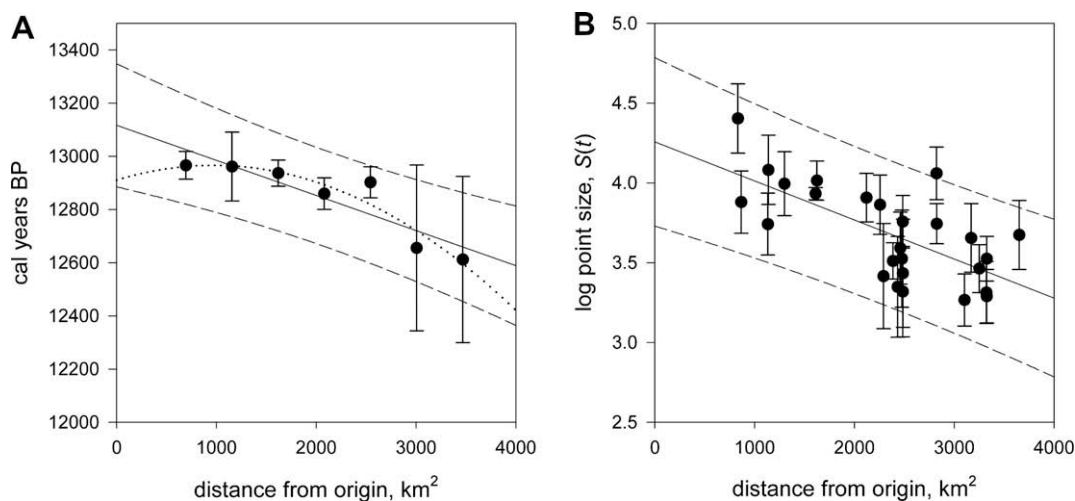
marriage (Hamilton and Buchanan, 2007; Hazelwood and Steele, 2004; Steele et al., 1998). In a spatially expanding population individuals will, on average, disperse during their lifetime as the population expands in space. This dispersal is not linear, but is best modeled as a random walk in two-dimensions (see Hazelwood and Steele, 2004). Thus, on an individual level, lifetime mobility is related to the two-dimensional area covered by the diffusive movement as well as the one-dimensional linear distance between place of birth and place of marriage or reproduction. Therefore, processes occurring within an expanding population at the individual, inter-generational level, such as the manufacture, use, and transmission of projectile point traditions are likely not only to be a function of distance, but also of area.

Results of the GLM indicate that while distance and area remain significant, site type and the interaction of site type and distance are non-significant, though the overall fit of the model is improved by considering these additional factors (GLM: see Table 3). Indeed, the GLM explains over half of the variation in point size as a function of distance from origin, space, and site type. The non-significance of site type likely results from the fact that although site type is non-uniform in space as generally camps occur in the east, and kills in the west, there is no significant difference in point size between kills and camps. In addition, although cached points are significantly larger than points at kill or camps and primarily a western Clovis phenomena, caches also occur in the east (i.e., Rummells-Maske and Lamb).

In sum, after controlling for the potential confounding factors of site type and raw material, point size decreases with distance from origin, as predicted by the combined model.

Hypothesis 3

Fig. 8A shows the frequency distribution of projectile point size, per gradient bin. Fig. 8B is a boxplot of log point size decomposed by gradient bin. The distribution within each bin is approximately lognormal, and the mean size decreases significantly with bin number. The slope of the regression of point size by time gives a direct estimate of the drift parameter (Fig. 9A). The regression results show that the drift parameter $\alpha = -0.002$, which gives the standard deviation of the copying error rate $\sigma_\varepsilon = 0.063$ (0.044–0.078) (5.3%). The confidence limits around this estimate encompass the Weber fraction (0.05, or 5%).

Fig. 7. Spatiotemporal gradients in Clovis radiocarbon dates and projectile point sizes. Solid lines are the fitted slopes, and the dashed lines are the 95% prediction intervals. (A) Plots of the average calibrated radiocarbon date per gradient bin by linear distance from origin (i.e., the mouth of the ice-free corridor), demonstrating that mean Clovis-age radiocarbon dates are younger the further from origin. The dotted line shows the quadratic regression fit, which is used in the GLM (see text and Table 3). (B) Regression of mean log point size (±1 standard deviation) for each of the 26 assemblages used in the analysis. The slope indicates that mean point size decreases with distance as predicted.

Table 3
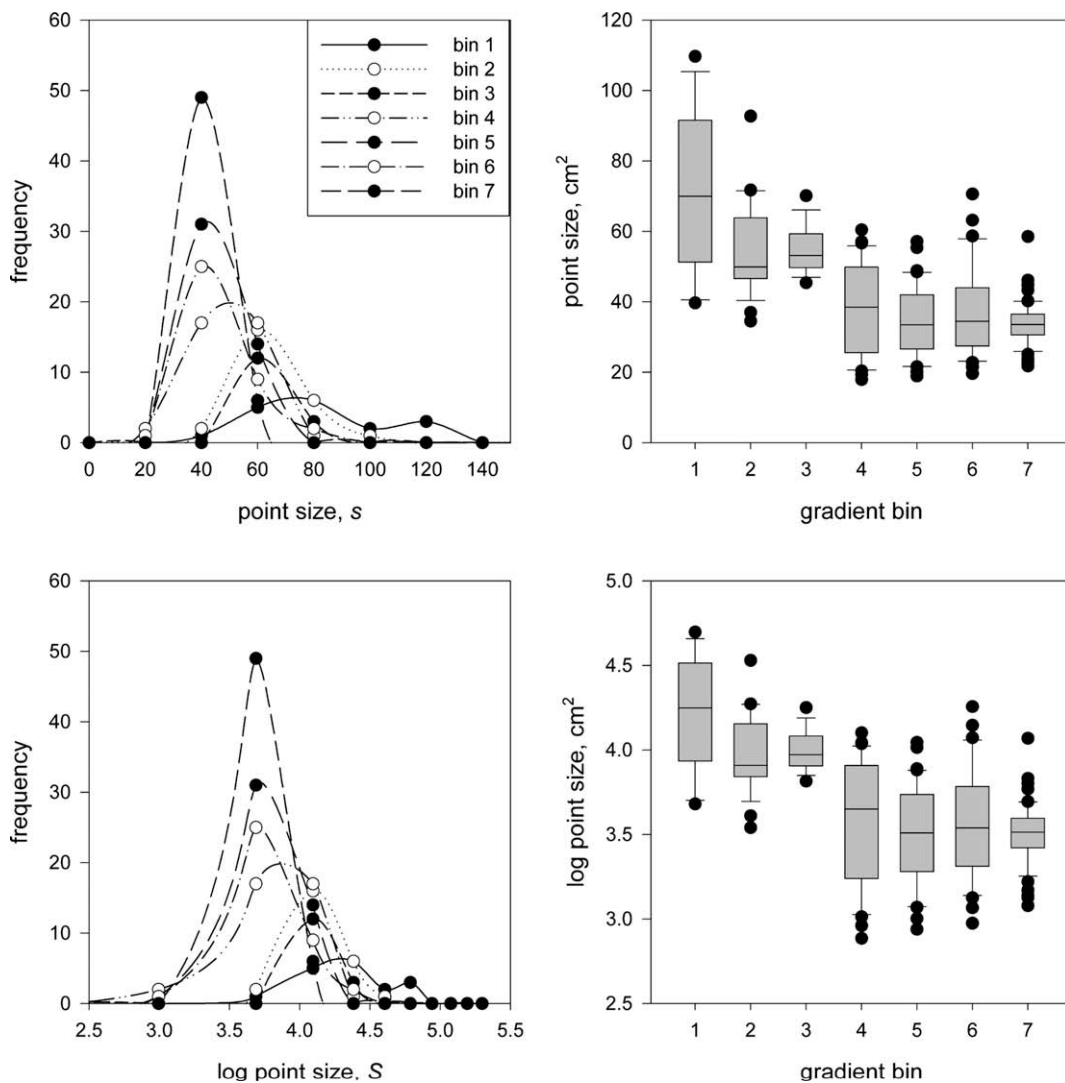Results for the general linear model of point size by distance, area and site type.

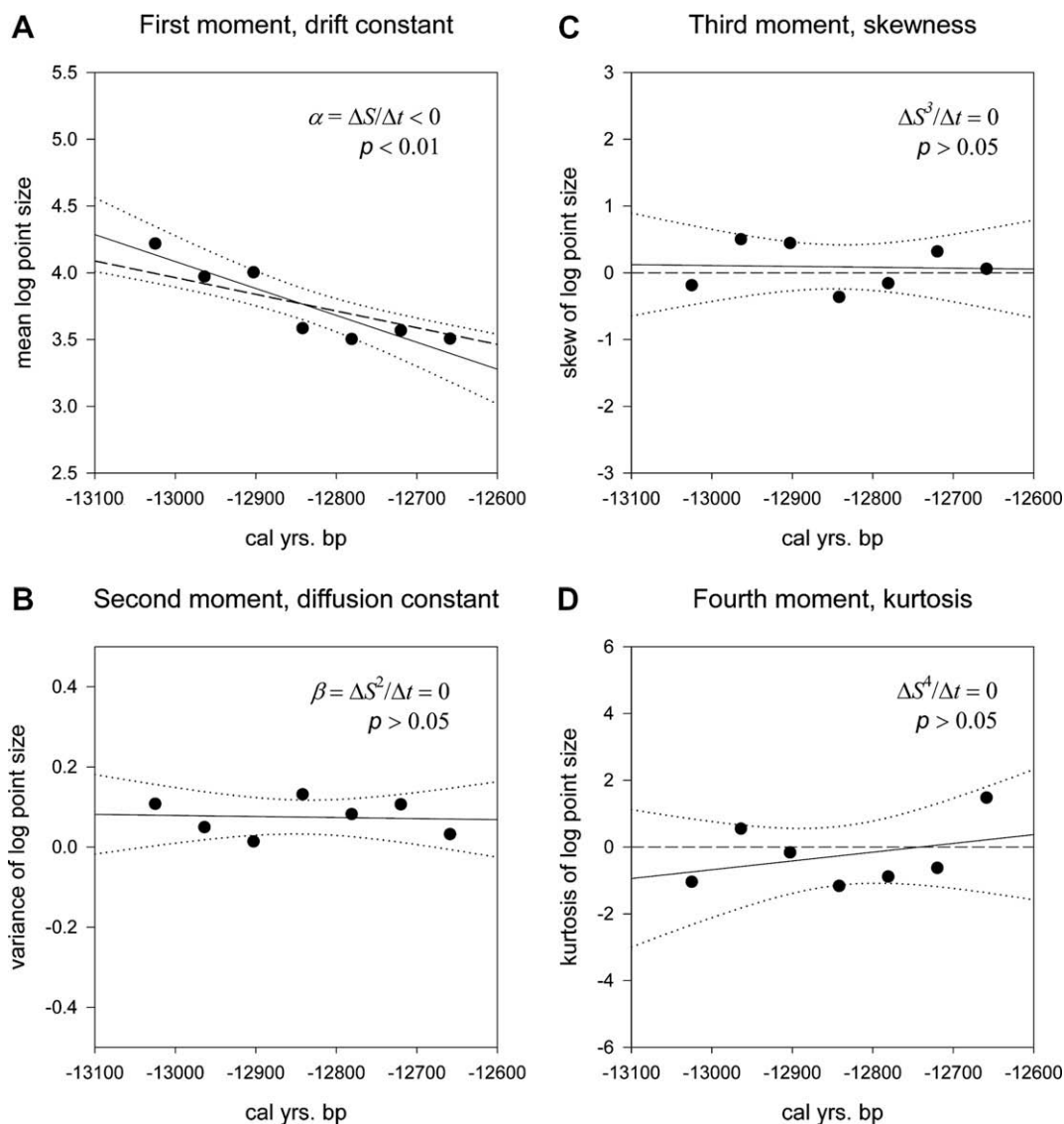| Source	DF	Seq SS	Adj SS	Adj MS	F	p
ANOVA tables						
Distance	1	9.998	0.560	0.560	9.20	0.003
Area	1	1.958	0.534	0.534	8.77	0.003
Type	2	3.806	0.043	0.021	0.35	0.704
Site type *						
Distance	2	0.095	0.095	0.047	0.78	0.460
Error	225	13.687	13.686	0.061		
Total	231	29.543				
Term		Coef	SE Coef		T	p
Coefficients						
Constant		4.730	0.373		12.68	0.000
Distance		−0.001	<0.001		−3.03 *	0.003 *
Area		<0.001	<0.001			
Site type						
Cache		0.078	0.2047		0.38	0.704
Camp		0.037	0.3445		0.11	0.915
Distance * *site type*						
Cache		0.0001	0.0001		1.24	0.216
Camp		−0.0001	0.0001		−0.89	0.376

r^2 = 53.67%.

In terms of estimating structural error, the standard deviation of the residuals from the autoregressive model is $\sigma_R = 0.145$, which gives the standard deviation of the error term in the transmission bias model $\sigma_\phi = 0.130$. Given that we have an estimate of the Weber fraction, and $\sigma_\varepsilon = 0.063$, the standard deviation of the structural error is then $\sigma_K = \sigma_\varphi - \sigma_\varepsilon = 0.067$. The relative proportion of the total variance due to copying error is given by $\sigma_\varepsilon^2 / \sigma_\phi^2$, which is about 23%, therefore copying error constitutes about one quarter of the variance in Clovis projectile point size. Considering that the structural error term we use here includes all other sources of variation in projectile point size, including sampling bias, raw material size and quality, use life, and preservation among many other factors, copying error is a considerable source of variation in Clovis projectile point size.

Hypothesis 4

A least-squares regression of variance per gradient bin by time shows no significant slope (Linear regression: $F_6 < 0.02$, $r^2 < 0.01$, $p > 0.9$) indicating that variance remains statistically constant over time. This suggests that variance is bounded by transmission bias as predicted by the BACE model. The first-order autoregressive

Fig. 8. Distributions of the Clovis projectile point sample. (A) Frequency distributions of the Clovis sample separated into the seven gradient bins. Each distribution is lognormal and shifts to the left with increasing bin number (see Fig. 7 for more details). (B) Boxplots of point sizes within each bin. (C) The same frequency distributions as A but linearized to the log scale. (D) Boxplots of point sizes within each bin.

Fig. 9. Regressions of moments per gradient bin by time (cal. years BP), giving estimates of the first four infinite moments. Dotted lines are 95% confidence limits around the fitted slopes, and dashed lines are the theoretically predicted moments. (A) Mean log point size decreases significantly with time, at a rate given by the drift constant, $\alpha = -0.002$, which encompasses the theoretically predicted value of -0.00125. (B) Point size variance remains constant over time, such that the diffusion constant $\beta = 0$ as predicted. (C) As predicted, skewness remains constant over time, and also bounds the predicted value of zero. (D) Although the kurtosis of the distributions has a slight positive trend over time (see Fig. 2B and C), the rate is non-significant as predicted, and bounds the predicted value of zero.

model gives the transmission bias parameter $\lambda = 0.38$. As indicated in Fig. 3, a bias parameter of >0.1 results in a rapid approach to equilibrium, and so an estimated parameter of about 0.4 indicates that biased transmission played an important role in the teaching and learning of Clovis projectile point technology.

As predicted both the rate of change in skewness and kurtosis are non-significant, consistent with the predictions of the model.

Discussion

Our analyses demonstrate that the Clovis projectile point sample provides support for all four hypotheses derived from the combined model, indicating that the BACE model is the appropriate null model for the cultural transmission of quantitative data.

First, the frequency distribution of Clovis projectile points is lognormal, as predicted by the multiplicative process of the cultural transmission. Second, on average Clovis projectile point sizes decrease with distance from the opening of the ice-free corridor, as predicted by the gradient model. This gradient maps onto a similar

gradient in the average age of radiocarbon dates shown in Hamilton and Buchanan (2007), where the earliest dates of Clovis occupation per gradient bin increase across North America with distance from the ice-free corridor. Therefore, our findings show that average point size decreases through time, as well as space. It then follows that these results indicate that the wave-like expansion of Clovis populations into North America is not only reflected in the spatiotemporal distribution of radiocarbon dates, but also in the average size of projectile points.

The lack of founder effects in the evolution of Clovis projectile point size suggests that rapidly growing Clovis populations were relatively demographically stable and did not fluctuate widely over time. Or at the least, localized extinctions of regional populations were rare enough not to affect the amount of cultural variation within the population as a whole. The absence of founder effects also suggests that as Clovis populations spread rapidly over the landscape they did not become geographically isolated. Instead, Clovis populations likely maintained broad social networks over large geographic expanses, which would have facilitated the flow

of both genetic and cultural information over time and space (see Hamilton et al., 2007a; Hamilton et al., 2007b). These social networks thus would have had the effect of stabilizing local and global demographic and cultural variation across the continent via horizontal transmission and/or shared cultural phylogenetic histories (Buchanan and Collard, 2007; Buchanan and Hamilton, in press). Indeed, despite some regional differences there is a noticeable qualitative similarity in Clovis projectile point form across the continent, and a clear historical relationship to subsequent Paleoindian projectile point styles in many areas of the continent (e.g., Folsom on the Plains and in the Southwest, Barnes in the Great Lakes, and Dalton and Suwannee in the Southeast).

Third, Clovis projectile point size decreases through time at a rate predicted by the Weber fraction, suggesting that spatial variation in Clovis projectile point size is due to drift processes caused by the accumulation of copying errors over multiple transmission events. Because the rate of reduction in projectile point size is almost exactly the rate predicted by drift due to copying errors, there is no evidence to suggest that the empirical size reduction at the continental level was driven by directional selection for smaller points, either due to changing ecological conditions, perhaps resulting in smaller prey sizes in the east, or as megafaunal prey went extinct toward the end of the Clovis period. However, while there is no evidence for direct selection for smaller points through time it is plausible that performance criteria, particularly the lower bound of the functional size of Clovis points also reduced through time as prey body size decreased, and so the rate of drift may have mapped onto changes in performance criteria. We want to emphasize that our results do not suggest that directional selection for point size never occurred, but that the overall trend in point size reduction over time at the continental scale was most likely due to neutral drift processes. Indeed, it is more than likely that while some traits were under direct selection, others were subject to drift.

It is interesting to note that the results we present here are consistent with the hypothesis that the variation in Clovis projectile point form across North America was primarily the result of drift (Morrow and Morrow, 1999), a hypothesis that finds support from a multivariate correlation analysis between regional measures of ecology, prey availability and selection, prey body sizes and projectile point form (Buchanan and Hamilton, in press). However, while regional variation in projectile points is primarily the result of drift, this does not mean that all aspects of Clovis projectile point form were a result of drift. On the contrary, this suggests that Clovis projectile point technology was highly stable and capable of performing well in the diverse environments of the North American Late Pleistocene, a result consistent with the finding of strong bias transmission in Clovis projectile point technology we present here.

Fourth, variance in projectile point size is statistically constant over time, consistent with bias social learning practices within Clovis populations. This finding is not surprising given that biased transmission is recognized as a dominant force in social learning within human societies (Henrich, 2001), and, as such, it is easily understandable why biased learning strategies would have played an important role in Clovis technologies. Clovis projectile point technology is complex and would have required a significant amount of investment both in terms of time and energy to learn effectively. Under these conditions it is likely that there was a significant amount of variation among the skill-level of flintknappers, such that recognized master flintknappers likely would have held considerable prestige. Indeed, judging from the size, quality, and over-engineering of some archaeological examples, especially cached points, flintknapping may also have been a form of costly signal. Additionally, in a fast moving and fast growing population subject to the widespread environmental changes of the North American late Pleistocene landscape conformist bias would also have been a highly effective strategy for social learning (see Boyd and Richerson, 1985;

Henrich and Boyd, 1998). This is because under circumstances where ecological conditions change on a generational level, the mean trait value is often optimal, leading to frequency-dependent bias, or conformism (Henrich and Boyd, 1998). If ecological conditions change much faster than this, social learning will favor trial and error learning leading to increased variance. Although the Clovis time period would have seen widespread ecological change over time and space, the rate of this change may not have been experienced within a lifetime (Alroy, 2001). As such, Clovis social learning likely involved a combination of both prestige bias and conformism, which had the effect of limiting variance over time.

Our mathematical model development and analysis indicates that the ACE model is a special case of the BACE model when the strength of bias, λ is zero. So, in general the BACE model is the appropriate null model for the evolution of continuous traits over time, as the strength of bias is always likely to be greater than zero in human populations. Importantly, the null model's major prediction is that the mean value of a continuous trait subject to cultural transmission will drift negatively through time due to the inherently multiplicative process of social learning. Deviations from this expectation can then be used to generate further hypotheses. For example, if the average size of projectile points decreased faster than the null model, this may suggest strong directional selection for smaller projectile points over time. For example, if we assume there are strict performance criteria to point sizes, directional selection for smaller point sizes would be expected to correlate with smaller prey sizes. On the other hand, if point size remained constant over time, this would suggest stabilizing selection for point size, and may suggest a relatively stable prey population. Similarly, increasing point size through time may suggest directional selection for larger points, or some other major shift in lithic economy or behavior. However, note that neither the ACE nor BACE models allow for positive drift in point sizes. This is due to the mathematics of the learning process. Eqs. 6 and 15 show that whenever the variance of the copying error rate is greater than zero (i.e., which could only occur in cases of 100% copying accuracy, perhaps due to standardized production), negative drift occurs deterministically. Positive drift could only occur mathematically if the probability distribution of copying error rates was heavily skewed to the left, in which case the model would violate the assumption of neutral unbiased copying errors, and so would reflect some form of directional selection.

The second major prediction of the BACE null model is that variance should asymptotically approach equilibrium, and so should remain statistically constant over time. This equilibrium is simply a mathematical result of the mean-reversion processes, where the probability of copying the mean is greater than zero (i.e., $\lambda > 0$). When the strength of bias is zero, then variance will increase linearly with time (see Fig. 3). However, as stated above, situations where the strength of bias is zero are expected to be extremely rare, if they ever occur at all, given the highly social nature of learning in human societies.

In conclusion, in this paper we have shown that the original formulation of the ACE model by Eerkens and Lipo (2005) leads to a remarkably rich body of quantitative theory with which to explore the archaeology of cultural transmission in human societies. Markov models of cultural transmission incorporate the essential stochasticity of social learning that contributes to the generation of archaeological variation, and are a flexible, yet straightforward method of generating the statistical predictions of cultural transmission over the long-term.

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