

Cultural traits as units of analysis

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Cultural traits have long been used in anthropology as units of transmission that ostensibly reflect behavioural characteristics of the individuals or groups exhibiting the traits. After they are transmitted, cultural traits serve as units of replication in that they can be modified as part of an individual's cultural repertoire through processes such as recombination, loss or partial alteration within an individual's mind. Cultural traits are analogous to genes in that organisms replicate them, but they are also replicators in their own right. No one has ever seen a unit of transmission, either behavioural or genetic, although we can observe the effects of transmission. Fortunately, such units are manifest in artefacts, features and other components of the archaeological record, and they serve as proxies for studying the transmission (and modification) of cultural traits, provided there is analytical clarity over how to define and measure the units that underlie this inheritance process.

Keywords: cultural traits; cultural transmission; ideational units; classes; design space

1. INTRODUCTION

Cultural traits are units of transmission that permit diffusion and create traditions—patterned ways of doing things that exist in identifiable form over extended periods of time. As with genes, cultural traits are subject to recombination, copying error, and the like and thus can be the foundation for the production of new traits. In other words, cultural traits can be both *inventions*—new creations—and *innovations*—inventions that successfully spread (Schumpeter 1934). Because they can exist at various scales of inclusiveness and can exhibit considerable flexibility, cultural traits have many of the characteristics of Hull's (1981) 'replicators'—entities that pass on their structure directly through replication (Williams 2002).

Archaeologists and other social scientists often distinguish between biologically based (innate) behavioural traits and cultural traits, the former being a reflection of one's genotype and the latter the result of learning (e.g. Williams 1992; Boone & Smith 1998). This is a false dichotomy (Shennan 2002; Mesoudi & O'Brien 2009). 'Biological' means living; thus, all human behaviour is biological. Further, 'innate' behaviours typically include cultural components, both innate and learned. Learning a language, a quintessential cultural trait, requires cultural transmission, but it also requires the appropriate mental facilities, which result from the interaction between an individual's genes and the environment (Nettle 2006). Thus, language is a cultural trait because it *requires* the transmission of cultural information *in addition to* other environmental and

genetic elements. Cultural transmission occurs when both the necessary genes and environmental factors (including cultural traits) are present. Cultural traits that are transmitted through behaviour are a fundamental component of human phenotypes and are one, but clearly not the only, component necessary for cultural transmission.

Once transmitted, cultural traits serve as units of replication in that they can be modified as part of an individual's cultural repertoire through processes such as recombination (new associations with other cultural traits), loss (forgetting) or partial alteration (incomplete learning, personal experience or forgetting select components) within an individual's mind (Eerkens & Lipo 2005). In this regard, cultural traits are analogous to genes in that organisms replicate them, but they are also replicators in their own right. However, the *transmission* of these units is behavioural, and it uses mutually understandable spoken or written language, physical imitation or some combination.

No one has ever seen a unit of transmission, either behavioural or genetic, although we can observe the effects of transmission. Genes and behavioural traits become units of transmission only in specific environmental contexts, meaning that although one can talk abstractly about them, their definition as an analytically useful unit depends on environmentally specific elements. Fortunately, such units are manifest in artefacts, features and other components of the archaeological record, and they serve as proxies for studying the transmission (and modification) of cultural traits (Leonard & Jones 1987; VanPool 2003). The applicability of an evolutionary framework to these traits has been previously defended (e.g. Lyman & O'Brien 1998; VanPool & VanPool 2003; Mesoudi & O'Brien 2009); here we point out only that these behavioural traits are transmitted between

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One contribution of 14 to a Theme Issue 'Cultural and linguistic diversity: evolutionary approaches'.

people in an evolutionary process of descent with modification. Our concern is with how to define and measure the units that underlie this inheritance process. What sort of unit will be useful for measuring cultural transmission?

2. KINDS OF UNITS

Evolutionary archaeologists have examined various units that have been proposed to track cultural transmission (e.g. Dunnell 1971, 1986; Lipo *et al.* 1997; O'Brien & Lyman 2000, 2002; Lipo & Madsen 2001), in the process emphasizing the critical distinction between two kinds of units—*ideational* and *empirical*. A projectile point is an empirical unit—we can see and feel it—but its properties are measured using ideational units, which include the characters and the various states in which they reside. The character 'notch angle' is an ideational unit, as are its various states (30°, 40–50°, and so on). Ideational units can be descriptive, used merely to characterize a thing (e.g. recording projectile-point colour for descriptive purposes), or they can be theoretical, created for specific analytical purposes (e.g. projectile-point notch-angle units such as 1–30°, 31–60° and 61–90°, each of which corresponds to a functional distinction) (Dunnell 1986). A *theoretical unit* is a special kind of ideational unit—one that has explanatory significance because of, and only because of, its theoretical relevance to the problem at hand. Colour could be a theoretical unit if we were interested in why prehistoric potters painted their bowls certain colours but not others, but it is unlikely that it would play a role in the functional analysis of projectile points.

Ideational units are important in two ways. First, they are essential to defining cultural traits, given that archaeologists study cultural replication indirectly through artefacts and other components of the archaeological record. Second, the transmission of cultural traits is contingent on ideational units, making them an essential component of cultural replicators. Humans use ideational units when learning and communicating behavioural information. For example, a manufacturer of, say, projectile points, thinks of his intended creation using ideational units: 'I need a 6-inch-long point that is 2 inches wide and has 60-degree notches instead of the usual 40-degree notches.' Those units—*inches* and *degrees*—cannot be anything else but ideational because we cannot 'see' or 'feel' them. The manufacturer then uses ideational units to create the object and can also describe the object using ideational units. The actual specimen that he creates—a 6-inch-long projectile point—is an empirical unit in that it *can* be seen and felt.

Ideational units reduce the need for repetitive, and costly, experimentation with, for example, each newly produced atlatl and dart. Our ability to forego repetitive experimentation sets humans apart from other culture-bearing animals and is based on cultural transmission, which itself is based on the ability to think in, as well as transmit and receive, ideational units (Mesoudi & O'Brien 2008c). In fact, behavioural transmission is typically focused on the transmission of specific ideational units in that they allow fidelity

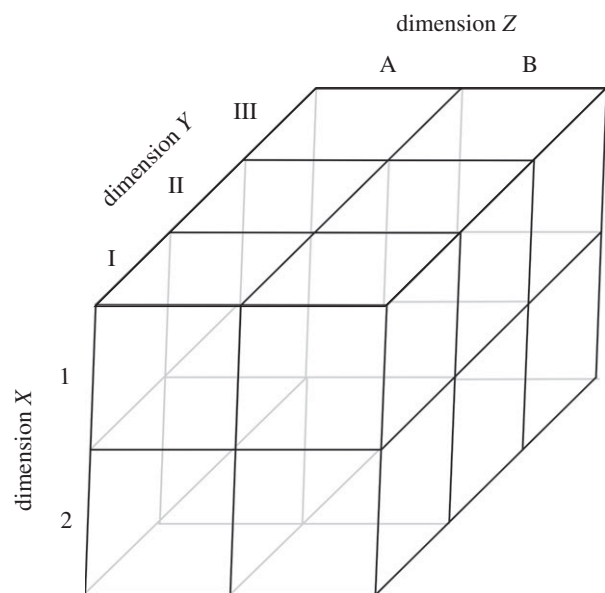


Figure 1. A simple three-dimensional classification system showing the intersection of the character states of each character. Twelve classes are represented ($2 \times 3 \times 2$), which collectively define the design space.

in cultural transmission by allowing an individual to copy the 'intent' as opposed to simply the 'object' of another. Notice that there are two things going on here: ideational units are used by both the person making a stone tool—*systemic* context—and the person later studying the tool—*archaeological* context (Schiffer 1972). The only difference between the two contexts is in terms of the ultimate role played by the units—replication in the systematic context, analysis in the archaeological context.

Some archaeological studies of transmission employ a particular kind of ideational unit, the *class*, which is a measurement unit that specifies the necessary and sufficient conditions that a specimen must possess to be classified as a member of that unit (class). The advantage of using this kind of classification system is that various combinations of ideational units that define cultural traits can be specified. We can consider the packages of cultural traits that are transmitted (classes with members), those that are not (classes without members), and the differential persistence of behavioural traits through time or space (changes in the occurrence or frequencies of particular classes). What does a class reflect? If a class has sustained replicative success (Leonard & Jones 1987), the short answer is behaviour that at least, in part, reflects cultural transmission. The class does not *reconstruct* a cultural trait any more than the distal breadth of a fossil hominid humerus reconstructs the underlying genes; rather, it serves as a proxy for one or more cultural traits.

Of considerable analytical interest is the concept of *design space*, an n -dimensional hyperspace (meaning that it is non-Euclidian) defined by the intersection of all possible character states of mutually exclusive characters. Figure 1 illustrates a three-dimensional space (X , Y and Z). There are 12 positions ($2 \times 3 \times 2$) that define our three-dimensional hyperspace—1-II-A,

2-III-B, and so on. Those positions are classes—mutually exclusive units defined by the intersections of character states of the three characters (*X*, *Y* and *Z*). We label these *paradigmatic classes* (Dunnell 1971; O'Brien & Lyman 2000). Although figure 1 shows a three-dimensional design space, the number of characters and character states included in a particular classification is unrestricted. Importantly, some classes may have no empirical members, meaning that those parts of our design space are empty. Empty design space is just as important analytically as filled design space. We point out that for the sake of simplicity, our treatment here is on a monothetic view of design space when in fact people often or mostly think about things as polythetic groups. This will have implications for our upcoming discussion of recipes and hierarchies.

Design-space analysis has been a focus of much of our recent work (e.g. O'Brien *et al.* 2001, 2002; VanPool 2003; Darwent & O'Brien 2006; Lyman *et al.* 2008, 2009) aimed at tracking the appearance and disappearance of characters and character states over time and space. An ongoing project studying the evolution of projectile points in the southeastern United States that date *ca* 11 050–10 500 radiocarbon years before the present illustrates our approach. Instead of using traditional artefact types, we used classes defined by eight characters with a variable number of character states (table 1 and figure 2). The selected characters are those that are expected to change the most as a result of cultural transmission (e.g. Beck 1995; Hughes 1998). Our classification gives us the ability to monitor changes in characters through time at the scale of single characters or packages of linked characters. As we discuss below, projectile points (and all other artefacts/features) are higher level traits that comprise any number of lower level traits. Classification used to define design space allows us to shift back and forth between different levels.

3. HIERARCHIES OF UNITS

Just as the human brain is equipped to recognize the difference between ideational and empirical phenomena, it is also equipped to arrange phenomena hierarchically (Atran 1998). This is manifest in the manufacture and use of such things as ceramic vessels, which are cultural traits that comprise hierarchically lower traits such as various kinds of temper or manufacturing techniques and themselves are parts of higher level traits such as diet and cuisine choices, food storage, and so on. Further, traits at the same level may be independent, in that their variation is not directly linked (e.g. temper type and form of painted design), yet may also be dependent on the same higher level traits (e.g. pottery use).

Pocklington & Best (1997) argue that appropriate units of selection for tracing cultural adaptation will be the largest units that reliably and repeatedly withstand transmission. These presumably will reflect multiple cultural traits, just as most somatic adaptations typically reflect multiple genetic sites. Why the largest unit? Pocklington and Best see two reasons. First, the evolution of smaller units is probably

Table 1. System used to classify projectile points from the midwestern and southeastern United States.

character	character state
I. location of maximum blade width	1. proximal quarter 2. second-most proximal quarter 3. second-most distal quarter 4. distal quarter
II. base shape	1. arc-shaped 2. normal curve 3. triangular 4. Folsomoid
III. basal-indentation ratio ^a	1. no basal indentation 2. 0.90–0.99 (shallow) 3. 0.80–0.89 (deep)
IV. constriction ratio ^b	1. 1.00 2. 0.90–0.99 3. 0.80–0.89 4. 0.70–0.79 5. 0.60–0.69 6. 0.50–0.59
V. outer tang angle	1. 93°–115° 2. 88°–92° 3. 81°–87° 4. 66°–80° 5. 51°–65° 6. ≤50°
VI. tang-tip shape	1. pointed 2. round 3. blunt
VII. fluting	1. absent 2. present
VIII. length/width ratio	1. 1.00–1.99 2. 2.00–2.99 3. 3.00–3.99 4. 4.00–4.99 5. 5.00–5.99 6. ≥6.00

^aThe ratio between the medial length of a specimen and its total length; the smaller the ratio, the deeper the indentation.

^bThe ratio between the minimum blade width (proximal to the point of maximum blade width) as a measure of 'waistedness'; the smaller the ratio, the higher the amount of constriction.

controlled by the transmission of cultural traits defined at a higher level. Second, the parallel transmission of multiple smaller scale units over long periods of time indicates that there is no significant conflict of interest among the sub-components (Bull 1994). From an evolutionary perspective, parallel transmission is the force that initiates the process by which multiple isolated elements begin to cooperate with one another and create larger scale structural integrity, which is the scale at which adaptations form.

Our classification produces units that are amenable to hierarchical arrangement, meaning that the units are nested. The evolutionary arrangement of four hypothetical units (taxa) created from eight characters is shown in figure 3*a*. The ancestral unit, *x*, undergoes

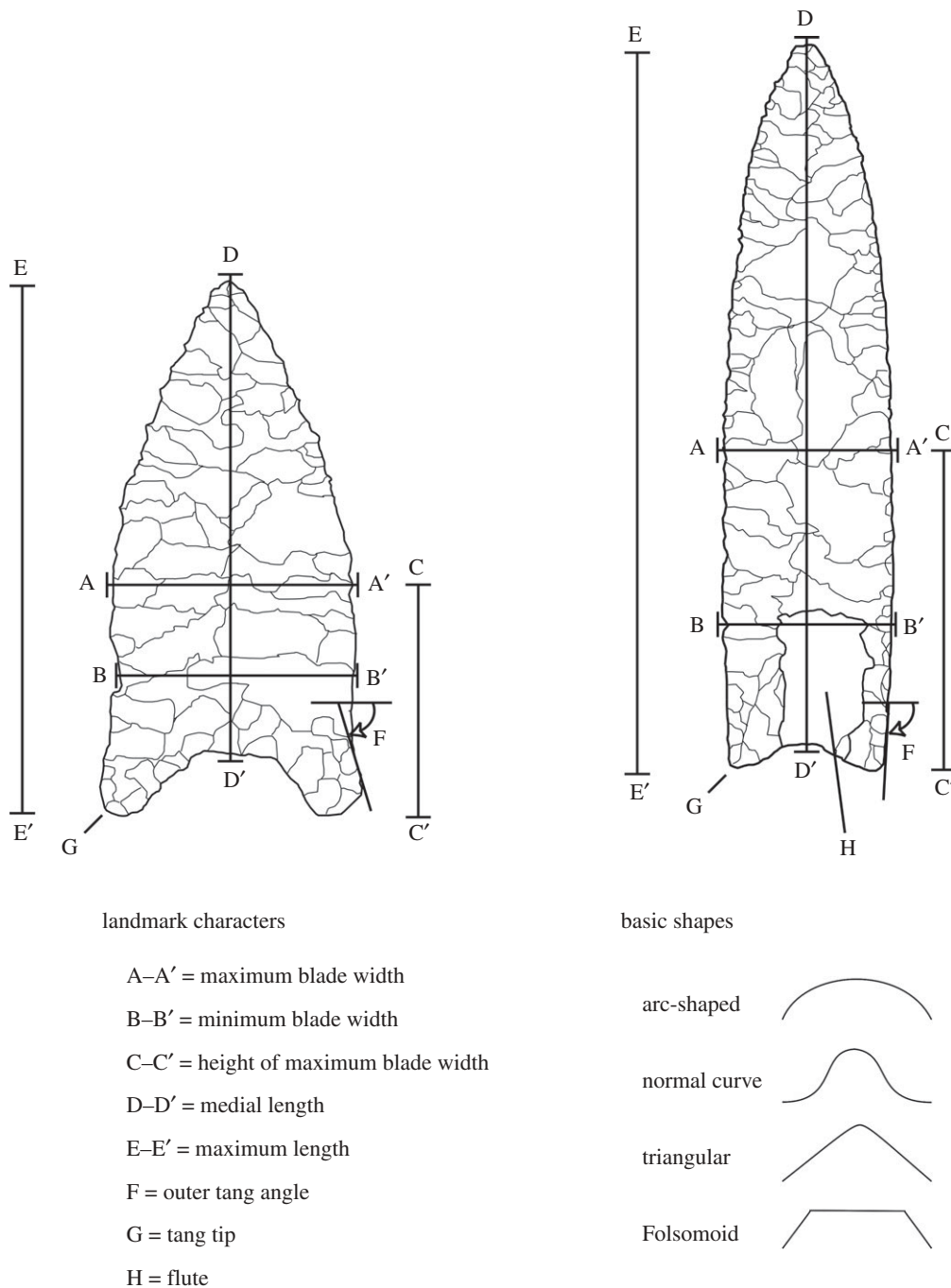


Figure 2. Locations of characters used in the analyses of projectile points from the midwestern and southeastern United States (from O'Brien *et al.* 2001). See table 1 for character states.

one character-state change, in character IV (1 → 2), to produce unit *y* (represented by 11222324). Unit *y* undergoes two state changes, in characters VII (2 → 1) and VIII (4 → 3), to produce unit *z* (11222313). Unit *z* undergoes one state change in character I (1 → 2) to produce unit 21222313. This arrangement is hierarchical in the sense of a nesting of less-inclusive, lower level units within more-inclusive, higher level units. To simplify, considering only characters that change states—I, IV, VII and VIII—and ranking the characters in the order listed in figure 3*a*, the hierarchy of possible combinations of character states gives the 16 possible classes as shown in figure 3*b*. Only four of the classes are actually represented by empirical specimens in figure 3*a*, but we reiterate that empty design

space—classes without members—can be analytically significant (Gould 1991), especially with respect to adaptation. For example, Henrich & Boyd (1998) ask why the aboriginal peoples of New Guinea do not fletcher their arrows, given the likelihood that people in coastal New Guinea have had considerable contact with and have observed others using fletching for centuries. The emptiness of design space raises the question ‘Why not?’ in a manner that lends itself to empirical examination.

4. RECIPES AS UNITS

The successful construction and use of tools—higher order cultural traits—typically involve the execution

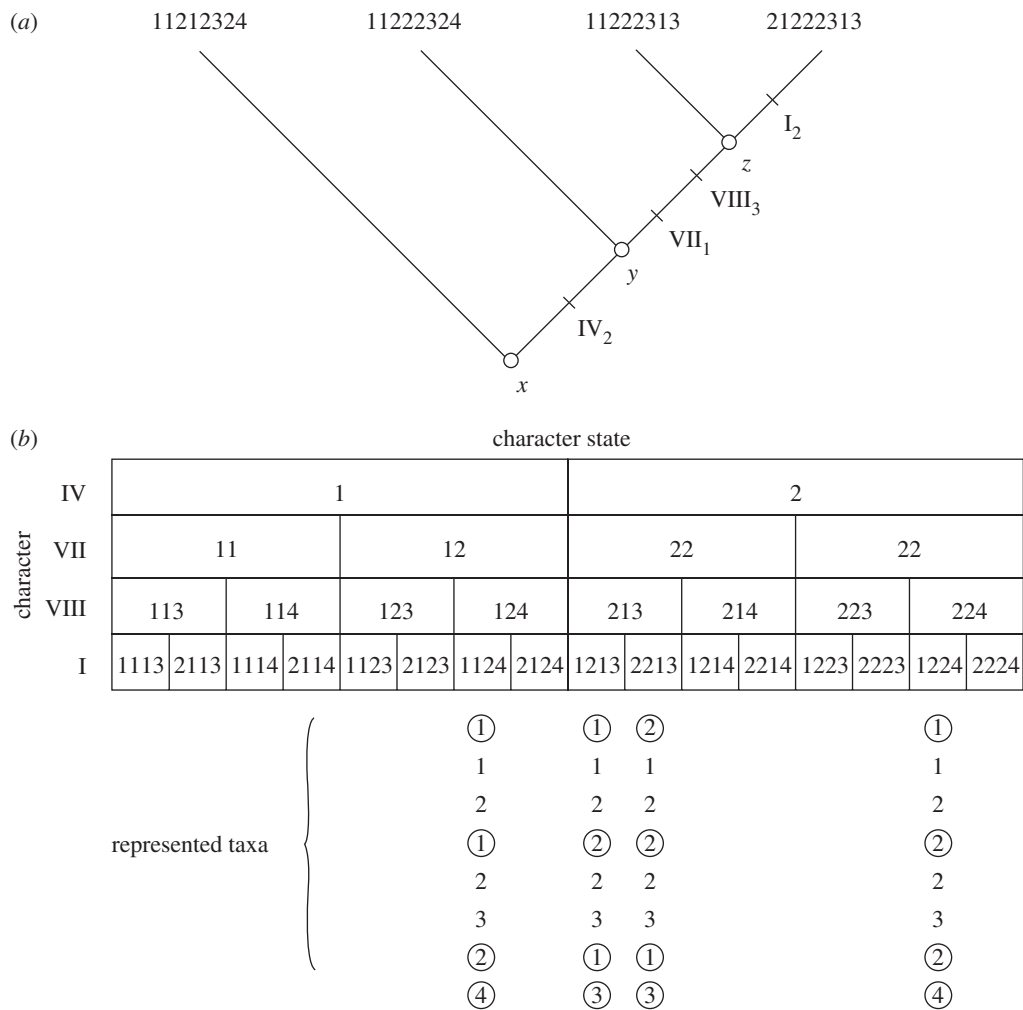


Figure 3. Phylogenetic (historical) arrangement of four fictional units (taxa) created from eight characters: (a) tree showing historical progression of character-state changes (arabic numerals identify the characters, and roman numerals identify the states of those characters); (b) nested hierarchical arrangement of character states showing empirically filled design space (the classes labelled 'represented taxa') and empty design space; character states common to all classes are not circled (from O'Brien *et al.* 2002).

of a lengthy sequence of actions (Bleed 2001), from the acquisition and preparation of materials to a tool's eventual discard, with each action functionally dependent on previous actions. Cognitive psychologists (see Mesoudi & Whiten 2004) have proposed that people represent tools as interlinked, hierarchical knowledge structures, incorporating behavioural scripts governing their construction and use, much like recipes—a concept that has been used on occasion in archaeology (e.g. Krause 1985; Schiffer & Skibo 1987; Neff 1992; Lyman & O'Brien 2003; Mesoudi & O'Brien 2008c).

The concept of recipe attends several of the difficulties inherent in the cultural-trait concept. If, as is evident, culture is highly plastic, then 'the location of the 'joints' in a cultural genome appear to be capable of varying from case to case, and perhaps from context to context' (Wimsatt 1999, p. 282). The seeming arbitrariness of cultural traits as cultural fragments gives them their viability as replicators and provides 'our ability to re-package and re-articulate cultural products into seemingly arbitrary larger or smaller constructions to be replicated and transmitted as units' (Wimsatt 1999, p. 283). This means 'most cultural products are

also compound products' (Wimsatt 1999, p. 285)—a characteristic not lost on early ethnologists (e.g. Driver & Kroeber 1932).

The same can be said for modern perspectives in biology, where it is becoming increasingly clear that 'the classical molecular concept of a gene as a contiguous stretch of DNA encoding a functional product is inconsistent with the complexity and diversity of genomic organization' (Prohaska & Stadler 2008, p. 215). In our minds, it is unquestionable that genes are units of function, and we have no issue with defining a gene as a unit that shows 'stronger cohesion to itself than to other components' (Prohaska & Stadler 2008, p. 219). We need to keep in mind, however, that for any given experimental protocol, 'we may be able to distinguish the function of higher level units from those of their components, thus functional units can be nested within each other' (Prohaska & Stadler 2008, p. 219). This perspective both recognizes that biological products can also be compound products and underscores our earlier discussion of ideational units, which can exist in the minds of the makers of tools just as they can in the minds of the archaeologists studying the tools. In both cases,

units can be manipulated at various scales, from that of small functional units—equivalent to ‘genes’ in the biological world—to that of larger, nested units. Recipes are nothing but large, nested ideational units.

We find the term ‘recipe’ to be useful for three reasons. First, the commonsensical meaning of the term captures the essence of most standard anthropological definitions of ‘cultural trait’: behavioural information that can be transmitted between people about how (and when, where, and why, to lesser extents) to produce something (that may or may not leave a material trace). Second, the recipe concept behaviourally links two general structures—ingredients and rules—that can be reconfigured to form different recipes and thus different products (Eerkens & Lipo 2007). As an important aside, the same is true in biology with respect to protein interaction networks, in which the same ‘ingredients’ can be activated in different orders by different rules to form different cellular products.

Two concepts employed in evolutionary biology are of interest here (Lyman *et al.* 2008). The first is *constraint*, in which some attribute of the phenomena being transmitted places mechanical or structural limitations on future potential variants. This results in *channelling* (Gould 2002), in which the transmission of a particular trait can be constrained by the transmission of a trait with which it is mechanically linked. Such a trait is said to *hitchhike*—the second concept—with a trait that is actually being sorted by processes such as selection, drift or infidelity of transmission (Hurt *et al.* 2001; Ackland *et al.* 2007).

The third useful characteristic of the term recipe is that recipes are ideational, with any given product being a more or less imperfect empirical manifestation of a recipe as a result of variation in raw materials, manufacturing skills, and so on. Given their ideational structure, recipes can be defined (and cultural transmission studied) at different scales. Thus they are ordered, encompassing several behavioural subroutines (e.g. preparation of material, production and use), each of which in turn can be subdivided into a sequence of constituent lower level actions required to complete each subroutine. This feature of recipes is helpful from an analytical standpoint in that the scale of units of cultural replication can vary according to analytical needs. That is, one can move back and forth between examining the basic building blocks of a recipe and examining the higher order groupings of those blocks into larger, more-complex blocks.

To examine these issues, Mesoudi & O'Brien (2008c) constructed a simple agent-based model designed to explore the conditions under which recipe-like knowledge structures are likely to emerge during cultural evolution. The model considered three types of vertical cultural transmission: hierarchical, holistic and diffusionist (‘piecemeal’ might be a better term to differentiate the process from the catch-all process long used in anthropology to refer to any kind of transmission). Hierarchically organized transmission, where agents could subdivide tool-making knowledge acquired from their parents into a recipe-like series of constituent subunits or subroutines (figure 4), was favoured over holistic

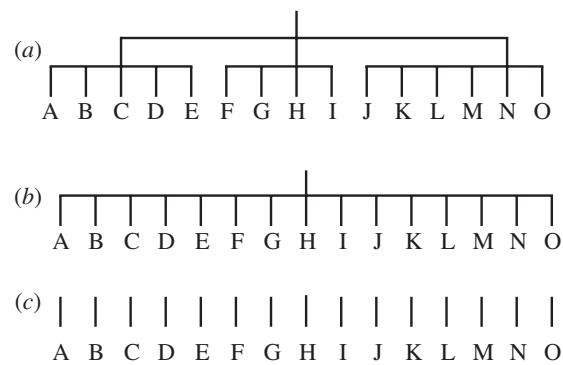


Figure 4. Three different models of behavioural organization (from Mesoudi & O'Brien 2008c). Although Mesoudi and O'Brien use the term ‘diffusionist’ organization, perhaps a better term would be ‘piecemeal’ organization. (a) Hierarchical organization; (b) holistic organization; (c) diffusionist organization.

transmission, where agents learned tool-making from their parents in an all-or-nothing fashion with no stable subunits (figure 4), *only* when there was some degree of error in the transmission process. This is because, for hierarchical transmission, errors affect only a single subunit; already-completed subunits are unaffected. Where there are no intermediate subunits, as in holistic transmission, errors disrupt the entire learning process (Simon 1962; Dawkins 1976b). The advantage of hierarchical transmission is maintained at equilibrium when transmission is also associated with some cost, which minimizes the amount of time spent learning from parents. Otherwise, holistic learners will eventually acquire the entire behavioural sequence despite the disruptive effect of transmission error. That cultural transmission exhibits both cost and error seems a realistic assumption, given that mastering the skills required to make and use tools typically requires repeated practice over several years (Eerkens 2000).

Hierarchical transmission is also favoured over diffusionist transmission, in which actions are acquired from the parent separately in piecemeal fashion (figure 4), *only* when subunits repeat in one or more recipe. This is because the overall cost of transmission is reduced: once a subunit is learned, it can be repeated in the same or a different artefact at no cost and with no error (Lyman & O'Brien 2003). Hierarchical transmission is therefore more likely to emerge when there are multiple recipes with multiple subunits and few actions per subunit.

Finally, the model also explored the advantage of hierarchical cultural transmission of behavioural knowledge from the previous generation relative to individual trial-and-error learning: the former is more likely to replace the latter when the former is less costly and features less error. This assumption is consistent with both theoretical predictions (the maximization of inclusive fitness) and ethnographic evidence (Mesoudi & O'Brien 2008c). Some degree of individual learning is retained when the selective environment changes, which vertical transmission alone cannot track (see Boyd & Richerson 1985).

A plausible scenario suggested by this model, therefore, is one in which there is an extended period of relatively low cost and relatively accurate vertical cultural transmission, where hierarchically structured behavioural knowledge is learned from the parental generation, along with less-frequent individual learning that is predominantly diffusionist and functions to track novel environmental change (Mesoudi & O'Brien 2008c).

Recent advances in evolutionary developmental biology, or 'evo devo' (Carroll 2005), have shown there to be several parallels between the hierarchically structured, recipe-like organization of cultural behavioural knowledge and the manner in which biological organisms develop (Callebaut & Rasskin-Gutman 2005). Phenotypic characters are often modular (Hansen 2003), such that different characters develop as partially self-contained modules, similar to the subunits of a behavioural recipe. These modules are ordered, with a small number of higher level regulatory genes triggering the growth of entire lower level modules, such as the *Hox* genes that control the growth of limbs or body segments (Carroll 1995). Consequently, bodies can be built by repeating modular body parts, such as limbs, teeth or body segments (Weiss 1990), in the same way that cultural subunits can be repeated in one or more recipes. These parallels suggest that the advantages of hierarchical organization—localization of error and repetition of subunits—are likely to generalize to many or all knowledge-gaining evolutionary systems (Dawkins 1976b).

5. DISCUSSION

Although there is considerable room for debate about cultural units, we find several points indisputable (Lyman *et al.* 2008) and hope that they will serve as cornerstones of all future evolutionary studies of cultural transmission. First, cultural traits are ideational replicative units composed of behavioural information transmitted through human interaction. Second, cultural traits are part of human phenotypes, but the traits themselves are populational. They can be tracked at an individual level across time and space, but trait evolution is observed at the level of the changing membership of a population and does not predict the life history of any individual trait. Third, traits aggregate into larger linked associations that can be manifest in the archaeological record. However, individual cultural traits cannot be directly reconstructed from the archaeological record because they are replicated behaviour, which is not wholly reflected in even the best-preserved archaeological contexts. Further, the material objects archaeologists recover typically reflect cultural-trait clusters (recipes of action) that can be indirectly traced through the replicative success of like artefacts (Leonard & Jones 1987). Recognizing that theoretical classes reflect, but do not reconstruct, cultural traits frees us from worrying about such things as identifying 'true' cultural traits, just as palaeobiologists do not seek to reconstruct specific genetic sequences from the morphological characteristics they study.

Four axioms follow from these premises (Lyman *et al.* 2008). First, cultural transmission creates lineages of artefacts as cultural traits replicate and change. At a larger scale, groups of phylogenetically related lineages form traditions, or clades (e.g. Jordan & Shennan 2003; Buchanan & Collard 2007; O'Brien *et al.* 2008; Lycett 2009). Second, the persistence of artefact classes over time monitors cultural transmission but at a scale higher than a single cultural trait (Lyman & O'Brien 1998; Lyman & Harpole 2002). If constructed using attributes that are culturally transmitted, cultural traits reflected in artefacts in the same class are related phylogenetically. Third, copying error, intentional or not, and experimentation create variation (Schiffer 1996; Eerkens & Lipo 2005). Fourth, selection reduces or stabilizes that variation.

Understanding the operation of selection and other evolutionary processes is simplified by properly understanding cultural traits as replicative units. To begin with, there probably will not be a one-to-one correspondence between only one cultural trait and its behavioural manifestation. Each cultural trait is linked more or less strongly (depending on selective context) within the transmission environment. Recombination *might* allow previously linked cultural traits to become independently transmitted, but this is unnecessary and may actually be mechanically impossible. Linked cultural traits further illustrate that cultural traits are replicative units, not just units of inheritance. For example, variants that are superior in one context can be selected against because they lack performance characteristics associated with different recipes of action. A key factor in explaining spatial-temporal patterns visible in culturally transmitted information will consequently be evaluating hierarchical relationships between culture traits and related recipes of action.

Although variation is continuously generated, we also expect that the rate of change in items such as projectile points will be episodic rather than constant. Studies of modern material culture have found patterned inventive activities, 'discernible as a clustering in time and space of similar inventions'—literally, a 'burst of variation,' termed *stimulated variation* (Schiffer 1996, p. 656). The analogous process in biological evolution is adaptive radiation, during which organisms enter new niches. We believe a similar temporal dynamic attends stimulated variation (Lyman & O'Brien 2000). Deficiencies in the performance characteristics of an artefact category result in a proliferation of variation (Petroski 1992), perhaps in a *cascade effect* as culture traits realign into new recipes of action (Schiffer 2005). Subsequently, variation will decrease as less-efficient variants cease to be replicated.

We recently began investigating such changes in the tempo of cultural-trait evolution as they are reflected in the replacement of the atlatl and dart by the bow and arrow (Lyman *et al.* 2008, 2009). Because of mechanical differences, attributes of dart points, especially those related to point size (arrow points are smaller than dart points) and the manner in which the points were fastened to shafts (hafting), had to be experimented with to find an effective combination

of attributes (classes) of points that could serve as arrow points (e.g. Beck 1995; Hughes 1998; Bettinger & Eerkens 1999). These efforts are archaeologically visible as both taxonomic diversity and morphological diversity within classes.

6. CONCLUSION

If Mayr (1973) is correct that behaviour is perhaps the strongest selection pressure operating in the animal kingdom, then we need to take it all that more seriously when the animals are humans. Cultural transmission is a primary determinant of behaviour, and there is little doubt that cultural transmission is one of the most effective means of evolutionary inheritance that nature could ever sculpt. Some (e.g. Gould 1996) argue that culture, through its highly creative transmission processes, has exempted humans from natural selection, and thus from evolution, but a growing number of social scientists are rejecting this myopic view. Instead, they are finding themselves in agreement with Bettinger & Eerkens' (1999, p. 239) claim that, 'it seems clear to us that cultural transmission must affect Darwinian fitness—how could it be otherwise? And Darwinian fitness must also bear on cultural transmission. Again, how could that not be true? ... To deny that would imply that the culturally mediated evolutionary success of anatomically modern humans is merely serendipitous happenstance'.

Considerable study has elucidated cultural-transmission processes—individual learning versus social learning, for example—and the strategies/biases that shape the results of transmission—conformist, prestige-based, indirect, content-based, and so on (e.g. Boyd & Richerson 1985; Henrich & Boyd 1998). If our intellectual forebears were able to look into the future, no doubt they would have been amazed at the progress that has been made in understanding transmission processes. But they probably would also be amused to see that the same issues with which they were wrestling in the early twentieth century relative to the units of transmission have a similar cast to them (Lyman 2008). As Shennan (2008, p. 3176) put it, the key question is, 'to what extent is it possible to identify the action of the various cultural evolutionary processes. ... on the basis of distributions of variation in the (more or less) present. ... or at various points in the past?' This requires us to understand both the ways in which humans gain cultural information and the structure of that information.

We have been able to model the relationships between process and structure for some time (e.g. Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985), but recent empirical investigations reflect our growing ability to empirically test such models (e.g. Bettinger & Eerkens 1999; Shennan & Wilkinson 2001; Henrich 2004; Kohler *et al.* 2004; Mesoudi & O'Brien 2008*a,b,c*). Archaeologists in particular are beginning to take what Dawkins (1976*a*) referred to as the 'meme's eye-view', or the perspective of the cultural attributes themselves (Shennan 2008). And when we reach down to the level of the artefact, and then down to the level of characters and character states, we begin to notice the incredible variation that exists.

That variation tells us that evolutionary change has taken place. It is our job to construct units that measure the change—its direction, tempo and scale.

Here is a closing example: Let us say that our analytical interest is on understanding how hunters and gatherers negotiate complex fitness topographies containing a variety of peaks, valleys, chasms and plateaus. Slight variations in initial conditions—the starting point on the fitness landscape—can drive two similar populations towards increasingly divergent adaptive 'peaks', or solutions (Henrich & Boyd 1998). We might propose that jumping from one optimum to another is difficult, requiring simultaneous alteration of a number of traits in just the right manner so as to land on a superior peak and avoid dropping into fitness valleys (Mesoudi 2008). How could we possibly structure research to address this proposition without detailed knowledge of the small-scale changes that occurred, either singly or as integrated packages (linked characters), in the phenotypic expressions of the actors involved? The answer is, we cannot.

We thank James Steele, Peter Jordan, and Ethan Cochrane for organizing the seminar at which this paper was presented. The paper benefited greatly from the comments of seminar participants, especially Carl Lipo, Mark Collard, Jamie Tehrani, and Stephen Shennan. We also thank two not-so-anonymous reviewers for their extremely helpful advice.

REFERENCES

- Ackland, G. J., Signitzer, M., Stratford, K. & Cohen, M. H. 2007 Cultural hitchhiking on the wave of advance of beneficial technologies. *Proc. Natl Acad. Sci. USA* **104**, 8714–8719. (doi:10.1073/pnas.0702469104)
- Atran, S. 1998 Folk biology and the anthropology of science: cognitive universals and cultural particulars. *Behav. Brain Sci.* **21**, 547–609. (doi:10.1017/S0140525X98001277)
- Beck, C. 1995 Functional analysis and the differential persistence of Great Basin dart forms. *J. Calif. Great Basin Anthropol.* **17**, 222–243.
- Bettinger, R. L. & Eerkens, J. 1999 Point typologies, cultural transmission, and the spread of bow-and-arrow technology in the prehistoric Great Basin. *Amer. Antiq.* **64**, 231–242. (doi:10.2307/2694276)
- Bleed, P. 2001 Trees or chains, links or branches: conceptual alternatives for consideration of stone tool production and other sequential activities. *J. Archaeol. Method Theory* **8**, 101–127. (doi:10.1023/A:1009526016167)
- Boone, J. L. & Smith, E. A. 1998 Is it evolution yet? A critique of evolutionary archaeology. *Curr. Anthropol.* **39**, S141–S173. (doi:10.1086/204693)
- Boyd, R. & Richerson, P. J. 1985 *Culture and the evolutionary process*. Chicago, IL: University of Chicago Press.
- Buchanan, B. & Collard, M. 2007 Investigating the peopling of North America through cladistic analyses of Early Paleoindian projectile points. *J. Archaeol. Sci.* **26**, 366–393.
- Bull, J. J. 1994 Virulence. *Evolution* **48**, 1423–1437. (doi:10.2307/2410237)
- Callebaut, W. & Rasskin-Gutman, D. (eds) 2005 *Modularity: understanding the development and evolution of natural complex systems*. Cambridge, MA: MIT Press.
- Carroll, S. B. 1995 Homeotic genes and the evolution of arthropods and chordates. *Nature* **376**, 479–485. (doi:10.1038/376479a0)

- Carroll, R. L. 2005 *Endless forms most beautiful: the new science of *evo devo* and the making of the animal kingdom*. New York, NY: Norton.
- Cavalli-Sforza, L. L. & Feldman, M. 1981 *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
- Darwent, J. & O'Brien, M. J. 2006 Using cladistics to construct lineages of projectile points from northeastern Missouri. In *Mapping our ancestors: phylogenetic approaches in anthropology and prehistory* (eds C. P. Lipo, M. J. O'Brien, M. Collard & S. J. Shennan), pp. 185–208. New York, NY: Aldine.
- Dawkins, R. 1976a *The selfish gene*. New York, NY: Oxford University Press.
- Dawkins, R. 1976b Hierarchical organisation: a candidate principle for ethology. In *Growing points in ethology* (eds P. P. Bates & R. A. Hinde), pp. 7–54. Cambridge, UK: Cambridge University Press.
- Driver, H. E. & Kroeber, A. L. 1932 Quantitative expression of cultural relationships. *U. Calif. Pub. Am. Archaeol. Ethnol.* **31**, 211–256.
- Dunnell, R. C. 1971 *Systematics in prehistory*. New York, NY: Free Press.
- Dunnell, R. C. 1986 Methodological issues in Americanist artifact classification. *Adv. Archaeol. Method Theory* **9**, 149–207.
- Eerkens, J. W. 2000 Practice makes within 5% of perfect: the role of visual perception, motor skills, and human memory in artifact variation and standardization. *Curr. Anthropol.* **41**, 663–668. (doi:10.1086/317394)
- Eerkens, J. W. & Lipo, C. P. 2005 Cultural transmission, copying errors, and the generation of variation in material culture and the archaeological record. *J. Anthropol. Archaeol.* **24**, 316–334. (doi:10.1016/j.jaa.2005.08.001)
- Eerkens, J. W. & Lipo, C. P. 2007 Cultural transmission theory and the archaeological record: providing context to understanding variation and temporal changes in material culture. *J. Archaeol. Res.* **15**, 239–274. (doi:10.1007/s10814-007-9013-z)
- Gould, S. J. 1991 The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. *Paleobiology* **17**, 411–423.
- Gould, S. J. 1996 *Full house: the spread of excellence from Plato to Darwin*. New York, NY: Harmony.
- Gould, S. J. 2002 *The structure of evolutionary theory*. Cambridge, MA: Belknap.
- Hansen, T. F. 2003 Is modularity necessary for evolvability? Remarks on the relationship between pleiotropy and evolvability. *BioSystems* **69**, 83–94. (doi:10.1016/S0303-2647(02)00132-6)
- Henrich, J. 2004 Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *Amer. Antiq.* **69**, 197–214. (doi:10.2307/4128416)
- Henrich, J. & Boyd, R. 1998 The evolution of conformist transmission and the emergence of between-group differences. *Evol. Hum. Behav.* **19**, 215–241. (doi:10.1016/S1090-5138(98)00018-X)
- Hughes, S. S. 1998 Getting to the point: evolutionary change in prehistoric weaponry. *J. Archaeol. Method Theory* **5**, 345–408. (doi:10.1007/BF02428421)
- Hull, D. L. 1981 Units of evolution: a metaphysical essay. In *The philosophy of evolution* (eds U. J. Jensen & R. Harré), pp. 23–44. New York, NY: St. Martin's Press.
- Hurt, T. D., VanPool, T. L., Leonard, R. D. & Rakita, G. F. M. 2001 Explaining the co-occurrence of attributes in the archaeological record: a further consideration of replicative success. In *Style and function: conceptual issues in evolutionary archaeology* (eds T. D. Hurt & G. F. M. Rakita), pp. 51–68. Westport, CT: Bergin and Garvey.
- Jordan, P. & Shennan, S. J. 2003 Cultural transmission, language, and basketry traditions amongst the California Indians. *J. Anthropol. Archaeol.* **22**, 42–74. (doi:10.1016/S0278-4165(03)00004-7)
- Kohler, T. A., VanBuskirk, S. & Ruscavage-Barz, S. 2004 Vessels and villages: evidence for conformist transmission in early village aggregations on the Pajarito Plateau, New Mexico. *J. Anthropol. Archaeol.* **23**, 100–118. (doi:10.1016/j.jaa.2003.12.003)
- Krause, R. A. 1985 *The clay sleeps*. Tuscaloosa, AL: University of Alabama Press.
- Leonard, R. D. & Jones, G. T. 1987 Elements of an inclusive evolutionary model for archaeology. *J. Anthropol. Archaeol.* **6**, 199–219. (doi:10.1016/0278-4165(87)90001-8)
- Lipo, C. P. & Madsen, M. E. 2001 Neutrality, 'style,' and drift: building models for studying cultural transmission in the archaeological record. In *Style and function: conceptual issues in evolutionary archaeology* (eds T. D. Hurt & G. F. M. Rakita), pp. 91–118. Westport, CT: Bergin and Garvey.
- Lipo, C., Madsen, M., Dunnell, R. C. & Hunt, T. 1997 Population structure, cultural transmission, and frequency seriation. *J. Anthropol. Archaeol.* **16**, 301–333. (doi:10.1006/jaa.1997.0314)
- Lycett, S. J. 2009 Are Victoria West cores 'proto-Levallois'? A phylogenetic assessment. *J. Hum. Evol.* **56**, 175–191. (doi:10.1016/j.jhevol.2008.10.001)
- Lyman, R. L. 2008 Cultural transmission in North American anthropology and archaeology, ca. 1895–1965. In *Cultural transmission and archaeology: issues and case studies* (ed. M. J. O'Brien), pp. 10–20. Washington, DC: Society for American Archaeology Press.
- Lyman, R. L. & Harpole, J. L. 2002 A. L. Kroeber and the measurement of time's arrow and time's cycle. *J. Anthropol. Res.* **58**, 313–338.
- Lyman, R. L. & O'Brien, M. J. 1998 The goals of evolutionary archaeology: history and explanation. *Curr. Anthropol.* **39**, 615–652. (doi:10.1086/204786)
- Lyman, R. L. & O'Brien, M. J. 2000 Measuring and explaining change in artifact variation with clade-diversity diagrams. *J. Anthropol. Archaeol.* **19**, 39–74. (doi:10.1006/jaa.1999.0339)
- Lyman, R. L. & O'Brien, M. J. 2003 Cultural traits: units of analysis in early twentieth-century anthropology. *J. Anthropol. Res.* **59**, 225–250.
- Lyman, R. L., VanPool, T. L. & O'Brien, M. J. 2008 Variation in North American dart points and arrow points when one or both are present. *J. Archaeol. Sci.* **35**, 2805–2812. (doi:10.1016/j.jas.2008.05.008)
- Lyman, R. L., VanPool, T. L. & O'Brien, M. J. 2009 The diversity of North American projectile-point types, before and after the bow and arrow. *J. Anthropol. Archaeol.* **28**, 1–13. (doi:10.1016/j.jaa.2008.12.002)
- Mayr, E. 1973 *Populations, species, and evolution*. Cambridge, MA: Harvard University Press.
- Mesoudi, A. 2008 An experimental simulation of the 'copy-successful-individuals' cultural learning strategy: adaptive landscapes, producer–scrounger dynamics, and informational access costs. *Evol. Hum. Behav.* **29**, 350–363. (doi:10.1016/j.evolhumbehav.2008.04.005)
- Mesoudi, A. & O'Brien, M. J. 2008a The cultural transmission of Great Basin projectile-point technology I: an experimental simulation. *Amer. Antiq.* **73**, 3–28.
- Mesoudi, A. & O'Brien, M. J. 2008b The cultural transmission of Great Basin projectile-point technology II: an agent-based computer simulation. *Amer. Antiq.* **73**, 627–644.

- Mesoudi, A. & O'Brien, M. J. 2008c The learning and transmission of hierarchical cultural recipes. *Biol. Theory* **3**, 63–72. (doi:10.1162/biot.2008.3.1.63)
- Mesoudi, A. & O'Brien, M. J. 2009 Placing archaeology within a unified science of cultural evolution. In *Pattern and process in cultural evolution* (ed. S. J. Shennan), pp. 21–32. Berkeley, CA: University of California Press.
- Mesoudi, A. & Whiten, A. 2004 The hierarchical transformation of event knowledge in human cultural transmission. *J. Cogn. Cult.* **4**, 1–24. (doi:10.1163/156853704323074732)
- Neff, H. 1992 Ceramics and evolution. In *Archaeological method and theory* (ed. M. B. Schiffer), vol. 4, pp. 141–194. Tucson, AZ: University of Arizona Press.
- Nettle, D. 2006 Language: costs and benefits of a specialized system for social information transmission. In *Social information transmission and human biology* (eds J. K. Wells, S. Strickland & K. Laland), pp. 137–152. Boca Raton, FL: CRC Press.
- O'Brien, M. J. & Lyman, R. L. 2000 *Applying evolutionary archaeology: a systematic approach*. New York, NY: Kluwer Academic/Plenum.
- O'Brien, M. J. & Lyman, R. L. 2002 The epistemological nature of archaeological units. *Anthropol. Theory* **2**, 37–57. (doi:10.1177/1463499602002001287)
- O'Brien, M. J., Darwent, J. & Lyman, R. L. 2001 Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the southeastern United States. *J. Archaeol. Sci.* **28**, 1115–1136. (doi:10.1006/jasc.2001.0681)
- O'Brien, M. J., Lyman, R. L., Saab, Y., Saab, E., Darwent, J. & Glover, D. S. 2002 Two issues in archaeological phylogenetics: taxon construction and outgroup selection. *J. Theor. Biol.* **215**, 133–150. (doi:10.1006/jtbi.2002.2548)
- O'Brien, M. J., Lyman, R. L., Collard, M., Holden, C. J., Gray, R. D. & Shennan, S. J. 2008 Transmission, phylogenetics, and the evolution of cultural diversity. In *Cultural transmission and archaeology: issues and case studies* (ed. M. J. O'Brien), pp. 77–90. Washington, DC: Society for American Archaeology Press.
- Petroski, H. 1992 *The evolution of useful things*. New York, NY: Vintage Books.
- Pocklington, R. & Best, M. L. 1997 Cultural evolution and units of selection in replicating text. *J. Theor. Biol.* **188**, 79–87. (doi:10.1006/jtbi.1997.0460)
- Prohaska, J. S. & Stadler, P. F. 2008 Genes. *Theory Biosci.* **127**, 215–221. (doi:10.1007/s12064-008-0025-0)
- Schiffer, M. B. 1972 Archaeological context and systemic context. *Amer. Antiq.* **37**, 156–165. (doi:10.2307/278203)
- Schiffer, M. B. 1996 Some relationships between behavioral and evolutionary archaeologies. *Amer. Antiq.* **61**, 643–662. (doi:10.2307/282009)
- Schiffer, M. B. 2005 The devil is in the details: the cascade model of invention processes. *Amer. Antiq.* **70**, 485–502. (doi:10.2307/40035310)
- Schiffer, M. B. & Skibo, J. M. 1987 Theory and experiment in the study of technological change. *Curr. Anthropol.* **28**, 595–622. (doi:10.1086/203601)
- Schumpeter, J. A. 1934 *The theory of economic development: an inquiry into profits, capital, credit, interest, and the business cycle*. Cambridge, MA: Harvard University Press.
- Shennan, S. J. 2002 Learning. In *Darwin and archaeology: a handbook of key concepts* (eds J. P. Hart & J. E. Terrell), pp. 183–200. Westport, CT: Greenwood Press.
- Shennan, S. J. 2008 Canoes and cultural evolution. *Proc. Natl Acad. Sci. USA* **105**, 3175–3176. (doi:10.1073/pnas.0800666105)
- Shennan, S. J. & Wilkinson, J. R. 2001 Ceramic style change and neutral evolution: a case study from Neolithic Europe. *Amer. Antiq.* **66**, 577–593. (doi:10.2307/2694174)
- Simon, H. A. 1962 The architecture of complexity. *Proc. Amer. Phil. Soc.* **106**, 467–482.
- VanPool, T. L. 2003 Explaining changes in projectile point morphology: a case study from Ventana Cave, Arizona. PhD thesis, Department of Anthropology, University of New Mexico, Albuquerque, NM.
- VanPool, T. L. & VanPool, C. S. 2003 Agency and evolution: the role of intended and unintended consequences of action. In *Essential tensions in archaeological method and theory* (eds T. L. VanPool & C. S. VanPool), pp. 89–114. Salt Lake City, UT: University of Utah Press.
- Weiss, K. M. 1990 Duplication with variation: metameric logic in evolution from genes to morphology. *Amer. J. Phys. Anthropol.* **33**, 1–23. (doi:10.1002/ajpa.1330330503)
- Williams, G. C. 1992 *Natural selection: domains, levels, and challenges*. New York, NY: Oxford University Press.
- Williams, P. A. 2002 Of replicators and selectors. *Q. Rev. Biol.* **77**, 302–306. (doi:10.1086/341995)
- Wimsatt, W. C. 1999 Genes, memes and cultural heredity. *Biol. Phil.* **14**, 279–310. (doi:10.1023/A:1006646703557)