Metadata of the article that will be visualized in OnlineFirst

1	Article Title		**Five Misunderstandings About Cultural Evolution**
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29		e-mail	
30		Received	
31	Schedule	Revised	
32		Accepted	
33	Abstract		Recent debates about memetics have revealed some widespread misunderstandings about Darwinian approaches to cultural evolution. Drawing from these debates, this paper disputes five common claims: (1) mental representations are rarely discrete, and therefore models that assume discrete, gene-like particles (i.e., replicators) are useless; (2) replicators are necessary for cumulative, adaptive evolution; (3) content-dependent psychological biases are the only important processes that affect the spread of cultural representations; (4) the "cultural fitness" of a mental representation can be

EDITOR'S PROOF

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34	Keywords separated by ' - '	Dual inheritance theory - Memes - Cultural evolution - Epidemiology of representations - Cultural transmission - Replicators
35	Foot note information	

Five Misunderstandings About Cultural Evolution   4

Joseph Henrich · Robert Boyd · Peter J. Richerson   5

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Recent debates about the utility of "memes" have revealed some fundamental   23
misunderstandings about the nature of cultural evolution. Memeticists and their   24
many critics seem to share the view that evolutionary principles can only be applied   25
to cultural evolution if culture can be thought of as arising from the transmission of   26

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gene-like replicators (Atran 2001; Blackmore 1999; Dennett 1995). The memeticists 27
believe that such particles (or at least close approximations) exist, and thus 28
Darwinian reasoning—which has proven so useful in biology—can be applied to 29
culture. Their critics argue that replicating particles do not exist, and therefore, that it 30
is inappropriate to apply Darwinian ideas to culture. While we think that culture is 31
clearly a Darwinian process (Mesoudi et al. 2004, 2006b), we argue that both camps 32
have been misguided by an overly enthusiastic analogy between genes and culture. 33

Because much of culture can be understood in the most general sense as 34
information stored in human brains—information that got into those brains by 35
various mechanisms of social learning—we think that population-dynamic concepts 36
and evolutionary models are extremely useful for understanding how such processes 37
work. *But,* and this is a big one, we maintain that constructing appropriate models of 38
cultural evolution demands that close attention be paid to the psychological and 39
social processes involved. From this broader approach, both the memeticists and 40
their critics labor under a number of recurrent misunderstandings about cultural 41
evolution. Here we focus on these five: 42

1. Mental representations are rarely discrete, and therefore models that assume 43
   discrete, gene-like particles (i.e., replicators) are useless (Atran 2001). 44
2. Replicators are necessary for cumulative, adaptive evolution (Dawkins 1976, 45
   1982). 46
3. Content-dependent psychological biases are the only important processes that 47
   affect the spread of cultural representations (Sperber 1996). 48
4. The "cultural fitness" of a mental representation can be inferred from its 49
   successful transmission through the population. 50
5. Selection can only occur if the sources of variation are random (Pinker 1997). 51

These assertions are often used to dismiss whole categories of thinking about 52
cultural evolution. For example, some anti-memeticists have suggested that if there 53
are no cultural replicators, or if selection requires random variation, researchers 54
interested in the distribution of representations can ignore cultural evolutionary 55
models that assume discrete traits (Atran 2001; Boyer 1994). Or, as some 56
memeticists have suggested, if cultural replicators exist and are operating in 57
cumulative evolution, one can ignore a lot of complicated mathematical theorizing— 58
it's just natural selection, after all (Blackmore 1999; Dennett 1995). However, none 59
of these claims is correct. In the rest of this paper, we will try to convince you of 60
these facts. 61

Discrete Replicator Models of Cultural Inheritance can be Useful Even 62
if Mental Representations are Never Discrete 63

A great deal of work on cultural evolution assumes that cultural traits can be 64
modeled as discrete, gene-like entities that are faithfully transmitted from one 65
individual to another. Memeticists like Blackmore (1999) and Aunger (2002) believe 66
cultural representations or, as they prefer, *memes* must be particulate for cumulative 67
cultural change to occur. Cultural evolutionary theorists (e.g., Boyd and Richerson 68
1995; Cavalli-Sforza and Feldman 1981; Henrich and Boyd 1998; Rogers 1989) 69

have devoted much effort analyzing models of cultural evolution in which cultural traits are assumed to be discrete—although it is sometimes overlooked that these theorists have also spent a substantial amount of effort analyzing the evolution of continuous (non-discrete) cultural traits.

Cognitive anthropologists have criticized such "replicator approaches," arguing that such thinking is at variance with two observations. First, Atran (2001, 2002) has suggested that there is no evidence that the mental representations that underpin cultural traits are discrete, gene-like entities. Instead, he argues that mental representations are continuously graded entities. Second, Sperber (1996), Atran (2001), and Boyer (1999) emphasize that, unlike genes, ideas are not transmitted intact from one brain to another. Instead, the mental representations in one brain generate observable behavior, a "public representation" in Sperber's terminology. Someone else then observes this public representation, and then (somehow) infers the underlying mental representation necessary to generate a similar public representation. The problem is that there is no guarantee that the mental representation in the second brain is the same as it is in the first. Any particular public representation can potentially generate an infinite number of mental representations in other minds. Mental representations will be replicated from one brain to another only if most people induce a unique mental representation from a given public representation. Moreover, inferential processes often systematically transform mental representations, so that unlike genetic transmission, cultural transmission is highly biased toward particular representations. Following Sperber (1996), we call the representations favored by processes of psychological inference (including storage and retrieval) "cognitive attractors."[1]

While the nature of the cognitive processes that give rise to social learning are very much a matter of debate (e.g., Rosenthal and Zimmerman 1978; Tomasello 1996; Whiten 2000), we think it is quite likely that the general picture painted by Sperber, Boyer, and Atran is correct—cultural transmission does not involve the accurate replication of discrete, gene-like entities. Nonetheless, we also believe that models which assume discrete replicators that evolve under the influence of natural-selection-*like* forces can be useful. In fact, we think such models are useful *because* of the action of strong cognitive attractors during the social learning.

The reason is simple: cognitive attractors will rapidly concentrate the cultural variation in a population. Instead of a continuum of cultural variants, most people will hold a representation near an attractor. If there is only one attractor, it will dominate. However, if, as seems likely in most cases, attactors are many, other selective forces will then act to increase the frequency of people holding a representation near one attractor over others. Under such conditions, even weak selective forces ("weak" relative to the strength of the attractors) can determine the final distribution of representations in the population.

Henrich and Boyd (2002) analyze a simple mathematical model to show that this verbal reasoning is cogent. In this paper we represent each individual's mental

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[1] In recent years our views and those of Sperber, Atran, and Boyer have largely converged. However, perhaps owing to their important contributions on numerous fronts, a legacy of published claims about the problems with formal models and the nature of cultural traits continues to sow confusion among many, especially those not well equipped to digest mathematical models.

representation as a numerical value (x) between zero and one. For example, x might represent an individual's beliefs about the moon. Individuals with $x=0$ perceive the moon as a self-aware, conscious entity with goals, emotions, and motivations—thus the moon's behavior can be understood using folk psychology (Leslie 1994). In contrast, individuals with $x=1$ see the moon as simply a big rock, lacking goals, consciousness, and emotions. These individuals attribute the moon's color, shape, and movement to the effects of non-agentic interactions with light and the gravity of other mindless bodies, governed by physical laws that operate throughout the Universe. Now, it is possible to imagine moon-concepts that mix these poles ($0 \leq x \leq 1$). One could believe, for example, that the moon's movement and shape are out of its control (governed by physical laws), while its color or hue expresses its mood, which in turn influences the weather. Or, perhaps the moon's color is 23% controlled by its emotions and 77% controlled by the laws of light refraction. One might also believe that on Tuesdays and Thursdays the moon is a goal-oriented agent; on Mondays, Wednesdays, and Fridays the moon is a big rock; and on the weekends these two alternate minute by minute. Such beliefs might seem odd to us because they violate intuitive expectations, which is why cognitive attractors might transform them. In contrast to intermediate concepts (x values), $x=1$ or 0 is "easier to think." The formal model described here uses a one-dimensional representation of x, but this easily extends to the n dimensions needed to capture the above example.

Individuals in the model acquire their mental representations by observing the behavior of others. Two cognitive mechanisms affect this learning process. First, *inferential transformation* captures the manner in which cognitive processes of acquisition, storage, and retrieval alter mental representations in ways to favor some representations over others—cognitive attactors. Because the two extreme represen- tations—"moon as person" and "moon as rock"—are easier to think, they act as cognitive attractors in our example. Individuals who observe behaviors that result from intermediate representations tend to infer mental representations closer to one of the two attractors. The second process, *selective attention*, captures the tendency for individuals to pay particular attention to some individuals more than others. For example, it could be that in a modern environment, where the representations favored by science are prestigious, people who hold the "moon as rock" representation are more successful than those who hold the alternative, and thus they attract more attention (and are more likely to be learned from). Finally we assume the effects of inferential transformation are *much stronger* than the effects of selective attention.

Figure 1 shows what happens to the distribution of mental representations. In the underlying simulation, we assumed every mental representation is equally common initially (this has no impact on the results). The effects of inferential transformation dominate the early part of the trajectory, rapidly causing almost everyone to have a representation close to one of the two attractors. Once everyone is clustered around one of the two attractors, the rest of the trajectory is dominated by the effects of selective attention. In Henrich and Boyd (2002) we showed analytically that, as long as there are multiple attractors, the resulting population dynamics and the final distribution of mental representations are *closely approximated by a discrete-trait replicator dynamics model* in which the discrete traits are the strong attractor locations. This result is confirmed by the simulations results shown in Fig. 1.
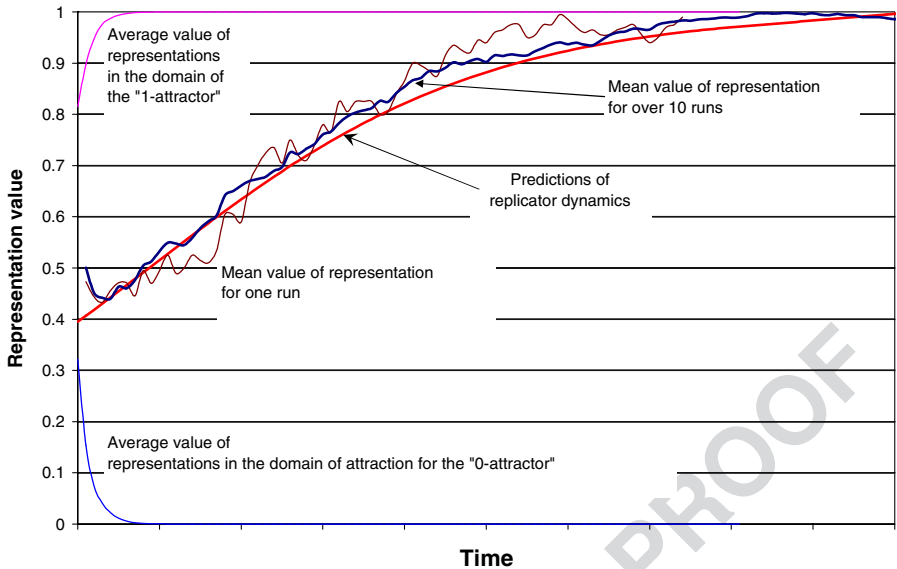
Fig. 1 Results from the simulation model described in the text. The two strong cognitive attractors are located at 1 and 0 (along Representation value). The overall evolution of the population is well approximated by a discrete model in which only weak selective forces are present

Two conclusions are important here: First, the selective processes (i.e., paying 159 attention to certain individuals) that generate cumulative adaptive evolution do *not* 160 depend on replication, fidelity, or longevity. This model shows that a replicator- 161 approximating process can arise and lead to cumulative adaptation even when 162 representations are non-discrete and are transformed during *every* acquisition. You 163 do not need to assume gene-like replicators exist to deploy replicator dynamics. 164 Second, we showed that the *stronger* the inferential transformations, the *better* the 165 replicator-dynamics approximation. Therefore, contrary to the common assumption 166 that a rich cognitive architecture relegates the selective process to a limited 167 importance, we showed that such assumptions imply that selective processes will be 168 critical to understanding the epidemiology of representations. 169

The above claims should *not* be interpreted as asserting that understanding 170 cognitive attractors and our rich cognitive architecture is unimportant for 171 understanding cultural evolution. In the above model, it is the attractors that create 172 quasi-discrete representations for selective forces to act on. What the analysis does 173 show is that if one believes human cultural transmission is substantially influenced 174 by potent attractors and rich cognition, one must also recognize the potential 175 importance of selective forces (even weak ones) in influencing cultural evolutionary 176 outcomes and the potential utility of replicator models, even though actual mental 177 representations may not be discrete. 178

Claidiere and Sperber (2007) have clarified and extended the scope of the above 179 findings using additional simulations. Their exploration confirms that replicator 180 dynamics remains a good approximation even when (1) attractors are moderately 181 strong and (2) selective forces are not at their maximum at any of the attractors. In 182 this second situation, the strong attractors become replicator-like and the attractor- 183

replicator with the greatest impact on selective forces (e.g., that which most 184
increases success) ultimately spreads through the population in a process captured by 185
replicator dynamics. However, their analysis also emphasizes that adding substantial 186
noise (stochasticity) to the transmission process makes replicator dynamics a poor 187
approximation, although selective forces remain important in understanding the 188
evolutionary dynamics and final distribution of representations. Such situations 189
require the classical continuous-trait models of cultural transmission (Boyd and 190
Richerson 1985; Cavalli-Sforza and Feldman 1981). In the next section, we show 191
how natural selection has equipped learners to cut through such transmission noise 192
using conformist and blending algorithms, and we discuss how such learning biases 193
favor the emergence of cumulative adaptive cultural evolution. 194

Replicators are not Necessary for Cumulative, Adaptive Cultural Evolution 195

Much confusion about cultural evolution traces to Dawkins's (1976, 1982) argument 196
that discrete, accurately copied, long-lived "replicators" are necessary for cumula- 197
tive, adaptive evolution. Dawkins argues that self-replicating entities are a 198
requirement for cumulative evolution and must have the following characteristics: 199

Fidelity. The copying must be sufficiently accurate that even after a long chain 200
of copies the replicator remains almost unchanged. 201
Fecundity. At least some varieties of the replicator must be capable of 202
generating more than one copy of themselves. 203
Longevity. Replicators must survive long enough to affect their own rate of 204
replication. 205

This argument has been repeated and elaborated by Dennett (1995), Blackmore 206
(1999), Aunger (2002), among others, and has convinced many people that discrete, 207
gene-like particles are a requirement for adaptive cultural evolution. 208

While we agree that the existence of replicators is *sufficient* for cumulative 209
adaptive evolution, they are not necessary. Any process of cultural transmission that 210
leads to accurate replication of the average characteristics of the *population* will 211
work. Accurate replication at the level of the gene (or meme) will have this effect, 212
but accurate replication at the population level can arise for other reasons as well. 213
Here are two examples. 214

Henrich and Boyd (2002) analyze a discrete trait model with very inaccurate 215
transmission. They assume that there are two mental representations, A and B. As 216
before, mental representations are transmitted when one individual observes the 217
behavior of a second individual and attempts to infer the underlying mental 218
representation that gave rise to that behavior. Now, however, we assume that this 219
process is very inaccurate—individuals make the wrong inference with probability 220
m. Formally, m plays a role identical to mutation in a genetic model. Genes are 221
replicators because m is tiny, say 10^{-6}. Here we are going to assume that m is a big 222
number like 0.2. When $m=0.5$ there is no transmission at all, so $m=0.2$ represents 223
very low fidelity transmission. Thus, if nothing else were going on, cumulative 224
adaptive evolution would be extremely unlikely. However, we also assume that 225
individuals have a psychological propensity for *conformist transmission*, an 226

assumption that is both theoretically and empirically well grounded (see below). 227
Suppose that each learner selects *n* different individuals to learn from. For each 228
individual, the learners attempt to infer what the underlying mental representation is 229
(either A or B) but make an error with probability *m* for each inference. Based on 230
these inferences, they then adopt what they think is the most common representation 231
in their sample. For example, suppose a learner selects five individuals. Three of 232
these five hold mental representation A, and the remaining two hold B. If our learner 233
estimates all five accurately, he will adopt A. If he gets one of two holding B 234
incorrect (and the rest correct), he will still adopt A. But, if he gets one of the three 235
holding A wrong, he will adopt B. Our results show that conformist transmission 236
effectively corrects even large errors in transmission, even when the inferential/ 237
transmission channel is 60% noise. The reason for this is simple: errors have a 238
bigger effect on populations in which one mental representation is common than in 239
populations in which both mental representations have similar frequencies. However, 240
when one representation is common, the conformist effect is also stronger and thus 241
systematically corrects for the effect of errors. Although this model is limited to two 242
traits, there is no reason to suspect that the insights derived are similarly limited. 243
Conclusion: fidelity of replication is not required for cumulative adaptation. 244

Here is a second example. For more than 20 years cultural evolutionary theorists have 245
analyzed blending models of cultural evolution (e.g., Cavalli-Sforza and Feldman 1981; 246
Boyd and Richerson 1985:71–79). In such models, no mental representations are 247
replicated, but nonetheless cumulative evolution is possible. To see this, suppose that 248
in deciding what length to make his arrow, a hunter samples *n* models from a larger 249
population and adopts as his mental representation (his arrow length) the average of 250
the lengths of the *n* models. Suppose *n*=3, and the arrow lengths of the three models 251
are 16 cm, 20 cm, and 21 cm. This means the hunter adopts an arrow length of 19 cm. 252
Note, this 19-cm meme is *not* represented among the *n* individuals sampled—there is 253
no replication, fecundity, or longevity. If we further assume that in selecting their *n* 254
models, individual preferentially focus on the best hunters, and that proximity to the 255
optimal arrow length (say 20 cm) contributes to a hunter's success (on average), then 256
blending will generate adaptive evolution on arrow length. Laboratory experiments 257
involving incentivized decisions indicate that such success-biased blending processes 258
are likely a reasonable approximation for some form of cultural transmission 259
(McElreath et al. 2005; Mesoudi 2008; Offerman and Sonnemans 1998). 260

Neither of these mechanisms results in the same kind of relatively "frictionless" 261
adaptation as genetic replication. Highly accurate, unbiased, genetic replication 262
allows minute selective forces to generate and preserve adaptations over millions of 263
years. Error-prone cultural replication, even when "corrected" by a conformist bias, 264
imposes modest, but still significant forces on the cultural composition of the 265
population. Similarly, blending inheritance rapidly depletes the variation in a 266
population necessary for selective processes ~~like~~ prestige-biased transmission to 267
have an effect. But, because the inferential processes that underlie cultural 268
transmission are noisy, it is likely that they can maintain lots of variation. However, 269
this also means that they are likely to create evolutionary forces that act to change 270
the mean, and thus compete with selective forces. 271

The contrasts between cultural and genetic evolution provide more reasons, not 272
fewer, for analyzing formal cultural evolutionary models. The forces that are 273

important for understanding cultural evolution (such as non-random errors and 274
blending) are likely not the same forces that are important for understanding genetic 275
evolution. Population-based models of cultural evolution can be useful, but they 276
have to pay careful attention to these differences. 277

Content-Dependent Psychological Biases are not the Only Processes that Affect the Spread of Cultural Traits

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Content bias, or how the content of memes "fit into" the cognitive structure of 280
human minds, is not the only important process for understanding cultural evolution 281
(Boyer 1994, 1999).[2] Genetically maladaptive memes about religion, food taboos, 282
ghosts, and so on, may readily spread because of their ability to exploit aspects of 283
human psychology in ways that make them more likely to be acquired, stored, and 284
transmitted. However, summarizing evidence from across the social sciences, 285
Henrich and Gil-White (2001) show that humans are quite selective in picking the 286
individuals they will learn from, or be influenced by ("imitate," if you will). Human 287
psychology seems geared up to selectively extract useful (locally adaptive) 288
information from the individual(s) most likely to possess such information. Skill, 289
success, and prestige all make individuals substantially more likely to be learned 290
from, or imitated. This psychological propensity for "model selectivity" seems to 291
operate across most, if not all, domains of culture (Henrich and McElreath 2006; 292
Henrich and Henrich 2007), from dialects and word choice to political opinions, 293
suicide, food preferences and technical innovations (such as using fertilizer). The 294
classic literature on the diffusion of innovations (Rogers 1995) is a rich source of 295
examples. This means that a meme's mimetic fitness (vs. genetic fitness) will depend 296
jointly on how attractive its content is to human brains and how it affects an 297
individual's likelihood of being selected as a cultural model by other individuals. 298

Consider the following example. In a fishing village on an Indonesian island, an 299
old man is out fishing at night in small boat. The next morning he is found dead in 300
his boat, which is filled with a massive catch. A rumor begins to spread that a 301
demon-fish, common in local mythology, sucked out the man's soul because he was 302
fishing at night. Individuals who believe this rumor stop fishing at night (which is 303
often the most productive time to fish). For simplicity, we assume that individuals 304
either believe the meme, or not. The variable p gives the frequency of individuals in 305
this large village who believe the fish-demon has returned and do not fish at night. 306
From the meme's perspective, the relative mimetic fitness of the demon-fish belief is 307
$\omega_f = \alpha + \gamma$, while the relative mimetic fitness of not believing the rumor is $\omega_n = \alpha + \varphi$. 308
The parameter α is the baseline mimetic fitness, γ is the strength of the meme's 309
content bias, and φ is the cost to an individual who bears it in terms of their 310
likelihood of being selected as a cultural model by a learner. An individual's 311
likelihood of being selected as a model is affected because not-fishing at night means 312

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[2] Broadly, "content bias" refers to any situation in which a meme's representational content influences its likelihood of transmission. Such biases arise from the interaction of the representational content of the meme and human psychologies. While this includes reliably developing aspects of human psychology (e.g., incest aversion favoring favor ubiquitous oedipal narratives; Johnson and Price-Williams 1996), it also includes the "fit" between different memes, or different experiences and certain memes (cultural psychologies).

fewer fish to sell, and thus less extra money for clothing, sugar, house maintenance, throwing feasts, and the children's health needs—all of which may make one more likely to be selected as a cultural model. Putting these expressions into standard replicator dynamics gives us

$$\Delta p = p(1-p)[\gamma - \varphi]$$

where Δp is the change in the frequency of rumor believers. This equation, as it stands, tells us that there are two potential stable equilibria: either everyone will come to believe the fish-demon story and cease all night fishing, or the success costs of not fishing will dominate and the rumor will not be favored in the long run. Clearly, just because the demon-fish story is fun to tell, easy to remember, built on widely believed local mythologies, and interacts with innate inferential machinery in interesting ways (Boyer 2001) does not guarantee it will spread if possessing the belief makes one less likely to be selected as a cultural model.

The point of this example is to show that the human mind's tendency to focus attention preferentially on certain individuals (independent of mimetic content) means the usual approach to memetic reproduction is insufficient. It further means that whether a particular genetic-fitness-reducing meme can spread, and how far it will spread, depends on the details—the dynamics of which are best understood by formally modeling the social and psychological processes involved. No categorical claims based on hand-waving arguments about the relationship between genetic and mimetic fitness are likely to hold, as Rogers (1989) demonstrates. For example, just because something is transmitted "horizontally" within a generation tells us nothing the genetic adaptiveness of those memes. We should also note at this point that the appropriateness of tracking fitness from the perspective of the meme (assigning fitnesses to alternative memes) or to individuals (or groups) is merely a modeling convenience. For example, just as with genetic evolution, it is not "more correct" to view fitness in association with memes, individuals, or groups. As with genetic models, the above model can be fully derived from the perspective of individuals, rather than memes, by specifying the individual's tendency to transmit particular ideas, rather than from the meme's ability to transmit itself. Different fitness tracking systems may allow certain aspects of the problem to be studied more or less effectively, but they are all formally identical at some level (McElreath and Boyd 2007).

Successful Diffusion is not a Measure of Fitness

Authors who adopt the selfish meme concept often give us no causal idea of what actually bestows different "fitnesses" of alternative memes. How do we know whether a bit of a tune or a catch phrase is a fit meme? Often, it seems, only by asking whether the meme has successfully spread.

This is dangerous territory. Used in this way, natural selection is a useless, or even misleading, tautology. For example, a recessive gene causing a severe vision disorder called achromatopsia has spread to roughly 30% of the population on the Micronesian island of Pingelap. Sufferers of achromatopsia cannot see well under any circumstances, and they are especially disadvantaged in the bright sunlight of a

tropical island. Nonetheless, there is no doubt that this gene spread on Pingelap 356
because people who carried it had more descendants than those who didn't carry the 357
gene. If we were to infer the relative fitness of the achromatopsia and normal alleles 358
from this spread, we would conclude that the achromatopsia allele had higher fitness. 359
However, this doesn't mean that achromatopsia was favored by selection, because 360
the achromatopsia didn't *cause* their increased reproductive success. Rather, it seems 361
that the gene was carried by members of a chiefly lineage whose social position 362
allowed them to survive the aftermath of a severe typhoon that struck the island during 363
the 1700s—it likely spread by a combination of drift and a chance covariation with 364
social status. The same kinds of phenomena are likely at work in cultural evolution. 365
Otherwise-deleterious or unattractive ideas and practices often spread because they 366
happen to be statistically correlated with attractive individuals or successful groups. 367
Why did the English language rapidly spread across North America during the 368
eighteenth and nineteenth centuries? Certainly not because it is an intrinsically more 369
attractive mode of expression than Cherokee or Apache. Rather, it spread because it 370
happened to be associated with the military advantages, technological innovations, and 371
infectious diseases that allowed English speakers to conquer the native cultures of North 372
America. Similarly, the Western business suit has also spread across the world in the 373
twentieth century not, we conjecture, because the four-in-hand tie is intrinsically more 374
attractive than its many alternatives, but because it happens to be associated with the 375
economic and military prowess of the West. 376

Evolutionary biologists escape this circularity in defining fitness because they 377
have *independent* means of predicting which genetic variants are more fit. Peter and 378
Rosemary Grant's (1986) famous studies of the evolution of beak depth in 379
Galapagos finches illustrate how this works. During a severe drought, the birds 380
evolved stouter beaks. We know this change is due to selection because the 381
investigation showed that (1) large, tough seeds predominated during the drought, 382
(2) finches with stouter beaks were better able to crack larger seeds, and (3) beak 383
stoutness is heritable. Similarly, we know that the human pelvis was shaped by 384
selection because we understand the biomechanics of bipedal locomotion. 385

Evolutionary biologists are also in the habit of subdividing their concepts— 386
selection especially—to create a rather diverse family of sub-concepts. These include 387
classics like Darwin's two kinds of sexual selection as well as modern concepts like 388
frequency- and density-dependent selection. The reason is that experimentalists are 389
typically concerned, like the Grants, with concrete details. The concrete cases of 390
selection involve everything that happens to heritably varying organisms as their daily 391
lives unfold. An incredible variety of things can and do happen, and evolutionary 392
biologists collect similar ones together using a rough-and-ready taxonomy to cope 393
with the otherwise overwhelming diversity. Notice that we have been doing the same 394
thing with the psychological forces that affect the distribution of representations. 395
Attractors are different from conformity, and both are different from prestige-based 396
imitation (see Richerson and Boyd 2005:69 for a taxonomy of forces). 397

These principles should also apply to the study of memes. The rapid spread of the 398
New World's sweet potato throughout highland New Guinea during the 1700s is 399
easy to understand. Sweet potatoes have higher yields and grow at higher altitudes 400
than yams, the previous staple. People noticed these properties and avidly adopted 401
the new crop. Here we have a causal theory that links evolved psychology (people 402

like to be well fed) with the preference for one cultural variant over another. In many cases, however, it is difficult to predict which representations will spread because we do not understand much about the underlying psychological or ecological processes (but see, for example, Martindale 1975; Rogers 1995; Taylor 1996). Why do we like particular musical forms or literary devices? Why do some religious beliefs spread while others fail? Why do some religious beliefs spread in some groups (e.g., Christianity in Polynesia) even while they decline in their homelands (Christianity in Europe)?

Even for technological traits, there are many puzzles such as the fact that throughout New Guinea the idea of fletching arrows has never caught on, while just across the Torres Strait in Australia the idea of bows and arrows *en toto* never spread, or why the Tasmanians abandoned or never adopted bone tools, cold-weather clothing, barbed spears, and fishing during their ten thousand years of isolation (Henrich 2004). These questions are not unanswerable in principle, but meme theory, as it stands, seems ill-equipped to tackle them. We believe that constructing a full-fledged theory of cultural evolution requires considering a longish list of psychological, social, and ecological processes that interact to generate the differential "fitness" of cultural variants.

Selection Does not Require Random Variation

Many people have argued that selection cannot affect cultural evolution because cultural variation, unlike genetic mutations, is not based on random copying errors. Instead, the argument goes, cultural changes are systematic, driven by attempts to innovate or by the cognitive machinery by which individuals make inferences about the beliefs of others, and this means selective processes are not important. For example, Pinker (1997:209) makes this argument in the following passage:

> A meme impels its bearer to broadcast it, and it mutates in some recipients: a sound of a word, or a phrase is randomly altered. Perhaps, as in Monty Python's *The Life of Brian*, the audience of the Sermon on the Mount mishears "Blessed are the peacemakers" as "Blessed are the cheesemakers." The new version is more memorable and comes to predominate in the majority of minds. It too is mangled by typos and speakos and hearos, and the most spreadable ones accumulate, gradually transforming the sequence of sounds. Eventually, they spell out "That's one small step for man, one giant leap for mankind." I think you'll agree that this is not how cultural change works. A complex meme does not arise by the retention of copying errors.

We will agree that Pinker provides a pithy example showing why selection isn't everything. The problem is that he then concludes that it is nothing. If selection does not explain complex design in cultural evolution *by itself*, then it is of no importance. This is mistaken. There is no doubt that, as people acquire and modify beliefs, ideas, and values, the variation that is generated can be highly non-random, and these non-selective processes shape cultural variation. But so what? Selection occurs *anytime* there is heritable variation that affects survival or reproduction (transmission). It does not matter whether the variation is random. In cultural evolution, unlike genetic

evolution, natural selection may compete with other important directional processes created by human psychology. In any given case, whether one or another force will predominate is an empirical issue.

We also think that Pinker overestimates the importance of conscious problem-solving in innovation (also see Mesoudi et al. 2006a, b). Pinker (1997:209) writes that innovation occurs when "some person knuckles down, racks his brain, musters his ingenuity, and composes or writes or paints or invents something." This pervasive "Myth of the Heroic Inventor," as scholars of the history of technology called it (Basalla 1988; Diamond 1997), fails to sufficiently recognize (1) the central importance in the history of science and technology of luck, happenstance, and recombination, and (2) that most great inventors actually make only incremental additions to the existing or emerging capacities or understandings of their times. We leave a complete defense of these views to the existing historical works that have confronted this in detail (e.g., Basalla 1988; Diamond 1997; Hager 2007; Meyers 2007; Sneader 2005; Williams 1987) but provide five illustrative examples here.

1. James Watt "invented" the steam engine in 1769 after repairing a Newcomen steam engine constructed 57 years earlier. This engine was modified from Thomas Savery's design of 1698, the components of which trace to seventeenth-century Europe and thirteenth-century China. After dissecting the steam engine, famed historian Joseph Needham concluded that "No single man was the father of the steam engine; no single civilization either" (quotation from Basalla 1988).

2. The discovery of penicillin, and the dawn of the age of antibiotics, began when Alexander Fleming returned from holiday to find that his Petri dishes had been contaminated with mold. Seeking to clean up his chronically messy laboratory, he dumped the whole batch of dishes into a laboratory sink where they sat until he retrieved an unsubmerged disk to show a visitor. He happened to notice that while the mold was growing fine, the staph was dead. Penicillin was discovered as a result of luck and messiness.

3. Establishing the germ theory of disease required obtaining pure cultures of bacteria. In the nineteenth century, dozens of researchers were trying to figure out how to do this, without success. Robert Koch solved the problem when, while cleaning up his laboratory, he ran across a half of a boiled potato that had been carelessly left for a few days. Koch noticed the growth of discrete reddish dots at different places on the white potato and realized that one needed a solid, not a liquid, medium. He went on to firmly link specific pathogens with specific diseases, and to develop his four postulates for making this link based on cultivating a pure culture (Hager 2007). None of this could have occurred without the carelessly left potato.

4. Edison's "invention" of the incandescent light bulb only improved on many other such bulbs patented between 1841 and 1878 by a wide variety of inventors. Of course, if you are from Britain, Sir Joseph W. Swan is the inventor of the incandescent light bulb, whereas if you are from Russia, it's A. N. Lodygin (Conot 1979).

5. The Wright brothers' invention of the airplane built on existing manned gliders and unmanned powered airplanes. Their contribution was a recombinant of existing lines of technology (Diamond 1997).

Pinker errs in conflating exemplars of a work within a tradition with the tradition itself. Mozart composed innovative symphonies but he did not invent the symphony. Watt built innovative steam engines but he did not invent the steam engine.

We emphasize, however, that even if Pinker's view of innovation is correct, this does not mean (1) that selective forces cannot operate (since they require only variation, not *random* variation), and (2) that cultural evolution cannot be understood and modeled as a population process. What is important is that one has to construct specific models of *cultural* evolution, based on what is known of the underlying individual-level decision processes.

Charting a Course: Foundations for a Unified Science of Cultural Phenomena

In this final section we briefly sketch some of the essential components for a successful research program in cultural evolution and human behavior. We do not strive here to take a full accounting of all the important and necessary domains of inquiry (see Mesoudi et al. 2006b; Richerson and Boyd 2005), but only to highlight certain areas.

Rich Psychology

Two key components of psychology are of most direct relevance to understanding cultural evolution. The first involves understanding how cognition directs social learning toward particular individuals or ideas, beliefs, and so on, and how cognition extracts, or makes use of, the socially available information in a population. For example, evolutionary theory applied to social learning predicts that individuals should use model-based cues of skill, success, health, prestige, and self-similarity (e.g., sex and ethnicity) to figure out who to pay particular attention to for cultural learning (Boyd and Richerson 1985: chapter 8; Henrich and McElreath 2006; Henrich and Gil-White 2001). Similarly, theory also indicates that individuals should, in the absence of decisive social information from skilled (or successful, etc.) individuals or high-quality environmental information, rely on copying the majoritarian behavior—conformist transmission (Boyd and Richerson 1985: chapter 7; Henrich and Boyd 1998). Recent work has also suggested that, to avoid exploitation during cultural learning by models that seek to convey one representation while actually holding another, natural selection has equipped learners to rely on inferentially potent displays when acquiring memes that can be cheaply transmitted using verbal (or other symbolic) communication. Inferentially potent displays are actions that would likely only be performed by those models who actually hold (believe in) the memes they have expressed verbally (Henrich 2007). Both experimental and field evidence support these different theoretical predictions to varying degrees (Henrich and Henrich 2007).

The second component of psychology involves inferential, storage, and recall processes (Sperber 1996). How do cognitive processes organize and interpret information coming in from the social world? The idea here is to open the black box of imitation. In acquiring something like tool-making skill, how do individuals decompose a continuous stream of behavior into steps? How do individuals infer the

goals of the individual they attempt to imitate? How do the building blocks of 535
inference (e.g., theory of mind, naïve physics, folk biology) shape the inferences 536
individuals draw from observing these selected cultural models (Atran 1998, 2002; 537
Boyer 2001)? Given that public representations of underlying mental representations 538
are nearly always incomplete, how do inferential processes reconstruct mental 539
representations? How do inference processes deal with the range of different public re- 540
presentations produced by a single individual? How do culturally acquired representations 541
influence subsequent learning processes? 542

Population Processes 543

Knowledge of psychological mechanisms and cognitive structures is insufficient to 544
predict the epidemiology of cultural representations in most cases. Understanding 545
the population-level consequences of individuals, each possessing learning psychol- 546
ogies and interacting, requires the construction of formal cultural evolutionary 547
models. Even with simple psychological assumptions such models have proven 548
useful in understanding a wide range of phenomena (Boyd and Richerson 1985), 549
including (1) the origins of ethnic groups (Boyd and Richerson 1987; McElreath 550
et al. 2003), (2) evolution of economic specialization and the emergence of large- 551
scale cooperation (Boyd and Richerson 1992; Henrich and Boyd 2001, in press; 552
Panchanathan and Boyd 2004), (3) conditions for technological accumulation 553
(Henrich 2004; Shennan 2001), (4) emergence of a culture of honor (McElreath 554
2003), and (5) dynamics of the diffusion of innovations (Henrich 2001). 555

Cobbling up from psychological mechanisms to population processes is also 556
increasingly informing research on larger-scale cultural evolutionary processes. 557
Important work arising from evolutionary archaeology and behavioral ecology is 558
exploring how to use archaeological, ethnographic, and historical data to reconstruct 559
cultural lineages, assess linkages between different cultural traits, recognize adaptive 560
processes, and predict migration patterns (Bentley et al. 2007; Collard et al. 2006; 561
Eerkens and Lipo 2005; Lipo et al. 2006; Shennan in press). 562

Ecological-Economic Processes 563

The fitness of cultural variants may be determined entirely by psychological forces, 564
but more commonly different variants have consequences in the environments in 565
which people live. These consequences will often interact with psychological forces 566
(Baum 2005). People will find some cultural variants useful in one environment and 567
another useful in a different environment; reinforcement at the individual level will 568
create content-based biases favoring different variants in different environments. 569
Similarly, economic success often translates into prestige and model-based cultural 570
transmission biases, and different activities lead to economic successes in different 571
economies. But residual effects not accounted for by psychology are also liable to be 572
common. The many forms of natural selection *are* candidates to influence cultural 573
evolution and to produce cultural fitnesses that *are* close analogs to genetic fitnesses. 574
But these effects are importantly different from those generated by psychological 575
processes (Richerson and Boyd 2005). 576

Evolutionary and Culture-Gene Coevolutionary Origins   577

What are the evolutionary origins of the psychological capacities that give rise to   578
cultural evolution? Understanding the origins of the psychological mechanisms   579
discussed above goes hand-in-hand with hypothesizing what the details of those   580
mechanisms might be. To date, we and our colleagues have explored the evolution   581
of, and trade-offs regarding, parent-offspring transmission (McElreath and Strimling 582
in press), conformist transmission, prestige-biased transmission, and ethnic biases   583
(McElreath et al. 2003). We have also sought to understand why human-like cultural   584
and cognitive abilities are so rare in nature (Boyd and Richerson 1996).   585

In our view, one of the most important, and least explored, avenues of   586
evolutionary inquiry in human behavior and psychology are the "Baldwinian"   587
processes that arise from the interaction of cultural and genetic transmission.   588
Cultural traditions manifestly change the environments faced by human genes   589
(Durham 1991; Henrich and Henrich 2007; Laland et al. 2000; McElreath et al.   590
2003; Richerson and Boyd 1998, 2000, 2005). This opens novel evolutionary   591
pathways that are not available to species that are not heavily reliant on social   592
learning for acquiring phenotype (Mesoudi and Laland 2007). Human teeth, lack of   593
body hair, digestive processes, malaria resistance, and manual dexterity certainly   594
cannot be understood without realizing that genes responded to the cultural   595
transmission of the use of clothing, fire, agriculture, and tools (Wrangham et al.   596
1999). Similarly, culture has likely shaped cognition, both directly and indirectly by   597
changing the selective environment faced by genes. Despite numerous physiological   598
examples ~~and~~ gene-culture coevolution and a rock-solid theoretical foundation,   599
mainstream evolutionary psychology (e.g., Pinker 1997; Tooby and Cosmides 1992)   600
has largely ignored gene-culture coevolution.   601

Methodological Pluralism   602

The theoretical and empirical demands of this program exceed those available in any   603
one discipline. Theoretically, tools have been drawn from population genetics,   604
communication theory, epidemiology, learning theory, statistics, and evolutionary   605
game theory. In the future, insight may come from fields as diverse as information   606
theory and statistical mechanics. Empirically, our program demands the integration   607
of both observational and experimental data from human biology, psychology,   608
economics and anthropology (e.g., Henrich et al. 2004; Mesoudi 2008), as well as   609
studies of processes of long-term change from paleoecology, history, and   610
archaeology (e.g., Henrich 2004; Richerson and Boyd 2005; Shennan 2003, in   611
press).   612

Conclusion   613

We believe that the Darwinian approach differs from traditional social sciences   614
approaches in ways that are not yet fully appreciated. All five misunderstandings we   615
describe here have a common theme. They result from a tendency to think   616

categorically rather than quantitatively. Take the meme controversy. The disputants take the main issue to be whether or not culture is highly analogous to genes. If so, then their evolution is to be explained by Darwinian fitness; if not, Darwinism is useless. If we are correct, this debate is a red herring. The proper approach is to recognize that the analogy between genes and culture is quite loose, and to build up a theory of cultural evolution that takes into account the actual properties of the cultural system (Mesoudi et al. 2006b). Culture has a much richer array of psychological processes with population level consequences than is the case for genes. But neither particular psychological forces nor the integrated effect of all such forces in any way rules out a role for natural selection, or vice versa. The matter turns entirely on how the numbers work out in the particular case at hand. Because its most complex examples are confined to our species, culture can hardly prove to be as diverse in its outcomes as organic evolution. However, we expect that it will turn out to be a baroque system. The balance of evolutionary forces on culture no doubt changed with the advent of mass literacy and mass media; no doubt economically important traits differ from symbolic ones; and so forth. To paraphrase something J. B. S. Haldane is supposed to have said: Culture is not only queerer than we imagine but, as of this moment, queerer than we can imagine.

References

Atran, S. (1998). Folk biology and the anthropology of science: cognitive universals and cultural particulars. *Behavioral and Brain Sciences*, *21*, 547–609.

Atran, S. (2001). The trouble with memes: inference versus imitation in cultural creation. *Human Nature*, *12*, 351–381.

Atran, S. (2002). *The religious landscape*. Cambridge: Cambridge University Press.

Aunger, R. (2002). *The electric meme: A new theory of how we think*. New York: Free Press.

Basalla, G. (1988). *The evolution of technology*. New York: Cambridge University Press.

Baum, W. M. (2005). *Understanding behaviorism: Behavior, culture, evolution*. Oxford: Blackwell.

Bentley, R. A., et al. (2007). Regular rates of popular culture change reflect random copying. *Evolution and Human Behavior*, *28*, 151–158.

Blackmore, S. (1999). *The meme machine*. Oxford: Oxford University Press.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.

Boyd, R., & Richerson, P. J. (1987). The evolution of ethnic markers. *Cultural Anthropology*, *2*, 27–38.

Boyd, R., & Richerson, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology & Sociobiology*, *13*, 171–195.

Boyd, R., & Richerson, P. J. (1995). Why does culture increase adaptability? *Ethology & Sociobiology*, *16*, 125–143.

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, *88*, 77–93.

Boyer, P. (1994). *The naturalness of religious ideas*. Berkeley: University of California Press.

Boyer, P. (1999). Cognitive tracks of cultural inheritance: how evolved intuitive ontology governs cultural transmission. *American Anthropologist*, *100*, 876–889.

Boyer, P. (2001). *Religion explained: The evolutionary origins of religious thought*. New York: Basic Books.

Cavalli-Sforza, L. L., & Feldman, M. (1981). *Cultural transmission and evolution*. Princeton: Princeton University Press.

Claidiere, N., & Sperber, D. (2007). The role of attraction in cultural evolution. *Journal of Cognition and Culture*, *7*, 89–111.

Collard, M., Shennan, S. J., & Tehrani, J. J. (2006). Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evolution and Human Behavior*, *27*, 168–184.

Conot, R. E. (1979). *A streak of luck*. New York: Seaview Books (distributed by Simon and Schuster).

Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford Unversity Press.

Dawkins, R. (1982). *The extended phenotype*. Oxford: Oxford University Press.

Dennett, D. (1995). *Darwin's dangerous idea*. London: Penguin Press.

Diamond, J. M. (1997). *Guns, germs, and steel: The fates of human societies*. New York: W.W. Norton & Co.

Durham, W. H. (1991). *Coevolution: Genes, culture, and human diversity*. Stanford: Stanford University Press.

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 Anthropological Archaeology*, *24*, 316–334.

Grant, P., & Grant, R. (1986). *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.

Hager, T. (2007). *The demon under the microscope*. New York: Three Rivers Press.

Henrich, J. (2001). Cultural transmission and the diffusion of innovations: adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change and much of sociocultural evolution. *American Anthropologist*, *103*, 992–1013.

Henrich, J. (2004). Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *American Antiquity*, *69*, 197–214.

Henrich, J. (2007). The evolution of costly displays, cooperation, and religion: Inferentially potent displays and their implications for cultural evolution. Economics and Evolution working paper series. Evolutionary Economics Group, MPI Jena, Germany. <Available at https://papers.econ.mpg.de/evo/discussionpapers/2007–21.pdf>

Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, *19*, 215–242.

Henrich, J., & Boyd, R. (2001). Why people punish defectors: weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*, *208*, 79–89.

Henrich, J., & Boyd, R. (2002). On modeling cultural evolution: why replicators are not necessary for cultural evolution. *Journal of Cognition and Culture*, *2*(2), 87–112.

Henrich, J, & Boyd, R. (In press). Division of labor, economic specialization, and the evolution of social stratification. *Current Anthropology*, in press.

Henrich, J., & Gil-White, F. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*, 165–196.

Henrich, J., & McElreath, R. (2006). Dual inheritance theory: The evolution of human cultural capacities and cultural evolution. In R. Dunbar, & L. Barrett (Eds.) *Oxford Handbook of evolutionary psychology* (pp. 555–570). Oxford: Oxford University Press.

Henrich, J. et al. (Eds.) (2004). Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies. Oxford: Oxford University Press.

Henrich, N. S., & Henrich, J. (2007). *Why humans cooperate: A cultural and evolutionary explanation*. Oxford: Oxford University Press.

Johnson, A. W., & Price-Williams, D. R. (1996). *Oedipus ubiquitous: The family complex in world folk literature*. Stanford: Stanford University Press.

Laland, K. N., Odling-Smee, J., & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, *23*, 131–175.

Leslie, A. M. (1994). ToMM, ToBY, and agency: Core architecture and domain specificity. In L. A. Hirschfeld, & S. A. Gelman (Eds.) *Mapping the mind: Domain specificity in cognition and culture* (pp. 119–148). Cambridge: Cambridge University Press.

Lipo, C. P. (Ed.) (2006). *Mapping our ancestors*. Piscataway, NJ: Aldine Transaction.

Martindale, C. (1975). *Romantic progression: The psychology of literary history*. Halsted: Washington Hemisphere.

McElreath, R. (2003). Reputation and the evolution of conflict. *Journal of Theoretical Biology*, *220*, 345–357.

McElreath, R., & Boyd, R. (2007). *Modeling the evolution of social behavior*. Princeton: Princeton University Press.

McElreath, R., & Strimling, P. (2008). When natural selection favors imitation of parents. *Current Anthropology*, in press.

McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology, 44*, 122–129.

McElreath, R., et al. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior, 26*, 483–508.

Mesoudi, A. (2008). The cultural transmission of Great Basin projectile technology: an experimental simulation. *American Antiquity, 73*, 3–28.

Mesoudi, A., & Laland, K. N. (2007). Culturally transmitted paternity beliefs and the evolution of human mating behaviour. *Proceedings of the Royal Society of London. B: Biological Sciences, 274*, 1273–1278.

Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Perspective: is human cultural evolution Darwinian? Evidence reviewed from the perspective of the Origin of Species. *Evolution, 58*, 1–11.

Mesoudi, A., Whiten, A., & Laland, K. N. (2006a). A science of culture: clarifications and extensions. *Behavioral and Brain Sciences, 29*, 366–383.

Mesoudi, A., Whiten, A., & Laland, K. N. (2006b). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences, 29*, 329–347.

Meyers, M. A. (2007). *Happy accidents: Serendipity in modern medical breakthroughs*. New York: Arcade.

Offerman, T., & Sonnemans, J. (1998). Learning by experience and learning by imitating others. *Journal of Economic Behavior and Organization, 34*, 559–575.

Panchanathan, K., & Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature, 432*, 499–502.

Pinker, S. (1997). *How the mind works*. New York: W. W. Norton.

Richerson, P., & Boyd, R. (1998). The evolution of ultrasociality. In I. Eibl-Eibesfeldt, & F. K. Salter (Eds.) *Indoctrinability, ideology and warfare* (pp. 71–96). New York: Berghahn Books.

Richerson, P., & Boyd, R. (2000). Complex societies: the evolutionary dynamics of a crude superorganism. *Human Nature, 10*, 253–289.

Richerson, P., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

Rogers, A. (1989). Does biology constrain culture? *American Anthropologist, 90*, 819–831.

Rogers, E. M. (1995). *Diffusion of innovations*. New York: Free Press.

Rosenthal, T. L., & Zimmerman, B. J. (1978). *Social learning and cognition*. New York: Academic Press.

Shennan, S. (2001). Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeology Journal, 11*, 5–16.

Shennan, S. (2003). *Genes, memes, and human history: Darwinian archaeology and cultural evolution*. London: Thames & Hudson.

Shennan, S. (in press). *Pattern and process in cultural evolution*. Berkeley: University of California.

Sneader, W. (2005). *Drug discovery: A history*. Chichester, England, and Hoboken, NJ: Wiley.

Sperber, D. (1996). *Explaining culture: A naturalistic approach*. Oxford, UK, and Cambridge, MA: Blackwell.

Taylor, G. (1996). *Cultural selection*. New York: Basic Books.

Tomasello, M. (1996). Do apes ape? In C. M. Heyes, & B. G. Galef Jr. (Eds.) *Social learning in animals: The roots of culture* (pp. 319–346). San Diego: Academic Press.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.) *The adapted mind* (pp. 19–136). New York: Oxford University Press.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science, 24*(3), 477–508.

Williams, T. (1987). *The history of invention*. New York: Facts on File.

Wrangham, R. W., et al. (1999). The raw and the stolen: cooking and the ecology of human origins. *Current Anthropology, 40*, 567–594.

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EDITOR'S PROOF

AUTHOR QUERY

AUTHOR PLEASE ANSWER QUERY.

Q1. Please provide an update on the publication status of McElreath and Strimling (2008), in press.