ARTICLES

DEMOGRAPHY AND CULTURAL EVOLUTION: HOW ADAPTIVE CULTURAL PROCESSES CAN PRODUCE MALADAPTIVE LOSSES—THE TASMANIAN CASE

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A combination of archeological and ethnohistorical evidence indicates that, over an approximately 8,000-year period, from the beginning of the Holocene until European explorers began arriving in the eighteenth century, the societies of Tasmania lost a series of valuable skills and technologies. These likely included bone tools, cold-weather clothing, hafted tools, nets, fishing spears, barbed spears, spear-throwers, and boomerangs. To address this puzzle, and the more general question of how human cognition and social interaction can generate both adaptive cultural evolution and maladaptive losses of culturally acquired skills, this paper constructs a formal model of cultural evolution rooted in the cognitive details of human social learning and inference. The analytical results specify the conditions for differing rates of adaptive cultural evolution, and reveal regimes that will produce maladaptive losses of particular kinds of skills and related technologies. More specifically, the results suggest that the relatively sudden reduction in the effective population size (the size of the interacting pool of social learners) that occurred with the rising ocean levels at the end of the last glacial epoch, which cut Tasmania off from the rest of Australia for the ensuing ten millennia, could have initiated a cultural evolutionary process that (1) kept stable or even improved relatively simple technological skills, and (2) produced an increasing deterioration of more complex skills leading to the complete disappearance of some technologies and practices. This pattern is consistent with the empirical record in Tasmania. Beyond this case, I speculate on the applicability of the model to understanding the variability in rates of adaptive cultural evolution.

La evidencia arqueológica y etnohistórica indica que, a lo largo de aproximadamente 8,000 años, desde el principio del Holoceno hasta la llegada de exploradores europeos en el siglo XVIII, las sociedades de Tasmania perdieron gran parte de su cultura tecnológica. Las herramientas que desaparecieron probablemente incluyen el hueso, ropa resistente al frío, los instrumentos enmangados, arpones, lanzas de púas, los lanza-lanzadores y los bumerangs. ¿Cómo es posible que se perdiera todo esto? Para resolver este misterio, y también esclarecer de forma más general cómo el conocimiento humano y la interacción social pueden generar adaptaciones y también la pérdida de las mismas, e inclusive malas adaptaciones, en este artículo se construye un modelo formal de la evolución cultural que se basa en detalles cognoscitivos del aprendizaje y la inferencia humanos en el ámbito social. Los resultados analíticos especifican los regímenes de condiciones bajo los cuales la evolución cultural genera adaptaciones, y también los regímenes contrastantes bajo los cuales se producen pérdidas que representan malas adaptaciones tanto de habilidades como de las tecnologías vinculadas con ellas. Más específicamente, los resultados sugieren que la reducción relativamente repentina en el tamaño eficaz de la población (el tamaño del grupo de aprendices sociales), es la causa más importante de estas pérdidas culturales. El motor ecológico de esta reducción fue el alza del nivel del mar en la época final de la glaciación pasada, que tuvo como efecto separar a Tasmania del resto de Australia durante los últimos diez milenios. La consecuencia fue un deterioro de las habilidades más complejas con las cuales contaba esta población. El expediente empírico de la arqueología en Tasmania confirma este patrón. Más allá de este caso particular, se presentan especulaciones acerca de la aplicabilidad de este modelo para entender la variabilidad en los índices de la evolución cultural adaptativa en el marco tecnológico.

This paper presents a model of cumulative cultural evolution that explicitly links certain cognitive aspects of cultural learning with social group characteristics (e.g., size, density, interconnectedness). My goal is to provide some general theoretical insights that show how our cognitive capacities for social learning (i.e., cultural transmission), which likely evolved via natural selection for their ability to extract adaptive information from the social environment (Boyd and Richerson 1985; Henrich and Gil-White 2001), generate varying rates of cultural/technological

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evolution, *including* regimes of technological loss or maladaptive change.[1] As a case example, I will apply predictions derived from the formal model to illuminate some of the curious aspects of Tasmanian cultural evolution observed from the beginning of the Holocene to the arrival of Europeans. Below, I first describe the Tasmanian case, and then develop a fairly general analytical model of cultural evolution, deriving its implications in relation to the available evidence. Next, I compare this model with alternative approaches. And finally, I briefly speculate about how the model might be used to illuminate other cases of rapid or uneven technological change in the archaeological record.

The Tasmanian Case

Archaeological evidence indicates that humans probably arrived in Tasmania about 34,000 years ago (Jones 1995). In reaching what would later become an island four-fifths the size of Ireland (67,800 km^2), Paleolithic foragers likely walked from Australia across a land bridge that would later become the Bass Strait. With the beginning of the end of the last glacial epoch, between 12,000 and 10,000 years ago, the Tasmanians were cut off from Australia by rising seas that severed the land bridge, and gradually filled the 200-km stretch to Tasmania (Bowdler 1982; Diamond 1977, 1978; Jones 1977a, 1995). When Europeans began arriving on Tasmania ten millennia later, they found a small group of societies that possessed the simplest technology of any known contemporary human group (McGrew 1987; Oswalt 1973, 1976). Not only was the Tasmanians' technology simple compared to the wider world, it was remarkably simple compared to both their contemporaries 200 km to the north in Australia, and to their own ancestors from the late Pleistocene and early Holocene (Jones 1977b, 1995).

Based on a combination of ethnohistorical and archaeological data, Tasmanians had by the time of European discovery likely lost, or never developed, the capacity to manufacture bone tools of any kind, cold-weather clothing, fishhooks, hafted tools, fishing spears, barbed spears, fish/eel traps, nets, spear-throwers, and boomerangs. To hunt and fight, Tasmanian men used only one-piece spears, rocks, and throwing clubs. In all, the entire Tasmanian toolkit consisted of only about 24 items, which contrasts starkly with aboriginal Australians just across the Bass Strait who possessed almost the entire Tasmanian toolkit plus hundreds of additional specialized tools including multipronged fishing spears, spear-throwers, boomerangs, mounted adzes, composite tools, a variety of nets for birds, fish and wallabies, sewn bark canoes, string bags, ground-edge axes, and wooden bowls for drinking (Jones 1974, 1976; Plomley 1966; Ryan 1981).

This ethnographic pattern had led some to mistakenly assume that Tasmanian technological evolution, for whatever reason, had stopped after splitting off from the mainland. It appears, however, that the Tasmanian technological suite and economic repertoire underwent some severe losses *after* being isolated—although these losses are mixed with some minor improvements in core lithic technologies (Jones 1977b; White and O'Connell 1982). The clearest evidence for this comes from the Holocene archaeological record for Tasmania, which is nearly continuous from 8000 B.P. to the ethnographic present. It shows a general pattern of change from a more complex toolkit to a less complex one. For example, while bone tools appear in several sites from Pleistocene Tasmania—dating back at least 18,000 years—the frequency, variety of types, and quality of bone tools show a gradual decline from 8,000 to 3,000 years ago, at which point bone tools drop entirely from the record. Seven thousand years ago the ratio of stone to bone tools at Rocky Cape was 3:1. Three thousand years later it was 15:1, and about 3,500 years ago bone tools disappear entirely from the record (Bowdler 1974; Jones 1977b; Ranson et al. 1983; Webb and Allen 1990). Ethnographically, there is not a single mention of bone tools, despite the efforts of observers to record the material culture (Jones 1974; Plomley 1966; Ryan 1981). In contrast, Aboriginal Australians deployed a vast array of fine bone tools (Jones 1977b; Lourandos 1997), and bone artifacts (double-row barbed points) have been dated to 89,000 B.P. in Africa (Brooks et al. 1995; Yellen et al. 1995).

Further, despite their cool maritime climate, the Tasmanians also appear to have lost the ability to make cold-weather clothing—a skill that likely allowed them to weather the last glacial maximum in a place that was only a few hundred kilometers north of an expanded Antarctica. For clothing, unlike their neighbors in southern Australia who wrapped themselves warmly in snug possum-skin cloaks, ethnographically recorded Tasmanians donned only wallaby skins, which they slung over their shoulders and tied with skin scraps. This was supplemented by spreading grease or ochre over their exposed skin. Interestingly, comparative ethnographic data from Australia, and detailed use-wear studies of Paleolithic finds, suggests that some of the bone tools that disappeared from the Holocene archaeological record were probably used to fashion cold-weather clothing (Jones 1977b, 1990; Webb and Allen 1990). Thus, the loss of bone tools and cold-weather clothing may be linked.[2]

Perhaps the most striking losses suffered by the Tasmanians during their long isolation involved their ability to catch bony or cartilaginous fish and their taste for such fish ("fish" here does not include shellfish, crustaceans, or mollusks). The archaeological record from 8,000 to 5,000 years ago indicates that Tasmanians relied heavily on fish, and fishing was probably the second-most common hunting activity. The available evidence indicates that fish were likely second only to seals in terms of calories, and they probably supplied about 21 percent of the meat—which is three times more than the third-ranked dietary item, wallabies (Jones 1977c:35). At this latitude, meat was undoubtedly a sizable portion of the total Tasmanian diet.[3] Nevertheless, by 5000 B.P. the frequency of fish bones was declining, and by 3800 B.P. fish disappeared entirely from the archaeological record all over Tasmania—yet, the relative proportions of other elements in the Tasmanians' diverse diet do not shift much (Jones 1977c). In concordance with the archaeological record, detailed ethnographic studies, including inspections of middens and fireplaces, confirm that fish was not a part of the Tasmanian diet when the Europeans arrived. Numerous historical accounts describe not only the Tasmanians' great surprise at seeing Europeans catching enormous amounts of fish (by all early accounts Tasmanian fishing was a great bounty), but also their disgust at the thought of eating fish, and their repeated refusals to accept offers of fish (in contrast to other offers that were readily accepted). Perhaps the most interesting, and widely overlooked, aspect of this is not the disappearance of fishing 3,800 years ago, but the fact that in the ensuing four millennia it never re-entered the economic repertoire—meanwhile a few hundred kilometers north at Bass Point, fishing never ceases, although technology likely shifted from spears to shell fishhooks (Jones 1977c).[4]

Although most Australian archaeologists accept the evidence that the Tasmanians stopped fishing at some point in prehistory (e.g., Bowdler 1980; Collett 1994; Horton 1979; Lourandos 1997; Vanderwal 1978), there may be reason to doubt that the Tasmanians ever fished at all. Bassett (2004) has argued that Jones' Rocky Cave data may be more consistent with a "seal-butchery interpretation," noting that the sizes and types of fish represented in the data can be understood as the contents of seals' guts. This hypothesis leaves open the question of why seal bones continue through the rest of the sequence, up to the ethnographic present, but fish bones do not. Nevertheless, regardless of the outcome of this debate, nothing about my argument or the model hinges on Tasmanian fishing in particular. Even if it turns out that the Tasmanians never fished at all, we are left with either the loss, or the lack, of a wide range of other technologies and practices vis-à-vis the Australian aboriginals. Fishing merely moves from the category of "lost" to that of "never evolved." As noted above, the aboriginals on the northern side of the Bass Strait relied on a wide range of fishing techniques that included fish traps, nets, barbed spears, and shell fishhooks. Furthermore, from the perspective of comparative ethnography, either category ("lost" or "never evolved") is equally puzzling, given the dependence on fishing observed among other cool-climate maritime foragers such as the Moriori of the Chatham Islands and the Ona and Yahgan of Tierra del Fuego. I will return to these issues later in the paper.

Looking at overall technological complexity, Oswalt (1973, 1976) performs a systematic comparative analysis of the complexity of food-getting technology that allows us to quantitatively contrast the ethnohistorically known Tasmanians with other foraging groups. His approach looks at the number of different technological forms and the number of functionally relevant (and differentiated) constituent parts in those forms to assess the aggregate complexity of each groups food-getting technology. (He also makes a persuasive empirical argument that while the number of constituent parts does not always predict a technology's effectiveness, it does strongly correlate with it.) In comparisons with 12 other foraging groups, including three temperate groups, three arctic groups, and five coastal or island groups, the ethnographically known Tasmanians come out in a distant last place. At the conclusion of his discussion, Oswalt writes (1973:92) of the Tasmanians, "*In technological terms they did not have any complex weapons* ["weapons" includes hunting tools], *nor did they make any composite instruments or weapons*. These factors set the Tasmanians apart from all other peoples in the world" [emphasis in original; brackets are mine].

The Model

To analyze the relationship between demography and cumulative cultural evolution, I constructed a simple model rooted in the available evidence on human social learning. This evidence, from both field and laboratory studies, shows that humans possess a psychological propensity to pay attention to, and attempt to imitate, particularly skillful, successful and/or prestigious individuals.[5] A tendency to orient one's social learning attention toward particularly skillful individuals ("cultural models") creates a selective force in cultural transmission that may, under some circumstances, generate cumulative adaptation.

To outline how this adaptive process could work, consider a population of *N* individuals who vary in a skill that involves at least some culturally transmittable components. The variable z_i gives a measure of this attribute for each individual *i*. Transmittable z_i skills might involve such things as net-manufacturing preferences (weaving practices, preferences for certain fibers), spear-throwing techniques, fishhook material selection, canoe-building techniques, bone-tool craft, and medicinal plant knowledge. This could be a quantitative measure of a skill like how straight an arrow shaft is, or it could measure the possession of several discrete skills. Each of the *N* individuals attempts to copy the most skillful individual, and z_h gives the skill of the most skilled individual, *h*. In attempting to imitate *h*, through a combination of imperfect imitation, experiments, errors, bad memories and ill-fortune, some individuals end up with higher *z* values than their chosen model (*h*), while others end up worse than *h*. If this combination of errors, luck, and experiments averages out such that the value of the skill averaged over the *N* individuals is unaffected, then the average skill of the *N* individuals after imitation ($\bar{z}$) will increase to z_h (now, $\bar{z} = z_h$). If everyone now imitates the new most skilled individual, *h'* (e.g., the new best net-maker), then the group average will again increase to that of the new most-skilled person, and the mean skill of the group will now exceed the skill of the initial best net maker ($\bar{z} = z_{h'} > z_h$). As this process repeats, skill-biased transmission combines with learning errors (or individual experimentation) to generate a process of cumulative cultural adaptation (Boyd and Richerson 1985:Chapter 8).

More realistically, if we assume that human inference is imperfect and individual experiments are costly and often inconclusive, then individuals will rarely achieve the level of skill demonstrated by their chosen model. This will be particularly true for complex skills that are difficult to figure out on one's own. Such low-fidelity cultural transmission means that cumulative cultural adaptation may not occur. Even if the inferential machinery of human minds were perfect, the transmission process would still result in a range of errors because behavioral (phenotypic) displays provide learners with only incomplete information from which to mentally reconstruct the underlying skill, strategies, and abilities (Henrich and Boyd 2002). Thus, to build a model that combines skill-biased (or success-biased, see Appendix D) cultural transmission with imperfect inference, I will make use of the Price equation (1). In its most basic form, this equation is a general statistical statement that applies to any evolutionary system; it is equally applicable to the evolutionary dynamics of genes, quantitative cultural traits, phonemes, and the frequency of hydrogen atoms in some distant galaxy (Frank 1998). The Price equation makes no assumptions about the discreteness of traits, transmission pathways, or transmission fidelity. For our purposes here, the Price equation usefully separates the effect of selecting particular cultural models (selective attention to skillful individuals) from the effects of errors in transmission, inferential processes and individual learning ("inference"):

$$\Delta\bar{z} = \underbrace{Cov(f, z)}_{Selective\ Transmission} + \underbrace{E(f\Delta z)}_{Incomplete\ Inference} \qquad (1)$$

As before, we begin with *N* individuals indexed by *i*. Each individual *i* has a *z*-value (z_i). This value measures the individual's skill, as described above.

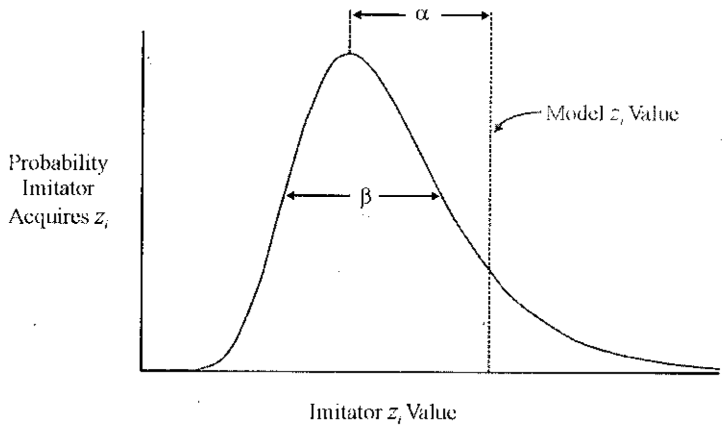

Figure 1. Gumbel distribution for imperfect imitation.

$\Delta\bar{z}$ represents the average change in skill (z) per time step—i.e., the rate of cultural evolution of skill z. If $\Delta\bar{z}$ is positive, then adaptive evolution is taking place—e.g., people are becoming better bone tool makers. If $\Delta\bar{z}$ is zero, the population is in equilibrium. If $\Delta\bar{z}$ is negative, then the population is losing skill (e.g., the bone tools are getting cruder). Also, associated with each individual is an f value. f_i gives the relative degree to which other individuals focus their social learning attention on i. If individuals tend to pay attention to particularly skilled individuals, f and z will be positively correlated. Said another way, f gives the relative likelihood that an individual with a particular z-value will be selected as a cultural model. $Cov(f, z)$ is the covariation between f_i and z_i, and gives the effect of selective cultural forces on $\Delta\bar{z}$. To simplify matters here, I will assume that all individuals successfully identify and attempt to copy the person with the highest value of z.[6] Note that our pool of N individuals could represent the same individuals (e.g., the same bone tool makers) from one season to the next, or it could represent different generations or age cohorts in a society. For thinking about the long-term cultural evolution in Tasmania, the latter is most relevant.

To capture the idea that inferential processes are incomplete, I assume that the inferential processes that underpin social learning are inaccurate in two ways: first, they are noisy, so that copiers never accurately replicate the z value of their model; and second, they are biased so that the behaviors acquired by copiers are, on average, less skilled than that of their model. More formally, as illustrated in Figure 1, individuals who attempt to copy a model with z-value, z_i, end up with a z-value drawn from a Gumbel probability distribution[7] with mode $z_i - \alpha$ and dispersion β. Typically, copiers acquire skills that are worse than their model's z-values by an amount α, but occasionally—through lucky guesses or errors—some individuals acquire z-values (skills) that are superior to their chosen model. The probability of that occurring for an individual is the area under the distribution to the right of the dashed line (the model's z-value). It's also worth noting that the probability of an exact copy is zero—there is no "replication" in this model (cumulative cultural evolution does not require "replicators": Henrich and Boyd [2002]).

For analytical purposes, it is important to remember that α and β arise from an interplay between the "things being learned" and human cognitive processes. If something is easy to imitate and people vary little in the inferences they make during the imitation process, then both α and β will be small—for perfect replication α and $\beta = 0$. If something is hard to imitate, but people tend to make the same kinds of mistakes, then α will be large, and β small. If something is difficult to accurately imitate, and people make wildly different inferences/mistakes, then α and β will both be large. If people generally make fairly accurate inferences in learning something, but sometimes diverge wildly in their efforts, α will be small and β large.

When particular skills/technologies are quite simple, it may be possible for individual learning, based on experience and/or experimentation, to swing the mode of the distribution to the other side of the selected model's z-value. Under such conditions, individual learning would combine with selective transmission (copying the skillful) to drive adaptive cultural evolution. However, both the ethnographic record and my own experience living among the Machiguenga of the Peruvian Amazon suggests that these circumstances are unlikely to apply to most human situations because of the amount of culturally learned know-how involved in human skills related to making and using such things as blowguns, bows, arrows, bowls, craft tools, spears, fishing nets, canoes, kayaks, etc., or in practices and knowledge related to such things as tracking, using medicinal plants, and processing foraged foods. After only a few generations, most of the improvements that can be made based on typical experiences and practical deductions will have already been incorporated into the basic cultural repertoire, leaving only the nonintuitive and difficult-to-figure-out modifications. This is not to say that the experience and experiments of some few individuals will not lead them to higher z-values, or that such information won't spread (via selective transmission) through the population. Rather, I argue that such individually based experiences and deductions won't happen on average across the population, and thus such processes won't (alone) be responsible for the population patterns of cultural evolution. It is the selective transmission of lucky errors and occasional experiments that drives much of the evolution of adaptive technology, skills, beliefs, and practices.

With this setup, we can derive equation (2) from the basic Price formulation shown above (Appendix A provides the technical details):

$$\Delta\bar{z} = -\alpha + \underbrace{\beta(\varepsilon + \mathrm{Ln}(N))}_{Always\ Positive} \qquad (2)$$

The two terms on the right side of (2) go in opposite directions: the first term ($-\alpha$), which represents the effect of low-fidelity transmission and inference bias, favors a decrease in the average skill in the population (favoring $\Delta\bar{z} < 0$), while the second term, which combines the effects of inaccurate inference and model selection, always favors adaptive cultural evolution ($\Delta\bar{z} > 0$; $\varepsilon \approx .577$, the Euler-Gamma constant). This means that whether the average skill in the population of social learners increases or decreases depends on the relative sizes of the two terms. Interestingly, the two components of human inference, α and β, have opposite effects on adaptive evolution. α operates against adaptive evolution, while β, the tendency of individuals to make *different* inferences from observing the same thing, *favors* adaptive evolution. The more individuals tend to make different inferences, the faster cultural evolution goes—or the more likely it is to be adaptive.

Most importantly for our purposes, N, the size of the pool of social learners, also positively affects adaptive evolution. The larger the population of interacting social learners, the faster adaptive evolution proceeds—or the more likely it is that selective forces will favor adaptive processes. N represents the effective number of social learners and may be substantially larger than the number of individuals in a social group as long as individuals interact sufficiently often with people from other groups. For Tasmania, both ethnographic description and the rapid diffusion of European practices suggest a fairly well-connected cultural population, at least for technologies (Jones 1977a, 1995). Thus, if we take Jones's estimate of 4,000 Tasmanians at the time of European contact,[8] assume a sexual division of labor, and ignore children, we can estimate $N = 1{,}000$. If we further ignore older individuals who are unlikely to acquire novel practices (20 percent of the population), $N = 800$. Of course, nothing in the analysis hinges on the exact number, and we are primarily interested in the qualitative insights, but this at least provides a point of reference.

By setting $\Delta\bar{z} > 0$, we can solve for the conditions under which selective transmission will drive adaptive cultural evolution, or generate maladaptive loss:

$$N^* > e^{(\frac{\alpha}{\beta} - \varepsilon)} \qquad (3)$$

N* is the critical number of social learners necessary to produce cumulative adaptive cultural evolution for a specified set of inferential processes (α and β values)—which relate to specific skills, techniques, or practices. This shows N* must exceed a threshold determined by the ratio of α to β. Larger values of α or smaller values of β will increase the minimum threshold size of the pool of social learners. If N* is less than this threshold, $\Delta\bar{z}$ will be less than zero, and these culturally acquired skills, knowledge, and related technologies will begin to ebb away. Plotting equation (3), Figure 2 illustrates the conditions for adaptive loss: parameter combinations above the line create adaptive evolution,

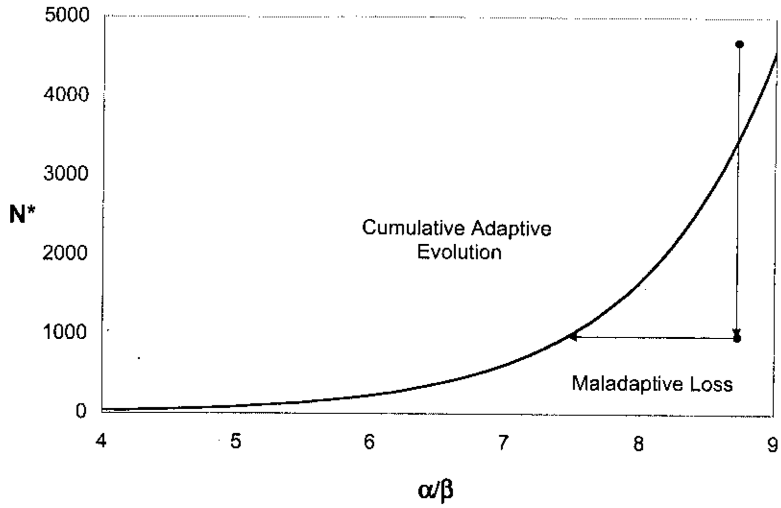

Figure 2. Regimes of Cumulative Adaptation and Maladaptive Loss.

while those below the line produce maladaptive deterioration.

To get an intuitive sense of what is going on here, consider what happens if each learner picks only one person ($N = 1$) and attempts to copy his skills. Under these conditions, learners would, on average, select only a model of average skill to copy, and thus would obtain a worse-than-average set of skills (assuming copies tend to be worse than the original). However, if learners can pick two models and learn from whichever of the two is the most skilled, then learners will (on average) learn from a better-than-average model, but they will still suffer the losses from imperfect inference and imitation. Picking from three potential models further improves the learner's chances of learning from a model sufficiently skilled to compensate for the losses inherent in any transmission process, and four models further improves things, etc. Cultural learning becomes cumulatively adaptive when the effect of having a larger set of models from which to pick the most skilled exceeds the losses from imperfect copying. This process is roughly analogous to the effect of sample size on assemblage diversity:[9] larger samples mean more variation, and variation is the fuel for the engines of any selective evolutionary process.

Based on these theoretical findings, Tasmanian technological losses may have resulted from a drop in N produced by the climatic change that isolated Tasmania from the social networks of southern Australia and cut the available land area in half.[10] Figure 2 depicts this vertical drop from a regime of cumulative adaptive evolution into one of maladaptive deterioration for specific "hard to learn" skills. After the drop, skill losses proceed fairly gradually, following the horizontal arrow to a new equilibrium. This point will involve technologies and practices with smaller values of α and/or larger values of β—that is, simpler technologies that are easier to accurately acquire, and/or vary. For example, throwing clubs and one-piece spears may substitute for bows and arrows, boomerangs, and bone-tipped, barbed spears in some sense, but they don't replace them in terms of equal effectiveness.

Different technologies and practices have different α and β values, so a drop in N will not influence all cultural products equally. Figure 3 shows two different technologies/skills that are associated with different values of α and β. For the more "complex skills" (harder to learn), larger pools of social learners are required to achieve cumulative cultural evolution, and sustain a more adaptive equilibrium: A drop from $N = 4{,}000$ to $1{,}000$ means a change from a slow rate of adaptation/improvement (a small positive value of $\Delta\bar{z}$) to a larger rate of maladaptive loss (a negative value of $\Delta\bar{z}$), while a similar drop for a "simpler skill" merely reduces the rate of cumulative adaptive evolution ($\Delta\bar{z}$ stays positive). Thus, this process will disproportionately target the most complex technologies and practices for deterioration—i.e., those that are the most difficult to learn (high values of α/β), and the least amenable to individual learning.

This prediction is consistent with the Tasmanian pattern. Extensive archaeological analyses and

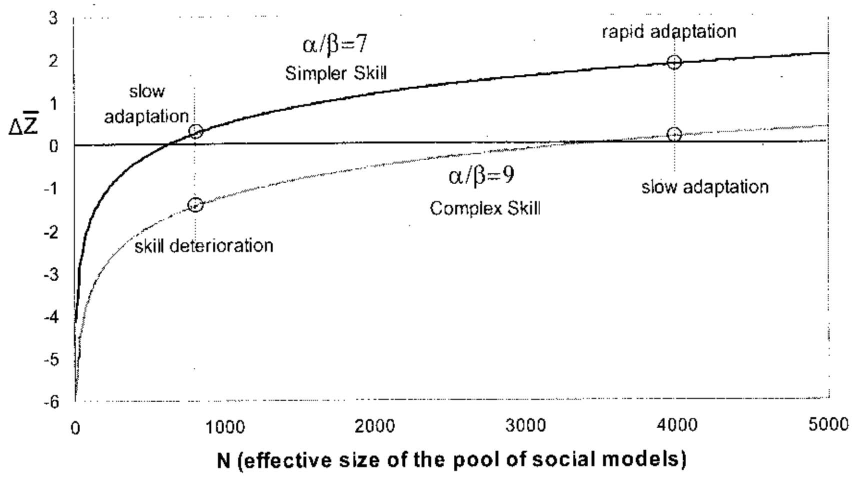

Figure 3. Differential effects of a drop in the size of the pool of social learners (*N*) on the evolution of "simple" and "complex" technologies.

historical ethnography suggest a continuous stone tool tradition from the Australian Paleolithic to the Tasmanian ethnographic present. Nevertheless, Jones's analyses of this stone-tool tradition also indicate some gradual improvement—smaller, finer tools manufactured using materials from more distant sources (Jones 1977b, 1995). Improvement in some skills/technologies and deterioration in others may seem intuitively odd, but this prediction arises directly from the above model (as illustrated in Figure 3). Simpler technologies can remain in the "cumulative regime" even when more complex tools have plummeted into the "maladaptive regime." As explained above, this occurs because the skills for producing and using simple tools are easier to acquire by imitation (smaller α) or are more strongly affected by individual learning (smaller α and larger β). This contrasts with the difficulty of learning how to make more complex tools such as fishing nets, boomerangs, arrows, sewn bark canoes, fishhooks, and fine bone implements.

With cultural learning in mind, compare the manufacturing process used by the maritime foragers of Tierra del Fuego to craft bone-tipped arrows and the shellfish-gathering approach recorded for Tasmanians. Among Fuegians, crafting bone-tipped arrows involved a 14-step process, seven different tools (four of which were specially crafted solely for making arrows), four types of wood (which all required straightening procedures), and six other materials (Lothrop 1928). The fine details associated with straightening gnarled wood, crafting barbed bone heads, and affixing the fletching involved techniques that are not easily figured out, and small errors have enormous impacts on performance. In contrast, the Tasmanian technique of diving for crustaceans (which was exclusively women's work) probably requires both the development of substantial physical skills and lots of practice, but seems less likely to benefit from observing particularly skilled models. Such risky diving techniques are not, to my knowledge, used by other cold-climate foragers, and may have evolved in the absence of more complex food-procurement technologies. My hope is that experimental archaeological work can test this claim—and even estimate α and β parameters for different kinds of tools and skills.

Adding Vertical Transmission has No Effect on the Qualitative Analysis

The empirical importance of vertical transmission (parent-offspring cultural transmission) is a matter of debate. Some work among small-scale societies suggests that vertical transmission may account for as much as 70 to 80 percent of the transmission of craft skills (Hewlett and Cavalli-Sforza 1986; Ohmagari and Berkes 1997; Shennan and Steele 1999), while other work in both small-scale and industrialized societies indicates that vertical transmission maybe of little importance (five percent) to understanding adult patterns of behavioral variation (Aunger 2000; Chen et al. 1982; Harris 1998; Lancy 1996; Plomin et al. 2000). In my view, recent methodological critiques of the data-gathering methods used in the studies favoring vertical transmission (Aunger 2000) has brought some of this evidence into question, and tipped the balance against vertical transmission as the central force in cultural transmission.[11] Nevertheless, the issue is far from settled, and vertical transmission may turn out to be crucial in certain cultural domains. This leads to the question: how would the presence of vertical transmission influence the important qualitative claims made above?

Vertical transmission can be incorporated directly into the above model by assuming that social learners copy the most skilled individual a proportion p of the time and imitate their parents a proportion $(1-p)$ of the time. Using the Price equation and following the above derivation yields (Appendix A shows the details):

$$\Delta\bar{z} = p\left[-\alpha + \beta(\varepsilon + \text{Ln}(N))\right] \quad (4)$$

Assuming $0 < p < 1$, equation (4) tells us two important things about adding vertical transmission: (1) the magnitude of the rate of cultural evolution will be reduced by the fraction p; and (2) the conditions demarcating the adaptive regime from the maladaptive regime (i.e., Figure 2; $\Delta\bar{z} > 0$) are *identical* to those derived above. From this, we can conclude that adding even large amounts of vertical transmission do not change the basic qualitative results.

Alternative and Complementary Explanations

Noncultural Explanations

One approach to dealing with the evidence of technological losses in the Tasmanian record, and the stark differences between the Tasmanians and their continental neighbors, has been to argue that all the tools, practices, and skills that the Tasmanians either lost, or never developed, can be explained as the product of adaptive decision making (cost/benefit analysis by individuals), rather than the adaptive cultural learning processes modeled above. Vanderwal (1978:123), for example, has argued that the loss of cold-weather clothing was actually an adaptive response to the cooling climate of the late Holocene; he says that spreading grease and ochre over the skin may be a more effective protection against the elements than clothing. Similarly, Allen has argued that dropping fish from the diet was an adaptive move for the Tasmanians, given their latitude and the availability of seals and mutton birds. Bassett (2004), Horton (1979), and Walters (1981) attempt similar arguments.[12]

Most of this work amounts to suggestions about how particular oddities in the Tasmanian record (usually fishing) might be understood as adaptive products of individuals making cost/benefit decisions. To explain the overall pattern, however, the approach needs to show how *all* bone tools, spear-throwers, barbed spears, ground-edge tools, durable boats, paddles, winter clothing, seal nets, bird snares, and all eating of any kind of fish during any season (caught by any method: fishhooks, spearing, traps, nets) were maladaptive choices in all parts of Tasmania for the last few thousand years of the Holocene. Unfortunately, in examining the implications of their approach, none of these authors takes seriously the challenge of comparative ethnography: if Tasmanian ecological conditions caused (via individual-level cost-benefit decision making) people to reject such things as fishing, bone tools, barbed points, etc., then we should observe similar patterns in similar places. In constructing their arguments, all of the above-mentioned authors make causal reference to the harsh maritime climate of Tasmania. However, whatever the details of the Tasmania climate, all these arguments must be rooted in the differences between the climate of Tasmania and those of southern Australia, only 200 km to the north. It's these differences that must account for the different historical trajectories and immense cultural divide. Thus, we should compare the suite of Tasmanian technologies and practices to foragers inhabiting environments similar to, or harsher (i.e., colder) than, Tasmania. Following this line, comparative work provides no support for the "harsh maritime climates" explanation for the Tasmanian pattern.

Consider the foraging populations that once inhabited Tierra del Fuego. Lying at 52° south latitude, the archipelago of Tierra del Fuego is 10° south of southern Tasmania and has a fully maritime climate. The incessant cold winds and range of vegetation are quite similar to Tasmania. Like the Tasmanians, the indigenous inhabitants of Tierra del Fuego were nomadic hunter-gatherers who organized themselves in either families or bands, and as in Tasmania, bands often controlled particular territories. Fuegians (referring specifically to the Ona and Yahgan) also relied on resources similar to the Tasmanians: seals, birds, shellfish, and land mammals (the guanaco substitutes for the wallaby). And, as they did with the Tasmanians, Europeans once believed these foragers represented a primitive, degenerate state of humanity. However, if we compare the technology of Fuegians to that of the Tasmanians, the differences are stark. Like the Tasmanians, the Fuegians were heavily reliant on seal hunting and sometimes used clubs in their hunting; however, unlike the Tasmanians, the Fuegians also used bows and arrows, seal-spears, and specialized seal-nets (manufactured from seal hide). Along with sealing, Fuegians also fished using baited fishing lines,[13] special barbed fishing spears, and fishing nets; in fact, fish comprised an important component of their diet (contra Allen 1979[14]). Both Yahgan and Ona made extensive use of bone in awls, barking tools, arrows, spatulas, and canoe manufacturing; in the Tasmanian archaeological record, bone tools disappeared 3,800 years ago and never re-enter. As in Tasmania, birds were an important food source for both the Yahgan and Ona; however, in addition to Tasmanian techniques, the Fuegians also used bows and arrows and bird snares. As noted, the Fuegians used a complex procedure to craft fine bone-tipped arrows, which were sanded, polished, and apparently deadly. Although Fuegian clothing appeared light by European standards, these foragers made capes (seal, otter, and guanaco skins sewn together), robes, undergarments, moccasins (seal skin), and leggings—compare this to the Tasmanians one-piece wallaby skins. Fuegians did, like the Tasmanians, make use of grease and ochre as protection against the cold, except that they integrated these with their clothing—often applying grease to the skin surface of their robes (contra Vanderwal 1978[15] and Bassett 2004). In comparing hunting technologies, the Fuegians deployed clubs, slings, at least two kinds of nets, bird snares, bows-and-arrows, and four kinds of specialized spears (all barbed; including a detachable harpoon with lead line for seals, porpoises, and whales). Tasmanians were limited to clubs, a single one-piece spear (without barbs), and a baited bird-blind trap. The island-dwelling Yahgan also used durable sewn bark canoes as their primary mode of transportation, and as an important tool in hunting and fishing. In contrast, some Tasmanians had crude, canoe-rafts that were capable of serving only limited transportation functions. To propel these watercraft, Tasmanian women had to swim in the cold waters alongside their canoe-rafts, pulling them along (or sometimes using sticks as paddles), while the Yahgan crafted efficient canoe paddles.[16] Given these comparisons, it is difficult to see how Tasmanian technology and practices can be realistically viewed as optimal responses for cold-climate maritime foragers.

I am *not* arguing that the Fuegians were optimal and the Tasmanians were not. Rather, what the above model shows is that cumulative adaptive cultural evolution is the joint product of our evolved cognitive abilities (which I assume are constant across the species) and sociodemographic factors. Consistent with the above model, the population of Tierra del Fuego was at least twice that of Tasmania, and more importantly, these semi-isolated groups appear to have maintained substantial contact with the larger groups to the north. Fuegian stylistic forms and technological details show clear evidence of diffusion with northern populations (e.g., Telhuenche and Araucanians). Fuegian basket-weaving techniques, baby cradles, and clothing were very similar to those used all along the Chilean coast. Unlike the Tasmanians, the Fuegians were not completely disconnected from the vast continent to the north for 10,000 years. Nevertheless, their partial isolation (which would affect N) might account for their degree of technological complexity vis-à-vis their northern neighbors or many Inuit groups in the Northern Hemisphere. The Fuegians lacked fishing traps, hide boats, axes, drills, spear-throwers, guanaco wool-weaving techniques, fishhooks, pottery, and tanning procedures (keep in mind, the Yahgan traveled by canoe, so the "too much to carry" argument does not work very well here). They also did not utilize several potential food sources, including wild celery, two kinds of cress, wild seapink, wild parsnips, scurvy grass and mushrooms (Lothrop 1928).

Broader comparisons of technology further support this demonstration. Oswalt has quantitatively compared the functional complexity of the food-getting technologies for 23 foraging groups drawn from desert, tropical, temperate, subarctic, and arctic climates. His analysis shows three things worthy of note. First, looking only at the six foraging groups from temperate climates, the analysis shows that the Tasmanians have substantially less complex food-getting technologies then the other five groups. In fact, the next most complex group scores more than twice that of the Tasmanians. Second, on average, temperate foragers show more (not less) food-getting technological complexity than either desert or tropical foragers, about the same as subarctic groups, and somewhat less than arctic foragers—so the Tasmanians remain an outlier even when environments are taken into account. Finally, when compared against the entire field of 23 foraging groups from a full range of environments, the Tasmanians tie with the tropical Tiwi for a distant last out of all the groups investigated. The fact that the Tiwi tie for last place further supports the thesis of this paper. At the time of European contact, about 5,500 Tiwi inhabited two islands 50 km off the northern coast of Australia and had experienced little contact with the mainland, apparently believing that the mainland was the "land of the dead." Thus, the functional complexity of their technology is limited by *N*. Oswalt's overall comparison of functional complexity is consistent with the more detailed technology-by-technology comparison above: comparative ethnography does not support the notion that the broad patterns in the ethnohistorical and archaeological record of Tasmania are explained by cost-benefit decision-making models.

What often goes unrecognized by those who take a behavioral ecological or rational choice approach to behavior when they look at a cultural evolutionary model (like the one here) is that such models are *perfectly* consistent with both approaches if one removes the assumption that individuals are omniscient beings with unlimited information processing abilities, and replace it with an informational constraint (i.e., information about costs and benefits is not free). As soon as one does this, natural selection favors forms of imitation like prestige-biased imitation (Henrich 2001, 2002; Henrich and Boyd 1998; Henrich and Gil-White 2001; Henrich and McElreath 2003), and rational actors will start imitating others (Alvard 2003; Henrich et al. 2001; Schlag 1998). Shennan's recent book makes an excellent case that behavioral ecological and cultural evolutionary approaches are naturally compatible. Behavioral ecological models provide a fitness-maximizing benchmark, and cultural transmission mechanisms provide a psychologically plausible process that can explain adaptation while simultaneously accounting for change, cultural history (why cultural phylogenies matter), patterns of diffusion, and maladaptation.

Cultural Drift Explanations

Cultural evolutionary drift provides another potentially complementary explanation for technological losses. The idea is that small, isolated populations are more likely to lose technologies through sampling errors in the cultural transmission process than are larger populations.[17] For example, if in a population of 10 adults, 8 made barbed spears and 2 prefer simple spears, we might expect the next generation of 20 individuals to have 16 barbed spear-users and 4 simple spear-users. However, in such a small population and when vertical transmission is very important, sampling error in transmission could lead to 8 barbed spear-users (vice 16) and 12 simple-spear users (vice 4) in the next generation. If this sampling error happens successively, barbed spears could disappear out of the population even if they are more adaptive than simple spears.

In considering drift explanations, four things should be noted: (1) drift will often be swamped by selective forces (like copying skilled individuals) unless vertical transmission dominates the evolutionary process (thus, the importance of drift turns on the aforementioned debate about vertical transmission); (2) drift cannot explain cumulative adaptive cultural evolution involving hard-to-figure-out skills; (3) unlike the analogous genetic case, cultural traits/skills lost through drift are not prevented from re-entering the population by the low "mutation rates" that characterize most genetic systems; and (4) drift is unlikely to systematically target the most complex practices, skills, and technologies.[18] I will take up points 2 through 4 in more detail.

Under some conditions drift may generate cultural losses when selective forces are weak or zero, which occurs both when cultural traits are neutral vis-à-vis selective forces, and when an evolutionary system is at (or often near) an equilibrium. However, drift cannot explain cumulative adaptation in general, nor can it explain the improvements observed in Tasmanian stone tool technologies. To explain cumulative adaptation, under the assumption of vertical transmission, anthropologists have added individual learning to vertical cultural transmission (Binford 1983; Boyd and Richerson 1985;

Chibnik 1981; Henrich 2001). As we saw above, vertical transmission alone does not produce cumulative adaptation. The "individual learning solution" to adaptation means that drift is unlikely to be important because the adaptive force of individual learning is not diminished in small populations. For drift to overpower individual learning, individual learning would have to be incredibly weak, which would mean even large populations would adapt extremely slowly—because the strength of individual learning does not increase in larger populations. And, even if drift could overcome individual learning to drive the loss of a particular skill or practice, individual learning could drive it right back toward the equilibrium value for an infinite population. The fact that bone tools and fishing disappeared from the archaeological record over 3,800 years before the Europeans arrived cannot be easily reconciled with the drift explanation because important skills would be reintroduced and spread during the ensuing millennia by individual learning and invention. Unlike adaptive alleles lost from an isolated island population via genetic drift, there is no reason why humans living on a cool island and relying primarily on marine resources could not come up with the ideas of warmer clothing and fishing equipment. Thus, the real trick involves not only explaining the disappearances, but also in figuring out why such useful ideas and skills were not reintroduced and spread during the subsequent millennia. Lacking the low mutation rates found in genes, cultural drift models provide no systematic selective pressure against the reintroduction or spread of useful skills. In short, the vertical transmission models that favor drift effects require individual learning for adaptive cultural evolution, but this required individual learning saps the effect of drift on losses by providing an adaptive force that opposes drift and can readily reintroduce lost technologies (unlike mutation).

In contrast, my model shows that even if particular individuals frequently developed superior skills, the interaction between social learning and demography is such that these skills won't spark cumulative evolution because small losses in transmission combined with an insufficient pool of cultural models will drive those skills right back out of existence. That is, such skills can be reinvented repeatedly, but still won't appear in the archaeological record.

Taking the fourth point, if drift alone were responsible for Tasmanian technological evolution, we should expect an archaeological record showing the following kinds of sequences: a disappearance, span of time, reintroduction, diffusion and improvement, span of time, a disappearance of something *different*, span of time, reintroduction, diffusion, and improvement, etc. Taken at face value, the Tasmanian record does not suggest such a stochastic process, and the mere fact that valuable technologies never reappeared indicates an evolutionary force that systematically targets complex skills. There are different ways of modeling drift, but the simplest approaches (e.g., Shennan 2001) will probabilistically target simpler technologies. This contrasts with both the Tasmanian archaeological record and the prediction of the above model.

In summary, drift may be important in some regimes of cultural transmission, but alone, it cannot explain many interesting aspects of the Tasmanian case.[19] With the qualitative insight from my model laid out, future theoretical work (which will likely require computer simulations) should combine drift and "imperfect learning" into the same model. Such an approach should seek out evolutionary regimes in one or the other processes dominant and look for predictive (empirically testable) patterns that distinguish the two regimes.

Conclusion

While the complete isolation of the Tasmanians for 10,000 years provides an extreme example, persistent technological losses among partially isolated cultural groups are substantially more common than is typically recognized. As early as 1912, in his paper "The Disappearance of Useful Arts," W. H. R. Rivers[20] argues that the scattered losses of canoes, bows and arrows, and pottery in Oceania cannot be explained consistently by economic factors such as the availability of raw materials or the diffusion of alternative technologies or practices. In the canoe case, he points to the Torres Islands, a small group of geographically isolated islands in the northernmost part of the Vanuatuan archipelago. The Melanesian inhabitants of these islands apparently lost the ability to make the kind of seaworthy canoes that they surely arrived in. At the time of Rivers' fieldwork in the early twentieth century, they were relying entirely on crude bamboo catamarans that were of no use in fishing and too flimsy for travel outside of the immediate island group (archaeological data indicates that inter-island travel was once common throughout the region). Adjacent to the Torres Islands, the inhabitants of the Banks Islands went for a time without canoes after having lost the manufacturing skills, but as of the mid-nineteenth century people on the largest island had gradually begun to re-acquire the skills—although their canoes were still crude compared to the ones built in the past, and still insufficient for travel outside the local island group. Rivers reports a similar finding regarding the evolution of sea-voyaging canoes into crude bamboo rafts in Mangareva (Gambier Archipelago). In none of these cases was there a lack of raw materials (as there might be elsewhere in Oceania), and it is difficult to argue that an island-dwelling people really don't need a good canoe. Admittedly, Rivers's evidence is not sufficiently detailed to make a strong case in favor of any particular model, but it does suggest that the "loss of useful arts" is not isolated to Tasmania.

In this paper, I have presented a simple model that synthesizes two important aspects of human social learning—selective choice of cultural models and imperfect inference—with a population's demographics. The model predicts the conditions for cumulative cultural evolution, cultural equilibria, and maladaptive losses vis-à-vis particular skills or practices. With respect to the Tasmanian case, it does *not predict* a general process of "devolution" applicable across the entire spectrum of cultural domains, or a "slow strangulation of the mind" (Jones 1977b:203). Instead, it precisely specifies the conditions under which particular skills will enter a regime of maladaptive deterioration until reaching a new less-well-adapted equilibrium. By assuming that all human groups share the same cognitive abilities, the model shows how different rates of regimes of cultural adaptation (which includes skills, technology, etc.) may result from the interaction between social and cognitive processes.

Beyond the Tasmanian case, this model may also be applicable to cases of rapid cumulative technological evolution, as it predicts that larger pools of interacting social learners will generate more rapid cultural change, and are capable of achieving higher equilibrium levels of skill, knowledge, and technological prowess. Two examples illustrate the range of potential applicability. First, among orangutans and chimpanzees, recent work yields results that appear consistent with the above model, and inconsistent with ecological explanations of the complexity of cultural repertoires. Carel van Schaik et al. (2003) show (1) that cultural similarity among different groups depends on geographic proximity—which is consistent with the importance of diffusion and a large N—and (2) that opportunities for association beyond close kin predicts the size of a group's cultural repertoire. At the same time, these authors also show that neither "food scarcity" nor "free time" predict the size of a group's cultural repertoire. Second, the logic suggests that Paleolithic populations may develop quite different degrees of technological complexity depending on how the availability of local resources (and many other potential factors) affect the frequency and intensity of social interaction. For example, technological differences between Neanderthals and anatomically modern humans (with similarly-sized brains) may result from differences in group size and sociality (N), rather than in genes related to cognitive abilities that, in-and-of-themselves, lead to improved tools. Increases in N, perhaps facilitated by climatic change or changes in social organization that promote local interaction or higher population densities, should precede periods of rapid technological evolution. Of course, population size, density, and degree of interaction are not independent from craft skill, environmental knowledge, and technological prowess, and the interaction of these demands further investigation. Nevertheless, the model presented here reveals a potentially important linkage between cultural learning, demography, and technological change that has previously been overlooked. This link connects demographic characteristics to cultural evolution in a manner that may shed new light on old problems.

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Appendix A: Details of the Derivation

Start with the Price equation (Price 1970, 1972) using relative fitness, f:

$$\Delta\bar{z} = \underbrace{Cov(f,z)}_{Selective\ Transmission} + \underbrace{E(f\Delta z)}_{Incomplete\ Inference} \quad (A1)$$

Assume that everyone copies the most skilled individual, h, so $f_h = 1$ and $f_{not\,h} = 0$, this reduces (A1) to (A2):

$$\Delta\bar{z} = z_h - \bar{z} + \Delta z_h \quad (A2)$$

For a population with skills distributed approximately according to the Gumbel (Extreme Value) distribution (as in Figure 1) with mode a (not α) and spread β, $\bar{z}$ ($= a + \beta\varepsilon$) is the mean value of z in the current population, and z_h is the expected value of the highest values drawn from a sample of size N.

$$z_h = N \int_{-\infty}^{\infty} e^{\frac{a-x}{\beta}} \left(e^{-e^{\frac{\alpha-x}{\beta}}} \right)^N x dx \quad (A3)$$

Fortunately, z_h (A3) can be approximated by (A4) with great accuracy (see Appendix B):

$$z_h \approx a + \beta(\varepsilon + \mathrm{Log}(N)) \quad (A4)$$

Using Figure 1, each individual also draws from a Gumbel distribution (α, β) to determine the size of her imitation error:

$$\Delta z_h = -\alpha + \beta\varepsilon \quad (A5)$$

Note that the spread parameters in these two Gumbel distributions are identical because all the variation in the distribution comes through imperfect imitation, so both the distribution of the existing population and the inference distribution are β.

Using the Gumbel distribution provides an important advantage: a wide range of distributions, which include the Gumbel distribution and the Normal distribution, yield the Gumbel distribution (approximately) when the extreme values are repeatedly sampled. This means the distribution will remain Gumbel throughout the evolutionary process, and only the parameters will change.

Substituting (A4) and (A5) into (A2) gives us equation (2), from the main text.

To add vertical transmission, we follow the same derivation as above, except now,

$$f_i = (1-p)w_i + pb_i w_h \quad (A6)$$

Here, w_i is the relative number of learners produced under vertical transmission. If the effect of natural selection on cultural variation is considered small relative to the psychological forces in the model, then $w_i = w$ for all individuals i. As in the text, p gives the proportion of reliance that individuals give to skilled-biased transmission. By setting $b_i = 0$ when $i \neq h$ and $b_h = 1$ when $i = h$ captures the notion that individuals copy the most skilled individual in the population. If (A6) is substituted into (A1), and (A1) is solved in the manner described above, the result is equation (4) from the main text.

Appendix B: Effect of Using A3 Approximation

To verify the accuracy of the above approximation (A4), I calculated the difference between this and the exact value of z_h (A3):

$$d = \left| N \int_{-\infty}^{\infty} e^{\frac{a-x}{\beta}} \left(e^{-e^{\frac{\alpha-x}{\beta}}} \right)^N x dx - (a + \beta(\varepsilon + \mathrm{Log}(N)) \right| \quad (A7)$$

Solving (A7) for the range of parameters relevant to the above models yield nearly perfect agreement. For many particular parameter combinations (e.g., whenever $\beta = 1$), (A7) reduces to exactly zero. Where analytical solutions are impossible, within the range from $3 < a < 12$, $0.1 < \beta < 5$ and $10 < N < 10{,}000$, numerical solutions never yielded $d > 10^{-14}$.

Appendix C: Effect of non-Gumbel Distribution

To examine the effects of changing the distribution of skill in the basic model, I replaced the Gumbel distribution (and its approximation) with a standard logistic distribution with mean α and spread parameter β. Following the above derivation gives this equation for the average change in the value of the skill:

$$\Delta\bar{z} = -\alpha - \mu + \frac{N}{\beta} \int_{-\infty}^{\infty} x e^{\frac{x-\mu}{\beta}} \left(1 + e^{\frac{x-\mu}{\beta}} \right)^{-(N+1)} \quad (A8)$$

To explore the relationship between N* (the threshold value of N described above) and bias against accurate learning (α), we can set $\Delta\bar{z} = 0$, $\beta = 1$; we can also set $\mu = 0$, as the initial position of the skill distribution does not affect the qualitative results—and that is what we are checking. This gives,

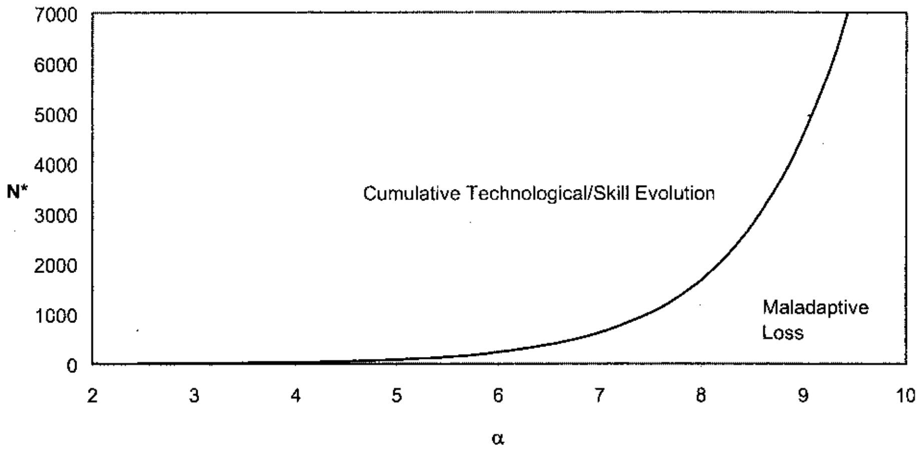

Figure 4. Threshold values of N* and α for the model using a logistic distribution.

$$\alpha = \Psi(N) + \varepsilon \quad \text{(A9)}$$

where $\psi(N)$ is the Digamma function at N. Plotting this in Figure 4 for a range of N values reveals no qualitative difference between the Gumbel distribution and the logistic.

Appendix D: Effect of Indirect Cues of Underlying Skill

What if an individual's skill is not directly observable? Suppose now that instead of skill, z measures success in some domain such as hunting (perhaps quantified in lifetime tapir kills), combat (in "heads-taken"), canoe making, or farming (in sacks harvested per hectare of wheat sown). Under these conditions, equation (1) would still govern the evolution of z. However, if we wanted to get at the underlying transmitted skills that produce particular values of z, we would have to specify how each skill contributes to an individuals' behavioral expression (to their success). For illustrative purposes, suppose z is hunting returns (a phenotypic measure) and y and ϕ are underlying skills related to prey pursuit time and arrow length—presumably there are many more relevant representations for hunting. Using a linear regression equation, we can express the causal relationship between mental representations y and ϕ on success, z, as follows:[21]

$$z_i = \mu + \lambda_1 y_i + \lambda_2 \phi_i + \varepsilon_i \quad \text{(A10)}$$

The λ's give the relative contribution of an individual's y and ϕ skills to their observed success, z_i. ε gives uncorrelated random error, and μ specifies the constant term. An individual's value of f might depend on her success (z), among other factors:

$$f_i = m + \rho_1 z_i + \rho_2 x_i + e_i \quad \text{(A11)}$$

Here, ρ_1 is the partial regression coefficient of f on z (x is "other factors" and e is the uncorrelated error term). It tells us how much success in z affects one's likelihood of being selected as a cultural model. Putting this into the basic Price formulation for $\Delta\bar{y}$ yields:

$$\begin{aligned} \Delta\bar{y} &= \mathrm{Cov}(f, y) + E(f\Delta y) \\ &= \rho_1 Cov(z, y) + E(f\Delta y) \end{aligned} \quad \text{(A12)}$$

Including the causal relation between y and z, we arrive at the following:

$$\Delta\bar{y} = \lambda_1\rho_1 \,\mathrm{Var}(y) + E(f\Delta y) \quad \text{(A13)}$$

The $\Delta\bar{y}$ term would have the same form as above, and depends on how difficult it is to infer the underlying y_i by observing the model's behavior. The remainder of the derivation proceeds as above.

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Notes

1. Maladaptive changes make individuals less able to survive and reproduce. In the case of technology, this involves changes that reduce the ratio of benefits (e.g., in effective food production) to costs (e.g., of manufacture). Such changes may entail shifts in tool or weapon designs (e.g., in materials, shape, etc.), reductions in the number of composite parts, and/or modifications in the details of their application (losses in the nuances of skilled technique).

2. It's worth noting that the Tasmanians may have lost the ability to make fire (Plomley 1966:225, footnote 5), an absence that has been ethnographically recorded elsewhere among small isolated groups (e.g., Holmberg 1950: Siriono; Oswalt 1973: Andamanese). However, Gott's in-depth investigation has bought this old claim into serious question. It seems that at least some social groups on Tasmania likely had the ability to make fire when the Europeans arrived. At best, it's uncertain.

3. The range of fish exploited extended to 30 species, indicating the likely use of sophisticated baited-box traps or tidal fish-traps; meanwhile the species most effectively exploited by simple spearing were absent (Colley and Jones 1988).

4. One might wonder why, if fish dropped out of the diet

because the necessary skills, knowledge or technologies related to fishing dropped out, the Tasmanians showed an aversion to eating the fish offered to them by the arriving Europeans. Given what is known about food aversions and disgust (Rozin et al. 2000), the most likely explanation is that once fish dropped out (3,500 years ago), subsequent generations were never exposed to the idea of eating these cold, slimy, smelly creatures, so default disgust reactions kicked in. That is, without cultural learning, humans tend to show disgust reactions toward the idea of eating slimy, smelly things. In my own ethnographic fieldwork, I had the same reaction (as the Tasmanians to fish) to the Machiguenga's habit of snacking on the slimy (fatty) insect larva taken from underneath fallen logs, and the Mapuche's taste for drinking hot sheep's blood right from the animal's neck (for the record, I forced myself to drink the blood, but would not eat the larva unless they were fried first). It's also worth noting that while the Tasmanians enthusiastically ate the bread the European explorers gave them, they refused to eat (and were averse to) the butter the Europeans wanted them to put on the bread. The same disgust logic applies.

5. Henrich and Gil-White (2001) ground this cognitive capacity in evolutionary theory, develop a set of interrelated predictions about human psychology and ethnography, and summarize the data in support of these predictions. Among other empirical findings, this work shows that both children and adults pay particular attention to highly skilled or successful individuals (often unconsciously) and preferentially imitate them in a variety of ways (including in ways that do not directly relate to their domain of skill).

6. In studying the conditions for maladaptive deteriorations in skill, this is a highly conservative assumption that favors cumulative cultural adaptation.

7. The details of this distribution do not qualitatively impact the results—see Appendix C.

8. Based on a lack of evidence for significant genetic drift between Victorian Aborigines and Tasmanians, Pardoe (1991) suggests that the estimate of 4,000 may be low.

9. Thanks to Fraser Neiman for pointing out the analogy to assemblage diversity.

10. The pre-Holocene peninsula of "Greater Tasmania" (115,000 km^2) was first severed from Australia between 12,000 and 13,500 B.P., leaving an ocean crossing of 60 km to the mainland. Over the next 6,000–7,000 years, rising seas further inundated the Bassian plain and reduced Tasmania to its present size of 67,800 km^2.

11. Moreover, more complex models and analyses may show that cultural transmission is a multistage process, linked to the developmental cycle: young kids may rely on vertical transmission for initial skill and knowledge acquisition, and subsequently rely on prestige-biased transmission in adolescence and adulthood. In making conclusions about transmission, researchers have often failed to take into account that such a multistage scheme would look, at equilibrium, like pure vertical transmission.

12. Also see Lourandos (1997:274–278), White and O'Connell (1982:157–170), Sim (1999), Parry (1981), Bowdler (1980) and Thomas (1981). For the most part, these have dealt exclusively with the loss of fish in the Tasmania record and do not address the broader puzzle.

13. Yaghan used a baited line and sinker to draw fish to the surface, at which point they would either snatch them by hand, or spear them.

14. As noted above, Allen (1979) has argued that dropping fish from the diet was an adaptive move for the Tasmanians, given their latitude and the availability of seals and mutton-birds. This explanation predicts that high-latitude coastal foragers (particularly island dwellers) all over the world should tend to drop fishing entirely from their economic repertoire, lose their ability to manufacture the technology, and learn to disdain the thought of eating fish. The empirical record does not support this prediction. Furthermore, wouldn't it be more adaptive to retain some fishing know-how, and a taste for fish, for use when other sources are scarce, or during the appropriate seasons?

15. Vanderwal's suggestion that it was the colder conditions of the late Holocene in Tasmania that caused people to drop their clothing in favor of grease and ochre leaves one wondering why the Tasmanians of the last glacial maximum did not abandon their clothing (the archaeological record provides bone tools consistent with clothing manufacture), and why neither the Aboriginals to the north (snug in skin cloaks) nor anyone in Tierra del Fuego stopped manufacturing winter clothing.

16. Similar comparisons can be made for the foraging inhabitants of the Chatham Islands (Skinner 1923; Sutton 1980), which lie at the same latitude as the southern extremes of Tasmania.

17. Shennan (2001) illustrates the effects of drift on a population's adaptiveness. Unfortunately, this model is somewhat difficult to apply directly to the Tasmanian case because it assumes populations are initially perfectly adapted to their environment.

18. Drift explanations do provide useful insights into evolutionary processes involving domains of culture not strongly affected by selective transmission (Lipo et al. 1997; Neiman 1995).

19. Interestingly, *genetic* drift appears to have had only a very small effect on the differences between Tasmanians and Australian Aborigines from Victoria (Pardoe 1991).

20. Rivers (1912) was republished in Rivers (1926).

21. In general, we can do this for any number of mental representations, and study the interaction of different mental representations.

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