LETTER

Understanding cumulative cultural evolution

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In a narrow critique of two early papers in the literature on cumulative cultural evolution, Vaesen et al. (1) misunderstand the work they criticize, mischaracterize multiple lines of research, and selectively ignore much evidence. While largely recycling prior criticisms, they provide no new models, evidence, or explanations (2).

Not only do their criticisms of Henrich's (3) and Powell et al.'s (4) modeling assumptions miss their mark (2), but Vaesen et al. (1) also ignore many other models that do not rely on these assumptions yet arrive at similar predictions. These other models variously include conformist transmission and explore these processes using nonnormal distributions, discrete traits, networks, etc. (2, 5). Of course, no one expects demographic/population variables to be the only things that matter; cultural packages related to clothing or housing, for example, will vary with latitude for reasons unrelated to demographics, risk, or mobility.

Vaesen et al. (1) are correct that these models assume that at least some individuals can sometimes assess the relative success or payoffs of different traits or individuals, but they are incorrect in claiming that there is little evidence for such learning. First, they ignore a vast body of laboratory evidence showing that infants, children, and adults use cues of success, skill, or competence in learning (2, 6). Second, Vaesen et al. (1) also ignore work showing that (*i*) Hadza and Ache foragers acquire cultural information obliquely from broad networks (7) and (*ii*) success biases are well documented in traditional populations (2). Finally, the studies cited by Vaesen et al. (1) do not support their claims about vertical transmission; instead, all support the two-stage learning process used by Henrich (3), Powell et al. (4), and many others. Here, individuals initially learn from their parents, and then update only if they observe others who are more successful than their parents. Evidence from fisher-horticulturalists and foragers support this pattern and shows that second-stage updating from nonparents is particularly prevalent in domains with high variation in skill/success. For example, Aka foragers learn from great hunters and prestigious shamans (2).

Vaesen et al. (1) ignore laboratory tests of these models (2). Using novel learning tasks, several experiments show how group size and interconnectedness influence the accumulation of skill, know-how, and complexity, and some demonstrate the "Tasmanian effect" (8). If the models are so poor, it is peculiar that they have withstood multiple experimental tests by independent researchers.

Vaesen et al. cite studies by Collard and coworkers (refs. 67, 70, 72, 73, 75, and 79 in ref. 1) that do not find a significant relationship between census population sizes and complexity. However, the theory explicitly predicts that it is the size of the population that shares information—the effective cultural population size (3)—that matters, and if there is extensive contact between local or linguistic groups, there is no reason to expect census population size to correspond to the theoretically relevant population (2). Inappropriately, Collard and coworkers used highly interconnected populations, and make no effort to measure these interconnections or deal with the conceptual problems of using census estimates (refs. 67, 70, 72, 73, 75, and 79 in ref. 1). Finally, Vaesen et al. (1) ignore important findings linking population size to both linguistic complexity and innovation rates (2, 9, 10).

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APPENDIX TO

UNDERSTANDING CUMULATIVE CULTURAL EVOLUTION

Joseph Henrich, Robert Boyd, Maxime Derex, Michelle Kline, Alex Mesoudi, Michael Muthukrishna, Adam Powell, Stephen Shennan and Mark G. Thomas

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Aiming to critique work linking population size and interconnectedness to cumulative cultural evolution, Vaesen et al. (2016) recycle previously published concerns (Read, 2006; Vaesen, 2012b) about two papers, one published 12 years ago and the other 7 years ago (Henrich, 2004; Powell, Shennan, & Thomas, 2009). This critique misunderstands these models, neglects much subsequent theoretical work, either misrepresents or disregards the large literature on cultural learning (including their own publications), overlooks a growing body of experimental work that directly tests these models, selectively ignores existing supporting empirical work, and remains blind to crucial conceptual flaws in supposedly "negative findings".

Here, because an exhaustive point-by-point refutation of all the issues with Vaesen et al. would run into hundreds of pages, we review just the major problems with their critique. Notably, because responding to their claims about the Tasmanian case requires a detailed review of the existing evidence, we have set aside this case for a separate paper. Importantly, however, readers should realize that the Tasmanian case represents merely one case example in a large empirical body of evidence that includes multiple other case studies, comparative observational studies of tools, languages and innovation, and a variety of laboratory experiments. Thus, theoretically, little hinges on this single example.

UNDERSTANDING MODELS AND ASSUMPTIONS

In evolutionary biology, models are constructed to be optimally simple in order to capture and explore particular theoretical ideas. Each model acts as a kind of "mental prosthesis" that further sharpens our intuitions about the relevant evolutionary processes. The deepest insights arise from stepping back to consider an entire class of models that target the same underlying process from different angles. Contrary to this standard approach, Vaesen et al. ignore a broad class of models that build on Henrich's and Powell et al.'s early contributions while recycling a grab bag of off-target and generally inaccurate criticisms. In this section, we first evaluate their critiques of Henrich's model, then of Powell et al.'s model, and then we turn to the large but neglected modeling literature.

THE TASMANIAN MODEL

Vaesen et al.'s first criticism of Henrich's model— hereafter the 'Tasmanian Model' — focuses on a tactical assumption that all learners can locate, attend to and learn from the single most skilled or knowledgeable member of the previous generation—a payoff-biased strategy Vaesen et al. call "Best." As Vaesen et al. note, Henrich made this assumption because it *operated against* the very theoretical point he was making — that a sudden reduction in the effective population size of cultural models could result in a gradual loss of cultural know-how leading to an equilibrium of less adaptive technologies or cultural products. If he'd assumed learners were worse at locating the most skilled and knowledgeable individuals, he would have made it *easier* for the errors or noise in the cultural transmission channel to generate technological deterioration—a loss of know-how or skill. Vaesen et al. then argue that if learners rely solely on: (1) vertical transmission, (2) unbiased transmission or (3) conformist transmission then the relationship between population size and complexity does not emerge.

There are two problems with this critique: (1) it ignores that Henrich had already formally considered this in his original paper (i.e., he did not rely solely on the extreme Best assumption), and (2) Vaesen et al.'s choice of cultural transmission mechanisms are inconsistent with both the theoretical literature on the evolution of cultural transmission and with the empirical literature on social learning. Other than obtaining their preferred result, there is no justification for choosing them.[1]

Let's begin with the first issue: the Tasmanian Model already includes a version of vertical/unbiased transmission. As background for the model, N is the effective population size of cultural models and the parameters α and β, respectively, capture the average loss in skill or know-how due to transmission noise and the spread around that distribution. The variable $\bar{z}$ gives the average skill or know-how in the population, so $\Delta\bar{z}$ gives the change in average value of $\bar{z}$ per generation or time step. Incorporating vertical transmission into the model (unbiased transmission would be equivalent here), Henrich (2004: 205) wrote:

> 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):
>
> $$\Delta\bar{z} = p\left[-\alpha + \beta(\varepsilon + Ln(N))\right] \tag{4}$$
>
> 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.

Vaesen et al. say they carried out simulations for this study to show that vertical transmission does not create the link between population size and complexity. But, they also could have looked at Henrich's equation (4) and set *p* = 0. This automatically gives $\Delta\bar{z} = 0$, meaning no cumulative cultural evolution occurs. So, Vaesen et al.'s simulations merely reconfirm what Henrich's original analytical model had already demonstrated.

Henrich's equation (4) also shows that if there is a little success-biased transmission (*p* > 0), then cumulative cultural evolution can occur but the positive or negative rate will be smaller according to the degree of reliance on vertical or unbiased transmission (that is, according to *p*). Thus, Henrich's original model suggests that Vaesen et al.'s simulations of exclusively vertical or unbiased transmission capture only a special case that does not even generalize to situations in which cultural transmission is mostly vertical and only a

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[1] Also note, this critique is not new. Vaesen et al. are recycling an old criticism by Read (Jones, 1995; O'Connell, Allen, & Hawkes, 2010), which Henrich (2006) dealt with at length a decade ago.

little payoff biased. Below, we will review the empirical evidence on actual human cultural learning to show the assumption of $p > 0$ is quite reasonable.

Vaesen et al. also point to models that implement *pure* conformist transmission (Vaesen, 2012b). Pure conformist transmission is an inappropriate choice since both theoretical and empirical research suggests that learners should, and do, use conformist transmission *in combination with other learning mechanisms*, including payoff-biased cultural learning. Nakahashi et al. (2012), for example, predict the use of conformist transmission in spatially variable environments but payoff-biased transmission in general, especially when facing temporally varying environments.[2] In some situations, these models predict a mix of payoff and conformist biases (also see Guzman, Rodriguez-Sickert, & Rowthorn, 2007; Kendal, Giraldeau, & Laland, 2009). Other work shows how conformist transmission operates synergistically with payoff or success-biased transmission to improve adaptive learning. For example, learners can first select a sample of cultural models of size k (say $k = 3$) from the population using success biased cultural learning. A young hunter might pick the three best hunters in the community. Then, precisely because our cultural transmission is error prone, learners apply a conformist algorithm like 'copy the majority or plurality' (Henrich & Boyd, 2002: Model 2). If payoffs do not vary or are too uncertain, this algorithm operates like pure conformist transmission. This obtains the adaptive benefits of using payoff or success-biased transmission while simultaneously increasing transmission fidelity using conformist transmission.

Empirically, the use of diverse and integrated cultural learning strategies is supported by much laboratory research (Efferson, Lalive, Richerson, McElreath, & Lubell, 2008; Mesoudi, 2011b; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). The most relevant studies are those that (i) pit payoff bias and conformity against one another, rather than only allowing participants to employ one of them in comparison to asocial learning, and (ii) use tasks that are relevant to cumulative technological change, i.e. where there are objective payoff differences between behavioral options. Three laboratory studies fulfill both of these criteria (Efferson et al., 2008; Mesoudi, 2011b; Molleman, van den Berg, & Weissing, 2014; also see Muthukrishna, Shulman, Vasilescu, & Henrich, 2013). McElreath et al. and Mesoudi both found that people preferentially employ payoff-bias over conformist transmission. Molleman et al. found individual differences in social learning strategies (some people prefer conformity, others payoff bias), but crucially this was partially task-dependent: in tasks with a clear payoff-difference between options, payoff bias was used more often, whereas in coordination tasks where it only mattered that you coordinate on other players' choices, conformist transmission was used more often. All this suggests that in tasks most relevant to cumulative cultural evolution (e.g. technology), cultural learning is likely to be payoff-biased. Now, Vaesen et al. might argue that these studies with WEIRD undergraduates (Henrich, Heine, & Norenzayan, 2010a)[3]

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[2] It's worth noting that there's almost complete agreement that environments were changing *temporally* in Tasmania during the Holocene (Cosgrove, 1999).

[3] WEIRD is a commonly used acronym that stands for Western, Educated, Industrialized, Rich and Demographic (Henrich, Heine, & Norenzayan, 2010b).

are irrelevant to past hunter-gatherer behavior, though that would be inconsistent since they themselves cite such WEIRD studies. In fact, Vaesen (2012a) builds his entire case about *human* cognition vis-à-vis other animals based on WEIRD studies. Nevertheless, below we review the literature on cultural learning based on evidence from infants, small-scale societies and chimpanzees. Together, this triumvirate provides ample evidence to expect these results to broadly generalize.

Next, Vaesen et al. criticize Henrich's definition of "complexity." We deal with this specific component of the critique in detail below, but at least part of the problem seems related to a basic failure to understand the process of operationalizing a theoretical concept in order to measure and test it. To see what we mean, consider that Henrich did not actually use the term "complexity" in developing his model. His model examines the cultural evolution of a variable that measures adaptive know-how or skills. Then, one has to apply the model to data. This is "operationalization." In moving to the data, Henrich then uses the word "complexity" for the first time because it is the term Oswalt (1973, 1976) used in creating a measure based on the number of distinct tool types and the number of discrete parts in each tool. Oswalt's measures are reasonable proxies if having more elements makes things harder to learn or keep in memory. Reasonable people can argue about the best way to operationalize the model; but this is not a critique of the model per se. A productive critique would be to offer alternative approaches to operationalization (how to better go from theory to test).

We also note that Vaesen et al.'s critique of Henrich's use of Oswalt's term "complexity" applies directly to all the empirical work of Collard and colleagues that Vaesen et al. cite later in their paper, in support of their position. If Henrich's operationalization of his theoretical concept into various tool complexity measures is useless, then all of the work of Collard and colleagues is similarly uninformative (Buchanan, O'Brien, & Collard, 2015; Collard, Buchanan, Morin, & Costopoulos, 2011a; Collard, Kemery, & Banks, 2005; Collard, Ruttle, Buchanan, & O'Brien, 2012; Collard, Ruttle, Buchanan, & O'Brien, 2013c). Overall, with regard to the Tasmanian Model, the only substantive issue brought up by Vaesen et al. involves the empirical question of the importance of some forms of payoff or success-related biases in small-scale societies—we address this below.

CRITIQUES OF POWELL ET AL.

Vaesen et al. state that Powell et al. make two key assumptions in their model, which they call into question. The first is the 'Payoff' assumption, that cultural transmission is a two-stage process, with parental inheritance followed by payoff-biased transmission where this leads to an improvement in performance. As is demonstrated elsewhere in this response, and contrary to Vaesen et al.'s claims, there is extensive evidence in support of this assumption for a wide range of activities where performance-based criteria are relevant.

The second assumption is what they call the 'Complexity Maximization' assumption, *"that when a population increases in size, its members will always opt to adopt more complex cultural traits*". The claim that this assumption is made is simply not true, so all the many points they go on to make about the problems with 'Complexity Maximization' are off base. The outcome of the simulations in terms of increased adaptive know-how or skill as per Henrich's model simply follows from the operation of payoff bias at the second stage of transmission in the context of varying cultural effective population sizes. Powell et al. do suggest at the end of the paper that there might be *"a degree of positive feedback on population density after the accumulation of culturally inherited skills"* (Powell et al., 2009: 1301), though as a conservative measure they do not explore it. However, given that we are dealing not with neutral traits but with traits where performance is relevant, the suggestion that improvements might result in increases in survival and reproductive success seems, to say the least, not unreasonable.

Vaesen et al. go on to a critique of Boserup's well-known model in which increased population pressure leads to subsistence stress that then spurs innovation. Although her model cannot be as easily dismissed as they seem to imagine (R. D. Lee, 1986; J. W. Wood, 1998), we acknowledge that other responses to subsistence stress are possible, as they point out. They then go on to ask, supposing Boserup is right and growth makes populations innovate, why do we need cultural transmission processes to account for cultural complexity. By answering this question we can also address the question of why the response to stress is not always innovation. The answer is histories of contact. Innovations cannot be simply called into being by the problems they would solve (Diamond, 1997), or at least only the simplest ones can be, like shortening the fallow period in Boserup's agriculture model. Instead, populations often go extinct due to an inability to innovate solutions (Diamond, 2005; Henrich, 2015). The probability of relevant local innovation is greatly increased by contact with the results of innovations in other groups, at least one of whom may have already arrived at a solution to the problem. A clear example of this is the Siberian Khanty borrowing features from Russian horse-drawn sledges in response to the shortcomings of their traditional designs in the face of the increased stress resulting from being pulled by snowmobiles (Jordan, 2015, and)—see 'cultural learning evidence' section for more detail. This 'contact' represents social connections that increase the effective population size of cultural models (Henrich, 2009).

This point is relevant to other papers that have found no relationship between population and measures of complexity. For example, Buchanan et al. (2015) in their study of the factors affecting the diversity of lithic point types in Texas prehistory find no relationship between the diversity of point types and their population proxy, arguing that it is environmental risk that leads to innovation in point design, but they dismiss the fact that bow-and-arrow technology arrived in the region by a process of diffusion from outside as a mere 'proximal factor'. This entirely misses the point that if people had not had contact with the result of the diffusion of bow-and-arrow technology through North America over the previous several thousand years this innovation would not have been available to them, however useful it might have been. Since the peoples of Australia never invented the bow and arrow, are we to assume that nowhere in the entire continent over 50,000 years did the ecological conditions produce the need for bows and arrows (but favored boomerangs)?

In the Abstract of their paper, Powell et al. explicitly state *"that demography is a major determinant in the maintenance of cultural complexity and that variation in regional subpopulation density and/or migratory activity results in spatial structuring of cultural skill accumulation"*. Indeed, one of the main findings in Powell et al. is that the effects of population density and migratory activity on cultural complexity are confounded (also see Grove, 2016). It is puzzling that Vaesen et al. choose not to mention this finding – preferring instead to isolate their target (population size) – yet in other parts of their paper and other studies they cite, they admit the possibility that inter-group contact influences cultural complexity. This confusion is repeatedly apparent in the *Empirical Assessment* section and in Fig. S5, where Vaesen et al. go on to make the novel claim that *any* increase in population size of any magnitude should immediately result deterministically in Upper Paleolithic-like technology. Powell et al. estimate – crudely, as is acknowledged – the critical value of effective population density required to *retain* the complex technology characteristic of the Upper Paleolithic in Europe. This calibration is then used to estimate the time of appearance of similarly complex technology in other regions with some success, as discussed below.

In the same section, Vaesen et al. highlight concerns over inferring regional effective population size through time from genetic data. Powell et al. cautiously used regional estimates from Atkinson et al (2008), based on Bayesian coalescent inference from modern mitochondrial DNA (mtDNA) sequences; they found congruence with the predictions of their model in regions where they considered the estimates of population size to be least problematic. As clearly stated in Powell et al., an important confounder of effective population size in these inference methodologies is population structure; changes in the latter can lead to signatures of changes in the former. Powell et al. therefore only considered as reliable inferences made for regions where there was reasonable evidence for population mixing (J. Z. Li et al., 2008; Rosenberg et al., 2002, both cited in Powell et al. in relation to this issue). This is the reason Powell et al. give as to why estimates for south, central and northern Asia may be incongruous, and are not "*… due to the low resolution of their single-locus population estimates, which were taken from Atkinson et al.*", as Vaesen et al. incorrectly assert.

In a recent study by Mazet et al. (2016), this confounding of size and structure in effective population size inference using genetic data was formally shown to stem from a parameter known as the inverse instantaneous coalescence rate. Mazet et al. (2016) also show that this issue applies to all coalescent-based population size inference methodologies developed to date that use genetic data, including multilocus/whole genome approaches such as PSMC (Pairwise sequentially Markovian coalescent: H. Li & Durbin, 2011) and MSMC (Multiple sequentially Markovian coalescent: Schiffels & Durbin, 2014), the latter of which Vaesen et al. cite as an alternative. Thus, recent studies have only enhanced the justification Powell et al. give for considering past population size change inferences from genetic data only in cases where there is evidence of population mixing (J. Z. Li et al., 2008; Rosenberg et al., 2002). Vaesen et al. critiques here off target.

Importantly, Powell et al. show that increased population size and/or increased migration (i.e. reduced population structure) will lead to increased cultural complexity, whereas Mazet et al. (2016) show that increased population size and/or decreased migration (i.e. increased population structure) will lead to increased neutral genetic diversity. Thus, in terms of effects on cultural or genetic diversity, population size and structure are confounded in opposite ways. The reason for this is that the model of Powell et al. (and of Henrich) are not neutral evolutionary models, whereas those used in inferences about population size from genetic data are. Unfortunately, this will limit the utility of coalescent-based ancestral population size inference using genetic data for studies on cumulative culture, unless population structure can be accurately controlled for.

KEY THEORETICAL LITERATURE IGNORED BY VAESEN ET AL.

Vaesen et al. ignore a large theoretical literature that supports the results of Henrich and Powell et al. A diversity of other models have explored the robustness of the assumptions made by those developed earlier, and reformulate the ideas in new and different ways—often extending the earlier insights. The upshot is that nearly all of the targeted theoretical criticisms leveled at Henrich and Powell et al. by Vaesen et al. have already been addressed by later (and sometimes earlier!) models (Enquist, Strimling, Eriksson, Laland, & Sjostrand, 2010; Grove, 2016; Henrich, 2009; Kobayashi & Aoki, 2012; Kolodny, Creanza, & Feldman, 2015; Lehmann, Aoki, & Feldman, 2011; Lehmann, Feldman, & Kaeuffer, 2010; Lewis & Laland, 2012; Mesoudi, 2011c; Pradhan, Tennie, & van Schaik, 2012; van Schaik & Pradhan, 2003). Vaesen et al. somehow missed most of these in their narrow focus on two older papers. Let us begin with extensions of the Tasmanian Model.

Subsequent studies not cited by Vaesen et al. have relaxed Henrich's assumption (p = 1, Equation (4)), including Powell et al. (2009), and still found a link between effective cultural population size and cumulative cultural evolution (Kobayashi & Aoki, 2012; Mesoudi, 2011c; Muthukrishna & Henrich, n.d.; Pradhan et al., 2012; van Schaik & Pradhan, 2003). The most direct reformulations of Henrich's model actually demonstrate its robustness. Kobayashi & Aoki (2012) reformulated Henrich's model in terms of maximum rather than mean complexity, and in a way that does not require the Price equation, as well as incorporating overlapping rather than discrete generations. For large population sizes, this model actually predicts a *larger* effect of population size than the original Henrich model.

Vaesen (2012b) adapted Henrich's model replacing the Gumbel distribution with a Normal distribution.[4] To the contrary, Vaesen (2012b: 5) found that *"Henrich's qualitative results still obtain under assumptions of Normality"*. A Normal distribution produces a slightly reduced effect of population size compared to the Gumbel, but in conceptual

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[4] The Gumbel distribution is an extreme value distribution with a double exponential. It can be characterized by two parameters, capturing the mode and scale. Compared to the Normal distribution, it has 'thick tails'.

models like this, such a relatively small difference in magnitude is irrelevant compared to the qualitative result. Nevertheless, what is often unappreciated is that selective processes like those modeled by Henrich often tend to converge toward a Gumbel distribution, not a Normal distribution. This is why Henrich originally used the Gumbel—it's a feature of rank-order statistics (Sornette, 2006). Under selective processes, it's very likely a better approximation than the Normal distribution—see below for an empirical test.

But, if any concern remains about the Gumbel distribution or other aspects of either Henrich or Powell et al.'s models, several other researchers have taken entirely different approaches and still arrived at the same place: a robust relationship between effective cultural population size and cumulative cultural evolution under some conditions. For example, Mesoudi (2011c) constructed an agent-based simulation that explicitly tracked individuals and their traits, and added realistic additional assumptions such as that individuals have lifetime limits on the amount of information they can acquire. Cultural complexity increased with population size under assumptions of both direct bias (copying effective traits) and indirect bias (copying the individual with the best overall set of traits).

A number of papers also illustrate the relationship between population interconnectedness or mobility and cumulative cultural evolution that both Henrich and Powell et al. emphasized (also see Grove, 2016). In a simulation model, Kempe et al. (2014) found that cultural complexity increases with the number of demonstrators, which is a sensible way of modeling interconnectedness. Kempe et al.'s finding dovetails with a modification that Kobayashi and Aoki (2012) made of Henrich's approach in which they modeled parameters for both the number of demonstrators per learner (k, interconnectedness) and the total population size (N). Both had important influences on cumulative cultural evolution. This represents another way of showing the mobility findings in Powell et al.

Still other modeling approaches converge on the same results from a different direction. In a model focused on only one trait, but which can be readily extended to multiple traits, Henrich (2009) showed the power of interconnectedness to spread hard-to-learn traits through a population. In a more extensive exploration, Enquist et al. (2010) demonstrated the effects of (1) population size, (2) interconnectednesss (number of demonstrators) and (3) number of social learning trials on the spread of a hard-to-learn trait. For a similar approach applied to primate evolution, see the work of Pradhan and her collaborators (Pradhan et al., 2012; van Schaik & Pradhan, 2003).

Using yet another modeling approach involving discrete traits, Lehmann et al. (2011) studied the number of independent traits possessed by individuals and populations. Though these traits did not build on each other or interact at all, the results still show that larger populations maintain more traits. In fact, Lehmann et al. (2011) show that *even under unbiased or vertical transmission* larger populations will tend to have greater cultural complexity—e.g., larger toolkits (more items). This is because in smaller populations discrete traits can be lost more easily (also see Shennan, 2001), in the same way that genetic drift reduces variation.

In a large simulation of genes and culture using an island model population structure, Muthukrishna et al. (n.d.) begin with a small population with little social learning, no two-stage learning life stage (as assumed by Henrich and Powell et al.) and no payoff-biased oblique learning.[5] Nevertheless, despite deliberately stacking the deck against social learning and oblique transmission by always giving individual learners an opportunity to improve their knowledge with a second round of individual learning, the model gives rise to a feedback loop that favors a heavy reliance on social learning, a two-stage learning lifecycle with a second stage of oblique learning, and pressure toward more potent payoff-biased oblique transmission. These predictions offer theoretical justification for Powell et al. and others modeling choice of a two-stage learning process and suggest an evolutionary pressure towards getting better at identifying the model with the most adaptive knowledge. Not surprisingly, the simulations also show how the robust relationships between population size, interconnectedness and cultural complexity evolve via culture-driven genetic evolution.

Finally, using a population-level model focused on cumulative cultural evolution, Kolodny et al. (2015) found that cultural complexity was strongly influenced by population size, as well as other factors such as innovation processes. This large simulation model looks nothing like the other models, yet arrives at the same conclusion.

In summary, a wide variety of different approaches, including both analytic and simulation-based models, from different authors with different assumptions about traits, distributions, modes of transmission, costs and behaviors have—at least under some conditions (like Henrich and Powell et al.)—reveal a causal link between population size or interconnectedness and cumulative cultural evolution. By focusing narrowly on the assumptions of two early models, Vaesen et al. give an unrepresentative and inaccurate picture of the current theoretical literature. Our more comprehensive review suggests that—theoretically—population size and interconnectedness should often be important drivers of cumulative cultural evolution, given that their effect is robust to changes in so many different modeling setups and assumptions. Of course, we also expect other factors, such as ecological climatic variables and the payoffs of improved technology, to influence cumulative cultural evolution both directly and indirectly, via their influence on population size and interconnectedness.

Thus, Vaesen et al.'s critique fails to address the large literature that has emerged in the wake of Henrich and Powell et al.'s publications. This means, independent of the value of their specific criticisms of Henrich and Powell et al., the overall critique is of little worth in considering the larger thrust of the current literature.

CRITIQUING THE DEFINITION OF "COMPLEXITY"

> *One problem with Henrich's definition of cultural complexity (11) is that it is not the only one that has been proposed. Simon (36), for instance, argued that*

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[5] During cultural transmission, learners sample from a Normal distribution, not a Gumbel.

> *cultural complexity should be defined in terms of the interdependencies among the components of cultural items. In contrast, Oswalt (37, 38) measured complexity of subsistence tool- kits by counting the number of different types of tool parts. The existence of other definitions of cultural complexity would not be a problem if the other definitions yielded the same results as Henrich's model (11), but such is not the case. Querbes et al. (39) have shown that Simon's definition (36) only yields a population size effect in some conditions. Currently, there are no grounds for preferring Henrich's definition (11) over those definitions put forward by other researchers. Therefore, the results of Henrich's model (11) are dependent on an unjustified definition of cultural complexity, as well as on an unjustified assumption about the nature of cultural transmission*. (Vaesen et al., 2016: 2)

Here, Vaesen et al. seem to be saying that if you define a term one way—e.g., the way Henrich, Read and Collard operationalized 'complexity' following Oswalt—but someone else has defined it another way, then you are wrong unless the same results are obtained using all prior definitions of the term.[6] This makes no sense to us.

Nevertheless, the description of the Querbes et al. model result cited here is incomplete and misleading. Querbes *et al.* (2014) attempt to embed Herbert Simon's (1962) definition of complexity within the *NK*-fitness landscape framework[7], first introduced by Kauffman & Levin (1987), to investigate the population size effect. Notwithstanding the surprising omission of any reference to over 20-years worth of literature on the fruitful application of NK-models to economic and technological systems (Auerswald, Kauffman, Lobo, & Shell, 2000; Frenken, 2006; S. A. Kauffman & Macready, 1995), their model *actually qualitatively recapitulates* Henrich's (2004) results, under the shared assumption of 'BEST' payoff bias (Querbes et al., 2014: final 2 paragraphs of Results and Fig. 4). Thus, the central criticism leveled by Vaesen et al. at the definition of complexity is completely misplaced, collapsing instead to a general criticism about the realism of the 'BEST' cultural learning bias, which allows identification of, and access to, the maximally skilled or knowledgeable cultural model. This off target critique is dispatched elsewhere in this response.

While downplaying this awkward – and from our point of view – confirmatory result, Querbes *et al.* (2014) instead expend a great deal of effort in describing the outcome of a 'WEIGHTED' payoff bias, under which cultural models are selected with a probability proportional to their fitness. The 'WEIGHTED' pay-off bias results in consistently higher z_{max} values in a larger population, yet the proposed transmission error model is almost

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[6] The quotation also fails to separate the theoretical concepts developed by Henrich (2004), where neither the term nor concept 'complexity' were involved, from the operationalization of the theory for the purpose of empirical testing—see prior comments.

[7] Briefly for clarity, the *N* parameter in the *NK* model refers to the number of fundamental 'units' or 'elements' in an organism's genome or, in this context, a cultural or technological system. *K* determines the average interconnectedness, or epistasis, between the *N* elements, such that a change in the state of one will result in a change in overall fitness determined by the states of *K* others. Querbes *et al.* use *P* to refer to different population sizes of cultural learners.

perfectly designed *a priori* to rapidly remove any variance in cultural model *z*-values, thus rendering the bias useless. Error operates to move the average naïve individual between 0.1 (μ=0.01, *N*=10) and 25 (μ=0.5, *N*=50) 'mutational steps' away from their chosen cultural model in *NK*-space. As the authors acknowledge, most of this range would distribute naïve individuals to *NK* locations with effectively randomly drawn *z*-values, even in highly correlated *NK*-space (i.e. relatively low *K*). So under much of this (μ,*N*) parameter space, their instantiation of 'WEIGHTED' payoff bias quickly converges to randomly sampling *NK*-space, such that all *z*-values approach 0.5 (i.e. the global mean) and thus the population size effect naturally disappears. With lower μ, a population size effect holds for the measure $\Delta\bar{z}$, only disappearing consistently for maximal, or near maximal, *K*. With $K \approx N$, or even for moderately large and increasing *K,* the *NK*-landscape exponentially rapidly becomes so rugged that even very local moves (i.e. small errors) result in completely uncorrelated *z*-values; the so-called 'complexity catastrophe' that limits the evolvability of the entire system (Kauffman & Weinberger, 1989). Querbes *et al.*'s model provides no mechanism for the apparently spontaneous emergence of complex cultural traits or artifacts in an *NK*-space so intricate that they cannot be transmitted assuming even the most minimal error. Again, for the measure $\Delta\bar{z}$ the population size effect exists up to moderately high *K*, although the high level of stochasticity demonstrated makes it difficult to judge when the effect disappears consistently. Rather than relying on the constant baseline comparator of population size *P*=10, for which the variance is likely too high to find a significant effect (as the authors note), pairwise comparisons between *P* = [10,20,50,100,500] might instead have been more informative.

Third, the attempt to operationalize Simon's (1962) definition of complexity, which is largely concerned with the central notion of hierarchy, actually reaches no further than brief mention in the Introduction and their Fig. 1 (which is taken from Stout (2011)). Querbes *et al.*'s model is explicitly non-hierarchical, and after the Introduction there is not another single mention of 'hierarchy' or discussion of how their model would speak to such complexity. Thus, Querbes et.al. create and operationalize another definition of 'complexity', different from Henrich and Simon. This would seem to run afoul of Vaesen et al.'s concern about the devastating impact of the co-existence of different definitions of the same word.

In total, Vaesen et al.'s critique of Henrich's use of the term "complexity" is misguided, which if it weren't invalid, would apply equally well to the work of the second author, Collard (as well as Read), whose null results are instead highlighted approvingly by Vaesen et al.

CULTURAL LEARNING EVIDENCE

Many models, including Henrich and Powell et al., assume that at least some individuals can assess the relative success or payoffs of different traits or of other individuals. Vaesen et al. are correct on this claim, but they are incorrect in stating that there is no real-world evidence of success- or payoff-biased cultural learning in small-scale societies.

The problems are threefold. First, Vaesen et al. ignore a vast body of carefully controlled laboratory evidence which shows that infants, young children, adolescents and adults in WEIRD societies use cues of success, skill, or competence in learning (e.g., Atkisson, O'Brien, & Mesoudi, 2012; Chudek, Brosseau, Birch, & Henrich, 2013; Chudek, Heller, Birch, & Henrich, 2012; P. L. Harris & Corriveau, 2011; Henrich, 2015; Henrich & Gil-White, 2001; Mesoudi, 2011b; Mesoudi & O'Brien, 2008; L. A. Wood, Kendal, & Flynn, 2013; Zmyj, Buttelmann, Carpenter, & Daum, 2008; Zmyj, Buttelmann, Carpenter, & Daum, 2010). They also ignore evidence for such biases in chimpanzees (R. Kendal et al., 2015). Converging evidence from both human infants and chimpanzees suggests that payoff- and model-based learning biases may be a reliably developing feature of our species and perhaps others, not a peculiarity of WEIRD people.

Second, Vaesen et al. ignore direct evidence for such cultural transmission patterns in foragers as well as other small-scale societies. Recent work among both Hadza and Ache foragers shows that people acquire cultural information (including about tool making) from diverse social networks that stretch well beyond their parents and even bands (Hill, Wood, Baggio, Hurtado, & Boyd, 2014). Meanwhile, evidence from both rural sociology and development economics documents the use of success- or payoff-biases in traditional societies for adopting novel technologies and economic practices (Banerjee, Chandrasekhar, Duflo, & Jackson, 2013; Conley & Udry, 2010; Rogers, 1995).

Finally, as we'll see below, the studies of learning and cultural transmission in small-scale societies that Vaesen et al. do venture to cite in fact *support* the two-stage model used by Henrich, Powell et al. and several other modelers when the breadth of the evidence is evaluated as a whole. In the two-stage model, children first learn from their parents or family members and then later consider updating using some form of biased oblique transmission. Empirically, essentially all of the available field studies are consistent with this picture, though some lack conclusive evidence to indicate whether the oblique transmission is influenced by cues linked to success, prestige, age, or payoffs. Perhaps the most comprehensive data comes from a decade long study of Yasawan marine-forager-horticulturalists in the South Pacific. Data from multiple studies by different researchers using different protocols supports both the two-stage model and the extensive use of cues related to prestige, success, skill and expertise (Henrich & Broesch, 2011; Henrich & Henrich, 2010; Kline, Boyd, & Henrich, 2013). In addition to these cues, Fijians also use older age as an indirect cue, which can effectively carry payoff information for a number of evolutionary reasons (Henrich, 2015; Laland et al., 2011; Rendell et al., 2010). Further, in the two stage model, learners should only update later in life, and when those most skilled or knowledgeable are substantially better than their parents or family (Henrich & Broesch, 2011). Consistent with this prediction, Fijians update via oblique transmission especially in highly variable domains of skill or success (Kline et al., 2013). Kline et al. capture this shift by comparing high- and low-skill tasks, learned at different ages. With both skill difficulty and with age, oblique transmission becomes more common, in contrast to vertical transmission. Crucially here, we see a single adaptive learning mechanism that produces rather different phenotypic patterns depending on the domains in question and the societal context. Moreover, Kline's (2015) review of the ethnographic record on teaching – a high-cost form of social learning –

reinforces the view that, across societies, cultural transmission can occur through oblique and horizontal as well as vertical transmission.

Here's a review of the most recent work on cultural learning in small-scale societies:

1. In a synthesis of how people learn to hunt in small-scale societies, MacDonald (2007: Table 1) reveals the two-stage pattern: early vertical learning followed by later-life oblique updating. Her qualitative data show that across populations, early childhood learning about hunting happens with fathers or both parents. Then, attention shifts toward learning by co-hunting with older peers and adult men during adolescence and adulthood. Given that hunting is usually a high variance domain, this fits the Yasawan pattern nicely as well as the prediction of the two-stage model.
2. Among Tsimane forager-horticulturalists, Schniter et al.'s (2015) extensive study found that although people acquire the *basic* foraging skills in their pre-reproductive life stages, they continue to update those skills throughout adulthood. Further, foraging knowledge among the Tsimaneʼ peaks during the post-reproductive life phase, after a person's children are self-sufficient. Elders' knowledge is both highly respected and broadly shared well beyond their children. In addition, elders focus on developing prowess in high-skill, low-strength tasks where vertical transmission is unlikely because the parents of post-reproductive individuals are likely dead. Paralleling this research team's findings, detailed studies by a separate team also show that the transmission of ethnobotanical skills and knowledge among the Tsimane is mostly oblique, not vertical or horizontal. In this study, learners are attending in particular to older, non-parents (Godoy et al., 2009).
3. Among Jenu Kuruba honey gatherers in India, Demps et al. (2012) found similar cohort-based shifts in cultural learning strategies. Specifically, her results show that fathers are highly important sources of learning in middle childhood, but less so in adolescence. Brothers and elder kin are increasingly important in adolescence and adulthood, depending on the particular skill learned.
4. Among Khanty foragers in Siberia, Jordan's analysis (2015) of ski designs reveals the two-stage learning process. Basic ski designs are passed on from parents to sons, who then continue experimenting with novel traits they either invent independently, or copy from others. Jordan writes, *"This cumulative two step process of inheritance and payoff-based adjustment is driven primarily via functional performance criteria…"* (Jordan, 2015: 183). He also notes the impact of several technologies learned from external contacts with other cultural traditions. These, by definition, cannot be vertically transmitted. For example, the newly adopted snowmobile created mechanical stresses on sledges that the traditional sledge design was not equipped to meet. One innovator produced a more robust hybridized design by borrowing features from Russian horse-drawn sledges.[8] At the time of Jordan's study this hybrid design was spreading across

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[8] On the other side of the world, Netsilik hunters observed the saws of early European explorers and copied the designs by using antler (2004).

different Khanty communities through kinship contacts, by a process of payoff-biased transmission, while trial-and-error experimentation was also continuing to occur (Jordan, 2015: 201).

5. Among Kalahari foragers, aspiring hunters accompany, observe and learn from expert trackers (Liebenberg, 1990). For example, Liebenberg (Liebenberg, 1990: 43) writes, *"Hunter-gatherers share their knowledge and experience* [about hunting] *with each other in story telling around the campfire"* (('[ ]' are our addition, also see Blurton Jones & Konner, 1976). Such sharing will create both oblique and horizontal transmission since foraging bands are mostly non-relatives (Hill et al., 2011).
6. Among Penan hunter-gatherers in Borneo, ethnographic observations support the two-stage transmission model, and also provide clear evidence of success- and payoff-biases (Puri, 1997). For example, Puri (1997: 401) writes, *"Experts often point out animals and children learn to pick them out and recognize key characteristics for identifying them."* Puri also discusses how the Penan adopted methods for teaching dogs to hunt from nearby farmers, and also adopted a hunting technique from other foraging groups that involves imitating macaque calls in order to attract pigs and deer. The *"most knowledgeable practitioners"* of this technique *"all learned it from Kenyah on the lower Kayan River, who say they learned it from Punan hunters that once lived in the Pujungan-Lurah-Bahau area."* The renowned Penan expert on the technique reports teaching it to his *"son, nephews and several Kenyah men of the Long Peliran during the last decade or so"* (Puri, 1997: 280). Thus, these foragers widely engage in expert-biased oblique transmission for crucial elements in their hunting repertoire.
7. Studying both Congo Basin horticulturalists and foragers, Aunger (2000) used patterns of association in foods taboos to show how these are learned from parents during adolescence but then are updated after the age of 20 based on non-familial social partners.

Aunger's (2000) work is particularly important because self-report studies with this same group suggest that the normative pattern of transmission is vertical, but that when the patterns are evaluated using behavioral metrics, a two-stage updating process emerges. That is, if you simply ask people who they learned from, they tend to report a parent. This is consistent with the normative model ("important things are learned from parents"), and suggests that either people report only their initial source of learning (stage 1) of a two-stage model (see Demps et al., 2012 for discussion), or that there really is no opportunity for stage 2 updating. However, Aunger (2000) compared measurable cultural traits of parents with their adult children, and found that children did not in fact match their parents' cultural traits; they had updated those traits after learning them from parents initially. This is similar to WEIRD societies, where despite common beliefs in parental socialization, horizontal and oblique cultural transmission dominates (J. R. Harris, 1995).

Lacking a psychologically-rich and evolutionarily-grounded theory, Vaesen et al. simply take each study separately and don't always find strong evidence for oblique payoff biases, so they conclude that the evidence is mixed. However, when such a theory is applied to the data as a whole and methodological differences are considered, the most likely explanation for the collection of results is that studies based on retrospective self-reports often capture only Stage 1 learning. This likely occurs for three reasons. First, Stage 1 (vertical or family transmission) occurs first and often involves certain basic skills, giving it priority in people's minds. Second, such retrospective self-report questions might simply evoke the local normative model for parental socialization (which might exist because Stage 1 exists). Third, the fact that learners only update obliquely when (a) variation exists among potential models and (b) other models are more successful or skilled than one's self or one's parents (Henrich & Broesch, 2011). This means that in some contexts, such as when traits are widely shared or adaptive processes have reached equilibria, no oblique updating will occur.

This can be seen in the classic study by Hewlett & Cavalli-Sforza (1986), where Aka participants self-reported learning most skills from their same-sex parents. However, in that same paper, Hewlett and Cavalli-Sforza report that Aka boys and young men learn hunting from great elephant hunters, and healing from prestigious shamans. This is evidence that expertise-biased oblique transmission was important, though not reported under the method Hewlett and Cavalli-Sforza used. In addition, without the possibility of horizontal transmission, it would be impossible to explain how the Aka adopted recently arrived crossbow technology. Again, viewed as a collection of facts about the world – rather than a simple tally of positive or negative results, this is all consistent with a two-stage model: learners update via oblique transmission only if novel traits or superior models are available, as in domains like elephant hunting and shamanism, where skill level varies to a great degree. Further, in later work based on decades of study of the same populations, Hewlett et al. (2011) point out that the 'vertical-transmission only' story contrasts with the daily lives of children, especially in middle childhood, when they spend large amounts of time in mixed-age peer groups or with alloparents. The authors conclude that in this context, it would be surprising if transmission and social learning were not taking place. Even in egalitarian hunter-gatherer groups like the Aka, there is individual variation in skill and specialized knowledge (Hewlett & Lamb, 2005) that would make learning from non-parent experts worthwhile in an evolutionary sense (McElreath & Strimling, 2008). As a whole, these studies demonstrate a breadth of evidence for the two-stage life history pattern of learning that Vaesen et al. argue does not characterize human learning. To the contrary, the data support theoretically motivated predictions that human learning is flexibly adaptive, with transmission occurring through different pathways over the life course depending on costs, benefits and opportunities (Henrich & Broesch, 2011; McElreath & Strimling, 2008).

In light of this, it's important to consider how the two-stage process would operate in populations of different sizes. The two-stage model posits that learners only engage in selective (payoff-biased) cultural learning when they encounter individuals of sufficient success, skill or know-how (vis-à-vis what they acquired from their parents) to compensate for the cost of their time, attention and learning. Crucially, in larger and more interconnected populations, the identical learner will be more likely to encounter such individuals—individuals with more and better skills, techniques and know-how. To make this more concrete, suppose learners use a heuristic along the lines of “if someone is 20% better than mom, do the work and copy them,” then one is just more likely to encounter someone who is sufficiently better than mom to fire up stage 2 cultural learning. With more nuanced theoretical insights like this one in mind, much of the supposedly ‘mixed findings’ found by Vaesen et al. transform into expected empirical patterns, consistent with an adaptive evolutionary hypothesis about human learning and life history (Henrich & Broesch, 2011).

LABORATORY EXPERIMENTS TESTING THE THEORY

Vaesen et al. make no mention of an entire literature that aims at testing the factors that affect cultural accumulation using laboratory experiments (Caldwell & Millen, 2010; Derex, Beugin, Godelle, & Raymond, 2013; Derex & Boyd, 2015, 2016; Kempe & Mesoudi, 2014; Muthukrishna, Shulman, Vasilescu, & Henrich, 2014). This approach was specifically developed to address the limitations associated with empirical studies based on ethnographical or archaeological records. For example, interpenetrating social networks, extended duration of enculturation and ill-defined cultural influences, can all be obstacles to the proper evaluation of effective cultural population sizes and may lead to inconsistent results when trying to link population size to cultural complexity. Lab experiments overcome these issues by asking groups of individuals to perform tasks specifically designed to track successive improvements across time under fully controlled conditions.

In the past few years, several independent teams have taken advantage of this approach to rigorously test theoretical predictions linking population size and interconnectedness to cultural accumulation. Using a variety of tasks (spanning from knot tying to jigsaw puzzles to virtual totem pole building) and two different experimental paradigms (transmission chains and closed group methods), these experiments have consistently confirmed that larger populations do develop more efficient skills and artifacts than smaller populations (Derex et al., 2013; Kempe & Mesoudi, 2014; Muthukrishna et al., 2013). The one study (Caldwell & Millen, 2010) that didn’t reveal a link between group size and skill is likely consistent with the theory once task difficulty is taken into account (for discussion, see Muthukrishna et al., 2013).

These experiments also show that smaller groups are more likely to suffer maladaptive losses of cultural knowledge, as predicted by Henrich’s model (Derex et al., 2013; Muthukrishna et al., 2013). Vaesen et al. express doubts about the veracity of maladaptive loss of cultural traits arguing that loss of knowledge will only lower tool efficiency without leading to disappearance. This argument rests on a naive understanding of the relationship between cultural knowledge and technology. Artifacts typically involve multiple interacting parts, each of which plays a role that can be functionally pivotal for the artifact as a whole. For example, losing knowledge associated with the production of bowstrings doesn’t make bows 10% less efficient, it will render bows nonfunctional and make knowledge associated with bow shape, arrow shafts or fletching irrelevant.[9] Thus, ignoring tipping points and considering the amount of cultural information as linearly correlated with measures of efficiency do not make sense. For this reason, information losses, such as those experimentally observed in small groups, are expected to lead to complex traits' disappearance in favor of simpler, functionally equivalent cultural traits (when alternatives exist). In fact, a recent dual task experiment demonstrated that small groups provided with demonstrations about how to produce both a simple, low-rewarding tool and a complex, high-rewarding tool were much more likely than larger groups to switch to the simple subsistence method, permanently losing the ability to exploit the more complex one that was associated with higher risk of failure (Derex et al., 2013).

Given Vaesen et al.'s criticism (albeit inaccurate) of the assumptions of Henrich and Powell et al.'s models, it is worth noting that participants in these experiments were not constrained to using the best available source of social information. Instead participants were provided with measures of other group members' success and were free to choose the source they wanted to learn from. Consistent with a rich theoretical literature investigating the ways that individuals should use social information, these experiments confirm (alongside many other experimental investigations of social learning strategies in adults and children Chudek et al., 2012; Mesoudi, 2011a; Morgan et al., 2012) that individuals do show payoff biased social learning and are likely to acquire adaptive cultural information horizontally. Crucially, although individuals do not often use the extreme 'Best' strategy, cumulative cultural evolution still occurs and both population size and interconnectedness still influence levels of skill and know-how.

Of course, such experiments are always susceptible to the criticism that they occur in the laboratory and thus lack ecological validity. To address this, Bell (2015) exploited a natural experiment in which women in Tonga were aiming to learn a new weaving technique. First, Bell documents non-vertical, skilled-biased cultural transmission among traditional weavers in Tonga—which further confirms the existence of skill-biased cultural learning in small-scale societies. Second, the actual distributions of weaving skills among these learners was Gumbel distributed, suggesting the Gumbel is the better distribution for modeling selective forms of cultural learning than the Normal (consistent with theory). More importantly, Bell estimates the α and β parameters in Henrich's model using this empirical data, and his analyses suggests that skill losses are quite plausible if instructors are insufficiently skilled. Finally, as if to confirm the possibility of losses, Bell notes that this weaving technique, which so impressed Captain Cook's expedition, was indeed lost on Tonga after European contact. Fortunately, an old, tattered specimen was recovered from a museum collection and used to begin reconstructing the sophisticated weaving method.

Overall, cumulative cultural evolution experiments and natural field experiments not only confirm theoretical predictions linking population size and cultural accumulation, but

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[9] This point is also relevant to Vaesen et al.'s critique of bone tools in the archaeological record of Tasmania. It's crucial to consider the entire adaptive package.

they also support the foundational assumptions of Henrich and Powell et al.'s models. Vaesen et al. need to explain why they think this relationship emerges so powerfully in the laboratory if it's not important in the real world.

MISSING POSITIVES AND QUESTIONABLE NEGATIVES

As direct empirical tests of the relationship between population size and cumulative cultural evolution, Vaesen et al. claim there are eight relevant studies, which by their scorecard includes 2 supportive studies and 6 negative results. However, this collection ignores 8 other studies that apply these ideas to both languages and innovation rates across cities as well as to archaeological contexts (Marquet et al., 2012) and non-human primates (Lind & Lindenfors, 2010; van Schaik et al., 2003). Meanwhile, Vaesen et al.'s list of 6 negative results triple counts studies that use the same or very similar datasets (Collard, Buchanan, & O'Brien, 2013a; Collard et al., 2005; Read, 2008), and even tosses in a study that doesn't provide any empirical tests at all (Codding & Jones, 2010). All of the negative results are bedeviled by a failure to properly operationalize and measure effective cultural population size.

SUPPORTIVE FINDINGS THAT WERE IGNORED

Let's start with the studies that connect language and population size, which were ignored by Vaesen et al. Since languages are learned entirely by cultural transmission, they can be thought of as culturally-acquired tools for communication, and cultural evolutionary models readily apply (Chater & Christiansen, 2010; Henrich, 2015). Testing cultural evolutionary models on language is potentially cleaner than focusing on physical tools, technical skills and technologies because (a) although linguistic borrowing does occur across language boundaries, both the coordinative nature of language and the communicative barriers it creates naturally isolate speaker communities from each other in a way not possible with technology, and (b) language is less likely to be heavily influenced by ecological variables or economic challenges (though ecology and climate probably have some effect, see Chapter 13 in Henrich, 2015 for discussion).

Recent work has linked population size, or the size of speech communities, to (1) the size of a language's phoneme inventory, (2) the size of the vocabulary, and (3) communicative efficiency. Evidence for the first pattern, a positive relationship between the size of speaker communities and the size of the phoneme inventory, comes from several independent studies by different authors using different databases (Atkinson, 2011; Moran, McCloy, & Wright, 2012; Wichmann, Rama, & Holman, 2011). The effect is not large but it is persistent. Next, focusing on basic vocabulary in Polynesia, Bromham et al. (2015) have shown that larger populations gain words more quickly than smaller populations and that smaller populations lose words more quickly. This may help explain why the languages of larger populations tend to have larger vocabularies and more grammatical tools (Henrich, 2015: Chapter 13). Finally, a preliminary analysis of European languages, for which large corpora are available, reveals that languages with larger speech communities have more efficient 'informational packing'—that is, words with less information shrink, smoothing the rate of information transmission and allowing you to convey more information more quickly (Muthukrishna & Henrich, 2016). This correlation is large and holds even when the relatedness among languages is considered.

In a separate domain, work by economists and physicists shows that larger cities are more innovative than smaller cities. Of course, in the modern world, technological products flow globally, so you wouldn't want to measure technological complexity by counting parts or tools. But, it turns out that the tacit know-how and subtle skills and interconnections that foster innovation cannot merely be written down and shipped to other places, though skilled people can move geographically. As a consequence, the logarithm of a city's population size is a powerful predictor of its innovativeness, measured as new patents, inventors or "supercreative" employment (Bettencourt, Lobo, Helbing, Kuhnert, & West, 2007; Bettencourt, Lobo, & Strumsky, 2007; Carlino, Chatterjee, & Hunt, 2007).[10]

At the other end of the complexity scale, Lind and Lindenfors (2010) show that the number of cultural traits in a chimpanzee group is correlated with the number of females but not males, in keeping with the observation that females show a greater frequency of tool use, that infants have more opportunities for social learning from their mothers, and that it is females rather than males that move between communities, thus potentially introducing novel traits from their natal group. Similarly, among orangutans, *"the size of the cultural repertoire at a given site is best predicted by the opportunities for oblique and horizontal social transmission during development"* (van Schaik et al., 2003: 103).

So, current evidence suggests that these cultural evolutionary models are important for foraging toolkits in non-human apes, small-scale agricultural societies and urban innovation, but, according to Vaesen et. al., not for human hunter-gatherers?

PURPORTEDLY NEGATIVE RESULTS

In their list of purportedly negative results we find one paper by Read and four papers by Collard and his collaborators (hereafter 'Collard'). These papers have two major problems, as well as a variety of minor issues. First, the manner in which they operationalize the theoretical concept of population size and interconnectedness, or *effective cultural population size*, makes obtaining null results for population variables quite likely. Second, these authors insist on pitting a set of ecological or climatic hypotheses as exclusive alternatives to population effects, rather than as additive or potentially interactive with population size. It's not hard to see how variables related to risk, productivity, terrain ruggedness, climatic change, geography, trade and mobility might influence effective population sizes (for approaches that aim to integrate these

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[10] Of course, a full explanation for this has to involve specialization and a division of labor. However, as we explain below, the importance of a division of labor or technical specialization is necessarily intimately entwined with the effects of population size and interconnectedness on cultural evolution.

views, see Henrich, 2004; Henrich & Henrich, 2010; Kline & Boyd, 2010; Marquet et al., 2012; Powell et al., 2009).

Collard and Read make much of the null results they find between their *census* population measures and various measures of toolkit complexity. However, we emphasize again that *the theory does not predict that cultural complexity will increase with census population size.* Rather, it is the size of the population that shares cultural information—what Henrich called the e*ffective population siz*e of cultural models, and Powell et al. attempted to quantify. If there is even moderate contact between groups, there is no reason to expect that this will be the same as the census population size. Much evidence indicates that the populations used in all these studies are interconnected in networks that stretch across broad regions. The population sizes used were based on convenience, often representing a few hundred individuals from within larger and interconnected ethno-linguistic groups. There's no reason to suspect that these groupings represent meaningful population size measures from the point of view of the theory being tested.

By analogy, consider that models from population genetics predict an increased mutational load in smaller populations because maladaptive alleles are more likely to spread to fixation. If Collard and colleagues were to show that these various hunter-gatherer communities, say in California and Oregon, didn't reveal the predicted difference in mutational load across communities of different sizes, would we count this as evidence against this piece of theoretical population genetics? We hope not; that is, unless Read, Collard and their colleagues provided some evidence that their samples were genetically isolated.

It's also worth noting that nearly all of the null results from Read and Collard *rely on the same source* (Binford, 2001) for their population size estimates (Collard, Buchanan, Morin, & Costopoulos, 2011b; Collard et al., 2013a; Collard, Buchanan, O'Brien, & Scholnick, 2013b; Collard et al., 2005; Read, 2008). This source is not only conceptually inappropriate to test the theory, as just explained, but these numbers are difficult to source and diverge substantially from other sources for the same variables (see below). Despite this, Vaesen et al. treat these results as if they are somehow independent tests of the hypothesis.

With regard to culture, there's no evidence to suggest the community census estimates used by Collard and Read were even partially isolated for technology or tools. For example, among large swaths of the Western Indian communities used in Collard et al. (2013b), both archeological and ethno-historical evidence reveals an extensive diffusion of technologies, from baskets and obsidian to bows and arrows, across these communities (Bettinger, 2015; Jordan & Shennan, 2003). Perhaps more strikingly, we know that large swaths of this territory were engaged in a pre-Columbian monetary economy using various regional shell currencies. In Northern California, the Yurok, Karok and Hupa formed a sort of monetary union (Bettinger, 2015; Heizer, 1978; Kroeber, 1925). Their shell money was acquired through extensive trade and interaction with the Klamath, Shasta and Tolowa (see Map 1), although its ultimate source was in British Columbia, mostly with the Nootka. The currency reached east to Atsugewi and south to the Mattole. Meanwhile, south to San Francisco, other communities used clamshells as currency. Below San Francisco, in the vast San Joaquin Valley as well as both in the interior and along coastal southern California, populations used shell beads called Olivella, which were produced at near industrial levels by the Chumash in Santa Barbara. Near the border of these currency regions, the Sierra Miwok used both clam shells and the Olivella, allowing them to maintain a currency exchange (Heizer, 1978; Kroeber, 1925). Despite such evidence, Collard treats the Hupa, Karoks, Yuroks and others as independent, culturally-isolated, populations.

With the concept of effective cultural population size in mind, one might want to look for natural groupings that share languages and ethnic identities or who control territory and marry endogamously. Collard et al.'s population partitions lack all such conceptually relevant attributes. In fact, the sources for Collard et al.'s data (Binford, 2001; Jorgensen, 1980) are clear that the primary reason for creating these different groupings was convenience. For example, Jorgensen (1980: 2) writes, *"At this point it should be clear that the terms "tribe" and "tribal" are used here in the most convenient sense."* He goes on to explain that, for example, the Spring Valley Shoshone and Reese River Shoshone, who spoke the same language and had *"very similar cultures"* (Jorgensen, 1980: 3), are considered separate groups only because these highly mobile foragers tended to occupy different geographic areas. Of course, Shoshone groups intermarry, intermix, form alliances for raiding and hold yearly communal rituals (Johnson & Earle, 2000; Steward, 1938; Sutton, 1986). Collard et al.'s data includes nine different Shoshone groups and 4 different Paiute groups as supposedly independent, culturally-isolated, populations.

To see just how suspect the assumption of even partial isolation is, Figure 1 plots all the data available from Binford and marks the subset of data used by Collard et al. as triangles. Now, look at the triangle marking the Panamint Shoshoni in the lower, middle part of the map. This Shoshoni community is surrounded by five other Shoshoni communities not considered by Collard. There's just no justification for considering the Panamint as culturally disconnected from the surrounding, nearby, Shoshoni groups. Similarly, Collard uses the Eastern Pomo but doesn't consider the Clear-Lake Pomo population right next door (look north of San Francisco Bay).

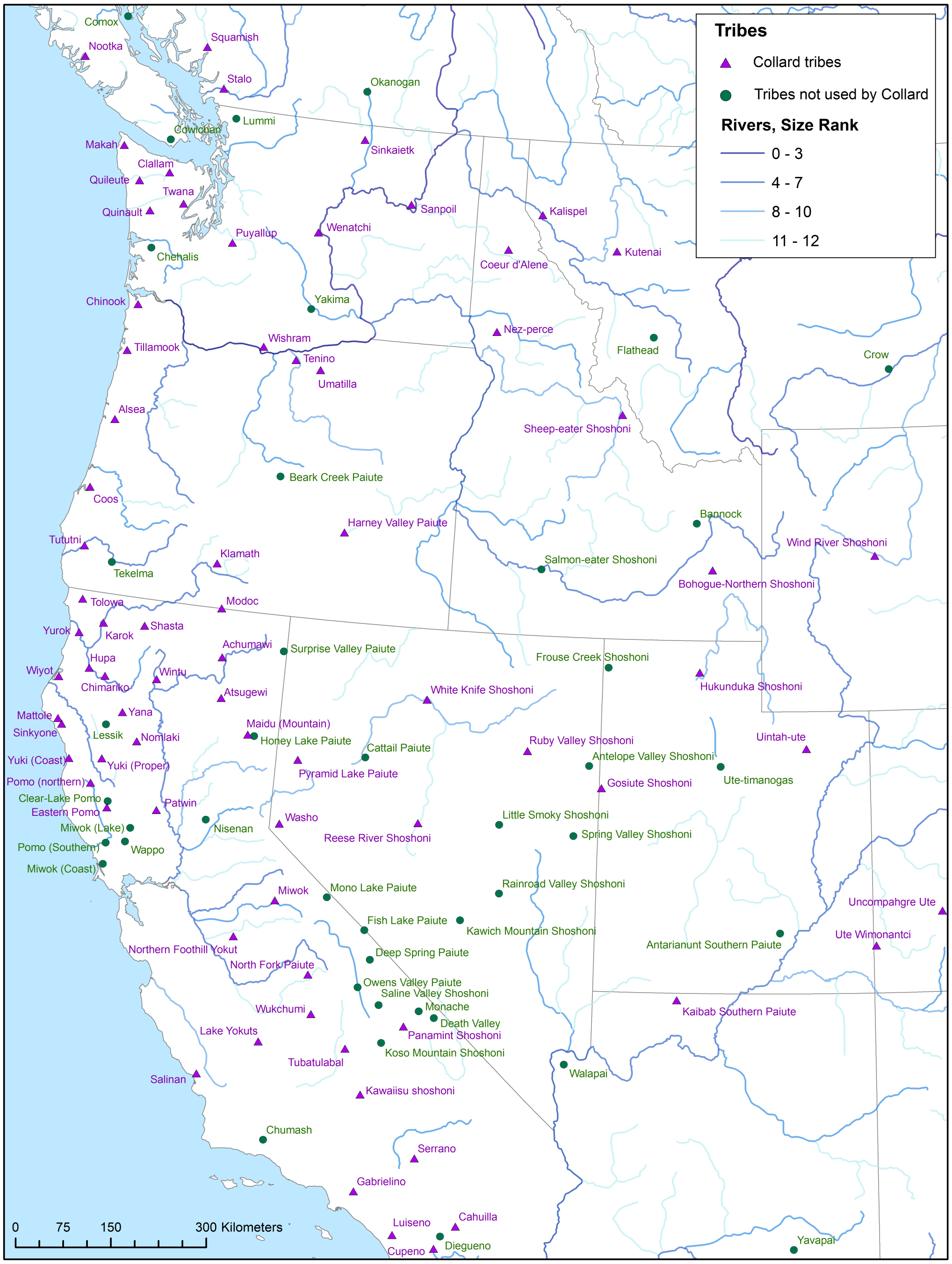

FIGURE 1. MAPS THE DATA FROM BINFORD FOR WESTERN (NON-ARCTIC) NORTH AMERICA, AND MARKS THOSE POPULATIONS USED BY COLLARD ET AL. (2013B). MANY OF THE SUPPOSEDLY CULTURALLY-ISOLATED POPULATIONS ARE ADJACENT TO OTHER POPULATIONS NOT CONSIDERED BY COLLARD.

The issue is that for Collard et al.'s analysis to provide a meaningful test of the hypothesis, these communities need to be at least somewhat isolated, in terms of the flow of techno-cultural information. But, the evidence shows some of the most extensive trading relationships in North America, including regional monetary systems, and broad diffusions of important technologies, like baskets and bows. This suggests these small groups were not isolated at all.[11] To put a fine point on this, imagine measuring the number of different tools used in U.S. cities and then showing a lack of relationship between city population and tool number. Would this be a good test of the hypothesis?

The identical issue applies to the slowly expanding global dataset of hunter-gatherers repeatedly used by Read (2008) and Collard et al. (2011a; 2013a; 2005). As noted, these analyses all draw their population data from the same source as Collard et al. (2013): Binford (2001). In describing this population number, Binford (2001: 117) explains that it *"refers to the total number of persons to whom the ethnographic description applies, …"* This number then seems to incorporate either the degree to which an ethnographer actually surveyed a particular region or the subjective willingness of different ethnographers to apply their generalizations to communities they may be less familiar with.

As a consequence, we wanted to get a better sense of where Binford's population size numbers come from, but have struggled to locate his sources. As an omnibus check, we compared the Binford population sizes for California hunter-gatherers (Figure 1) with those supplied by Baumhoff (1971) and Keeley (1992, 1995).[12] Baumhoff reviews the history and quality of census estimates for Western North American (non-arctic) hunter-gatherer populations, and isolates only 28 communities for which actual hard numbers exist—as opposed to the plentiful wild guesses that can be found in published sources. Of these 28, we found 15 that match communities in Binford (Table 1). While Keeley's numbers match Baumhoff on 14 out of 15 of these communities, Binford matches Baumhoff on only 1 out of 15. With two exceptions, Binford's estimates are all lower and their deviation ranges from 24 to 4,036 *percent*. For example, Binford gives the population size of North Foothills Yokut as 360 people while Baumhoff gives 3,900 people.

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[11] Collard et al. (2013b) purport to address the question of controlling for the interconnectedness among local groups. Essentially, they correlated the distance between groups with the absolute *number* of tools or technologies each group has. This is uninformative. Under this measure, groups could seem very similar but share none of the same tools or technologies. Or, two groups might look quite different because one group has 10 tools and another 20 tools. But, actually, it could be that all 10 tools possessed by the first group are also possessed by the second. Not surprisingly, there's little relationship between distance and absolute tool number. A far better idea would have been to calculate the percentage of shared inventory, and examine the relationship to distance. Using many of the same Western Indian populations used by Collard, Jordan and Shennan (2003) show that closer groups are technologically much more similar, even after removing the effects of ecology. This re-confirms the questionable nature of Collard's assumptions.

[12] Thanks to Bob Bettinger for the data.

Table 1: Population size estimates for North American foragers from three sources

Populations	Binford (Collard)	Baumhoff	Keeley	Percentage difference
Tolowa	2,562	2,400	2,400	-6
Yuki- Coast	750	750	750	0
Yurok	2,500	3,100	3,100	24
Hupa	1,000	1,475	1,475	48
Eastern Pomo	940	1,410	1,410	50
Sinkyone	1,300	2,076	2,076	60
Yuki- Proper	4,000	6,880	6,880	72
Karok	1,500	2,700	2,700	80
Mattole	652	1,200	1,200	84
Pomo- northern	3,360	7,010	7,010	109
Wiyot	1,390	3,200	3,200	130
Wappo	1,170	4,600	4,600	293
Miwok- Lake	227	900	900	296
North Foothills Yokuts	360	3,900	3,900	983
Mono Lake Paiute	170	7,032	3,640	4,036

The large uncertainty suggested by the divergent population estimates indicates that, even if these were conceptually appropriate populations, the total lack of precision on these population measures means that null results should be expected even if a true causal relationship exists—because of the attenuation bias generated by errors in measurement).

Overall, the null results reported by Vaesen et al., which include several studies that use much of the same data, rely on questionable population numbers that uniformly fail to operationalize the crucial variable—effective cultural population size—in any defensible way.

Collard's (2013a; 2013b; 2013c) only defense for his use of such a dubious population measure is to point to another of his studies, where despite using *"continental populations"*, he and his collaborators do find a strong positive result for the relationship between population size and technological complexity. He argues that the positive result in this study means his operationalization of population size in the other studies is fine. However, the operationalization of effective cultural population size in this one study *is completely different* from Collard's other studies. The populations in this study are much larger, and often represent linguistically distinct groups who marry endogamously, mark tribal distinctions with ethnic markers and defend exclusive territories (unlike, e.g., the various Shoshoni and Paiute subpopulations). Unsurprisingly, the population data used here doesn't come from Binford but instead from the eHRAF and other unspecified sources. Compared to local groups drawn from Binford, which range from the low hundreds (92 people is the low) to the low thousands, these populations range from the low thousands into the tens of millions. Large groups include "Korea," "Rwanda" and

"Vietnam" instead of the "Northern Foothill Yokut" and "Lake Yokut". Even the small groups are well-recognized ethno-linguistic groups. Moreover, and contrary to Collard's claims about these being "continental populations", this sample includes many islands, peninsulas and other geographically isolated groups. Island populations in this sample include Tikopia, a Cook Island, Vanuatu, Okinawa, Truk, and Sri Lanka. South Korea is a Peninsula. The sample also includes geographically isolated populations like the Mapuche and Tarahumara. The Mapuche, for example, inhabit a narrow strip of the Chilean coast that is bordered on the east by the Andes, on the west by the Pacific, on the south by Patagonia, and to the north by the Atacama Desert—moving in any direction would have required them to give up agriculture (Faron, 1968; Stuchlik, 1976). Thus, the operationalization of effective cultural population size used to construct this dataset, intentionally or otherwise, is totally different from that used in other studies (Collard et al., 2011a; Collard et al., 2013a; Collard et al., 2013b; Collard et al., 2005; Read, 2008). With a different and more appropriate operationalization, you get a different answer (for a study that takes care in operationalizing effective population size, see Kline & Boyd, 2010).

Finally, we note that in these studies the authors often make an "either/or" argument. They seem to think that either it's all about ecological or economic factors, or it's all about population size and interconnectedness. By contrast, we argue that ecological, climatic and economic factors can matter both directly, by altering the costs and benefits, and indirectly, by for example influencing carrying capacity or population interconnectedness. This can be seen in Henrich's original paper in which climatic shifts caused rising seas that isolated Tasmania from the rest of Australia, effectively shrinking the size of the pool of cultural learners. The ultimate cause is climate, not population. However, because the primary mode of human adaptation is cultural (via social learning, see Boyd & Richerson, 1985), our individual-level ability to adapt is influenced by the size of the pool of people that we can access, and the overall capacity for populations to adapt is influenced by a population's size and interconnectedness.

THE EVOLUTION OF SPECIALIZATION

Vaesen et al. treat economic specialization as an exclusive, alternative explanation for the relationship between population size and cultural complexity. We entirely agree that specialization plays a key role in understanding rates of cultural evolution, especially in more complex societies. However, it is not sufficient to point to the existence of specialization as a possible challenge to the relationship between sociality and cultural complexity nor control for it as if it were an exogenous, independent, variable. A more productive approach is to develop a broader and more comprehensive account of cultural evolution in which cumulative cultural evolution is interwoven with the emergence of specialization: How and why does specialization evolve in human societies given its relative absence in non-human primates? What's the relationship between cumulative cultural evolution and the emergence of specialization?

Cultural evolutionary models have begun to explore these questions (e.g., Henrich & Boyd, 2008). Henrich and Boyd's model predicts that persistent specialization (social stratification) is favored when there is surplus production and specialists benefit from divisions of this surplus. These strata are more persistent when mixing between subpopulations is restricted. More recently, Henrich (2015) has argued that specialization itself is a response to the ever spiraling accumulation of skills and know-how, driven by factors such as population size and interconnectivity. Consider the earliest case of specialization—the division of labor between males and females in enduring pair-bonds. Because our species possesses pair-bonds with substantial paternal investment, men can specialize in some kinds of skills, ecological knowledge or know-how while women specialize in others. This coordination is facilitated by the fact that shared offspring create fitness interdependence in the couple.[13] Each sex can then get relatively better at their areas of specialization compared to the situation in which every adult must develop at least a minimum level of skill in all fitness-relevant domains. The pair, and thus the offspring, does better. Thus, Henrich argues, informational specialization—which underlies economic specialization—emerges in human societies as a solution to limits imposed by our cognitive capacity. Adaptations that empower cumulative culture, such as more accurate learning biases selecting who to learn from and higher fidelity transmission through mechanisms such as formal education (for others, see Muthukrishna & Henrich, 2016), can be deployed within a circumscribed domain. Thus populations that evolve specialization under certain conditions can generate more rapid cumulative cultural evolution and maintain greater equilibrium levels of cultural know-how. But, of course, there are always tradeoffs, as the case below illustrates.

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[13] In the male-female collaboration proposed here, men can contribute to their offspring and households in a variety of ways, including subsistence contributions, ecological knowledge, childcare, the cultural transmission of valued know-how, protection and disaster assistance. Most work in this arena has focused on subsistence contributions (Hawkes, 1991), where the most recent studies indicate that fathers often make important subsistence contributions (Gurven & Hill, 2009, 2010; B. M. Wood & Marlowe, 2013, 2014). Nevertheless, debate continues on these issues (Hawkes, O'Connell, & Coxworth, 2010; Hawkes, O'Connell, & Jones, 2014). Men may also contribute via their ecological knowledge (e.g., weather patterns, flowering cycles, animal movements and behavior preferences), which may influence camp movements and campsite selection. Similarly, both recent syntheses and detailed ethnographic studies suggest that men make important household contributions, including through childcare, in at least some forager societies (Hewlett, 1991; Kramer, 2010; Sear & Mace, 2008). And notably, as both Vaesen et. al.'s and our reviews' emphasize, fathers may also play an important role in transmitting expertise on things like hunting to their sons. So, even if it turns out that men make no subsistence contribution at all to their households, they may still make key contributions to the information economy, via cultural transmission. This is, in fact, particularly critical by Vaesen et. al.'s account, since they argue for the predominance of vertical cultural transmission. Finally, the importance of male contributions to household protection (skill in weapon use or defensive tactics) or survival during periods of famine, drought or other disasters (e.g., waterhole locations during droughts) has not been a focus of investigation but may present critical fitness contributions (Henrich, 2015; R. Lee, 1979).

The importance of understanding the relationship between specialization and cultural evolution is revealed by cases of craft specialization in complex societies. Vaesen et al. attempt to use craft specialization as evidence against the general population and complexity argument, but craft specialization actually supports the argument. For example, Roux (2010) showed that in the 5th and 3rd millennia BCE Levant, specialist potters using wheel coiling were very few in number and were attached to an elite, making items solely for them. At the end of these periods, social and economic upheavals affecting the elites led to the demise of these specialist production and transmission networks. This was the case even though the techniques they used were more efficient than the prevalent hand-making techniques; the transmission networks were small and limited and therefore fragile. It was only later that wheel coiling became and remained prevalent, after the transmission networks became *"large enough for the technological feature to have sufficient redundancy to resist historical events"* (Roux, 2010: 228). This example illustrates the value of a comprehensive and integrated view of cultural evolution.

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