

# Population size does not explain past changes in cultural complexity

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**Demography is increasingly being invoked to account for features of the archaeological record, such as the technological conservatism of the Lower and Middle Pleistocene, the Middle to Upper Paleolithic transition, and cultural loss in Holocene Tasmania. Such explanations are commonly justified in relation to population dynamic models developed by Henrich [Henrich J (2004) *Am Antiq* 69: 197–214] and Powell et al. [Powell A, et al. (2009) *Science* 324(5932): 1298–1301], which appear to demonstrate that population size is the crucial determinant of cultural complexity. Here, we show that these models fail in two important respects. First, they only support a relationship between demography and culture in implausible conditions. Second, their predictions conflict with the available archaeological and ethnographic evidence. We conclude that new theoretical and empirical research is required to identify the factors that drove the changes in cultural complexity that are documented by the archaeological record.**

cultural evolution | demography | Upper Paleolithic transition | Tasmania | cultural complexity

The idea that demography affects cultural evolution has a long history in archaeology. The relationship has been characterized in two main ways. The older of the two, which is rooted in the work of Malthus and Boserup, focuses on the interaction between demography and the environment, especially the effects of population pressure (1–9). Recently, this Malthusian–Boserupian approach has been eclipsed by what may be called the “population size approach” (10–13). This approach contends that population size alone affects cultural evolution. Its key claim is that increases in population size lead to increases in cultural complexity, whereas decreases in population size result in decreases in cultural complexity.

The population size approach has had a major impact on archaeology in the past few years. For example, several authors have suggested that the appearance of indicators of behavioral modernity results from an increase in population size rather than from a change in cognitive abilities (10, 14–16). Others have used population size decrease to explain the loss of certain technologies, such as the abandonment of the bow and arrow in Northern Europe during the Late Glacial period (17, 18). Still others have invoked population size to explain apparent instances of cultural stability. Hopkinson et al. (19), for example, suggest that small population size explains the conservatism of the Acheulean. Such has been the growth of interest in the population size approach that the author of a recent review describes it as having “changed how archaeologists think about socio-cultural change” (ref. 20, p. 11).

The putative link between population size and cultural complexity that is at the core of the population size approach was identified with formal models. This paper offers a combined theoretical and empirical assessment of the most influential of these models (11, 12). For a model to provide a credible explanation for a pattern in the archaeological record, it must meet two conditions: Its components (i.e., its assumptions, simplifications, definitions) must be defensible, and it must be consistent with empirical data from relevant cases. Accordingly, we begin by describing the models of Henrich (11) and Powell et al. (12). We then investigate whether their assumptions and definitions can be

justified. Subsequently, we evaluate the fit of the models to ethnographic and archaeological data. The results of our evaluation cast doubt not only on the use of the models of Henrich (11) and Powell et al. (12) to explain patterns in the archaeological record but also on the population size approach in general.

## Models of Henrich and Powell et al.

In this section, we briefly outline the main elements of the models of Henrich (11) and Powell et al. (12). More technical descriptions of the models are provided in *Supporting Information* and *Figs. S1–S4*.

Henrich (11) developed his model to explain a key part of Jones' (21) interpretation of the archaeological record of Tasmania. Jones (21) argued that Tasmania experienced a slow cultural decline from the beginning of the Holocene until contact with Europeans. Henrich (11) avers that the decrease in the complexity of the Tasmanians' technology has to do with their isolation from mainland Australia following the rise of sea levels 12–10 kya. Henrich (11) contends that the latter event would have reduced the pool of interacting social learners, and that this reduction would have led to reduced cultural complexity.

At the heart of Henrich's model (11) is a process of cultural transmission we will call “Best.” In Best, each individual in the older generation has a skill level that expresses how proficient he or she is at performing a given skill. Individuals in the younger generation learn the skill from the most skilled member of the older generation, but this copying process is inaccurate. Consequently, members of the younger generation will, on average, be worse at the skill than members of the older generation. It is at this point that strength in numbers becomes important: Larger populations have a higher probability of giving rise to learners who achieve a level of skill as high as or even higher than the level of skill of the most skilled member of the older generation. Conversely,

## Significance

Archaeologists have long tried to understand why cultural complexity often changed in prehistory. Recently, a series of highly influential formal models have suggested that demography is the key factor. According to these models, the size of a population determines its ability to invent and maintain cultural traits. In this paper, we demonstrate that the models in question are flawed in two important respects: They use questionable assumptions, and their predictions are not supported by the available archaeological and ethnographic evidence. As a consequence, little confidence can be invested in the idea that demography explains the changes in cultural complexity that have been identified by archaeologists. An alternative explanation is required.

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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.

One major problem with Complexity Regression is that it treats an individual's skill level as fixed, which is inconsistent with the large body of literature on skill acquisition that has been published over the past 30 y. The literature in question indicates that skill level is heavily influenced by practice time (40). Learners can thus improve their ability to perform a given skill by practicing it, which in turn implies that a population can counter the effects of the loss of gifted learners on skillfulness by investing more time in learning skills.

Complexity Regression is problematic in yet another respect. Consider a population that uses fishing nets and is able to catch 100 fish per day. The population is struck by an infectious disease and loses some members. As a consequence of this loss, their skill level decreases and they are now worse at catching fish (e.g., they can only catch 90 fish per day). How might they respond? One option is to switch to a simpler skill like hand-line fishing, which is what Henrich (11) assumes will happen. However, there are several other possibilities. One is that the population might do nothing because population pressure has relaxed to such an extent that its members can survive on the lower returns from net fishing, because the decreasing benefits of net fishing are offset by decreasing costs (e.g., catching fewer fish per day requiring a smaller fishing team), because switching costs do not outweigh the lower returns from net fishing, and/or because tradition demands it. Alternatively, the population might compensate for the lower returns by relying more on other resources, by storing more food, or by engaging in more trade with other populations (5, 41–43). In these cases, if the strategy prevents a further decline in population size, the population can continue fishing with nets rather than switching to a simpler skill. Generally, whereas the outcome of an analysis of costs and benefits can be expected to vary greatly from case to case, Complexity Regression assumes only one possible outcome.

In sum, then, Henrich's model (11) does not withstand theoretical scrutiny. There are problems with both of its key assumptions and with the definition of cultural complexity it relies on.

**Powell et al.'s Model.** Given that Powell et al. (12) use the same definition of cultural complexity as Henrich (11), and that we have already explained why that definition is problematic, we will focus on the two assumptions made by Powell et al. (12) when constructing their model: Payoff and Complexity Maximization. To reiterate, Payoff is the assumption that cultural transmission is a two-stage process in which learners first undergo vertical transmission and then have the opportunity to improve their skill level by selecting another cultural parent proportional to the parent's skill level, whereas Complexity Maximization is the assumption that when a population increases in size, its members will always opt to adopt more complex cultural traits.

Payoff suffers from the same problems as Best. The fact that Vaesen (23) has shown that a number of copying processes do not yield an association between population size and skillfulness means that the results of Powell et al.'s model (12) also are not independent of the transmission process they assume. Equally problematically, there is no empirical support for Payoff. The first part of Payoff is in line with the available ethnographic evidence, which, as we explained earlier, suggests that vertical transmission is important early on (24–28). However, Payoff's second part cannot be justified on empirical grounds. One study has reported evidence for payoff biases in the transmission of skills related to fishing, growing yams, and using medical plants among indigenous Fijians (44), but the aforementioned studies by MacDonald (34) and Jordan (35) indicate that other societies use other forms of oblique transmission. Consequently, Payoff cannot be assumed to be universal.

Complexity Maximization has shortcomings too. One of these shortcomings is the fact that a number of the items that appear

during the Upper Paleolithic are tools or tool parts. The issue here is that increasing the complexity of a tool can, beyond a certain level, negatively affect its performance. This phenomenon is well known in industry (45), but it also applies to the tools produced by small-scale societies. Consider the type of harpoon used by contact-era Inuit to hunt seals in open water. Such harpoons typically had floats attached to them to make it more difficult for the seal to dive. It is obvious that there is a point at which adding more floats would make such a harpoon more difficult to use. The harpoon would be more complex but less effective. Given that complexity can negatively affect the performance of tools, it is unlikely that a population will always opt to adopt more complex tools.

It is difficult to justify Complexity Maximization in relation to the other elements of the Upper Paleolithic as well. There is no evidence that contemporary people maximize the complexity of their symbolic behavior, ritual artifacts, musical instruments, etc. Recent history certainly offers examples of change leading to increased complexity, but it also provides plenty of instances of change that reduced complexity. Given this fact, there is no reason to assume that ancient populations were "cultural complexity maximizers" in relation to their symbolic behavior, ritual artifacts, musical instruments, etc.

Complexity Maximization might be thought to fit with Boserup's suggestion that increased population density may induce subsistence stress and that such stress prompts innovation. However, both theoretical and empirical work has shown that increased population density cannot be assumed to lead to innovation (5, 46–48), let alone innovation of a complexity-increasing kind. We have already outlined one reason for the failure to establish a robust link between increased population density and innovation: Innovation is only one of several options available to people to relieve subsistence stress. The alternatives to innovation include migration, exchange, and higher reliance on resources already in the subsistence base (5, 41–43). A further problem with justifying Complexity Maximization by means of Boserup's hypothesis is that it is not clear what Powell et al.'s model (12) adds. If population growth forces populations to innovate, there is no need to invoke cultural transmission processes to explain increases in cultural complexity.

So, Powell et al.'s model (12) does not withstand theoretical scrutiny either. Its key assumptions are problematic, and so is the definition of cultural complexity it relies on.

### Empirical Assessment of the Predictions of the Models of Henrich and Powell et al.

In the previous section, we showed that there are theoretical reasons to be skeptical about the use of the models of Henrich (11) and Powell et al. (12) to interpret the archaeological record. In this section, we demonstrate that the predictions of the models are inconsistent with the available empirical evidence. We begin by showing that the models do not do a good job of explaining the archaeological patterns they were developed to explain. Subsequently, we review studies in which ethnographic and archaeological data have been used to test one of the key predictions of the models of Henrich (11) and Powell et al. (11) and the other models that underpin the population size approach, namely, that there should be a positive correlation between population size and cultural complexity. We show that the majority of these studies do not support this prediction.

**Henrich's Model and the Cultural History of Tasmania.** As noted earlier, Henrich (11) developed his model to explain a key part of Jones' (21) interpretation of the archaeological record of Tasmania, which is that the Tasmanians experienced a loss of cultural complexity during the Holocene. Drawing on the results of his model, Henrich (11) argued that Tasmania's isolation from the mainland led to a reduction of the pool of social learners, and that this reduction, in turn, resulted in the Tasmanians being unable to sustain the skills necessary to produce a complex toolkit. This hypothesis has been widely accepted as accurate, so much so that the idea that decreases in population size have a negative impact on cultural complexity is now often referred to as

“the Tasmanian effect” (e.g., ref. 49, p. 272). However, it is not, in fact, supported by the available ethnographic and archaeological data.

For Henrich’s hypothesis (11) to be correct, the skills abandoned by the Tasmanians must have been more complex than those skills they practiced afterward. Bone points are the only type of artifact that the Tasmanians are known to have stopped producing (22). Bone points have been recovered at several sites that date to the Late Pleistocene or Early Holocene (50), but bone points were not among the tools used by Tasmanians at the time of contact with Europeans. Hence, there is no doubt that sometime in the past few thousand years, probably *ca.* 4 kya, the Tasmanians stopped making bone points. Consequently, the key question is “Were any of the skills that the Tasmanians practiced after they stopped producing bone points more complex than bone point manufacture?”

The bone points produced by Late Pleistocene/Early Holocene Tasmanians would not have been difficult to make. Their production involved a few simple actions, including fracturing long bones and rubbing the broken ends on an abrasive surface (50). As such, they would have been easier to produce than some of the artifacts that the Tasmanians made after 4 kya. Among these more-difficult-to-manufacture items are woven baskets, seaworthy bark canoes, waterproof shelters, and certain stone tools (51). The skills involved in the production of bone points would also have been less complex than the skills involved in a number of the economic and ritual activities that Tasmanians engaged in after 4 kya. These activities include the mining, alteration, and distribution of ochre (52); the creation of necklaces from human bones and pierced shell beads (53); body scarification (54); and funerary rituals (53). Thus, a number of the skills that the Tasmanians practiced after they stopped producing bone points were more complex than bone point manufacture.

It is also worth noting that much knowledge transfer in Tasmanian Aboriginal society took place through song, dance, and stories. Robinson’s (55) diaries make numerous references to the Tasmanians’ cosmology and creation myths. Similarly, Clark (56) describes a rich repertoire of song and dance that persisted into the 1830s. There can be no doubt that many of these songs, dances, and stories would have been more difficult to learn, and therefore more complex according to Henrich’s definition of cultural complexity (11), than bone point production. Thus, Henrich’s hypothesis (11) fails on this count too.

Given that many of the activities that the Tasmanians were recorded doing at the time of contact with Europeans were more complex than manufacturing bone points, there is no reason to believe that the Tasmanians experienced a loss of cultural complexity as a result of the negative impact on skillfulness of their isolation from groups on the Australian mainland. (For a more detailed treatment of the Tasmanian case, we refer the reader to [Supporting Information](#).)

**Powell et al.’s Model and the Upper Paleolithic Transition.** To reiterate, Powell et al.’s goal (12) was to explain the interregional variation in the timing of the Upper Paleolithic transition. Having developed their model, they carried out a two-step empirical analysis. First, they used molecular data to estimate when different regions of the world would have reached the same population density as Europe at the start of the Upper Paleolithic. They then compared the population estimates with the timing of the Upper Paleolithic transition in the other regions of the world. Their rationale was that if the start of the Upper Paleolithic in Europe represents a substantial increase in cultural complexity as most archaeologists believe, and if cultural complexity is dependent on population size, then the Upper Paleolithic transition should occur in other regions when they have reached the same population density as Europe at the start of the Upper Paleolithic.

However, Powell et al.’s analysis (12) is inadequate as a test of their model. According to the model, populations should accumulate complexity whenever their size increases and not just when they reach a critical size, let alone a critical density. A better procedure is to examine whether the Upper Paleolithic transition

in various regions of the world took place around the time population size started to increase. Such a reanalysis, in which one assumes that Powell et al.’s (12) population estimates are reliable, that their dates for the Upper Paleolithic transition in various parts of the world are accurate, and that it is unproblematic to use a package of traits to characterize modernity [but see the severe criticism by other researchers (57–62)], yields nontrivial violations of the predicted association in Sub-Saharan Africa, Northern and Central Asia, Southern Asia, and Australia (a more detailed treatment is provided in [Fig. S5](#)).

Some of these incongruities also appear in Powell et al.’s two-step analysis (12). The authors suggest these incongruities are due to the low resolution of their single-locus population estimates, which were taken from Atkinson et al. (63). However, a recent multilocus study (64) does not settle the issue in favor of Powell et al.’s analysis (12). These new estimates give rise to a different set of mismatches. Most notably, they suggest that the Upper Paleolithic transition took place in Africa at a time when populations were shrinking (90–75 kya) and that the Upper Paleolithic appeared in Europe at a historic population low ([Fig. S6](#)). The fact that this new set of population size estimates challenges the lynchpin of Powell et al.’s analysis (12), the coincidence between the Upper Paleolithic transition and a relatively high population density in Europe, clearly calls into question the reliability of Powell et al.’s results (12).

Significantly, it is not just a question of which set of genetic data-derived population size estimates to believe. Recent studies by Klein and colleagues (e.g., 65) address whether larger human population sizes might explain the sporadic occurrence of more complex behavior in the South African Middle Stone Age and whether long-term population increase over the course of the Middle Stone Age could explain the emergence of the Later Stone Age at roughly 50 kya. For both cases, they failed to find any association.

Thus, Powell et al.’s model (12) also fails to explain convincingly the archaeological pattern it was developed to explain. There is no clear link between the Upper Paleolithic transition and demography.

**Tests of the Predicted Correlation Between Population Size and Cultural Complexity.** Population size is not the only factor that has been argued to affect cultural complexity. Environmental risk (66, 67) and mobility (68, 69) have also been suggested to influence it. Therefore, an adequate test of the prediction that there should be a positive correlation between population size and cultural complexity is one in which population size is evaluated alongside at least one other putative driver. So far, eight studies meet this criterion (67, 69–75).

The results of two of the studies are consistent with the prediction. Kline and Boyd (71) found an association between toolkit complexity and population size in a sample of 10 fisher-farmer groups from Oceania, whereas Collard et al. (72) found the same thing in a sample of 45 small-scale food-producing groups from several continents. In contrast, the results of the other six studies are not consistent with the prediction (67, 69–75). None of them identified a relationship between population size and cultural complexity when other potential driver variables were taken into account. Four of them found that cultural complexity was only correlated with proxies for environmental risk (67, 70, 73, 75). Another found that cultural complexity was correlated with both environmental risk and mobility. The remaining study concluded that a change in ecological and demographic conditions is more likely to have caused the relevant change in cultural complexity than is population size (74). Thus, the prediction has not fared well in the studies in which it has been adequately tested. The most that can be said about the relationship between population size and cultural complexity is that it is an inconsistent one.

In fact, even this conclusion may overstate the support for the population size approach. Larger societies tend to have a more complex social organization (76, 77), which often includes specialization of tasks (67, 73, 78). Task specialization has the potential to affect the complexity of a society’s cultural repertoire because individuals need not master all skills and can focus on learning a small number of more complex tasks (e.g., blacksmithing, carpentry). Task specialization and the mechanism of

the formal models of Henrich (11) and Powell et al. (12) work differently. In the former case, complexity is regulated by increased practice time and by the number of types of specialists; in the latter, complexity is regulated by a population's size-dependent ability to bring forth gifted individuals. Critically, for present purposes, the introduction of task specialization into a population is likely to increase complexity even though it implies a reduction of the effective population size for certain skills (i.e., a reduction from the entire pool of possible cultural parents to a pool merely consisting of specialist parents). Consequently, unless task specialization is controlled for, finding a correlation between population size and cultural complexity does not support the hypothesis that population size drives cultural complexity via the former's impact on transmission accuracy. Neither Kline and Boyd (71) nor Collard et al. (72) included task specialization as a control variable. Thus, their results do not necessarily support the population size approach.

### Concluding Remarks

The recent rise in popularity of the population size approach within archaeology has, to a large extent, been based on the formal models presented by Henrich (11) and Powell et al. (12) and their apparent ability to explain the decline in cultural complexity in Tasmania in the Early Holocene and the regional variation in the timing of the Upper Paleolithic transition, respectively. In this paper, we have shown that these models have serious shortcomings from a theoretical perspective. Their results are dependent on their assumptions, and their assumptions cannot be justified empirically. In addition, there is no reason to prefer the definition of cultural complexity they use over any of the other definitions that have been put forward. We have also shown that the models fit the available empirical data poorly. The ethnographic and archaeological data from Tasmania are not consistent with Henrich's model (11), and the available evidence pertaining to the Upper Paleolithic transition is not in line with Powell et al.'s model (12). Thus, the models do not fit the archaeological patterns they were developed to explain. Furthermore, most adequate tests of the most basic prediction of the models—that there should be a positive correlation between population size and cultural complexity—have returned results that are inconsistent with the prediction.

We contend that these findings cast serious doubt on the population size approach within archaeology. The fact that the two most influential models have serious shortcomings is clearly

a cause for concern. However, the problem is wider than that. The prediction that there should be a positive correlation between population size and cultural complexity is not specific to the models of Henrich (11) and Powell et al. (12). It is a prediction of all of the models that have been developed by proponents of the population size approach (10, 13). Thus, the failure of the majority of tests of the prediction to support it casts doubt not just on the models of Henrich (11) and Powell et al. (12), but on the population size approach in general.

What then, if not population size, drives the increases and decreases in cultural complexity that are documented by the archaeological record? We have already briefly mentioned the three most obvious possibilities. One is changes in population pressure as per the Malthusian–Boserupian approach. Another is changes in the degree of task specialization in the context of changes in the degree of social complexity. The third possibility is changes in environmental risk. None of these potential explanatory factors is free of problems. That population size does not correlate with cultural complexity in the majority of studies discussed in the previous section is difficult to square with the Malthusian–Boserupian idea that population pressure spurs innovation, or at least it is to the extent that population size is a good proxy for population pressure, and that innovation involves increases in complexity. It is also difficult to square with the notion that changes in task specialization drive changes in cultural complexity, because the latter predicts a correlation between population size and cultural complexity. One problem with the hypothesis that changes in cultural complexity are driven by changes in the level of environmental risk is that although a number of studies have supported its predictions (67, 70, 73, 75), some have failed to do so (72, 79). The implication of this is that environmental risk is probably not a universal driver of changes in cultural complexity. Further theoretical and empirical research is required to identify the factor or, as we think more likely, the set of factors that drove the changes in cultural complexity that are documented by the archaeological record.

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- Childe VG (1936) *Man Makes Himself* (Watts, London).
- Binford LR (1968) Post-Pleistocene adaptations. *New Perspectives in Archeology*, eds Binford SR, Binford LR (Aldine, Chicago), pp 313–341.
- Renfrew C (1973) *Before Civilisation* (Knopf, New York).
- Earle TK (1980) A model of subsistence change. *Modeling Change in Prehistoric Subsistence Economies*, eds Earle TK, Christenson AL (Academic, New York), pp 1–29.
- Redding RW (1988) A general explanation of subsistence change: From hunting and gathering to food production. *J Anthropol Archaeol* 7(1):56–97.
- Mellars P (2005) The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. *Evol Anthropol* 14(1):12–27.
- Stiner M, Kuhn S (2006) Changes in the “connectedness” and resilience of Paleolithic societies in Mediterranean ecosystems. *Hum Ecol* 34:693–712.
- Richerson PJ, Boyd R, Bettinger RL (2009) Cultural innovations and demographic change. *Hum Biol* 81(2-3):211–235.
- Vegvari C, Foley RA (2014) High selection pressure promotes increase in cumulative adaptive culture. *PLoS One* 9(1):e86406.
- Shennan SJ (2001) Demography and cultural innovation: A model and some implications for the emergence of modern human culture. *Cambridge Archaeological Journal* 11(1):5–16.
- Henrich J (2004) Demography and cultural evolution: Why adaptive cultural processes produced maladaptive losses in Tasmania. *Am Antiq* 69(2):197–214.
- Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324(5932):1298–1301.
- Premo LS, Kuhn SL (2010) Modeling effects of local extinctions on culture change and diversity in the paleolithic. *PLoS One* 5(12):e15582.
- Brumm A, Moore MW (2005) Symbolic revolutions and the Australian archaeological record. *Cambridge Archaeological Journal* 15(2):157–175.
- James HVA, Petraglia M (2005) Modern human origins and the evolution of behaviour in the later Pleistocene of South Africa. *Curr Anthropol* 46(Suppl 5):S3–S27.
- Langley MC, Clarkson C, Ulm S (2011) From small holes to grand narratives: The impact of taphonomy and sample size on the modernity debate in Australia and New Guinea. *J Hum Evol* 61(2):197–208.
- Riede F (2008) The Laacher See-eruption (12,920 BP) and material culture change at the end of the Allerød in Northern Europe. *Journal of Archaeological Science* 35(3): 591–599.
- Dev S, Riede F (2012) Quantitative functional analysis of Late Glacial projectile points from northern Europe. *Lithics* 33:40–55.
- Hopkinson T, Nowell A, White M (2013) Life histories, metapopulation ecology, and innovation in the Acheulian. *PaleoAnthropology* 2013:61–76.
- French JC (2015) Demography and the palaeolithic archaeological record. *Journal of Archaeological Method and Theory* 39:193–209.
- Jones R (1971) The demography of hunters and farmers in Tasmania. *Aboriginal Man and Environment in Australia*, eds Mulvaney DJ, Golson J (Australian National Univ Press, Canberra, Australia), pp 271–287.
- Andersson C, Read D (2016) The evolution of cultural complexity: Not by the treadmill alone. *Curr Anthropol*, in press.
- Vaesen K (2012) Cumulative cultural evolution and demography. *PLoS One* 7(7):e40989.
- Hewlett BS, Cavalli-Sforza L-L (1986) Cultural transmission among Aka pygmies. *Am Anthropol* 88(4):922–934.
- Shennan S, Steele J (1999) Cultural learning in hominids: A behavioural ecological approach. *Mammalian Social Learning*, eds Box HO, Gibson KR (Cambridge Univ Press, Cambridge, New York), pp 367–388.
- Ohmagari F, Berkes K (1997) Transmission of indigenous knowledge and bush skills among the western James Bay Cree women of subarctic Canada. *Hum Ecol* 25:197–222.
- Boyette AH (2013) Social learning during middle childhood among Aka foragers and Ngandu farmers of the Central African Republic. PhD thesis (Washington State University, Pullman, WA).
- Hattori S (2006) Diversity and variability of plant knowledge among adult Baka hunter-gatherers in Cameroonian rainforests. *Proceedings of Kyoto Symposium* (Kyoto Univ Press, Kyoto, Japan), pp 229–235.
- Aunger R (2000) The life history of culture learning in a face-to-face society. *Ethos* 28:445–481.

30. Reyes-García V, et al. (2009) Cultural transmission of ethnobotanical knowledge and skills: An empirical analysis from an Amerindian society. *Evol Hum Behav* 30(4): 274–285.
31. Demps K, Zorondo-Rodríguez F, García C, Reyes-García V (2012) Social learning across the life cycle: Cultural knowledge acquisition for honey collection among the Jenu Kuruba, India. *Evol Hum Behav* 33(5):460–470.
32. Tehrani J, Collard M (2009) On the relationship between interindividual cultural transmission and population-level cultural diversity: A case study of weaving in Iranian tribal populations. *Evol Hum Behav* 30(4):286–300.
33. Kline MA, Boyd R, Henrich J (2013) Teaching and the life history of cultural transmission in Fijian villages. *Hum Nat* 24(4):351–374.
34. MacDonald K (2007) Cross-cultural comparison of learning in human hunting: Implications for life history evolution. *Hum Nat* 18(4):386–402.
35. Jordan P (2014) *Technology as Human Social Tradition: Cultural Transmission Among Hunter-Gatherers* (Univ of California Press, Oakland, CA).
36. Simon HA (1962) The architecture of complexity. *Proc Am Philos Soc* 106(6):467–482.
37. Oswalt WH (1973) *Habitat and Technology: The Evolution of Hunting* (Holt, Rinehart, & Winston, New York).
38. Oswalt WH (1976) *An Anthropological Analysis of Food-Getting Technology* (Wiley, New York).
39. Querbes A, Vaesen K, Houkes W (2014) Complexity and demographic explanations of cumulative culture. *PLoS One* 9(7):e102543.
40. Ericsson KA, Charness N (1994) Expert performance: Its structure and acquisition. *Am Psychol* 49(8):725–747.
41. O'Shea J (1981) Coping with scarcity: Exchange and social storage. *Economic Archaeology: Towards an Integration of Ecological and Social Approaches*, British Archaeological Reports, International Series 96, eds Sheridan A, Bailey G (British Archaeological Reports, Oxford), pp 167–183.
42. Halstead P (1981) From determinism to uncertainty: Social storage and the rise of the Minoan palace. *Economic Archaeology: Towards an Integration of Ecological and Social Approaches*, British Archaeological Reports, International Series 96, eds Sheridan A, Bailey G (British Archaeological Reports, Oxford) pp 187–213.
43. Halstead P, O'Shea J (1982) A friend in need is a friend indeed: Social storage and the origins of social ranking. *Ranking, Resource, and Social Exchange*, eds Renfrew C, Shennan S (Cambridge Univ Press, Cambridge, New York), pp 92–99.
44. Henrich J, Broesch J (2011) On the nature of cultural transmission networks: Evidence from Fijian villages for adaptive learning biases. *Philos Trans R Soc Lond B Biol Sci* 366(1567):1139–1148.
45. Sessions R (2008) *Simple Architectures for Complex Enterprises* (Microsoft, Redmond, WA).
46. Bronson B (1975) The earliest farming: Demography as cause and consequence. *Population, Ecology, and Social Evolution*, no. 53-78, ed Polgar S (Aldine, Chicago).
47. Hammel EA, Howell N (1987) Research in population and culture: An evolutionary framework. *Curr Anthropol* 28(2):141–160.
48. Cowgill GL (1975) On causes and consequences of ancient and modern population change. *Am Anthropol* 77(3):505–525.
49. Richerson PJ, Boyd R (2005) *Not by Genes Alone: How Culture Transformed Human Evolution* (Univ of Chicago Press, Chicago).
50. Hiscock P (2008) *Archaeology of Ancient Australia* (Routledge, London).
51. Cosgrove R (2015) Raw material movement and past Tasmanian Aboriginal interaction: Implications for understanding isolated human population dynamics. *Archaeology in Oceania* 50(Suppl 1):69–81.
52. Sagona A, ed (1994) *Bruising the Red Earth: Ochre Mining and Ritual in Aboriginal Tasmania* (Univ of Melbourne Press, Melbourne).
53. Jones R (1967) Middens and man in Tasmania. *Nat Hist* 18:359–364.
54. Plomley NJB (1992) The Tasmanian tribes and catirices as tribal indicators among the Tasmanian Aborigines. Queen Victoria Museum and Art Gallery, occasional paper no. 5 (Queen Victoria Museum and Art Gallery, Launceston, TAS, Australia).
55. Plomley NJB, ed (1966) *Friendly Mission: The Tasmanian Journals and Papers of George Augustus Robinson, 1829-1834* (Tasmanian Historical Research Association, Hobart, Australia).
56. Clark J (1987) Devils and horses: Religious and creative life in Tasmanian Aboriginal society. *The Flow of Culture: Tasmanian Studies*, ed Roe M (Australian Academy of the Humanities, Canberra, Australia), pp 50–72.
57. Holdaway S, Cosgrove R (1997) The archaeological attributes of behaviour: Difference or variability? *Endeavour* 21(2):66–71.
58. McBrearty S, Brooks AS (2000) The revolution that wasn't: A new interpretation of the origin of modern human behavior. *J Hum Evol* 39(5):453–563.
59. Belfer-Cohen A, Hovers E (2010) Modernity, enhanced working memory, and the Middle to Upper Paleolithic record in the Levant. *Curr Anthropol* 51(Suppl 1): S167–S175.
60. Bar-Yosef O, Wang Y (2012) Paleolithic archaeology in China. *Annu Rev Anthropol* 41:319–335.
61. Shea J (2011) *Homo sapiens* is as *Homo sapiens* was: Behavioral variability versus “behavioral modernity” in Paleolithic archaeology. *Curr Anthropol* 52(1):1–35.
62. O'Connell JF, Allen J (2007) Pre-LGM Sahul (Pleistocene Australia-New Guinea) and the archaeology of early modern humans. *Rethinking the Human Revolution*, eds Mellars P, Boyle K, Bar-Yosef O, Stringer CB (McDonald Institute for Archaeological Research, Cambridge, UK), pp 395–410.
63. Atkinson QD, Gray RD, Drummond AJ (2008) mtDNA variation predicts population size in humans and reveals a major Southern Asian chapter in human prehistory. *Mol Biol Evol* 25(2):468–474.
64. Schiffels S, Durbin R (2014) Inferring human population size and separation history from multiple genome sequences. *Nat Genet* 46(8):919–925.
65. Klein RG, Steele TE (2013) Archaeological shellfish size and later human evolution in Africa. *Proc Natl Acad Sci USA* 110(27):10910–10915.
66. Torrence R (1989) Re-tooling: Towards a behavioral theory of stone tools. *Time, Energy and Stone Tools*, ed Torrence R (Cambridge Univ Press, Cambridge, New York), pp 57–66.
67. Collard M, Buchanan B, O'Brien MJ, Scholnick J (2013) Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunter-gatherers. *Philos Trans R Soc Lond B Biol Sci* 368(1630):20120412.
68. Shott M (1986) Technological organization and settlement mobility: An ethnographic examination. *J Anthropol Res* 42(1):15–51.
69. Read D (2008) An interaction model for resource implement complexity based on risk and number of annual moves. *Am Antiq* 73(4):599–625.
70. Collard M, Kemery M, Banks S (2005) Causes of toolkit variation among hunter-gatherers: A test of four competing hypotheses. *Canadian Journal of Archaeology* 29(1):1–19.
71. Kline MA, Boyd R (2010) Population size predicts technological complexity in Oceania. *Proc Biol Sci* 277(1693):2559–2564.
72. Collard M, Ruttle A, Buchanan B, O'Brien MJ (2013) Population size and cultural evolution in nonindustrial food-producing societies. *PLoS One* 8(9):e72628.
73. Collard M, Buchanan B, O'Brien M (2013) Population size as an explanation for patterns in the Paleolithic archaeological record: Caution is needed. *Curr Anthropol* 54(Suppl 8):S388–S396.
74. Codding BF, Jones TL (2010) Levels of explanation in behavioral ecology: Understanding seemingly paradoxical behavior along the Central Coast of Alta California. *California Archaeology* 2:77–92.
75. Buchanan B, O'Brien M, Collard M (2015) Drivers of technological richness in prehistoric Texas: An archaeological test of the population size and environmental risk hypotheses. *Arch Anth Sci*, 10.1007/s12520-015-0245-4.
76. Carneiro RL (1967) On the relationship between size of population and complexity of social organization. *Southwest Journal of Anthropology* 23(3):234–243.
77. Naroll R (1956) A preliminary index of social development. *Am Anthropol* 58(4): 687–715.
78. Price TD, Brown JA (1985) Aspects of hunter-gatherer complexity. *Prehistoric Hunter-Gatherers: The Emergence of Cultural Complexity*, eds Price TD, Brown JA (Academic, Orlando, FL), pp 3–20.
79. Collard M, Buchanan B, Morin J, Costopoulos A (2011) What drives the evolution of hunter-gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. *Philos Trans R Soc Lond B Biol Sci* 366(1567):1129–1138.
80. Klein R (2000) Archeology and the evolution of human behavior. *Evol Anthropol* 9(1):17–36.
81. Mithen S (1996) *The Prehistory of the Mind: The Cognitive Origins of Art and Science* (Thames & Hudson, London).
82. Wynn T, Coolidge F (2007) *Did a Small but Significant Enhancement in Working Memory Capacity Power the Evolution of Modern Thinking? Rethinking the Human Revolution*, eds Mellars P, Boyle K, Bar-Yosef O, Stringer C (McDonald Institute Monographs, Cambridge, UK), pp 79–90.
83. Henrich J (2006) Understanding cultural evolutionary models: A reply to Read's critique. *Am Antiq* 71(4):771–782.
84. Gilligan I (2007) Clothing and modern human behaviour: Prehistoric Tasmania as a case study. *Archaeology in Oceania* 42(3):102–111.
85. Jones R (1990) From Kakadu to Kutikina: The southern continent at 18,000 years ago. *The World at 18,000 BP. Low Latitudes*, eds Soffer O, Gamble G (Unwin Hyman, London), Vol 2, pp 264–295.
86. Taylor R (2007) The polemics of eating fish in Tasmania: The historical evidence revisited. *Aborig Hist* 31:1–26.
87. Williams AN (2013) A new population curve for prehistoric Australia. *Proc Biol Sci* 280(1761):20130486.
88. Cosgrove R, Pike-Tay A, Roebroeks W (2014) Tasmanian archaeology and reflections on modern human behavior. *Southern Asia, Australia and the Search for Human Origins*, eds Dennell R, Porr M (Cambridge Univ Press, Cambridge, New York), pp 15–188.
89. O'Connell J, Allen J (2004) Dating the colonization of Sahul (Pleistocene Australia-New Guinea): A review of recent research. *Journal of Archaeological Science* 31(6):835–853.
90. Webb SG (1989) *The Willandra Lakes Hominids* (Australian National University, Research School of Pacific Studies, Canberra, Australia).
91. Summerhayes G, Allen J (1993) The transport of Mopir obsidian to late Pleistocene New Ireland. *Archaeology in Oceania* 28(3):144–148.
92. Summerhayes GR, et al. (2010) Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science* 330(6000):78–81.
93. Groube L, Chappell J, Muke J, Price D (1986) A 40,000 year-old human occupation site at Huon Peninsula, Papua New Guinea. *Nature* 324(6096):453–455.
94. O'Connell J, Allen J, Hawkes J (2010) Pleistocene Sahul and the origins of seafaring. *The Global Origins and Development of Seafaring*, eds Anderson A, Barrett J, Boyle K (The McDonald Institute for Archaeological Research, Cambridge University, Cambridge, UK), pp 57–68.
95. Fullagar R, Field J (1997) Pleistocene seed grinding implements from the Australian arid zone. *Antiquity* 71(272):300–307.
96. Geneste J-M, David B, Plisson H, Delannoy J-J, Petchey F (2012) The origins of ground-edge axes: New findings from Nawarla Gabarnmang, Arnhem Land (Australia) and global implications for the evolution of fully modern humans. *Cambridge Archaeological Journal* 22(1):1–17.
97. Morse K (1993) Shell beads from Mandu Mandu Creek rock-shelter, Cape Range peninsula, Western Australia, dated before 30,000 b.p. *Antiquity* 67:877–883.
98. Balme J, Morse K (2006) Shell beads and social behaviour in Pleistocene Australia. *Antiquity* 80(310):799–811.

99. Allen J, Gosden C, Jones R, White JP (1988) Pleistocene dates for the human occupation of New Ireland, northern Melanesia. *Nature* 331(6158):707–709.
100. Flannery TF, White JP (1991) Animal translocation. Zoogeography of New Ireland mammals. *National Geographic Research and Exploration* 7:96–113.
101. Leavesley M (2006) Late Pleistocene complexities in the Bismarck Archipelago. *Archaeology of Oceania: Australia and the Pacific Islands*, ed Lilley I (Blackwell, Carlton, Australia), pp 189–204.
102. Slack MJ, Fullagar RLK, Field JH, Border A (2004) New Pleistocene ages for backed artefact technology in Australia. *Archaeology in Oceania* 39(3):131–137.
103. Mellars P, French JC (2011) Tenfold population increase in Western Europe at the Neandertal-to-modern human transition. *Science* 333(6042):623–627.
104. Dogandžić T, McPherron SP (2013) Demography and the demise of Neandertals: A comment on 'Tenfold population increase in Western Europe at the Neandertal-to-modern human transition'. *J Hum Evol* 64(4):311–313.
105. Cosgrove R (1990) *The Archaeological Resources of Tasmanian Forests: Past Aboriginal Use of Forested Environments* (Tasmanian Department Parks, Wildlife and Heritage, Hobart, Australia).
106. Cosgrove R (1995) Late Pleistocene behavioural variation and time trends: The case from Tasmania. *Archaeology in Oceania* 30(3):83–104.
107. Holdaway S, Porch N (1996) Dates as data. An alternative approach to the construction of chronologies for Pleistocene sites in southwest Tasmania. *Report of the Southern Forests Archaeological Project: Site Descriptions, Stratigraphies and Chronologies*, ed Allen J (School of Archaeology, La Trobe University, Bundoora, Australia), Vol 1, pp 251–277.
108. Lourandos H (1983) 10,000 years in the Tasmanian highlands. *Australian Archaeology* 16:39–47.
109. Lourandos H (1997) *Continent of Hunter-Gathers: New Perspectives in Australian Prehistory* (Cambridge Univ Press, Cambridge, New York).
110. Vanderwal R (1978) Adaptive technology in southwest Tasmania. *Australian Archaeology* 8:107–127.
111. Williams AN, Ulm S, Turney CSM, Rohde D, White G (2015) Holocene demographic changes and the emergence of complex societies in Prehistoric Australia. *PLoS One* 10(6):e0128661.
112. Hewitt G, Allen J (2010) Site disturbance and archaeological integrity: The case of Bend Road, an open site in Melbourne spanning Pre-LGM Pleistocene to Late Holocene periods. *Australian Archaeology* 70:1–16.
113. Sim R (1998) The archaeology of isolation? Prehistoric occupation in the Furneaux group of islands, Bass Strait, Tasmania. PhD thesis (Research School of Pacific and Asian Studies, Australian National University, Canberra, Australia).