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Original Article

An experimental demonstration of the effect of group size on cultural accumulation ☆

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ABSTRACT

Cumulative culture is thought to have played a major role in hominin evolution, and so an understanding of the factors that affect cultural accumulation is important for understanding human evolution. Population size may be one such factor, with larger populations thought to be able to support more complex cultural traits. This hypothesis has been suggested by mathematical models and empirical studies of small-scale societies. However, to date there have been few experimental demonstrations of an effect of population size on cultural accumulation. Here we provide such a demonstration using a novel task, solving jigsaw puzzles. 80 participants divided into ten transmission chains solved puzzles in one of two conditions: one in which participants had access to one semi-completed puzzle from the previous generation, and the other in which participants simultaneously saw three semi-completed puzzles from the previous generation. As predicted, the mean number of pieces solved increased over time in the three-puzzle-per-generation condition, but not in the one-puzzle-per-generation condition. Thus, our experiment provides support for a hypothesized relationship between population size and cultural accumulation. In particular, our results suggest that the ability to simultaneously learn from multiple cultural models, and combine the knowledge of those multiple models, is most likely to allow larger groups to support more complex culture.

1. Introduction

Cultural evolution is likely to have played a crucial role in hominin evolution. Examples of this include the spread of cooking and tool-use in earlier hominin species (Carmody & Wrangham, 2009; Foley & Lahr, 2003), and agriculture and writing in our own (Goody & Watt, 1963; O'Brien & Laland, 2012). Moreover, while social learning and cultural differences between populations are common in several non-human species (Galef & Laland, 2005), cumulative culture, defined as cultural traits that are dependent on other cultural traits (Boyd & Richerson, 1996; Enquist, Ghirlanda, & Eriksson, 2011), may be unique to hominins (e.g. Dean, Kendal, Schapiro, Lambeth, Thierry, & Laland, 2012). Cumulative culture is often characterised by the presence of traits that are too complex to have been invented by a single individual, instead having accumulated over multiple generations (Boyd & Richerson, 1996; Tomasello, Kruger, & Ratner, 1993). Such traits are ubiquitous in human domains such as technology, science, and mathematics (Basalla, 1988; Hodgkin, 2005; Longair, 2003), and clearly played a crucial role in our current ecological success. Thus, an understanding of the factors that help or hinder the emergence of cumulative culture is important for understanding hominin evolution.

One factor that has been proposed to be related to the emergence and maintenance of cumulative culture is population size. In an influential paper, Henrich (2004) constructed a mathematical model providing a potential mechanism by which population size partly determines the cultural complexity attainable by that population. In Henrich's model, a population of a given size reproduces in discrete generations, and in each generation every adult member of the population acquires a cultural trait which can be more or less functional, the functionality being measured quantitatively. For example, the trait could be a bow-and-arrow, and its functional measurement how far it shoots, or the trait could be a stone handaxe and its functional measurement how sharp it is. Each individual acquires the trait by copying the single individual in the previous generation with the most functional (i.e. ‘best’) version of the trait. However, they copy this individual imperfectly, so that most individuals make copying errors and acquire a version of the trait that is worse than that of their model, and a few individuals innovate successfully and acquire a version of the trait that is better than that of their model. This imperfect copying process is assumed to be random, so that each individual acquires a trait of different quality compared to other individuals.

Henrich (2004) showed that, given these assumptions, a population of a given size can maintain the transmission of a trait only up to a given functional level, or ‘complexity’. Versions of the trait with greater complexity than the stable level will tend through transmission to get worse, and versions with lesser complexity than the stable

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level to improve, until the stable level is reached. This stable level increases with the size of the population, because the more individuals there are, the greater is the chance that large gains in functionality will occur through innovation and be copied by the next generation. In essence, more innovation takes place in larger populations. The stable level is of course determined by other factors in addition to the size of the population, most importantly its inherent complexity and difficulty to learn. Henrich's model has been extended by Powell, Shennan, and Thomas (2009; see also Shennan, 2001) to look at population density and migration between sub-populations; by Mesoudi (2011a) to include the cost of acquiring more complex knowledge; and by Kobayashi and Aoki (2012) to the case of overlapping rather than discrete generations.

Empirical support for the link between population size and cultural accumulation is generally supportive. Henrich (2004) himself used his model to explain the loss of various technologies (e.g. complex bone tools, spears, boomerangs, fire-making) in Tasmania after rising seas cut it off from Australia approximately 11,000 years ago, thereby creating a smaller sub-population. Powell et al. (2009) used their extended model to explain the emergence of 'modern human behavior' (e.g. symbolic artefacts, complex tools, musical instruments) during the Pleistocene, noting that human population density in Africa, Europe and the Middle East was, according to estimates made using population genetic data and theory, similar at the times when these behaviours emerged. Four studies have investigated the relationship between population sizes of hunter-gathering and food-producing societies on the size and complexity of their toolkits. Collard, Kemery, and Banks (2005) did not find a relationship in a sample of 20 hunter–gatherer populations mainly from North America; Kline and Boyd (2010) did find a relationship with both toolkit size and complexity among 10 Oceanic island populations; Collard, Buchanan, Ruttle, and O'Brien (2011) also did find a relationship with both toolkit size and complexity among 45 food-producing societies from around the world, but not among a similar sample of 34 hunter–gatherer societies; and finally, Collard, Ruttle, Buchanan, and O'Brien (2013) similarly found a relationship with both toolkit size and complexity among 40 food-producing societies from around the world. At greater time depths, Lycett and von Cramon-Taubadel (2008) showed that Acheulean handaxe diversity fitted the predictions of a serial founder effect model, i.e. diversity decreased with predicted decreasing population size as early hominins migrated from an African origin (see also Lycett & Norton, 2010). Thus, there is clearly some empirical support for a link between population size and cultural accumulation.

However, Henrich's (2004) model provides not only a population-level prediction – that cultural complexity should be dependent on population size – but also an individual-level mechanism underpinning that prediction. Regarding the latter, a crucial aspect of Henrich's model is that new, unknowledgeable individuals acquire their cultural knowledge from a single individual of the previous generation, and that this individual has the highest cultural complexity of their generation (i.e. individuals employ success-biased oblique cultural transmission). Under this mechanism, the population-size effect therefore works because larger populations are more likely, by chance, to contain highly successful individuals who are copied by the subsequent generation. While the assumption of success-biased cultural transmission is a reasonable one (see, for example, McElreath, Bell, Efferson, Lubell, Richerson, & Waring, 2008; Mesoudi, 2008, 2011b), learning from just a single individual may be less plausible. Indeed, Enquist, Strimling, Eriksson, Laland, and Sjöstrand (2010) found analytically that cultural transmission from multiple individuals is more likely to maintain knowledge in a population than learning from a single individual, albeit in a non-cumulative cultural system. One might expect that learning from multiple skilled individuals, and combining their knowledge in each generation, would be at least as effective a mechanism for maintaining and accumulating complex cultural knowledge than relying on just the most-skilled individual, particularly when such knowledge can be easily combined. Under this alternative mechanism, then, the population-size effect outlined by Henrich (2004) would still occur, but would occur instead because in larger populations, there are more models available from whom knowledge can be additively combined.

While archaeological and paleoanthropological studies of the kind described above can address the general prediction of cultural–demographic models (a positive relationship between population size and cultural complexity), they cannot test the validity of the underlying mechanism responsible for this effect, given that we cannot directly observe cultural transmission dynamics in long-dead populations (e.g. whether people typically copied one or more individuals, or whether they copied successful individuals). As such, even though there is general support for the link between population size and cultural complexity, this may not necessarily be through the mechanism assumed in existing models. To probe such mechanisms, laboratory experiments are needed, in which cultural transmission dynamics can be directly observed and factors can be isolated and their effects precisely measured (Mesoudi & Whiten, 2008).

To date, three studies have experimentally tested the link between population size and cultural accumulation. Caldwell and Millen (2010) asked participants to build paper airplanes that would fly as far as possible, with participants observing either one, two, or three previous participants building their paper airplanes as well as those participants' completed airplanes. They did not find that the distance the airplanes flew increased more rapidly or to a higher level as the number of models increased. Derex, Beugin, Godelle, and Raymond (2013) had groups of 2, 4, 8 or 16 participants design computer-generated arrowheads (a simple trait) and fishing nets (a complex trait), allowing participants to copy the design of one other participant given information about other participants' success. Derex et al. found that only in the two larger groups (8 and 16) were the simple designs improved, and the complex designs maintained, over successive generations. Finally, Muthukrishna, Shulman, Vasilescu, and Henrich (2014) had chains of participants – either one per generation or five per generation – draw a symbol using a complex graphics software package, or tie a complicated knot. Written instructions, final products and/or videotaped behaviour were transmitted between generations. As predicted, the symbols drawn by chains of five participants increased in complexity due to increasingly effective instructions compared to the chains of single participants, and the knots tied by chains of five participants were more likely to be maintained than the knots tied by the chains of single participants.

Derex et al. (2013) and Muthukrishna et al. (2014) therefore provide support for the overall prediction that cultural complexity is more likely to be maintained and accumulated in larger groups, although Caldwell and Millen (2010) found no effect. Regarding the mechanism, both Derex et al. (2013) and Muthukrishna et al. (2014) found that Henrich's (2004) assumption of success-biased transmission from a single model is a plausible means by which the population-size effect works. However, none of these studies provided a proper test of the alternative mechanism outlined above, where information is integrated from multiple sources. Derex et al. (2013) only allowed participants to learn from a single person at a time, given information about other participants' relative success. Muthukrishna et al. (2014) allowed the five-per-generation participants to view the solutions of all five previous participants simultaneously, potentially allowing the integration of multiple participants' knowledge, but in practice participants predominantly copied the single most successful participant of those five. Caldwell and Millen's (2010) participants could also view two or three models simultaneously, but the task used, building paper airplanes, was not conducive to integrating information across models because different airplane designs may be incompatible. That is, combining elements of