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Population size predicts technological complexity in Oceania

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Much human adaptation depends on the gradual accumulation of culturally transmitted knowledge and technology. Recent models of this process predict that large, well-connected populations will have more diverse and complex tool kits than small, isolated populations. While several examples of the loss of technology in small populations are consistent with this prediction, it found no support in two systematic quantitative tests. Both studies were based on data from continental populations in which contact rates were not available, and therefore these studies do not provide a test of the models. Here, we show that in Oceania, around the time of early European contact, islands with small populations had less complicated marine foraging technology. This finding suggests that explanations of existing cultural variation based on optimality models alone are incomplete because demography plays an important role in generating cumulative cultural adaptation. It also indicates that hominin populations with similar cognitive abilities may leave very different archaeological records, a conclusion that has important implications for our understanding of the origin of anatomically modern humans and their evolved psychology.

Keywords: technological complexity; demography; cultural evolution

1. INTRODUCTION

Humans occupy a greater diversity of habitats, use a broader range of resources and form a wider array of social systems than any other animal species. This diversity is often explained in terms of human cognitive ability—we are able to adapt to a wide range of environments because we are cleverer than other creatures (e.g. Tooby & Devore 1987). A number of authors have argued that cumulative cultural adaptation plays an essential role in allowing humans to adapt so widely (see Richerson & Boyd (2005) for references). Humans are much better at learning from conspecifics than any other animal, allowing human populations to gradually create technologies, knowledge and institutions too elaborate for any one person to invent. One important corollary of this hypothesis is that larger populations will generate more complex cultural adaptations than smaller, isolated ones (Neiman 1995; Shennan 2001; Henrich 2006; Powell *et al.* 2009). Here, we test this prediction empirically and show that in Oceania around the time of early European contact, large, well-connected populations had more complicated marine foraging technology than did small, isolated populations.

Two models of cumulative cultural adaptation predict that large populations will have more diverse and more complex tool kits than small, isolated populations. First, cultural transmission is subject to a process analogous to genetic drift (Neiman 1995; Shennan 2001)—in finite populations, the number of people adopting a variant is affected by sampling variation. This means that cultural variants are lost by chance when their practitioners are not imitated. For instance, the most

knowledgeable net maker may not be copied because he/she is poor, unsociable or dies unexpectedly, and thus her special skills would be lost to the population. The rate of loss owing to cultural drift will be higher in small populations than in larger ones because such random losses are more likely. Lost traits can be reintroduced by the flow of people or ideas from other populations, so the equilibrium amount of variation depends on the rate of contact between groups.

Second, social learning is subject to error, and since errors will usually degrade complex adaptive traits, most ‘pupils’ will not attain the level of expertise of their ‘teachers’. In this way, inaccurate learning creates a ‘treadmill’ of cultural loss, against which learners must constantly work to maintain the current level of expertise. This process is counteracted by the ability of individuals to learn selectively from expert practitioners, so that cumulative cultural adaptation happens when a rare pupil surpasses his/her teachers (Henrich 2004, 2006). Learners in larger populations have access to a larger pool of experts, making such improvements more likely. As in the cultural drift models, contact between populations replenishes adaptive variants lost by chance, leading to higher levels of standing variation and thus more adaptive traits (Powell *et al.* 2009). Of course, ecological and economic factors may affect the kinds of tools that people use. We do not claim that such factors are unimportant. Rather, models of cultural adaptation predict that in the same economic and ecological circumstances, smaller, isolated populations will have simpler tool kits.

Existing empirical evidence bearing on this hypothesis is mixed. There are a number of examples of the degradation of technology in small, isolated island populations. For instance, the Tasmanian tool kit gradually became simpler after isolation from mainland Australia (Diamond 1978; Henrich 2004, 2006; but see Read 2006), and other Pacific groups have abandoned

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apparently useful technologies such as canoes, pottery and the bow and arrow (Rivers 1926). Elsewhere in the world, the isolated Polar Inuit lost kayaks, the leister and the bow and arrow when all knowledgeable people died during a plague, only to have these skills reintroduced by long-distance migrants from Baffin Island (Rasmussen 1908; Golden 2006). Neither of two systematic tests of this hypothesis found any relationship between population size and tool kit diversity or complexity (Collard *et al.* 2005; Read 2008). However, the sample used in both analyses did not include any measure of contact between populations and was drawn mostly from northern coastal regions of the western North America where intergroup contact was probably common (Balikci 1970; Jordan 2009), but difficult to estimate. If, as the cultural adaptation models predict, frequent contact between groups mitigates the effects of small population size, then the results from these analyses do not provide a test of the models.

Here, we examine the effects of population size and contact on the complexity of marine foraging tool kits among island populations in Oceania. Because island populations are geographically bounded and separated by significant distances, it is possible to estimate population sizes and contact rates with a reasonable degree of accuracy. The groups in our sample exploit similar marine ecosystems, and thus by focusing on marine foraging tools, we minimize the effect of ecological variation. The groups also share a common cultural descent, minimizing the potential impact of cultural history. Analysis of these data indicates that both the number of tools used for marine foraging and the average complexity of tools are higher in large populations than in small, isolated ones.

2. MATERIAL AND METHODS

Our sample is drawn from the electronic Human Relations Area Files (eHRAF) (World Cultures Ethnography Database 2008) and consists of information on indigenous marine foraging tool kits from 10 island societies (table 1). Rates of contact are defined as high or low by the eHRAF Culture Summaries. Finer-grained measures of contact were not available. We collected ethnographic excerpts indexed by eHRAF as *fishing*, *marine foraging* or *fishing gear*. We used these excerpts to generate a list of all marine foraging tools and coded each of those tools in terms of complexity. Tool types were established using the following criteria: (i) tools had different names and at least one non-overlapping function, (ii) tools had different mechanical structures, or (iii) tools were made through different production processes. The number of tool types varied from 13 in Malekula to 71 in Hawaii.

Tool complexity was quantified by the number of 'techno-units'. A techno-unit was defined by Oswalt (1976, p. 38) as 'an integrated, physically distinct and unique structural configuration that contributes to the form of a finished artefact'. Techno-unit counts are based on verbal descriptions, illustrations and photographs from the eHRAF and ranged from one techno-unit (e.g. a stick used for prying shellfish from the reef) to 16 techno-units (e.g. an untended crab trap made of a bamboo tube and baited lever); see the electronic supplementary material for an example of techno-unit coding. In contrast to Oswalt, we include decorative elements in the techno-unit counts because the production of any part

Table 1. Data on population size, contact and tool kits for each population in our sample. (Data were coded from the electronic Human Relations Area Files ethnographic database. Total number of tools includes artefacts for which there was no techno-unit (TU) information available; mean TU are based only on tools for which TU information was available. The proportion of tools with TU information ranged from 55% to 78% for each group and is not significantly associated with mean TU (Pearson's $r = -0.089$, $p = 0.404$, $n = 10$).)

culture	population	contact	total tools	mean TU
Malekula	1100	low	13	3.2
Tikopia	1500	low	22	4.7
Santa Cruz	3600	low	24	4.0
Yap	4791	high	43	5.0
Lau Fiji	7400	high	33	5.0
Trobriand	8000	high	19	4.0
Chuuk	9200	high	40	3.8
Manus	13 000	low	28	6.6
Tonga	17 500	high	55	5.4
Hawaii	275 000	low	71	6.6

of the tool may be socially learned, and thus subject to the dynamics of the cultural transmission process upon which both models are based. If a given tool was present in more than one society's tool kit, we coded that tool independently for each society where information was available. Next, we computed the mean of these techno-unit estimates. We then used the mean as the techno-unit estimate for that tool across all societies where it was present, replacing the original independent estimates. This helped to control for potential coder and/or ethnographer bias and worked against our hypotheses by decreasing variation between groups.

We used log-transformed population size, tool number and tool complexity data because both the treadmill and drift models predict a concave relationship between population size and technological complexity. We attempted to control for variation in marine biodiversity using the number of fish genera per region as listed in Fishbase (Froese & Pauly 2009) as a covariate. To control for the variation in the importance of fishing, we used data on per cent of subsistence that comes from fishing data compiled for eHRAF by Ember *et al.* (1992), Ember (2008) and by Huber *et al.* (2004). Previous analyses indicate the risk of resource failure is associated with increased tool complexity (Torrence 2000; Collard *et al.* 2005). To control for this possibility, we included a number of measures of such risk including: (i) seasonality and productivity (latitude and effective temperature), (ii) vulnerability to catastrophic storms (total cyclones, and mean and total wind speeds for those cyclones for the past 10 years), and (iii) drought risk (mean annual number of rainy days and standard deviation in daily rainfall). Effective temperature is a measure created by Bailey (1960) and used by Binford (2001) and Collard *et al.* (2005) as a measure of ecosystem abundance (see the electronic supplementary material for details). With the exception of Hawaii, all data on cyclones were gathered from Australian Severe Weather (2009). For Hawaii, we used cyclone data from the National Weather Service (2009) online. All other weather data were gathered from Weatherbase (2009). Similarly, for each society we used three measures, taken from the eHRAF collection description, to control for the amount of ethnographic effort: number of publications, total pages of publications in eHRAF and number of authors.

We did not use tool counts for the two island populations available in Oswalt (1976): the Pukapuka and the Tiwi. Although including these groups does not qualitatively alter our results (see the electronic supplementary material), we do not think it is appropriate to mix sources in this way. We were careful to choose our ethnographic sources ahead of time based on inclusion in the eHRAF, and then used consistent methods to infer the number of tool types and the number of techno-units. There may have been systematic error in our estimates of the absolute numbers of tools owing to the fact that ethnographers did not describe all tool types, but by being consistent in the way we chose and coded the ethnographies, we hoped to preserve the relative size of the numbers on different islands.

3. RESULTS

Analysis of these data support the hypothesis that gradual cultural evolution causes large populations to have a greater number of more complex cultural adaptations than small, isolated populations in three ways.

First, larger island populations have a larger repertoire of tools than smaller island populations (figure 1). In a linear regression model, the effect of population size on the number of tools is strong and highly significant ($\beta = 0.805$, $p = 0.005$). The other explanatory variables had smaller standardized coefficients, and the Akaike information criterion with a second order correction (AICc) information theoretic statistic indicates that population size is a much better predictor than any other single explanatory variable (table 2).

We also performed a series of regressions that combined population size and one of the alternate explanatory variables (table 2). The effect of population size on the number of tools remains strong and, in most cases, remains significant or close to significant at conventional levels. None of the alternative explanatory variables were significantly associated with the number of tools, and when AICc weights for all models that include population size are summed, the total is 0.7157 (with 1 being the maximum). This suggests that any effective model in our set will include population size as a dependent variable.

Second, both models of cultural adaptation predict that contact will be less important in larger populations. Our data provide some support for this prediction. Figure 1 shows that four of the five high-contact societies have more tool types than expected based on their population size. These five societies all fall in the intermediate range of population size. Low-contact groups tended to have fewer tools than expected while high-contact groups tended to have more (Mann-Whitney, $U = 5$; one-tailed exact $p = 0.075$, $n = 5$; t -test, one-tailed $p = 0.052$, $n = 10$). AICc results suggest that contact is important, with the model that includes contact and population size ranked as the second-best model (table 2).

Finally, both models of cultural adaptation predict that complex tools will be especially prone to loss because it is harder to learn how to make them (Henrich 2004), and they will be more affected by cultural drift if component parts of a tool are the units of inheritance. This prediction is supported by the data (figure 2). The mean number of techno-units is significantly higher in larger populations than in smaller populations ($\beta = 0.706$, $p = 0.022$).

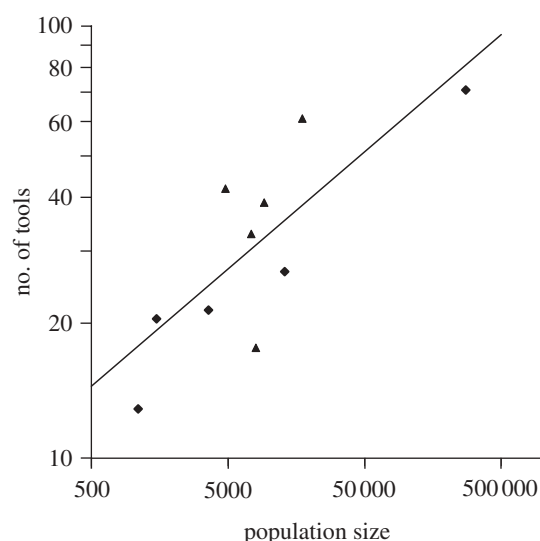


Figure 1. Number of tools as a function of population size. Larger populations have significantly more tool types than smaller populations. The trend line is based on a linear regression of the logarithm of the number of tools against the logarithm of population size ($\beta = 0.805$, $p = 0.005$, $n = 10$). Four of five low-contact groups have fewer tools than expected, whereas four out of five high-contact groups exceed the expected number of tools. Diamonds, low contact; triangles, high contact.

Again standardized coefficients for most of the alternate explanatory variables are substantially smaller. However the standard deviation of rainfall has a substantial effect on tool complexity. The AICc information theoretic statistic indicates that population size is the best individual predictor, but standard deviation of rainfall is a fairly close second (table 3). In a series of regressions that include population size and one of the alternative variables, population size remains a strong predictor of tool complexity, and none of the alternative predictors are significantly associated with tool complexity. Once again, the sum of AICc weights for all models that include population size ($w = 0.6692$) suggests that any informative model in our set will include population size. According to the AICc statistic, population size and contact is the sixth most-preferred model for predicting tool complexity, with population and standard deviation in rainfall being the most-preferred (table 3).

To assess the robustness of our coding method and of our sample composition, we retested our main finding—that population size predicts number of marine foraging tools—with a revised dataset. First, we had research assistants recode number of tools for four groups in our sample and used these numbers instead of those from the original coder, and used Oswalt's (1976) data on Trukese (in eHRAF, Chuuk) instead of our original coder's estimate of the number of tools. These changes do not qualitatively alter our main result (see the electronic supplementary material for details). Second, we added two groups available in Oswalt's sample but not available in the eHRAF (the Pukapuka and the Tiwi) to the sample. Using this new dataset ($n = 12$), we again find our main result: population size predicts the number of tools in a group's marine foraging tool kit (see the electronic supplementary material for details).

Table 2. Each row gives the standardized regression coefficients and significance values for a multiple regression in which the dependent variable is the logarithm of number of tool types and the independent variables are the logarithm of population size and one of the alternative variables. (The coefficients for population size are large and mostly significant, whereas the coefficients for the control variables are smaller and none are close to significant. Significance values based on bootstrap analysis show a similar pattern (see the electronic supplementary material for details). Models are arranged in order of best fit according to the AICc information theoretic statistic. The AICc value for a regression with only the constant is 0.63.)

	β	significance		β	significance	AICc	AICc weight
population	1.04	0.002	fish genera	-0.413	0.110	-3.39	0.06513
population	0.792	0.006	contact	0.259	0.239	-3.21	0.05956
population	0.824	0.006	mean maximum cyclone wind speed	-0.206	0.361	-3.12	0.05711
population	0.733	0.014	publications	0.205	0.396	-3.11	0.05663
population	0.988	0.017	mean rainfall per year	0.249	0.455	-3.08	0.05592
population	0.871	0.007	mean rainy days per year	0.175	0.476	-3.07	0.05570
population	0.918	0.012	sum of maximum wind speeds for all cyclones	-0.188	0.510	-3.06	0.05539
population	0.858	0.010	total cyclones	-0.123	0.628	-3.03	0.05454
population	0.783	0.010	latitude	0.635	0.112	-3.03	0.05451
population	0.724	0.069	importance of fishing	0.008	0.979	-3.01	0.05381
population	0.844	0.019	standard deviation rainfall per year	0.065	0.822	-3.00	0.05378
population	0.819	0.014	effective temperature	0.030	0.908	-3.00	0.05362

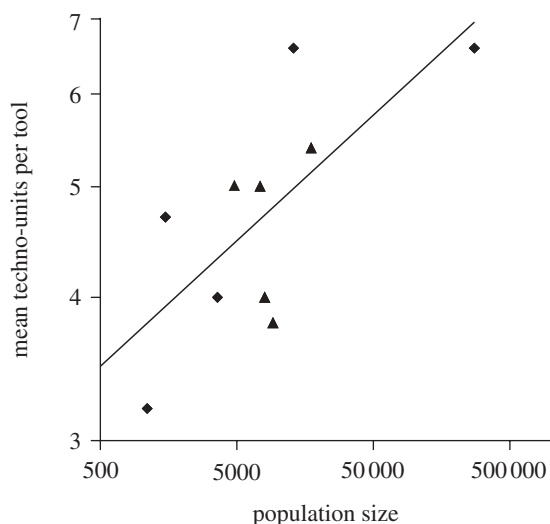


Figure 2. Mean number of techno-units by population size. Larger populations have significantly more complex tools than smaller populations. The trend line is based on a linear regression of the logarithm of mean techno-units per tool against the logarithm of population size ($\beta = 0.706$, $p = 0.022$, $n = 10$). Diamonds, low contact; triangles, high contact.

4. DISCUSSION

There is much evidence that ecological factors affect subsistence practices and therefore the size and complexity of the optimal tool kit (Bird & O'Connell 2006), and there are a number of hypotheses about which factors are most important. For example, Oswalt (1976) argued that hunting mobile prey requires larger, more complex tool kits than gathering immobile resources, Torrence (2000) hypothesized that tool kits are larger in environments in which the risk of resource shortfall is high and Shott (1986) posited that mobile populations have smaller tool kits than sedentary ones. In a systematic test of these hypotheses, Collard *et al.* (2005) found that latitude was the only predictor of technological complexity and interpreted this result as

supporting the hypothesis that risk of shortfall is the most important factor.

The present analysis is aimed at answering a different question: do population size and intergroup contact affect the cultural processes that allow populations to evolve tool kits that are adaptive in their environment? We believe that individuals rarely invent new tools from scratch; instead the knowledge about how to make and use the myriad of highly adaptive tools that characterize human populations accumulates gradually over time as people learn from others, make incremental improvements and then serve as models for the next generation. If this view of human adaptation is correct, the ability of human populations to evolve the optimal tool kit as determined by ecological factors will depend on constraints imposed on cultural adaptation by population size and the rate of contact between populations. To test this hypothesis, we chose to study island populations because they are ecologically similar and because population size and contact rates are easier to estimate than in continental populations. Then by limiting the analysis to marine foraging tools, we hoped to minimize the effects of ecological variation on tool kit complexity. Thus, our observation that larger populations have more kinds of marine foraging tools and more complex tools than smaller, isolated populations supports the hypothesis that gradual cultural evolution plays an important role in human adaptation.

There are three alternate explanations of the relationship between population size and tool kit complexity, but none explains the relationship between contact and tool kit complexity. First, it is possible that more complex marine foraging technology increases the local carrying capacity, resulting in larger population sizes. But it is not clear why rates of contact would be linked to larger population sizes. Second, large populations have more domains of specialization (Carneiro 1967), and this might lead to a more diverse tool kit. This only provides a competing explanation if increased specialization is not caused by the increase in tool complexity itself, but by some other correlate of population size. For example, economies of scale in large populations might permit

Table 3. Each row gives the standardized regression coefficients and significance values for a multiple regression in which the dependent variable is the logarithm of average number of techno-units per tool and the independent variables are the logarithm of population size and one of the alternative variables. (The coefficients for population size are large and mostly significant, whereas the coefficients for the control variables are smaller and none are close to significant. Significance values based on bootstrap analysis are larger, but show a similar pattern (see the electronic supplementary materials for detail). Models are arranged in order of best fit according to the AICc information theoretic statistic. The AICc value for a regression with only the constant is -2.91 .)

	β	significance		β	significance	AICc	AICc weight
population	0.514	0.143	standard deviation rainfall per year	-0.321	0.337	-4.33	0.05504
population	0.727	0.026	mean maximum cyclone wind speed	-0.205	0.453	-4.27	0.05355
population	0.907	0.048	mean rainfall per year	0.274	0.494	-4.26	0.05317
population	0.798	0.029	effective temperature	0.201	0.511	-4.25	0.05301
population	0.828	0.038	sum of maximum wind speeds for all cyclones	-0.203	0.551	-4.24	0.05270
population	0.715	0.030	contact	-0.144	0.600	-4.23	0.05238
population	0.702	0.033	importance of fishing	-0.103	0.710	-4.22	0.05215
population	0.732	0.030	latitude	-0.127	0.652	-4.22	0.05209
population	0.757	0.036	total cyclones	-0.120	0.694	-4.21	0.05189
population	0.632	0.093	fish genera	0.128	0.705	-4.21	0.05186
population	0.670	0.052	mean number of rainy days per year	-0.096	0.747	-4.20	0.05171
population	0.722	0.039	publications	-0.044	0.883	-4.19	0.05137

higher degrees of specialization. However, this does not explain the relationship between tool kit complexity and rates of contact. Finally, it may be that an increase in population size and subsequent resource scarcity may cause a population to broaden its diet to include resources with lower rates of return, which in turn inspires the invention of technologies that make food-handling (and thus foraging in general) more efficient (Hawkes & O'Connell 1992). Again, this cannot explain the importance of contact. In addition, we would expect some effect of ecological variables such as seasonality, productivity or resource risk were this the case. However, it is important to realize that this mechanism and the cultural evolutionary models discussed above are compatible: one concerns determinants of optimal tool kit breadth, the other constraints on achieving that breadth. In fact, the models that best explained tool complexity in our dataset included population size as well as a measure of contact, cyclone winds or rain variability. A more extensive study of the impact of intergroup contact on tool kit complexity may help to explain why such results have not been found in previous studies.

Our results also have important implications for the evolution of human cognition. Archaeologists sometimes assume that the cognitive abilities of a hominin species can be inferred from the complexity of the artefacts that they have produced. For example, the use of ochre and other signs of modernity appear sporadically in the archaeological record of Africa during the late Middle Pleistocene. Since it seems unlikely that cognitively complex hominins evolved and then disappeared from Africa, some archaeologists have suggested that the finds are incorrectly dated or otherwise artefactual (Klein 1999). However, if population size affects technological complexity, other interpretations become plausible. For example, Powell *et al.* (2009) have argued that the geographical patterning of the first emergence of markers of modern human culture, and their subsequent spatio-temporal transience, are better explained by changes in population size than by a late, species-wide cognitive

revolution. Similarly, Hill *et al.* (2009) have argued that the sporadic appearance of sophisticated tools during the Late Stone Age in Africa can be understood as the result of climate-induced fluctuations in population size. Our study provides empirical support for these arguments.

These findings are a first step in understanding the nature of cumulative cultural gains and losses. Although our sample size is small and our analysis is restricted to a limited range of tool types, our results suggest that cultural drift or the treadmill mechanism may have influenced the evolution and adaptive radiation of *Homo sapiens* as a cultural species.

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