PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. B 2013 **368**, 20120412, published 7 October 2013

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Cite this article: 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. Phil Trans R Soc B 368: 20120412.
http://dx.doi.org/10.1098/rstb.2012.0412

One contribution of 15 to a Theme Issue 'Tool use as adaptation'.

Subject Areas:
behaviour, evolution, cognition

Keywords:
hunter–gatherers, western North America, technological richness, risk hypothesis, population-size hypothesis, mobility hypothesis

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2012.0412 or via http://rstb.royalsocietypublishing.org.

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Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunter–gatherers

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Identifying factors that influence technological evolution in small-scale societies is important for understanding human evolution. There have been a number of attempts to identify factors that influence the evolution of food-getting technology, but little work has examined the factors that affect the evolution of other technologies. Here, we focus on variation in technological richness (total number of material items and techniques) among recent hunter–gatherers from western North America and test three hypotheses: (i) technological richness is affected by environmental risk, (ii) population size is the primary determinant of technological richness, and (iii) technological richness is constrained by residential mobility. We found technological richness to be correlated with a proxy for environmental risk—mean rainfall for the driest month—in the manner predicted by the risk hypothesis. Support for the hypothesis persisted when we controlled for shared history and intergroup contact. We found no evidence that technological richness is affected by population size or residential mobility. These results have important implications for unravelling the complexities of technological evolution.

1. Introduction

Technology has been crucial to the evolutionary success of our lineage. Without technology, it is unlikely that hominins would have become so numerous or occupied such a wide range of habitats. There is also reason to think that important features of the hominin body have coevolved with technology, including hand form and hair density [1,2]. Thus, in order to understand human evolution, we have to determine which factors influence technological evolution. Small-scale societies are of particular importance in this context because hominin history is dominated by such societies. Current evidence indicates that the hominin clade originated about 7 Myr ago [3]. Large-scale societies—those with tens of thousands of members, cities and impersonal social institutions—did not appear until the Holocene [4]. Hence, for 99% of the time that hominins have existed as a distinct lineage, they have lived in small-scale societies.

There have been a number of attempts to identify the factors that influence the evolution of food-getting technology [5–21], but there has been little work on the factors that affect the evolution of other technologies used by small-scale societies. The study reported here is an attempt to begin to fill this gap. We focused on variation in the total number of material items and techniques among hunter–gatherers from western North America during the early contact period and tested three hypotheses: (i) that the number of material items and techniques is affected by environmental risk, (ii) that population size is the primary determinant of the number of material items and techniques, and (iii) that

the number of material items and techniques is constrained by residential mobility. These hypotheses were inspired by the aforementioned work on the causes of variation in the number and intricacy of the tools that small-scale societies use to obtain food.

2. Background

The foundations for systematic research on food-getting toolkits were laid by Oswalt [5,6], who devised several measures of toolkit structure. One is the total number of subsistants, which Oswalt defined as a tool that is employed directly in the acquisition of food. Oswalt suggested that the total number of subsistants is an indicator of the size of a toolkit. Other researchers have referred to this variable as toolkit 'diversity' [8,9,11,15], but that term is potentially confusing. In ecology, 'taxonomic diversity' has two dimensions: 'richness' and 'evenness'. The former refers to the number of taxa in a community, landscape or region, whereas the latter refers to how similar the taxa in a community, landscape or region are in terms of numbers of individuals [22]. Thus, in order to reduce the potential for confusion, we refer to the total number of subsistants as 'toolkit richness' rather than 'toolkit diversity'. Oswalt's second measure of toolkit structure is the total number of technounits. Formally, a technounit is an 'integrated, physically distinct and unique structural configuration that contributes to the form of a finished artifact' [6, p. 38]. More simply, technounits are the different kinds of parts of a tool. The total number of technounits included in a toolkit is a measure of its 'complexity' [5,6,8,9,15,16]. Oswalt's third measure of toolkit structure is the average number of technounits per subsistant, which is calculated by dividing the total number of technounits in a toolkit by its richness value. Again, this is a measure of toolkit complexity [5,6,8,9,15].

Four hypotheses have been put forward to explain variation in the structure of small-scale societies' food-getting toolkits. The diet hypothesis was developed by Oswalt [6], who argued that the structure of a group's toolkit is affected by the group's degree of reliance on mobile resources because such resources are more difficult to exploit and therefore require more complex tools than immobile resources. Oswalt also argued that, because aquatic animals are more mobile than terrestrial animals, groups that depend on aquatic animals will have more complex toolkits than groups that rely on terrestrial animals. The latter point has also been made by Osborn [12].

The risk hypothesis has its roots in Torrence [8], in which she hypothesized that as time stress increases, hunter–gatherers produce more-specialized tools because they tend to be more effective. Because specialized tools usually have more parts than generalized tools, production of specialized tools increases both toolkit richness and toolkit complexity. Subsequently, Torrence [9] argued that time stress was only a proximate cause of toolkit variation and that the ultimate cause is the risk of resource failure. The use of more specialized, and therefore more elaborate, tools reduces risk of resource failure. Thus, groups that experience high risk of failure will produce toolkits that are richer and more complex than the toolkits of groups that experience lower risk of resource failure.

Shott [11] proposed the mobility hypothesis, which states that toolkit richness and complexity are influenced by residential mobility. This relationship exists, Shott argued, because carrying costs constrain the number of the tools a group can employ regularly. Groups that move frequently and/or long distances each year can be expected to have less-rich toolkits than those that move less frequently and/or shorter distances. The corollary of this is that the tools employed by highly mobile groups will be less specialized than those used by less-mobile groups, because they will be applied to a broader range of tasks.

The population-size hypothesis is based on modelling work carried out by Shennan [23] and Henrich [16]. Shennan showed that larger populations have an advantage over smaller ones when it comes to cultural innovation as a result of the decreasing role of sampling effects as populations get larger. When populations are large, there is a greater probability of fitness-enhancing innovations being maintained and deleterious ones lost than when populations are small. Henrich demonstrated that population size can also affect the probability of more complex skills being invented and maintained. In Henrich's model, learners preferentially copy the most skilled practitioner with some amount of error. The probability distribution that determines the amount of error is such that a learner will only occasionally get a better result than the previous best. The likelihood of this occurring is partly dependent on population size because in large populations even improbable events occur occasionally, and the larger the population, the more likely this is. Consequently, toolkit richness and complexity will be influenced by population size [13–15,21].

Recently, there have been a number of attempts to determine which hypothesis offers the best explanation for the variation in the structure of food-getting toolkits of ethnographically documented hunter–gatherers. Collard *et al.* [15] tested the hypotheses by subjecting data for 20 hunter–gatherer groups to stepwise multiple regression. They found that the only significant predictors of toolkit richness and complexity were the proxies for risk of resource failure they employed. Henrich [14] used Collard *et al.*'s dataset to investigate the impact of risk, mobility and diet on toolkit complexity, and found that risk was the only factor that explained a significant proportion of the variation in complexity. Read [20] argued that Collard *et al.*'s results are problematic, because they depend on their choice of regression technique. He then reported a study in which he reassessed the relative merits of the hypotheses using several types of multiple regression. Read employed Oswalt's [6] toolkit-structure data and the same proxy data as Collard *et al.* but used additional toolkit variables and another proxy for risk of resource failure, growing season. Read found that in majority of his analyses toolkit-structure measures were most strongly influenced by risk but were also affected—to a lesser extent—by mobility. In another study, Collard *et al.* [16] tested the risk hypothesis with data from hunter–gatherer groups living on the coast and plateau of the Pacific Northwest in the early contact period. Their analyses suggested that the plateau is a more risky environment than the coast. However, the predicted differences in the number and intricacy of the groups' food-getting tools were not observed. Collard *et al.* argued that their results likely indicate that the impact of risk is dependent on the scale of risk differences among groups: when risk differences are large, risk is the most important influence on toolkit structure. However, when risk differences among groups are small, other factors are as, if not more, influential as determinants of toolkit structure.

There have also been several attempts in recent years to test the hypotheses with data from recent small-scale farming and pastoralist societies [17,18,21]. Kline & Boyd [21] examined the impact of population size on marine foraging toolkits of 10 farming and fishing groups from Oceania. They found that population size had a significant impact on both the number of tools and the average number of technounits per tool. Collard *et al*. [17] investigated whether the toolkits of small-scale farmers and herders in the historic period were influenced by risk of resource failure. They applied simple linear and multiple regression analysis to toolkit and environmental data for 45 groups from five regions of the world. Their analyses did not support the risk hypothesis. None of the environmental variables had a significant impact on the toolkit variables. Collard *et al*. [18] investigated whether the subsistence toolkits of small-scale food producers are influenced by population size in the manner suggested by the population-size hypothesis. They applied simple linear and stepwise multiple regression analysis to data from 45 non-industrial farming and pastoralist groups to test the population-size hypothesis. Results of the analyses were consistent with the predictions of the hypothesis: both the richness and complexity of the toolkits of the food producers were positively and significantly influenced by population size in the simple linear regression analyses. The multiple regression analyses demonstrated that these relationships are independent of the effects of risk of resource failure, which, as we explained earlier, is the other main factor that has been found to influence toolkit richness and complexity in non-industrial groups. Collard *et al*. concluded from this that population size influences toolkit structure in non-industrial food-producing groups.

Currently, then, it appears that the food-getting toolkits of hunter–gatherers and small-scale farmers and herders are influenced by different factors. Among-group variation in hunter–gatherer food-getting toolkits seems to be driven primarily by risk of resource failure. Other factors may be more important in certain regions, but at the global scale, risk of resource failure is the dominant influence. By contrast, risk of resource failure does not seem to influence among-group variation in the food-getting toolkits of food producers. Rather, differences in the richness and complexity of the food-getting toolkits of food producers appear to be the result of differences in population size.

3. Material and methods

To reiterate, in this study, we tested the predictions of three hypotheses concerning variation in the total number of material items and techniques. To be consistent with the terminology discussed in §2, we refer to this variable as 'technological richness'. The first hypothesis is a generalization of the idea that risk of resource failure affects food-getting toolkit-richness structure. It contends that technologies are developed primarily to deal with environmental risks. Risk of resource failure is one of the most important of these risks, but there are several others, including risk of obtaining in sufficient water, risk of failing to maintain body temperature and risk of infectious disease. According to this hypothesis, technological richness should increase as the riskiness of the environment increases. The second hypothesis holds that technological richness is dependent on population size. The modelling work on which the idea that the structure of food-getting toolkits should be influenced by population size is not specific to food-getting tools. Shennan [23] and Henrich [13] modelled the impact of population size on generic cultural traits and a generic skill, respectively. Thus, there is reason to think that the population-size hypothesis is applicable to technological richness and not just to food-getting toolkit richness. The third hypothesis is a generalization of the mobility hypothesis. To reiterate, at the heart of the latter hypothesis is the idea that humans can carry only a limited number of items. Obviously, this should hold for most forms of technology, not just for food-getting tools. Therefore, there is reason to think that the mobility hypothesis might also hold for technological richness. We did not investigate the impact of diet on technological richness, because diet has not been found to have an impact on food-getting toolkit structure independent of risk, mobility and population size in recent studies [15,20]. In addition, we could not identify an obvious theoretical reason why diet should impact technological richness (as opposed to food-getting toolkit richness).

The groups used in the study resided in western North America during the early contact period and are classified as hunter–gatherers. Western North America corresponds roughly to the major physiographic region known as the North American Cordillera, which comprises the Rockies, the Coast Ranges in the states of California, Oregon, Washington and the province of British Columbia, and a series of intermontane plateaus. Ecologically, western North America is highly variable. It includes alpine and subalpine habitats as well as areas of temperate rainforest, boreal forest and desert. The early contact period in western North America began in the sixteenth century and ended in the early twentieth century. Hunter–gatherers are popularly understood to be people who live in small, egalitarian groups, subsist on wild plants and terrestrial game, and move frequently. However, historically there were also hunter–gatherers who lived in hierarchically organized communities of hundreds of people, were heavily dependent on aquatic resources and moved relatively infrequently, if at all. Both types of groups existed in western North America at the time of European contact and are represented in the sample.

Data on technological richness were obtained from Jorgenson's *Western North American Indians* [24]. We extracted data for 45 of the 46 traits in Jorgenson's 'technology and material culture' category. The only trait we did not include was no. 149, 'maize cultivated at time of first contact with Europeans'. We did not include this trait because of the study's focus on hunter–gatherers. Multistate traits were recoded into presence/absence. For example, Jorgenson included three states for trait no. 142, 'Fish nets and seines': (i) probably no nets, (ii) only small hand nets, and (iii) gill nets and seines. We created two traits out of this trait: presence/absence of the use of only small hand nets, and presence/absence of the use of gill nets and seines. Forty-one of the 45 traits had to be recoded. After recoding, there were 99 traits (see the electronic supplementary material). A group's value for technological richness is simply the number of times the group is coded as 'present' for the 99 traits.

Next, we added data for several potential driver variables to the dataset. The variables in question are species richness, net aboveground productivity (NAGP), effective temperature, mean rainfall for the wettest month (RHIGH), mean rainfall for the driest month (RLOW), population size and total distance moved per year during residential moves (DMV). NAGP is the amount of new cell life that is added to a given location by photosynthesis and growth in a year (measured in grams per square metre per year). Also known as 'warmth', effective temperature was developed to aid understanding of the impact of temperature on the distribution of living and fossil plants [25]. It is defined as the temperature characteristic of the start and finish of the period in which plant growth occurs [25].

Data for species richness were obtained from Jorgenson [24], who recorded the presence/absence of 124 plants and animal

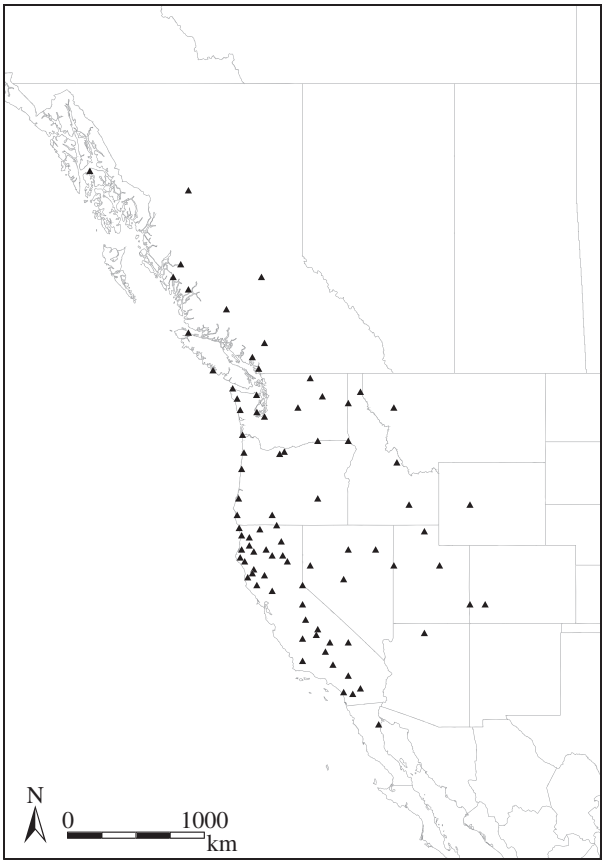

Figure 1. Map of western North America showing locations of the 85 groups in the sample.

species within the area occupied by each group. These include 54 wild plant species, 29 sea mammal species, 19 terrestrial mammal species, 18 freshwater, saltwater and anadromous fish species and four game bird species. A group's value for species richness is the number of times the group is coded as 'present' for traits in the following categories: 'number of sea mammals present in group's area' (traits 63–91), 'number of land mammals present in group's area' (traits 93–111), 'number of fish present in group's area' (traits 113–124, 126–131) and 'number of game birds present in group's area' (traits 134–137).

Data for the other driver variables were taken from Binford's *Constructing frames of reference: an analytical method for archaeological theory building using hunter–gatherer and environmental data sets* [26], which is widely regarded as the single best source of socioecological data on contact-period hunter–gatherers. We were able to obtain values for NAGP, effective temperature, RHIGH, RLOW and population size from Binford for 85 of the groups for which Jorgenson [24] provides technological and species richness data (see figure 1 for distribution of groups). We were able to obtain values for DMV from Binford for only 59 of those groups.

After compiling the dataset, we tested all the variables for normality with the Kolmogorov–Smirnov test. Several variables—species richness, NAGP, RHIGH, RLOW, population size and DMV—were found to be non-normally distributed. They were log-transformed as a consequence. After transformation, the variables in question had distributions that conformed to the expectations of a normal distribution according to the Kolmogorov–Smirnov test.

Subsequently, we used simple parametric correlation analysis to examine the relationship between technological richness and each of the seven potential driver variables. Because multiple tests were conducted, Benjamini & Yekutieli's [27] method of significance-level correction was used to reduce type I error rates. We used this method rather than the better-known Bonferroni correction, because it has been shown to balance the reduction of type I and type II error rates better than Bonferroni correction [28]. The analyses were carried out in PASW (SPSS) 19.

Thereafter, we used stepwise multiple regression analysis to determine which potential driver variables had a significant effect on technological richness independent of the other potential driver variables. We used the *F*-test as the selection criterion. We chose to use the *F*-test for two reasons. First, we wanted to be consistent with the analyses presented in our earlier studies to make this work as comparable as possible [15]. Second, we chose a model-simplification method (the *F*-test) over model-selection methods (e.g. AIC and BIC), because we wanted to distinguish among several competing hypotheses. Although both approaches have known shortcomings [29], we chose a simplification method because our goal was to identify the single most important predictor. It should be noted however, that using the corrected AIC as the selection criteria in the stepwise regression analysis yields qualitatively similar results.

We carried out two stepwise regression analyses. In one we included species richness, NAGP, effective temperature, RHIGH, RLOW and population size as potential driver variables. This analysis tested the environmental-risk and population-size hypotheses. In the other analysis, we added DMV to the set of potential driver variables and tested all three hypotheses. Sample size in the first analysis was 85; in the second it was 59. In both analyses, we assessed the variance inflation factor (VIF), which quantifies the severity of multicollinearity in a regression analysis. When multicollinearity is substantial (usually regarded as above 10), the resulting tests may suffer from low power and may be spurious [30]. None of the variables in the stepwise multiple regression models had a VIF above 2. These analyses also were carried out in PASW (SPSS) v. 19.

Lastly, we entered species richness, NAGP, effective temperature, RHIGH, RLOW and population size into a generalized linear model (GLM). The goal of this analysis was to examine the impact of the potential driver variables on technological richness while controlling for the potential confounding effects of shared history and intergroup cultural transmission. We incorporated shared history and intergroup cultural transmission into the GLM by including language-phylum affiliation and the presence/absence of specialist agents of barter or trade between communities as factors. Data for both variables were taken from Jorgenson [24]. Because technological richness is a count variable, the Poisson distribution was specified when generating the GLM. The Kolmogorov–Smirnov test confirmed that the variable technological richness was not significantly different from an underlying Poisson distribution ($z = 0.653$, $p = 0.787$). Once again, PASW (SPSS) v. 19 was used to carry out the analysis.

The same test predictions were used in all the analyses. The environmental-risk hypothesis predicts that technological richness should correlate negatively and significantly with species richness, NAGP, effective temperature, RHIGH and/or RLOW. The mobility hypothesis predicts that technological richness should be negatively and significantly correlated with DMV, whereas the population-size hypothesis predicts that technological richness should be positively and significantly correlated with population size.

4. Results

The 85 groups vary markedly in technological richness. The minimum value for technological richness is 20; the maximum is 53. The average value for technological richness is 32.72 (s.d. $\pm$ 6.82).

Table 1 and figure 2 summarize the results of the simple correlation analyses. Technological richness correlated

Table 1. Results of Pearson correlations between technological richness and potential driver variables. See §3 for details of abbreviations. Technological richness correlates significantly with three driver variables: richness, NPP and RLOW. The relationships between technological richness and species richness and RLOW are consistent with the environmental-risk hypothesis.

driver variable	*r*	*p*-value
species richness	−0.336	0.002*
NAGP	−0.279	0.010*
effective temperature	0.179	0.102
RHIGH	−0.189	0.084
RLOW	−0.366	0.001*
DMV	0.012	0.931
population size	−0.219	0.044

*Significant correlation using Benjamini and Yekutieli's [27] alpha correction; the critical value for seven tests is $\alpha = 0.01928$.

significantly with species richness, NAGP and RLOW, and did so in the direction predicted by the environmental-risk hypothesis, i.e. the relationships were negative. Technological richness was not significantly correlated with the mobility variable DMV or with population size. Thus, the simple correlation analyses supported the environmental-risk hypothesis but not the other two hypotheses.

Results of the first stepwise multiple regression analysis are summarized in table 2. To reiterate, this analysis included only species richness, NAGP, effective temperature, RHIGH, RLOW and population size, and therefore tested only the environmental-risk and the population-size hypotheses. A single variable was included in the final model as a significant influence on technological richness: RLOW. The effect of RLOW on technological richness was negative, as predicted by the environmental-risk hypothesis. The effect of population size on technological richness was non-significant and negative, which is inconsistent with the predictions of the population-size hypothesis. Thus, the analysis supported the environmental-risk hypothesis but not the population-size hypothesis.

Results of the second stepwise multiple regression analysis—the one that included DMV as well as species richness, NAGP, effective temperature, RHIGH, RLOW and population size and therefore tested all three hypotheses—are summarized in table 3. Again, only one variable was included in the model as a significant influence on technological richness. This variable was RLOW, which is one of the risk proxies. The effect of RLOW on technological richness was negative, as predicted by the environmental-risk hypothesis. Thus, the analysis supported the environmental-risk hypothesis but not the other two hypotheses.

Table 4 summarizes the GLM. Only one variable included in the model has a significant influence on technological richness when language-phylum affiliation and the presence/absence of specialist agents of barter or trade between communities were included as factors. This variable was RLOW. Consistent with the predictions of the environmental-risk hypothesis, the effect of RLOW on technological richness was negative. Thus, in line with the results of the other analyses, the GLM supported the environmental-risk hypothesis but not the other two hypotheses.

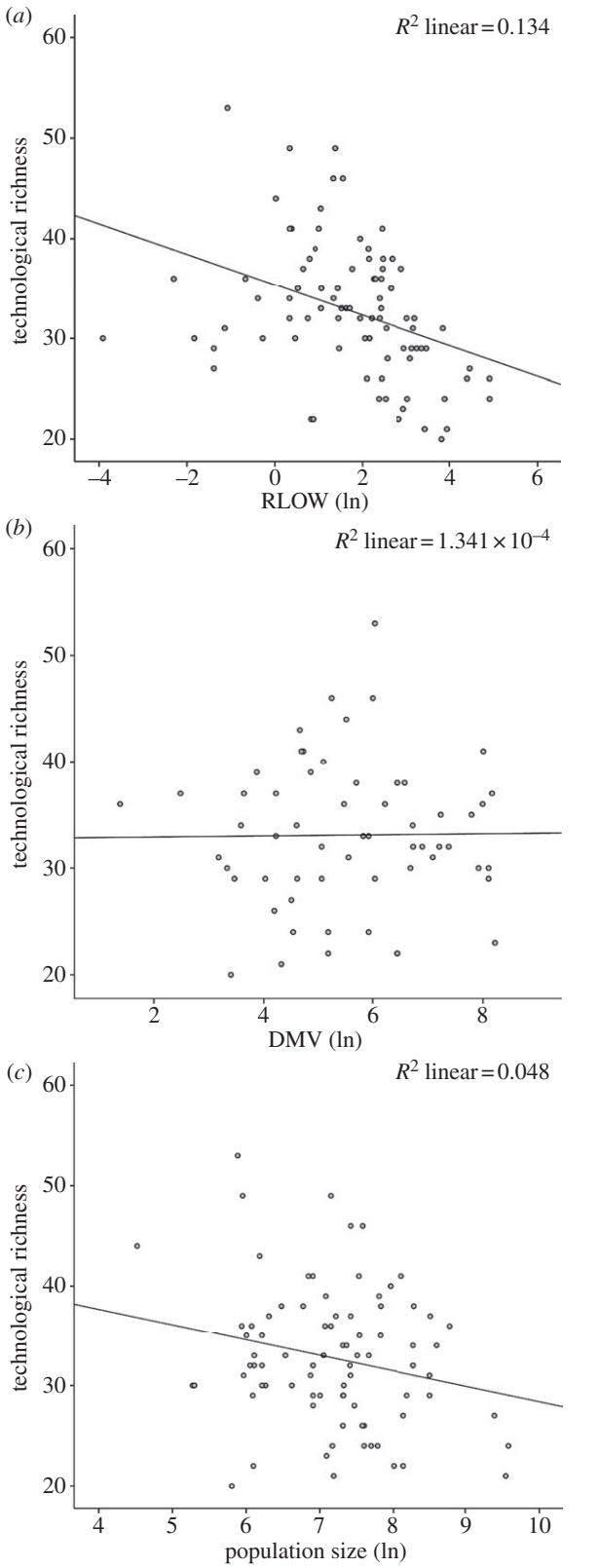

Figure 2. Scatterplots illustrating relationships between technological richness and potential driver variables relevant to each hypothesis: (*a*) technological richness versus RLOW (environmental risk), (*b*) technological richness versus DMV (mobility hypothesis) and (*c*) technological richness versus population size (population-size hypothesis). See §3 for details of abbreviations. The relationship between technological richness and RLOW is consistent with the environmental-risk hypothesis. The direction of relationship between technological richness and DMV is consistent with the mobility hypothesis, but the relationship is not significant. The relationship between technological richness and population size is neither significant nor in the direction predicted by the population-size hypothesis.

Table 2. Results of stepwise multiple regression for technological richness and six potential driver variables ($n = 85$). See §3 for details of abbreviations. The variable RLOW is the only significant driver variable in the final model ($r^2 = 0.134$, $F = 12.824$, d.f. = 1,83, $p = 0.001$). The relationship between technological richness and RLOW is consistent with the environmental-risk hypothesis. The relationship between technological richness and population size is inconsistent with the population-size hypothesis. Statistical significance in probability tests indicated by asterisks.

final model	β	*p*-value	VIF
RLOW	−0.366	0.001*	—
excluded variables			
population size	−0.186	0.069	1.009
effective temperature	−0.090	0.499	1.678
species richness	−0.208	0.075	1.308
RHIGH	−0.071	0.517	1.135
NAGP	−0.124	0.300	1.354

*$p \leq 0.05$.

Table 3. Results of stepwise multiple regression for technological richness and seven potential driver variables ($n = 59$). See §3 for details of abbreviations. The variable RLOW is the only significant driver variable in the final model ($r^2 = 0.104$, $F = 6.614$, d.f. = 1,57, $p = 0.013$). The relationship between technological richness and RLOW is consistent with the environmental-risk hypothesis. The relationship between technological richness and population size is inconsistent with the population-size hypothesis. The relationship between technological richness and DMV is inconsistent with the mobility hypothesis. Statistical significance in probability tests indicated by asterisks.

final model	β	*p*-value	VIF
RLOW	−0.322	0.013*	—
excluded variables			
population size	−0.176	0.168	1.023
effective temperature	−0.036	0.817	1.529
species richness	−0.160	0.294	1.445
RHIGH	−0.093	0.495	1.157
NAGP	0.132	0.370	1.357
DMV	0.017	0.894	1.000

*$p \leq 0.05$.

5. Discussion and conclusion

Results of the study reported here were unambiguous: technological richness among early contact-period hunter–gatherers of western North America was correlated with one of the proxies of environmental risk, mean rainfall for the driest month, and the direction of the relationship was consistent with the predictions of the environmental-risk hypothesis. By contrast, we found no evidence that technological richness was correlated with population size in the manner predicted by the population-size hypothesis or that technological richness was correlated with residential mobility in the manner predicted by the mobility hypothesis.

Results of this study obviously parallel results of the work on the food-getting toolkits of hunter–gatherers discussed earlier [9,14,15,20]. There would appear to be two potential explanations for this. One is that food-getting technology dominates the dataset used in this study, and therefore the dataset is not substantively different from those used in the work on food-getting toolkits. If this were the case, the similarity between this study's results and the results of the work on hunter–gatherer food-getting toolkits would not add much to our understanding of technological evolution in small-scale societies. The other potential explanation is that the finding that risk of resource failure is the primary influence on the richness and complexity of food-getting toolkits of hunter–gatherers is only a part of a bigger picture in which risk is a general influence on the technology of hunter–gatherers. The first potential explanation seems unlikely because only 22 of the 99 technological traits used in this study relate to the acquisition of food (see the electronic supplementary material). Thus, it would seem that the reason the results of this study parallel the finding that risk of resource failure is the primary influence on the structure of food-getting toolkits of hunter–gatherers, is that the influence of risk on hunter–gatherer technology is not limited to the tools they use to obtain food. Rather, it appears that environmental risk is a pervasive influence on the technology of hunter–gatherers, certainly on that of groups in western North America.

Results of this study have implications for understanding cultural evolution more generally. Recently, a number of authors have argued that population size is a key factor in cultural evolution [13,21,23,31–33]. Two previous studies tested the population-size hypothesis with toolkit data from hunter–gatherers and found no support for the hypothesis [15,20]. However, it has been argued that the lack of support for the population-size hypothesis in these studies is due to the fact that the authors did not take into account intergroup cultural transmission and therefore did not accurately measure the effective population size for cultural traits [34]. This study's failure to support the population-size hypothesis cannot be rejected so offhandedly, because the second set of analyses controlled for a key form of cultural transmission and still failed to support the population-size hypothesis. As such, this study suggests that the claim that population size is a key factor in cultural evolution perhaps needs to be tempered. Population size undoubtedly has the *potential* to impact cultural evolution, and undoubtedly *does* in some instances, as we [18] and others [21] have shown, but it cannot be assumed to *always* have an effect. Under certain conditions, its influence appears to be outweighed by other factors. Such conditions, this study suggests, are found among many hunter–gatherer groups.

A supplementary analysis provides further support for this conclusion. Another approach that has been used to reduce the effects of intergroup cultural transmission is to use island populations to test the population-size hypothesis. Kline & Boyd [21] employed this approach in their study of toolkit richness and complexity among populations of Oceania. They investigated the impact of population size on marine foraging toolkits of 10 farming and fishing groups and found that population size had a significant impact on the number of tools used by the groups. In their study, Kline & Boyd reasoned that because island populations of Oceania are geographically bounded and separated by significant distances, they are less likely to be impacted by

Table 4. Results of GLM using technological richness and six potential driver variables ($n = 85$). Technological richness is the dependent variable. All driver variables were log-transformed prior to analysis. The Poisson probability distribution was used with a log-link function. Statistical significance in probability tests indicated by asterisks.

parameter	β	s.e	Wald χ^2	p-value
(intercept)	4.825	0.5104	89.374	0.000
Aztec–Tanoan language phylum	−0.027	0.0721	0.141	0.707
Penutian language phylum	0.051	0.0582	0.782	0.377
Hokan language phylum	0.113	0.0689	2.686	0.101
phylum 4[a]	0[b]	—	—	—
groups with no trade specialists	−0.054	0.0638	0.707	0.400
groups with trade specialists	0[b]	—	—	—
species richness	−0.049	0.0629	0.610	0.435
population size	−0.033	0.0233	2.012	0.156
NAGP	−0.100	0.0955	1.087	0.297
effective temperature	−0.036	0.0221	2.714	0.099
RHIGH	0.043	0.0580	0.556	0.456
RLOW	−0.034	0.0159	4.620	0.032*

[a]Language phylum 4 includes the following language families: Algonkian, Eyak-Athapaskan, Wakashan, Chimakuan, Salishan and Na-Dene.
[b]Set to zero because this parameter is redundant.
*$p \leq 0.05$.

intergroup transmission and thus less likely to affect their population estimates relative to continental populations.

To test the possibility that the distances separating the groups in our sample had an effect on how much sharing they engaged in, we conducted an additional analysis examining the correlation between the distances between groups and the differences in the number of technological traits each group had with one another. To do this, we ran a Mantel matrix correlation test between the distances among groups (specifically, we calculated great circle arcs among groups using the latitude and longitude for each group) and a matrix of the differences in numbers of technological traits recorded for each group. If continental groups shared more often with local groups, we would expect a significant positive correlation for this test, where groups in close proximity also share similar numbers of technological traits (regardless of the total number of traits). This was not the case. Results of the Mantel test indicate *no* significant correlation between distance between groups and the differences in the number of technological traits they possess ($r = 0.0651$, $z < 0.000$, $p = 0.1085$). This suggests that continental populations are *not* more likely to share technological traits based on proximity.

The idea that island populations are less likely candidates for intergroup cultural transmission is intuitively appealing, but there are several possibilities why this may not be the case. For example, it has been well documented that physically isolated groups in Oceania spend enormous amounts of time and energy visiting other island populations and establishing extensive exchange networks [35,36]. This pattern of contact among populations in Oceania has been validated and extended into the past by archaeologists. For example, Cochrane & Lipo [37] have shown that the Lapita people, who colonized most of Oceania, were in contact and engaged in sharing of material culture with one another for more than 200 years. By contrast, we suggest that neighbouring populations in continental settings should be expected to engage in *less* sharing. Although neighbouring populations may have more frequent contact relative to island populations separated by significant distances, the form of contact was not always conducive to sharing and often was antagonistic. We suggest that it is the proximity of some groups—usually those occupying similar environments—that would discourage sharing of technological knowledge and traits as a result of the competition over resources. Freely sharing technological traits in these situations could be detrimental to a group's competitive edge over neighbouring groups.

The failure of this study to support the population-size hypothesis also has implications for the interpretation of the archaeological record. In the past few years, a number of researchers have argued that population size may explain several long-debated patterns in the Palaeolithic archaeological record. Shennan [23], for example, has suggested that the so-called 'creative explosion' of the late Middle Stone Age and Upper Palaeolithic might have resulted from a large, climate-driven increase in population size. In a follow-up paper, Shennan and co-workers [31] proposed that population size might also explain why many cultural innovations seem to have appeared, disappeared and then reappeared during the Late Pleistocene. Along similar lines, Premo & Kuhn [32] have argued that two key features of the Middle Palaeolithic and Middle Stone Age archaeological records—an absence of directional technological change and the reappearance of previously existing cultural behaviours—might be a function of a high rate of extirpation of small, isolated groups and subsequent repopulation. This study's failure to support the population-size hypothesis casts doubt on these explanations because all humans appear to have been hunter–gatherers during the Palaeolithic. If the technology of ethnographically documented hunter–gatherers is not affected by population size, there is little reason to think that the technology of

Palaeolithic hunter–gatherers would have been affected by population size. Based on the results of this study, the patterns in question more probably reflect adjustment to different levels of environmental risk.

Two possibilities for further research suggest themselves. One is to repeat the analyses reported here with data for groups that relied on domesticated resources for most of their calories and nutrients. As we explained earlier, the work on food-getting toolkits of small-scale societies that has been carried out over the past 40 years suggests that the toolkits of hunter–gatherers are influenced by risk but not by population size, whereas the food-getting toolkits of small-scale famers and pastoralists are influenced by population size but not by risk [9,14,15,17,18,20,21]. Results of this study suggest that this may be a more general pattern, but an analysis of technological richness in food-producing groups is required to confirm that such is the case.

The other possibility for further research is to repeat the analyses reported here with data for groups from the Pacific Northwest. As we indicated earlier, one of the studies of the food-getting toolkits of hunter–gatherers did not support the risk hypothesis [16]. To reiterate, that study focused on the food-getting toolkits of hunter–gatherers from the coast and plateau regions of the Pacific Northwest. At the moment, it is not clear why the toolkits of these groups do not vary in the manner predicted by the risk hypothesis. Repeating the analyses reported here with the data for groups from the Pacific Northwest would shed light on this issue by indicating whether the lack of fit with the risk hypothesis is specific to the groups' food-getting tools or is a more general phenomenon.

Acknowledgements. We are very grateful to the late Joseph Jorgenson for providing us with the data used in the study. We are also grateful to three anonymous referees and to guest editor Christian Rutz for their comments on the manuscript, which improved it greatly. The opinions expressed in this paper are those of the authors and do not necessarily reflect the views of the funding bodies that support them.

Funding statement. M.C. is supported by the Canada Research Chairs Program, the Social Sciences and Humanities Research Council, the Canada Foundation for Innovation, the British Columbia Knowledge Development Fund, and Simon Fraser University. B.B. is supported by the University of Missouri and Simon Fraser University. J.S. is supported by the National Science Foundation (grant no. 1064534) and Simon Fraser University.

References

1. Marzke MW. 1997 Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.* **102**, 91–110. (doi:10.1002/(SICI)1096-8644(199701)102:1<91::AID-AJPA8>3.0.CO;2-G)
2. Pagel M, Bodmer W. 2003 A naked ape would have fewer parasites. *Proc. R. Soc. Lond. B* **270**, S117–S119. (doi:10.1098/rsbl.2003.0041)
3. Brunet M *et al*. 2002 A new hominid from the Upper Miocene of Chad, central Africa. *Nature* **418**, 145–151. (doi:10.1038/nature00879)
4. Trigger B. 2003 *Understanding early civilizations: a comparative study*. New York, NY: Cambridge University Press.
5. Oswalt WH. 1973 *Habitat and technology: the evolution of hunting*. New York, NY: Holt, Rinehart, and Winston.
6. Oswalt WH. 1976 *An anthropological analysis of food-getting technology*. New York, NY: Wiley.
7. Oswalt WH. 1977 Northern Athapaskan food-getting technology. In *Problems in the prehistory of the North American subarctic: the Athabaskan question* (eds JW Helmer, S Vandyke, FJ Kense), pp. 120–123. Calgary, Canada: Archaeological Association of the University of Calgary.
8. Torrence R. 1983 Time budgeting and hunter–gatherer technology. In *Hunter–gatherer economy in prehistory* (ed. G Bailey), pp. 11–22. Cambridge, UK: Cambridge University Press.
9. Torrence R. 1989 Re-tooling: towards a behavioral theory of stone tools. In *Time, energy and stone tools* (ed. R Torrence), pp. 57–66. Cambridge, UK: Cambridge University Press.
10. Torrence R. 2001 Hunter–gatherer technology: macro- and microscale approaches. In *Hunter–gatherers: an interdisciplinary perspective* (eds C Panter-BrickRH Layton, P Rowley-Conwy), pp. 99–143. Cambridge, UK: Cambridge University Press.
11. Shott M. 1986 Technological organization and settlement mobility: an ethnographic examination. *J. Anthropol. Res.* **42**, 15–51.
12. Osborn AJ. 1999 From global models to regional patterns: possible determinants of Folsom hunting weapon design diversity and complexity. In *Folsom lithic technology: explorations in structure and variation* (ed. DS Amick), pp. 188–213. Ann Arbor, MI: International Monographs in Prehistory.
13. Henrich J. 2004 Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *Am. Antiquity* **69**, 197–218. (doi:10.2307/4128416)
14. Henrich J. 2006 Understanding cultural evolutionary models: a reply to Read's critique. *Am. Antiquity* **71**, 771–782. (doi:10.2307/40035890)
15. Collard M, Kemery MD, Banks S. 2005 Causes of toolkit variation among hunter–gatherers: a test of four competing hypotheses. *Can. J. Arch.* **29**, 1–19.
16. 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. *Phil. Trans. R. Soc. B* **366**, 1129–1138. (doi:10.1098/rstb.2010.0366)
17. Collard M, Ruttle A, Buchanan B, O'Brien MJ. 2012 Risk of resource failure and toolkit variation in small-scale farmers and herders. *PLoS ONE* **7**, e40975. (doi:10.1371/journal.pone.0040975)
18. Collard M, Ruttle A, Buchanan B, O'Brien MJ. In press. Population size and cultural evolution in non-industrial food-producing societies. *PLoS ONE*.
19. Read D. 2006 Tasmanian knowledge and skill: maladaptive imitation or adequate technology. *Am. Antiquity* **71**, 164–184. (doi:10.2307/40035327)
20. Read D. 2008 An interaction model for resource implement complexity based on risk and number of annual moves. *Am. Antiquity* **73**, 599–625.
21. Kline MA, Boyd R. 2010 Population size predicts technological complexity in Oceania. *Proc. R. Soc. B* **277**, 2559–2564. (doi:10.1098/rspb.2010.0452)
22. Colwell RK. 2009 Biodiversity: concepts, patterns and measurement. In *The Princeton guide to ecology* (ed. SA Levin), pp. 257–263. Princeton, NJ: Princeton University Press.
23. Shennan SJ. 2001 Demography and cultural innovation: a model and some implications for the emergence of modern human culture. *Cam. Arch. J.* **11**, 5–16.
24. Jorgenson JG. 1980 *Western Indians: comparative environments, languages and cultures of 172 Western American Indian tribes*. San Francisco, CA: Freeman.
25. Bailey HP. 1960 A method of determining the warmth and temperateness of climate. *Geografiska Annaler* **42**, 1–16. (doi:10.2307/520173)
26. Binford LR. 2001 *Constructing frames of reference: an analytical method for archaeological theory building using hunter–gatherer and environmental data sets*. Berkeley, CA: University of California Press.
27. Benjamini Y, Yekutieli D. 2001 The control of false discovery rate under dependency. *Ann. Stat.* **29**, 1165–1188. (doi:10.1214/aos/1013699998)
28. Narum SR. 2006 Beyond Bonferroni: less conservative analyses for conservation genetics. *Conserv. Genet.* **7**, 783–787. (doi:10.1007/s10592-005-9056-y)

29. Hegyi G, Garamszegi LZ. 2011 Using information theory as a substitute for stepwise regression in ecology and behavior. *Behav. Ecol. Sociobiol.* **65**, 69–76. (doi:10.1007/s00265-010-1036-7)
30. Zar JH. 2010 *Biostatistical analysis*, 5th edn. Upper Saddle River, NJ: Pearson Prentice Hall.
31. Powell A, Shennan S, Thomas MG. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 1298–1301. (doi:10.1126/science.1170165)
32. Premo LS, Kuhn SL. 2010 Modeling effects of local extinctions on culture change and diversity in the Paleolithic. *PLoS ONE* **5**, e15582. (doi:10.1371/journal.pone.0015582)
33. Mesoudi A. 2011 Variable cultural acquisition costs constrain cumulative cultural evolution. *PLoS ONE* **6**, e18239. (doi:10.1371/journal.pone.0018239)
34. Boyd R, Richerson P, Henrich J. In press. The cultural evolution of technology: facts and theories. In *Cultural evolution: society, technology, language and religion* (eds PJ Richerson, MH Christiansen). Cambridge, MA: MIT Press.
35. Malinowski B. 1920 Kula; the circulating exchange of valuables in the archipelagoes of eastern New Guinea. *Man* **20**, 97–105. (doi:10.2307/2840430)
36. Malinowski B. 1922 *Argonauts of the Western Pacific: an account of native enterprise and adventure in the archipelagoes of Melanesian New Guinea*. London, UK: Routledge.
37. Cochrane EE, Lipo CP. 2010 Phylogenetic analyses of Lapita decoration do not support branching evolution or regional population structure during colonization of Remote Oceania. *Phil. Trans. R. Soc. B* **365**, 3889–3902. (doi:10.1098/rstb.2010.0091)