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Research

What drives the evolution of hunter–gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest

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Recent studies have suggested that the decisions that hunter–gatherers make about the diversity and complexity of their subsistence toolkits are strongly affected by risk of resource failure. However, the risk proxies and samples employed in these studies are potentially problematic. With this in mind, we retested the risk hypothesis with data from hunter–gatherer populations who lived in the northwest coast and plateau regions of the Pacific Northwest during the early contact period. We focused on these populations partly because the northwest coast and plateau differ in ways that can be expected to lead to differences in risk, and partly because of the availability of data for a wide range of risk-relevant variables. Our analyses suggest that the plateau was a more risky environment than the northwest coast. However, the predicted differences in the number and complexity of the populations' subsistence tools were not observed. The discrepancy between our results and those of previous tests of the risk hypothesis is not due to methodological differences. Rather, it seems to reflect an important but hitherto unappreciated feature of the relationship between risk and toolkit structure, namely that the impact of risk is dependent on the scale of the risk differences among populations.

Keywords: toolkit variation; risk; subsistence; hunter–gatherers; northwest coast; plateau

1. INTRODUCTION

Identifying the factors that influence the number and intricacy of the tools that hunter–gatherers use to obtain food is an important task for researchers interested in the evolution of culture. The reason for this is twofold. First, artefacts linked to the acquisition and processing of food dominate our main source of information about the evolution of hominin culture, the archaeological record. Recent discoveries suggest that hominins have been producing material culture for 3.4 Myr [1,2]. More or less all of the artefacts that have been recovered from the first 3.3 Myr of this time period appear to have been employed in subsistence activities. Artefacts that were used for purposes other than subsistence increased in frequency around 100 000 years ago [3,4], but subsistence-related artefacts continued to make up a substantial portion of the archaeological record well into the Holocene. One implication of the dominance of the archaeological record by subsistence-related artefacts is that to understand the evolution of hominin culture, we have to understand the evolution of hominin subsistence technology. Second, hominin history is dominated by hunting and gathering. Current evidence indicates that the hominin clade originated about 7 Myr ago [5]. The earliest evidence for farming dates to around 11 500 years ago [6,7]. Thus, for 99 per cent of the time that hominins have existed as a distinct lineage, they have relied on wild resources. The obvious corollary of this is that to understand the evolution of hominin subsistence technology, we have to understand the evolution of hunter–gatherer subsistence technology.

In this paper, we report a study in which we used data from early contact-era hunter–gatherer

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populations living in the Pacific Northwest to reassess the most widely supported of the hypotheses that have been put forward to account for the variation in the structure of the toolkits that hunter–gatherers use to obtain food. This hypothesis holds that the differences among hunter–gatherer populations in the number and intricacy of the tools they use to obtain food reflect differences in the level of risk of resource failure experienced by the populations. We begin by outlining a method that anthropologists have developed to quantify toolkit structure. We then describe the main hypotheses that have been put forward to account for the variation in the structure of hunter–gatherer toolkits. Next, we review the results of recent tests of these hypotheses, and explain why a reassessment of the risk hypothesis is warranted. Subsequently, we describe our study. Lastly, we discuss the results of our study in relation to the results of previous work on the causes of variation in the structure of hunter–gatherer toolkits.

2. A METHOD OF QUANTIFYING TOOLKIT STRUCTURE

Oswalt [8,9] laid the foundations for systematic research on the factors that influence hunter–gatherer toolkit structure by developing a cross-culturally applicable typology of tools and several measures of toolkit structure. Oswalt limited his studies to tools that are employed directly in the acquisition of food, which he termed 'subsistants'. Oswalt recognized three types of subsistants: instruments, weapons and facilities. Instruments are 'hand-manipulated subsistants that customarily are used to impinge on masses incapable of significant motion and relatively harmless to people' [9, p. 64]. A digging stick is perhaps the most obvious example of an instrument. A weapon is 'a form that is handled when in use and is designed to kill or maim species capable of significant motion' [9, p. 79]. Weapons include boomerangs, crossbows and toggle-headed harpoons. A facility is 'a form that controls the movement of a species or protects it to man's advantage' [9, p. 105]. A deadfall trap is an example of a facility. Oswalt also drew a distinction between simple and complex tools. A simple tool 'retains the same physical appearance before, during, and after it is brought into play' [8, p. 27], while a complex one 'always has more than one component and its parts change in their physical relationship to one another during use' [8, p. 28]. The weapons mentioned earlier illustrate this distinction. Boomerangs are simple weapons, whereas crossbows and toggle-headed harpoons are complex weapons.

Oswalt [9] devised three measures of toolkit structure. The first is the total number of subsistants (STS), which is an indicator of the size or what Torrence [10–12] and Shott [13] called the 'diversity' of a toolkit. The second is the total number of 'technounits' (TTS). Put simply, technounits are the different kinds of parts in a tool. More formally, a technounit is an 'integrated, physically distinct, and unique structural configuration that contributes to the form of a finished artefact' [9, p. 38]. The total number of technounits included in a toolkit is a measure of its 'complexity' [9,10–12]. Oswalt's third measure of toolkit structure is the average number of technounits per subsistant (AVE). Again, this is a measure of toolkit complexity [9,10–13].

Recently, some additional toolkit structure variables have been proposed. Henrich [14] introduced the sum of the technounit counts for the most complex instrument, weapon, untended facility and tended facility in a given toolkit (MXT). Read [15] has proposed three new toolkit structure variables. One of these is the number of complex subsistants, where—following Oswalt [9]—a complex subsistant is one whose parts change their physical relationship to one another during use (NCT). Read's other two variables are the number of technounits in complex subsistants (CSTS) and the number of complex subsistant types (CTTS).

3. FACTORS HYPOTHESIZED TO INFLUENCE TOOLKIT STRUCTURE

Numerous factors have been hypothesized to drive hunter–gatherer toolkit structure [9,10–21], but attention has been focused primarily on the nature of the resources exploited for food, risk of resource failure, residential mobility and population size. A primary role for the first of these in shaping hunter–gatherers' decisions regarding the structure of their toolkits was initially proposed by Oswalt [9]. Based on an analysis of the toolkits and diets of 20 hunter–gatherer populations, Oswalt argued that there is a relationship between a population's degree of reliance on mobile resources and the complexity of its toolkit. He suggested that the exploitation of resources that are mobile is more difficult and therefore demands more complex tools than the exploitation of immobile resources. Thus, populations that rely on animals can be expected to have more complex toolkits than populations whose diets are plant dominated. Oswalt also argued that, because aquatic animals are more mobile than terrestrial animals, populations that depend on aquatic animals are likely to have more complex toolkits than populations that hunt mainly terrestrial animals.

The latter point has also been made by Osborn [18]. Osborn argued that when considering hunter–gatherer toolkit structure, it is important to recognize that the organizational demands of terrestrial hunting differ from those of aquatic hunting and fishing. He then reported the results of an analysis in which the diversity and complexity of 21 populations' toolkits were correlated, first, with the percentage contribution to their diets made by terrestrial animals, and then with the percentage contribution to their diets made by marine animals. Osborn found that, generally, the procurement of marine animals explained more of the variability in toolkit diversity and complexity than terrestrial animal procurement (marine r^2 range = 0.12–0.54; terrestrial r^2 range = 0.02–0.44). The only toolkit complexity measure that correlated more strongly with terrestrial animal procurement than with the procurement of marine animals was the diversity of simple instruments (terrestrial $r^2 = 0.28$; marine $r^2 = 0.12$).

The notion that risk of resource failure is the chief influence on hunter–gatherer toolkit structure has its roots in Torrence [10]. In this paper, Torrence focused on time stress. She hypothesized that as time stress increased, hunter–gatherers could be expected to produce more specialized tools and therefore more diverse and complex toolkits. Torrence tested the time stress hypothesis by measuring the statistical association between toolkit structure and latitude in Oswalt's [9] sample of 20 hunter–gatherer populations. She employed latitude as a proxy for time stress on the grounds that, all other things being equal, the length of the growing season for plants decreases with increasing latitude. The significance of this, according to Torrence, is that as latitude increases, the number of edible plants available for hunter–gatherers decreases, and therefore they have to depend more heavily on animal resources, which as noted above are more taxing as far as search and pursuit time are concerned. Torrence's analyses strongly supported the time stress hypothesis. She found that toolkit diversity and complexity were positively and significantly correlated with latitude.

Subsequently, Torrence [11,12] abandoned the time stress hypothesis in favour of one based on risk, which she defined as the effects of stochastic variation in the outcome associated with some behaviour. She explained that she had come to believe that the necessity for increasing speed of capture and for budgeting limited time are merely the proximate causes of the variation in toolkit structure, and that the ultimate causes of the variation are the timing and severity of risk. Torrence went on to argue that the use of more specialized and therefore more elaborate tools reduces the risk of resource failure. Thus, populations that experience high resource failure risk will produce toolkits that are diverse and complex, whereas those that experience lower resource failure risk will settle for more simple toolkits. In support of her revised hypothesis, Torrence highlighted the correlation that she had previously identified between toolkit structure and latitude, as well as the correlation that Oswalt had found between toolkit structure and degree of reliance on mobile resources. She argued that the former correlation supports the risk hypothesis because distance from the equator is a proxy for overall resource abundance, which in turn is a proxy for the scale of risk. The correlation between toolkit structure and degree of reliance on mobile resources supports the risk buffering hypothesis, Torrence argued, because a prey's mobility affects the probability of a hunter–gatherer capturing it: the higher the mobility, the larger the risk of failure.

The hypothesis that residential mobility influences hunter–gatherer toolkit structure was proposed by Shott [13]. Such a relationship exists, he argued, because carrying costs constrain the number of the tools a population can employ regularly. Thus, according to Shott, populations that move frequently and/or long distances every year will have less diverse toolkits than those that move less frequently and/or shorter distances. The corollary of this is that the tools employed by highly mobile populations will be less specialized than those used by less mobile populations, since they will be applied to a broader range of tasks. Shott carried out two sets of analyses to test the mobility hypothesis. The first set of analyses focused on residential mobility. These analyses employed data for 14 historically documented hunter–gatherer populations. Shott carried out parametric and non-parametric analyses in which the number of subsistants and average number of technounits per subsistant were correlated with several measures of mobility, including number of residential moves per year, distance travelled annually during residential moves in kilometres, average length of each residential move in kilometres and total area occupied in square kilometres. In the second set of analyses, which were based on samples that were smaller than those used in the first set of analyses, Shott examined the relationships between the technological variables and two measures of logistic mobility, the number of days spent in the main winter camp and intensity of land use. In addition to examining the correlations between the technological variables and measures of mobility, Shott carried out analyses that evaluated the strength of the statistical association between the technological variables and effective temperature and net primary productivity on the grounds that Kelly [22] argued that these variables play a role in structuring hunter–gatherer mobility strategies.

The results of Shott's first set of analyses were mixed. Toolkit diversity and mobility frequency were found to be significantly and negatively correlated, suggesting that, as predicted, populations that move frequently employ a smaller number of subsistants than groups that are more sedentary. However, the rest of the residential mobility-focused analyses did not support the mobility hypothesis. Toolkit diversity was not significantly correlated with total distance covered per year; toolkit complexity was not significantly correlated with either frequency of residential moves per year or the average distance covered during those moves, and neither toolkit diversity nor toolkit complexity was significantly correlated with territory size. The results of the second set of analyses were also mixed. Shott found that there was a significant positive correlation between toolkit diversity and number of days at the winter camp, which supports the mobility hypothesis. But toolkit diversity was not significantly correlated with intensity of land use, and toolkit complexity was not significantly correlated with either number of days at the winter camp or intensity of land use. Lastly, Shott found that the relationships between the technological variables and the two environmental parameters, effective temperature and net primary productivity, were not significant.

The hypothesis that hunter–gatherer toolkit structure is affected by population size was independently proposed by Collard *et al.* [21] and Henrich [23]. Collard *et al.* suggested that the diversity and complexity of hunter–gatherer toolkits might be influenced by population size in the light of cultural evolutionary modelling work carried out by Shennan [24]. Shennan employed two models, both of which were adapted from a population genetics model developed by Peck *et al.* [25]. In Peck *et al.*'s model, mutations can be either beneficial or deleterious; there is a correlation between an allele's fitness prior to mutation and its post-mutation fitness, and many mutations produce only very small changes in fitness. In his models, Shennan treated cultural innovations as equivalent to Peck *et al.*'s mutations. To create his first model, Shennan altered Peck *et al.*'s model so that transmission was only possible from one parent to one offspring. To produce his second model, Shennan modified Peck *et al.*'s model to allow transmission between individuals belonging to different generations where the older individual is not the biological parent of the younger individual. In simulation trials, Shennan found that there was a marked increase in the mean fitness of the population as effective population size increased, and that this occurred regardless of whether transmission was purely between relatives or involved unrelated individuals too. Shennan concluded from these results that larger populations have a major advantage over smaller ones when it comes to cultural innovation due to the decreasing role of sampling effects as populations get larger. When effective population size is large, there is a far greater probability of fitness-enhancing innovations being maintained and deleterious ones being deleted than when the effective population size is small. Collard *et al.* argued that a corollary of Shennan's findings is that, because each technounit represents an innovation, small populations can be expected to have less complex toolkits than large ones. Thus, there should be a significant positive correlation between population size, on the one hand, and measures of toolkit diversity and complexity, on the other hand.

Henrich [23] also drew on a cultural evolutionary model to argue that hunter–gatherer toolkits should be affected by population size. However, his model differs from Shennan's [24] in a number of respects. Henrich's model assumes that when copying a behaviour, especially a complex one, individuals will try to imitate the most skilful person in their population. Most people will not do as well as the best practitioner, but occasionally an individual will strike it lucky and, in a failed attempt to imitate, produce a behaviour that gives a better result than the previous best. This then becomes the new goal for the rest of the population. As a result, so long as the new behaviour is not more difficult to copy than the previous best, the skill level of the whole population will be improved. If the new behaviour is more difficult to copy than the previous best, the population's skill level will probably not improve. Thus, the likelihood of cumulative cultural evolution is partly dependent on the difficulty of copying a new behaviour. It is also partly dependent on population size, since in large populations even improbable events—in this case arriving at a behaviour that gives a better result than the previous best—occur now and again, and the larger the population is, the more likely this is. Depending then on the difficulty of copying a new behaviour, a larger or smaller population size will be required for cumulative cultural evolution to take place. It follows that, for a level of copying difficulty, if the size of the interacting population changes for some external reason, then this will affect the rate of cumulative cultural evolution. If population size increases, then the probability of cumulative improvement increases. On the other hand, if population size drops, then it is likely that the number of adaptive cultural behaviours will decline, because the probability of someone improving on the existing situation, or even equalling the current best, is small. Thus, in the next generation, the best individual to copy is likely to be slightly worse than in the generation before, and this process will be repeated through the generations, until some equilibrium is reached. Henrich argued that his model explains the apparent loss of cultural adaptations in Tasmania after it became separated from the Australian mainland with rising sea levels at the end of the last Ice Age, since this isolation meant that the Tasmanians were no longer part of a larger interacting continental population.

4. RATIONALE FOR CURRENT STUDY

Three recent studies have compared the relative merits of the nature of the food resources, risk of resource failure and residential mobility as explanations for variation in hunter–gatherer toolkit structure, and reached different conclusions [14,15,21]. Collard *et al.* [21] tested the competing hypotheses by subjecting Oswalt's [9] toolkit structure data and a series of proxies for the putative explanatory factors to stepwise multiple regression. They found that the only significant predictors of STS, TTS and AVE were the two proxies for risk of resource failure they employed, effective temperature (ET) and net above ground productivity (NAGP). As part of a reply to Read [26], Henrich [14] used Collard *et al.*'s [21] dataset to investigate the impact of ET, NAGP, number of residential moves per year, the percentage contribution of terrestrial animals to the diet and the percentage contribution of aquatic animals to the diet on MXT. He found that ET was the only variable that explained a significant proportion of the variation in MXT. Read [15] argued that Collard *et al.*'s [21] results are problematic because they are dependent on the authors' choice of regression technique. He then reported a study in which he reassessed the relative merits of the three putative explanations for hunter–gatherer toolkit structure using several types of multiple regression. Read used Oswalt's [9] toolkit structure data and the same proxy data as Collard *et al.*'s [21], but also used additional toolkit variables and another proxy for risk of resource failure. The additional toolkit variables he employed are NCT, CSTS and CTTS. The additional risk proxy Read used is the length of the growing season (GS). Read found that in the majority of his analyses, the measures of toolkit structure were most strongly influenced by GS but were also affected—to a lesser extent—by the number of residential moves per year. He went on to create a model in which toolkit structure is driven by the interaction between GS and number of residential moves per year.

Currently, then, it appears that risk of resource failure is the most important of the factors that have been hypothesized to affect hunter–gatherer toolkit diversity and complexity. However, the studies that support this conclusion suffer from potentially important shortcomings. One concerns the proxies for risk of resource failure used by Collard *et al.* [21] and Read [15]. To reiterate, Collard *et al.*'s risk proxies were ET and NAGP, while Read's were ET, NAGP and GS. While these variables are undoubtedly closer to the factors that directly affect hunter–gatherer technological decision-making than the other proxy for risk that has been used, latitude, they all relate to primary biomass (i.e. plants and other organisms that obtain their energy directly from the solar radiation), and there is a reason to think that the availability of primary biomass is less important to hunter–gatherers than the availability of secondary biomass in the form of animals [27]. As such, there is a reason to retest the risk hypothesis with data pertaining to the availability of secondary biomass. Another shortcoming is that none of the studies included what Torrence [11,12] contends is the key risk variable—species diversity. Lastly, there is a reason to be concerned about the sample used by Collard *et al.* [21], Henrich [14] and Read [15]. By any standard, 20 populations is a small sample. A modest sample need not be problematic if it is representative, but the sample in question is not representative. It is biased towards high-latitude environments and also coastal environments [21]. Accordingly, it is not clear whether we can be confident about the conclusions drawn in any of the studies.

The study we report here was designed to address the first of these shortcomings. In the study, we tested the risk hypothesis with data from hunter–gatherer populations living in the Pacific Northwest in the early contact period. We focused on these populations not only because the climates and ecologies of the two main regions in which they lived—the northwest coast and the plateau—differ in ways that can be expected to lead to differences in the risk of resource failure, but also because data pertaining to the availability of secondary biomass are available. As such, they allow a more precise test of the risk hypothesis to be carried out.

5. PREDICTIONS TESTED IN CURRENT STUDY

The study focused on 16 hunter–gatherer populations. Eight of these populations lived on the northwest coast, and eight on the plateau. The northwest coast populations are, from north to south, the Tlingit, Kwa'Kwa'Ka'Wk (Kwakiutl), Nuu-Chan-Nulth (Nootka), Coast Salish, Makah, Upper Stalo, Twana and Quinalt. The plateau populations are—again from north to south—the Shuswap, Lillooet, Thompson, Okanogan, Coeur D'Alene, Sanpoil/Nespelem, Flathead and Klamath. The approximate spatial distribution of the populations is shown in figure 1.

The northwest coast extends from Yakutat Bay in Alaska to Cape Mendicino in California. It is bounded by the Pacific Ocean on the west and by the Chugach, Coast and Cascade mountain ranges on the east. Much of the northern and central northwest coast is indented by deep fjords and contains many islands, while the southern portion consists of a relatively straight exposed coastline without islands. Many

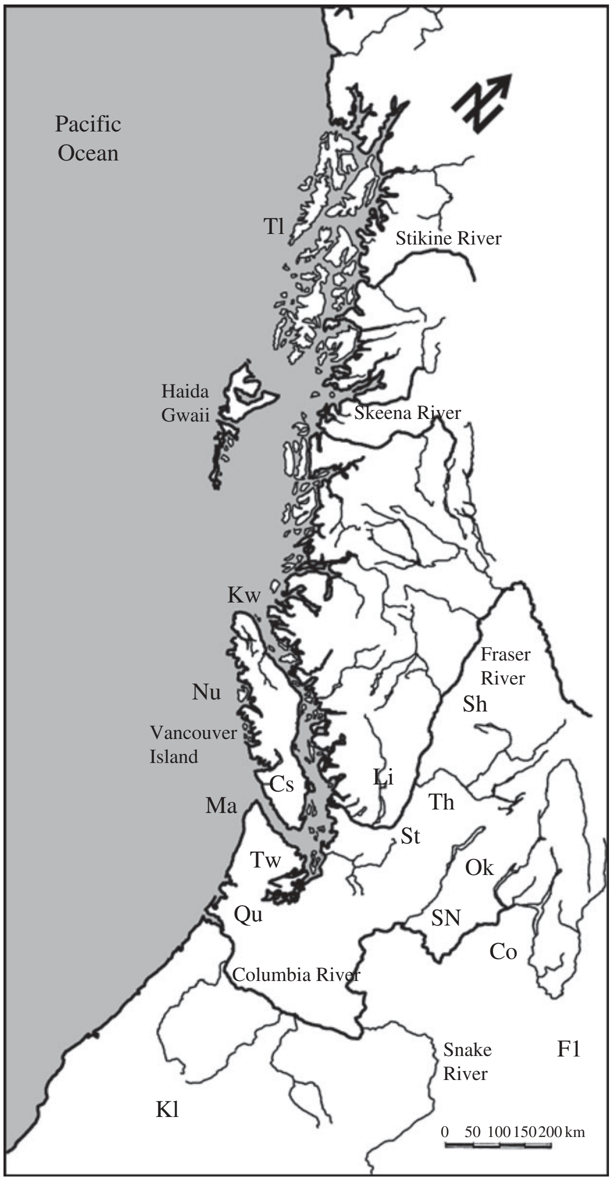

Figure 1. Map showing the approximate locations of the 16 hunter–gatherer populations included in the study. The abbreviations for the populations are as follows: Tl, Tlingit; Kw, Kwa'Kwa'Ka'Wk; Nu, Nuu-Chan-Nulth; Cs, Coast Salish; Ma, Makah; St, Upper Stalo; Tw, Twana; Qu, Quinalt; and the abbreviations for the groups in the plateau region are as follow: Sh, Shuswap; Li, Lillooet; Th, Thompson; Ok, Okanogan; Co, Coeur D'Alene; SN, Sanpoil/Nespelem, Fl, Flathead; Kl, Klamath.

large rivers including the Stikine, Nass, Skeena, Fraser and Columbia flow westward across the region. The climate of the northwest coast is temperate. Summer temperatures rarely exceed 18°C, and winter temperatures rarely drop below 0°C. Annual rainfall is relatively high, with many locations receiving more than 2000 mm of rain per year. Dense coniferous forests cover nearly the entire region. Upwelling cool, nutrient-rich waters support a highly productive local marine food chain. Halibut, sealions and grey whales are among the species resident in the waters of the northwest coast. In addition, massive runs of salmon and several other fish species usually occur once a year. By comparison, the terrestrial fauna of the northwest coast is much less abundant.

The plateau is bounded by the Coast Mountains in the west, the Rocky Mountains in the east, the Subarctic in the north and the Great Basin in the south [28]. The region consists of steep mountains, rolling hills, river valleys and several large lake systems. Almost the entire region is drained by the Columbia and Fraser River systems. The climate of the plateau is more extreme than that of the northwest coast. Summers tend to be very hot and winters very cold. In addition, there is much less precipitation than on the northwest coast. The ecology of the plateau is diverse, and is influenced by altitude and precipitation. Typically, lower elevation areas are dominated by shrub and bunchgrass steppe, while higher elevations are dominated by xeric montane forests (ponderosa and lodgepole pine) intermingled with some mesic montane forests (western hemlock and western red cedar) [29]. Not surprisingly, the plateau has far fewer aquatic animal species than the northwest coast. Less obviously, its terrestrial fauna is more diverse than that of the northwest coast.

The differences between the climates and ecologies of the northwest coast and plateau are such that it seems likely that the hunter–gatherers who occupied the latter faced greater risk of resource failure than the hunter–gatherers who occupied the former. Thus, if the risk hypothesis is correct, the toolkits of the plateau populations should have been more diverse and complex than those of the northwest coast populations.

6. COMPARISON OF RISK ON THE NORTHWEST COAST AND THE PLATEAU

We began by testing the hypothesis that risk of resource failure was higher for the populations that lived on the plateau than for the populations that lived on the northwest coast. We collected data for environmental variables relevant to testing the risk hypothesis for each of the 16 populations. These variables included ET, NAGP, GS, mean temperature of the coldest month (MCM), mean temperature of the warmest month (MWM), mean annual rainfall (RMEAN), mean rainfall for the wettest month (RHIGH), mean rainfall for the driest month (RLOW) and species richness (RICH). Data for ET, NAGP, GS, MCM, MWM, RMEAN, RHIGH and RLOW were obtained from Binford [20]. Data for RICH were taken from Jorgensen [30].

Once we had collected the environmental data, we subjected them to principal components analysis (PCA). We pursued this course of action because risk of resource failure is likely influenced by multiple environmental variables, and is therefore unlikely to be adequately represented by a single such variable. We reasoned that, because principal components reflect covariation among two or more variables, principal components derived from multiple environmental variables might approximate risk of resource failure more closely than any of the individual variables. We employed the Kaiser criterion for principal component extraction, and therefore only extracted principal components with eigenvalues that exceeded unity. A total of two principal components were extracted in the PCA. The first principal component (PC1) accounted for approximately 64.5 per cent of the variation in the dataset, and the second (PC2) for a further 25.2 per cent. The scores for these principal components were incorporated into the dataset alongside the values for the environmental variables.

Table 1. Results of t-tests in which northwest coast and plateau hunter–gatherer populations' values for nine risk variables and four toolkit structure variables were compared. MCM, Mean temperature of coldest month; MWM, mean temperature of warmest month; ET, effective temperature; RMEAN, mean annual rainfall; RHIGH, mean rainfall for wettest month; LRLOW, natural log of mean rainfall for driest month; GS, growing season; NAGP, net above ground productivity; PC1, first principal component obtained in PCA of environmental variables; PC2, second principal component obtained in PCA of environmental variables. The Bonferroni-corrected significance level for this analysis was 0.005.

variable	northwest coast mean	plateau mean	predicted direction?	p
MCM	3	−5	Y	0.000[a]
MWM	16	19	Y	0.002[a]
ET	12	12	N	0.727
RMEAN	1652	458	Y	0.001[a]
RHIGH	263	68	Y	0.001[a]
LRLOW	4	2	Y	0.001[a]
GS	7	6	Y	0.375
NAGP	740	324	Y	0.000[a]
RICH	50	28	Y	0.000[a]
PC1	0.86	−0.86	Y	0.000[a]
PC2	0.21	−0.21	Y	0.412

[a]Statistically significant difference.

Subsequently, we used the t-test to evaluate the significance of the differences between the northwest coast and plateau populations in the environmental variables. Prior to carrying out the t-tests, we tested all the variables for kurtosis and skewness. None of the variables was found to exhibit significant kurtosis, and only one variable was significantly skewed. This variable, RLOW, was $\log_e$ transformed to avoid violating the assumptions of the t-test. In the t-tests, we used the Bonferroni correction to adjust the significance level to account for the fact that we were carrying out multiple unplanned tests. The Bonferroni correction modifies the critical value by dividing it by the number of tests conducted [31]. We carried out a total of 11 tests. Thus, the significance level was 0.005.

Most of the environmental variables not only differed between the northwest coast and plateau in the expected direction, but also did so significantly. RMEAN, RHIGH, RLOW, MCM, GS, RICH and PC1 were all significantly lower for the plateau than for the northwest coast, while MWM was significantly higher for the plateau than for the northwest coast (table 1). The remaining three environmental variables—GS, ET and PC2—were not significantly different between the two subsamples. However, GS and PC2 differed between the northwest coast and plateau in the expected direction. Thus, overall, the environmental variables supported the idea that the plateau is a more risky environment for hunter–gatherers than the northwest coast.

7. COMPARISON OF TOOLKIT STRUCTURE ON THE NORTHWEST COAST AND PLATEAU

Using Oswalt's [8,9] methodology, we recorded the subsistants and technounits of six of the northwest coast populations (the Kwa'Kwa'Ka'Wk, Nuu-Chan-Nulth, Coast Salish, Makah, Upper Stalo and Quinalt) and seven of the plateau populations (Shuswap, Lillooet, Thompson, Okanogan, Coeur D'Alene, Sanpoil/Nespelem and Flathead). We obtained subsistant and technounit data for the remaining three populations (the Twana, Tlingit and Klamath) from Oswalt [9].

From the subsistant and technounit data, we calculated Oswalt's [9] three statistics for describing toolkit structure, total number of subsistants (STS), total number of technounits (TTS) and average number of technounits per tool (AVE). We also computed the statistic proposed by Henrich [14], the sum of the technounit counts for the most complex instrument, weapon, untended facility and tended facility in a given toolkit (MXT). We did not calculate Read's [15] toolkit structure statistics—the number of complex subsistants, the number of technounits in complex subsistants and the number of complex subsistant types—because we are not convinced by Read's rationale for using them and because trials showed that they are redundant with one or more of the other toolkit structure statistics. In addition, trials also showed that Read's number of complex subsistant types statistic is excessively prone to subjectivity.

Subsequently, we used the *t*-test to evaluate the significance of the differences between the northwest coast and plateau populations in the toolkit structure variables. As in the previous analysis, the variables were tested for kurtosis and skewness prior to the *t*-tests being carried out, and the Bonferroni correction was used to adjust the significance level to account for the fact that we were carrying out multiple unplanned tests. None of the variables was found to exhibit significant kurtosis, and none was significantly skewed. Applying the Bonferroni correction reduced the significance level to 0.013.

None of the toolkit variables was found to differ significantly between the northwest coast and the plateau populations (table 2). Moreover, none of the toolkit variables differed between the northwest coast and the plateau populations in the expected direction. The mean values for the northwest coast populations were all higher than the mean values for the plateau populations. Thus, the comparison of the toolkit variables did not support the predictions of the risk hypothesis.

Table 2. Results of *t*-tests in which northwest coast and plateau hunter–gatherer populations' values for four toolkit structure variables were compared. STS, Total number of subsistants; TTS, total number of technounits; AVE, average number of technounits per subsistant; MXT, sum of technounit counts for the most complex instrument, weapon, untended facility and tended facility in a toolkit. The Bonferroni-corrected significance level for this analysis was 0.013.

variable	northwest coast mean	plateau mean	predicted direction?	p
STS	39	39	N	0.984
TTS	212	178	N	0.350
AVE	5	5	N	0.038
MXT	37	31	N	0.097

8. DISCUSSION

The climate and ecological variables we examined strongly suggest that the plateau is a more risky environment than the northwest coast. According to the risk hypothesis, this should mean that plateau hunter–gatherer populations created more diverse and complex toolkits than hunter–gatherer populations on the northwest coast. However, the results of our comparison of the toolkits of hunter–gatherers from the plateau and northwest coast were not consistent with this prediction. The plateau populations in our sample did not create more diverse and complex toolkits than the northwest coast populations. As such, the results of our study do not support the risk hypothesis.

There are several possible explanations for the discrepancy between the results of our analyses and the results of the analyses reported by Collard *et al.* [21], Henrich [14] and Read [15], which, as we explained earlier, supported the risk hypothesis. One is that our research protocol was inadvertently biased against identifying the impact of risk of resource failure on toolkit structure. It is possible that classifying the environments of the two groups as 'lower risk' and 'higher risk' and then comparing the groups' values for the toolkit structure variables with the *t*-test is too crude. To evaluate this possibility, we ran a series of correlation analyses in which each toolkit structure variable was correlated with each risk variable. As in the *t*-tests, the *p*-value was divided by the number of tests to account for the fact that we were carrying out multiple unplanned tests ($p = 0.001$). These analyses did not support the risk hypothesis either. None of the risk variables was significantly correlated with the toolkit structure variables (table 3). Thus, it does not seem to be the case that the discrepancy between the results of our analyses and the results of the analyses reported by Collard *et al.* [21], Henrich [14] and Read [15] can be explained by our research protocol.

Another possible explanation for the discrepancy between the results of our analyses and the results of the analyses reported by Collard *et al.* [21], Henrich [14] and Read [15] concerns the risk variables we used. It could be that, contrary to what we have been assuming, our risk variables do not reflect risk of resource failure as well as the risk variables employed by Collard *et al.* [21], Henrich [14] and Read [15]. However, this explanation is also unsatisfactory. The reason for this is that our set of risk variables included all the risk variables employed by Collard *et al.* [21], Henrich [14] and Read [15]. To reiterate, Collard *et al.* used effective temperature and net above ground productivity as proxies for

Table 3. Results of correlation analyses in which toolkit structure variables were correlated with risk variables. The upper value in each cell is the Pearson correlation coefficient; the lower is the *p*-value. After the Bonferroni correction, the significance level for the analyses was 0.001.

	MCM	MWM	ET	RMEAN	RHIGH	LRLOW	GS	NAGP	RICH
STS	−0.030	0.015	0.073	−0.216	−0.209	−0.408	−0.250	−0.032	−0.011
	0.913	0.956	0.789	0.421	0.438	0.117	0.351	0.907	0.969
TTS	0.201	−0.510	0.161	−0.033	−0.019	−0.152	−0.009	0.178	0.243
	0.456	0.850	0.551	0.903	0.943	0.575	0.973	0.508	0.365
AVE	0.509	−0.106	0.289	0.348	0.370	−0.331	0.477	0.464	0.569
	0.440	0.696	0.278	0.186	0.159	0.211	0.062	0.070	0.021
MXT	0.384	−0.180	0.138	0.298	0.301	0.204	0.056	0.367	0.474
	0.142	0.506	0.609	0.261	0.257	0.448	0.836	0.162	0.064

risk, Henrich employed effective temperature and Read used effective temperature, net above ground productivity and growing season. It might be objected that our first set of *t*-tests did not find a significant difference between the effective temperature values for the two groups of populations, and that this is consistent with the risk hypothesis. However, it is clear from the regression analyses reported in the previous paragraph that this result is misleading, and that effective temperature does not, in fact, impact the toolkits of the Pacific Northwest populations in the manner predicted by the risk hypothesis. As such, the discrepancy between the results of our analyses and the results of the analyses reported by Collard *et al.*, Henrich and Read is not a consequence of our choice of risk proxies.

A third possibility is that our results differed from those of Collard *et al.* [21], Henrich [14] and Read [15] because the risk hypothesis holds at the global scale, but not necessarily at the regional level. It is feasible that risk of resource failure is the dominant influence on toolkit structure variation when differences in risk of resource failure are large—as seems likely to be the case between, say, Africa and the Arctic—but is less influential when differences in risk of resource failure are small. In such situations, other factors may be equally, if not more, important. The results of a recent study by Kline & Boyd [32] are consistent with this idea. Kline & Boyd used data from Polynesian fisher–farmer populations to test the hypothesis that population size influences cultural evolution. They found that population size has a significant impact on both number of subsistants and average number of technounits per subsistant, which is consistent with the predictions of the population size hypothesis. Significantly for present purposes, Kline & Boyd selected the populations in their sample to minimize risk differences, and when they evaluated the relative importance of risk and population size, they found—as expected—that population size was more important than risk. This is consistent with the hypothesis that risk is the dominant influence on toolkit structure variation when risk differences are large, but becomes less important than other factors as risk differences among populations decrease.

To evaluate the possibility that our results differ from those of Collard *et al.* [21], Henrich [14] and Read [15] because the importance of risk versus other factors is dependent on the magnitude of the differences in risk among populations, we carried out a further analysis. First, we combined our TTS and ET data with Collard *et al.*'s [21]. Next, we generated 20 ten-population subsamples by random sampling with replacement, log transformed the values for ET (LET) and calculated the variance of LET for each subsample. Subsequently, we computed the Pearson correlation coefficient for the correlation between the number of technounits and LET for each subsample. Lastly, we correlated the variances for LET with the Pearson correlation coefficients. We reasoned that if the hypothesis is correct, there should be a significant negative correlation between variance of LET and the strength of the relationship between TTS and LET. The reason the relationship should be negative is that toolkit diversity and complexity are predicted to increase as ET decreases, since low-ET locations are expected to be more risky than high-ET locations. The analysis supported the hypothesis. As predicted, there was a significant negative correlation between the variances for LET and the Pearson correlation coefficients ($r = -0.450$, $p = 0.046$). As such, it seems reasonable to conclude that our results differ from those of Collard *et al.* [21], Henrich [14] and Read [15] not because there is a problem with our analyses, but rather because the importance of risk versus other factors is dependent on the magnitude of the differences in risk among populations.

With regard to future research, there are two obvious challenges. One is to further evaluate the idea that the influence of risk is dependent on the scale of risk differences among populations. This will require additional regional comparisons and/or studies that compare populations from parts of the world that are geographically separate but have similar levels of risk. In addition, there is a need to confirm that the results of the global-scale analyses are reliable and do not simply reflect population history [33]. The other challenge is to determine what influenced hunter–gatherer toolkit structure in the Pacific Northwest during the early contact period. If risk of resource failure was not the main influence, what was? Based on the findings of Henrich [14] and Kline & Boyd [32], population size is an obvious possibility to investigate. The study reported by Rendell *et al.* [34] suggests that degree of reliance on copying may also be worth considering.

9. CONCLUSIONS

A number of recent studies have supported the hypothesis that the diversity and complexity of hunter–gatherer toolkits are driven by risk of resource failure such that populations living in more risky environments create and use more diverse and complex toolkits than populations living in less risky environments [14,15,21]. In the study reported here, we carried out a further test of the risk hypothesis using data from hunter–gatherer populations who occupied the Pacific Northwest in the late nineteenth and early twentieth centuries. Our analyses indicated that the two main regions of the Pacific Northwest—the northwest coast and the plateau—differ significantly in variables that can be expected to affect risk of resource failure. Specifically, they indicated that the plateau is a more risky environment than the northwest coast. According to the risk hypothesis, this should mean that plateau hunter–gatherer populations created more diverse and complex toolkits than hunter–gatherer populations on the northwest coast. However, the results of our comparison of the toolkits of hunter–gatherers from the two regions were not consistent with this prediction. The plateau populations did not create more diverse and complex toolkits than the northwest coast populations. As such, the results of our study did not support the risk hypothesis. The discrepancy between our results and those of previous tests of the risk hypothesis is not due to methodological differences. Rather, it seems to reflect an important but hitherto unappreciated feature of the relationship between risk of resource failure and toolkit structure, namely that the impact of risk is dependent on the scale of the risk differences among populations. It appears that when risk differences are large, risk is the most important influence on toolkit structure variation. However, when risk differences among populations are small, other factors are as, if not more, influential as determinants of toolkit structure variation.

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