

Niche Construction and the Toolkits of Hunter–Gatherers and Food Producers

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Abstract In the study reported here we examined the impact of population size and two proxies of risk of resource failure on the diversity and complexity of the food-getting toolkits of hunter–gatherers and small-scale food producers. We tested three hypotheses: the risk hypothesis, the population-size hypothesis, and a hypothesis derived from niche construction theory. Our analyses indicated that the toolkits of hunter–gatherers are more affected by risk than are the toolkits of food producers. They also showed that the toolkits of food producers are more affected by population size than are the toolkits of hunter–gatherers. This pattern is inconsistent with the predictions of both the risk hypothesis and the population-size hypothesis. In contrast, it is consistent with the predictions of the niche construction hypothesis. Our results indicate that niche construction has affected the evolution of technology in small-scale societies and imply that niche construction must be taken into account when seeking to understand technological variation among food producers and the technological changes that occurred in association with the various transitions to farming that have occurred over the last 10,000 years.

Keywords Food producers · Hunter–gatherers · Niche construction theory · Pastoralists · Farmers · Population size · Risk · Toolkits

Introduction

Niche construction theory (NCT) has become increasingly popular in biology and ecology over the last 15 years (e.g., Erwin 2008; Post and Palkovacs 2009; Cuddington 2012; Laland and O'Brien 2012; Odling-Smee and Laland 2012; Schielke et al. 2012) but has been little used in anthropology over the same time period, despite the fact that *Homo sapiens* is the most obvious example of a niche-constructing organism (Laland and Brown 2006; Smith 2007a). To date, NCT has been discussed in just over a dozen archaeological papers (Bleed 2006; Smith 2007a, b, 2009, 2011, 2012; Broughton et al. 2010; Laland and O'Brien 2010; Riel-Salvatore 2010; Bleed and Matsui 2011; Riede 2011; Rowley-Conwy and Layton 2011; Wollstonecroft 2011; O'Brien and Laland 2012; Zeder 2012), and about the same number of contributions have discussed NCT in relation to living humans (Laland et al. 2000, 2001, 2007, 2010; Laland and Brown 2006; Laland 2008; Gerbault et al. 2011; Kendal et al. 2011; Rendell et al. 2011; Rowley-Conwy and Layton 2011; O'Brien and Laland 2012).

It is likely that anthropologists have been slower to embrace NCT than biologists and ecologists because it is newer to anthropology than to biology and ecology (O'Brien and Laland 2012). However, our conversations with colleagues suggest that there is at least one other reason why archaeologists and sociocultural anthropologists have not employed NCT more often, and that is the paucity of empirical studies that demonstrate its usefulness

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for understanding anthropological problems. In our experience, discussions with fellow anthropologists about NCT often end in, “Yes, but where’s the beef?” or questions to that effect. With that in mind, we decided to see whether we could design an empirical study that used NCT to shed light on an issue that a number of anthropologists have investigated over the last 30 years—the causes of cross-cultural variation in the structure of subsistence toolkits (e.g., Oswalt 1973, 1976; Torrence 1983, 1989; Shott 1986; Osborn 1999; Collard et al. 2005, 2011; Read 2008; Kline and Boyd 2010).

Investigating the causes of variation in the number and intricacy of food-getting tools among human populations is an important task for anthropologists. Such variation is one of the most obvious aspects of the ethnographic record. In addition, artifacts linked to the acquisition and processing of food dominate the archaeological record. Recent discoveries suggest that hominins have been producing tools for 3.4 million years (McPherron et al. 2010). The majority of the tools that have been recovered from the first 3.3 million years of this time period appear to have been employed in subsistence activities. Tools used for purposes other than subsistence increased in frequency around 100,000 years ago (d’Errico and Stringer 2011; Foley and Lahr 2011), but subsistence-related items continue to comprise a substantial portion of the archaeological record well into the Holocene. Thus, to understand both the ethnographic and archaeological records, we have to understand the causes of variation in subsistence technology.

In line with previous work on the causes of toolkit variation (e.g., Torrence 1983, 1989; Shott 1986; Osborn 1999; Collard et al. 2005, 2011; Read 2008; Kline and Boyd 2010), we used an approach to analyzing toolkit structure that was developed by Oswalt (1973, 1976). Oswalt devised two primary variables for quantifying toolkit structure. One is the total number of subsistants (STSs). A subsistant is a tool used for subsistence, and STS is an indicator of the size, or what Torrence (1983, 1989) and Shott (1986) call the diversity, of a toolkit. The other variable is the total number of technounits (TTS). Oswalt (1976, p. 38) defined a technounit as an “integrated, physically distinct, and unique structural configuration that contributes to the form of a finished artifact.” In other words, technounits are the different kinds of parts of a tool (e.g., shaft, spearhead, binding). TTS is a measure of toolkit complexity (Oswalt 1976; Torrence 1983, 1989).

We quantified toolkit diversity and complexity in a sample of hunter–gatherers and a sample of small-scale food producers and used the data to test the predictions of three hypotheses. The first hypothesis focuses on risk of resource failure. The idea that risk of resource failure drives variation in subsistence toolkits has its roots in Torrence’s (1983) paper “time budgeting and hunter–gatherer technology,” 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, the production of specialized tools increases not only toolkit diversity but also toolkit complexity. Subsequently, Torrence (1989) argued that time stress was likely only a proximate cause of toolkit variation and that the ultimate causes are the timing and severity of risk of resource failure. She argued further that the use of more specialized, and therefore more elaborate, tools reduces risk of resource failure. Thus, populations that experience high risk of failure will produce toolkits that are diverse and complex, whereas those that experience lower risk of resource failure will produce simpler toolkits.

The second hypothesis posits that toolkit diversity and complexity are driven by population size. This hypothesis is rooted in the work of Shennan (2001), who used a population-genetics model to investigate the impact of population size on cultural evolution when innovations affect fitness. He employed two variants of a population-genetics model that was developed by Peck et al. (1997) to assess the relative benefits of sexual and asexual reproduction. In their 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. Shennan (2001) began by altering Peck and colleagues’ model so that transmission was possible only from one “cultural parent” to one “cultural offspring.” To produce his second model, Shennan (2001) modified Peck and colleagues’ 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 (2001) found a marked increase in the mean fitness of the population as effective population size increased. In the trials of the first model, there was a 10,000-fold increase in the mean fitness value of the population as effective population size increased from 5 to 50. In trials of the second model, in which cultural traits were adopted from non-biological parents 5 % of the time, the population’s mean fitness value increased a thousandfold as the effective population size increased from 5 to 25, and then increased by around 5 times as effective population size increased from 25 to 75. Shennan’s (2001) simulation studies showed that larger populations have a major advantage over smaller ones when it comes to cultural innovation as a result of the decreasing role of sampling effects as populations increase. When effective population size is large, there is a far greater probability of fitness-enhancing cultural innovations being maintained and deleterious ones being lost than when effective population size is small. In the latter situation, innovations that are maintained tend to be less

beneficial in terms of reproduction and also less attractive for imitators. One 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 populations. Thus, there should be a significant positive correlation between population size and measures of toolkit structure.

The third hypothesis we tested draws on NCT. It holds that the subsistence toolkits of small-scale food producers should be less influenced by risk of resource failure and more influenced by population size than the subsistence toolkits of hunter-gatherers. Part of the rationale for this hypothesis is that although both hunter-gatherers and food producers engage in niche construction, food producers are more potent niche constructors than hunter-gatherers (Smith 2007a, b, 2009, 2011). One corollary to this is that food producers should be more buffered from the type of large-scale environmental variation that increases or decreases risk of resource failure. This in turn should mean that the structure of their toolkits is less directly influenced by variation in macro-environmental factors than the toolkits of hunter-gatherers. The other part of the rationale for the hypothesis is that food producers' greater intensity of niche construction results in their having, on average, larger populations than hunter-gatherers. According to the results of Shennan's (2001) modeling work, the impact of population size on cultural complexity increases magnitudinally as population size increases. A corollary is that population size should have a more profound impact on the diversity and complexity of the toolkits of food producers than on the diversity and complexity of the toolkits of hunter-gatherers.

Materials and Methods

Data

We calculated STS and TTS for 34 hunter-gatherer populations and 45 small-scale food-producing populations (Table 1) using information from ethnographic sources varying in age from the late 1800s to the mid-twentieth century. Food producers were defined as populations that derived the majority of their food from pastoralism, horticulture, or intensive agriculture and relied on locally manufactured technology at the time fieldwork was conducted. Hunter-gatherers were defined as groups subsisting primarily on wild resources at the time of fieldwork.

In addition to collecting values for the number of STSs and TTSs, we generated values for two proxies for risk of resource failure—latitude and effective temperature (ET). Torrence (1989, 2001) argued that latitude is a good global

Table 1 Names and locations of populations in the samples

Group	Location
Food-producing groups	
Akamba	Kenya
Aymara	Peru
Azande	Sudan
Garo	India
Gikuyu	Kenya
Guarani	Paraguay
Gwembe Valley Tonga	Zambia
Haddad	Chad
Hopi ^a	USA
Huron ^a	Canada
Jivaro	Ecuador
Kapauku	Indonesia
Kogi	Colombia
Korea	South Korea
Lepcha	India
Lur	Iran
Malay ^a	Malaysia
Malekula	Vanuatu
Mapuche	Chile
Mataco	Bolivia
Maya ^a	Guatemala
Monguor	China
Ojibwa ^a	Canada
Okinawa	Japan
Ovimbundu	Angola
Pawnee	USA
Pima ^a	USA
Pukapuka	Cook Islands
Quichua	Ecuador
Rwanda	Rwanda
Sema Nega ^a	India
Seminole	USA
Sinhalese	Sri Lanka
Somali	Somalia
Tanala	Madagascar
Tarahumara	Mexico
Tikopia	Solomon Islands
Trukese	Micronesia
Tuareg	Algeria
Vietnamese	Vietnam
Walapai ^a	USA
Yanomami	Venezuela
Yuma ^a	USA
Zapotec	Mexico
Zuni ^a	USA
Hunter-Gatherers	
!Kung San	Kalahari Desert

Table 1 continued

Group	Location
Alacaluf	Chile
Angmagsalik	Greenland
Botocudo	Brazil
Caribou Inuit	Canada
Chenchu	India
Copper Inuit	Canada
G/Wi	Botswana
Great Andamanese	Andaman Island
Groote-eylandt	Australia
Guato	Brazil and Bolivia
Hadza	Tanzania
Ingalik	USA
Ingulik Inuit	Canada
Klamath	USA
Mbuti	Congo Region
Nabesna	USA
Nharo	Southern Africa
Northern Arenda	Australia
Ona	Tierra del Fuego
Owens Valley Paiute	USA
Punan	Malaysia
Siriono	Bolivia
Surprise Valley Paiute	USA
Tanaina	USA
Tareumiut Inuit	USA
Tasmanians	Tasmania
Tiwi	Australia
Tlingit	USA
Twana	USA
Veddas	Sri Lanka
Yahgan	Tierra del Fuego
Yaruro	Venezuela
Yukaghir	Russia

^a Population estimates are unavailable

proxy for risk because resource abundance decreases with distance from the equator. We used ET as a second proxy measure of risk because it captures local environmental factors that small-scale societies are more likely to respond to and that are not captured by latitude. ET is calculated using mean warmest and mean coldest temperatures and the following equation:

$$ET = ([18WM] - [10CM]) / (WM - [CM + 8]),$$

where WM is the mean temperature (in °C) of the warmest month of the year, and CM is the mean temperature of the coldest month (Bailey 1960). The first constant in the Eq. (18) is the mean minimal temperature that will sustain tropical plant life. The second (10) is the temperature limit

of polar climates for the warmest month (the minimal mean temperature at the boundary between polar and boreal environments). The third (8) is the minimal mean temperature at the beginning and end of the growing season. ET values for the hunter–gatherer groups were taken from Binford (2001). ET values for the food producers were calculated from temperatures presented in several open-access sources of climatic information.¹ As far as possible, we used temperatures from the same period as the toolkit data. For ease of interpretation, prior to the analyses we inverted the signs of the ET values. This meant that both latitude and ET were expected to have a significant positive impact on toolkit diversity and complexity.

Lastly, we collected population-size information for each hunter–gatherer and food-producing group. Estimates for the hunter–gatherer groups were taken from Binford (2001). For the food-producing groups, we obtained population estimates from the Human Relations Area Files, which is a Web-accessible, key-word-searchable collection of ethnographies. We were unable to collect population estimates for 10 of the 45 food-producing groups in the time available.

Analyses

Having compiled the dataset, we assessed the normality of the variables with the Kolmogorov–Smirnov test. Only one of the five variables, population size, departed significantly from the expectations of a normal distribution, and we log-transformed it. After transformation, all five variables had distributions that conformed to the expectations of a normal distribution according to the Kolmogorov–Smirnov test. Analyses were carried out in PASW (SPSS) 18. Subsequently, we carried out 12 linear-regression analyses. We ran six regressions using STS as the dependent variable and the two risk variables and population size as the independent variables. Three of these analyses used the hunter–gatherer data and three used the food-producer data. We then ran a similar set of six regressions using TTS as the dependent variable. Again, three analyses used the hunter–gatherer data and three used the food-producer data. Because we effectively carried out multiple unplanned tests, we used Benjamini and Yekutieli's (2001) method of significance-level correction. We employed this method rather than the commonly used Bonferroni correction because it has been shown to balance the reduction of type-I and type-II error rates better than Bonferroni correction (Narum 2006). Using this method, our significance level

¹ www.climatetemp.info/; www.weatherbase.com/weather/countryall.php3?refer; www.wrcc.dri.edu/CLIMATEDATA.html; www.tutiempo.net/en/Climate.

was reduced from $\alpha = 0.05$ to $\alpha = 0.016$. The regressions were done using PASW (SPSS) 18.

Predictions

We defined predictions regarding the effects of the risk variables and population size on STS and TTS for each hypothesis (Fig. 1). In relation to the niche construction hypothesis, we reasoned that because food producers engage in more niche construction than hunter-gatherers, they should be more buffered from risk. Consequently, the relationship between risk variables and measures of toolkit structure should be stronger in the hunter-gatherer sample than in the food-producer sample (Fig. 1a). We also predicted that under the niche construction hypothesis the relationship between population size and the measures of toolkit structure should be stronger among food producers than among hunter-gatherers (Fig. 1b). The reason for this is that Shennan’s (2001) modeling work suggests the impact of population size on innovation increases as population increases. The populations in our food-producer sample tend to be larger than the populations in our hunter-gatherer samples. It follows, therefore, that there should be a stronger relationship between population size and the measures of toolkit structure among food producers than among hunter-gatherers.

Predictions for the other two hypotheses are simpler. Under the risk hypothesis, the relationship between risk variables and toolkit variables is predicted to be positive in both samples (Fig. 1c), whereas population size should not

impact STS or TTS in either sample (Fig. 1d). The population-size hypothesis has the opposite predictions to the risk hypothesis. It predicts that risk should not impact either STS or TTS (Fig. 1e) and that the relationship between population size and toolkit variables should be positive (Fig. 1f).

Results

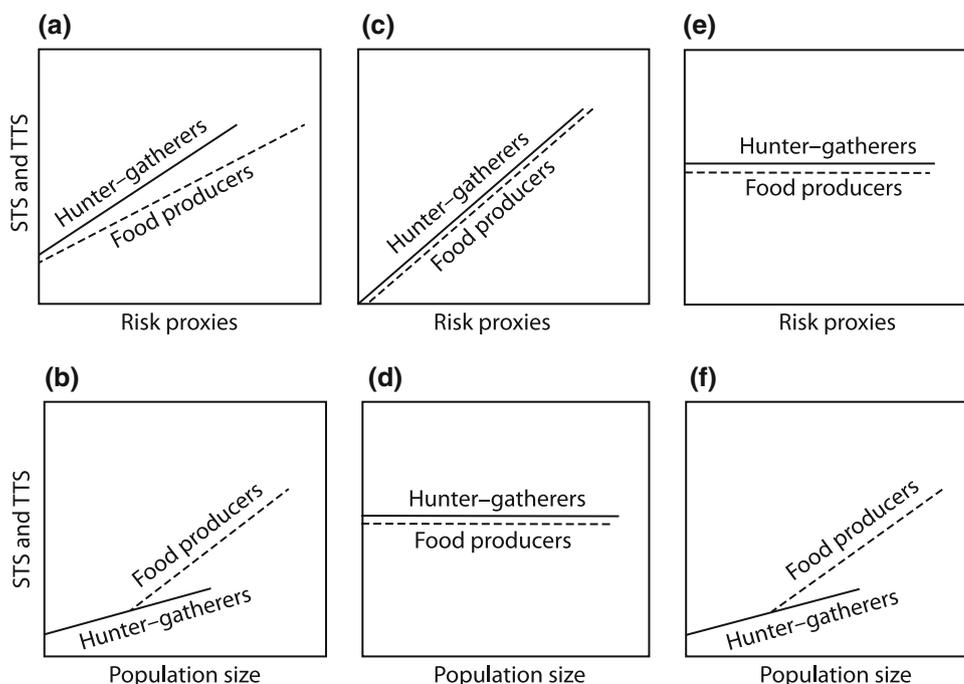
Table 2 and Fig. 2 summarize results of analyses in which STS and TTS were regressed on latitude. STS was significantly and positively related to latitude among the hunter-gatherers but not among food producers. The relationship between STS and latitude in the food-producer sample was positive but not statistically significant. TTS was positively

Table 2 Results from the linear regression analyses of STS and TTS on latitude for hunter-gatherers ($df = 32,33$) and food producers ($df = 43,44$)

	r^2	F	p	Slope	y-intercept
STS-HG	0.528	35.87	<0.000*	0.422	5.89
TTS-HG	0.494	31.19	<0.000*	2.299	1.81
STS-FP	0.001	0.06	0.815	0.049	43.20
TTS-FP	0.005	0.23	0.632	0.542	142.16

* Rejecting null hypothesis that the sample comes from a population with a slope of 0. Significance level is adjusted using Benjamini and Yekutieli’s (2001) alpha correction; the critical value for 12 tests is $\alpha = 0.016$

Fig. 1 Predicted outcomes of the three hypotheses of the relationship between the number of tool types, or subsistants (STS), and the complexity of the tools as measured by the number of technounits (TTS) and risk proxies and population size for hunter-gather groups and food-producing groups: **a, b** niche construction hypothesis, **c, d** risk hypothesis, **e, f** population-size hypothesis



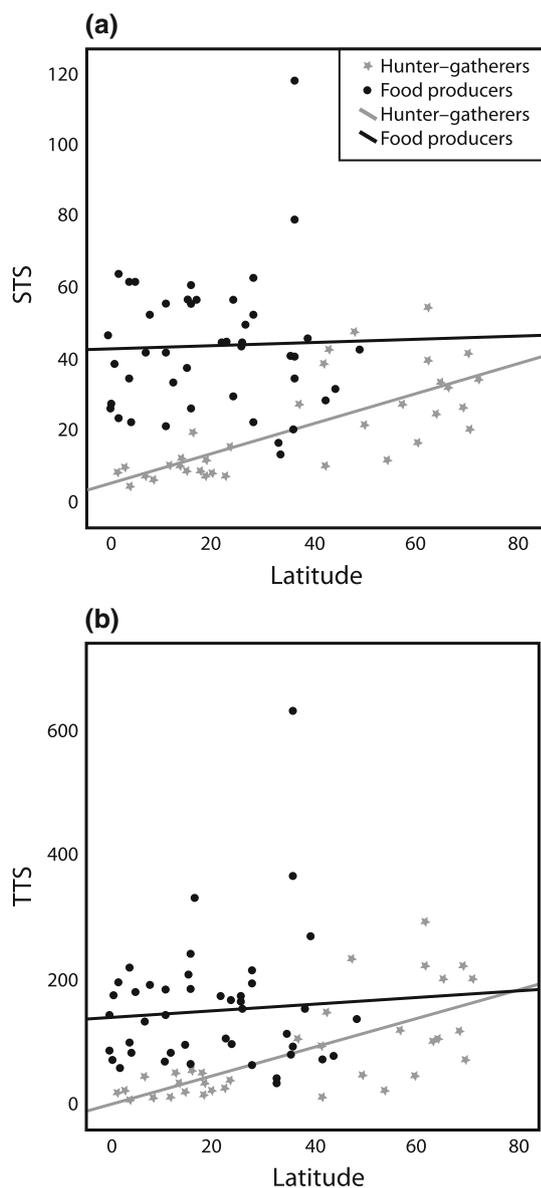


Fig. 2 The relationship between latitude and **a** the number of different tool types (STS) and **b** the complexity of the tools as measured by the number of technounits (TTS) used by hunter-gatherer groups and food-producing groups

related to latitude in both samples but significant only in the hunter-gatherer sample.

Table 3 and Fig. 3 summarize results of analyses in which STS was regressed on the inverse of ET. STS was positively related to decreasing ET in both samples, but it was significant only in the hunter-gatherer sample. The pattern was the same for TTS.

Table 4 and Fig. 4 summarize results of analyses in which STS and TTS were regressed on population size. STS was positively related to population size in both samples but was significant only in the food-producer sample. The pattern was the same for TTS.

Table 3 Results from the linear-regression analyses of STS and TTS on the inverse of ET for hunter-gatherers ($df = 32,33$) and food producers ($df = 43,44$)

	r^2	F	p	Slope	y-intercept
STS-HG	0.445	25.63	<0.000*	0.182	48.71
TTS-HG	0.367	18.57	<0.000*	9.314	226.17
STS-FP	0.000	0.01	0.910	0.095	45.78
TTS-FP	0.001	0.03	0.864	0.785	166.24

* Rejecting null hypothesis that the sample comes from a population with a slope of 0. Significance level is adjusted using Benjamini and Yekutieli's (2001) alpha correction; the critical value for 12 tests is $\alpha = 0.016$

When the scatterplots and r^2 values are compared to the predictions of the three hypotheses, it is clear that the results of the analyses are consistent only with the niche construction hypothesis. The lack of an effect of risk on the toolkits of the food-producer sample is not in line with the predictions of the risk hypothesis. Nor is the finding that population size affects the toolkits of the food-producer sample. Similarly, neither the presence of an effect of risk on the toolkits of the hunter-gatherer sample nor the lack of an effect of population size on the toolkits of the hunter-gatherer sample is consistent with the population-size hypothesis.

Discussion

We examined the impact of population size and two proxies of risk of resource failure on the diversity and complexity of the food-getting toolkits of hunter-gatherers and small-scale food producers to test the predictions of three hypotheses: the risk hypothesis, the population-size hypothesis, and a hypothesis derived from NCT. Our analyses indicated that the toolkits of hunter-gatherers are more affected by risk than are the toolkits of food producers. They also showed that the toolkits of food producers are more affected by population size than are the toolkits of hunter-gatherers. This pattern is inconsistent with the predictions of both the risk hypothesis and the population-size hypothesis. In contrast, it is consistent with the predictions of the niche construction hypothesis.

The obvious implication of our findings is that niche construction has affected the evolution of technology in small-scale societies. Specifically, our findings suggest that the greater frequency and impact of food producers' niche-constructing activities have altered the selection pressures on technological decisions and the demographic context in which they are made, such that the dynamics of technological evolution among food producers are different from the dynamics of technological evolution among

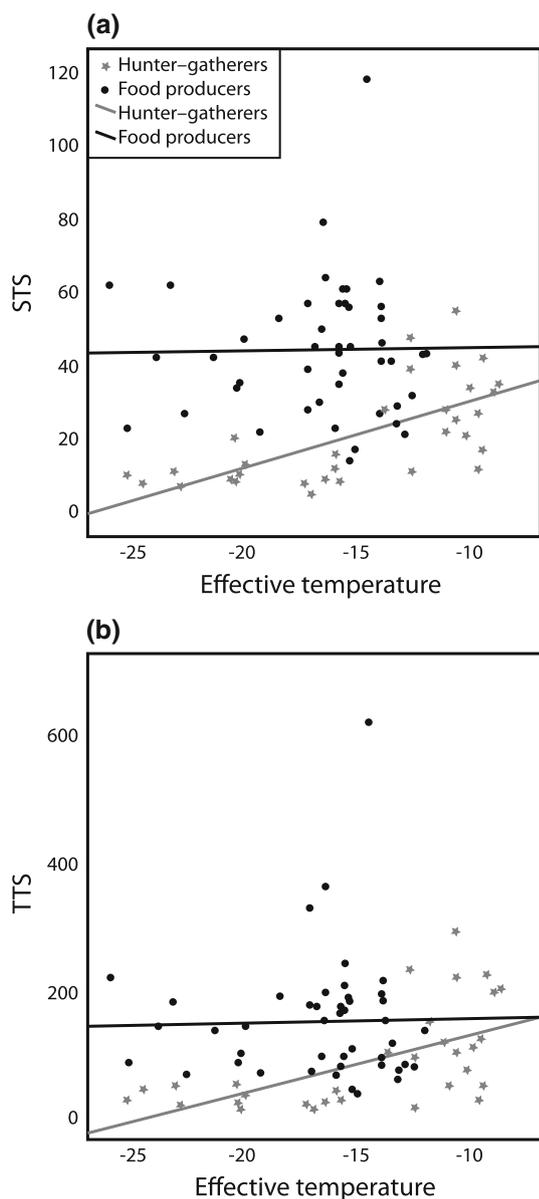


Fig. 3 The relationship between ET and **a** the number of different tool types (STS) and **b** the complexity of the tools as measured by the number of technounits (TTS) used by hunter-gatherer groups and food-producing groups

hunter-gatherers. One key corollary is that the effects of niche construction should be considered when seeking to understand technological variation among food producers. Another important corollary is that niche construction should be taken into account in attempts to understand the technological changes that occurred in association with the various transitions to farming that have occurred over the last 10,000 years.

With regard to future research, two possibilities suggest themselves. One concerns the impact of niche construction on hunter-gatherer subsistence technology. Over the last 35 years, Woodburn (1979, 1980, 1982, 1988) has

Table 4 Results from the linear-regression analyses of STS and TTS on population size for hunter-gatherers ($df = 32,33$) and food producers ($df = 33,34$)

	r^2	F	p	Slope	y-intercept
STS-HG	0.048	1.61	0.213	2.580	3.64
TTS-HG	0.030	0.98	0.330	11.425	7.56
STS-FP	0.236	10.18	0.003*	3.112	10.57
TTS-FP	0.268	12.08	0.001*	18.53	-49.40

* Rejecting null hypothesis that the sample comes from a population with a slope of 0. Significance level is adjusted using Benjamini and Yekutieli's (2001) alpha correction; the critical value for 12 tests is $\alpha = 0.016$

convincingly argued that hunter-gatherers can be divided into groups whose subsistence activities usually have an immediate return and groups for whom there is often a delay between carrying out a food-getting behavior and its payoff. Woodburn calls these groups "immediate-return-system" (IRS) hunter-gatherers and "delayed-return-system" (DRS) hunter-gatherers, respectively (Woodburn 1988). The Hadza of Tanzania and the !Kung of Namibia are perhaps the best-known examples of IRS hunter-gatherers, whereas the Kwakiutl and Nootka of the Pacific Northwest Coast are examples of DRS hunter-gatherers.

One key difference between the two systems, Woodburn argues, is that DRS hunter-gatherers often improve or increase the yield of wild products with human labor, whereas IRS hunter-gatherers rarely do so (Woodburn 1982). Among the activities that Woodburn cites as examples of the ways in which DRS hunter-gatherers improve or increase the yield of wild products with human labor are selective culling and tending wild food-producing plants. Both activities are forms of niche construction. Thus, if Woodburn is correct, there may be substantial differences in niche construction between IRS hunter-gatherers and DRS hunter-gatherers. Specifically, it is possible that the latter are more potent niche constructors than the former. An obvious corollary of this is that niche construction may impact the subsistence toolkits of DRS hunter-gatherers more than the toolkits of IRS hunter-gatherers. If so, then the differences between food producers and hunter-gatherers that we have identified in the present study should be replicated to some degree between DRS hunter-gatherers and IRS hunter-gatherers.

The other possibility for future research concerns the impact of niche construction on the toolkits of food producers. We included both farmers and pastoralists in our sample of food producers. We did so because we were focusing on the differences between hunter-gatherers and food producers in general. However, it would be interesting to investigate whether niche construction impacts the subsistence toolkits of farmers and pastoralists differently.

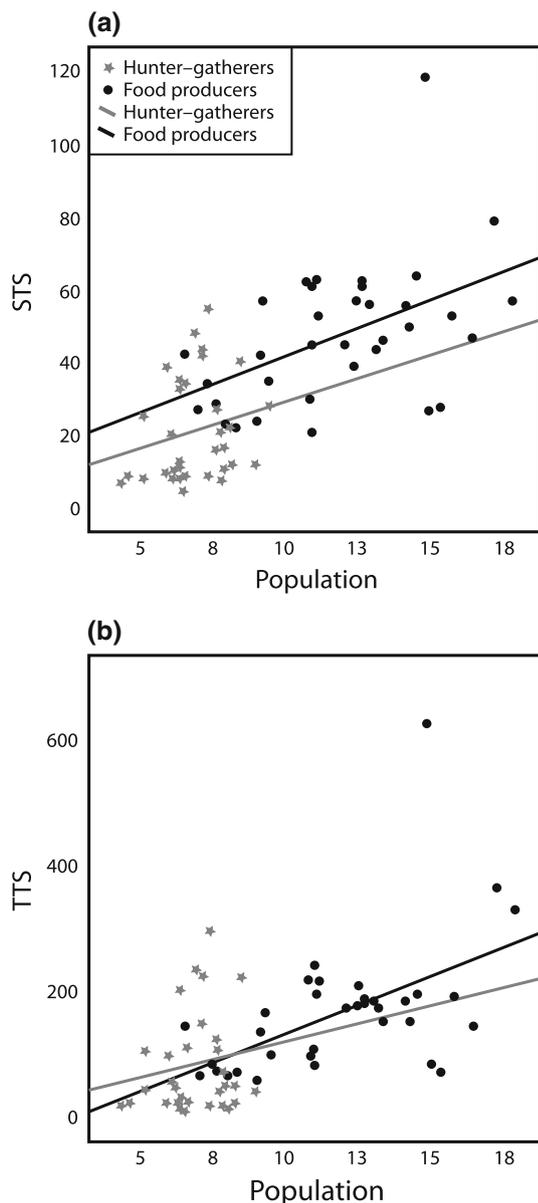


Fig. 4 The relationship between population size (log-normal) and **a** the number of different tool types (STS) and **b** the complexity of the tools as measured by the number of technounits (TTS) used by hunter-gatherer groups and food-producing groups

The niche-construction activities of farmers often seem to be more numerous and impactful than those of pastoralists. Given this, we might expect the differences between food producers and hunter-gatherers we have identified in the present study to also be replicated to some degree between farmers and pastoralists.

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