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Population ecology

Hunter–gatherers have less famine than agriculturalists

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The idea that hunter–gatherer societies experience more frequent famine than societies with other modes of subsistence is pervasive in the literature on human evolution. This idea underpins, for example, the 'thrifty genotype hypothesis'. This hypothesis proposes that our hunter–gatherer ancestors were adapted to frequent famines, and that these once adaptive 'thrifty genotypes' are now responsible for the current obesity epidemic. The suggestion that hunter–gatherers are more prone to famine also underlies the widespread assumption that these societies live in marginal habitats. Despite the ubiquity of references to 'feast and famine' in the literature describing our hunter–gatherer ancestors, it has rarely been tested whether hunter–gatherers suffer from more famine than other societies. Here, we analyse famine frequency and severity in a large cross-cultural database, in order to explore relationships between subsistence and famine risk. This is the first study to report that, if we control for habitat quality, hunter–gatherers actually had significantly less—not more—famine than other subsistence modes. This finding challenges some of the assumptions underlying for models of the evolution of the human diet, as well as our understanding of the recent epidemic of obesity and type 2 diabetes mellitus.

1. Introduction

The idea that our hunter–gatherer ancestors frequently experienced periods of famine or food shortages is pervasive across the field of human biology, palaeoanthropology and evolutionary psychology and is increasingly influential in the field of evolutionary medicine. This idea informs theoretical models in these disciplines ranging from life-history theory in biology to rational choice theory in economics [1–4]. Very few hunter–gatherer societies still exist as they did traditionally, as distinct genetic or cultural groups. This makes directly testing for the 'thrifty' genotype or phenotype across contemporary hunter–gatherer populations effectively impossible and makes ethnographic data all the more important. While we cannot know for certain whether our ancestors faced frequent food shortages or famines, we can examine the evidence that food insecurity characterizes the hunter–gatherer lifestyle generally. To explore this premise, we analyse a large ethnographic cross-cultural database, which contains data on frequency and severity of famine in hunter–gatherer societies and agricultural societies. We specifically examine these data as they relate to two hypotheses: (i) hunter–gatherers suffer more famine, which has resulted in the thrifty genotype adaptation in humans and (ii) hunter–gatherers ethnographically described in the last century (since the mid-1800s) mostly lived in unproductive habitats because more powerful people had taken over better, more productive habitats.

The thrifty genotype hypothesis, proposed by Neel [5], suggested that our hunter–gatherer ancestors experienced frequent feast and famine cycles. Those with 'thriftier' genotypes stored calories in the form of fat more readily and were thus better able to survive and reproduce. This hypothesis is one

Table 1. Famine in warm-climate hunter–gatherers versus cold-climate hunter–gatherers (n1, sample of warm-climate hunter–gatherers ET $\geq$ 13; n2, cold-climate hunter–gatherers ET $<$ 13).

variable	n1	n2	*U*	*p*
ordinary nutritional conditions and endemic starvation	11	14	64.5	0.501
occurrence of short-term starvation	18	15	125.0	0.735
occurrence of seasonal starvation	18	15	107.5	0.325
occurrence of famine	19	14	47.5	0.001** warm lower
severity of famine	16	9	41.5	0.084 warm lower
persistence of famine	17	7	19.5	0.009** warm lower
recurrence of famine	18	9	50.0	0.118
contingency of famine	13	6	9.5	0.007** warm lower

*Significant at 0.05, **significant at 0.01.

potential evolutionary explanation for the human predisposition to type 2 diabetes mellitus (T2DM) and obesity, but see Speakman [6] for other evolutionary explanations. Early evidence for the thrifty genotype hypothesis was presented as case studies from the Samoans, Pima Native Americans and Yanomami, because they experienced rapidly increasing levels of obesity after abandoning their traditional diets. However, these groups had actually been practising non-intensive agriculture (often horticulture with hunting) for a long time [7–9]. These early case studies actually support the idea that it was the 'westernization' of the diet, rather than the transition to agriculture that has caused the increased incidence of obesity and T2DM in these populations. Nevertheless, several recent diet books are based on the premise that humans are adapted to a diet that consists regularly of periods of feast and famine—and thus recommend periodic fasting [10,11].

While some groups privilege hunter–gatherers as evolutionary models (and embrace the feast and famine model), others believe that the hunter–gatherers described by ethnographers are of little utility for understanding ancestral human habitats or mode of subsistence. These researchers contend that hunter–gatherers documented in the last century occupy marginal habitats as a consequence of the greater power and development of the agricultural societies that have pushed them out of better habitats [12–14]. However, the only real test of habitat quality of hunter–gatherers (as measured by net primary productivity or NPP) [15–17] found that once Arctic groups were removed, hunter–gatherers' habitats were not less productive than intensive agriculturalists [18].

To the best of our knowledge, only two studies [19,20] have analysed famine and food shortages across different modes of subsistence. Neither of these studies considered habitat quality in their analyses, and neither found differences in the frequency of famine between hunter–gatherers and agriculturalists. However, approximately half of the hunter–gatherer societies in both studies are Arctic or subarctic, whereas very few agriculturalists live in the Arctic or subarctic. Thus, the agricultural versus hunter–gatherer societies in these samples are not comparable in terms of climate and habitat. Our study is the first to report that, controlling for habitat quality, hunter–gatherers have less famine than agriculturalists.

2. Material and methods

For this study, we use the standard cross-cultural sample [21], which consists of 186 cultural provinces of the world. It is primarily a sample of preindustrial societies coded from ethnographies conducted before the disappearance of many of these societies, including 36 hunter–gatherer societies with eight variables relating to famine (see the electronic supplementary material, appendix S1 for a detailed account of the sample and coding of variables) [21,22]. We define warm climate as having an effective temperature (ET) greater than or equal to 13°C, because 12.75 is defined as the plant dependence threshold [15]. ET is calculated from mean temperature of the warmest and coldest months and reflects the variability of the local climate [23]. We used a five year average of NPP estimates (2000–2004) from sensors on a NASA satellite (called MODIS) [24,25]. All statistics were performed with SPSS v. 19, except the principle components analysis, which was performed in R v. 3.0.0.

3. Results

We first compared warm-climate hunter–gatherers and cold-climate hunter–gatherers using Mann–Whitney *U*-tests (table 1). Warm-climate hunter–gatherers had a significantly lower frequency of famine than cold-climate hunter–gatherers in two variables: occurrence of famine and persistence of famine. Also, planning for famine (contingency of famine) was significantly more common in cold-climate hunter–gatherers than warm-climate hunter–gatherers (table 1).

We then compared hunter–gatherers versus agriculturalists, only using societies with ET $\geq$ 13° (see the electronic supplementary material, appendix S2*a*–*c* for a breakdown of famine in hunter–gatherers versus each other subsistence category e.g. horticulturalists, pastoralists and intensive agriculturalists). Mann–Whitney *U*-tests (table 2) showed the same pattern of significantly better background nutritional conditions in warm-climate hunter–gatherers. Three measures of famine frequency all showed significantly less frequent famine in hunter–gatherer societies than in agricultural societies: occurrence of famine, persistence of famine and recurrence of famine. Hunter–gatherers had significantly less frequent famine than agriculturalists (ET $\geq$ 13 in all societies) across five of the eight variables (see the electronic supplementary material, appendix S3 for descriptive statistics).

Table 2. Famine in warm-climate hunter–gatherers versus other warm-climate subsistence modes (n1, hunter–gatherers; n2, horticulturalists, pastoralists, intensive agriculturalists combined, all ET $\geq$ 13).

variable	n1	n2	*U*	*p*
ordinary nutritional conditions and endemic starvation	14	64	298.5	0.039* hunter–gatherers lower
occurrence of short-term starvation	15	114	820	0.717
occurrence of seasonal starvation	15	113	726.5	0.349
occurrence of famine	14	114	417	0.001** hunter–gatherers lower
severity of famine	9	71	214.5	0.088 hunter–gatherers lower
persistence of famine	7	67	100.5	0.008** hunter–gatherers lower
recurrence of famine	9	85	226	0.013** hunter–gatherers lower
contingency of famine	6	69	55.5	0.002** hunter–gatherers lower

*Significant at 0.05, **significant at 0.01.

Table 3. ANOVA famine in warm-climate hunter–gatherers versus other warm-climate subsistence modes.

variable	n1	n2	*F*	*p*	power
ordinary nutritional conditions and endemic starvation	14	18	21.6	0.015* hunter–gatherers lower	0.705
occurrence of short-term starvation	15	39	0.87	0.356	0.150
occurrence of seasonal starvation	15	39	2.3	0.136	0.319
occurrence of famine	14	38	14.1	0.000** hunter–gatherers lower	0.957
severity of famine	9	21	3.2	0.087 hunter–gatherers lower	0.402
persistence of famine	7	27	7.6	0.010** hunter–gatherers lower	0.763
recurrence of famine	9	33	6.2	0.017* hunter–gatherers lower	0.683
contingency of famine	6	25	11.6	0.002** hunter–gatherers lower	0.907

*Significant at 0.05, **significant at 0.01.

Two measures of periodic famine were not significantly different between hunter–gatherers and non-hunter–gatherers (occurrence of short-term starvation and occurrence of seasonal starvation). This is because neither warm-climate hunter–gatherers nor agriculturalists experience frequent or regular bouts of seasonal or short-term starvation (see the electronic supplementary material, table S4 for an analysis of famine by societies within a particular NPP range).

We then compared hunter–gatherers to agriculturalists, but controlled for habitat quality. We first performed a principal components analysis on our habitat variables (NPP and ET) to control for colinearity ($r = 0.599$, $p < 0.001$, $n = 180$). We then used that first principal component as a single control variable for habitat quality in an ANOVA comparing famine rates in hunter–gatherers versus agriculturalists (table 3). In this analysis, the same five of the eight variables were significantly lower in hunter–gatherers than in agriculturalists. We included *post hoc* power estimates for better assessment of type II errors stemming from our necessarily small sample size of hunter–gatherer societies.

4. Discussion

Warm-climate hunter–gatherers actually experience fewer famines than societies with other modes of subsistence. This is an important result, because these findings do not support the association between frequent famine and hunter–gatherer lifestyles. It may suggest that if there is a 'thrifty genotype', it has a more recent origin and may have swept human populations since the advent of agriculture, as suggested by Prentice *et al*. [26]. While few people would assert that any people of today live exactly as early humans did, our results provide some evidence that hunter–gatherers documented over the last century were not all living in strictly marginal habitats. By contrast, by definition cold-climate hunter–gatherers live in marginal habitats. As a consequence, cold-climate hunter–gatherers have many derived cultural adaptations to cope with more frequent food shortages, such as infanticide of females, food storage, long-distance migrations, marine hunting technology and complex trade networks [27–28]. These adaptations should be considered carefully, as coping with food shortages may have played an important role early in the evolution of agriculture. Nevertheless, cold-climate hunter–gatherers are not the best models for most of human evolutionary history, as they occupy a relatively recent, narrow niche [29].

Although in good years agriculturalists may reap far more calories per unit of land than hunter–gatherers, hunter–gatherers can and do move in times of drought or flood—something that agricultural populations are limited in doing [16]. That said, few traditionally living, non-industrialized agriculturalists (e.g. horticulturalists, pastoralists or early intensive agriculturalists societies) suffer the rates of obesity or T2DM seen in western, industrialized nations. Human food preferences are for the most calorically dense foods (fat and sugar), which were in short supply in every mode of subsistence until relatively recently in human evolutionary history.

One aspect of our hunting and gathering past that may contribute to the current obesity epidemic is that simple hunter–gatherers have been described as 'immediate return' [30], that is, they make use of resources immediately and completely rather than waiting, storing or cultivating. It would not have been adaptive for simple hunter–gatherers to ration food intake or to pass up calorically dense foods. This explanation does not require a 'thrifty genotype', but rather a genetic or cultural adaptation that causes 'immediate return' behaviour with respect to food resources paired with a preference for foods that are high in calories. While this once would have been an adaptive trait, with greater access to calorically dense foods it is now a liability.

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