Abstract only

# "Civilisation" and the thrifty genotype

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Over the past 30 years, Neel's "thrifty" genotype concept has received much support from investigators interested in diabetes and the health consequences of changing from traditional to more westernised diets. In many cases, the "thrifty" genotype was interpreted in a local context by people working in a limited geographical area. It is increasingly clear, however, that the "thrifty" genotype effects are present in populations throughout the world. In fact, there is a good chance that the majority of the world's population do indeed carry the "thrifty" genotype, although since a westernised diet is far from universally available, the negative consequences of the genotype have yet to be expressed.

Diabetes, obesity, and other diseases may indeed be the price paid for civilisation in the context of a "thrifty" genotype. We point out, however, that the negative consequences of the "thrifty" genotype seen in modernising populations with westernised diets today do not necessarily provide an explanation for why the "thrifty" genotype disappeared from some populations (mostly European and European-derived) in the past. Our assumption is that given its broad distribution today, the "thrifty" genotype was once universal in human populations; the problem then, is to explain the evolution of the "non-thrifty" genotype in those populations in which it is no longer seen.

The idea that "civilisation" has worked to select out (or relax selection for) the "thrifty" genotype is untenable, although this is the view accepted implicitly by most workers in the field. To be fair, it should be pointed out that they are mostly concerned with explaining the presence, not absence, of diabetes and other diseases in certain populations, and the "thrifty" genotype serves this purpose.

There are several reasons to not accept the face validity of the idea that civilisation has selected out the "thrifty" genotype:

1) the notion that agricultural populations are less susceptible to food stress and famine than hunter-gatherer populations is quite contentious; in fact, the conventional wisdom has been at various times that agricultural populations are more susceptible to food shortages and are more prone to famine;
2) the dietary history of Europe, the part of the world where the "thrifty" genotype is least common, indicates that most people, most of the time lived under conditions of food stress; we will briefly review data pertaining to the Roman, Anglo-Saxon, and Medieval periods;
3) agricultural populations in New World civilisations probably had diets that were no worse than those found in their Old World counterparts; the Old World diet of today and of the past 200 years or so is, of course, one greatly modified by the introduction of plants from the New World.

In summary, the idea that civilised populations have provided a flush dietary environment for thousands of years is insupportable, and opportunities for the expression of negative sequelae of the "thrifty" genotype in European populations, for example, have occurred only relatively recently (less than 100 years). In other words, all things being equal, a typical consumer in the year 1650 say, no matter where he or she lived, would have benefited more from possessing a "thrifty" genotype, than from not possessing it. But given that today most European populations would appear to have a "thrifty" genotype frequency of less than 10% (and some much less), and the opportunities for strong selection against the genotype have been relatively rare over the past few hundred years, how can we explain the high frequency of the "non-thrifty" genotype in these populations? We see four possible explanations:

1. *The traditional explanation.* It is absent in Europe because they have had the benefits of a westernised diet for centuries and paid the price for civilisation long ago. As discussed above, there are problems with this explanation.
2. *Chance.* The "thrifty" genotype may have been lost in these populations due to a genetic bottleneck at some point or some other random evolutionary factor. This seems unlikely given that there are good reasons to expect that it would be selected for; also it is difficult to test.
3. *Social factors.* In a complex, large-scale society, access to food and especially quality food may be influenced by factors far different from those seen in a hunter-gatherer society. After a period of food shortage, who

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comes out best in the end may depend less on metabolism and more on social status and economic power. This could lead to a relaxation of selection for the "thrifty" genotype, but it seems unlikely that it could have played a major role given that elites in a society are by definition rare.

4. *Interaction with another specific nutritional factor.* In most formulations of the "thrifty" genotype concept, the characterisation of the "civilised diet" is usually done in very general terms. However, particular dietary factors could interact with the "thrifty" genotype making it far less beneficial to its possessors. We suggest one such dietary factor- lactose.

Besides the "thrifty" genotype, Europeans are out-of-step with most of the rest of the world in that they (or at least most of them) can digest lactose (the sugar found in mammalian milk) throughout their lifetimes, and do not turn off the production of the enzyme lactase at weaning as most normal mammals do. Selection for this ability is clearly associated with the herding of cows and other milk-producing animals, who provide a good, potentially steady nutritional source. More critically in the European context may be that lactose facilitates the absorption of calcium, and in high-latitude areas with low sunlight, acts as a substitute in calcium metabolism for vitamin D, which is normally synthesised with exposure to sunlight. Consumption of lactose therefore protects against rickets and other diseases or conditions associated with low calcium intake.

We have looked at more than 40 populations for which data are available concerning both lactose absorption rates and type II diabetes rates. Overall, there is an absence of populations exhibiting high lactose absorption rates and high diabetes rates. For the total sample, the (negative) correlation between lactose absorption and diabetes rate is significant although not particularly high. If we remove from consideration populations that were not likely to have had westernised diets (eg, in PNG, Africa, perhaps in Northern Canada) at the time of diabetes assessment, then the correlation is much stronger. Further, although the data for the Pima and Papago are in the "right" direction (ie, very low lactose absorption rates and high diabetes rates), their inclusion in the data set reduces the correlation as derived from the rest of the world's populations, since their diabetes rates are almost double that for any other population. In summary, diabetes rates and lactose absorption rates are highly negatively correlated in populations with a westernised diet.

Why should this be the case? At a metabolic level, there is no direct link between the two. Whether or not one produces lactase in adulthood has nothing directly to do with how one deals with glucose in blood. In individuals with type II diabetes, there is no correlation with lactose absorption ability. However, studies indicate that although lactose is a disaccharide (glucose-galactose; the galactose is converted to glucose in the liver), it is absorbed very quickly into the bloodstream and is metabolised essentially as a simple sugar. Furthermore, the insulin response to lactose in milk is five times higher than would be expected, and approaches that for straight glucose. If there is a primary difference between westernised and traditional diets, it is the substitution of simple sugars in the diet in place of complex carbohydrates.

Since the correlation between lactose absorption and the "non-thrifty" genotype cannot be explained physiologically, then perhaps an historical explanation is worth considering. The consumption of lactose was selected for in certain populations, perhaps due to the combined effects of milk availability, high latitude, and the facilitation of calcium uptake. Individuals who consume milk do have an increased simple sugar load relative to that typically seen in a hunter-gatherer diet. Thus the ability to consume lactose constituted a change in the environment in which the "thrifty" genotype was expressed. Although there was not necessarily an overall increase in the quality of the diet or in calories available in these populations, there was a dietary stress that could have lead to selection against the "thrifty" genotype, especially if the short-term benefits of consuming lactose (which would have a greater influence in early life) outweighed the long-term benefits of the "thrifty" genotype.