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Protein Selection and Avoidance Strategies of Contemporary and Ancestral Foragers: Unresolved Issues [and Discussion]

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Protein selection and avoidance strategies of contemporary and ancestral foragers: unresolved issues

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SUMMARY

During seasonal or inter-annual periods of food shortage and restricted total calorie intake, ethnographically and ethnohistorically documented human foragers, when possible, under-utilize foods that are high in protein, such as lean meat, in favour of foods with higher lipid or carbohydrate content. Nutritional studies suggest that one reason for this behaviour stems from the fact that pregnant women, particularly at times when their total calorie intake is marginal, may be constrained in the amount of energy they can safely derive from protein sources to levels below about 25% of total calories. Protein intakes above this threshold may affect pregnancy outcome through decreased mass at birth and increased perinatal morbidity and mortality. This paper briefly outlines the evidence for the existence of an upper safe limit to total protein intake in pregnancy, and then discusses several facets of the issue that remain poorly understood. The paper ends by raising two basic questions directed especially toward specialists in primate and human nutrition: is this protein threshold real and demographically significant in modern human foraging populations? If so, does an analogous threshold affect pregnant female chimpanzees? If the answer to both of these questions is yes, we can then begin to explore systematically the consequences such a threshold might have for the diet and behaviour of early hominids.

1. INTRODUCTION

The origins of our earliest hominid ancestors, and the factors that led to that origin, have attracted the attention of scholars since the time of Darwin. The diet of these early bipeds has always been of prime interest, and quite understandably attention has most often focused on the role of hunting and meat eating (Gordon 1987; Hill 1982). The reasons for this focus are obvious. Animals are large packages of high-quality protein as well as calories. They are also among the most obvious high-quality food sources in the open semi-arid savannas of sub-Saharan Africa, where our earliest ancestors are believed to have first arisen (Klein 1989). In addition, consistent with expectations drawn from optimal foraging theory, animals are highly ranked among the food choices of modern hunters and gatherers, peoples who provide the inspiration for many of our current models about hominid origins and evolution (e.g. Binford 1978; Bunn *et al.* 1988; O'Connell *et al.* 1988; Winterhalder & Smith 1982). Moreover, even our closest living primate relatives, the chimpanzees, are now known to hunt and consume meat on a fairly regular basis, a strong argument that the common ancestors of both chimpanzees and humans probably also did so (Teleki 1981; Wrangham 1977). Finally, stone tools and fossil animal bones – the latter commonly displaying distinctive cut-marks produced when a carcass is dismembered and stripped of edible flesh with a sharp-edged stone flake – are found together on many Plio-Pleistocene archaeological sites, convincing proof that by at least 2.0 to 2.5 Ma before present (BP) these early hominids did in fact eat meat (Bunn 1986; Isaac & Crader 1981). In contrast, plant remains are absent or exceedingly rare on these ancient sites and their role in early hominid diet, therefore, can only be guessed on the basis of their known importance in contemporary forager diets, as well as their potential availability in Plio-Pleistocene environments (for example, see Peters *et al.* (1984); Sept (1984)). Thus few today doubt that early hominids ate meat, and most would agree that they probably consumed far more meat than did their primate forebears. Instead, most studies nowadays focus primarily on how that meat was procured: that is, whether early hominids actively hunted animals, particularly large-bodied prey, or scavenged carcasses that had already been partly consumed and abandoned by other predators (see, for example, Binford (1981); Blumenschine (1987, this symposium); Bunn (1986); Potts (1982); Shipman (1983)).

I fully concur with the view that meat was a regular and important component of early hominid diet. For this the archaeological and taphonomic evidence is compelling. Instead, what concerns me is how much of their energy, on average, was actually obtained from meat. And was the amount of meat in early hominid diet constrained just by their lack of adequate technological and organizational means for procuring large and often dangerous animals, or were there also intrinsic nutritional factors that, at least seasonally, may have limited the extent to which early hominids could rely on meat for calories, independent of the quantity that was potentially available on the landscape? Although there seems little doubt that technological and organizational constraints were im-

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portant, there is growing evidence to suggest that nutritional constraints may also have been significant. As these nutritional arguments have been presented in detail elsewhere (Speth 1983, 1987, 1989, 1990; Speth & Spielmann 1983), I will only briefly outline them here, and use the remainder of this paper as an opportunity to identify specific critical facets of this 'excess protein' argument that remain poorly understood and that require for their solution further input from specialists in the fields of human and primate nutrition.

2. THE 'EXCESS PROTEIN' ARGUMENT

Whereas meat can obviously provide calories as well as protein, there is an upper limit to the total amount of protein (plant and animal combined) that one can safely consume on a regular basis. This limit – best expressed as the total number of grams of protein per unit of lean body mass that the body can safely handle – is about 300 g or roughly 50% of one's total calories under normal, non-stressful conditions. This means that, on average, at least half of one's daily energy must be derived from non-protein sources, either fat, oils, or carbohydrates. Protein intakes above this threshold, especially if they fluctuate sharply from day to day, may exceed the rate at which the liver can metabolize high levels of amino acids, and the body can synthesize and excrete urea, leading to impairment of liver and kidney function, as well as other potentially serious health consequences, and perhaps even death (Cahill 1986; McArdle *et al*. 1986; McGilvery 1983; Miller & Mitchell 1982; Speth 1990; Whitney & Hamilton 1984). Clearly, this is a large amount of protein, far in excess of the levels normally seen in the diets of ethnographically documented hunters and gatherers, with the notable exception of the Eskimos, whose all-meat diet often led to protein intakes that approached 40–45% of calories (see Speth (1989) and references therein). Thus, if this were the only limit, it would be of little concern to us in reconstructing early hominid diet, as virtually no one postulates regular per capita protein intakes anywhere near this magnitude some 2.0 to 2.5 Ma BP in the Plio-Pleistocene.

However, there is a small but growing body of evidence suggesting that the safe upper limit to total protein intake for pregnant women may, in fact, be much lower and, if substantiated by further nutritional research, could be much more relevant to our understanding of the food choices of modern hunters and gatherers and perhaps early hominids as well. A woman's protein needs increase during pregnancy, and these requirements must be met in order for her to produce a viable, healthy offspring. Extremely low maternal protein intakes, below about 5–6% of calories, may be detrimental to the health of the foetus (Martorell & Gonzalez-Cossio 1987; National Academy of Sciences 1985; Winick 1989). As maternal protein intakes increase above this minimum threshold, mass at birth and foetal health generally improve. However, several recent studies suggest that supplementation of maternal diets with protein in excess of about 25% of total calories (i.e. above about 100–150 g), even in diets that are otherwise balanced and calorically adequate, may lead to declines, not continued gains, in infant birth mass, and perhaps also to increases in perinatal morbidity and mortality and even cognitive impairment. Premature infants appear to be most vulnerable to high maternal protein supplements (Rush *et al.* 1980; Rush 1982, 1986, 1989; Sloan 1985; Worthington-Roberts & Williams 1989, p. 88).

Birth masses may also decline when the mother's total calorie intake is restricted (Brooke 1987; Lechtig *et al.* 1978; National Academy of Sciences 1985; Wray 1978), but the decline appears to be most extreme when her diet is both low in energy and high in protein (Martorell & Gonzalez-Cossio 1987; Rush 1989; Winick 1989). This is illustrated, for example, by data from Motherwell, a small community in Scotland, where for 30 years pregnant women were advised to consume a comparatively low energy diet consisting of about 1500 kcal and 85 g of protein (*ca.* 23% of total calories). Birth masses of Motherwell infants over this period were, on average, about 400 g lower than those of infants born in Aberdeen during the same period (Kerr-Grieve *et al.* 1979; Winick 1989). This striking decline in average mass at birth rivals the declines seen during wartime famines (Kerr-Grieve *et al.* 1979; Rush 1989).

The relevance of this threshold to the present discussion is that for a major segment of a foraging population – the pregnant women – as much as 70% of their daily calories may have to be obtained from non-protein sources. During much of the year this may pose little or no problem, as women traditionally do most of the plant food collecting in these groups, a division of labour that normally assures them access to ample supplies of carbohydrates and oils (Lee & DeVore 1968). But during seasonal or inter-annual low points in food availability (i.e. the late winter and spring in temperate and northern latitudes or the late dry season and early rainy season in more southerly latitudes), as edible wild plant foods become scarce, unreliable, or more costly in time or effort to procure, the pregnant females in particular may face an increasingly difficult task of maintaining adequate non-protein energy intakes (Speth 1983, 1989, 1990; Speth & Spielmann 1983). These recurrent seasonal or inter-annual resource low points, therefore, may become critical adaptive 'bottlenecks' (Wiens 1977) for hunters and gatherers, and their responses to these hold important clues to understanding the foraging behaviour and food choices of both modern and pre-modern human foragers.

3. UNRESOLVED ISSUES

(*a*) *Contemporary human foragers*

The preceding section outlined the basic framework of the 'excess protein' issue, looking in particular at the amount of protein that can be safely ingested by pregnant women. But there are many facets of this argument that remain poorly understood, and in this section I specifically focus on these aspects.

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First, the very existence of an upper limit to the amount of protein a pregnant women can safely consume on a regular basis remains controversial among nutritionists. Assessing the relationship between dietary protein intake and pregnancy outcome has been compounded by difficulties in obtaining reliable, quantitative data on the amount and nutritional composition of foods consumed by women over the course of their pregnancies, as well as by problems in controlling for differences among subjects, both before and during pregnancy, in factors such as height; body mass; overall health; the use of drugs, alcohol and cigarettes; economic status and level of education. As a consequence, many of the presently available studies suffer from flaws in research design and measurement precision (for a detailed review of prior research, see Rush (1989)).

Second, and perhaps more importantly, the actual mechanisms by which high dietary protein intakes impinge on the health and well-being of the developing foetus remain to be worked out (see Rush 1989; Sloan 1985).

Third, it is not yet clear whether high protein intakes are deleterious to the foetus throughout the course of a pregnancy or only during a particular trimester. Because the developing foetus is particularly susceptible to teratogenic substances during the first trimester, the period of embryonic organogenesis, this may also be the time in a pregnancy when excessive protein intakes would be most problematic. Interestingly, this is also the trimester in which 'pregnancy sickness', as well as intense food aversions and food cravings, are most in evidence and, in cross-cultural studies, meat and meat odours are among the most common and widespread aversions, whereas carbohydrates are among the most common cravings (Dickens & Trethowan 1971; Hook 1978; Profet 1989; Tierson *et al.* 1985). One also finds widespread and seemingly irrational food taboos and inequitable sharing practices among traditional hunter-gatherer and horticultural societies that effectively limit or block pregnant women from access to meat (Aunger 1991; Speth 1990; Spielmann 1989). Unfortunately, however, no one has yet examined these practices to determine whether they are in effect throughout the course of a pregnancy or only during a particular trimester. Despite the many uncertainties, these factors together provide very tentative evidence that high levels of protein may be deleterious to the foetus primarily or exclusively during the first trimester of pregnancy.

Fourth, if high protein intakes are, in fact, detrimental to pregnancy outcome, how did pregnant women in traditional Eskimo and other northern latitude foraging societies cope with this problem? These peoples commonly consumed average daily protein intakes in excess of 25% of total calories and levels on the order of 40–45% were not uncommon (e.g. Draper 1977; see also discussion and references in Speth (1989, 1990)). What did pregnant women in arctic and subarctic environments consume to avoid high protein intakes? Unfortunately, the existing dietary and nutritional literature for these groups is extremely sketchy, providing little quantitative data on diet broken down by sex, and none according to reproductive status. As a consequence, I can offer only a few tentative suggestions here that may serve as working hypotheses for future nutritional research among these groups. For example, pregnant women probably consumed greater proportions of fat in their diet than did other adults (H. V. Kuhnlein, personal communication). They also appear to have augmented the meagre carbohydrate component of their diet by collecting berries and other terrestrial plant foods (see, for example, Eidlitz (1969); Giffen (1930); Nickerson *et al.* (1973)), as well as kelp washed up on the beach or harvested through the ice in winter, by extracting the fat-rich fly larvae from the hides of caribou and reindeer, and by consuming the partly digested stomach and rumen contents of mammalian and avian herbivores (H. V. Kuhnlein, personal communication; Eidlitz 1969).

The fifth and final issue concerns the significance of the protein threshold in terms of its actual or potential demographic impact on foragers. What is the relationship between excessive protein consumption by a pregnant woman, particularly during periods of reduced overall energy intake, and the level of perinatal morbidity and mortality? Anthropologists have long suspected that seasonally marginal calorie intakes play an important role in the low completed fertility of extant foraging populations such as the Kalahari San or Bushmen and the Australian Aborigines (see, for example, Howell (1979, 1986); Lager & Ellison (1987)). The arguments presented here suggest that high dietary protein intakes during these seasonal 'bottlenecks' may also play a role.

(*b*) *Living higher primates*

Up to this point, I have been concerned with the existence and nature of a dietary protein threshold among pregnant women in contemporary human foraging populations. Obviously, even if the threshold proves to be both real and demographically significant in modern humans, this in no way shows that such a threshold also existed in early hominids. This is clearly a much more difficult problem to deal with. Although less than ideal, a common way of approaching this sort of problem is to see if an analogous phenomenon exists in our closest living primate relatives, the chimpanzees. If the answer is yes, this would suggest that a protein threshold was also present in the common ancestor of both chimpanzees and modern humans and hence probably also in Plio-Pleistocene hominids. Thus, the next step is to raise the same issues concerning chimpanzees that were raised above for contemporary foragers: do female chimpanzees face seasonal or interannual shortfalls in resource availability and total energy intake (see, for example, Wrangham (1975, 1977) for evidence of substantial seasonal body mass fluctuations in chimpanzees)? Does the absolute amount and proportional contribution of protein in their diet increase during these stressful periods, as their principal fruits (generally comparatively low-protein foods) become less abundant or accessible (e.g.

Wrangham 1975)? Is there any evidence for the existence of a protein threshold in pregnant chimpanzee females above which pregnancy outcome is negatively impacted? If so, what proportion of total calories can safely come from protein? Does the threshold persist over the entire course of the pregnancy or only during a particular trimester? What, if any, is the potential demographic impact of excessive protein intakes? And how do female chimpanzees cope behaviourally and dietarily with the threshold? These are issues clearly in need of explicit investigation by specialists in primate and human nutrition.

4. SUMMARY AND CONCLUSIONS

This paper raises many more questions than it answers. To summarize briefly, there is a growing body of nutritional evidence to suggest that pregnant women may face a dietary constraint, at least during the first trimester of pregnancy, in which their protein intake (plant and animal combined) must be kept below about 25–30% of their total daily energy intake, to protect the health and well-being of the developing foetus. This constraint may be most critical to forager women during seasonal or inter-annual periods of reduced overall food availability. For most modern human populations, particularly those in western industrial nations, protein intakes rarely approach this threshold and it is probably therefore of little or no significance. Among ethnographically and ethnohistorically documented foragers, however, protein intakes approaching and even exceeding this level are actually fairly common, especially during the late winter – spring in temperate and northern latitudes and the late dry season – early rainy season in the tropics and sub-tropics. At such times, foragers are faced with reduced overall energy intakes and they may be forced to rely increasingly on foods, such as seeds, nuts and meat, that are protein-rich but often low in fat. For pregnant females, such times may place the developing foetus at increased risk. This paper basically seeks further input from nutritionists and primatologists to help answer two basic questions: is this protein threshold real and demographically significant in modern human foraging populations, and does a similar threshold affect pregnant female chimpanzees? If the answer to both of these questions is yes, we can then begin to explore systematically the implications such a threshold might have for the diet and foraging strategies of early hominids.

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Discussion

E. M. WIDDOWSON (*9 Boot Lane, Barrington, Cambridge, U.K.*). Dr Speth's paper raises some interesting questions about protein metabolism. We did an experiment on rats many years ago (Cabak *et al.* 1963) in which some were fed a low-protein diet in measured amounts, but they did not eat enough of it to maintain body mass. Others had a high-protein diet (48 % protein) in restricted amounts so that their mean mass remained the same as those on the low-protein diet. A third group had a normal rat diet and they served as the controls. A third of the animals having the high-protein, restricted-energy diet died during the experiment, but none of the others. Those that remained had high concentrations of urea and low concentrations of glucose in their blood. Does Dr Speth think a high-protein diet exerts a harmful effect primarily when the energy intake is restricted?

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O. T. Oftedal (*Smithsonian Institution, Washington D.C., U.S.A.*). I agree with Dr Widdowson that the relationship between protein excess and energy requirements may be particularly important. The examples of polar and Western explorers that Dr Speth cites were often under conditions of extreme energy demand due to cold exposure or severe physical exhaustion. Under such circumstances, low-fat diets (i.e. lean tissues) may well fail to meet energy demands despite deamination and catabolism of amino acids as an energy source. In subfreezing conditions explorers might also have difficulty obtaining enough melted water to sustain urea excretion via urine formation. I suspect that primates in arid conditions that do not have access to drinking water may be limited in their ability to use high protein foods due to water shortage. Dr Speth might also want to examine the literature on high-protein diets for dogs as this has been somewhat of a controversial issue, at least in the United States.

J. D. Speth. All of the studies I am aware of point to the combination of high dietary protein intake together with low total energy intake as potentially the most problematic situation. Thus, in the case of human foragers or hunter-gatherers, high protein intakes are most likely to pose a problem primarily at times of year when their total food intake is restricted, in other words, during the winter and spring in more northerly latitudes or during the dry season in the tropics and subtropics. At such times the most vulnerable segment of the population may be the pregnant women.

R. A. Foley (*Department of Biological Anthropology, University of Cambridge, U.K.*). In view of the fact that the occurrence of 'protein starvation' seems specific to high-latitude populations and individuals in periods of winter, could it be that this phenomenon is associated with high energy expenditure due to the thermoregulatory problems of living at very cold temperatures?

J. D. Speth. Although 'protein starvation' has been mentioned most commonly and explicitly in the ethnographic and explorer literature of the northern latitudes, the phenomenon is by no means restricted just to these parts of the world. For example, by the end of the dry season in the tropics and subtropics, foragers may be faced with marginal or inadequate total energy intakes, perhaps exacerbated by heavy work loads, forcing them to obtain the bulk of their energy from fat-depleted game. Under these circumstances, high protein intakes pose the same problem they do in the arctic and subarctic. In fact, shortage of water may make the problem even more acute.

P. Van Soest (*324 Morrison Hall, Cornell University, New York, U.S.A.*). High protein consumption had been a feature of some dietary fads in the United States designed to promote weight loss. This is regarded as hazardous by many doctors who point out the dangers of uremic poisoning in subjects with liver or kidney disease. High-protein diets may mean diets low in both carbohydrates or fat. Low carbohydrate plus fat sets the need for gluconeogenesis from amino acids to maintain body glucose needs. The production of NH_3 from this process plus that from protein used for energy may overload the liver capacity for urea synthesis. NH_3 is extraordinarily toxic to tissue cells. One theory of colon cancer is based on this concept. The cost of energy to detoxify one gram of ammonic nitrogen is about 45 kJ. This is a high energy cost. Ruminants are very sensitive to overfeeding of protein.

The calcium-phosphorous ratio of meat is about 1:15, whereas requirements are 2:1. Thus meat is grossly deficient in calcium and excessive in phosphorus. A nutrition problem for lions and cats in zoos, and dogs fed high-meat diets, is the occurrence of rickets.