Energy Source, Protein Metabolism, and Hunter–Gatherer Subsistence Strategies

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During late winter and spring, hunter–gatherers in temperate, subarctic, and arctic environments often relied on diets that provided marginal or inadequate caloric intakes. During such periods, particularly when stored food supplies dwindled or were used up entirely, lean meat became the principal source of energy. Nutritional problems associated with high-protein, low-energy diets are discussed. These problems include elevated metabolic rates, with correspondingly higher caloric requirements, and deficiencies in essential fatty acids. The relative benefits of adding fat or carbohydrate to a diet of lean meat are evaluated in light of the protein-sparing capacities of these two nutrients. Experimental data indicate that although both enhance high-protein, low-energy diets, carbohydrate is a more effective supplement than fat. Given the nutritional inadequacies of a lean-meat diet, the paper concludes with a discussion of alternative subsistence strategies that increase the availability of carbohydrate or fat at the critical time of year.

INTRODUCTION

The problem of seasonal and long-term nutritional stress has received much attention in recent anthropological and archaeological research (e.g., Newman 1975; Wetterstrom 1976; Cox 1978; Hitchcock 1978; Laughlin and Brady 1978; Dirks 1980; Minnis 1981). Thus far, the focus of most studies has been on the effects of, and responses to, inadequate calorie and/or protein intake in contexts where the diet consists predominantly of carbohydrate and low levels of protein. Here we propose to examine the reverse situation: recurrent periods of moderate to severe

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caloric stress in contexts where carbohydrate intake is low, and where protein intake may at times provide as much as 85 or 90% of the total calories. In the following discussion we show that (1) many hunter—gatherers recurrently relied on protein as a principal source of calories at certain times of the year, and (2) such reliance could lead to marginal or inadequate energy intake and other nutritional deficiencies in the hunter—gatherer diet. We examine the causes of these deficiencies and suggest subsistence strategies that would buffer hunter—gatherers against such potential periods of stress.

Our concern is with periods of high *lean* meat (i.e., high protein) consumption, when carbohydrates and animal fat would have been scarce or unavailable to hunters and gatherers as sources of calories. We became interested in this situation when our research on late prehistoric and early historic adaptations in the Southern High Plains indicated that hunters and gatherers were adopting a variety of subsistence strategies in the late winter and spring that avoided the consumption of lean bison meat (Speth 1983; Spielmann 1982). Fat-depleted animals were avoided and lean cuts of meat were abandoned by hunters at spring-season kill sites despite the facts that spring was generally a time of food scarcity in the region and bison was the only readily available subsistence resource. To better understand this seemingly paradoxical subsistence behavior, we turned to the nutritional literature to determine if there were in fact serious problems associated with high lean meat intake that might compel hunter—gatherer populations to adopt alternative subsistence strategies.

While our original concern was with hunters and gatherers in temperate grassland environments, this discussion also applies to hunter—gatherer populations in other sharply seasonal environments (e.g., inland arctic, subarctic, northern deciduous forest). In environments such as these, late winter and spring were often times of recurrent food shortage, hunger, weight loss, and starvation (for a few ethnographic examples, see Anastasio 1972; Bean 1972; Goldschmidt 1951:417; Steward 1938:19—20, 27, 46; Kelly 1964:22; Hodge 1907:51—52; Silberbauer 1981:274—275; Gusinde 1961:284; Piddocke 1965; Balikci 1968; Grinnell 1972:258; Hayden 1981:414—415 and references therein; see also Wilmsen 1978; Truswell and Hansen 1968; Shephard 1974:287, 1980:329; Rode and Shephard 1973:172; Høygaard 1941:68 for quantified examples of seasonal weight loss in hunter—gatherers). Recent studies in paleopathology document similar periodic nutritional stress in populations of prehistoric hunters and gatherers, including those in so-called "nonmarginal" habitats (see Huss-Ashmore *et al.* 1982:434—450 and references therein; Buikstra 1976, 1981; McHenry 1968; McHenry and Schulz 1978; Cassidy 1972).

In late winter and spring, reliable alternative resources such as small mammals, fish, and stored plant foods often became scarce or unavailable, and hunter−gatherers had to rely on large ungulate species for a major part of their diet. It is precisely at this time of year, however, that a diet composed largely or entirely of ungulate meat may lead to caloric and other nutritional deficiencies because the ungulates themselves are experiencing nutritional stress and becoming fat-depleted.

UNGULATE CONDITION AND ITS CONSEQUENCES FOR HUNTER−GATHERER DIETS

Male ungulates may lose up to 10 or 15% of their body weight during the fall rut due to high energy expenditure and reduced forage intake. As a consequence, they often enter winter in comparatively poor condition. If nutritional shortages occur during winter, their body-fat reserves begin to be depleted and their overall condition declines through late winter into spring. Females often enter winter with more reserves than males; their condition therefore may be somewhat better in early spring. Later in the spring, however, pregnant or lactating females decline in condition to a level below that of males. Thus, both sexes are in poorest condition in the spring, and both may have become severely fat-depleted (Allen 1979; Anderson *et al.* 1972; Nordan *et al.* 1968; Peterson 1977; Pond 1978; Riney 1955; Sinclair and Duncan 1972; Binford 1978:40).

With plant foods largely unavailable in this season, and in situations where stored carbohydrate reserves were nearly or entirely exhausted, the hunter−gatherer diet would have been composed mainly of protein with whatever fat remained in the meat. As the following ethnographic and historic accounts document, high reliance on lean meat can lead to serve nutritional stress. For example, Stefansson has described the deleterious effects of subsisting on the lean meat of rabbits in northern latitudes. These animals are notoriously low in body fat, and reliance on them for food leads to a condition known as "rabbit starvation."

> If you are transferred suddenly from a diet normal in fat to one consisting wholly of rabbit you eat bigger and bigger meals for the first few days until at the end of about a week you are eating in pounds three or four times as much as you were at the beginning of the week. By that time you are showing both signs of starvation and of protein poisoning. You eat numerous meals; you feel hungry at the end of each; you are in discomfort through distention of the stomach with much food and you begin to feel a vague restlessness. Diarrhoea will start in from a week to 10 days and will not be relieved unless you secure fat. Death will result after several weeks. (Stefansson 1944:234)

Observations similar to those of Stefansson are common in the ethno-

graphic literature. The following examples further illustrate the inadequacy, in northern latitudes, of a diet based on lean meat.

> The quantity of food consumed at one meal naturally varies according to the amount of fat it contains. Men and dogs will half-starve on a diet of lean caribou-meat, however plentiful, whereas half the quantity of blubbery seal-meat will satisfy their desires and keep them well nourished. (Copper Eskimo, Canada; Jenness 1923:100)

> If people had only rabbits at such times they would probably starve to death, because these animals are too lean. The same might be true if they could get only thin moose. People cannot live on lean meat alone, but if they have enough fat they can survive indefinitely. (Kutchin, Alaska; Nelson 1973:142)

There are many similar observations in the ethnohistoric literature, and these are by no means confined to the arctic. For example, Warren A. Ferris, while trapping in the Bear River Valley of Utah in 1830, made the following observations concerning the poor sustenance provided by lean buffalo.

> We killed here a great many buffalo, which were all in good condition, and feasted, as may be supposed, luxuriously upon the delicate tongues, rich humps, fat roasts, and savoury steaks of this noble and excellent species of game. Heretofore we had found the meat of the poor buffalo the worst diet imaginable, and in fact grew meagre and gaunt in the midst of plenty and profusion. But in proportion as they became fat, we grew strong and hearty. . . . (Phillips 1940:42)

Jedediah Smith led a group of trappers along the Klamath River in California in May 1828. According to Dale Morgan (cited in Allen 1979:457),

> . . . the party made only 3 miles on the 18th, which taxed their strength to the utmost. 'The men were almost as weak as the horses, for the poor [spring] venison of this country contained little nourishment.'

Finally, Randolph B. Marcy in the winter of 1857–1858 provided an illuminating comment regarding the inadequacy of a diet based on fat-depleted meat.

> We tried the meat of horse, colt, and mules, all of which were in a starved condition, and of course not very tender, juicy, or nutritious. We consumed the enormous amount of from five to six pounds of this meat per man daily, but continued to grow weak and thin, until, at the expiration of twelve days, we were able to perform but little labor, and were continually craving for fat meat. (Marcy 1863:16)

Of particular interest are frequent references to situations in which hunters avoided or abandoned animals they considered too lean for use in favor of fatter animals, even when the hunters themselves were short of food. A typical example was recorded by Lewis and Clark in December 1804.

> Captain Lewis went down with a party to hunt. They proceeded about 18 miles; but the buffalo having left the banks of the river they saw only two, which were so poor as not to be worth killing. . . . (Coues 1893:211)

In February 1805 Lewis and Clark made another, similar entry in their diary.

> Captain Clark returned last evening with all his hunting party. During their excursion they had killed 40 deer, 3 buffalo, and 16 elk; but most of the game was too lean for use. . . . (Coues 1893:233)

As a final example, Jacob Fowler, during his expedition to the Rocky Mountains of Colorado, made the following comment in his journal in February 1822.

> Hunters out Early—Killed one Cow Buffelow With In four Hundred yards of Camp—but so Poor the meat Was not Worth Saveing. . . . (Coues 1898:97; spelling as in original)

To summarize, the above data indicate that a diet composed largely of lean meat (i.e., mainly protein with small amounts of fat), even in quantities that would appear to satisfy caloric requirements, can result in serious nutritional problems. Hunters apparently were keenly aware of the deleterious effects of a lean-meat diet, and, when possible, abandoned lean animals for fatter ones, even when they were short of food (see also Jochim 1981:81 and Hayden 1981:394–398 for discussions of the importance of fat in hunter–gatherer diets).

PROTEIN METABOLISM

The nutritional literature provides interesting insights into the reasons why diets composed largely of lean meat should have the negative effects described in the above quotes, and suggests which alternative sources of energy should be preferentially sought to supplement such a diet. We briefly review pertinent aspects of this literature to (1) delineate several key problems peculiar to meeting caloric needs under high-protein, low-energy diets, and (2) derive a series of subsistence activity responses which hunter–gatherers may be expected to make to cope with periods of adequate protein intake but caloric deficiency.

Specific Dynamic Action

One aspect of protein metabolism relevant to this issue concerns the high "specific dynamic action" (SDA) of protein ingestion. The SDA of food refers to the rise in metabolism or heat production (diet-induced thermogenesis) resulting from the ingestion of food (Chaney and Ross 1971:45; Briggs and Calloway 1979:32; Barnes 1976:12–13; Houssay *et al.* 1955:455–456; Taylor and Pye 1966:39–40; Guthrie 1975:94–95; Bigwood 1972:xxii; Rothwell and Stock 1979; Wing and Brown 1979:22; Bourlière 1964:336). The SDA of a diet consisting largely of fat is about 6–14%, while that of a diet high in carbohydrates is about 6%. In striking

contrast, the SDA of a diet consisting almost entirely of protein may be as high as 30%; or, in other words, for every 100 calories of protein ingested, up to 30 calories are needed to compensate for the increase in metabolism. Thus, persons whose diets are high in protein experience higher metabolic rates than those whose diets are composed largely of carbohydrate. For example, members of Eskimo populations, at least 90% of whose caloric needs were traditionally met by meat and fat (cf. Draper 1980:263; Høygaard 1941), had basal metabolic rates 13 to 33% above the DuBois standard, which is based on the metabolic rates of populations consuming western diets (Itoh 1980:285).

In a series of experiments, Long (1946) demonstrated that elevated metabolic rates such as those observed among the Eskimos are not solely a response to low arctic temperatures (see also Rodahl 1952; LeBlanc 1957). He observed significant increases in the rate of heat production with the administration of high-protein diets over a considerable range of air temperatures, and irrespective of the type or amount of clothing worn by the subjects in his experiments.

Similarly, two arctic explorers, V. Stefansson and K. Andersen, in a study conducted in the temperate environs of New York, subsisted for an entire year on an all-meat diet. With an intake of lean meat (ca. 3% fat), the increase in their metabolic rate varied from 14.6 to 25.0% above basal levels. In one test the increase was 45.3%. On a diet in which fat provided about 75% of their calories, the increased heat production ranged from 8.6 to 22.3% (McClellan *et al.* 1931; McClellan and DuBois 1930). It may be concluded from these data that heavy or complete reliance on fat-depleted meat would have *elevated* the total energy needed to support a group of hunters at a time of year when total caloric intake was very likely to have been restricted.

If we examine the caloric requirements of body maintenance, i.e., the calories needed for basal metabolic functions, ingestion of food, and protein balance, the impact of a high-protein diet on basic caloric needs becomes evident. Table 1 provides two different estimates of basal metabolic rates for an adult male weighing 53 kg and an adult female weighing 46 kg. These weights, based on FAO/WHO developing country standards (1973:82), are below the standard weights for industrialized countries and are assumed to be representative of hunter–gatherer body weights. The estimates of basal metabolic rate do *not* include energy expended for metabolic processing of food (SDA), and thus an additional energy increment amounting to about 20% of the basal rate, a median figure based on the ranges of SDA values given above, must be added to estimate caloric requirements under conditions of high protein intake. Thus, as the "Total" column in Table 1 indicates, under a high-protein diet, simply to maintain the calories necessary for basal metabolism and the metabolic

TABLE 1
BASIC CALORIC REQUIREMENTS UNDER A HIGH-PROTEIN DIET

Sex	Weight (kg)	BMR[a] (kcal)	SDA[b] (kcal)	Total (kcal)	Source (BMR)
Male	53	1600	320	1920	Payne (1972:303)
Male	53	1525	305	1830	FAO/WHO (1973:108)
Female	46	1350	270	1620	Payne (1972:303)
Female	46	1338	268	1606	FAO/WHO (1973:108)

[a] Basal metabolic rate.
[b] Specific dynamic action (20%).

processing of food, an adult male requires about 1800–1900 kcal/day, and an adult female about 1600 kcal/day. In comparison to a more balanced diet, whose SDA would be between about 6 and 10% rather than 20% (Briggs and Calloway 1979:32; Guthrie 1975:95), a diet composed almost entirely of lean meat requires at least 9% more calories to satisfy the same basic metabolic and physiological functions. As the above studies indicate, SDA values approaching 30% are not uncommon on all-meat diets, and at these levels at least 18% more calories are required to meet basic metabolic needs.

We can translate these caloric requirements into estimated per capita daily quantities of lean meat consumed. However, to do this we must first provide quantitative estimates of the percentage fat content of meat from wild animals, and particularly of meat from animals at the low point of their annual cycle of condition. In the present discussion we will concern ourselves entirely with large ungulates such as deer, antelope, caribou, and bison. These and other large mammals were principal targets of hunter–gatherer procurement activities. The importance of specific smaller animals during the winter and spring will be considered later.

Standard food composition tables, such as Watt and Merrill (1963), are of limited utility in this endeavor. First, very few wild ungulates have been investigated by food scientists, because these animals play an insignificant nutritional role in the modern world. Values for the amount of fat in meat of cattle, sheep, and other domestic species are far more numerous in the literature, but these figures are inappropriate in the present context since domestic animals have undergone centuries or millennia of selective breeding in favor of high levels of fat. In addition, domestic animals are often fed supplemental rations during seasons of low natural

forage availability, and many are fattened on high-protein or high-energy "finishing" rations just prior to slaughter.

For the relatively small number of wild ungulates that have been analyzed, often only a single value is reported, and seldom is there any indication given as to whether this value represents a specific muscle or meat cut, or a composite of several cuts (e.g., "venison" of deer). These studies also rarely indicate the sex of the animals analyzed, nor do they report the reproductive status of the animals at the time of slaughter (i.e., whether pre- or post-rut in males; whether pregnant, lactating, or barren in females). Furthermore, most published values are derived from animals that presumably were slaughtered while in peak condition, whereas in the present context we are most concerned with animals at their annual low point in condition.

It should be pointed out, however, that the few minimum values that do exist for wild ungulate meat may nevertheless tend to underestimate somewhat the actual amount of fat available to hunter−gatherers in a carcass, because the values do not include subcutaneous and visceral fat deposits, fat in the bone marrow, and so forth. On the other hand, as will be discussed more fully below, many of these fat reserves may become largely or totally depleted during the winter and spring, bringing the available fat levels more in line with the values for meat alone.

In contrast to the nutrition literature, studies in wildlife biology have been very much concerned with the fat levels of wild ungulates. The amount of fat in the carcass of an animal, such as a deer or antelope, provides a very useful indicator of its overall condition, and therefore plays a critical role in management practices (cf. Harris 1945; Riney 1955). Wildlife specialists have devised a series of expedient indices (e.g., kidney fat index, thickness of backfat, girth measurements) which permit them to estimate condition in the field without having to resort to far more costly and time-consuming quantitative laboratory determinations of actual fat content (cf. Riney 1955). Unfortunately, these indices are very difficult to translate into data comparable to the percentage fat values of meat provided by nutritionists.

In a few cases total carcass fat has also been determined, either by densitometric techniques or by analyzing samples from homogenized carcasses. These whole-body estimates provide a reasonably accurate measure of the total amount of fat in the carcass. However, the whole-body figures overestimate the amount of fat generally available to hunter−gatherers by including lipids, such as bone grease, that are very costly in terms of time and labor for hunters to extract from the carcass.

An additional problem arises in using data from the wildlife literature. To obtain large sample sizes, data collected over several months, or even over several years, are frequently pooled. The resulting averages tend to

obscure the impact of below-average years on the condition of the animals; and it is the minimum fat levels that are most critical to the subsistence behavior of hunters and gatherers.

Table 2 provides comparative data on the fat levels of several large wild ungulates that are known to have been of importance to hunters and gatherers in various parts of the world. Entries are included only when data are available in the form of percentage fat content. This unfortunately eliminates the bulk of observations on wildlife in which overall animal condition is assessed only by means of fat indices. It should also be noted that techniques for extracting fat have improved over the years; as a consequence, some of the values from the earlier studies listed in the table may tend to underestimate actual fat levels.

Despite the obvious shortcomings of the data presented in Table 2, they do indicate that "minimum" fat levels in the meat of many wild ungulates may reach extremely low values in the winter and spring (or in the late dry season and early rainy season in arid tropical areas). Most values are probably less than 2%, and it may not be uncommon for levels to drop below 1%. Moreover, many of the principal fat deposits in an animal may disappear completely, and others may be largely depleted (Harris 1945; Riney 1955; Ransom 1965; Sinclair and Duncan 1972; Pond 1978). For example, Anderson (1981:74) notes that in Colorado mule deer, "subcutaneous fat was entirely lacking in mature males and near minimal in mature females during winter." Harris (1945) made similar observations in a study of both white-tailed and mule deer in the Black Hills of South Dakota. In many of the deer he examined, the subcutaneous fat had been totally depleted by mid-February and by the end of the month fat deposits in the body cavity, including fat around the intestines, kidneys and heart, also had been completely mobilized. Dauphiné (1976) observed that 100% of the backfat in the *average* adult barren-ground caribou had been depleted by spring, and that 70% of the abdominal fat had been mobilized. In adult Scottish red deer stags, rump fat disappeared entirely, and in females was reduced to negligible levels (Mitchell *et al.* 1976). Trout and Thiessen (1968) reported that 80% of the mule deer collected in late winter and spring in southwestern Idaho were in poor condition. They described this condition class as having no subcutaneous fat, less than 10% of the intestines covered by mesentary fat, and kidney fat totally depleted or present only in small patches. Stockle *et al.* (1978) observed zero percent fat levels during the spring around the kidneys and heart in 15−18% of male white-tailed deer and in approximately 10% of female white-tailed deer collected from various localities in the southeastern United States. Adult male elk in Michigan had little or no visceral fat following the rut (Moran 1973).

Significant reduction of fat levels in bone marrow has also been re-

TABLE 2

PERCENTAGE FAT CONTENT OF SELECTED WILD UNGULATES

Animal	Part (Sex)	Season killed	Fat (%)	Source
Cattle (Domestic)				
(*Bos taurus*)	Whole-body (Steer)	?	32.6	Keys *et al.* (1950)
(*Bos taurus*)	Whole-body	Emaciated	1.9	Keys *et al.* (1950)
(*Bos taurus*)	Whole-body	?	13.6–39.5	Pearson *et al.* (1968)
(*Bos taurus*)	Whole-body	?	15.1–38.8	Garrett (1968)
Antelope				
(*Antilocapra americana*)	Ham	August	4.5	Cook *et al.* (1949)
(*Antilocapra americana*)	Ham	October	1.2	Cook *et al.* (1949)
(*Antilocapra americana*)	Loin	August	6.0	Cook *et al.* (1949)
(*Antilocapra americana*)	Loin	October	1.1	Cook *et al.* (1949)
(*Antilocapra americana*)	Shoulder	August	4.3	Cook *et al.* (1949)
(*Antilocapra americana*)	Shoulder	October	0.9	Cook *et al.* (1949)
Deer				
(*Odocoileus* spp.)	Venison, lean	?	6.0	Chatfield (1940)
(*Odocoileus* spp.)	Venison, lean	?	4.0	Watt and Merrill (1963)
(*O. hemionus*)	Ham + loin	August	4.5	Cook *et al.* (1949)
(*O. hemionus*)	Ham + loin	January	0.9	Cook *et al.* (1949)
(*O. hemionus*)	Whole-body (M)	Dec. – Apr.	4.9	Anderson *et al.* (1969)
(*O. hemionus*)	Whole-body (F)	Dec. – Apr.	6.0	Anderson *et al.* (1969)
(*O. hemionus*)	Whole-body (M)	Summer	16.9 ± 7.1	Anderson *et al.* (1972)
(*O. hemionus*)	Whole-body (M)	Winter	5.4 ± 1.7	Anderson *et al.* (1972)
(*O. hemionus*)	Whole-body (F)	Fall	12.5 ± 3.2	Anderson *et al.* (1972)
(*O. hemionus*)	Whole-body (F)	Spring	6.9 ± 3.1	Anderson *et al.* (1972)
(*Capreolus capreolus*)	Whole-body	Winter	7.7 ± 2.0	Weiner (1973)

	Part	Season	Value	Reference
Caribou				
(*Rangifer tarandus*)	?	March	1.1–1.2	Mann *et al.* (1962)
(*Rangifer tarandus*)	Shoulder	?	1.7	Farmer *et al.* (1971)
(*Rangifer tarandus*)	?	?	1.2	Schaefer (1977)
(*Rangifer tarandus*)	?	?	1.2	Berkes and Farkas (1978)
(*Rangifer tarandus*)	Muscle	?	2.0–3.6	Wo and Draper (1975)
Bison				
(*Bison bison*)	Hump (M)	Fall	5.0	Morris *et al.* (1981)
(*Bison bison*)	Rib steak (Steer)	Fall	3.0–3.6	Dickinson (1976)
(*Bison bison*)	Breast	Fall	3.7	Wilber and Gorski (1955)
(*Bison bison*)	Composite, cooked	?	2.8	Deethardt (n.d.)
Moose				
(*Alces alces*)	?	March	1.1	Mann *et al.* (1962)
(*Alces alces*)	?	?	1.5	Berkes and Farkas (1978)
(*Alces alces*)	?	?	1.1	Schaefer (1977)
Waterbuck				
(*Kobus defassa*)	Whole-body	?	0.2–3.4	Smith (1970), Ledger (1968)
Wildebeest				
(*Connochaetes taurinus*)	Whole-body	?	0.8–6.4	Smith (1970), Ledger (1968)
Impala				
(*Aepyceros melampus*)	Whole-body	?	0.5–4.7	Smith (1970), Ledger (1968)
Topi				
(*Damaliscus korrigum*)	Whole-body	?	0.8–3.5	Smith (1970), Ledger (1968)

ported in many ungulates. Anderson *et al.* (1972), for example, observed mean spring-season fat levels of 31.9% ± 28.0 in male mule deer femora. Values of less than 20% were reported by Ratcliffe (1980) in the femora and humeri of a small sample of roe deer. Comparably low fat levels were noted by Stockle *et al.* (1978) in southeastern white-tailed deer femora during the spring. Alabama white-tailed deer femora from animals visually assessed to be in poor condition had a mean fat content of 27.09% ± 7.32 (Baker and Lueth 1967). Greer (1968) reported fat levels of less than 0.25% in femora of winter-killed elk. He also observed values of less than 1% in live elk collected during the spring. Franzmann and Arneson (1976) recorded an average fat level of 8.5% ± 4.1 in femora of winter-killed moose. Finally, although no actual figures are provided, Peterson (1977) found that bone marrow was almost totally fat-depleted in moose from Isle Royale, Michigan that had died of malnutrition during the late winter and spring.

We can now return to our original objective of determining the daily per capita quantity of lean meat that hunter–gatherers would have to consume in late winter and spring to fulfill their basic caloric requirements. Based on the discussion above, the meat of wild ungulates at the low point in their annual cycle of condition probably ranged in fat content from as low as 0.9% to a maximum of about 1.5–2.0%. Although the major fat deposits most readily accessible to hunter–gatherers (i.e., subcutaneous and visceral fat) may be largely if not entirely depleted at this time of year, there may be smaller amounts of fat remaining in places such as the bone marrow which, while labor-intensive to extract, will augment the total fat intake. Thus, we will assume that the average amount of fat available to the hunters ranges between about 2 and 3%. The protein content of meat is relatively constant at about 21% (cf. Watt and Merrill 1963).

Table 3 provides estimates of the number of kilograms of meat necessary to meet the basic daily caloric requirements for adult males and females that were presented in Table 1. Given a diet composed entirely of lean meat (2–3% fat), a male would have to consume between 1.7 and 1.9 kg (3.7–4.2 lb.) of meat per day, and a female between 1.5 and 1.6 kg (3.3–3.5 lb.) simply to satisfy basic metabolic needs.

These estimates do *not* include calories for any form of physical activity. Inclusion of calories to cover physical activity will substantially *raise* this need, especially since hunting requires high energy expenditure (Shephard 1974:284). For example, both summer and winter caribou hunting among traditional Canadian Eskimos require approximately 3600 kcal per 24-hour period (Shephard 1978:51). To meet these energy needs, a hunter would have to consume between 3.4 and 3.6 kg (7.5–7.9 lb.) of lean meat per day. It is important to keep in mind that the increase in hunter–gatherer caloric requirements just outlined is occurring during a

TABLE 3
DAILY LEAN-MEAT REQUIREMENTS UNDER A HIGH-PROTEIN DIET

Sex	Basic caloric requirement (kcal/day)	Lean meat[a] (2% fat) (kg/day)	Lean meat[a] (3% fat) (kg/day)
Male	1830–1920	1.8–1.9	1.7–1.8
Female	1600	1.6	1.5

[a] Adipose tissue (fat and moisture), 7.5 kcal/g; protein, 4 kcal/g (McLaren 1981:32, Rodahl and Issekutz 1965:8).

season in which ungulate body weight has declined, and hence the take per animal is reduced. Moreover, herds in the spring may be widely dispersed or highly mobile in response to reduced forage availability. Thus, locating subsistence resources may become particularly difficult at this time of year and require much greater amounts of strenuous activity.

Finally, there is evidence that appetite may be depressed sharply when the protein content of the diet is high (cf. Mayer 1980:565, 575; Krauss and Mayer 1963, 1965; Henry et al. 1953). This would exacerbate the problems for hunter–gatherers of meeting their caloric needs on a diet of lean meat.

To summarize, late winter and spring would have been seasons in which hunter–gatherers may have had to rely largely on lean meat to satisfy their energy needs. Such reliance would have substantially *raised* their caloric requirements during a period of time when subsistence resource availability was at its lowest ebb.

Protein-Sparing Action of Fat and Carbohydrate

A second aspect of protein metabolism of interest to us here is the protein-sparing effect of nonprotein dietary energy. Protein-sparing is an important nutritional consideration when ingested protein is being utilized for providing energy. Since the body's energy needs must be fulfilled before protein needs can be met, under conditions of marginal or inadequate caloric intake, the amino acids of ingested protein are degraded, and the nonnitrogenous residues are converted to glucose or fat or are oxidized directly to meet the body's energy needs. This utilization of amino acids for energy makes protein unavailable to the body for its normal uses, and thus body protein is not replenished. Under conditions of severe caloric shortage, skeletal muscle protein will also be broken down to provide glucose for organs that do not use fat for energy.

Both fat and carbohydrate exert a protein- or nitrogen-sparing action on

protein metabolism (Munro 1964; Richardson *et al.* 1979; Gelfand *et al.*
1979; Peret and Jacquot 1972; Goodhart and Shils 1980:820, 1128; Sim *et
al.* 1979). This means that when either source of energy is increased, the
loss of body protein is reduced. Numerous studies have demonstrated,
however, that under conditions of marginal calorie, protein, or glucose
intake the protein-sparing effect of carbohydrate is much greater than that
of fat (Allison 1951; Allison *et al.* 1946; Calloway 1975; Calloway and
Spector 1954; Gelfand *et al.* 1979; Miller 1973; Munro 1964, 1978; Nettle-
ton and Hegsted 1975, 1977; Richardson *et al.* 1979; Rosenthal and Allison
1951; Torún and Young 1981; Young and Bier 1981; see also McClellan *et
al.* 1930; Rodahl and Issekutz 1965).

> It has long been known that if fat and carbohydrate are given in isocaloric amounts
> they do not exert an equal protein-sparing effect, and that carbohydrate is more
> effective than fat in promoting the utilization of dietary protein. (Richardson *et al.*
> 1979:2224)

Protein metabolism is often studied indirectly by monitoring the
amounts of nitrogen ingested and excreted (Guthrie 1975:64−66). If the
amount of nitrogen lost is lower than the amount taken in, the individual is
in positive nitrogen balance; i.e., protein is being gained. Similarly, if the
amount excreted exceeds the amount ingested, the individual is in nega-
tive nitrogen balance; i.e., protein is being lost. One indication of the
greater protein-sparing effect of carbohydrate is that when it is adminis-
tered to fasting subjects there is a noticeable decline in the amount of
nitrogen excreted. No improvement in nitrogen balance is obtained when
fat is given to fasting individuals. Another indication is that when fat is
substituted for carbohydrate, while holding total dietary protein and
energy intake constant and at marginal to inadequate levels, nitrogen
losses increase sharply.

One important reason for the greater protein-sparing effect of carbohy-
drate as compared to fat is that certain organs, particularly the brain and
nervous system, require glucose as an energy source. If only fat and
protein comprise the diet, this glucose must be derived largely from the
degradation of protein, leading to higher nitrogen losses from such a diet.

Munro (1964) suggested that increased nitrogen output, resulting from
substitution of fat for carbohydrate, was a transient phenomenon lasting
at most about 15 days. More recent studies by Richardson *et al.* (1979),
however, indicate that the negative nitrogen balance produced by fat
substitution may persist for longer periods and may have a much more
detrimental impact. They observed that

> on average, the net protein utilization . . . could be raised by about 13% when the
> diet provided the majority of the energy from carbohydrate. (Richardson *et al.*
> 1979:2223)

Of particular interest, Richardson *et al.* (1979:2223) noted a considerably greater protein-sparing effect (values approaching 50%) in individuals whose caloric intake was marginal and who were losing weight.

It is important to note that virtually all of the experimental studies to date concerning the protein-sparing action of fat and carbohydrate have involved considerably smaller total protein intakes than those with which we have been concerned in the present discussion. Thus, the magnitude of the difference in protein-sparing capacity of the two nutrients remains somewhat speculative in situations where marginal to inadequate caloric intakes consist almost entirely of protein. Given the experimental data we do have, however, it is clear that when *both* total calories *and* protein are in short supply, such as might occur seasonally in many nonarctic habitats, the relative protein-sparing efficiencies of fat and carbohydrate will be nutritionally significant. Under these conditions, carbohydrate resources should be preferentially sought over fat resources.

ESSENTIAL FATTY ACID DEFICIENCY

Another potentially serious problem faced by hunters and gatherers is a deficiency of essential fatty acids (EFA), particularly linoleic acid (Holman 1968; Mead 1980; Alfin-Slater and Aftergood 1980). Symptoms of EFA deficiency are rarely expressed in adults, because of the large reserves of essential fatty acids in their body fat. In rapidly growing infants, however, an inadequate EFA intake may be far more serious, especially in situations where the mother is malnourished and the infant is weaned to a low-fat diet (Holman 1968; Mead 1980). Major consequences of EFA deficiency include severe skin lesions, impaired water balance, reduced growth, and greater susceptibility to infection. The deleterious effects of EFA deficiency are exacerbated if caloric shortages are ameliorated with low-fat, high-protein supplements, such as skim milk, that promote growth (Mead 1980:226).

Essential fatty acid deficiencies may have posed a serious nutritional problem for hunters and gatherers during late winter and spring, if caloric intake declined to marginal or inadequate levels, stored plant foods were used up, and lean meat became the principal source of energy in the diet. Meat is a relatively poor source of linoleic acid. Plant foods such as corn and various oil-rich seeds contain much higher proportions of this critical fatty acid (Mead 1980).

Minimum requirements for linoleic acid in humans are somewhat controversial. In adults the level is commonly placed at approximately 2% of total calories, or about 7.5 g for an adult male on a daily caloric budget of 3000 kcal (Alfin-Slater and Aftergood 1980:135; McLaren 1981:95). The

TABLE 4

LINOLEIC ACID CONTENT OF UNGULATE MEAT, ADIPOSE TISSUE, AND MARROW

Animal	Part	Linoleic acid content (%)	Lipid class analyzed	References
Deer	Venison (lean)	Trace	Total fatty acids	Watt and Merrill (1963)
Cattle	Beef carcass (trimmed)	<1	Total fatty acids	Watt and Merrill (1963)
Bison	Liver (tissue)	2.00	Triglycerides	Evans (1964)
Antelope	Kidney fat	2.61	Total fatty acids	Booren et al. (1973)
Elk	Kidney fat[a]	2.85	Triglycerides	Garton et al. (1971)
Elk	Subcutaneous fat[a]	2.00	Triglycerides	Garton et al. (1971)
Caribou	Kidney fat[a]	1.80	Triglycerides	Garton et al. (1971)
Caribou	Subcutaneous fat[a]	1.15	Triglycerides	Garton et al. (1971)
Moose	Kidney fat[a]	2.40	Triglycerides	Garton et al. (1971)
Moose	Subcutaneous fat[a]	2.25	Triglycerides	Garton et al. (1971)
Deer	Kidney fat[a]	3.85	Triglycerides	Garton et al. (1971)
Deer	Subcutaneous fat[a]	3.35	Triglycerides	Garton et al. (1971)
Dall Sheep	Marrow (front limb)[b]	3.55	Total fatty acids	West and Shaw (1975)
Bighorn Sheep	Winter marrow (front limb)[b]	2.62	Total fatty acids	Turner (1979)
Bighorn Sheep	Summer marrow (front limb)[b]	2.23	Total fatty acids	Turner (1979)
Bighorn Sheep	Winter marrow (rear limb)[c]	2.53	Total fatty acids	Turner (1979)
Bighorn Sheep	Summer marrow (rear limb)[c]	2.05	Total fatty acids	Turner (1979)
Caribou	Marrow (front limb)[b]	2.50	Total fatty acids	Meng et al. (1969)
Caribou	Marrow (rear limb)[c]	2.64	Total fatty acids	Meng et al. (1969)

[a] Average of male and female values.
[b] Average of humerus, radius, metacarpus, and phalanges.
[c] Average of femur, tibia, metatarsus, and phalanges.

minimum daily requirement for infants is about 0.5% of calories (Cuthbertson 1976:559).

Available data concerning the linoleic acid content of various tissues in wild and domestic ungulates are presented in Table 4. Most of these data reflect the fatty acid composition of adipose tissue. Values tend to fall between 2 and 3%. Very few figures are available for the linoleic acid content of lean meat, the portion of the carcass of most concern to us in the present discussion. The data presented by Watt and Merrill (1963) for venison and various cuts of beef suggest that linoleic acid values in lean meat generally fall below 2% and often well below 1% (i.e., "trace"). It should also be pointed out that all of the figures in Table 4 are derived from animals in peak condition. It is clear, however, that linoleic acid levels vary with season, attaining maximum values in late fall and winter and minimum values in late spring and summer (Turner 1979; Link et al. 1970). Thus, typical levels of linoleic acid in lean meat available to hunter—gatherers in late winter and spring probably rarely exceeded 2%.

Table 5 summarizes the amount (and percentage of total calories) of linoleic acid in lean meat, using an EFA value of 2% and a total fat content of 2%. It is clear from these data that linoleic acid intakes would seldom have reached 1 g, or only about 0.3% of total calories. These values are well below the minimum recommended levels for infants and adults.

While these low values do not necessarily imply linoleic acid deficiency in adults, they do suggest that a more susceptible cohort, the infants, may be experiencing severe stress. With lower fat reserves to draw upon than adults, infants should be affected more severely by short-term, seasonal linoleic acid deficiencies. We expect that, owing to the greater susceptibility to infection that accompanies a deficiency in linoleic acid, infant mortality may rise in hunter—gatherer populations that rely seasonally on lean-meat diets.

Lack of fat in the human diet has effects other than reduction in essential fatty acid intake. For example, adequate fat is important in calcium

TABLE 5
LINOLEIC ACID LEVELS IN HUNTER—GATHERER DIET

Lean meat (kg) (2% fat)	Total[a] calories (kcal)	Linoleic acid content (2%)		
		Amount (g)	Calories (kcal)	Percentage of total calories
1.5	1530	0.6	5.4	0.35
2.5	2550	1.0	9.0	0.35
3.5	3570	1.4	12.6	0.35

[a] Fat, 9 kcal/g; protein, 4 kcal/g.

absorption (Alfin-Slater and Aftergood 1980:120–121) and as a source of fat-soluble vitamins (Morton 1970). In addition, high protein intake tends to inhibit calcium absorption (Linkswiler 1976:234–236) and may lead to imbalances in the body's acid-base levels (Briggs and Calloway 1979:368; Goldberger 1975). Though we lack quantitative data concerning the consequences of seasonal restrictions in fat intake on these metabolic processes, the existence of deficiencies other than those on which we have focused our discussion should be noted.

HUNTER–GATHERER FORAGING STRATEGIES

The above observations concerning the specific dynamic action of protein ingestion, the protein-sparing effect of dietary carbohydrate, and essential fatty acid deficiencies resulting from lean-meat diets have important implications for understanding certain critical aspects of hunter–gatherer subsistence behavior. Let us assume in the following discussion that we are dealing with hunting and gathering populations in temperate grassland, subarctic, or inland arctic environments during the late winter and spring. As mentioned above, this is the most stressful period of the year, one often characterized by diminishing stored food supplies, the scarcity or absence of collectible plant foods, and a decline in total per capita calorie intake.

To compensate for declining total energy levels and dwindling food reserves, hunter–gatherers in these environments may be forced to increase their emphasis on hunting large ungulate species such as deer, elk, moose, caribou, and bison. Since these animals are also subsisting on diets of declining nutritional worth, their body-fat reserves are becoming depleted and the hunters will be taking in increasing proportions of lean meat.

It is clear from the above discussion, however, that because of the high specific dynamic action of protein and the low levels of linoleic acid, lean-meat diets provide an inefficient and often inadequate source of sustenance for hunters and gatherers at times when their intake of carbohydrate and total energy is restricted. As a consequence, in anticipation of recurrent (e.g., seasonal) periods when caloric needs cannot be met by lean meat consumption, it is expected that hunters and gatherers will concentrate on subsistence strategies that increase the availability of carbohydrate and/or fat at the critical time of year. Three types of strategies would achieve this result:

(1) increasingly selective procurement and processing of animals with high fat content,

(2) storage of fat- and carbohydrate-rich foods,
(3) exchange for fat- or carbohydrate-rich foods.

During seasons of potential caloric deficiency, hunter−gatherers may become much more selective in procuring fat animals and in processing fat-rich body parts (cf. Speth 1983). When possible, hunter−gatherers may shift their hunting emphasis from potentially fat-depleted ungulates to animal species that normally maintain higher levels of body fat in winter and spring. These include bear, beaver, certain species of fish, various migratory waterfowl, and others, depending of course on habitat and abundance (cf. Rogers 1972; see Aleksiuk and Cowan 1969a, 1969b for data on seasonal fat-level fluctuations in beaver).

The second strategy, storage of fat or carbohydrate, has two components. First, humans can accumulate reserves of body fat. As Munro (1964:431) and Peret and Jacquot (1972:90) point out, an excess of body fat is a protection against wastage of body proteins during severe dietary restriction. An ethnographic example of this practice, though not pertaining to meat consumption per se, is the late-summer gorging on *pitahaya* (organ-pipe cactus) fruits by hunter−gatherers in Baja California, who, as a consequence, became quite corpulent (J. Baegert, cited in Castetter and Bell 1937:31; see also Lee 1979:272). The practice of accumulating body fat reserves in times of plenty to supply energy in times of nutritional stress also may help account for the seemingly anomalous gorging on meat at bison kills frequently noted by early North American travelers and explorers (see discussion in Wheat 1972:108−109).

Second, hunter−gatherers may augment their supplies of storable fat through labor-intensive activities such as rendering bone grease. Preparation of bone grease involves smashing the bone, heavy limb elements as well as lighter vertebrae and ribs, and then boiling the small pieces of bone in water until the grease is extracted. Grease is skimmed off the water and placed in skin containers to harden. Among nomadic groups lacking pottery, the laborious boiling process is accomplished by heating rocks in a fire and transferring them to a perishable container such as a skin bag that contains the broken-up bones (see Binford 1978 for a description of grease rendering). Commonly, the rendered fat is mixed with an equal proportion of pulverized, jerked lean meat to make pemmican, an energy-rich food that can be stored for several years if kept dry (Stefansson 1956:179, 188).

The degree of mobility and the transport capabilities of the population, however, may place severe constraints on the amount of fat that can be stored. Problems of this nature probably obtained, for example, for many prehistoric Plains hunter−gatherer populations who wintered off the

Plains, but whose transportation facilities (dogs and humans) limited the quantities of fat, or fat plus meat (pemmican), that could be transported from kills made on the Plains.

In light of the greater protein-sparing capacity of carbohydrate compared to fat, and the higher essential fatty acid content of many plant foods, hunter–gatherers, when possible, may place equal or greater emphasis on building up storable carbohydrate reserves during the fall than on hunting, particularly in areas where adequate supplies of fat cannot be reliably produced (see, for example, the discussion in Lee 1968). Thus, we propose that higher quantities of carbohydrate will be included in hunter–gatherer diets than would be expected given the relative availability of carbohydrate and protein in these environments.

Where neither fat surpluses nor carbohydrate-rich wild plant foods are available in adequate quantities to store for winter use, hunter–gatherers may supplement their carbohydrate/fat reserves by consuming insects (including fly larvae in spring caribou hides), seaweed, the entrails of ptarmigans and the stomach contents of caribou, bark, and a variety of other foods (cf. Eidlitz 1969; Nickerson et al. 1973).

Trade for fat or carbohydrate with other populations provides another widely practiced alternative. For example, Nunamiut Eskimos who relied heavily on caribou for subsistence annually traded for fat and seaweed with coastal-dwelling Taremiut (Gubser 1965; Spencer 1959; Eidlitz 1969:50). The same situation obtained for inland Athabascan groups who traded skins, blankets, and tools to Eskimo and Northwest Coast populations in return for seal, whale, or oulachen oil (Olson 1936; Birket-Smith and de Laguna 1938; People of 'Ksan 1980:89ff.; Kuhnlein et al. 1982).

Where storage is not feasible due to group mobility, hunter–gatherers may rely on the storage capacities of horticultural populations and make seasonal trips to horticultural villages to trade for carbohydrate resources. Hunter–gatherer exchange of meat with horticultural populations in return for carbohydrates is documented for many areas of the world (e.g., Peterson 1978; Turnbull 1965; Hammond and Rey 1953; Ewers 1954; cf. Spielmann 1982). In temperate climates such exchange coincided with seasons during which hunter–gatherers were experiencing reduction in available food resources and probably nutritional stress.

Limited cultivation by hunter–gatherers has also been documented (e.g., Peterson 1978; Thomas 1935). Such cultivation is often sporadic and does not approach the efficiency of full-time horticulturists. Little research has been conducted concerning the significance of these limited amounts of cultivated carbohydrates in the hunter–gatherer diet. The argument presented here would suggest that this desultory cultivation is a buffering strategy which provides a backup source of carbohydrate during

seasons in which lean meat becomes an increasingly large proportion of the diet.

CONCLUSIONS

In this paper we have focused on alternative strategies open to hunter—gatherers to cope with nutritional deficiencies which occur seasonally in environments where ungulate meat forms the principal available resource in late winter and spring. In environments where alternative, fattier species such as beaver, raccoon, or migratory waterfowl are normally available in the spring, heavy reliance on lean ungulate meat and its associated nutritional problems might nevertheless occur periodically during "bad" years in which the number of smaller game animals is significantly depressed. It is also possible that such reliance may occur chronically in areas of the subarctic where caribou constitute the primary, year-round subsistence resource (cf. Burch 1972). Thus, while the emphasis of our discussion has been on the consequences of recurrent, winter—spring reliance on ungulate meat, the susceptibility of populations to the deficiencies discussed above actually ranges over a continuum from periodic to seasonal to chronic, depending on the frequency with which lean ungulate meat constitutes a major part of the hunter—gatherer diet.

In addition, these same arguments may be extended to situations in which climatic, environmental, demographic, or other changes lead to long-term reductions in available energy. Under such conditions, selection may favor a permanent shift in the subsistence strategies of hunters and gatherers toward greater emphasis on carbohydrate resources. The apparent increase in reliance on plant foods in many parts of the world following the end of the Pleistocene might profitably be explored from this perspective. The greater protein-sparing capacity of carbohydrate under conditions of marginal calorie or protein intake may also help to explain why hunter—gatherers in the early Holocene began to invest time and energy cultivating plants, despite the meager returns many of these cultigens would have provided in their early stages of domestication. Similarly, a long-term increase in the availability of carbohydrates, due, for example, to the introduction of a cultivated plant species, may alter the importance to hunter—gatherers of animal fat, and may lead to permanent changes in the animal species they procure, the parts they select during butchering and processing, the importance of marrow production and grease rendering, and the season of the year they hunt or trap. The inadequacies of a lean-meat diet and the noninterchangeability of fat and carbohydrate clearly open a number of interesting avenues of research that remain to be explored in detail.

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