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"Neanderthals, Vitamin C, and Scurvy"

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Running Title: 'Neanderthals, Vitamin C, and Scurvy'

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Abstract

This paper explores the role of vitamin C (ascorbic acid) in the foodways of hunter-gatherers both ethnohistoric and Paleolithic—whose diet seasonally or over much of the year, of necessity, was comprised largely of animal foods. In order to stave off scurvy, such foragers had to obtain a minimum of about 10 mg per day of vitamin C. However, there is little to no vitamin C in muscle meat, being concentrated instead in various internal organs and brain. Even ruminant stomach contents, despite the abundance of partially digested plants, contains almost none. Moreover, many of the "meatiest" anatomical units in a carcass, such as the thigh muscles or "hams" associated with the femur, are extremely lean in most wild ungulates, making them nutritionally much less valuable to northern foragers than archaeologists commonly assume (for example, Inuit and other indigenous peoples of the arctic and subarctic commonly use the thigh meat as dog food). Vitamin C is also the most unstable vitamin, rapidly degrading or disappearing when exposed to water, air, light, heat, and pH levels above about 4.0. As a consequence, common methods of preparing meat for storage and consumption (e.g., drying, roasting, boiling) may lead to significant loss of vitamin C. There are two effective methods of minimizing such loss: (1) eating meat raw (fresh or frozen); and (2) eating the meat after it has been putrefied. Putrefaction has distinct advantages that make it a common, if not essential, way of preparing and preserving meat among northern latitude foragers and, for the same reasons, very likely also among Paleolithic foragers in the colder climes of Pleistocene Eurasia. Putrefaction "pre-digests" the meat (including the organs), making it much less costly to ingest and metabolize than raw meat; and it lowers the pH, greatly increasing the stability of vitamin C. These observations offer insights into critical nutritional constraints that likely had to be addressed by Neanderthals and later hominins in any context where their diet was heavily meatbased for a substantial part of the year.

Keywords: Hunter-Gatherers; Neanderthal; Diet; Vitamin C; Scurvy; Putrid Meat.

1. Introduction

While this paper is focused squarely on certain nutritional problems confronting Neanderthals living in the colder climes of Middle and Late Pleistocene Eurasia, many of the same issues apply equally well to Upper Paleolithic and later foragers occupying broadly comparable environments. Some important differences do arise, however, stemming in particular from the increasing use in the Upper Paleolithic of fish and small game, and these will be discussed below where appropriate.

As with just about every other facet of Neanderthal life, from their technological organization and mobility patterns to their mental capacities and ultimate demise, Neanderthal diet and subsistence practices have been sources of constant and often contentious debate. There is one thing, however, about which there seems to be fairly widespread agreement, sometimes explicit, though most often implicit: meat from large to very large animals generally provided the cornerstone of Neanderthal diet (e.g., Bocherens et al., 2005; Gaudzinski-Windheuser and Roebroeks, 2011; Richards et al., 2000; see discussion in Morin et al., 2016). This view is hardly surprising. There is no mistaking the fact that many Middle Paleolithic sites are jam-packed with animal bones. In fact, they sometimes occur in such numbers and densities that the accumulations resemble a veritable éboulis of bones. And unambiguous traces of human involvement, such as charring, impact fractures, and cutmarks, more often than not are found on the bones of the larger-bodied taxa. In striking contrast, plant remains are noteworthy for their scarcity or absence. So as one might expect, much of the debate has not been about the role of plant foods in Neanderthal diet (preservation bias and, until recently, limited methodologies were sufficient to render that debate largely moot); instead the discussion has been about how Neanderthals went about procuring their meat.

Throughout the better part of the 20th century, hunting seemed like the obvious answer, a view that by and large was simply taken as a given. But then, beginning in the 1980s (and most vociferously in North America), many in the profession began to deny early hominins, and in short order Neanderthals and their southern African contemporaries as well, the wherewithal needed to bring down large game (e.g., Binford, 1981, 1984, 1988; Blumenschine, 1987). Their weapons, and perhaps even their mental capacities, were thought to have been no match for the large, fleet-footed, and sometimes dangerously aggressive animals like mammoth, rhino, bison, aurochs, and probably even large antlered prey like red deer and reindeer. Instead, archaeologists and paleoanthropologists alike had no qualms about relegating our ancestors prior to the Upper Paleolithic to a life of opportunistic scavenging, eking out a precarious existence off what scraps of meat and marrow they could glean from carcasses that the "real" predators of the time had killed, gorged upon, and then abandoned helter-skelter across the landscape (Trinkaus, 1987:130).

Though the scavenging scenario was widely persuasive in both scholarly and popular circles, especially in discussions of early hominins, but also with regard to Neanderthals, it began to crumble in the 1990s. Armed with new ideas and innovative methods of analysis, zooarchaeologists brought forth compelling evidence that hominins across the span of the Pleistocene had early or primary access to carcasses; that is, they somehow were able to get at

the prey before carnivores like hyenas, large cats, and wolves had time to devour a kill on the spot or carry off the choicest parts. Thus, the "passive scavengers" of the 1980s morphed into the "power scavengers" of the 1990s, foragers endowed with sufficient prowess to be able to drive off their hungry competitors from a kill (Bunn, 2001). Some even took an important step further and argued that Neanderthals were not just capable of scaring off ferocious predators, they in fact were *bona fide* "big game" hunters in their own right (e.g., Marean and Kim, 1998).

As the field evolved, zooarchaeologists started carefully examining the age structure of the larger mammals in Middle Paleolithic faunal assemblages and, in case after case, found that prime adult animals rather than juveniles and old-timers were unexpectedly well represented, in fact often over-represented. This surprising discovery was not only at odds with the age structure typical of kills made by most non-human predators, it was also at odds with any sort of scavenging scenario (Gaudzinski and Roebroeks, 2000; Speth, 2013a). Thus, "Neanderthal the scavenger" (in whatever guise) gradually gave way as a new image took its place, the one to which much of the profession subscribes today: Neanderthals were "top predators," formidable hunters fully capable of killing even the largest and most dangerous prey.

The "top predator" view of course found its firmest grounding in the fact that most Middle Paleolithic faunal assemblages are dominated, often overwhelmingly so, by the bones of large mammals, including not only an array of medium to large ungulates, but also a surprising number of mammoth and in some places even rhino remains (Bratlund, 2000; Gaudzinski and Roebroeks, 2000; Morin et al., 2016; Rendu et al., 2012; Speth, 2013a). No doubt, this picture is biased by sampling issues (big bones, or their large, robust fragments, are more likely than small ones to be preserved, and they are also more likely to be recognized and recovered in excavations). And until fairly recently there has been a common tendency among zooarchaeologists to devote the lion's share of their attention to the large animals when talking about subsistence, while focusing more on the small mammals, birds, and reptiles when reconstructing paleoclimates and paleoenvironments, as well as when attempting to resolve taphonomic issues. Nevertheless, there is no denying that larger mammals (deer-sized and up) are very prominent in many Middle Paleolithic assemblages, making it quite clear that Neanderthals did in fact focus a lot of their hunting effort on the "big ones."

The "top predator" view also gained considerable additional support, as well as a kind of scientific "legitimacy," from the work of biochemists, whose stable isotope studies of Neanderthal skeletal remains revealed elevated $\delta^{15}N$ values that placed these archaic humans high up on the food chain, right up there with hypercarnivores like wolves, hyenas, and cave lions (Bocherens, 2011).

But the "top predator" scenario is not without its problems. First and foremost, there is a widespread misapprehension among zooarchaeologists—and among those who consume the results of such studies—about what the animal bones can actually tell us regarding the role of meat in past human diets. Contrary to what many in the profession would seem to assume, faunal remains can only reveal to us the relative proportions of different animals in an assemblage; they tell us nothing about the actual contribution of meat to the daily or annual diet, expressed in terms of kcal (or kg) of meat per person per day: "Stone tools and butchered animal bones almost certainly indicate that early *Homo* ate meat..., but they reveal nothing about meat's relative

dietary importance" (Sponheimer and Lee-Thorp, 2009:192). This problem persists even if we convert raw bone counts (e.g., NISP, Number of Identifiable Specimens; or MNE, Minimum Number of Elements) into estimates of the number of animals that are represented in an assemblage (MNI or Minimum Number of Individuals) (Grayson, 1984). Regrettably, despite these attempts to inject greater rigor and interpretive power into zooarchaeological investigations, there still is no way to translate NISP, MNE, or MNI values into per capita daily meat consumption. Put bluntly, lots of bones does not necessarily mean lots of meat in an individual's or a group's daily or annual diet.

There are many reasons for this unfortunate constraint on zooarchaeological interpretation. Leaving aside the plethora of taphonomic biases that can greatly complicate such reconstructions (Lyman, 1994), we seldom know the actual number of people that inhabited a site at a particular moment in time, nor can we be certain about the precise length of each individual episode of occupation. Additionally, we never have sufficient data or chronological precision to look at the hunting returns of an individual, or of a larger social unit, over an entire year. Instead, we have to content ourselves with samples that are complex palimpsests of the (partial) hunting returns generated by an unknown number of discrete hunting events made by an unknown number of people over an unknown period of time, plucked from a settlement system of unknown spatial scale and organizational structure. In short, while we can say with some confidence that foragers in the past hunted more of species "X" than of species "Y", the faunal data by themselves will probably never tell us how many animals were actually killed by a particular social unit over the course of a year; and, more importantly, such data remain silent when it comes to determining the *nutritional* contribution that each taxon made to an individual's or a group's average daily or annual meat intake.

The isotope approach has its problems as well. First of all, nitrogen values tell us about an organism's protein intake, and since many plant foods are deliberately selected by foragers for their starch or oil content, and since many contain far less protein than meat does, trophic reconstructions based on nitrogen isotopes are likely to be biased, at times sharply so, in favor of the meat component of the diet (Bocherens, 2009:244). One can expect this bias to be greatest when dealing with human remains from contexts where plant foods are likely to have played a major dietary role (e.g., the $\delta^{15}N$ values from skeletal remains that date to warmer climatic episodes such as interglacials and interstadials, or that derive from geographic areas that generally experienced less harsh climatic conditions).

It is also important to keep in mind that Neanderthals, their $\delta^{15}N$ values notwithstanding, were not hypercarnivores. It is certainly true that traditional northern foragers such as the Inuit (traditionally referred to as "Eskimos"), and presumably the more meat-dependent hominins of the Middle and Upper Paleolithic, do (or did) resemble hypercarnivores in one important respect: both are (or were) capable of consuming diets comprised almost entirely of meat. But that's where the similarity stops. Thus, while wolves, hyenas, and felines can thrive on a diet in which protein provides as much as 70% of total energy (Schermerhorn, 2013:2), northern latitude hunter-gatherers (and presumably Paleolithic foragers as well) would experience dire health consequences, and even death, within a matter of weeks if their protein intake regularly exceeded roughly half that amount (i.e., ca. 35% of total kcal) (Cordain et al., 2000; Speth, 2010). In other words, fat is far more important to the survival of meat-dependent humans (including

Neanderthals) than it is to hypercarnivores.

This difference may help explain why Neanderthals, and later humans, routinely targeted prime adults, the age cohort with the highest overall fat levels, while hypercarnivores could make do with fat-poor juveniles and fat-depleted old adults (their capture of course also posed less risk of injury and failure). This important contrast is easily missed in dietary reconstructions based on $\delta^{15}N$ values. Neanderthal hunters would have had to exercise far greater selectivity than hypercarnivores with regard to the species, age, sex, reproductive state, and overall condition of the animals they targeted and the body parts they processed and consumed (*contra* White et al., 2016). At times and in contexts where plant foods were scarce or unavailable, hunting wasn't just a matter of opportunistically killing an animal and bringing home the meat. To survive the coldest months of the year, hunters had to provide fat in substantial quantities on a regular basis—in fact, as much as 60% or more of total calories (Cordain et al., 2000; Speth, 2010).

Though beyond the scope of this paper, it is worth noting that we still don't fully understand how Neanderthals managed to obtain sufficient fat from their animal resources (see Costamagno, 2013:220; Marean, 2005:352). They undoubtedly made heavy use of the obvious and most readily accessible lipids, such as the fat deposits under the skin, around the internal organs, in the marrow cavities of the limb bones and other elements, and in the brain and tongue. But there is another source of fat in an animal that played an extremely important role in the survival of ethnohistorically documented foragers throughout the circumpolar regions—the "grease" (lipids) within the spongy cancellous tissue of bones. Historically, northern foragers invested considerable time and effort to recover these lipids, systematically breaking up the bones into small fragments, a time-consuming activity in its own right, and then thoroughly boiling them until the fat rose to the top of the container and could be skimmed off for later use (Eidlitz, 1969; Saint-Germain, 2005). We have yet to determine whether Neanderthals possessed the boiling technology needed to render lipids in a similar manner from animal bones; and, if not, how they might have compensated for the likely seasonal, if not annual, shortfall in available non-protein calories (Speth, 2015).

2. Scurvy

Before proceeding, I need to digress briefly to clarify some potentially ambiguous terminology. The word "meat" can convey different meanings in different scholarly and popular contexts. Thus, when archaeologists talk about meat, I suspect they are thinking mostly about muscle. More often than not, they treat the internal organs, not only as a category distinct from meat, but also as marginally important tidbits or "add-ons" in the grand scheme of things. This creates a dilemma when talking about hunting in northern latitudes (and very likely when considering Neanderthal and Upper Paleolithic subsistence as well). As I will discuss further below, adequate intake of vitamin C is absolutely vital to survival when relying, whether seasonally or year-round, on a heavily "meat"-based diet, but this critical micronutrient occurs at low to negligible levels in muscle. Instead, most is concentrated in the internal organs and brain. In addition, the muscle from wild ungulates is much leaner than analogous cuts from domestic animals, in part because it is not marbled with fat (Speth, 2010). Taken together, these shortcomings significantly diminish the nutritional worth of muscle as a food for northern

foragers, contrary to the value or "utility" typically ascribed by archaeologists to the "meatiest" body parts of an ungulate (as represented in faunal assemblages by their associated skeletal elements). So it is important in what follows that I make clear when using the word "meat" whether I am talking about just muscle, or about everything edible on an animal (i.e., muscle, fat, internal organs, brain, blood, etc.; but excluding the skin, except when dealing with marine mammals and perhaps birds). Unfortunately, common usage of the word "meat" in the English language does not make this task easy. Thus, henceforth, when referring specifically to muscle, I will use either the word "muscle" by itself or the phrase "(muscle) meat," and when referring to the total yield of edible products from an animal (often identified as "byproducts" in the meat science literature), I will express it as "meat (sensu lato)" or, for simplicity, just "meat (s.l.)."

So, how does all of this relate to Neanderthals and the issue of scurvy in the Middle Paleolithic? Scurvy is an insidious disease caused by an inadequate intake of vitamin C (ascorbic acid) that can seriously compromise an individual's health and, if not brought in check in time, will very likely lead to death. The best and most readily available sources of vitamin C are fresh fruits and raw or lightly cooked vegetables. Thus, for hunter-gatherers consuming a broad mix of plant and animal foods, scurvy would seldom pose much of a threat. However, animal foods as a class, while rich in B vitamins (Hassan et al., 2012b; Lombardi-Boccia et al., 2005), are notoriously poor sources of vitamin C (see below). Moreover, vitamin C is very unstable, and readily and rapidly degrades as foods are prepared for storage and consumption. This means that traditional foragers inhabiting the more northerly latitudes have had to overcome a serious challenge in finding foods with adequate and reliable levels of this critical vitamin, and in developing ways to prepare them that preserve what little vitamin C might initially have been present. That they were successful in coping with their vitamin C-poor resource base is clearly shown by the fact that outbreaks of scurvy, while commonplace among Euroamerican explorers, fur-trappers, missionaries, and military expeditions to the north, were rare among the region's traditional indigenous inhabitants (Fediuk et al., 2002:222; Hayes, 1859:116; Stefansson, 1918; Thomas, 1927:1560). By looking closely at how northern foragers dealt with the scarcity of vitamin C, we can gain a better understanding of how heavily meat (s.l.)-dependent Neanderthals and their Upper Paleolithic successors might have coped with comparable nutritional challenges during the many millennia they inhabited the colder reaches of Middle and Late Pleistocene Eurasia.

In the West one doesn't hear much about scurvy nowadays, in large part because many of our foods are fortified with vitamin C and many people also take daily supplements. However, well into the 20th century scurvy remained a major debilitating disease and a significant cause of death. Historically, one most often hears about scurvy as the scourge of the seas, and affliction that led to the demise of a staggering number of sailors, particularly during the centuries of European exploration and colonization. Nothing makes this clearer than the death toll among British sailors just in the few centuries between 1500 and 1900—over one million! And if comparable records were available for the rest of Europe during this same period, the figure would be substantially greater (Carpenter, 1986; McCord, 1965, 1971).

But scurvy was by no means confined to sailors and the high seas. Carpenter (1986), for example, reviews the terrible losses suffered by early explorers, fur-trappers, missionaries, and military expeditions in the far north, most especially those who failed to adopt indigenous

foodways. Scurvy raised its ugly head in many other contexts as well. For example, during the Middle Ages scurvy may have been endemic during the long, harsh winters of northern Europe (Drymon, 2008:114). Participants in the California gold rush in the late 1840s suffered heavily from scurvy, as did fortune seekers in the late 19th-century Alaskan and Yukon gold rushes (Buffum, 1850; Stefansson, 1960:162). The disease may also have been widespread during the great famine in Ireland (1845–1852), when the potato, the poorer inhabitants' principal source of vitamin C, was destroyed by a blight (Geber and Murphy, 2012). Scurvy was also a serious and widespread threat to armies in the field, as for example during the Crusades (Drymon, 2008:114), during Napoleon's 1801 Egyptian campaign (Wood, 2008), among French and other troops during the Crimean War in the 1850s (Baudens, 1862), and among Union and Confederate soldiers during the American Civil War in the 1860s (Secretary of War, U.S. War Department, 1884). More recently, the British army fighting in the Near East in World War I suffered serious losses from scurvy (Stefansson, 1960:162), as did soldiers in campaigns against the Italians in Ethiopia in the mid-1930s. So too did American troops fighting in World War II. And in some parts of the world scurvy is still very much with us. Fain (2005:125), for example, notes that more than 100,000 cases of the disease were reported among refugee populations in the horn of Africa in the 1990s.

James Lind (1753), an 18th-century Scottish medical officer in the British Royal Navy and a pioneer in the study of scurvy, described its symptoms in considerable detail, and explored at length the disease's possible causes and remedies. He recognized the antiscorbutic power of citrus juices, but unfortunately did not understand that boiling the juice in copper kettles to reduce the liquid to a more compact and easily transportable concentrate effectively destroyed whatever vitamin C it originally had contained. While recent medical research has greatly advanced our understanding of the etiology of scurvy, Lind's observations of British sailors afflicted with the disease, though made more than two and a half centuries ago, still provide valuable insights into scurvy's progression (Hirschman and Raugi, 1999; see also Stefansson, 1918:1718). Among the first symptoms to manifest themselves are overall fatigue and lassitude, as well as weight loss, irritability, and depression. Since many other disorders can produce similar symptoms, the early stages in the disease can be quite difficult to identify. However, as the disease progresses, physical manifestations become increasingly apparent. Among some of the first are changes in facial complexion, roughening of the skin, and edema or swelling, particularly in the lower extremities. These are followed by more severe conditions, many of which stem from compromised collagen formation. The blood vessels are particularly impacted at this stage, giving rise to the appearance of numerous tiny petechiae (red spots) on the skin (hemorrhagic manifestations of fragile and broken capillaries), as well as larger reddish to purplish bruise-like blotches. Wound healing also becomes severely impaired (Akikusa et al., 2003; Fain, 2005; Hirschman and Raugi, 1999; Hodges et al., 1971; Institute of Medicine, Food and Nutrition Board, 2000:101; Sheraz et al., 2015). At this stage, agonizing pain and bleeding within the joints also develop, as well as osteoporosis, bone resorption, and other pathological conditions. The combined effect of these changes can be so severe that the patient becomes totally immobilized and bedridden. In the more advanced stages of the disease, the gums begin to bleed and recede, and teeth may become loose. If the vitamin deficit persists beyond this point, death usually follows, often quite suddenly.

3. Vitamin C

What is the minimum vitamin C intake needed to stave off scurvy? The Institute of Medicine, Food and Nutrition Board (2000:95) established the Recommended Dietary Allowance (RDA) for vitamin C at 90 mg/day for adult men and 75 mg/day for adult women. These values were deliberately set far higher, however, than the amount actually needed to prevent the onset of scurvy. Arne Høygaard, for example, found that on "sledging journeys of long duration in the Arctic, less than 15 mgm. ascorbic acid a day effectively prevents scurvy" (Høygaard and Rasmussen, 1939:943). A few years later, in a classic experimental study, The Medical Research Council (1948:857) concluded that the "minimal protective dose" of vitamin C was as little as 10 mg per day and, according to Hodges et al. (1971:432, 440, 442), perhaps as little as 6.5 mg if the individual is not performing under physical or emotional stress.

Vitamin C (L-ascorbic acid) is a water-soluble vitamin biosynthesized in mammals from glucose by means of a series of enzymes in the liver. While most mammals are capable of producing their own, humans, as well as most primates, guinea pigs, some birds, fruit-eating bats, and many fish have lost that capacity due to the inactivity of the gene that produces L-gulonolactone oxidase. This enzyme is critical to the process, as it catalyzes the last step in the biosynthesis of ascorbic acid. Without L-gulonolactone oxidase, humans, primates, and others are unable to produce their own vitamin C; instead, they must get this critical micronutrient from their food (Bender, 2003:357; Chatterjee, 1973; Clemens and Tóth, 2016:2; Cummins, 1992; Institute of Medicine, Food and Nutrition Board, 2000:95–96; Matsui, 2012:597; Smirnoff et al., 2004:10).

Vitamin C serves many important functions in the body (summarized in Asard et al., 2004; and in Institute of Medicine, Food and Nutrition Board, 2000), serving for example as a co-factor in a number of key enzymatic reactions, and as an extremely important antioxidant. And, as already indicated, vitamin C plays a pivotal role in the normal formation of collagen.

How long does it take for scurvy to develop once vitamin C intake drops below the 10 mg per day minimum noted above? Unfortunately, there are few such studies, and their conclusions are not entirely comparable. One source of uncertainty stems from the difficulty of recognizing scurvy in its earliest stages, since the most common symptoms are fatigue, lassitude, irritability, weight loss, and depression, all symptoms that can arise from a variety of other causes, not just scurvy. Another potentially complicating factor may arise from differences in the initial reserves or body pools of vitamin C in the serum and cells of the subjects under observation. Given these and other uncertainties, it is not surprising that estimates vary quite widely in the few available sources. In the earliest of these, Hodges et al. (1971:442) provide the shortest estimate, from 84 to 97 days (~2.8–3.2 months). In contrast, in a more recent study Bender (2003:372) suggests a much longer interval, with symptoms taking anywhere from 4 to 6 months to become manifest. Perhaps the most reliable and useful look at the issue comes from Fain (2005:125), who subdivides the early onset of the disease into discrete, clinically detectable stages:

Serum ascorbic acid levels become undetectable 41 days [1.4 months] after the initiation of a diet deficient in vitamin C, cell depletion occurs

after 121 days [4 months], and the first skin lesions develop after 132 days [4.4 months]. Dental abnormalities occur after 6 months. The constellation of clinical symptoms develops after 1–3 months of a diet containing no vitamin C at all, when the total body pool falls below 300 mg and the serum ascorbic acid level decreases below 2.5 mg/l....

One conclusion that we can draw from Fain's data is that the earliest stages of the disease can only be pinpointed reliably using internal clinical criteria, not external physical manifestations. Not surprisingly, the highly visible (and most infamous) features of scurvy, the characteristics so often mentioned in the historical literature (e.g., *petechiae*, bleeding gums, loose teeth), don't become apparent until long after the initial onset.

There is no question of vitamin C's considerable nutritional importance to northern foragers. Unfortunately, vitamin C is also the most labile or unstable of the vitamins, easily leached from foods in the presence of water, and subject to rapid degradation and loss when exposed to oxygen, heat, light, and elevated pH levels (Bender, 1979; Kizlaitis et al., 1964; Nobile and Woodhill, 1981; Rose and Nahrwold, 1982; Sheraz et al., 2015; Soliman et al., 1987). Given the unstable nature of vitamin C, many of the more obvious means by which circumpolar peoples might prepare meat (s.l.) for storage or consumption are likely to contribute to the demise of this critical micronutrient. Thus, drying or smoking meat (s.l.) can destroy most or all of what little vitamin C might have been present originally. Even frozen meat (s.l.) is vulnerable to vitamin loss through the presence of oxygen, the activity of various endogenous and microbial enzymes in the food, the shape and size of the portions selected for freezing, the cellular integrity of the food when frozen, and many other factors (e.g., Giannakourou and Taoukis, 2003). Cooking, whether by roasting, stewing, or boiling, can also lead to substantial losses. The magnitude of these losses can be mitigated to varying degrees by keeping the cooking time to a minimum, the temperature low and, when boiling, by consuming the broth along with the meat (s.l.) (Harry and Frink, 2009:334; McClellan and DuBois, 1930:661–662; Stefansson, 1918:1717, 1935:183). Not surprisingly, boiling in the northern latitudes was almost always brief and very light, in fact fondue-like in the words of Frink and Harry (2008:111). Spray (2002:36) makes a similar point:

[T]he term 'boil' might be a misnomer. Not once did I see a bubbling pot. Rather, the liquid gently shimmered at a perfect poaching temperature. With a limited heat source, if a pot did boil, it was only for a short time.... Sometimes only a tiny amount of water was needed to braise or steam. But no matter the exact cooking method, the descriptive term was always 'boiled.'

Eating meat (*s.l.*) while fresh and still raw is one of the best ways to minimize vitamin C losses, and northern foragers are renowned for consuming meat (*s.l.*) in its uncooked state (e.g., Eidlitz, 1969; Sinclair, 1953; Spray, 2002). But there is also a downside to eating meat (*s.l.*) raw. Cooked meat (both muscle and organs) is easier to chew and, most importantly, it is much less costly energetically to metabolize than its uncooked counterpart (Boback et al., 2007; Carmody et al., 2011; Carmody and Wrangham, 2009; Dietz and Erdman, 1989; Speth, 2010, 2017; Williams and Erdman, 1999). Thus, there is a trade-off between the energetic savings one gets

from cooking meat (*s.l.*) versus the risk one faces of losing the meat's (*s.l.*) precious vitamin C content, the critical micronutrient needed to stave off scurvy when subsisting for extended periods on a heavily meat (*s.l.*)-based diet.

As already alluded to earlier, the stability of ascorbic acid is very much dependent on the pH of the food, with broad consensus that vitamin C fares much better at low (more acidic) pH's. The question is how low? Not surprisingly, estimates vary. The rate at which vitamin C disappears at different pH's is sometimes determined *in vivo* in domestic livestock by directly sampling the rumen contents through a fistula. In other cases, analogous experiments are conducted *in vitro*. As might be expected, the results of these two approaches aren't always the same. The techniques and equipment used to measure the vitamin C concentrations also differ, again with some loss of comparability. Nevertheless, there does seem to be broad agreement that vitamin C begins to become stable at a pH of about 4.0, and increasingly stable as pH values drop below 3.0 (Aditi and Graham, 2012:2508; Cheigh et al., 1994:196; Farahmand et al., 2006:259; Gallarate et al., 1999:240–241; Harris, 1988:4; MacLeod et al., 1996:2; Nobile and Woodhill, 1981:23; O'Connor et al., 1989:438, 441; Ødum, 1993:368–370; Rose and Nahrwold, 1982:390).

These pH studies help to explain why eating the chyme or partially digested plant matter in the stomach of ruminants like reindeer, while providing a valuable source of carbohydrates and B vitamins, is not a viable way of acquiring vitamin C (Speth, 2017). The pH of the gastric juice in ruminants is quite high (i.e., more alkaline than in humans and other monogastrics), with values typically ranging between 5.5 and 7.5. At pH values above 4.0, and especially when the values reach or exceed 5.5, vitamin C degrades very rapidly, most disappearing from the rumen within a matter of hours (Aagnes et al., 1995:589; Beasley et al., 2015; Dressman, 1986; Erb et al., 1947; Evans et al., 1988; Gurusinghe, 2001:88; Hatton et al., 2015; Hoppe, 1977:5–6; Ichimura et al., 2004:392; Knight et al., 1941; Murray and Schusser, 1993; Nilsson et al., 2006:77; Vallenas P. and Stevens, 1971).

4. Vitamin C in Arctic and Subarctic Animal Resources

Now let us look at the amounts of vitamin C available to northern latitude foragers. Circumpolar peoples did, of course, have some access to plant foods, some such as berries quite rich in vitamin C; but, aside from the stomach contents of hares and ptarmigans (see below), berries collected in summer but frozen for winter use, and teas made from conifers and certain other plants, most of their vegetal sources of ascorbic acid were only available during the relatively short summer months (Arnason et al., 1981:2197; Cordain et al., 2000:686, their Table 2; Draper, 1978; Nickerson et al., 1973; Spray, 2002:34–35). Thus, for the colder months of the year northern foragers were heavily dependent on meat (*s.l.*) for their vitamin C. The data are summarized in Table 1 and shown graphically in Figure 1 (all values are for raw meat (*s.l.*)).

INSERT TABLE 1 ABOUT HERE

Table 1. Vitamin C content for various aquatic and terrestrial animal resources by body portion. All values are for raw meat and organs expressed in mg/100 g. Published sources are indicated in

brackets.a

INSERT FIGURE 1 ABOUT HERE

Figure 1. Vitamin C content (mg/100 g) in aquatic and terrestrial animals by taxonomic group and body portion (raw).

What is perhaps most surprising about the vitamin C content of meat (s.l.) is how little there is in muscle. Instead, by far the highest concentrations are found in the internal organs and brain. Interestingly, this also seems to be the case in marine and freshwater fish (Fediuk, 2000; Moreau and Dabrowski, 1998:10282; Ríos-Durán et al., 2006:150, their Table 1; Rodahl, 1949). This seemingly minor nutritional "shortcoming" of muscle meat raises an important point about the way archaeologists often think about the transport decisions of northern latitude hunters in the past. Archaeologists place great stock in "utility indices," such as Binford's (1978) Modified General Utility Index (MGUI), and Metcalfe and Jones's (1988) more recent and simplified Food Utility Index (FUI). Both of these indices, while also incorporating marrow and grease in their derivation, nonetheless give considerable weight to the amount of (muscle) meat that is present in the different anatomical parts of an animal. Using either index, the femur (i.e., the element associated with the thigh muscles or "hams") emerges as the number one anatomical unit in the typical ungulate carcass (i.e., its rank is 100% when the indices are standardized). Yet, in most wild ungulates this is not only one of the leanest cuts, but also one that is largely devoid of vitamin C. As a consequence, traditional northern peoples often fed the thigh meat to their dogs! By implication, it seems very likely that, for both Eurasian Neanderthals and their Upper Paleolithic successors, the principal value of the femur as a food derived, not from its associated muscle mass, but from its substantial content of fat-rich marrow (Morin, 2007; Morin and Ready, 2013).

For themselves, the hams are either fed to the dogs, which must have their share, or cut up for drying. The white man's "choice cuts" are not the Eskimo's or the Indian's favorites, and as a rule are not the first choice of the out-door man who is cooking in the field with primitive appliances. (Anderson, 1918:61)

It is seldom among the Alaska and Mackenzie River Eskimos that caribou hams are eaten when there is enough of other meat. The hams, some of the entrails, the lungs and liver, the outside meat from the neck and brisket, and the tenderloin are the food of the dogs. (Stefansson, 1921:232)

One leg of meat after another was buried in the snow with the flat side to the heat; this was the food for the dogs, which first had to be thawed out.... When the pot was empty, we each put to good use the titbit roasting on our respective spits. Here, too, only the meat nearest the bone is eaten, the coarser cuts, such as would be used as a "roast" by civilized people, being eliminated and thrown to the dogs. The true delicacies consist of liver, heart, kidney, fat, marrow, breast, and head of caribou. (Ingstad, 1992:186)

Binford (1978) echoes these earlier observations, noting that the Nunamiut on numerous occasions used dried (muscle) meat, including dried strips cut from the thighs or "hams," as dog food rather than as human food.

There is one thing that is troubling about the Stefansson quote. He explicitly includes caribou (*Rangifer tarandus*) liver among parts usually fed to the dogs rather than to humans, despite the fact that this organ is an excellent source of vitamin C. That Stefansson's view of the liver is not merely an editorial lapse is shown by the fact that he reiterates this same position elsewhere in his writings (e.g., Stefansson, 1953:231, 236, 316). We'll probably never know how and why he came to this conclusion, but it runs counter to the opinion expressed in all of the northern latitude dietary and nutritional studies I consulted (e.g., Fediuk, 2000; Kuhnlein et al., 2006; Sinclair, 1953:72), not to mention scores of ethnographic and ethnohistoric accounts, both New World and Old World (e.g., Burch, 1988:68; Eidlitz, 1969:71, 73–74; Ingstad, 1992:186, 258). Caribou and reindeer livers were often eaten raw or frozen, and sometimes after first being fermented or putrefied. Banfield (1957) summarizes the issue succinctly, not only emphasizing the importance of caribou liver in the diet of northern peoples (*contra* Stefansson), but also echoing the sentiment expressed by those quoted earlier that the hind end of an ungulate like caribou, despite its obvious "meatiness," was not generally ranked as highly by traditional arctic and subarctic foragers as archaeologists would expect.

The primary human use of caribou is for meat. White trappers choose the hind quarters, Eskimos prefer the head and rib-basket. All agree that the tongue is the greatest delicacy, being only slightly superior to the liver. (Banfield 1957:13)

It is clear from Table 1 and Figure 1 that an animal's internal organs, not its muscles or its fat deposits, provide by far the most important sources of ascorbic acid (Hassan et al., 2012a:4). In fact, the richest sources of this vitamin are the adrenal, thymus, spleen, and pituitary glands (Harrison and May, 2009; Hediger, 2002; Svirbely, 1933). Other important sources are the brain and liver. Some fish roe may also be rich in vitamin C (see below), as is muktuk or mattak, the skin and underlying blubber of certain whales (the term is sometimes also applied, particularly in nutritional reports, to the skin and blubber of other marine mammals such as walruses; e.g., Andersen, 2005; Fediuk, 2000; Innis and Kuhnlein, 1987:107). In point of fact, the vitamin C appears to be concentrated primarily in the skin or epidermis, much less so in the blubber, which often has negligible or marginal amounts. Since Middle Paleolithic exploitation of fish—and hence fish roe—and marine mammals seems to have been sporadic at best, limited largely to coastal regions, and relatively late, these potential sources of vitamin C are more relevant to Upper Paleolithic and later foragers than to Neanderthals (Hardy and Moncel, 2011; Richards and Trinkaus, 2009; Stringer et al., 2008). It is not surprising that northern foragers prioritized fat rather than muscle in order to avoid what has often been called "rabbit starvation," the deleterious effects of excessive protein intakes (Speth, 2010), but it is also clear that these foragers had to target the internal organs of their prey in order to assure that their intake of vitamin C was adequate. Thus, as already noted in discussing the femur, arctic and subarctic foragers may often have considered an animal's overall yield of (muscle) meat less important than its internal organs, body fat content, and even its highly useful hide (see discussion in Speth,

2013b:181–182, 2018:212–213). We need to keep these complexities in mind when using utility indices to decipher Neanderthal and later butchering and transport decisions in the colder reaches and climes of Pleistocene Eurasia.

The muscle meat from horses (equids) deserves additional comment. Horses were widely hunted throughout much of Eurasia during the Middle and Upper Paleolithic and were clearly an important food resource for both Neanderthals and modern humans (Morin et al., 2016). Not only do equids provide a valuable source of monounsaturated and polyunsaturated lipids, including α -linolenic acid, an essential omega-3 fatty acid (Guil-Guerrero et al., 2013; Rossier and Berger, 1988:37), but there are hints in the literature that horsemeat might also be useful as an antiscorbutic. If true, horsemeat would be unlike the muscle meat of most other ungulates, which is widely considered to be, at best, a very marginal source of vitamin C. One such hint is historical in nature. During Napoleon's 1801 Egyptian campaign, his military surgeon, Dominique-Jean Larrey, used fresh (unsalted) horsemeat, mostly from young Arabian horses, to treat several thousand soldiers stricken with scurvy (Hall, 1814:390–393; Wangensteen et al., 1972; Wood, 2008). The other piece of evidence suggesting that horsemeat (i.e., muscle) might have more than trace levels of vitamin C comes from a study by Rossier and Berger (1988:38), who report a value of 3.4 mg/100 g (for unspecified meat cuts).

But there are reasons to question the value of horsemeat as an antiscorbutic. For one thing, Larrey doesn't make clear exactly what he included under the heading of "horsemeat." Was it only muscle meat or did it include internal organs as well? Larrey also fed his patients a variety of foods, drinks, and liquid concoctions, including at least some lemons and some unspecified bark, so it is impossible to know how much of the vitamin C actually came from horsemeat as opposed to other sources (Hall, 1814:390–393). Moreover, in addition to the vitamin C value published by Rossier and Berger (1988), I have managed to find only two other values for raw horsemeat (Lee et al., 2007:72; Nutrition Monitoring Division and Anderson, 1989:202), and these are "not detected" (for *M. longissimus dorsi* muscle) and 1 mg/100 g (for unspecified meat cuts), respectively. Finally, it is worth pointing out that there are numerous studies of the B vitamins in horsemeat, while studies of its vitamin C content are noteworthy for their scarcity. This fact alone, in my view, suggests that the muscle tissue from equids is not a viable antiscorbutic. Of course, the only way to clarify this issue is through additional analyses.

There are two small animal resources we have yet to consider that may have become important, especially during the Upper Paleolithic, for their content of vitamin C. These are ptarmigans (*Lagopus* spp.) and hares (*Lepus* spp.) (e.g., Conard et al., 2013:180, 184; Morin et al., 2016). Given their small size, these animals would not have been major sources of calories except when captured in considerable numbers (see Nelson, 1973:133). Ptarmigan, depending on species (*Lagopus lagopus* and *L. mutus*), sex, and season, typically weigh only about 0.45 kg to 0.65 kg (Angerbjörn and Flux, 1995; Best and Henry, 1994; Crile and Quiring, 1940:226; Mortensen et al., 1985:26; West and Meng, 1968:428). Mountain and Arctic hares, *Lepus timidus* and *L. arcticus*, respectively, are somewhat heavier, falling between about 2.5 kg and 3.5–4.5 kg; Crile and Quiring, 1940:247; Hewson, 1968:251). Ptarmigans and hares were often regarded by indigenous peoples as "starvation foods," particularly at times or in contexts where they had limited access to their "preferred" resources—animals like caribou, fish, or marine mammals. Moreover, ptarmigans and hares were most heavily exploited during the harshest months of the

year—winter and early spring (Burch, 1988:73–76; Friedman, 1934; Hall, 1969:77; Irving et al., 1967:77–78; Magdanz et al., 1967; Nansen, 1893:93–94; Nelson, 1973:133; Soffer, 1985:342–343). And, of course, having to subsist on the extremely lean meat (*s.l.*) of hares in the arctic and subarctic gave rise to the expression "rabbit starvation," a debilitating and potentially life-threatening condition brought about by a diet insufficient in *non-protein* calories (Stefansson, 1960:30). And finally, as is the case with muscle tissue generally, the flesh from these animals has negligible amounts of ascorbic acid (see Table 1).

Despite their diminutive size, these putatively "marginal" foods may have been critical to the survival of northern foragers, not just for their yield of calories during tough times, but because of the precious vitamin C content of the digesta or chyme in their stomachs. As already noted, caribou and reindeer stomach contents were frequently eaten in the arctic and subarctic, and may have provided a valuable source of partially digested carbohydrates as well as B vitamins (Kuhnlein and Turner, 1991:24). But because of the elevated pH in the ruminant stomach (typically falling between 5.5 and 7.5), most of whatever vitamin C may have been present in the forage disappears within a matter of hours once it reaches the rumen. Not so with ptarmigan and hares, whose stomach contents—and, in the case of ptarmigan, all of the entrails as well—were also frequently eaten (Andersen, 2005; Cheeke, 1987:20; Pálsson, 2001:291; Rodahl, 1949; Schaefer, 1981:113). Nansen (1893:91-92) provides a vivid description of the relish with which Greenland Eskimos devoured the innards of ptarmigans, while at the same time viewing their fat-poor flesh as famine food: "Another dish, which will doubtless shock many Europeans, is the entrails of ptarmigans. In this case they do not confine themselves to the stomachs, but devour in a twinkling the viscera with their contents. The remainder of the ptarmigan they sell to the traders for a penny or less...." The pH in the ptarmigan's stomach (both proventriculus and gizzard), as in most other birds, averages between about 1.0 and 2.6, sufficiently acidic to preserve the vitamin C in the bird's food (Denbow, 2000; Farner, 1943, 1960; Joyner and Kokas, 1971; Koelz, 1992; Smit, 1968). And like other monogastrics, including humans, lagomorph stomachs are also very acidic, with pH values ranging between 1.0 and about 2.0 or 2.5 (Brewer, 2006:10; Cheeke, 1987:20; Lebas and Gidenne, 2005; Smith, 1965; Yu and Tsen, 1993:271).

So, based on pH values, whatever vitamin C may be present in the foods eaten by ptarmigans and hares stands a good chance of being preserved in their stomachs. Unfortunately, after an extensive search of the literature, I was unable to find any published vitamin C values for the stomach contents of ptarmigans and only one for hares (see Table 1). So what follows is clearly speculative until actual measurements become available. Nevertheless, the potential is there, since the levels of ascorbic acid in the principal plant foods eaten by these animals during winter and spring, the months when scurvy poses the greatest threat to northern foragers, is quite remarkable (Gustafson, 1954; Rodahl, 1944). Not surprisingly, the diets of both ptarmigans and hares vary seasonally and geographically, but several species belonging to just two genera of brushy or shrubby plants—*Salix* (willow) and *Betula* (birch)—figure very prominently in their diets (Angerbjörn and Flux, 1995; Best and Henry, 1994; Gasaway, 1976; Pulliainen, 1972; Pulliainen and Tunkkari, 1987; Weeden, 1969; West and Meng, 1966). Both animals eat the leaves, buds, stems, twigs, and bark of these plants. However, with the exception of newly emerged willow leaves and tender young shoots early in the spring (Ager and Ager, 1980:34; Heller, 1966:29–30), most parts from these plants, particularly as they mature, become largely or

entirely inedible. But once partially digested in the stomachs of ptarmigans and hares, the chyme may prove to be an excellent winter-spring source of vitamin C.

Finally, there is one other resource that may have become important during the Upper Paleolithic—fish roe. A diversity of evidence (e.g., archaeological, isotopic, artistic) points to the increasing importance of fish following the Middle Paleolithic (Adán et al., 2009; Richards and Trinkaus, 2009). If so, it is equally likely that fish roe entered the diet as well, and may not only have provided an additional source of lipids, most notably long-chain polyunsaturated fatty acids such as DHA (Tocher and Sargent, 1984), but also another valuable way of obtaining vitamin C (see Table 1). I should point out, however, that I have found only a few published sources that document the vitamin C content of roe actually used for food by traditional Inuit or other northern peoples. Two of these studies (Fediuk et al., 2002:229 and Rodahl, 1949:38) found very high vitamin C levels (nearly 50 mg/100 g and 25 mg/100 g, respectively), while a third (Mann et al., 1962:72) found more modest values ranging from as low as 2 to as high as 13 mg/100 g, with an average of 7.5 mg/100 g. Though Mann et al.'s values are not high, even fish roe with a vitamin C content of 7 or 8 mg/100 g is nearly enough to fulfill the minimum requirement needed to stave off scurvy. And the levels reported by Fediuk and Rodahl, if verified by future studies, would constitute truly "rich" sources for foragers subsisting for part or all of the year on a heavily meat-base diet.

In contrast, scattered throughout the more general fisheries and food science literature there are a fair number of reports of ascorbic acid levels for fish roe that are much lower, in fact often below 1.0 mg/100 g (e.g., Bledsoe et al., 2003:337). Why there should be such a tremendous range in values remains unclear. Fediuk et al. (2002:222) comment at some length on this issue, and suggest that much of the variability likely arises from differences in sample selection and preparation, as well as problems with experimental protocols and measurement procedures. So, to be honest, I cannot say with surety that roe was a major source of vitamin C for fish-using northern foragers or for their ancestors in the Upper Paleolithic, but it remains a possibility worth looking into further.

Among ethnohistorically documented foragers in cold temperate and more northerly latitudes, roe was often eaten raw, in fact frequently squeezed directly from the freshly caught fish. This of course would assure the viability of whatever vitamin C might be present in the eggs. Interestingly, however, the pH of raw roe across a spectrum of different species is quite high, with values typically falling between 5.5 and 6.5 (Bekhit et al., 2009:321; Bledsoe and Rasco, 2006:161-18; Bledsoe et al., 2003:347; Himelbloom and Crapo, 1998:627). At such high pH values, the vitamin C in the roe would probably dissipate quickly. It is perhaps not surprising, therefore, that the most common practice throughout the arctic and subarctic was to deliberately ferment or putrefy the roe in above-ground boxes or bags, or in underground pits. As already indicated, this approach would lower the resource's pH, not only inhibiting the germination of *Clostridium* spores, but also greatly enhancing the likelihood that its vitamin C content would not be lost, as well as reducing the chances that the polyunsaturated lipids in the roe would become rancid (de Laguna, 2000:287; Elliott, 1887:56–57; Jewitt, 1849:88; Morice, 1909:597; Spray, 2002:38).

5. Vitamin C and Food Processing

As already discussed, the surest way to get enough vitamin C when living on a heavily meat (*s.l.*)-based diet is to religiously consume the organs, not just the muscle meat, and to eat both either fresh and raw, or frozen. But we have also alluded to the costs of these practices. Raw meat (*s.l.*), whether fresh or frozen, is not only tough and time-consuming to chew, it is much more costly to metabolize than cooked meat (*s.l.*). Cooking serves as a way of "pre-digesting" meat (*s.l.*) before it is ingested, by softening the food and denaturing the proteins, breaking them down into their component peptides and amino acids (Boback et al., 2007; Carmody et al., 2011; Carmody and Wrangham, 2009; Dietz and Erdman, 1989; Speth, 2010; Williams and Erdman, 1999). On the other hand, cooking increases the likelihood that some or all of the vitamin C will be lost or degraded, the magnitude of the loss depending on how long the food is cooked, the temperatures that are reached, and whether the cooking involves boiling. Since most animal food, whether terrestrial or aquatic, marine or lacustrine, contains relatively little vitamin C to start with, any further loss can be nutritionally significant.

An alternative strategy is to deliberately putrefy the meat (s.l.), a technique frequently used, even today, by foragers in the arctic and subarctic: "... Eskimo tribes often live for several months in succession on putrid meat or fish without ever developing scurvy, while Eskimos working for white men or living on purchased provisions have it quite as readily as Europeans living on the same sort of diet" (Stefansson, 1918:1717). As explored in some detail in Speth (2017), once an animal is killed and it no longer draws in oxygen, aerobic bacteria in the body cavity and tissues rapidly deplete the remaining oxygen supply and are replaced by obligate and facultative anaerobic forms, including various species of lactic acid bacteria (LAB). One outcome of this turnover in the microflora is a significant lowering of the pH, creating an environment favorable to the preservation of whatever vitamin C was originally present in the (muscle) meat and organs. Traditional Inuit often putrefied meat and fish in below-ground pits which they deliberately lined with highly acidic leaves, a practice that would not only contribute to the stability of the vitamin C, but might also help create or maintain an environment favorable to the desired microflora (Spray, 2002:34-35). Putrefaction also offers many of the same benefits that one gets from cooking: it effectively "pre-digests" the meat (s.l.) before it is ingested, softening it and denaturing the proteins, breaking them down into peptides and amino acids (Fadda et al., 2002; Forbes et al., 2017; Ordóñez and de la Hoz, 2007; Petäjä-Kanninen and Puolanne, 2007). Moreover, the anaerobic environment inhibits oxidation of the fats (i.e., prevents them from going rancid), and the putrefaction process begins the breakdown (lipolysis) of the lipids, liberating a range of nutritionally beneficial free fatty acids (Forbes et al., 2017; Vasundhara et al., 1983).

Thus, putrefaction accomplishes many of the same things as cooking, but without the need for fire, and hence without the need for fuel. In northern latitudes, dead wood suitable for firewood is often a scarce resource; and even when wood is abundant, as in the boreal forests of the subarctic, it may often be too green or too wet to burn effectively (Henry et al., 2018). Unlike the Inuit, most Neanderthals and their Upper Paleolithic successors would rarely have had access to combustible oil from marine mammals, and at times may have found it necessary to rely on bones as a substitute fuel (Costamagno et al., 2009; Morin, 2010). This practice of course would have precluded their use as a source of dietary lipids, whether by consuming crushed bone-meal

directly or by rendering the fat from the cancellous tissue of the bones.

Interestingly, the methods used by traditional northern foragers to putrefy meat (s.l.) and fish, such as storage in pits, wooden boxes, bogs, ponds and rivers, rock cairns, and seal pokes, created an environment that was hostile to invading pathogens, keeping both meat (s.l.) and fish safe to eat for weeks, even months or longer, its foul smell and maggot infestations notwithstanding (Alakomi et al., 2000; Axelsson, 2004; Caplice and Fitzgerald, 1999; de Moreno de LeBlanc et al., 2015; Fadda et al., 2002; Farouk et al., 2014; Frink and Giordano, 2015; Holzapfel and Wood, 2014; Liu et al., 2014; Ray and Joshi, 2015; Riley and Chavan, 2007; Ross et al., 2002; Singh et al., 2012; Stadnik and Kęska, 2015). In fact, there is no evidence that Inuit or northern Athabaskan (Dené) peoples suffered from outbreaks of botulism—a debilitating and often deadly condition brought on by a neurotoxin produced by Clostridium botulinum—until the 1970's and 1980's, when well-intentioned Euroamericans introduced more "sanitary" methods such as sterilized plastic bags and bottles in which to putrefy their animal foods (Chiou et al., 2002; Fagan et al., 2011; Shaffer et al., 1990). Apparently, by sterilizing the containers the microfloral community or ecosystem (bacterial and probably also fungal), that previously had maintained an environment sufficiently acidic (pH well below 4.5) and inhospitable for Clostridium spores to germinate, was disrupted, turning putrefied meat (s.l.) and fish, once safe to eat, into dangerous and potentially deadly foods (Brown, 2000:159-160; Kastman et al., 2016; Lund and Peck, 2013:106-107; Plowman and Peck, 2002:689; Zhang et al., 2018; Rachel Carmody, personal communication, June 2018).

What about the disgust response that most Euroamericans experience when they encounter rotten meat (*s.l.*) (e.g., disapproving facial expressions, gag reflex, nausea)? Many psychologists over the years have argued that our revulsion to common disgust elicitors, such as rotten meat (*s.l.*), maggots, feces, vomit, and urine, comes hard-wired at birth, very likely selected for as a mechanism to protect infants from ingesting dangerous pathogens, especially during the vulnerable immediate-post-weaning period. More recent studies, however, suggest that children may not even recognize a disgust response, or be able to distinguish it from anger, until they are at least five years old, and probably older, clearly well beyond the critical post-weaning period (Herz, 2012:46–47; Rozin et al., 2008:765; Widen and Russell, 2010). Instead, it increasingly looks as though the substances that elicit the disgust response are culturally demarcated and learned in early infancy, not genetically-based universals (Liberman et al., 2016:9480; Rottman, 2014). One example selected from hundreds of similar observations in the ethnohistoric literature beautifully illustrates the absolute relish with which northern foragers regarded thoroughly putrid, foul-smelling, maggot-infested meat (*s.l.*).

Ikwa...returned in a jubilant frame of mind, and announced his discovery of a cached seal. He asked Mr. Peary if he might bring the seal to Redcliffe in the boat, saying it was the finest kind of eating for himself and family. We could not understand why this particular seal should be so much nicer than those he had at Redcliffe; but as he seemed very eager to have it, we gave him the desired permission, and off he started, saying that he would be back very soon. About half an hour later the air became filled with the most horrible stench it has ever been my misfortune to endure, and it grew worse and worse until at last we were forced to make an

investigation. Going to the corner of the cliff, we came upon the Eskimo carrying upon his back an immense seal, which had every appearance of having been buried at least two years. Great fat maggots dropped from it at every step that Ikwa made, and the odor was really terrible. Mr. Peary told him that it was out of the question to put that thing in the boat; and, indeed, it was doubtful if we would not be obliged to hang the man himself overboard in order to disinfect and purify him. But this child of nature did not see the point, and was very angry at being obliged to leave his treasure. After he was through pouting, he told us that the more decayed the seal the finer the eating, and he could not understand why we should object. He thought the odor 'pe-uh-di-och-soah' (very good)." (Diebitsch-Peary, 1894: 59–60)

6. Summary and Conclusions

Vitamin C is a vital nutrient essential for normal collagen formation and for many other functions. With insufficient vitamin C over a period of about 2–3 months, an individual will likely fall victim to scurvy, a debilitating disease that almost inevitably ends in death if the vitamin shortfall is not alleviated. Even though the minimum amount of the vitamin needed to stave off scurvy is only about 10 mg per day, there is very little vitamin C in either muscle meat or in fat. So, if northern hunter-gatherers preferentially targeted the "meatiest" parts of the animal—the muscle masses that archaeologists typically prioritize in their thinking—these foragers would probably have disappeared from the scene in fairly short order. The calories and protein from (muscle) meat and the non-protein calories from fat are clearly essential to survival in the north. But so too is vitamin C. And in order to assure adequate intakes of ascorbic acid, they had to prioritize the brain and internal organs, particularly the adrenals, spleen, pituitary, thymus, liver, and even the testes and eyes. It is perhaps not all that surprising, then, that Inuit commonly used the (muscle) meat from the element with the highest meat or food utility—the femur—as dog food, not human food. Speculating here, it is even conceivable that Binford's (1978) original Drying Utility Index and Friesen's (2001) revised Meat Drying Index might better serve as proxies for (muscle) meat that is of marginal value to northern foragers, precisely because of its lack of both fat and vitamin C. This would be an interesting issue to explore further.

To add to the nutritional difficulties facing northern foragers, ascorbic acid is the most labile of the vitamins, easily degraded or lost when exposed to water, air, heat, light, and pH levels above about 4.0. This means that drying meat (s.l.) for storage and any form of heat-based cooking, whether by roasting or boiling, may contribute to loss of the vitamin. One can circumvent this problem by eating the meat (s.l.) raw, either fresh or frozen. This has a major drawback, however, as raw meat (s.l.) is energetically much more costly to metabolize than cooked meat (s.l.). The alternative is to putrefy it. Putrefaction accomplishes many of the same things that cooking does, but without the need for scarce fuel or for vitamin-degrading heat. Moreover, the bacteria involved in the putrefaction process lower the pH, often well below 4.0, creating an acidic environment that is much more conducive to the preservation of vitamin C.

It is evident from the ethnohistoric record that northern foragers were very successful in avoiding scurvy. It is also clear that they did so with a mix of foodways, sometimes lightly cooking their meat (s.l.), sometimes eating it raw while still warm from the animal's body, at other times frozen, and at still other times in a thoroughly putrid state. These strategies were not mutually exclusive and were often used in conjunction with each other or in close succession. Unfortunately, we still lack sufficient information to make any sort of predictive statements about when northern foragers might rely more heavily on one or another of these strategies. However, a closer and more thorough reading of the ethnohistoric literature might reveal some rewarding insights into how these different practices fit together into an overall food system.

To the extent that Neanderthals, as well as modern humans in the Upper Paleolithic, had to subsist for extended periods of the year on a diet that was heavily meat (*s.l.*)-based, they too almost certainly faced the threat of scurvy (Guil-Guerrero, 2017). But unlike the conclusions drawn by Guil-Guerrero, I suspect that Neanderthals successfully figured out how to cope with the problem, much like their more modern descendants—by systematically consuming the organs and brains of their prey, by frequently eating their foods raw, perhaps at times frozen, and sometimes very lightly cooked. It is also very likely that they too ate some of their meat (*s.l.*) thoroughly putrefied. Putrefaction is probably the most effective strategy for preserving the vitamin C while at the same time minimizing the caloric costs of metabolizing the protein and fat. At the moment, all of this remains rather speculative. But perhaps by explicitly laying out these expectations, it will give biochemists, molecular biologists, microbiologists, and other specialists a clear research target that they are far better equipped to address than we archaeologists.

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Table 1. Vitamin C content for various aquatic and terrestrial animal resources by body portion. All values are for raw meat and organs expressed in mg/100 g. Published sources are indicated in brackets.^a

MAI	RINE MAMMALS
	spida = Phoca hispida = P. foetida)
Meat	1.6 [F], 0.7-2.0 [A], 3.0 [G]
Liver	23.8 [F], 11.9-18.0 [A], 35.0 [G], 18.0 [Ho]
Brain	14.9 [F]
Pancreas	7.0 [A] [Ho]
Heart	2.0 [A] [Ho]
Eye	3.2 [F], 10.0 [A]
Testis	9.4 [A]
Thymus	26.0 [A]
Blood	0.0 [F], 3.0 [Ho]
Blubber	
	0.0 [Ho]
Mattak [Muktuk] [Epidermis]	03.0 [A], 17.0 [Ho] cal (Erignathus barbatus)
Meat Bearded se	01.0 [G], <0.5 [Hj]
Liver	9.0 [Hj
	le (Delphinapterus leucas)
Meat (dried)	1.1 [F], 4.2 [St], <1.0 [Hj]
Liver	16.2 [St], 19.0 [Hj]
Kidney	
Brain	8.1 [St] 18.0 [St]
Pancreas	
	22.0 [St]
Heart	6.4 [St]
Adrenal Gland	97.3 [St]
Mattak [Muktuk] [Epidermis]	36.0 [F], 38.0 [G], 38.0 [St], 25.0 [Hj]
Blubber	5.0 [G], 5.3 [St]
	(Monodon monoceros)
Meat	<0.6 [Hj]
Mattak [Muktuk] [Epidermis]	31.5 [F]
	(Odobenus rosmarus)
Meat	1.0 [F]
Mattak [Muktuk] [Epidermis]	0.7 [F]
	FISH
	FISH har (Salvelinus alpinus)
Arctic Cl Meat (Flesh)	
Meat (Flesh)	har (Salvelinus alpinus)
Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F]
Meat (Flesh) Sculpin Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.)
Meat (Flesh) Sculpin Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] ttefish (Coregonos nasus)
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.)
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Cariboo	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS in (Rangifer tarandus)
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Cariboo Meat	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS tu (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha]
Meat (Flesh) Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS to (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS in (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS in (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G]
Meat (Flesh) Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Cariboo Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha]
Meat (Flesh) Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS to (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F]
Meat (Flesh) Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha]
Meat (Flesh) Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS to (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Polar B	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] Itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS In (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F] ear (Ursus maritimus)
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Polar B	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS to (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F] ear (Ursus maritimus) 1.0 [G]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Polar B Meat Domest Stomach Contents	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F] ear (Ursus maritimus) 1.0 [G] tic Cattle (Bos taurus) 0.0 [K]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribot Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Polar B Meat Domest Stomach Contents	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] tefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS to (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F] ear (Ursus maritimus) 1.0 [G] tic Cattle (Bos taurus)
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Cariboo Cariboo Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Meat Polar Book Stomach Contents Mountain Hare (Limba)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS in (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.8 [G] in (Fill of the salar indius) 1.0 [G] itic Cattle (Bos taurus) 0.0 [K] itic pur variabilis = Lepus timidus) 1.3 [A], 1.3 [R]
Meat (Flesh) Sculpin Meat (Flesh) Broad White Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Caribor Meat Liver Kidney Heart Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Meat Domest Stomach Contents Mountain Hare (L Meat Liver	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS u (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.0 [F] ear (Ursus maritimus) 1.0 [G] tic Cattle (Bos taurus) 0.0 [K] eepus variabilis = Lepus timidus) 1.3 [A], 1.3 [R] 4.8 [R]
Meat (Flesh) Sculpin Meat (Flesh) Broad Whi Meat (Flesh) Atlantic Meat (Flesh) Liver Roe Cisco Roe TERRE Cariboo Cariboo Meat Liver Kidney Heart Marrow (Limbs) Subcutaneous Fat Kidney Fat Stomach Contents Meat Polar Book Stomach Contents Mountain Hare (Limba)	har (Salvelinus alpinus) 1.2 [F] (Myoxocephalus spp.) 1.1 [F] itefish (Coregonos nasus) 2.8 [F] Salmon (Salmo salar) 1.4 [R] 8.9 [R] 25.1 [R] (Coregonus spp.) 49.6 [Fe] STRIAL MAMMALS in (Rangifer tarandus) 0.9 [F], 1.4 [G], 0.0 [Ha] 23.8 [F], 11.9 [Ha] 8.9 [F] 2.6 [F] 0.0 [Ha] 1.8 [G] 0.0 [Ha] 1.9 [F] ear (Ursus maritimus) 1.0 [G] tic Cattle (Bos taurus) 0.0 [K] sepus variabilis = Lepus timidus) 1.3 [A], 1.3 [R]

Muskox (Ovibos moschatus)		
Meat	0.8 [R], 1.5 [G]	
Liver	10.4 [R]	
Kidney	5.9 [R]	
Brain	12.8 [R]	
Pancreas	3.9 [R]	
Heart	1.5 [R]	
Tongue	1.0 [R]	
Testis	18.2 [R]	
Eye	0.7 [R]	
Amniotic Fluid	0.4 [R]	
Subcutaneous Fat	0.0 [R]	
Stomach Contents	0.5 [R]	
BIRDS		
Ptarmigan ($Lagopus mutus = L. muta$)		

Meat 1.7 [F], 1.2 [G], <2.0 [Hj]

^a[A] (Andersen, 2005), [F] (Fediuk, 2000), [Fe] (Fediuk, 2002), [G] (Geraci and Smith, 1979), [Ha] (Hassan et al., 2012), [Hj] (Hjarde et al., 1952), [Ho] (Høygaard and Rasmussen, 1939), [K] (Knight et al., 1941), [R] (Rodahl, 1949), [St] (St. Aubin and Geraci, 1980).

