

Theoretical perspectives on the dietary role of small animals in human evolution

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Résumé

Le paradigme majeur retenu pour rendre compte de l'exploitation des petits animaux découle du principe d'évaluation des bilans énergétiques impliqués. Les modèles qui s'en inspirent dérivent tous de « l'écologie évolutive », en particulier des modèles d'évaluation des spectres de consommation (« Diet Breadth model ») qui ne prennent en compte que les facteurs de dépense énergétique. Dans cet article, on compare et critique le rôle des petits animaux à travers les résultats fournis par l'évaluation des bilans énergétiques, par une approche que nous qualifions « d'écologie nutritionnelle ».

Abstract

The dominant paradigm for explaining small animal use has been an ecological one based on the capture of energy. The derived models are all variants of Evolutionary Ecology, in particular the Diet Breadth model with its use of energy as the sole currency. In this paper we compare and contrast the study of small animal use through energy-based models with an approach we refer to as Nutritional Ecology.

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In the past, archaeologists studying Palaeolithic and Mesolithic subsistence in Europe and the Near East noted specialized large game hunting economies characterized the former and generalized Broad Spectrum economies the latter (*e.g.* Binford, 1968 ; Clark, 2000 ; Hayden, 1981 ; Neeley, Clark, 1993 ; Straus, 1996). Despite increasing evidence of regional variability in subsistence, this perception remains steadfast. This is due to a number of reasons such as : a biased archaeological record of animal bones taken as an accurate reflection of past human diet ; theoretical emphasis on energy-based foraging models ; and the intensity of research in areas where glacial climatic conditions curtailed plant diversity, thus limiting the options available to prehistoric people.

One current argument is that human diet became much more meat-focused early in human evolution, and this subsistence change was related to brain evolution and the colonization of temperate Eurasian latitudes (*e.g.* Isaac, Crader, 1981 ; Aiello, Wheeler, 1995 ; Stiner, 2002). This change culminated in the hunting economies of Middle and Upper Palaeolithic peoples in Eurasia. Small terrestrial game, aquatic resources and plants entered the diet only after large-game populations became depressed due to hunting pressures brought on by ever-increasing Pleistocene human populations and/or climate change which altered game habitats. Recent work suggests that Late Upper Palaeolithic humans may not have negatively impacted large game populations and that a dietary shift occurred much earlier than the Pleistocene-Holocene transition (Grayson, Delpech, 1998, 2003 ; Delpech, 1999 ; Stiner 2001 ; Hockett, Haws, 2003). Stable isotope and trace element studies lend support to the idea that Neanderthals were highly carnivorous while early modern humans ate a slightly more diverse diet (Richards *et al.*, 2001 ; Bocherens *et al.*, 1999). The explanations for the shift to a more diversified diet during the latter Pleistocene are still framed in terms of population pressure on resources (Stiner 2001), though others such as niche differences between two competing human populations, and nutritional decisions resulting in greater reproductive success of modern humans, have been proposed (Hockett, Haws, 2003, 2004).

In recent decades, the dominant paradigm for explaining small animal use has been one based on the capture of energy (*e.g.* Broughton, 1997 ; Stiner *et al.*, 2000). The derived models are all variants of Optimal Foraging Theory (OFT or OF) borrowed from ecology and economics. The Diet Breadth model, with its use of energy as the sole currency to explain prehistoric foraging behaviour, has led many archaeologists to view small animals as marginal resources in human subsistence because the model always ranks large mammals higher than small animals on a net-energy return scale (*e.g.* Davidson, 1976, 1989 ; Aura, Pérez Ripoll, 1995 ; Simms, 1987).

Recent studies utilizing evolutionary approaches that focus on the reproductive advantages of consuming all essential nutrients vital to human health rather than energy alone provide an alternative view of the significance of small animals in human evolution. This paradigm is referred to as nutritional ecology. After reviewing some of the theoretical underpinnings of OFT and its application in

archaeology, we use nutritional ecology to show how changing currencies can alter perceptions of small animal use through time.

Evolutionary ecology and human behavioural ecology

Evolutionary ecology is defined by Winterhalder and Smith (1992, p. 5) as « the application of natural selection theory to the study of adaptation and biological design in an ecological setting. » The evolutionary ecology approach to explaining human behaviour is known as Human Behavioural Ecology (HBE) (Winterhalder, Smith, 2000). The most commonly utilized set of models applied to archaeology are OF models borrowed from ecology (Winterhalder, 1981 ; Broughton, O'Connell, 1999 ; Winterhalder, Smith, 2000). Although these models are thought to have their roots in economic theory (MacArthur, Pianka, 1966), critical concepts such as energy maximization that form the core of OFT can be traced back to early nineteenth century European chemists and physicians such as William Prout and Justus von Liebig. One primary assumption of OFT in archaeology is that natural selection has shaped human behaviour to adapt to environments by harvesting resources with maximum energy efficiency. Adaptation is measured in net energy capture, while success is determined by net acquisition rate (Winterhalder, 1981). Though energy in general is the most common currency, others can also be used although they almost never are (Jochim, 1976 ; Winterhalder, 1981 ; Keene, 1983).

Diet breadth models

The basic assumption in OF models is that maximization of energy return rates is the primary goal of foraging (Kelly, 1995). Resources are ranked according to post-encounter return rates, based on the amount of energy gained per unit time after encounter, usually kilocalories per hour. Two of the approaches used in this framework are patch choice and prey choice models. Patch choice models recognize that human foragers rarely target single resources and rarely procure individual animals in the day-to-day search for food. The assumption is that camps are moved from one place to another to maximize the net-energy return of patches of the highest ranked food resources in heterogeneous environments. In archaeology, these models (*e.g.* Zeanah, 2000) are highly speculative. Without realistic paleoenvironmental reconstructions, archaeologists cannot use them in periods for which there is no modern analogue because it is impossible to know what the densities, spatial layouts, and precise resource availabilities would have been. With such an incomplete record, one cannot accurately rank food patches and predict what decisions would have been made. In most cases, patch choice models cannot be adequately tested against the archaeological record.

In archaeology, prey choice models that rank individual species have been used more frequently than patch choice models. The main assumption is that

foragers will always take the highest ranked prey when encountered, and if these species do not satisfy the caloric needs of the group others will be added to the diet in descending order of net-energy return.

« Logical arguments suggest and empirical data from experimental and ethnographic settings demonstrate... that, for singly-handled animal prey, post-encounter return rates are generally scaled to prey body mass. Among Holocene North American vertebrates in particular, the larger the animal, the higher the post-encounter return rate. This fact, combined with the proposition that overall foraging return rates declined in the late Holocene, leads to the prediction that low-ranked (smaller-sized) vertebrates should have become more important in human diets at this time... » (Broughton, O'Connell, 1999, p. 155).

Despite long search time, large game are usually the highest ranked resource because the caloric yield is great enough to lower handling costs significantly. Small game are often more abundant and thus have lower search costs, but their pursuit costs are usually considered higher because more effort goes into their capture. Also, their small package size results in a lower post-encounter return rate requiring a higher harvest rate to make them worth the effort. Therefore, the abundance of a resource does not determine its inclusion in the diet. Extremely abundant, low-ranked resources may be ignored as long as high-ranked resources are sufficiently encountered (Winterhalder, 1981 ; Bettinger, 1991 ; Kelly, 1995).

Accordingly, if foragers are subsisting on occasional large game but mostly plants or small animals they are assumed to be adapting to a population-resource imbalance due to resource depression caused by either overharvesting of high-ranked game, climate-induced environmental changes or possibly some other factor which has lowered the return rate for the highest ranked resource, forcing people to add previously uneaten, lower ranked resources to the menu. If small game are being eaten to any significant degree, then « economic intensification » is generally assumed to have occurred through time (*e.g.* Smith, 1998 ; Zvelebil, 1990). Arguably, regions with generalized hunter-gatherer diets probably reflect low frequencies of highly ranked resources, most often large game. Either the environment is « poor » to begin with or resource depression has occurred due to climate change or over-harvesting.

Seeking alternative models for human foraging behaviour

The reliance on energy as the sole currency in diet breadth models may underestimate the value of many resources. Fat and protein content plays a critical role in hunter-gatherer food choices (Speth, Spielmann 1983). Although the diet breadth models rank small game such as rabbits lower than deer, for example, because of a lower kcal/kg yield, the protein/kg of meat in rabbits and deer is nearly equal (Erlandson, 1988 ; Hockett, Bicho, 2000). In addition, return rates can change due to technology, seasonal changes in animal behaviour and nutri-

tive value, or variations in forager skill level (Kelly, 1995). Further, prey choice models rank the net energy return of capturing individual animals, or « singly-handled animal prey ». However, many if not most animal prey (whether large or small) are pursued with the intent of taking multiple individuals. The prey choice approach also ignores critical variables such as the abundance of small game that can, in fact, render their return rates higher than large game on a consistent basis that can be scheduled for capture by foragers (Madsen, Schmitt, 1998).

From a philosophical standpoint, OF models refer to the foraging habits of nonhuman animals such as black birds, flying squirrels and goldfish. OF modelers in archaeology essentially assume the same selective processes that shape the foraging habits of these nonhuman animals also shape the foraging habits of humans. To many anthropological archaeologists, however, symbolic-oriented cognition influences sociocultural change in ways that cannot always be explained through energy maximization and Neo-Darwinian models. Put another way, humans engage their social and ecological environments in ways that are fundamentally different than the behaviours of the animals that gave rise to OF models in ecology (*e.g.* Ingold, 2000).

According to HBE, natural selection favours genes that code behaviours that produce reproductively more fit individuals. In foraging theory, energy maximization enables greater reproductive success so humans will adapt to changing environmental conditions by selecting food resources to provide the most energy with the least amount of effort. While ethnographic and experimental research has been used to support OF models (Hawkes *et al.*, 1991), more recent evolutionary ecology approaches have recognized reasons other than energy maximization behind subsistence decisions (Hawkes *et al.*, 2001). These authors observed that hunters did not take large game primarily to provide food for their families but to acquire mating status. Thus, self-interested individuals were engaging in behaviours that precluded maximizing energy for the group. O'Connell (2000) discussed a similar pattern among Australian aboriginal hunters. Ultimately, however, these authors relate these behaviours to reproductive fitness: better hunters « show-off » to mate with better mothers who better provide for their children. We are not suggesting that this interpretation applied to a specific modern group is necessarily in error; we simply note that even OF modellers in archaeology have found that human behaviour may be unrelated to energy maximization.

This renders human decisions about what paths to pursue under conditions encouraging sociocultural change less predictable than accounted for in prey choice models (Binford, 2001). For example, during the European mid-Early Upper Palaeolithic, human subsistence choices did not conform to the predictions of prey choice models, as so-called « lower-ranked » small animals were regularly consumed during a time when humans were arguably tethered to easily-culled, abundant herds of large game (Richards *et al.*, 2001; Pettitt *et al.*, 2003). In southern Iberia, rabbits were intensively exploited throughout the Upper Palaeolithic in the absence of resource depression (Hockett, Haws, 2002; Haws, 2003).

Although Winterhalder and Smith (2000, p. 52) call human behaviours unrelated to the maximization of energy intake or the improvement of reproductive fitness of individuals « ancillary variables », we think these are not « ancillary » to explaining the historical trajectories of sociocultural change. This does not mean that natural selection does not act on human choice and behaviour ; it simply means that the study of human behaviour can be best understood through a non-reductionist set of models that may include those that are fundamentally different from the Neo-Darwinian approach. As Politis and Saunders (2002, p. 127) point out, « ideological imperatives » such as food taboos create serious problems for optimality models when high-ranked large game are ignored for non-energetic reasons. Perceptions of « taste » also complicate applications of prey choice models to human behaviour. Meehan (1983) observed that Anbarra women preferred less abundant, harder to gather shellfish that provided fewer post-encounter calories but were better tasting. In both cases the absence of higher-ranked resources in a potential archaeological assemblage might be misconstrued as evidence for diet breadth expansion due to resource depression.

Finally, we find that OF models in archaeology are untenable for a theory of human demography (Hockett, Haws, 2004). The nutritional factors that impact human mortality are not solely or primarily based on caloric intake or net energy returns. We seek to develop a model of the impact of subsistence decisions on the demographic patterns of human foragers that is compatible with the knowledge of human demographers, nutrition scientists, and medical researchers.

Nutritional ecology and human dietary choice

We suggest that nutritional ecology offers a more comprehensive means of understanding the consequences of prehistoric dietary choice because the model is grounded in assumptions that take into account the current state of knowledge about the nutritional parameters that affect human demographic trends. We recently defined nutritional ecology as « the study of the relationship between essential nutrient intake and its effects on overall human health, including growth and maintenance in individuals and general demographic trends in populations » (Hockett, Haws, 2003, p. 211). The nutritional ecology approach also assumes that natural selection acts upon human dietary choices and that reproductive success may be enhanced by those choices. However, we reject the notion embedded in the prey choice model that resource selection is determined by the net acquisition rate of energy.

Nutritional ecology recognizes that it is the balanced intake of essential nutrients (proteins, fats, carbohydrates, vitamins, minerals and water) that leads to lower foetal-to-infant and maternal mortality and greater life expectancy in human populations (Hockett, Haws 2003, 2004). In a nutritional ecology approach, foraging efficiency is not measured in net energy return of calories from the environment, rather in the diversity of essential nutrient intake of which energy consumption plays a critical, albeit not the sole, role. It simply states that

those human foragers that consume a more balanced diet of essential nutrients may have greater reproductive success than those who consume a less balanced diet.

The nutritional ecology model requires that a number of critical assumptions be accepted: (a) that human foragers may make dietary choices that result in a balanced diet whether by accident or intention, (b) that balanced nutrient intake from a wide diversity of food sources results in better health, (c) that better health leads to lower foetal-to-infant and maternal mortality rates and greater reproductive success, and (d) that lower foetal-to-infant and maternal mortality rates and higher reproductive success are necessary for population growth.

Subdividing animals by general taxonomic categories such as terrestrial mammals, birds, shellfish, fish, marine mammals and reptiles regardless of size or the amount of calories they provide per unit animal may be useful in discussions of long-term trends in human health. Most terrestrial mammals provide a relatively rich supply of several essential nutrients, and are energy-dense. However, shellfish provide carbohydrates missing from terrestrial game. Fish and shellfish are relatively rich sources of vitamin-D and vitamin-E. Birds provide rich sources of fats and nearly twice the kilocalories per hundred grammes of flesh than terrestrial mammals, shellfish and some fish. Thus, different types of animals provide different sources and amounts of essential nutrients (fig. 1). Importantly, because most fish, shellfish, and birds come in relatively small packages, small animals (including terrestrial small game such as leporids), together with plants

Essential Nutrients	Terrestrial Mammals (muscle)	Terrestrial Mammals (organs)	Shellfish	Birds	Fish	Plants	Reptiles ¹
Energy (kcal)	119	195	74	215	166	132	89
fat	2.8	10.0	0.97	14.1	8.1	2.5	0.50
protein	22.0	20.0	12.8	21.7	21.7	8.3	19.8
carbs	0	4.0	2.6	0	0	14.8	0
Non-Caloric							
C	0.17	12.7	13.0	3.6	0.17	32.5	-
Thiamin	0.22	0.16	0.08	0.19	0.22	0.13	0.12
Riboflavin	0.26	2.4	0.21	0.20	0.31	0.19	0.15
Niacin	4.8	9.4	1.8	4.2	5.9	1.1	1.1
B-6	0.34	0.50	0.06	0.53	0.40	0.07	0.12
B-12	4.6	27.6	49.4	0.65	6.6	-	1.0
A (IU)	0	9196	300	118	322	138	100
Folate	7.4	105.0	16.0	21.0	16.7	2.4	15.0
D	0	0.75	4.0	-	8.0	-	-
E	0.20	1.2	1.0	0.70	0.25	2.2	0.50
Calcium	9.5	10.8	46.0	22.5	145.7	110	118
Iron	3.4	4.1	14.0	5.4	1.7	3.0	1.4
Potassium	338	313	314	288	416	387	230

¹ Reptile values are based on the green turtle.

Fig. 1. Macronutrient and some micronutrient values of various types of foods (see Hockett, Haws, 2003 for further details).

which are often more micronutrient dense than animal foods, provide the key to the balanced intake of essential nutrients and one critical element to greater reproductive success in human foragers (Hockett, Haws, 2003, 2004).

Besides protein, fat and carbohydrate, humans require many micronutrients for the proper development of the human foetus and the health and well-being of the mother (*e.g.* Fall *et al.*, 2003). Some argue that hunter-gatherer diets are naturally diverse and they will consume the necessary nutrients by default. Jochim (1998) argued that foods high in energy are naturally high in protein and fat, and they will also provide all of the necessary amino acids, vitamins and minerals. However, as Stini (1971, p. 63) wrote, « ...proteins are necessary to supply the necessary balance of essential amino acids and vitamins and minerals are often not available in adequate quantities in foods that are excellent energy sources. » Therefore, one cannot assume that maximizing energy will result in adequate essential nutrient intake.

If subsistence changes through time in specific places are characterized by an older focus on large game animals followed by an increasing dependence on small animals, plant foods, or both, OF modellers in archaeology interpret these changes as a reduction in foraging efficiency due to population pressure on resources or habitat loss through climate change. Recently, Hockett and Haws (2003, 2004) showed how a nutritional ecology approach alters the concept of « foraging efficiency » and changes causal and chronological relationships among subsistence and demographics during the Pleistocene. Ironically, humans maximizing caloric intake may exhibit higher foetal-to-infant mortality rates and shorter life expectancies than those who eat a more balanced diet of essential nutrients. Therefore, energy maximizing may inhibit population growth. In fact, a highly carnivorous diet is energy inefficient compared to an omnivorous one due to energy loss at each trophic level. Energy loss also limits population size, thus explaining why the highest-level carnivores are also the rarest animals (Colinvaux, 1993). Humans feeding as top carnivores adapted to large game hunting would not have been able to grow their populations. This is confirmed by Delpech (1999) who argued that Late Pleistocene humans in Europe north of the Alps (adapted to large game) experienced population boom and bust along with changing ungulate biomass.

A number of recent articles have commented on the potential consequences of a diverse diet. Erlandson (2001) specifically noted the importance of incorporating shellfish as part of a diverse subsistence base that may have led to population increases through time (see also Parkington, 2001). From a nutritional ecology perspective, then, increases in human population densities may be a result of changes in human diet rather than demographic pressures forcing dietary changes. From a demographic perspective, this explains why European Upper Palaeolithic foragers who consumed more small, non-terrestrial game and plant foods within increasingly restricted territories probably had a selective advantage over those groups « optimally foraging » at a higher trophic level in head-to-head competition. By lowering trophic level, anatomically modern

humans would have enabled population growth necessary to swamp the Neanderthals genetically.

Researchers can use nutritional ecology to investigate whether specific dietary strategies over time may have led to decreased foetal-to-infant and maternal mortality rates and increased longevity, and if so, whether these strategies could lead to the spread of human populations at the expense of others. Importantly, all types of essential nutrients must be included to structure a model that is compatible with current knowledge about the way diet affects human demographic patterns. In nutritional ecology, small animals, and in particular non-terrestrial game (as well as plant foods), play central roles in human dietary diversity, health patterns, and reproductive fitness.

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