Food Remains, Food Webs and Ecosystems

M. K. JONES

Department of Archaeology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, U.K.

Summary. It is the aim of this paper to take stock of recent developments in the techniques of bio-archaeology towards the reconstruction of past food webs, and to highlight some areas in which their dynamics could be usefully pursued. Reconstruction of these webs is explored in the first two sections following the introduction, the first dealing with new developments in recognition and identification of the building blocks, and the second with exploring the linkages between them. The third and fourth sections consider some possibly characteristic features of human webs and the detection of stress and change within them.

1. Introduction

This conference marks a threshold that has been passed in the understanding and reconstruction of past food economies. Over the last decade, a number of volumes have addressed the difficulties of binding together independent and sometimes very detailed archaeological studies of particular foods into a coherent, and at least semi-quantitative analysis of early economies (cf. Sheridan and Bailey 1981, Jones M. 1983). A recurrent proposal within those volumes was that various ecosystem models, such as have been gaining increasing currency in early palaeolithic studies, (cf. Foley 1977, 1986) had considerable potential for studies of Holocene sites that were yielding in some cases enormous quantities of bio-archaeological data (Thomas 1983, 1989). At the same time it remained clear that the quantification of those various categories of data recovered was fraught with difficulties. We now see the burden of providing this quantitative overview being lifted as the study of

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human teeth and bones, human faeces, and vessels used directly in the consumption of food, are showing the potential to provide this information by chemical and isotopic means (*cf.* the papers by Evershed *et al.* and van der Merwe in this volume).

As these latter approaches break new ground in providing the broader framework of food consumption, the way becomes more open for the techniques of bio-archaeology to enrich those patterns with extremely fine qualitative detail. The two developments that enhance progress in this area are first the new methodologies that have grown within bio-archaeology over the last decade, and second, the fast growth in interest in the form and structure of food webs in various parts of the natural world (Pimm 1982; Lawton and Warren 1988). We are now considerably closer to being able both to build past human food webs through direct evidence of what their components are and how they are energetically or nutritionally linked, and to explore the dynamics of those constructed webs and consider the consequences for the trajectories of past human ecosystems.

2. Identifying the building blocks

Identification of food remains has traditionally been based on the visual comparison between modern reference collections and macroscopic archaeological fragments of durable plant and animal tissues or various forms of cast or mineral replacement fossil. Where such fragments survive, they contain considerable morphological detail, but their survival is restricted in range. This is less problematic for animals used as food, as the majority have at least some skeletal element, than it is for plant foods, of which a very large number are composed of non-durable tissues (*cf.* Harris 1969). Thus the critical research in this area has been, and continues to be, in extending the range through identifying new tissues, and in improving separation techniques.

The plant tissues most amenable to conventional analysis have been seeds and fruits of neolithic and later periods. There have been major gaps in palaeolithic food plants of all types, and root, tuber, leaf and stem foods for all periods, but these gaps are gradually closing (*cf.* Harris and Hillman 1989). At the Institute of Archaeology University College London, a great deal of success has been achieved in identifying fragmented parenchymatous tissues, which are proving a promising route to the identification of bulky plant foods such as tubers (Hather 1988). Similarly, at the Environmental Archaeology Unit at York University a wide range of stem tissues such as *Allium* have been successfully identified, as well as a number of economic non-food plants, on the basis of epidermal fragments retaining their stomata (Tomlinson 1985). The identification of fragmentary vegetative tissue in general will have major significance in coprolite studies, where their survival is sufficient for some quite detailed analyses (Hillman 1986).

At the same time as the range is being extended, so the precision of taxonomic identification within food species is being enhanced in two ways. First, the cellular structure may often be more tightly genetically defined than the gross morphology so often relied upon in visual comparison, and there is in some cases a very direct relationship between cell size and levels of ploidy. Thus scanning electron microscopy has proved of great value in distinguishing cereal species (Körber-Grohne 1981, Körber-Grohne and Piening 1980) though the technique is not without practical difficulties in terms of within-tissue variation (S. Colledge pers. comm.). A second method of identification with undoubted long-term potential is the incorporation of the range of chemical methods discussed by Evershed *et al.* and Hedges and Sykes (both in this volume) with the study of the food fragments themselves. Two notable and promising examples are the isolation of taxonomically specific lipids from ancient cereals (McLaren *et al.* 1991) and of DNA from both plant and animal foods (*cf.* Hedges and Sykes, this volume)

Thus the state of play on improved identification is generally involving a continuing move from the macroscopic to the cellular, sub-cellular and chemical levels of analyses. This move is relaxing the traditional restraints on both the range of organs and tissues that can be successfully identified, and the genetic range and precision that can be entertained. In the case of DNA analysis at least, this potentially takes us for the first time beyond the range of genotypes that are extant in our current collections of reference material.

3. Food web interactions

Palaeo-economic studies have quite naturally concentrated on those food web interactions directly connecting with humans, in other words the plant and animal foods consumed by the humans themselves, and analyses of the skeleton and faeces of the humans themselves. In order to reach a dynamic understanding of the food web as a whole, that approach needs to be extended to other members of the past food webs we study. It is in other words fruitful to ask the same questions about the nutritional status of the animals associated with humans as we ask about the humans themselves, and indeed related questions about the nutritional status of the plants on which they feed.

Much work has been initiated in this direction. For example, the analyses of human teeth and jaws to explore diet, nutrition and health are well advanced (Hillson 1989, Hillson and Jones 1989), and some of these analyses

are now being considered in the context of domestic animals. One example is the study of hypoplasia, a term referring to certain developmental defects that appear around the tooth crown (Hillson 1986, 127). Current research is demonstrating how these defects, which correlate with a range of metabolic and nutritional deficiencies, can be closely linked to life histories of the individuals concerned, by association with the cyclical physiology of tooth growth (Hillson 1989, Hillson and Jones 1989). They have been widely examined in human and hominid populations, and the analyses are now being explored in the context of non-human teeth, for example pig teeth, which have already been shown to be amenable to this kind of analysis. Periodontal disease can also be examined in the context of diet, ecology, and health (Hillson 1986, 305) and this too applies to animals as well as to humans. A further example is tooth microware analysis, also applied to a range of human and hominid specimens to establish the categories of food into which the teeth came into contact (Hillson 1986, 186) is currently being developed at Sheffield for application to domesticated animals (I. Mainland pers. comm.).

Faecal analyses have also been extended to animals. An example is a study by Robinson and Rasmussen (1989) of the waterlogged neolithic lake village deposits at Weier, north east Switzerland. Animal dung deposits were used to demonstrate the use of cereal grains and "leafy hay" (stripped tree foliage) in animal fodder. Gay Wilson's work on animal dung from a Roman well also provides evidence for the use of grain as fodder (Wilson 1979).

Extending methodology from humans to animals also applies to identifying their food sources directly, and this returns us to a problem already discussed, namely that the animals we use as food have tended to be heavily dependent on soft plant tissues that do not survive well. Studies of the rich waterlogged deposits of urban sites have allowed the recognition of meadow hay, for example in the Roman phases of Carlisle and York, together with some of its associated fauna, including horse roundworm eggs (Hall and Kenward 1990, Goodwin and Huntley in McCarthy 1991). The elusiveness of any similar evidence in prehistory may be as much to do with the relative importance of leafy hay from woodland, as opposed to meadow hay. At Sheffield work is in progress identifying leafy hay from insects and other "marker" fossils, including associated insects, pollen and dendrochronological traces (P. Halstead pers. comm.).

The nutritional status of plants must of be approached in a quite different way. The direct analysis of elemental assimilation in actual plant tissues has considerable potential but is in its early stages. Current research at Durham for example is examining trace element profiles fixed within carbonised wheat grains (J. Langston pers. comm.). Rather better established is a community ecology approach to the nutrient and water status of those communities exploited for plant food, and by implication the plant foods themselves. Analyses of the autecology and synecology of arable weed species has implicated nitrogen deficiency as a major problem of later prehistoric crop production, alongside concurrent problems in the hydrological management of the agricultural landscape (Jones M. 1984, 1988a, 1988b). This analytical approach is being given further statistical rigour through the application of various forms of multivariate analysis (Jones G. 1991).

In summary, the major moves forward have been in the extension of existing methodologies for the study of human remains to other members of the human food web, and in addition, the use of community ecological approaches to the primary levels of the food web.

4. Characteristic aspects of human food webs

It is frequently the case, at least in the Holocene, that the components of human food webs are extensively connected, not just by transfers of energy and nutrients from the consumed to the consumer, but also by transfers of information in the reverse direction, to "workgates" at lower trophic levels, steering energy flows in chosen directions (*cf.* Ellen 1982, chapter 5). These workgates that abound in "managed" ecosystems perhaps provide the sharpest definitions we can articulate around such concepts as environmental management and agriculture.

The archaeological recognition of management, including agriculture, has moved more and more away from dependence on oversimplistic correlates of a "domestication event" to examining direct evidence for these workgates. This represents in part a legacy of the work of Eric Higgs and his colleagues who suggested we split up the concept of domestication into more tangible component units, and stimulated a taphonomic route to the rediscovery of the processes people applied to their food plants and animals (Higgs 1972, 1975).

Isolating these processes has itself become ever more closely focussed. At first depending on the physical alterations visible on bones and seeds, our methods now focus also on the physiological response of plants and animals during their lives to human action (Higgs 1972, 1975). Best established in this field is the skeletal response of domestic animals to the wide range of "lifestyles" to which we subject our animals. An obvious example is the use of animals for traction, and the influence on forelimb morphology (Armour-Chelu and Clutton-Brock 1985). Plant taphonomy has only more recently moved from studying the physical separation of components (Hillman 1984, Jones G. 1984, Jones M. 1985) to this kind of morphological detail. Current research at Cambridge is exploring the relationship between harvest time and fruitstone morphology, and at London, extensive work has been conducted on the structural and molecular effects of cooking and digestion, an example of which is the use of electron spin resonance to elucidate thermal histories of food plants (Hillman *et al.* 1985).

Moving from a more obvious characteristic feature of Holocene human food webs to a more speculative one, a recurrent theme of interest in theoretical ecology has been the degree of interconnectedness or "connectance" of food webs, expressed as the proportion of theoretically possible feeding links that have actually been established in the real food chain (De Angelis 1975, Gardner and Ashby 1970, May 1972, Rosenzweig 1971). Some of this work has overturned an intuitive presumption that high levels of connectance bind the system together and thus endow it with greater stability. Indeed the reverse would appear to be true and systems would instead be expected to stabilise at lower levels of connectance.

Now that a number of detailed bio-archaeological studies of particular Holocene human food webs are in existence, or at least well on the way to publication, we can begin to make some provisional observations on apparent levels of connectance. What seems to be emerging is not a simple linear pattern towards stable levels of connectance, but instead levels that fluctuate considerably in space and time, frequently reaching levels that seem high in comparison with non-human webs. We can see this divergence in connectance by contrasting some inland and coastal food webs in the later British Holocene, both of which have received considerable attention from bio-archaeologists.

This can be illustrated by reference to the Viking coastal midden site of Freswick, Caithness (Rackham *et al.* 1984), where up to a metre of midden deposits yielded evidence of such terrestrial domesticates as ox, sheep/goat, domestic fowl, cultivated oats and six-row barley, a few wild dry land plants and animals that may have been consumed, together with over 20 species of coastal and marine molluscs, crustaceans and fish. In addition, both peat and seaweed were collected, both of which may plausibly have entered the human food web.

We can contrast this sustained dietary breadth with the progressive narrowing that is evident in later prehistoric terrestrial communities in Britain. There is much evidence that inland neolithic communities retained a fairly broad web, drawing on domesticated plant and animals as well as wild animals, nuts and fruits, but that this web contracted progressively towards the end of prehistory, as diet was more and more restricted to grain crops and domestic animals, bound together by much sharing of plant foods and secondary products within this restricted species group (Grant 1981; Jones M. 1983, 1988a) before broadening out again in the historic period (*cf.* Greig 1991). Little has as yet been done to examine how these very variable degrees of connectance interact with information transfer along the workgates of the food web, beyond the intuitive observation that highly connected webs are also highly "managed". In turn their relationship with various forms of "stability" and "resilience" has much to offer, if indeed those concepts are the appropriate ones to articulate in the case of highly changeable systems (*cf.* Allen and Starr 1982, McGlade and Allen 1986).

In summary, recent theoretical ecology provides bio-archaeology with a language with which to define with greater precision the particularly human aspects of food webs. The next modelling steps are in their infancy, but the methodology nevertheless exists to move in that direction. That move involves consideration of such features as connectance and workgate structures in the context of deflection and change.

5. Deflection and change within past food webs

While, as mentioned at the outset, direct quantification of populations from bio-archaeological data has always been a particularly problematic area, those data have proved and are proving extremely well suited to the recognition of ecological stress within past human food webs, largely because the "scars" of that stress affect the ecosystem in so many of its parts. This has ranged from structural stress within the soils supporting the food webs (Dimbleby 1962, Limbrey 1975), nutritional stress in both the plant communities at the base of the food web (Jones M. 1984), and the herbivores feeding upon them (Baker and Brothwell 1980), and extending towards the human remains themselves (e.g., papers in *Journal of Archaeological Science* 11, 1984).

We can also find more finely tuned records of food web deflection in quite subtle demographic shifts, as exemplified by Andrew Jones' work on fish, which has examined a range of modifications of fish populations in conjunction with human exploitation (Wheeler and Jones 1989). Around the city of York for example, the development of early mediaeval "pollution" would appear to be mirrored in shifts in the fish consumed by its inhabitants (Jones A. 1988).

The extended campaign of bio-archaeological research that English Heritage has sponsored on a series of urban sites has also provided a detailed record of another gradual deflection of the human food web. As a corollary of the dense occupation of relatively protected settlements, our large and medium sized competitors have been held at bay, and energy within our food webs is instead more and more deflected to the invertebrates and microorganisms that are able to flourish in an ecosystem which is densely packed spatially. York is a key example, where the proliferation of invertebrate competitors can first be seen in positions in the food web adjacent to humans, such as the high populations of grain beetles in the Roman town. During the course of the first millennium AD this proliferation applies more and more to the humans themselves, as is dramatically illustrated by the incidence of intestinal worms. While nematode eggs are likely to have been but the tip of an iceberg of less visible diseases and parasites, they provide an extremely useful marker that can to some extent be quantified through time (cf. Hall et al. 1983, Hall and Kenward 1990)

6. Future directions

It was argued at the outset that advances in molecular, chemical and radiometric analyses have set a new agenda for bio-archaeology. The direct examination of surviving fragments of past human food webs is gradually being liberated from those questions they were least suited to answer, and instead, through analyses with these newer techniques, can provide the qualitative framework for a much more structured examination of the particular place of humans in past food webs. Much of this work has yet to be conducted, but what I hope to have demonstrated is that the bio-archaeology of the last twenty years has produced a data-set, and a key series of pilot studies, that provide a secure foundation for such a project.

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References

- Allen, T.F.H. and Starr, T.B. 1982; *Hierarchy: Perspectives for Ecological Complexity* (Chicago, Chicago University Press).
- Armour-Chelu, M. and Clutton-Brock, J. 1985: Notes on the evidence for the use of cattle as draft animals at Etton. In Pryor, F. et al. Excavations at Etton, Maxey, Cambridgeshire 1982–1984, Antiquaries Journal 65, 297–302.
- Baker, J.R. and Brothwell, D. 1980: Animal Diseases in Archaeology (London, Academic Press).

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- Brown, T.A. and Brown, K.A. (in press): Ancient DNA and the archaeologist. Antiquity.
- De Angelis, D.L. 1975: Stability and connectance in food web models. Ecology 56, 238-243.
- Dimbleby, G.W. 1962: The Development of British Heathlands and their Soils. (Oxford, Oxford Forestry Memoir 23).
- Ellen, R. 1982: Environment, Subsistence and System: the Ecology of Small Scale Formations (Cambridge, Cambridge University Press).
- Foley, R.A. 1977: Space and energy. In Clarke, D.L. (editor), *Spatial Archaeology* (London, Academic Press) 163-188.
- Foley, R.A. 1986: Another Unique Species: Patterns in Human Evolutionary Ecology (London, Longman).
- Gardner, M.R. and Ashby, W.R. 1970: Connectance of large dynamic (cybernetic) systems: critical values for stability. *Nature* 228, 274.
- Grant, A. 1981: The significance of deer remains at occupation sites of the Iron Age to the Anglo-Saxon period. In Jones, M.K. and Dimbleby, G.W. (editors), *The Environment of Man: the Iron Age to the Anglo-Saxon Period* (Oxford, British Archaeological Reports British Series 87) 205-213.
- Greig, J.R.A. 1991: The British Isles. In van Zeist, W., Wasylikowa, K. and Behre, K.E. (editors), *Progress in Old World Palaeoethnobotany* (Rotterdam, Balkema) 299-334.
- Hall, A.R., Kenward, H.K., Williams, D. and Grieg, J.R.A. 1983: Environment and living conditions at two Anglo-Scandinavian sites. *Archaeology of York* 14/4.
- Hall, A.R. and Kenward, H.K. 1990: Environmental evidence from the Colonia. The Archaeology of York 14/6.
- Harris, D.R. 1969: Agricultural systems, ecosystems and the origins of agriculture. In Ucko, P.J. and Dimbleby, G.W. (editors), *The Domestication and Exploitation of Plants and Animals* (London, Duckworth) 3–15.
- Harris, D.R. and Hillman, G.C. 1989: Foraging and Farming: the Evolution of Plant Exploitation (London, Unwin Hyman).
- Hather, J.G. 1988: The Morphological and Anatomical Interpretation and Identification of Charred Vegetative Plant Remains (London, University of London PhD Thesis).
- Higgs, E.S. (editor) 1972: Papers in Economic Prehistory: Studies by Members of the British Academy Major Research Project in the Early History of Agriculture (Cambridge, Cambridge University Press).
- Higgs, E.S. (editor) 1975: Palaeoeconomy: being the Second Volume of Papers in Economic Prehistory by Members of the British Academy Major Research Project in the Early History of Agriculture (Cambridge, Cambridge University Press).
- Hillman, G.C. 1984: Interpretation of archaeological plant remains: the application of models from Turkey. In van Zeist, W. and Casparie, W. (editors), *Plants and Ancient Man* (Rotterdam, Balkema) 1–41.
- Hillman, G.C. 1986: Plant foods in ancient diet: the archaeological role of palaeofaeces in general and Lindow Man's gut contents in particular. In Stead, I.M., Bourke, J.B. and Brothwell D. (editors), *Lindow Man: the Body in the Bog* (London, British Museum) 99-115.
- Hillman, G.C., Robins, G.V., Odowole, D., Sales, K.D., and McNeil, D.A.C. 1985: The use of electron spin resonance spectroscopy to determine thermal histories of cereal grain. *Journal* of Archaeological Science 12, 49–58.
- Hillson, S.W. 1986: Teeth (Cambridge, Cambridge University Press).
- Hillson, S.W. 1989: Teeth; some current developments in research. In Roberts, C.A., Lee, F. and Bintliff, J. (editors), *Burial Archaeology: Current Research, Methods and Developments* (Oxford, British Archaeological Reports British Series 211) 129-149.
- Hillson, S.W. and Jones, B.K. 1989: Instruments for measuring surface profiles: an application in the study of ancient human tooth crown surfaces. *Journal of Archaeological Science* 16, 95–105.
- Jones, A.K.G. 1988: Provisional notes on fish remains from archaeological deposits at York. In

Murphy P.J., and French C. (editors), *The Exploitation of Wetlands* (Oxford, British Archaeological Report British Series 186) 113-127.

- Jones, G.E.M. 1984: Interpretation of archaeological plant remains. In van Zeist, W. and Casparie, W. (editors), *Plants and Ancient Man* (Rotterdam, Balkema) 43-61.
- Jones, G.E.M. 1991: Numerical analysis in archaeobotany. In van Zeist W., Wasylikowa K. and Behre K-E., Progress in Old World Palaeoethnobotany (Rotterdam, Balkema).
- Jones, M.K. 1983: Integrating the Subsistence Economy (Oxford, British Archaeological Report International Series 181).
- Jones, M.K. 1984: Regional patterns in crop production. In Cunliffe, B.W. and Miles, D. (editors) Aspects of the Iron Age in Central Southern Britain (Oxford, Oxford University Committee for Archaeology Monograph 2) 120-124.
- Jones, M.K. 1985: Archaeobotany beyond subsistence reconstruction. In Barker, G. and Gamble, C. (editors), *Beyond Domestication in Prehistoric Europe* (London, Academic Press) 107-128.
- Jones, M.K. 1988a: The arable field: a botanical battleground. In Jones, M.K. (editor), Archaeology and the Flora of the British Isles: Human Influence on the Evolution of Plant Communities (Oxford, Oxford University Committee for Archaeology Monograph 14) 86-92.
- Jones, M.K. 1988b: The phytosociology of early arable weed communities, with special reference to southern Britain. In *Festschrift: Udelgard Körber-Grohne. Der prähistorische Mensch und sein Umwelt* (Stuttgart, Konrad Theiss Verlag) 43-51.
- Körber-Grohne, U. 1981: Distinguishing prehistoric grains of *Triticum* and *Secale* on the basis of their surface patterns using the scanning electron microscope. *Journal of Archaeological Science* 8, 197–221.
- Körber-Grohne, U. and Piening, U. 1980: Microstructure of the surfaces of carbonised and non-carbonised grains of cereals as observed in scanning electron and light microscopes as an additional aid in determining prehistoric findings. *Flora* 170, 189–228.
- Lawton, J.H. and Warren, P.H. 1988: Static and dynamic explanations for patterns in food webs. Trends in Ecology and Evolution 3, 242-4.
- Limbrey, S. 1975: Soil Science and Archaeology (London, Academic Press).
- May, R.M. 1972: Will a large complex system be stable? Nature 238, 413-414.
- McCarthy, M.R. 1991: The Roman Waterlogged Remains and Late Features at Castle Street Carlisle: Excavations 1981/2. Fascicule 1 (Cumberland and Westmoreland Antiquarian and Archaeological Society Research Series 5).
- McLaren, F.S., Evans, J. and Hillman, G.C. 1991: Identification of charred seeds from epipalaeolithic sites of S.W. Asia. In Pernicka, E. and Wagner, G.A. (editors), Archaeometry '90 (Basel, Birkhäuser Verlag) 797-806.
- McGlade, J. and Allen, P. 1986: Disequilibrium models of human ecosystems. Science and Archaeology 28, 44-50.
- Pimm, S.L. 1982: Food Webs (London, Chapman and Hall).
- Rackham, D.J., Batey, C.E., Jones, A.K.G. and Morris, C.D. 1984: Freswick Links, Caithness: report on environmental survey 1979. Circaea 2, 29–55.
- Robinson, D. and Rasmussen, P. 1989: Botanical investigations at the Neolithic Lake Village at Weier, North East Switzerland. In Milles, A., Williams, D. and Gardner, N. (editors), *The Beginnings of Agriculture* (Oxford, British Archaeological Reports International Series 496) 149–163.
- Rosenzweig, M.L. 1971: Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science 171, 385–387.
- Sheridan, A. and Bailey, G.N. (editors) 1981: Economic Archaeology: Towards an Integration of Ecological and Social Approaches (Oxford, British Archaeological Reports International Series 96).
- Thomas, K.D. 1983: Agricultural and subsistence systems of the third millennium B.C. in

north-west Pakistan: a speculative outline. In Jones, M. (editor) Integrating the Subsistence Economy (Oxford, British Archaeological Report International Series 181) 279–314.

- Thomas, K.D. 1989: Hierarchical approaches to the evolution of complex agricultural systems. In Milles, A., Williams, D. and Gardner, N. (editors), *The Beginnings of Agriculture* (Oxford, British Archaeological Reports International Series 496) 55-73.
- Tomlinson, P. 1985: Use of vegetative remains in the identification of dyeplants from waterlogged 9th-10th century AD deposits at York. *Journal of Archaeological Science* 12, 269–283.

Wheeler, A. and Jones, A.K.G. 1989: Fishes (Cambridge, Cambridge University Press).

Wilson, D.G. 1979: Horse dung from Roman Lancaster: a botanical report. Archaeo-Physika 8, 331–349.