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CHICAGO JOURNALS

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Reviewed work(s):

Source: *Current Anthropology*, Vol. 37, No. 3 (Jun., 1996), pp. 529-539

Published by: [The University of Chicago Press](#) on behalf of [Wenner-Gren Foundation for Anthropological Research](#)

Stable URL: <http://www.jstor.org/stable/2744553>

Accessed: 13/02/2013 09:59

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Dietary Variability among Prehistoric Forager-Farmers of Eastern North America¹

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Until recently, subsistence studies have tended to emphasize one type of variability over others as a focus of inquiry: long-term, directional change. However, in order to explain such trends (including the origin and growing importance of agricultural subsistence), it is critical to document variability that occurs on a relatively restricted temporal scale and along nontemporal dimensions. For example, plant food consumption is likely to be sensitive to short-term seasonal changes in food availability. Analyses of agricultural origins in many regions (e.g., Cowan 1985, McCorriston and Hole 1992, Wills 1988) emphasize the causal significance of seasonality and the role played by crops as storable resources. In addition, the costs and benefits of producing, processing, and consuming crops were probably somewhat different for women and men, children and adults, large households and small ones. These costs and benefits also varied according to the part of the plant used and the cultural and environmental context of use.

Neglect of these issues in studies of prehistoric subsistence has been largely a product of limitations inherent in the data base. Most investigators of archaeobotanical materials, for example, work with remains that represent carbonized waste from refuse deposits. Occasionally they are able to recover desiccated or waterlogged material that is well-preserved in its noncarbonized, organic state and offers a more complete record of plant use. Analysis of such material gives us the opportunity to generalize about changes in the processing and disposal of plant products but provides no direct evidence of consumption. Furthermore, refuse deposits must usually be regarded as representing a sort of aver-

age behavioral pattern of sequential communities over a period of time. Although advances have been made in identifying differences in production, processing, and consumption patterns between households (Hastorf 1990) and other small community groups (Gumerman 1994), variability, which is the basis of evolutionary change (Braun 1990:63-63; Dunnell 1980:38; O'Brien and Holland 1990:40-41), is obscured in the resulting analyses.

In contrast to midden refuse, human paleofeces offer direct evidence of food consumption by individuals (who differ in gender, age, and social status) in a variety of environmental and cultural contexts. Refined analytic techniques make it possible for us to obtain information about these and other dimensions of prehistoric dietary variability in unprecedented detail. Our goal is to demonstrate the potential of such an approach with reference to recently obtained paleodietary data from Salts Cave and Mammoth Cave, Mammoth Cave National Park, Kentucky.

PALEODIETARY RESEARCH IN THE MAMMOTH CAVE AREA

Salts Cave and Mammoth Cave are part of the Mammoth Cave system, an extensive network (the world's longest) running through a karstic plateau in west-central Kentucky (Crothers and Watson 1993) (fig. 1). These caves were exploited for minerals by prehistoric people, primarily during the mid-3d millennium B.P. Because of the constant humidity and temperature in many of the cave interiors as well as the exsiccating effect of some of the minerals, organic materials (including human paleofeces) are extremely well preserved. Remains of this type from Salts Cave and Mammoth Cave have provided key evidence for the early development in eastern North America of agriculture based on native crops (Watson 1974a; Yarnell 1969, 1974). Paleofecal data were particularly critical in demonstrating a substantial dietary role for cultivated plant species. Overall, 127 paleofeces have been analyzed from Salts and Mammoth; 100 samples were studied for their macrobotanical content by Yarnell (1969, 1974) and 27 by Stewart (1974). In addition, pollen from paleofeces was analyzed by Schoenwetter (1974) and Bryant (1974). Yarnell (1969, 1974) estimates that approximately 74% of the Salts Cave diet was composed of plant foods that were either cultivated (about 42%) or a product of habitats created by agricultural activity (another 32%). Skepticism about the representativeness of this dietary pattern diminished in view of corroborating evidence from the vestibule, or entry chamber, of Salts Cave, where numerous carbonized seeds of crop plants were deposited during the main period of cave utilization (Gardner 1987, Yarnell 1974).

The present project was devised to expand and refine this database by applying new analytic techniques to a series of 12 paleofecal samples collected from Salts and Mammoth. Each specimen provided material for accelerator radiocarbon dating and was processed for macrore-

1. © 1996 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/96/3703-0007\$1.00. We are grateful to Patty Jo Watson for the opportunity to work with the Salts Cave and Mammoth Cave material. Washington University in St. Louis and The Ohio State University provided financial support for our research, which was carried out in collaboration with the Cave Research Foundation Archaeological Project. Spencer Tomb and Heather Almquist-Jacobsen assisted with identification of Asteraceae pollen. Stephen Bicknell drafted figures 1, 3, and 4. Vaughn Bryant, Paul Gardner, Bruce Smith, Patty Jo Watson, and one anonymous referee provided valuable comments that helped us to improve the quality of the manuscript.

FIG. 1. *The Mammoth Cave system.*

mains, parasite remains, and pollen. We do not report on faunal remains (which were poorly represented in the specimens) or parasites (analysis of which is still in progress). Related research also produced a pioneering effort to extract and measure steroids in the paleofeces in order to determine the sex of the individuals who deposited them (Sobolik et al. 1995, Whitten 1994). In this paper we synthesize results from these different lines of evidence to discuss the implications of variability in plant use by the prehistoric forager/farmers of the Mammoth Cave area along three major dimensions: temporal (both long-term and seasonal), interindividual, and contextual.

DIMENSIONS OF DIETARY VARIABILITY

Long-term temporal variability. For the Mammoth Cave area, there now exists an extensive series of radiocarbon dates that provide a sound chronological framework for early food production (Gardner 1987, Kennedy n.d., Kennedy and Watson n.d., Watson 1974a). All directly dated paleofeces fall between ca. 2,700 and 2,250 B.P., although there are indications of earlier (Late Archaic period, ca. 4,000 to 2,700 B.P.) exploration of the

cave interior and occupation of Salts Cave vestibule (Gardner 1987, Kennedy n.d., Kennedy and Watson n.d.). Judging by these determinations and by analyses of paleofecal content, crops had become a significant portion of the diet of the people using the caves before 2,500 B.P.

Within the time period represented by the paleofeces, there is evidence of considerable dietary continuity in that the same types of plant foods were consumed regularly. In fact, diet has been judged as having remained quite consistent during the period of major cave use (Watson 1969:77). With the availability of 12 directly dated paleofeces that span this period, there is an opportunity to evaluate this conclusion. Is there perhaps a trend toward consumption of greater quantities of cultivated plant products?

After calibration (using CALIB version 3.0; Stuiver and Reimer 1993), radiocarbon ages of the most recently collected 12 specimens fall within the 3d millennium B.P. and form a continuous series with considerable overlap at the two-sigma level (table 1, fig. 2, Kennedy and Watson n.d.). The total of 14 determinations (including duplicates for 2 samples that were run to test for mold contamination) are significantly different at the .05 level

TABLE 1
AMS Radiocarbon Determinations for Salts Cave and Mammoth Cave
Paleofeces

Specimen ^a	Radiocarbon Age (Uncalibrated B.P.)	Laboratory Number ^b	Calibrated Age (Years B.P.) ^c
MCF-1A	2,335 ± 75	AA-10079	2,707 (2,340) 2,147
MCF-1B	2,485 ± 70	AA-10080	2,752 (2,710, 2,630, 2,490) 2,346
MCF-2	2,575 ± 65	AA-10081	2,780 (2,740) 2,464
MCF-3	2,365 ± 70	AA-10082	2,712 (2,350) 2,159
MCF-4	2,485 ± 70	AA-10083	2,752 (2,710, 2,630, 2,490) 2,346
MCF-5	2,605 ± 70	AA-10084	2,846 (2,750) 2,478
MCF-6	2,700 ± 80	AA-10085	2,954 (2,780) 2,720
SCF-1	2,570 ± 70	AA-10086	2,782 (2,740) 2,369
SCF-2	2,410 ± 70	AA-10087	2,729 (2,360) 2,322
SCF-3	2,605 ± 80	AA-10088	2,854 (2,750) 2,464
SCF-4A	2,590 ± 70	AA-10089	2,794 (2,740) 2,468
SCF-4B	2,580 ± 70	AA-10090	2,788 (2,740) 2,377
SCF-5	2,500 ± 80	AA-10091	2,760 (2,710, 2,620, 2,580, 2,540, 2,530, 2,510) 2,345
SCF-6	2,703 ± 62	AA-111738	2,935 (2,780) 2,742

NOTE: Calibrated ages were calculated using CALIB Version 3.0 (Stuiver and Reimer 1993). Calibration datasets are from Stuiver and Pearson (1993) for MCF-1A, MCF-3, and SCF-2 and Pearson and Stuiver (1993) for all others.

^aMCF = Mammoth Cave feces; SCF = Salts Cave feces.

^bAll ¹⁴C measurements were conducted at the NSF-Arizona AMS Facility, University of Arizona, Tucson.

^cTwo-sigma maximum (calibrated ages) two-sigma minimum.

($\chi^2 = 22.40$). However, if the two oldest samples (SCF-6 and MCF-6) are removed, the remaining 12 are statistically the same ($\chi^2 = 19.70$), indicating a high probability that the majority of the paleofeces were deposited around the same time. The remaining pair represent a somewhat earlier entry into the cave. The contents of specimens from these two temporal groups do not appear to differ in any significant way; all 12 contain some remains of crops, although their quantity and the species represented vary widely. However, the earlier sample may be too small to reflect any differences in composition that might differentiate it from the later group.

Thus, Watson's (1969) original assessment of considerable dietary stability during the Early Woodland period cannot be further evaluated using these data, given the likelihood that most of the paleofecal specimens form a contemporaneous group. However, direct dating of paleofeces should prove to be a useful tool in future paleodietary studies, particularly if it can be used on a large sample of specimens that can be grouped chronologically. This technique, especially if it proves possible to reduce the size of standard deviations of radiocarbon determinations, offers the prospect of tracing dietary change over relatively brief periods of time.

Seasonality. The question of why cultivated plants acquired subsistence importance demands attention to cyclical variation in diet that occurs at a restricted temporal scale in response to seasonal variation in resource abundance. The importance of crops as stored foods intended to be consumed during the winter and spring

(when plant foods are in short supply) was emphasized in earlier Mammoth Cave area research (Watson 1974, Yarnell 1974). Other researchers (e.g., Cowan 1978a, 1985; Gremillion 1993a, 1995) have explored similar causal links between food storage and food production for the Cumberland Plateau to the east of Mammoth Cave, where a similar record of early plant domestication has been found. Seasonal variations in resource abundance have also been cited as causal factors in initial cultivation of crops in other regions (McCorriston and Hole 1992, Wills 1988).

Previous analyses of paleofeces from Salts Cave and Mammoth Cave revealed seasonal variation in the consumption of crop plants. For example, Yarnell (1969) noted that maygrass (*Phalaris caroliniana*), whose grains ripen in early summer, was generally either extremely abundant or present in trace amounts. Furthermore, when it was abundant maygrass tended greatly to exceed other crops in quantity. Maygrass seeds and pollen are often associated with strawberry (*Fragaria virginiana*) and blackberry (*Rubus* sp.), both of which are late-spring-summer fruits likely to be eaten fresh (Bryant 1974, Yarnell 1969). In contrast, several of the other crop taxa (including sumpweed [*Iva annua*], chenopod [*Chenopodium berlandieri*], and sunflower [*Helianthus annuus*]) were frequently associated with hickory (*Carya* sp.) and seldom occurred with maygrass (Marquardt 1974). Thus, it seems likely that sumpweed, sunflower, and chenopod (as well as hickory) were stored and consumed out of season, often in quantity. In contrast, may-

FIG. 2. Calibrated age ranges for 12 paleofecal specimens. Solid bars, calibrated one-sigma ranges; empty bars, calibrated two-sigma ranges. The total of 14 determinations includes duplicates taken from MCF-1 and SCF-4. The chart was produced using CALIB Version 3.0 (Stuiver and Reimer 1993).

grass was apparently utilized when available. Although maygrass is considered a crop plant (Cowan 1978b), because of its early availability (before other crops and nuts were harvestable) it was probably not stored in any quantity, if at all.

Studies of pollen (Bryant 1974, Schoenwetter 1974) provided information on seasonal utilization of the caves. Many of the feces were deposited during the spring and summer months, although there is evidence of activity throughout most of the year (Watson 1974, Yarnell 1974). However, in the earlier work most of the specimens studied for macrobotanical content were not subjected to pollen analysis. We have analyzed both pollen and macrobotanical content of each specimen to maximize chances of documenting seasonal variation in plant food consumption.

Pollen remains found in paleofeces can be classified as either economic pollen or background pollen. Economic pollen enters the body through the intentional consumption of flowers or seeds or through the unintentional ingestion of pollen adhering to plant parts used

as ingredients in medicinal teas or foods. In contrast, background pollen is ingested during respiration or as a contaminant of food and water. This type of ingestion is prevalent during the pollination season of a plant (e.g., spring in the case of pine and oak and fall for ragweed and juniper). Economic pollen from known crops may have been stored with crop seeds and fruits (either intentionally or unintentionally) and is therefore a poor indicator of seasonality. Analysis of economic noncrop pollen and background pollen is more useful for seasonality determination because the presence of pollen in a sample usually reflects the season in which a plant blooms.

Most of the pollen grains identified in the paleofeces are probably economic pollen. Of these, only one represents economic noncrop pollen (the mustard family, Brassicaceae). Mustard pollen made up 58% of pollen from sample SCF-3, which is therefore likely to represent spring deposition (figs. 3 and 4). Background pollen was usually not observed in the samples in large enough frequencies to indicate seasonality. Three exceptions are sample SCF-3, in which 19% of the pollen was hickory;

FIG. 3. Crop remains and selected pollen taxa from Salts Cave and Mammoth Cave paleofeces.

sample SCF-6, in which 13% of the pollen was oak (*Quercus* sp.); and sample MCF-5, in which 4% of the pollen was oak. Both trees bloom in the spring, and neither type of pollen is likely to be ingested with the nutmeats (which could have been stored and consumed out of season).

Samples without sufficient quantities of noncrop pollen did contain some seeds that reflect seasonality (fig. 4). Seeds of wild or weedy taxa producing fruits or small grains are assumed not to have been stored. MCF-5 and MCF-6 contain strawberry seeds from fruits that would most likely have been eaten fresh in the late spring, as well as maygrass, which ripens during May and June. These occurrences indicate that MCF-5 and MCF-6 were probably deposited in the late spring or early summer. Summer or early fall deposition is likely for MCF-1, MCF-2, MCF-4, SCF-1, and SCF-5, based on the occurrence of weed seeds such as nightshade (*Solanum*), amaranth (*Amaranthus*), knotweed (*Polygonum*), poke (*Phytolacca americana*), wood sorrel (*Oxalis*), and/or panic grass (*Panicum*). These plants typically have long seasons of flowering and fruiting that last from early or

midsummer until first frost. Maygrass in MCF-2 and MCF-4 suggests early to midsummer, although the trace amounts represented might have been retained for some weeks in the intestine and been deposited later in the year. SCF-2, SCF-4, and MCF-3 lack small noncrop seeds. However, high frequencies of grass pollen in SCF-2 probably represent warm-season ingestion. SCF-4 contains cucurbit pollen, which is unlikely to have stored well and was probably ingested in summer. Because of the lack of other seasonal indicators in MCF-3, we suggest that it was deposited in the winter.

Many of the specimens indicate that crops were stored and consumed out of season (fig. 4). This pattern is represented by the four samples deposited during spring or early summer (SCF-3, SCF-6, MCF-5, and MCF-6). Assuming that maygrass was consumed at harvest, MCF-2 and MCF-4 contain stored crops and/or hickory nut (presumably also stored). SCF-4 represents summer consumption of squash/gourd (*Cucurbita*) flowers along with stored seeds of the same taxon and other crops. MCF-1, SCF-1, SCF-2, and SCF-5 may have been deposited during the late-summer–early-fall harvest season

FIG. 4. Probable season of deposition of Salts Cave and Mammoth Cave paleofeces based on macrobotanical and pollen evidence. Ranges of seed and pollen production represent estimates for species likely to have been found in west-central Kentucky. Sources for seed seasonality: Asch and Asch (1977), Cowan (1985), and Radford, Ahles, and Bell (1968).

and therefore do not necessarily contain stored foods. If MCF-3 was in fact deposited in winter, the chenopod contained in it was stored.

Although it appears likely that crops were consumed over much of the seasonal cycle, no obvious seasonal patterning in the dietary importance of crops emerges from analysis of our sample. However, the potential for such an investigation is high given consistent application of analytic and quantitative methods to a larger data base.

Interindividual variability. The issue of interindividual variability in diet is seldom addressed in prehistoric subsistence research, primarily because of the lack of relevant evidence. However, consumption of particular kinds of foods (including crops) probably varied widely within as well as between communities. Differences of this kind are likely to be relevant to why food production began and succeeded when and where it did. For example, the use of crop-based gruels to wean infants appears to have accompanied the intensification of food production in the midcontinental United States (Braun 1987, Buikstra et al. 1987). Differences in diet and health between social ranks in stratified societies (Powell 1988, 1991) also indicate that the benefits of food production cannot be assumed to have been identical for all individuals within a community. Fortunately, paleofecal analysis gives us the opportunity to examine interindividual variability in food consumption. Furthermore, it holds the potential for comparing diet between major subgroups within a population.

When comparing individual specimens, the source of variability can be difficult to determine. First of all, there is no way of telling at the present time whether specimens of similar age were deposited by the same or different individuals (although DNA analysis makes this a very real possibility for the near future; see, for example, Sutton, Malid, and Ogram 1995). Even if we assume that the specimens are from different individuals, the possible underlying causes of dietary differences are many: seasonality, year-to-year variation in productivity of different taxa, individual food preferences, and individual physiology and health status. One inference that is supported by available data, however, is that meals eaten by contemporaneous individuals (perhaps by the same individual) are as likely to vary widely in crop content as they are to be similar in this respect. How can we determine whether these differences reflect systematic dietary patterns within a food-producing community?

One way to approach this question is to consider food consumption by different subgroups. Analysis of fecal steroids offers one method for determining the biological sex of individuals as a basis for identifying gender differences in diet. Ratios of hormones in the 12 specimens from Salts Cave and Mammoth Cave strongly suggest that the cave explorers responsible for the fecal deposits were predominantly or exclusively male (Sobolik et al. 1995, Whitten 1994). There may not have been significant differences in male and female diet among early forager-farmers of the Mammoth Cave area, but if cavers were of one sex the probability of ever finding

out is low. However, one very important piece of information has been obtained: that gender is not likely to account for dietary variability represented in the paleofeces.

When in the caves, adult males frequently ate crop seeds, probably on a daily basis; however, quantities consumed varied considerably. Comparison of samples of similar age and season of deposition permits elimination of some potential causes of variation and allows for identification of behavioral differences between individuals within similar environments. For example, samples SCF-1 and MCF-2 produced nearly identical radiocarbon determinations (table 1) as well as macrobotanical and pollen profiles that are similar with respect to seasonality (summer-fall) (figs. 3 and 4). Both contain high percentages of crop remains as well as panic grass, poke, and amaranth seeds and small amounts of hickory. However, whereas MCF-2 is dominated by chenopod, SCF-1 has a more or less equal mix of squash, chenopod, and sunflower. This analysis shows that much of the variation in plant food consumption observed in these paleofecal samples may be attributable to seasonal patterns of resource abundance and that in similar environmental contexts diet composition among cavers may in fact have been quite consistent. On the other hand, no single crop species was invariably chosen as the primary component of meals by different individuals or by the same individuals on different occasions. Future comparisons of this kind utilizing larger samples may help to clarify this issue.

Variability in the context and character of plant use. A final dimension of variability is the cultural context of plant use. Although subsistence research tends to emphasize nutritional content, plants have a multitude of other uses that may well have some bearing on the process of domestication. The prehistoric seed crops of eastern North America, although probably primarily important for the food value of their seeds and fruits, also produced flowers, stems, leaves, and roots and probably had nonfood uses. Various modes of use are likely to have had different utility depending on their environmental and cultural context. For example, consumption of food would have been subject to varying constraints at a riverine base camp, on a caving expedition, and on an overnight hunting trip.

Midden refuse seldom gives us direct evidence for how plants were used (Sobolik 1994) or for what purpose (as food, medicine, or construction material or in ritual). Paleofeces most likely underrepresent the ingestion of meat, particularly of large animals, because of the absence of large bone remains (Sobolik 1993). However, they offer more precise information on exactly what parts were used. In many plants, pollen is present at the same time and found in the same location as seeds and/or fruits. For example, chenopod and sunflower fruits both ripen in the same location as residual pollen. With the ingestion of these seeds and/or fruits, pollen is automatically ingested as well, either intentionally or unintentionally. If a flower type is frequently ingested, the soft flower parts will most likely be digested, leaving

only the pollen intact in the sample. Pollen may thus indicate the intentional consumption of flowers or seeds or the intentional or unintentional ingestion of pollen adhering to other plant parts for medicinal teas or foods (Bryant 1974, Sobolik and Gerick 1992). Pollen, depending on size and structure, becomes caught in the intestinal lumen, allowing it to be excreted in fecal samples for up to one month after ingestion (Kelso 1976, Williams-Dean 1978). Consequently, the pollen content of paleofeces does not reflect one meal but rather may be a product of numerous meals containing a variety of pollen types (Sobolik 1988, Williams-Dean 1978).

Previous studies have indicated that paleofeces and modern human feces that contain pollen frequencies above 100,000 grains/gram contain recently ingested and easily recognized economic pollen (Sobolik 1988, Sobolik and Gerick 1992). Paleofecal samples that contain pollen concentrations between 99,000 and 25,000 grains/gram probably contain economic pollen types that are not as easy to recognize because pollen ingestion was not recent; and samples that have pollen concentration values less than 25,000 grains/gram may contain economic pollen, but this pollen will not be recognized because ingestion may have taken place many days and even weeks ago.

An example of an economic pollen type found in paleofeces from the caves is sumpweed, as indicated by the high pollen concentration values of the samples in which it occurs and its extremely high frequencies in six of the samples. Two of the specimens that contain high frequencies of sumpweed pollen exhibit pollen concentration values indicating the recent ingestion of economic pollen, and the remaining four samples contain pollen concentration values indicating the probable ingestion of pollen, although not as recently (fig. 3). Sumpweed pollen was thus probably ingested either as food or along with sumpweed achenes.

Evidence of a similar pattern is offered by the presence of significantly high frequencies of cheno-am pollen (Chenopodiaceae and/or *Amaranthus*) and chenopod seeds, high-spine pollen (sunflower type) and sunflower achenes, sumpweed pollen and sumpweed achenes, and maygrass grains/glumes and Poaceae (grass) pollen. However, the combination of Cucurbitaceae (squash family) pollen and cucurbit seeds in sample SCF-4 indicates that cucurbit flowers were intentionally ingested at the same time as cucurbit fruits (or seeds) because cucurbit flowers and fruit production take place in spatially separate locations on the plant. Mustard pollen was observed in high frequency in sample SCF-3, indicating the intentional ingestion of mustard pollen and flowers. Mustard seeds were not observed in this sample, which suggests either that mustard seeds were ingested and excreted many days before sample deposition or that mustard flowers were ingested independently of the seeds, most likely as medicine.

Broadening the geographical scale brings subsistence diversity according to environmental context into sharp focus. In the Mammoth Cave area, it is only within the caves themselves that remains of domesticated plants

dating to the 3d millennium B.P. are abundant. Rockshelters in Mammoth Cave National Park with Early Woodland components have yielded little evidence of food production with the possible exception of bottle gourd (*Lagenaria siceraria*) (Gremillion 1990, Wagner 1978, Watson 1985). However, such contemporaneous noncave data sets are limited in number and thus are unlikely to be an adequate reflection of subsistence variability. For the period prior to ca. 3,000 B.P. (the traditional boundary between the Late Archaic and Early Woodland periods in Eastern Woodlands prehistory), the prevalent environmental context of evidence for early food production is just the opposite, with noncave sites such as rockshelters and shell middens in and near the Green River floodplain providing the bulk of the data (Crawford 1982, Gremillion 1990, 1994, Marquardt and Watson 1983, Wagner 1978, Watson 1985).

These Late Archaic collections of botanical material (which date primarily to the mid-4th millennium B.P.) are no match for the later cave assemblages in either quantity or variety. Shell middens have produced no evidence of food production save remains of gourd/squash (which, in light of our present understanding of the evolution of *Cucurbita pepo*, may represent a wild gourd rather than, or as well as, a garden crop [Cowan and Smith 1993, Decker 1988, Decker-Walters et al. 1993, Smith, Cowan, and Hoffmann 1992]). Possible seed crops represented at nearby Peter Cave (which is actually a rock shelter rather than a true cave) include gourd/squash, chenopod, and knotweed, but only chenopod is abundant and exhibits morphological evidence of domestication (Crawford 1982, Yarnell 1993).

Although limited in quantity, archaeological evidence of the use of crops outside the caves by their Late Archaic predecessors challenges the contention that the caver's mode of plant use is an aberration, a special diet of "trail mix" that was consumed only in special contexts (see discussions in Gardner 1987 and Watson 1985:128). The rock shelters of this region, unlike the deep caves, were suitable for a wide range of human activities and are likely to represent a larger subset of subsistence practices. Thus, the occurrence of cultivated plants at such sites indicates that they were consumed in settings lacking the constraints on food choice imposed by the rigors of cave exploration. Compelling evidence of a similar context for early food production is provided by midden-derived plant remains from rock shelters on the Cumberland Plateau, located approximately 200 km to the northeast of Mammoth Cave (Gremillion 1993b). Furthermore, the fact that remains of crops were deposited in quantity at the entrance of Salts Cave as well as within the cave itself suggests that they were unlikely to have been used exclusively as "trail mix."

The presence of crop remains amongst midden refuse in noncave locations does not necessarily argue for the widespread and generalized adoption of an agricultural diet in the Mammoth Cave area. However, paleofeces from rock shelters on the Cumberland Plateau that have been directly dated to ca. 3,000 B.P. have been found in some cases to contain substantial quantities of crop

seeds (Gremillion 1995). Domesticated chenopod was at least present in the diet of these populations several centuries earlier (Smith and Cowan 1987). Thus, even if heavy consumption of crop seeds during the Early Woodland in the Mammoth Cave area was limited to caving expeditions, such a specialized dietary role was not necessarily typical of early farming populations in the uplands of the midcontinental United States.

Variable preservation of organic remains is a major factor influencing the archaeological record of food production found in different environmental situations. The exceptional opportunities for survival of organic remains found in dry cave passages and in some rock shelters account to some degree for the substantial archaeological record of early food production at such sites. In contrast, the collections of charred crop seeds that amply document the early development of food production at nonsheltered sites in the larger river valleys of the Midwest and Mid-South to the west of Mammoth Cave (e.g., Asch and Asch 1985, Chapman and Shea 1981, Crites 1991, Johannessen 1984) have survived in spite of the great potential for rapid mechanical and chemical breakdown of plant tissues in such environments. Thus, it seems unlikely that preservational factors are solely responsible for the absence of a record of agricultural subsistence of similar composition and age from open sites in the Mammoth Cave area. The intensity of archaeological research is implicated as well as geographical variability in the behavior of prehistoric people. Systematic comparison of the formation processes affecting different site types between regions should help to clarify the extent to which the paleofecal evidence (necessarily restricted to sheltered sites) is representative of subsistence behavior over a broad range of environmental contexts.

CONCLUSIONS

Our study illustrates the advantages of applying multiple analytic techniques to prehistoric paleofecal material as a method for investigating dietary variability. Many types of variability (seasonal, interindividual, functional, environmental) are relevant to the explanation of long-term subsistence change and merit comprehensive documentation. Although in most cases the complexity of plant use is obscured in the archaeological record, the feasibility of this line of research is greatly enhanced by continuing methodological innovation aimed at the fullest possible exploitation of direct evidence for the diet of individuals. Awareness of the many dimensions of variability within and between prehistoric farming communities of eastern North America (Fritz 1990, Gremillion 1995, Scarry 1993) continues to grow in the wake of the application of new analytic techniques and resulting refinement of the evidential basis for prehistoric subsistence.

Direct assessment of the age of individual paleofecal specimens holds considerable potential for tracking subsistence change. The small size and apparent contemporaneity of our sample prohibits assessment of fluctuation in the dietary role of crops during the major period

of cave use. However, larger samples in combination with smaller standard deviations for radiocarbon dates would provide opportunities for delineation of subtle changes in crop usage over relatively brief periods of time. Such a database would also permit us to pinpoint times of initial introduction of individual crops and intensification of farming in order to correlate these human behavioral changes with environmental and social variables.

Combined pollen and macroplant data provide a strong evidential basis for seasonality of crop consumption and have allowed us to substantiate the claim that stored crops were an important part of the caver diet. The fact that crops were consumed year-round indicates that they were not reserved for periods of shortage but integral components of human diets. However, the frequent consumption of crop seeds out of season suggests that their role as storable resources may have been an important determinant of their dietary importance. Whether the storability of food crops was a key factor influencing the initiation of plant domestication and farming can be determined only through recovery and analysis of paleofecal material from the 4th millennium B.P.

Preliminary comparisons of samples of similar age and seasonal profile indicate that, although any conclusive statements about interindividual dietary variability would at this point be premature, this line of investigation holds much promise for the future. Our preliminary assessment does suggest that consistent consumption of crop seeds had high utility for cave explorers but that the mix of species used was likely to be quite variable. This pattern contrasts with the dietary reliance of many Late Prehistoric populations in eastern North America on a single staple carbohydrate source, maize (Smith 1989). Analysis of fecal steroids (Sobolik et al. 1995, Whitten 1994) has shown further that our subjects are males and demonstrates that we have the potential to examine gender differences in diet.

Our analyses have also allowed us to document the consumption of pollen and/or flowers (items that are usually not preserved in open sites) as food and/or as medicine. Such conclusions may provide insights into the domestication, management, or persistent utilization of plants whose uses in prehistory are imperfectly understood. For example, gourd/squash (*C. pepo*) was used for its fruits (both as containers and as food) and its seeds (Cowan n.d.). Our research demonstrates that its flowers were also consumed prehistorically in eastern North America. These multiple uses help explain the millennia-long ecological association between prehistoric human populations and this species. Pollen evidence from paleofeces also provides information on the medicinal and/or nutritional usefulness of plants such as the mustards, whose seeds are seldom recovered archaeologically. The same is probably true of many medicinal plants, whose preparation methods often ensured the destruction or alteration of anatomical structures that make identification of macroremains possible.

Finally, we have considered variability in the spatial context of plant use in the Mammoth Cave area by proposing explanations for the contrast between cave inte-

rior, on the one hand, and noncave and cave entrance archaeobotanical assemblages, on the other. These explanations remain incomplete, but the variation between site types and preservational contexts in the frequency of crop remains illustrates the need for attention to the full range of environmental settings used by prehistoric populations. There is no reason, on theoretical or empirical grounds, to assume that crops were equally important in all contexts. Thus, in order to document and explain the behavior of early forager-farmers accurately, we need to consider the constraints and opportunities offered by nonagricultural as well as agricultural activities.

For the most part, our study complements and confirms the results of earlier investigations of the prehistoric forager-farmers of the Mammoth Cave area (Watson 1969, 1974). However, by utilizing newly available techniques we have refined our understanding of early food-producing societies in eastern North America and charted some potentially profitable directions for future research into the origins and development of agriculture worldwide.

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Is Reproductive Synchrony an Evolutionarily Stable Strategy for Hunter-Gatherers?¹

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The human female has a number of striking reproductive and sexual characteristics, ones that are rare or unusual in the context of mammals or primates more gen-

erally. Among these are concealed rather than advertised patterns of ovulation and the lack of periodic restriction to sexual activity. In recent years two other sexual traits have been given prominence. The first is that women can have very conspicuous blood loss during menstruation, and the second is a tendency under some circumstances for them to synchronise their ovulatory cycles and, in particular, menstruation. These traits have all been ascribed evolutionary significance.

Knight (1991) has linked these physiological and other anthropological observations together to construct a comprehensive model for the role of female sexual behaviour in the evolution of modern human cultural and cognitive systems. His argument in essence is as follows: Human females conceal their period of ovulation. In contrast to the situation with many mammals, there is no overt advertisement of when ovulation occurs or when the female is sexually and reproductively receptive. Chimpanzees and baboons, for example, both have major genital swelling around the time of ovulation. In contrast, human females have a more marked period of menstruation, with relatively high levels of blood loss, which can give rise to visible signals. This signal, Knight argues, is the inverse of signalling ovulation. Females will be infertile, and so in effect by the high visibility of menstrual bleeding they are signalling to males that conception cannot occur even if there is sexual activity. This gives menstruation, although a characteristic of all anthropoid primates, an additional significance for humans beyond the purely physiological. In Knight's model this significance is enhanced by the fact that some women have been observed to synchronise their menstrual cycles. Some reports have indicated that under certain circumstances women living in close proximity will converge in their ovulatory cycles in such a way as to end up menstruating at approximately the same time (and, by implication, presumably ovulating simultaneously as well).

Knight has placed the occurrence of visible signalling and menstrual synchronisation in an evolutionary context. For much of their evolution, human females would have lived in small groups in close proximity to each other. Synchronisation of menstrual cycles, possibly related to lunar cycles, would have occurred. The selective pressure leading to this would have been the reproductive advantages accruing to women when their reproductive behaviour was coordinated. Women who synchronised their reproduction within a group would have had enhanced evolutionary fitness. In Knight's model this would have arisen through the following set of circumstances: These small groups of women would have regularly been signalling to men that they were infertile, and because this would have been universal within the group there would have been no direct reproductive benefit to men arising from copulation. Females' signalling infertility in concert, Knight argues, would have encouraged males to increase their economic efforts on the grounds that there would have been little advantage in guarding females. By reducing male competition for females, the synchronised regulation of periods of fertility and infertility would have acted as a stimulus to male

1. © 1996 by The Wenner-Gren Foundation for Anthropological Research. All rights reserved 0011-3204/96/3703-0008\$1.00. We thank Chris Knight for his constructive comments on an earlier draft of this paper, a version of which was also presented at the conference he organised on ritual and the origins of culture at the School of Oriental and African Studies, London, in March 1994.