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The “cultural filter,” human transport of mussel shell, and the applied potential of zooarchaeological data

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Abstract. Large assemblages of animal bones and/or shells from archaeological sites can provide data valuable for modern conservation efforts, e.g., by providing accurate historical baselines for species reintroductions or habitat restoration. Such data are underused by natural scientists, partly due to assumptions that archaeological materials are too biased by prehistoric human actions (the so-called “cultural filter”) to accurately reflect past biotic communities. In order to address many paleobiological, archaeological, or applied research questions, data on past species, communities, and populations must first be demonstrated to be representative at the appropriate level. We discuss different ways in which one kind of cultural bias, human transport of specimens, can be tested at different scales, using freshwater mussel shells from prehistoric sites in the Tombigbee River basin of Mississippi and Alabama to show how representativeness of samples can be assessed.

Key words: applied zooarchaeology; conservation biology; cultural bias; freshwater mussels; Tombigbee River basin, Mississippi.

INTRODUCTION

Zooarchaeologists routinely analyze assemblages of archaeological bones and/or shells containing thousands to tens of thousands of specimens. The resulting data have value within a contemporary management context via what has come to be known as “applied zooarchaeology” or “applied paleozoology” (Lyman 1996, 2006, 2011, Lyman and Cannon 2004, Wolverson et al. 2011). It is accurate to say that the use of such data is not yet mainstream in conservation biology, despite the fact that thousands of zooarchaeological assemblages have been recovered (with more recovered every day). One reason for this situation is that, when confronted with unexpected findings from the zooarchaeological record (e.g., major range extensions or, conversely, the absence of an expected taxon in a particular locale), natural scientists may propose prehistoric human transport of fauna (for subsistence or trade), the avoidance of particular species because of cultural “tastes,” or other nonrandom human actions (also known as, the “cultural filter” [Daly 1969]) as the responsible factor (e.g., Matteson 1959:53, Murphy 1971:22, Robison 1983, Casey 1987:117–118, Call 1992:249, Myers and Perkins 2000, Haag 2009a:111). Unfortunately, such reactions do not often occur in the

arena of peer-reviewed publication where zooarchaeologists can debate the merits of archaeological faunal data. Instead, authors of this paper (and other zooarchaeologists) commonly encounter such reactions after conference presentations, in reviews of papers and grant proposals, and in technical reports written by zoologists cum zooarchaeologists. Thus, the “cultural filter” has taken on mythical importance outside of archaeology that is increasingly difficult to counter unless zooarchaeologists assert the value of paleozoological data and the merits of analytical approaches that are mainstream in zooarchaeology and paleontology.

The failure of natural scientists to fully appreciate the worth of zooarchaeological data, while understandable, is problematic for a number of reasons: (1) it often involves arguing from negative evidence; (2) it assumes that zooarchaeologists have not considered cultural bias in their analyses and interpretations; (3) it ignores what actually is known about prehistoric human behavior; and (4) it enforces self-fulfilling prophecies about preindustrial species ranges and faunal community characteristics. The practical result is that these valuable data remain largely ignored by the very people (conservation biologists) who could put them to best use (Frazier 2007, Humphries and Winemiller 2009). It is important, therefore, to discuss a suite of approaches for assessing how well zooarchaeological assemblages represent past ecological communities, species, and populations. Without such discussion, attempts to address research questions involving past species bio-

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geographic ranges or other applied topics can be dismissed as biased and “pseudo-scientific.”

Zooarchaeological data may, of course, be structured to varying degrees by several types of bias, including cultural selection, differential inter- and intrasite preservation, sampling error, recovery methods, and differing skill levels between individual analysts (Payne 1972, Uerpman 1973, Reitz and Wing 2008:6). Studies of such factors have a long history in zooarchaeology and paleontology (see summary by Lyman 1994). The literature on the topic is immense, and conceptually sophisticated models for exploring taphonomic pathways have become common (e.g., Butzer 1982, Grayson 1984, Schiffer 1987, Lyman 1994, 2008, Dincauze 2000, Lyman and Ames 2004, Reitz and Wing 2008). Most zooarchaeologists receive at least some training in taphonomic analysis, the study of the transition of organic materials (e.g., bones and shells) from the biosphere into the lithosphere (sedimentary deposits) (Lyman 1994, 2010). Taphonomy provides a systematic approach to understanding the effects of a variety of cultural and natural processes on animal remains during their accumulation and depositional histories (Nagaoka et al. 2008). Bone and shell fragments routinely are inspected for immanent properties of butchery, weathering, carnivore and rodent gnaw damage, burning, acidification through soil exposure or digestion, a variety of fragmentation agencies, and evidence of multiple other kinds of taphonomic processes. In short, zooarchaeologists are patently aware of biases that shape archaeological faunal assemblages and consider such biases when extrapolating from their data to past community characteristics. Unfortunately, this taphonomic work is not well known outside the discipline, leading to a loss of applied value as outlined previously.

Our purpose in this paper is not to convey data to test paleobiological or zooarchaeological research hypotheses, but to address the very assumption of representativeness in zooarchaeological assemblages. To do this, we explore the nature of the cultural filter as expressed in one particular kind of archaeological faunal remains: the shells of freshwater unionid mussels (Mollusca: Bivalvia: Unionidae) that accumulated as food waste at sites around the world. Various sorts of bias in this class of material have been addressed elsewhere (Peacock 2000, Peacock and Chapman 2001, Wolverson et al. 2010, see also Muckle 1994). Here, we focus primarily upon ways in which one purported bias, the cultural transport of shellfish, can be formally tested as a hypothesis at three different scales: the specimen, assemblage, and watershed levels.

Test implications

To test any hypothesis about past species biogeography or faunal community composition, both highly relevant to modern conservation biology and restoration ecology, we first must consider how it is that zooarchaeologists can determine whether or not samples are

so culturally biased as to be representative in only a limited way. If shell samples are representative of past shellfish communities, then assemblages should pass several tests. First, at the species level, individuals harvested from the same localities should exhibit similar shell morphology and isotopic chemistry. That is, if individuals from multiple streams were transported long distances by prehistoric people, one would expect a range in morphology and perhaps several different modes in metric traits within the same species. As well, one would expect a large range of isotopic chemical signatures in the same species. However, if species were harvested from local streams, and are thus representative of past ecological conditions near the site from which they were recovered by archaeologists, then morphology and isotopic chemistry should be less variable. The logic is that long-distance transport effectively samples a host of streams with different hydrological and isotopic chemical regimes, thus introducing higher variability in both parameters.

Similarly, predictions about representativeness can be made at the assemblage level. Samples from a locality (multiple sites within close geographic proximity, or samples from different contexts at a particular site) should be from the same prehistoric mussel population. Smaller samples, if representative, therefore should nest within larger ones in terms of taxonomic composition, as it has been established in ecology and paleozoology that taxonomic richness increases with sample size (references in Lyman 2008). If cultural transport led to sampling of species from different streams, especially streams at a distance, then small samples might not nest within larger ones. Within a locality, much as in contemporary ecology, if the full suite of species in an area is sampled, the species–area curve should asymptote as sample size increases. If the curve does not “sample to redundancy,” it could be that people transported new and different species from substantial distances. Similarly, if zooarchaeological samples are representative of past local mussel community composition, then the taxonomic composition of samples should sort along geographical gradients, such as upstream and downstream and among watersheds.

What we propose are multiple lines of evidence for determining whether or not cultural transport or other mechanisms bias archaeological mussel assemblages in terms of how well such samples represent past ecological conditions. The more lines of evidence, from species morphology and isotopic chemistry to assemblage composition (e.g., nesting and sampling to redundancy) that suggest sampling of local streams, the less likely that cultural transport was in play and the more confident the zooarchaeologist or ecologist can be in the representativeness of samples. As an example of assessing archaeological sample quality (i.e., representativeness) at the watershed level, we offer a case study from the Tombigbee River drainage in Mississippi and Alabama.

BACKGROUND ON ARCHAEOLOGICAL MUSSEL SHELL

An example of remains holding value for conservation biologists is freshwater mussel shell, a common constituent of archaeological sites across North America (e.g., Gallagher and Bearden 1980, Parmalee et al. 1980, 1982, Lyman 1984, Lippincott 1997, 2000, Butler and Campbell 2004, Culleton 2006) and elsewhere in the world. Native Americans exploited these animals over the entire span of the Holocene to a greater or lesser extent, depending on local abundance, human population pressure, and other factors (Peacock 2002). Accumulations range in size and density from a few scattered valves within a site matrix to immense "shell mounds" that may be hectares in area and several meters thick (Webb and DeJarnette 1942, Marquardt and Watson 2005), where millions of valves accumulated over the centuries (Haag 2009a). In addition to providing subsistence, mussels provided a raw material (shell) useful for tools, beads, and other lapidary items, and pottery temper (e.g., Theler 1990a, b, Lippincott 1997, Myers and Perkins 2000, Warren 2000). However, with very rare exceptions (e.g., Theler 1991, Warren 2000), the proportion of modified valves is far too low to have any significant effect on the taxonomic makeup of assemblages (Peacock 2000), and shells that have been modified for use as tools are immanently recognizable (Claassen 1998) and routinely reported.

By the time systematic surveys of America's waterways were undertaken by natural scientists, conditions in many streams were substantially altered from their preindustrial states (Bogan 1998, 2006). Archaeological shell assemblages thus often hold surprises in terms of species representation and relative proportions. For example, *Pleurobema decisum*, the southern clubshell, was by far the most common species in the main stem upper-central Tombigbee River of Mississippi and Alabama in prehistoric times (Robison 1983, Peacock 2000, 2002), a situation that has never been recorded historically (Peacock et al. 2011). Early naturalist records suffer from incomplete coverage, errors in identification, poor curation practices, and other problems (Hughes and Parmalee 1999:29, Hoke 2000, Haag 2009b). As a result of such biases, preindustrial ranges and past mussel community characteristics simply cannot be known in their entirety without accessing archaeological data.

An excellent example in this regard is the discovery of an "Ozarkian" species, *Cyprogenia aberti*, at a number of archaeological sites along eastern tributaries of the Mississippi River, in the Yazoo River and Big Black River drainages of Mississippi (Bogan 1987, Peacock and James 2002, Jones et al. 2005, Peacock et al. 2011). The species also has been reported from sites in northern Louisiana (e.g., Peacock and Chapman 2001, Saunders et al. 2005). While rare at most sites, it could be locally abundant; for example, Peacock and James (2002) found it to be the fourth most common species at a site in Hinds County, Mississippi. No living populations of this

species are known in Mississippi today (Jones et al. 2005). Current range maps (e.g., Oesch 1984: Fig. 144) show *C. aberti* as being limited to waterways issuing from the Ozark and Ouachita uplands of northern Arkansas, southern Missouri, and west into southeastern Kansas and northeastern Oklahoma. If one assumes that mussels were obtained locally in prehistoric times, then our historical understanding of this nationally threatened species (Williams et al. 1993) is limited, given that it once lived in radically different environments from where it is currently found. Another species, *Plethobasus cyphyus*, found "principally in streams above the Ozarkian crest" (Branson 1983:52), also was widespread throughout the Yazoo Basin (also known as the Mississippi Delta) in prehistoric times (Peacock et al. 2011). A small remnant population of this mussel recently was discovered in the Sunflower River in Mississippi (Jones et al. 2005), corroborating the range evidence derived from archaeological data.

As alluded to above, such taxonomic "surprises" may be informally attributed by biologists to the importation of shellfish, especially if the suspect shells are relatively rare in archaeological assemblages. From an optimal foraging theory standpoint, it is unlikely that shellfish were commonly transported long distances as food. Long-distance transport of food items correlates positively with caloric return (Binford 1978, Broughton 1999, Stiner et al. 1999, Nagaoka 2002, Cannon 2003, Munro 2004). Shellfish are exploited in patches (beds), and individuals offer very low caloric returns (Parmalee and Klippel 1974, but see Erlandson 1988 for protein values). They also are quite heavy in the shell, making bulk transport difficult. Such transport is a possibility, however, and has been specifically posited in particular archaeological cases (e.g., Johnson 1985, Theler 1990a, 1991, Warren 2000). Shellfish (or shells) also could have been transported for reasons other than food: e.g., for ritual, medicinal, or lapidary purposes. Such supposition may be cast as a hypothesis testable in various ways, at different scales of analysis: specimen level, assemblage level, and watershed level.

METHODS FOR ASSESSING CULTURAL TRANSPORT

Specimen-level scale

Morphometrics.—According to the "Law of Stream Position," headwater forms tend to be less obese (smaller width/length ratio) compared to large-river forms of the same mussel species (e.g., Ortmann 1920, Ball 1922, Eager 1978, Tevesz and Carter 1980, Imlay 1982, Roper and Hickey 1994, Timm 1994, Zieritz and Aldridge 2009, Hornbach et al. 2010). Shell sculpture (knobs and tubercles) also varies with stream reach (e.g., Hornbach et al. 2010), although results of analyses in this regard have been mixed (e.g., Ball 1922, Imlay 1982, Watters 1994, Peacock and Seltzer 2008). Theoretically, significant phenotypic differences in shell form suggest different source areas for particular archaeological specimens, whether it be downstream distance or

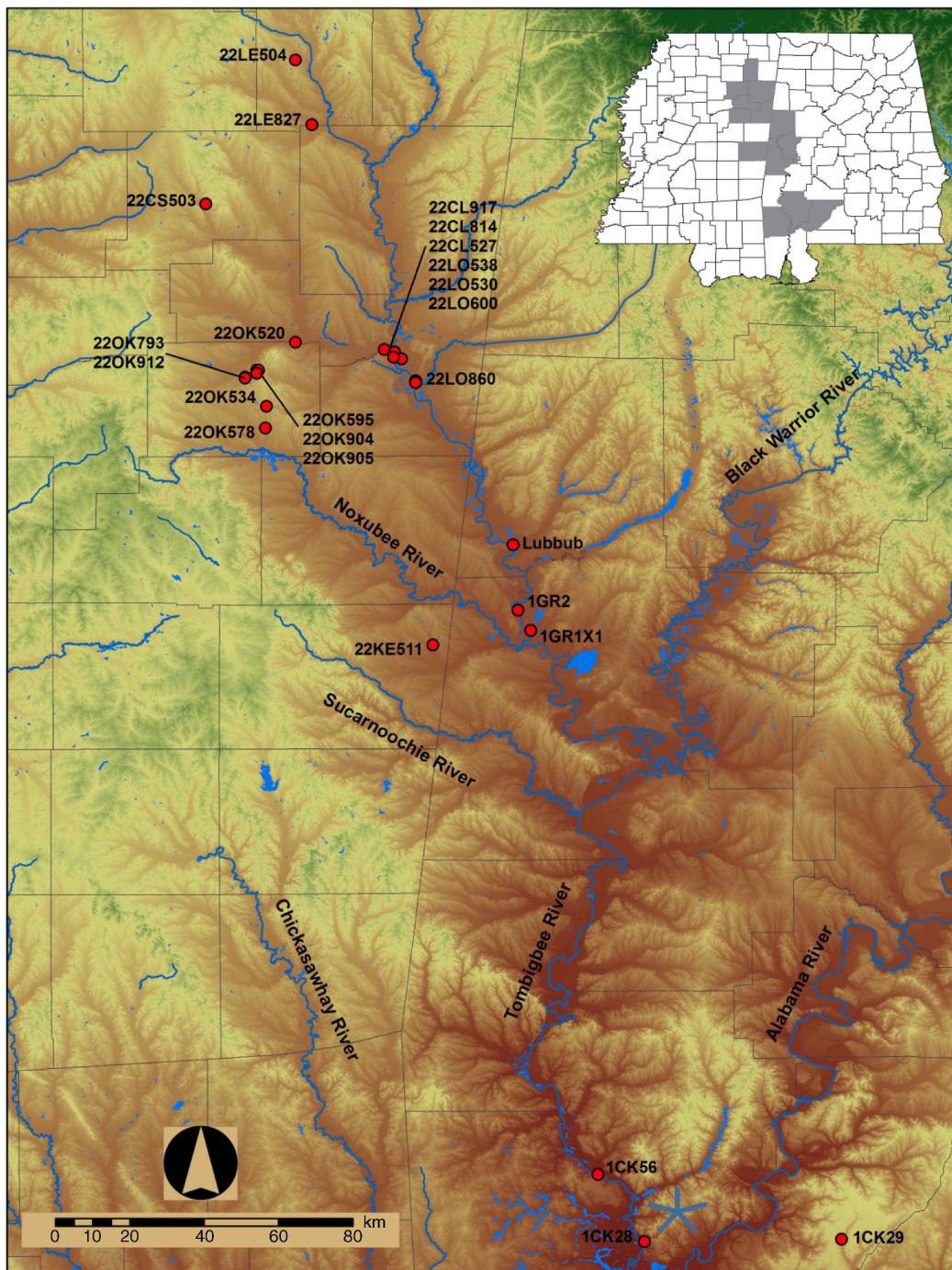


FIG. 1. Map of the Tombigbee River drainage, Mississippi and Alabama, USA. Archaeological sites with unionid shell material are denoted by red circles. Archaeological site numbers follow the Smithsonian Trinomial System, with states ordered alphabetically (Mississippi is number 22), followed by a county code (e.g., OK is Oktibbeha County), followed by a sequential site number.

different habitats within a given stream segment, and such differences may be quantifiable via morphometric analysis of archaeological shell. There are, however, several issues zooarchaeologists must consider when conducting morphometric analysis. Nonenvironmental factors that can affect shell form include growth stage

and sexual dimorphism. Additionally, archaeological shell often is fragmented so that traditional measures like length may not be available, necessitating the measurement of more robust shell features (e.g., Peacock and Mistak 2008, Peacock and Seltzer 2008, Randklev et al. 2009). Such features (e.g., pallial line to

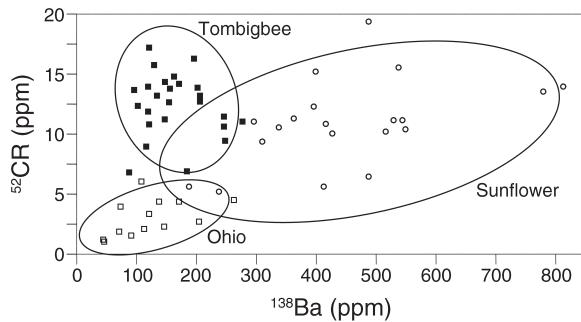


FIG. 2. Biplot of barium vs. chromium in mussel shells from archaeological sites in the Sunflower, Ohio, and Tombigbee River drainages. Ellipses represent 90% confidence intervals. The unit ppm refers to parts of the element per million parts of material ablated from different seasonal growth rings in mussel shell.

lateral tooth) have been shown to correlate positively with measurements used by biologists to characterize population structures (Peacock 2000).

Traditionally, morphometric analysis has been a cumbersome process involving the measurement by hand of landmark features on shell exterior and/or interior surfaces (e.g., Hazay 1881, Buchner 1910, Israel 1910, Grier and Mueller 1926, Bloomer 1938). Recent advances in geometric morphometrics, such as elliptical Fourier shape analysis (Crampton and Haines 1996, Scholz and Hartman 2007), are making such analyses both more efficient and more accurate in terms of environment-related features (Zieritz and Aldridge 2009). Methods are based on digital image analysis and employ Cartesian coordinates of landmarks. Researchers can use digitizers on specimens to obtain coordinates and outlines. These analyses maintain geometric data (Corti 1993) in a concise manner. Although complex, geometric morphometric image analysis has several advantages over traditional morphometric methods. For example, researchers can evaluate variables they did not initially plan to measure without the original specimens (Rohlf 1990). Geometric morphometric methods also provide the ability to analyze fragmented shell (Scholz and Hartman 2007). Size variation in a study sample can be addressed with Procrustes analysis: study specimens are scaled, translated, and rotated to remove size differences from the data set and to place each specimen in the same coordinate plane. In this way, shape differences between specimens are reflected in differences between the coordinate values of their landmarks. Researchers can then run standard multivariate tests to analyze these differences within a sample or across sample populations (Rohlf 1990, Slice 2007). Rohlf (1990) cautions that the variables that most easily record the shape of a specimen are not always the same variables that should be used in morphometric analysis. There are multiple ways to represent a group of landmarks, and the choice of specific variables should be justified in terms of their

function or development. For example, variables meant to measure the elongation of features should differ from those meant to show the degree to which features are “bent” (degree of vertical change in two directions over a given horizontal distance, as measured from a center point).

Researchers must keep in mind that, even in prehistoric times, average shell sizes in a mussel population could be reduced by human predation pressure (e.g., Peacock and Mistak 2008). One final, complicating factor in the morphometric analysis of archaeological shell is that watercourses evolve, leading to different environmental pressures and consequently different phenotypic responses in mussels over time (Caughron 2009). At sites occupied for centuries or millennia, which are common in eastern North America, such changes in shell size/shape (e.g., Klippel et al. 1978) could confound the use of morphometrics in sourcing studies. For example, Peacock and Seltzer (2008) found significant differences in pustule density and shell obesity (width/length) for specimens derived from different strata at a single site that were thousands of years apart in age. Thus, corroborative methods such as chemical sourcing should be employed.

Chemical sourcing.—Filter-feeding shellfish, including freshwater mussels, are in approximate chemical equilibrium with their aquatic environments (e.g., Lee and Wilson 1969, Jeffree et al. 1995, Dettman et al. 1999, Markich et al. 2002). In freshwater systems, each stream or stream segment is to some extent chemically distinct due to the representation of different geological areas (drainage basins) of various sizes. Major chemical differences may be expected between drainages in radically different geographical settings (e.g., piedmont vs. lower coastal plain). Such differences are reflected in the shell chemistry of freshwater mussels, providing the theoretical foundation for sourcing via the “provenience

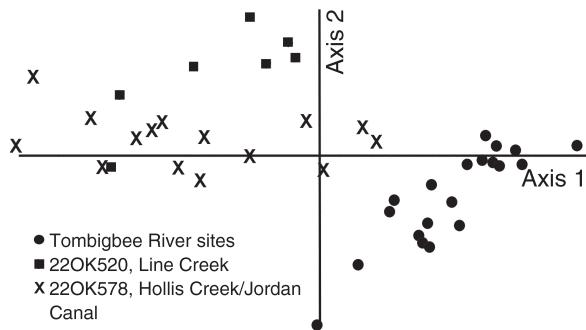


FIG. 3. Results of correspondence analysis of data on 46 elements taken from archaeological shell in the Tombigbee River drainage, eastern Mississippi. Analysis was done via PC-Ord (McCune and Mefford 1997) and employed Bray-Curtis ordination, using Bray-Curtis original endpoint selection, Sorenson (Euclidian) residual distance calculation, and element scores calculated by weighted averaging. Axis 1 accounts for 83.27% of the variation; axes 1 and 2 combined account for 94.47% of the variation.

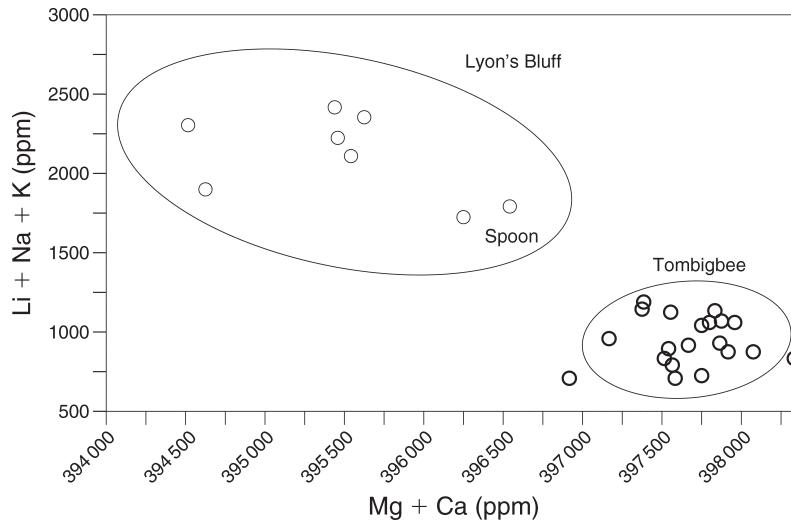


FIG. 4. Bivariate plot of elements showing chemical separation of shells from Tombigbee River sites and shells from Lyon's Bluff. Ellipses represented 90% confidence intervals. The figure is from Peacock et al. (2010: Fig. 4); used with permission.

postulate" if chemical differences related to a source outweigh other factors (such as post-depositional diagenesis) influencing shell chemistry. A recent diagenetic study at Lyon's Bluff (22OK520), a village site in Mississippi, using X-ray diffraction, scanning electron microscopy, and petrographic analysis, revealed no significant differences in microcrystalline structure or elemental makeup in mussel shell specimens (fragments unidentifiable to species) ranging over 450 years in age (Collins 2011). For an explanation of site number codes, see Fig. 1 legend.

Research employing laser ablation-inductively coupled plasma mass spectrometry (LA-ICP MS) indicates that the provenience postulate applies to mussel shell from archaeological sites (e.g., Peacock et al. 2007). Shell specimens from a number of different sites in Mississippi (Fig. 1) and Kentucky have been analyzed, with data taken for 46 elements (see Peacock et al. [2010] for analytical protocols). Fig. 2 is a sample biplot showing chemical separation of shell from sites of various ages in the Tombigbee (sites 22LO520, 22LO527, 22OK520, 22OK578), Sunflower (site 22SU531), and Ohio River (site 15CL58) drainages. (See Peacock [2008] and Peacock et al. [2011] for site and assemblage descriptions.) Fig. 3 is an ordination diagram showing the level of precision that can be achieved using this method. Data from Tombigbee River drainage shells were analyzed using correspondence analysis employing all 46 elements. Two sites (22LO530 and 22LO527) located within 3.5 km of one another on the main stem of the Tombigbee River in eastern Mississippi are chemically indistinguishable. However, shells from sites on tributary streams (Line Creek [site 22OK520] and Hollis Creek/Jordan Canal [site 22OK578]) feeding into the Tombigbee from the west show good chemical separation from the main river

and between tributaries. This separation was achieved even though all three sites fall within a 35 km radius circle.

The shell analyzed was from general midden deposits and was assumed to represent food detritus (and hence a local chemical signature). A possible exception was noted at one site. On the basis of phenotype, a prehistoric (ca. AD 1400) shell "spoon" retrieved from a grave at site 22OK520, located on a tributary stream in the Tombigbee River drainage, was hypothesized to be an import from the main river valley, minimally 25 km away (Peacock et al. 2010). This artifact is fashioned from a right valve of *Lampsilis straminea claibornensis*, the only specimen of this relatively inflated, smooth-shelled, "downstream" phenotype thus far recovered from the site, where the compressed and highly sculptured "upstream" form, *L. s. straminea*, is common in an assemblage of over 900 valves. To test whether the spoon had been imported to the site from the main river valley, the chemical sourcing method mentioned above was applied to the spoon and several valves of *L. s. straminea* from 22OK520. The resulting chemical data were compared to data derived from shells from main stem Tombigbee River sites, also analyzed via LA-ICP MS. The results (Fig. 4) indicate that the spoon was manufactured from shell obtained locally, as it grouped chemically with other shells from 22OK520, distinct from shells from main-river sites (Peacock et al. 2010).

Assemblage-level scale

Context.—Some clues as to whether shellfish were imported to a site can be derived from the contexts in which the specimens were deposited. If extra-local species were occasionally brought in for food, it is reasonable to assume that they were brought in batches.

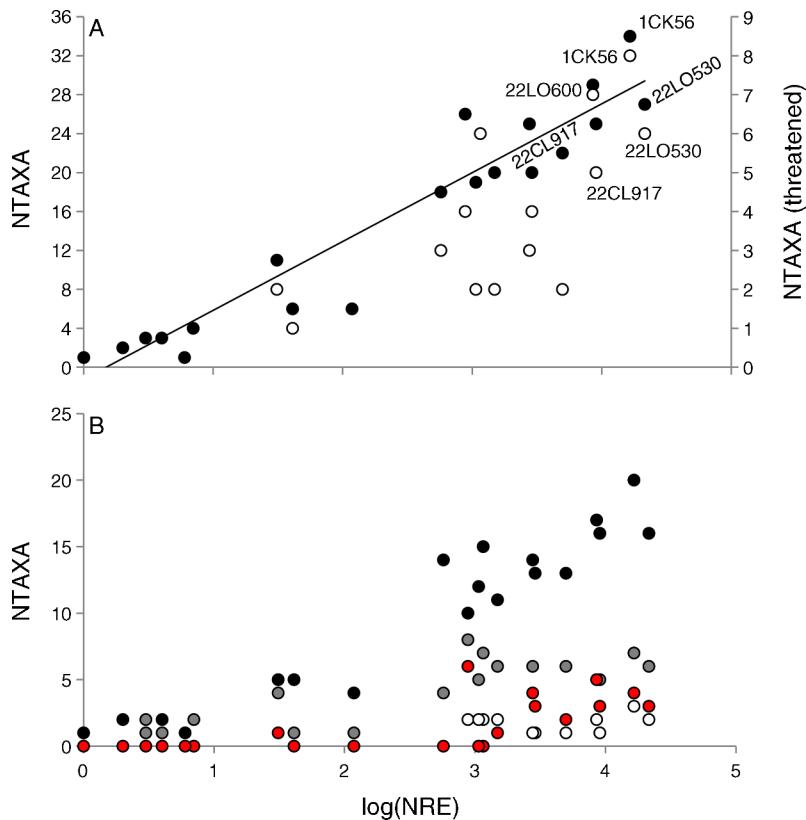


FIG. 5. (A) Black circles denote the relationship between total unionid nonrepetitive element (NRE) (sample size) and NTAXA (number of unionid species), and open circles denote the relationship between unionid NRE (sample size) and NTAXA (threatened or federally endangered, threatened, or extinct unionid species). The simple best fit line ($r^2 = 0.92$, $P < 0.05$) is shown for the relationship between NRE and NTAXA; sites above or below this line have higher or lower NTAXA values than is predicted by the regression analysis. (B) The relationship between total unionid NRE (sample size) and NTAXA (number of unionid species per shell preservation category). Shell categories were defined following Wolverton et al. (2010) as follows: Category 1, black circles, unionid shells with high sphericity and density; Category 2, open circles, unionid shells with high sphericity and moderate density; Category 3, gray circles, unionid shells with moderate sphericity and high density; Category 4, red circles, unionid shells with low sphericity and density. For both graphs, sample size and preservation are important factors that influence the presence of a given mussel species.

Because of their perishable nature, the animals presumably would have been consumed quickly. (The same caveat applies even if the meat was shucked out for smoking or other preservation measures. Shucking/smoking could have taken place elsewhere, in which case animals could be transported without shells). Although shells resulting from such short-term events could have been scattered about, there is no apparent reason to think that people would have wasted effort doing so. The assumption, then, is that extra-local shell should be found in concentrations representing short-term episodes of processing and disposal, and given the extra effort required for transport, such concentrations also might be expected to occur outside deposits of everyday domestic debris (e.g., on mound flanks). The shells of locally available shellfish also presumably accumulated via a series of short-term depositional events, but more frequent use of an abundant, near-at-hand resource would have led to more constant incorporation into general midden deposits.

An example is provided by *Rangia cuneata* (marsh clam) shells found in unionid mussel middens at a number of prehistoric sites on the Lower Tombigbee River in southern Alabama (e.g., McGregor and Dumas 2010). Archaeological specimens are found significantly north of where this brackish-water species occurs today (E. Peacock, S. W. McGregor, and A. A. Dumas, *unpublished manuscript*). Although the numbers are small (e.g., Peacock 2009), marsh clam shells are not found together in archaeological contexts, as would be expected if batches of shellfish were being brought in from afar, consumed, and the waste discarded. Instead, shells are found scattered throughout general midden deposits, suggesting that marsh clams were locally present in low numbers in the river and were being gathered along with mussels in prehistoric times (E. Peacock, S. W. McGregor, and A. A. Dumas, *unpublished manuscript*). *Rangia cuneata* are capable of tolerating low-salinity conditions, so it is feasible that they occurred in the Lower Tombigbee River in the past

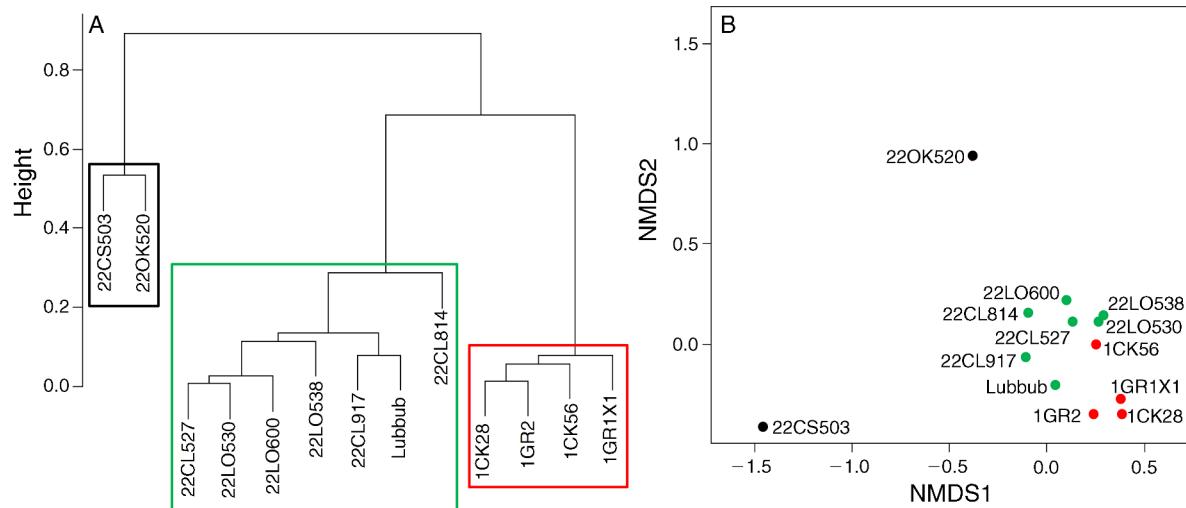


FIG. 6. (A) Hierarchical cluster analysis (group average) using Horn's index of dissimilarity for abundance data from archaeological sites with sample sizes (NRE) ≥ 100 . Abundance data were converted to proportions to control for differences in sample size. Colored rectangles denote significant clusters ($R = 0.99$, $P < 0.05$; ANOSIM). The correlation analysis between the calculated and plotted similarities was 0.96, indicating a good representation of actual similarities. (B) Nonmetric multidimensional scaling (NMDS) using Horn's index of dissimilarity for abundance data from archaeological sites with sample sizes (NRE) ≥ 100 . The stress, a measure of goodness of fit, was 0.03, indicating a good representation of actual similarities. As with the cluster analysis, abundance data were converted to proportions to control for differences in sample size between archaeological sites. For both analyses, the geography in the Tombigbee River drainage is the dominant factor in structuring unionid community composition at these sites.

when sea level was higher than today (E. Peacock, S. W. McGregor, and A. A. Dumas, *unpublished manuscript*). If they were being transported into the area from farther south, other, less tolerant brackish/salt water invertebrate and vertebrate species also could have been imported to the Lower Tombigbee sites, but no such demonstrably extra-local fauna have been found (e.g., Klippel and Synsteliën 2009).

Watershed-level scale

For the Tombigbee River drainage in Mississippi and Alabama, we have data on 71 984 mussel valves identifiable at least to genus (with a minimum of 43 species represented) from 23 sites in nine counties in Mississippi and Alabama (see Peacock 2009, McGregor and Dumas 2010, Peacock et al. 2011; and E. Peacock, S. W. McGregor, and A. A. Dumas, *unpublished manuscript*, for original data tables), that allow us to look at sample characteristics throughout the drainage basin.

Sample size and taphonomy.—Logistic species–area curves can be used to assess whether multiple samples in a watershed reach an asymptote in terms of discovery of rare species with increased sampling (Wolff 1975, Lyman 2008, Peacock, *in press*). A related technique, nestedness (Wright et al. 1998), can be used to determine whether the assemblage of species represented in smaller samples simply constitute subsets of larger samples in a watershed (Lyman 2008). If so, this suggests that differences in samples from different sites within a watershed relate to sampling intensity and/or clinal

changes in species distributions, not to differences in cultural filters.

For studies using archaeological shell to characterize past mussel community composition, the target variable of interest is often the presence of state or federally listed species (NTAXA [threatened]) or taxonomic richness (NTAXA [number of unionid species]). Measures of richness are sensitive to sample size effects. Species–area curves are used to evaluate correlations between sample size andNTAXA (see Lyman and Ames 2007, Lyman 2008) to determine the magnitude and degree to which these variables are biased by sample quality.

Fig. 5A demonstrates this relationship for archaeological sites in the Tombigbee River drainage. The quantitative unit used here is the nonrepetitive element (NRE), defined as an exoskeletal part that occurs only once per individual mollusk (e.g., right or left valves) that can be identified to taxon based on diagnostic morphological characteristics (Mason et al. 1998). In this example, as sample size (NRE) increases, the number of species, including those that are federally listed, also increases. If local environments are sampled adequately, as in modern ecological communities, taxonomic richness asymptotes with additional sampling once the rarest species are encountered; this is referred to as sampling to redundancy (Lyman 2008:146–152). Given this relationship, it is not surprising that the addition of archaeological sites with larger sample sizes results in the occurrence of rare species. Assuming that habitat and preservation were similar at sites, an

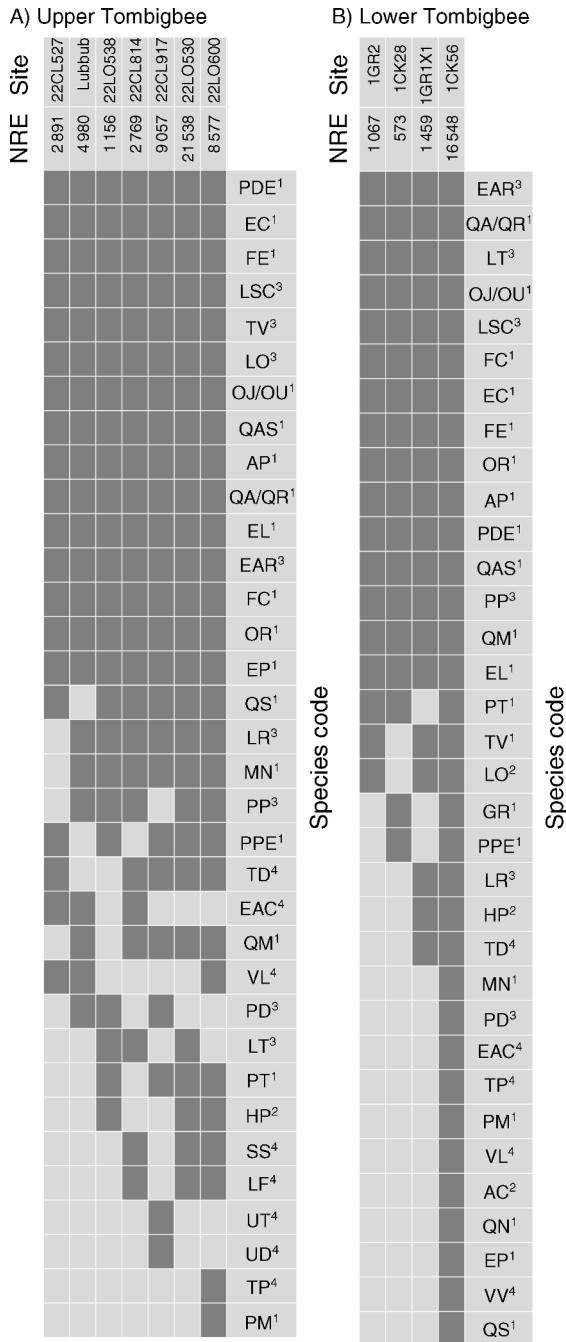


FIG. 7. Nestedness diagrams of archaeological sites in the Tombigbee River drainage. The diagrams are based on groupings identified in the cluster and nonmetric multidimensional scaling (NMDS) analyses. For each diagram, codes for unionid species are listed at the top, and their presence at a given archaeological site is denoted by a dark-shaded square; the numerical superscripts for each species correspond to shell preservation categories described in Wolverson et al. (2010). For explanations of the species codes, see Table 1. Sample size (NRE) is also presented for each archaeological site. The nested “temperatures” (heat of disorder; see *Watershed-level scale: Sample size and taphonomy*) for diagram A (upper Tombigbee faunal component) and diagram B (lower Tombigbee faunal component) are 21.9° and 7.1°, respectively. The tributary

increase in sample size increases the likelihood of the recovery of rare species in archaeological faunas.

Another point to consider is whether sample size is the sole determinant for NTAXA and the occurrence of rare species. For a number of assemblages in the Tombigbee River drainage, NTAXA differs among assemblages with similar sample sizes, which indicates that factors other than sample size influence species occurrence. For example, 22LO530 has lower NTAXA compared to 1CK56, despite having a similar sample size. Both sites are located on the Tombigbee River but are separated geographically (Fig. 1), which suggests that differences in NTAXA between these sites stem from regional dissimilarities in habitat and species pool. In contrast, the disparity in NTAXA for 22LO600 and 22CL917 is probably attributed to site-specific differences in preservation, because both assemblages have similar sample sizes and are located in the same geographic area. This last example highlights the concept that preservation and geographic locality must be assessed in addition to sample size to determine whether rare species are local in origin.

Even when nestedness, morphology, and/or isotopic chemistry indicate that shells were not transported long distances and are thus representative of past local communities, the zooarchaeologist may confront differential preservation of shell as a biasing factor. Recent studies demonstrate that preservation of freshwater mussel shells is largely dependent on shell density and shape (Wolverson et al. 2010). Specifically, spherical and dense mussel shells are more likely to be preserved in archaeological contexts than less spherical and less dense shells. As a result, the probability of occurrence for poorly preserved shells is dependent on past abundance and sample size of a given assemblage. Fig. 5B illustrates this point: as sample size increases, the number of species with low-density and nonspherical shells also increases. If species with fragile shell morphology are encountered in a sample, and if a species-area curve indicates sampling to redundancy, the conclusion that a particular sample represents the past local community in terms of taxonomic composition is supported.

As an additional test of this proposition, geographic locations of mussel shell assemblages from sites can be assessed with ordination and other classification methods (see Peacock 2000, and *in press*, for further details). Such methods commonly are used by ecologists to classify communities on the basis of similarities between sample sites (Krebs 1999). For archaeological faunal assemblages, they can be used to evaluate how species composition changes with respect to geographic location. Fig. 6 shows a statistically significant separation ($R = 0.99$, $P < 0.05$; ANOSIM) between sites, based on the geography of the Tombigbee River drainage. Archaeo-

← faunal component was omitted because there were only two sample sites within this cluster/grouping.

logical sites (22CS503 and 22OK520) located on tributaries are separated from sites on or near the Tombigbee River. Sites on the Tombigbee River are separated based on their relative stream location. This separation is based on the condition of habitats from which these species were collected. For example, unionid species from 22CS503 and 22OK520 are characteristic of tributary streams (Peacock et al. 2011), whereas those from the upper and lower faunal components of the Tombigbee River are typical of medium- and large-sized rivers (Peacock 2000, Peacock and Seltzer 2008; E. Peacock, S. W. McGregor, and A. A. Dumas, *unpublished manuscript*). Moreover, although they are statistically different, the fact that the groupings/clusters for the Tombigbee River are more similar than those for nearby tributaries indicates that mussel shells from these sites are probably local in origin. If this were not the case, the groupings/clusters likely would consist of a mix of species with different habitat preferences. That is, species adapted to small, slow-flowing streams would be clustered with those adapted to large, fast-flowing rivers. Of course, this relies on the assumption that modern habitat preferences for a given mussel species are the same as they were in the past (Warren 1991). We presume this is the case for the Tombigbee River drainage because most of the shell assemblages are no more than ~1300 years old, excepting site 22LO538, which has two shell-bearing strata, one dating to ca. AD 700–1000 and one dating to ca. 4490–3660 BC (Atkinson 1974, Peacock and Seltzer 2008).

A valid question regarding these clusters/groupings is whether they are “real,” given that community composition is influenced not only by prehistoric habitat but also by sample size and preservation. That is, are samples of different sizes within each group/cluster derived from the same underlying population? This hypothesis can be tested by examining the nestedness of shellfish faunas in terms of taxonomic composition to determine if assemblages with smaller sample sizes are subsets of those with larger samples. A nested subset pattern is measured on a scale from 0 (perfectly nested faunas) to 100 (no nestedness) degrees and is referred to as the “heat of disorder” or “temperature” (see Lyman 2008:168–170 for further details). For archaeological sites on the Tombigbee River, the upper river grouping has a nested temperature of 21.9°, and the lower river grouping has a temperature of 7.1° (tributary assemblages were omitted because only two sites had samples large enough for consideration). A visual examination of this nested pattern (Fig. 7, Table 1) shows that small samples nest within larger samples in terms of taxonomic composition. Closer examination reveals that the species absent from archaeological sites with small samples are those with easily fragmented shells. This figure is illustrative of our point that rare species collected from an assemblage are not a priori evidence for long-distance transport.

TABLE 1. Definitions for unionid mussel species codes used in Fig. 7.

Mussel species codes and scientific names
AC, <i>Arcidens confragosus</i>
AP, <i>Amblema plicata</i>
EAC, <i>Elliptio arcata</i>
EAR, <i>Elliptio arca</i>
EC, <i>Elliptio crassidens</i>
EL, <i>Ellipsaria lineolata</i>
EP, <i>Epioblasma penita</i>
FC, <i>Fusconaia cerina</i>
FE, <i>Fusconaia ebena</i>
GR, <i>Glebulia rotundata</i>
HP, <i>Hamiota perovalis</i>
LCA, <i>Lasmigona complanata alabamensis</i>
LF, <i>Leptodea fragilis</i>
LO, <i>Lampsilis ornata</i>
LR, <i>Ligumia recta</i>
LS, <i>Lampsilis straminea</i> ssp.
LSC, <i>Lampsilis straminea claibornensis</i>
LSS, <i>Lampsilis straminea straminea</i>
LT, <i>Lampsilis teres</i>
MA, <i>Medionidus acutissimus</i>
MN, <i>Megaloniaia nervosa</i>
OJ/OU, <i>Obovaria jacksoniana/unicolor</i>
OR, <i>Obliquaria reflexa</i>
P, <i>Pleurobema</i> cf. <i>verum</i>
PD, <i>Plectomerus dombeyanus</i>
PDE, <i>Pleurobema decisum</i>
PM, <i>Pleurobema marshalli</i>
PP, <i>Potamilus purpuratus</i>
PPE, <i>Pleurobema perovatium</i>
PT, <i>Pleurobema taitianum</i>
QA/QR, <i>Quadrula apiculata/rumphiana</i>
QAS, <i>Quadrula asperata</i>
QM, <i>Quadrula metanevra</i>
QN, <i>Quadrula nobilis</i>
QS, <i>Quadrula stapes</i>
SS, <i>Strophitus subvexus</i>
TD, <i>Truncilla donaciformis</i>
TP, <i>Toxolasma parvum</i>
TT, <i>Toxolasma texasense</i>
TV, <i>Tritogonia verrucosa</i>
TTR, <i>Truncilla truncata</i>
UD, <i>Unioemerus declivis</i>
UT, <i>Unioemerus tetralasmus</i>
VL, <i>Villosa lienosa</i>
VV, <i>Villosa vibex</i>

CONCLUSIONS

We do not contend that natural scientists have ignored data on archaeological mussel shell; indeed, a number of publications in the biological literature would belie such an assertion (e.g., Ortman 1909, Parmalee 1956, Stansbery 1966, Murphy 1971, Murray 1981, Barber 1982, Taylor and Spurlock 1982, Call and Robinson 1983, Gordon 1983, Robison 1983, Neves et al. 1997:51–52, Hughes and Parmalee 1999, Williams and Fradkin 1999, Lyons et al. 2007, Haag 2009a, Randklev et al. 2010). There also exists a body of work reflecting cross-disciplinary collaborations between archaeologists and natural scientists (e.g., Hughes and Parmalee 1999, Peacock et al. 2005, McGregor and Dumas 2010, Wolverton et al. 2010, 2011). We do contend, however, that archaeological faunal data in general remain underused. Part of the reluctance to

employ such data in modern resource management contexts may stem from reasonable concerns related to preservation and sampling biases. However, consideration of such biases is a standard part of zooarchaeological procedure, and the extent to which the data are shaped by such biases (and hence their general utility in an applied context) can readily be assessed. A less reasonable fear concerns the extent to which prehistoric faunal assemblages are shaped by the cultural filter, as via human transport. We do not assert that such transport never occurred, but that such a suggestion should be treated as a hypothesis and tested by various means at different scales, rather than being assumed with consequent disregard of important data.

The spatial patterning evident in statistical analyses of archaeological mussel data suggests that, in most cases, all or most of the shell recovered from particular sites came from waterways adjacent to those sites, an assertion that makes sense from an optimal foraging theory perspective. We believe it is safe to assume that the large assemblages typically recovered from archaeological sites adequately represent past mussel communities once the various types of potential bias are accounted for (Barber 1982, Cvancara 2000). Such tests as we have discussed herein can be applied to all kinds of animal remains derived from archaeological deposits. We recommend that natural scientists approach zooarchaeological data in general from a perspective of "innocence before guilt." The rewards will be increased interdisciplinary cooperation and results of real applied value in the complex world of natural resource management, especially where particularly sensitive organisms like freshwater mussels are concerned.

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