

Evolutionary Ecology, Resource Depression, and Niche Construction Theory: Applications to Central California Hunter-Gatherers and Mimbres-Mogollon Agriculturalists

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Published online: 17 July 2010
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Abstract Evolutionary ecology is a theoretical framework that has been widely applied to problems in human evolution and prehistory. Because the approach often focuses on how behavioral adjustments to changing socio-ecological conditions create novel selective pressures that in turn drive other changes in morphology and behavior, it draws on the same evolutionary logic that underlies niche construction theory. We illustrate here the important role that niche construction has played in archaeological applications of evolutionary ecology with two detailed case studies: one from Late Holocene hunter-gatherer populations in Central California and one from Mimbres-Mogollon agriculturalists in New Mexico. These examples illustrate that evolutionary ecology-based approaches, with an emphasis on formal predictive modeling, allow for the incorporation of niche construction as it affects model parameters with reference to specific problems involving past behavior. Further modeling and empirical applications will expand the synergies between these complementary approaches and advance our understanding of the human past.

Keywords Evolutionary ecology · Niche construction theory · Resource depression · Human behavioral ecology

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Introduction

Evolutionary ecology (EE) is a theoretical framework that has been widely applied to problems in human evolution and prehistory and can be defined as the application of natural selection theory to the study of adaptive design in behavior, morphology, and life history (Bird and O'Connell 2006; Broughton and Cannon 2010; Winterhalder and Smith 1992). In practice, archaeological applications of EE are typically concerned with understanding how socio-ecological conditions structured the past behaviors or morphologies that archaeologists and paleoanthropologists are interested in studying. One of the distinguishing characteristics of the EE approach is that it makes use of formal optimization models that are designed to explore the fitness-related costs and benefits of behavioral or morphological alternatives in specific socio-ecological contexts. The EE approach builds on traditional archaeological interest in human–environment interrelationships, but it allows such issues to be studied in a way that is much more theoretically sound and methodologically rigorous than is usually the case. Theoretical soundness derives from EE's concern with explicitly specifying the parameters that are hypothesized to affect the costs and benefits of phenotypic alternatives, and methodological rigor is enabled by the identification of variables that can be measured in order to test propositions derived from the theory. Because EE often focuses on how behavioral adjustments to changing socio-ecological conditions create novel selective pressures that in turn drive other changes in morphology and behavior, these applications draw on the same evolutionary logic that underlies niche construction theory (NCT).

Developed primarily over the last two decades, the central premise of the niche construction perspective is that the activities of organisms can modify the environment so as to alter selective pressures for themselves and descendants inheriting that environment. The perspective thus views niche construction as a unique evolutionary process—a cause of evolution rather than simply a product of it. While the concept is strongly intuitive, and niche construction is more easily observed than natural selection, it has hidden complexities and significant implications for evolutionary dynamics (*e.g.*, Day *et al.* 2003; Gray 1988; Laland *et al.* 1999; Laland and Brown 2006; Lewontin 1983; Odling-Smee *et al.* 2003).

We illustrate here the important role that niche construction has played in archaeological applications of EE with two case studies from the Late Holocene of western North America. These examples illustrate that EE-based approaches, with an emphasis on formal predictive modeling, allow for the ready incorporation of niche construction as it affects model parameters with reference to specific problems involving past human behavior.

Evolutionary Ecology and Niche Construction Theory

Linking Evolutionary Ecology and Niche Construction

The optimization logic used in EE assumes that organisms will adapt to changing socio-ecological conditions in ways that maximize fitness, whatever the proximate

genetic, physiological, cultural, or cognitive mechanisms that may underlie the adaptation and whatever the specific source of the changing conditions. EE models are thus used to generate predictions about adaptations that result from selective pressures stemming from environmental changes extrinsic to the organism, as well as those that result from modifications of the organism's own making—and the latter represents an important symmetry between niche construction and EE. In a nutshell, EE models predict specific changes in human phenotypes as a result of changes in socio-ecological conditions, and to the extent that the changes in those conditions are due to human action, niche construction plays the catalytic role. In addition, niche construction also occurs to the extent that the phenotypic changes that result from altered socio-ecological conditions themselves create new selective pressures. A hypothetical application of the encounter contingent “prey model” from foraging theory—a subfield of EE dealing with foraging behavior—illustrates these types of linkages.

The prey model (see Stephens and Krebs 1986) predicts that foragers will select only prey items with post-encounter return rates high enough to maintain or increase the overall net caloric return rate while foraging within a resource patch. Since overall patch returns are a function of resource densities and encounters, declining abundances of and encounters with high-return prey types are predicted to lead to the expansion of the suite of prey types taken from that patch. Most notable here, the prey model predicts widening diet breadth regardless of the specific cause for declining encounters with high-ranked prey—that cause may be an extrinsic environmental change or human-induced prey depression. In the case of the latter, prey depression represents a case of negative niche construction, where niche-constructing activities change environments in ways that decrease fitness (see Odling-Smee *et al.* 2003:47). Thus, it is niche construction that affects a key parameter of the prey model, overall net patch return rates, declines which drive the model-predicted change in subsequent foraging behavior, namely, reduced prey selectivity or a widening of within-patch diet breadth. Archaeological tests of these propositions may involve temporal trends in faunal taxonomic abundances and other data bearing on environmental change, as well as skeletal indicators of increasing harvest pressure (*e.g.*, Broughton 2002; Cannon 2003; Nagaoka 2002; Wolverton *et al.* 2008).

Anthropogenic reductions in prey abundances constitute an obvious case of niche construction to which the prey model predicts that foragers should respond by increasing diet breadth. Perhaps less obvious, but no less important, is that the increase in diet breadth itself may constitute further niche construction: incorporation of new resources into the diet may result in major changes in selective pressures, as the case studies discussed below illustrate. This further highlights the overlap between EE and NCT. Indeed, the NCT conception of evolution as a cumulative process in which once incidence of niche construction leads to another should come as second nature to practitioners of EE.

Evolutionary Mechanisms in EE and NCT

The prey model example discussed above raises the question of what proximate sources underlie the specific behaviors or other phenotypic characters under study,

and both EE and NCT hold that several different transmission and inheritance mechanisms may be operative depending on the nature of the phenotypic trait involved. Both approaches also hold that behavioral changes—an important source of niche construction—can represent virtually instantaneous facultative adjustments to changing environmental contexts. The cognitive machinery allowing such adjustment is thus the product of natural selection, whereas specific behavioral responses are not.

Applications of EE, especially those in archaeological contexts, usually do not explicitly address these issues of evolutionary mechanisms (see Cannon and Broughton 2010), but recent work in NCT has provided a heuristic framework for conceptualizing the contexts under which facultative, cultural, or genetic systems may be at work (Fig. 1; from Odling-Smee *et al.* 2003:338). As depicted in Fig. 1, “route 1” consists of cases in which behavioral adjustments to changing socio-ecological conditions modify selection pressures that drive further cultural change. For example, a human-induced depletion of large ungulates may drive a shift to more intensive fishing, which, in turn, would alter selective pressures to favor technology (*e.g.*, netting) that would increase the efficiency of harvesting fish resources. Individuals thus adopt behavioral practices that are adaptive under the modified conditions but genetic evolution is absent or minimal; rather, facultative behavioral changes or cultural inheritance are clearly involved in these contexts.

On the other hand, if the cultural/behavioral response is insufficient to counteract the behaviorally induced environmental change, the latter can drive selective pressures that may change genetic frequencies in human populations. This is the “route 2” response, depicted in the lower of the two feedback loops in Fig. 1 (Odling-Smee *et al.* 2003). Using the example above, suppose that the behavioral shift to intensive fish exploitation took place but that netting technologies were not available due, say, to a lack of suitable plant fiber raw materials. Genetic-based natural selection may then begin to play an important role and favor such features as smaller adult body size to cope with lower food availability or other adaptive

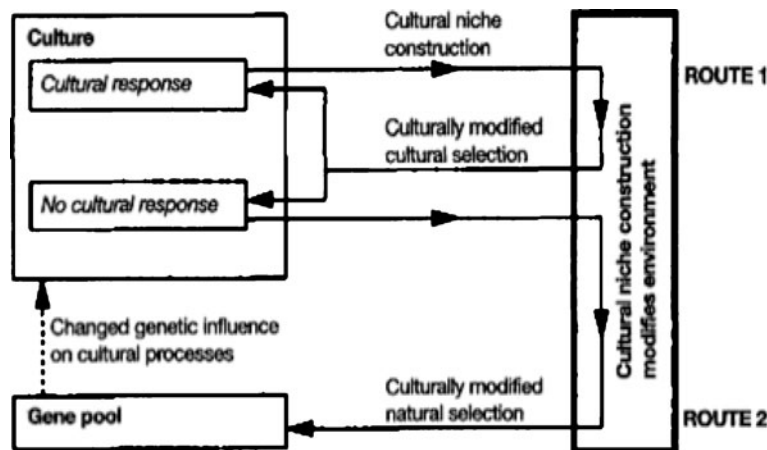


Fig. 1 Routes of niche construction. See text for discussion (from Odling-Smee *et al.* 2003: Fig. 9.1, p. 338)

characteristics associated perhaps with intensive exposure to cold water (e.g., thicker layers of subcutaneous fat), insofar as fishing intensified in the absence of any new technology.

It is also possible that genetic changes resulting from niche construction (route 2) can influence further cultural or facultative behavioral responses, as depicted by the dashed arrow at the bottom left in Fig. 1. Smaller adult body size driven by the processes described above might, for example, influence the energetics associated with watercraft use in the pursuit of fish resources. Behavioral or cultural niche construction can thus potentially drive repeated cycles of evolutionary change. These forms of feedback are rarely considered in standard evolutionary analyses, but are an important component of the niche construction perspective (Day *et al.* 2003; Odling-Smee *et al.* 2003).

Previous applications of EE in archaeology and paleoanthropology illustrate the range of proximate mechanisms underlying the expression of phenotypic variants that may be involved and include examples of both of these primary routes by which human populations can respond to their own behavioral or cultural niche construction. Paleoanthropological applications have addressed aspects of the early hominin biological phenotype—such as life history characteristics and brain enlargement—that were certainly under relatively direct genetic control (Kaplan *et al.* 2000; O’Connell *et al.* 1999). Moreover, these applications argue that evolutionary changes in these aspects of the phenotype stemmed from niche construction—specifically, changes in behavior in the realm of subsistence and mating—that may or may not have been under such direct genetic control. Other examples, by contrast, address patterns of persistence and variability in technology, and archaeologists have long recognized that such patterns may be largely a product of cultural transmission. Finally, the case studies we elaborate below address prehistoric subsistence behavior, which can reasonably be assumed to have been at least in part an expression of facultative adjustment, as is the case, for example, when a forager decides whether to pursue a resource based on cues to the likelihood of encountering alternative resources during a foraging trip. However, it is also likely that cultural transmission has played some role in subsistence behavior in many situations, as is the case, for example, when elders provide children instruction in farming, food processing, or hunting and gathering activities. Given that EE models are demonstrably applicable regardless of the proximate mechanisms in play, users of these models would likely benefit from more explicit consideration of the perspective on these mechanisms that NCT provides.

Evolutionary Ecology, Niche Construction, and Resource Depression: Case Studies

Many examples of the use of niche construction in EE-based approaches to the human past model the effects of population growth and resource depression on subsequent changes in human behavior. These represent examples of perturbatory niche construction or cases where organisms actively change components of their environments in specific spatiotemporal contexts. As we alluded to above, resource

depression refers to reductions in the encounter rate of prey species (or other resources) caused by the activities of the predator (Charnov *et al.* 1976), and foraging theory has provided a theoretical foundation to explore this phenomenon in archaeological settings all over the world. Most important, resource depression can be a potent form of niche construction (Laland *et al.* 2001) in that it alters selective environments that influence many other facultative behavioral adjustments and, in some settings, genetic changes in human populations. Examples relate to a diverse array of topics including human colonization, agriculture, and technological change. Analyses of prehistoric resource depression thus have far-reaching implications, and consequently, they represent one of the better developed areas in the archaeological application of EE (see reviews in Broughton 2002, 2004a, b; Grayson 2001; Lupo 2007). We highlight below two archaeological case studies that demonstrate the role resource depression plays as a form of niche construction.

Resource Depression Affecting Diet Breadth, Violence, Human Health, and Stature in the Prehistoric Sacramento Valley, Central California

The causes of dietary change and their consequences for changes in health and violence are fundamental issues in human prehistory (*e.g.*, Cohen 1981; LeBlanc 1999; Lambert and Walker 1991; Larsen 1995; Martin and Goodman 2002), and many of these elements can be deductively integrated within EE approaches that incorporate a major role for niche construction. In the NCT framework (Fig. 1), resource depression represents a cultural or behavioral niche construction factor that modifies the environment. The predicted behavioral responses (route 1) include: (1) widening diet breadth and increasing use of low-return resources and (2) increases in interpersonal violence that are anticipated from models of territorial defense under conditions of broader diets that favor intensive use of resources with dense concentrations in stationary, spatially confined clumps (*e.g.*, Broughton and O'Connell 1999).

To the extent that these behavioral responses are unable to offset the declining returns driven by resource depression, changes in the selective environment that would affect the human genotype (route 2 effects) are also predicted to occur due to factors related to nutrition. Insofar as increases in morbidity and mortality result from the new environmental conditions, enhanced selection related to stronger physiological or immune responses to disease and nutritional stress is anticipated. Such selective conditions could be inferred from changes such as reduced adult body size and an increased prevalence of skeletal indicators of disease or nutritional stress.

These hypotheses derived from integrating EE models of behavioral response with NCT suggest that faunal and floral evidence for resource depression and widening diet breadths should co-vary with human skeletal indicators of morbidity, mortality, stature, and interpersonal violence. We test these hypotheses next using data derived from Late Holocene hunter-gatherers of the lower Sacramento Valley of Central California.

In several respects, the lower Sacramento Valley is an ideal setting to examine these issues since it was represented by one of the highest—if not the highest—ethnographically documented population density of hunter-gatherers anywhere in North America (Cook 1976; Driver and Massey 1957). Previous archaeological

research has also documented that those populations expanded dramatically over about the last 4,000 years (Dickel *et al.* 1984; Rosenthal *et al.* 2007; White 2003b). In addition, the region is characterized by a high diversity and abundance of lower-return plant (*e.g.*, acorns, grass seeds) and small vertebrate (*e.g.*, rodents, small resident fishes) resources, with many of the latter characterized by high *r* (intrinsic rate of population increase) values and resilience to harvest pressure. These attributes can promote continued expansion of human forager densities despite concurrent depression of high-return prey resources (see Belovsky 1988; Byers and Broughton 2004; Winterhalder and Goland 1997; Winterhalder and Lu 1997).

On the empirical side, the region has produced a rich sample of Late Holocene archaeological vertebrate faunas and human skeletal samples, and over the last several decades, increasingly refined analyses of those materials have been directed at issues related to prey depression and human paleopathology (Bartelink 2006; Broughton 1994a; Rosenthal *et al.* 2007; White 2003a). These data now allow a systematic evaluation of the potential role that resource depression played as a niche construction variable affecting trends in diet breadth, violence, and human health and stature across the Late Holocene in the Sacramento Valley.

Faunal Evidence for Resource Depression in the Sacramento Valley

Several systematic assessments of the faunal evidence for resource depression and intensification in the Sacramento Valley have been recently presented (Broughton 1994a, 2004a; White 2003a), and we briefly update and synthesize the currently available evidence here. Since we are interested in evaluating the evidence of diachronic trends in animal utilization, it is essential to control for spatial variation in the natural abundance of various faunal resources. Following earlier work, we thus confine the present analysis to archaeological faunas derived from sites located in very similar environmental contexts. Specifically, we focus on sites located within 5 km of the main stem of the Sacramento River between 38° and 40° North latitude. Detailed archaeological vertebrate data are available from 15 site components in this region (Table 1 and Fig. 2).

The prehistoric inhabitants of these sites would have had access to the vertebrate faunas of four primary vegetation zones: freshwater marsh, grassland, oak woodland, and riparian forest. In addition, aquatic resources, especially fishes, could have been taken in both lentic (warm oxbow and floodplain lakes, swamps, and sloughs) and riverine habitats, namely, the swifter, cooler waters of the main channel of the Sacramento River. The sites were occupied over the past 4,000 years and were represented by substantial midden deposits, house floors, and high densities of artifacts including animal bone—all indicative of residential occupations. To maintain consistency with the published literature, uncalibrated radiocarbon years before present is the timescale used in this section (Bouey 1995; Broughton 1994a, 2004a; White 2003a).

Paleoenvironmental Background A secure documentation of human resource depression as a form of niche construction requires, of course, that other factors that can influence resource abundances be controlled. As a result, such analyses routinely incorporate paleoenvironmental evidence for possible non-human-based

Table 1 Occupation Dates, Screen Size, and References for the Sacramento Valley Faunal Assemblages

Site (component)	Screen size (in.)	Occupation date (B.P.)			References
		Initial	Terminal	Midpoint	
CA-BUT-12	1/8	550	250	400	Broughton (1994a)
CA-SAC-329	1/8	1170	350	760	Schulz <i>et al.</i> (1976), Broughton (1994a)
CA-COL-158 (A), CA-COL-245/H (A)	1/4, 1/16 ^a	740	910	825	White (2003a)
CA-COL-158 (D)	1/4, 1/16	970	1180	1075	White (2003a)
CA-SAC-145	1/8	2020	150	1085	Simons <i>et al.</i> (1978), Broughton (1994a)
CA-SAC-43	1/8	2400	600	1500	Schulz (1995), Simons (1995)
CA-BUT-288	1/4	3000	300	1650	Cole (1986), Broughton (1994a)
CA-COL-247 (S1A)	1/4	1550	2159	1855	White (2003a)
CA-COL-247 (S1B)	1/4, 1/16	2200	2750	2475	White (2003a)
CA-GLE-101	1/4	4240	1060	2650	Valente (1990), Broughton (1994a)
CA-GLE-105	1/4	3750	2000	2875	Bayham and Broughton (1990), Broughton (1994a)
CA-COL-247 (S2)	1/4, 1/16	2750	3222	2986	White (2003a)
CA-SJO-68	–	4350	2980	3665	Ragir (1972), Broughton (1994a)
CA-COL-247 (S3)	1/4, 1/16	3460	4385	3923	White (2003a)

^a All Colusa Co. sites reported in White (2003a)—for these sites, mammals were recovered with 0.25 in. and fish with 0.0625 in.

causes for trends in animal utilization. To thus clearly establish the human contribution to changes in faunal densities, we briefly summarize paleoenvironmental trends that appear to have affected the Holocene abundances of the high-ranked taxa of primary interest here: artiodactyls and large anadromous fishes, including salmon (*Oncorhynchus* spp.) and sturgeon (*Acipenser* spp.). Although artiodactyls and these fishes occupy widely disparate habitat systems and although the individual species within each group exhibit unique responses to climatic variability, current evidence suggests that Holocene climatic change would have impacted both groups in generally similar ways.

Artiodactyls

Recent research has documented that the population densities of most western artiodactyls, including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn, (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*), were strongly influenced by Holocene changes in the seasonality of temperature and precipitation, as well as changes in annual effective precipitation and primary productivity (Broughton *et al.* 2008; Byers and Broughton 2004). Briefly, the combined influences of enhanced seasonality and low annual effective precipitation

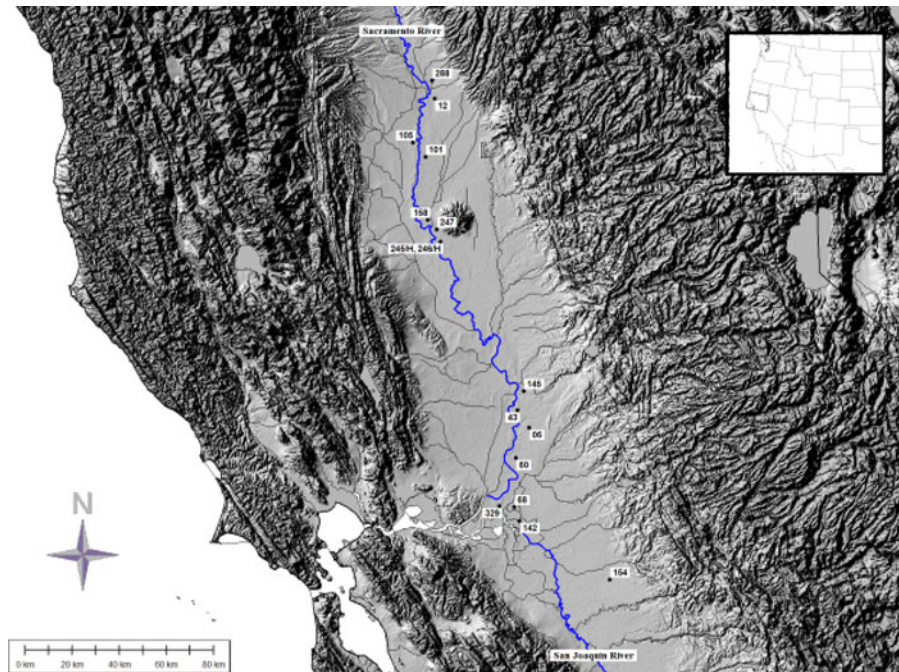


Fig. 2 Map of the Sacramento Valley indicating site locations discussed in the text

appear to have maintained most artiodactyl populations at low densities for much of the early and Middle Holocene. On the other hand, the Late Holocene, after 4000 B.P., was characterized by the most equable temperature of the late Quaternary and was also marked by several periods in which the high equability occurred together with a favorable precipitation regime, namely, high overall effective precipitation coupled with a summer-wet pattern. Many western archaeofaunas, including many in California, reflect these patterns by exhibiting low relative frequencies of artiodactyls until the Late Holocene (Broughton *et al.* 2008).

These climatic trends appear to be reflected in paleoenvironmental records from locations in or directly adjacent to the Sacramento Valley (*e.g.*, Goman and Wells 2000; Malamud-Roam *et al.* 2006; Meko *et al.* 2001; West 2002). We can thus anticipate climate-based increases in artiodactyls between about 4000 and 3000 B.P. in this setting, other things equal. Moreover, since no linear directional changes in the critical climatic factors are evident across the period from about 3000 B.P. to the historic period, declining proportional abundances of artiodactyls over this time should be related to other factors.

Anadromous Fishes: Salmon and Sturgeon

The climatic trends described above also have implications for changes in the abundances of salmon and sturgeon in the Sacramento River system. Although run sizes of these fishes are clearly affected by a mosaic of climatic factors that influence both the ocean and freshwater life stages, hot and dry conditions are widely viewed as having detrimental impacts on most populations of eastern Pacific salmon and sturgeon (*e.g.*, Chatters *et al.* 1995; Healey 1991; Kohlhurst *et al.* 1991). More

specifically, arid conditions are associated with reduced streamflow, increased salinity of estuarine nurseries, later onset of fall freshets, higher water temperatures, and higher siltation of streams—all factors that reduce the reproductive success of these fishes. Trends in the natural abundance of anadromous fishes should thus have paralleled those for artiodactyls, with low densities characterizing the Middle Holocene and an expansion of run sizes occurring between about 4000 and 3000 B.P. Fluctuations in the hydrological regime clearly occurred after 3000 B.P. in the Sacramento rivershed, including a possible muted expression of the Medieval Climatic Anomaly, but no linear directional shifts in critical variables are apparent (e.g., Goman and Wells 2000; Meko *et al.* 2001; Malamud-Roam *et al.* 2006; West 2002). Given these data, linear declines in abundances of anadromous fishes over the past 3,000 years would be more consistent with anthropogenic factors.

Sacramento Valley Archaeofaunas With one exception, 0.75-in. (0.64 cm), 0.125-in. (0.32 cm), and/or 0.0625-in. screens were used to collect the vertebrate remains from the sites in the study sample. Dating of the sites and site components is generally coarse-grained and based primarily on radiocarbon assay, obsidian hydration, and artifact typologies and is discussed elsewhere (Table 1; Bouey 1995; Broughton 1994a; White 2003a, b). The midpoints of the occupational ranges are used to establish an ordinal sequence of the assemblages that are used in the statistical analyses to follow. In those analyses, we use the number of identified specimens as a measure of relative abundance whenever these data are available (see Grayson 1984). However, only minimum numbers of individuals values are available for two of the assemblages (CA-SAC-145 and CA-SAC-329), and we use them here for these cases.

A variety of archaeological indices of resource depression have been developed over the last several decades, with taxonomic abundance indices being one of the most routinely employed. Drawing from prey model logic, temporal declines in high-ranked prey should reflect reductions in the encounter rate or density of the species in the surrounding environment over the time during which the fauna accumulated. Such trends not only provide an index of foraging efficiency and diet breadth (Bayham 1979; Broughton 1994a, b, 1995, 1997), but if other potential causes for changes in high-ranked prey densities (e.g., environmental change) can be ruled out, they are strongly indicative of resource depression.

Using abundance indices to document resource depression requires ordinal scale estimates of the ranking or profitability of potential prey items, usually measured as e/h , where e represents the net energy gain of a resource and h represents the handling costs associated with acquiring and processing it. For a variety of reasons, body size has been a commonly employed proxy for prey ranks in archaeological applications, a convention that is supported by considerable empirical evidence. To our knowledge, there are now ten ethnographic or experimental data sets in existence that include return rates for suites of vertebrate prey types consisting of five or more taxa or prey types. In each of these cases, the direction of the relationship between return rate and body size is positive, and in eight of them, the correlations are significant despite differences in prey mobility (see Bird *et al.* 2009; Broughton *et al.* 2010 for detailed discussion on the issue of prey mobility in relation to return rates). The two cases that fail to yield significant correlations are those that are

characterized by very narrow ranges of prey sizes (see Broughton *et al.* 2010; Morin 2010). And while the empirical data certainly show exceptions to this rule of thumb, they also indicate that taxa widely separated in size are far less likely to exhibit overlapping ranks. Artiodactyls and lagomorphs, for instance, taxa we use in abundance indices below, show no overlap in return rates, with artiodactyls consistently yielding higher returns. We also note that the two empirical studies that focus on fish—resources especially relevant to the Sacramento Valley case discussed here—conform to the general positive body size–return relationship.

Mammals and fishes dominate most Sacramento Valley archaeological faunas, and we therefore focus on these classes. Following previous research (Broughton 1994a, 2004a), we evaluate evidence for declines in the proportionate abundance of several taxonomic pairs that differ markedly in body size: large- and medium-sized mammals compared to small resident fishes; artiodactyls compared to lagomorphs; artiodactyls compared to small resident freshwater fishes; artiodactyls compared to both rodents and lagomorphs; and large anadromous fishes (salmon and sturgeon) compared to small resident freshwater fishes (Table 2; see Broughton 1994a for details on the size differences in these taxa).

As is clear from Table 2, substantial variation in sample size exists in the Sacramento Valley faunal collections, and this must be taken into account in assessing whether or not apparent trends in the data are statistically significant. Cochran's test of linear trends is a chi-square-based statistical method that does just that. The test is analogous to a form of regression analysis in which relative abundance values are weighted according to their associated sample sizes (Cannon 2001b; Zar 1999). The relevant test statistics for the Sacramento Valley relative abundance data are presented in Table 3, and Figs. 3, 4, 5, 6, and 7 provide graphical depictions of these data.

In general, these data indicate declines in the proportionate representation of large-sized taxa, and consequently in foraging efficiency, across the Late Holocene in the Sacramento Valley. In fact, the only taxonomic pair that does not indicate a significant linear decline is the abundance of anadromous fishes compared to smaller resident taxa. However, as Fig. 7 suggests, anadromous fishes appear to increase in abundance across the early sites in the study sample—those with midpoint occupations dating between 4300 and 2500 B.P.—a trend that is anticipated from the paleoenvironmental summary above. Such an increase may also be suggested in the indices incorporating artiodactyls for similar reasons (Figs. 3, 4, 5, and 6). Evidence for Late Holocene anthropogenic depressions may thus be more appropriately focused on sites post-dating these climate-based increases—those dating after 2800 B.P. Indeed, if the four sites with midpoint occupations dating to before 2800 B.P. are excluded from the analysis, all of the indices indicate significant linear declines through time (Table 4). We also observe that while the methods used to recover the faunas (*e.g.*, screen size) varied, this does not appear to affect the overall patterns in these data. Similar trends in these indices are apparent, for instance, in analyses using subsets of those assemblages collected with 0.25-in. screens (see Broughton 1994a) or when recovery methods are otherwise held constant (see White 2003a). The overall consistency of these patterns, uncorrelated with linear trends in paleoenvironmental conditions after 2800 B.P., is strongly indicative of resource depression.

Table 2 Numbers of Identified Specimens of Major Faunal Categories for the Sacramento Valley Assemblages

Site (component)	Midpoint date	Small, resident fishes	Large/medium mammals	Anadromous fishes	Artiodactyls	Lagomorphs	Rodents	Total
CA-BUT-12	400	1,600	47	249	25	15	55	1,991
CA-SAC-329 ^a	760	1,603	23	17	10	2	85	1,740
CA-COL-158 (A), CA-COL-245/H (A) ^b	825	590	142	327	39	1	–	1,099
CA-COL-158 (D) ^b	1,075	89	22	143	13	4	–	271
CA-SAC-145 ^a	1,085	2,535	14	3	6	4	71	2,633
CA-SAC-43	1,500	5,066	800	194	503	63	682	7,308
CA-BUT-288	1,650	31	45	20	24	14	340	474
CA-COL-247 (S1A) ^{b, c}	1,860	–	14	–	12	1	–	27
CA-COL-247 (S1B) ^{b, c}	2,475	45	11	47	8	0	–	111
CA-GLE-101	2,650	23	202	30	87	42	239	623
CA-GLE-105	2,875	17	207	2	65	15	134	440
CA-COL-247 (S2) ^b	2,986	38	38	17	25	2	–	120
CA-SJO-68	3,665	7	190	0	109	41	23	370
CA-COL-247 (S3) ^b	3,923	137	11	84	7	1	–	240
Total		11,781	1,766	1,133	933	205	1,629	17,447

^a Values are minimum numbers of individuals^b Rodent materials from this site were not studied^c Fish materials from this site were not studied

Table 3 Chi-Square and Cochran's Test of Linear Trends for the Sacramento Valley Sites

Faunal pairing	Chi-square	<i>p</i> value	Chi-square linear trend	<i>p</i> value
Large-medium mammals: small resident fishes	4,617.97	0.000	1,815.60	0.000
Artiodactyls: lagomorphs	79.96	0.000	20.77	0.000
Artiodactyls: small resident fishes	3,388.58	0.000	1,097.61	0.000
Artiodactyls: rodents + lagomorphs	290.29	0.000	13.64	0.000
Large anadromous fishes: small resident fishes	2,904.21	0.000	0.061	0.804

Plant Use: Acorns and Small Seeds

These trends in the archaeofaunal data are closely paralleled by changes in prehistoric plant utilization in the Sacramento Valley, especially as reflected in the intensity of acorn and small seed use. Experimental and ethnographic data bearing on the handling times and caloric yields for these resources consistently indicate that both yield modest to low return rates. Return rate estimates for California acorn species range from 1,350 to 850 kcal/h, while those for small seeds produce somewhat lower values between 1,200 and 200 kcal/h (*e.g.*, Barlow and Heck 2002; Hawkes and O'Connell 1981; Simms 1987). These returns are substantially lower than most animal resources: estimates for medium-sized (lagomorphs) and large (artiodactyls) mammals range from roughly 6,000 to over 30,000 kcal/h. Given the evidence presented above for declining overall foraging returns in the Sacramento Valley across the Holocene, we can thus anticipate increasing use of both acorns and small seeds over this period of time.

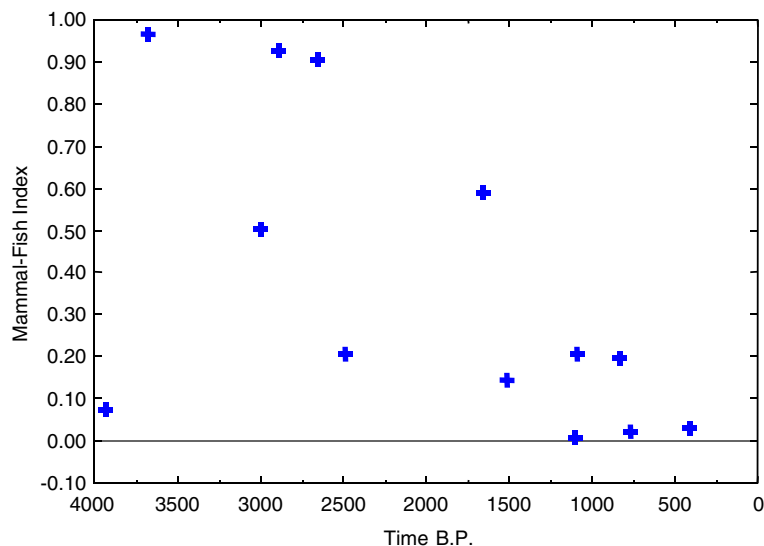


Fig. 3 Changing proportionate representation of large and medium mammals compared to small resident fishes from the Sacramento Valley sites

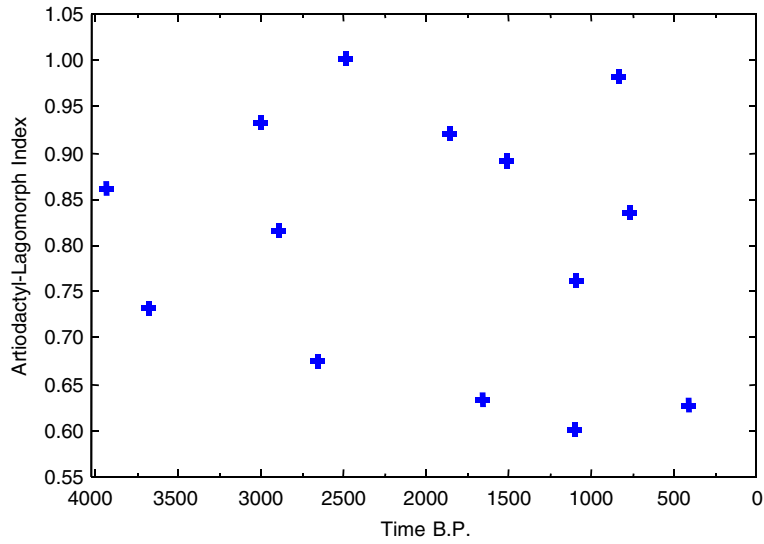


Fig. 4 Changing proportionate representation of artiodactyls and lagomorphs from the Sacramento Valley sites

In the most comprehensive analysis conducted to date, Wohlgemuth (2004) summarized archaeobotanical data from 48 Central California archaeological sites, including many located in the lower Sacramento Valley. Trends documented from this analysis are largely consistent with expectations, although there is considerable spatial and temporal variability. Acorn macrofossils are found in some of the earliest sites—those dating between 10,000 and 7,000 B.P.—and their use appears to have

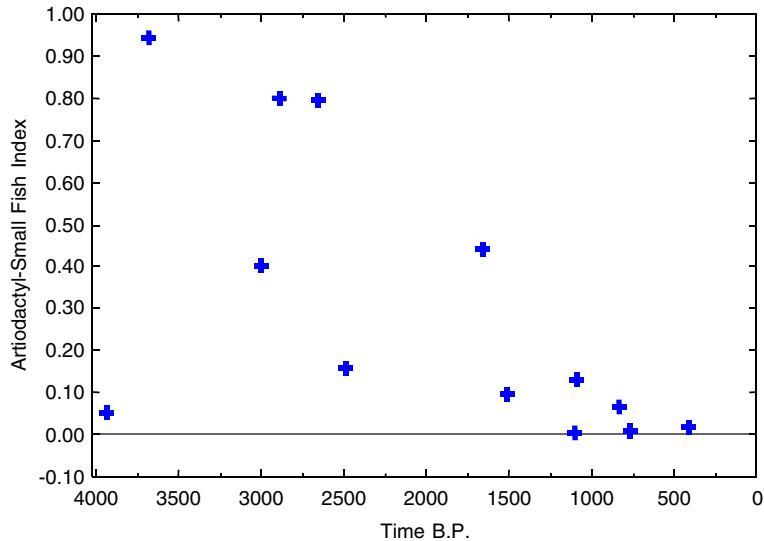


Fig. 5 Changing proportionate representation of artiodactyls compared to small resident fishes from the Sacramento Valley sites

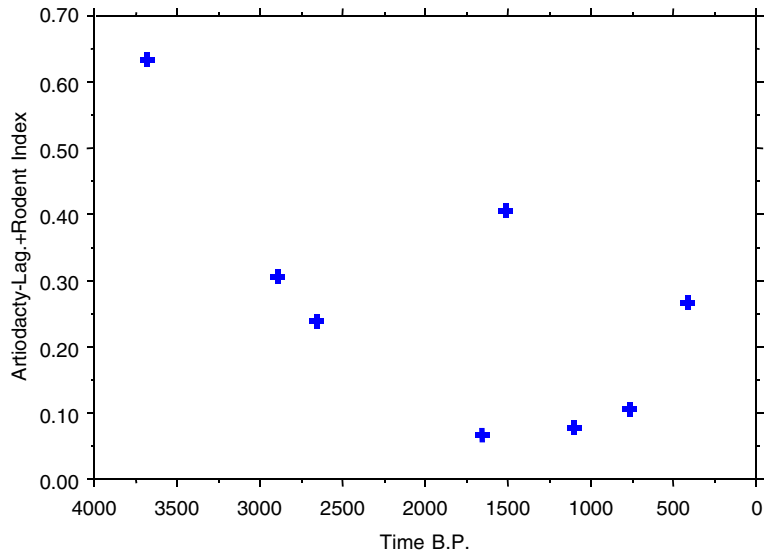


Fig. 6 Changing proportionate representation of artiodactyls compared to small lagomorphs and rodents from the Sacramento Valley sites

increased during the Middle Holocene; however, artifact and site feature data (mortars, detoxification pits) suggest that acorns were still used relatively casually during this time. A sharp increase in acorn macrofossils does not occur until between 2,500 and 1200 B.P. and appears to signal their intensified use, and probably storage, likely reflecting the initial emergence of acorn-intensive economies reported in Central California ethnographies.

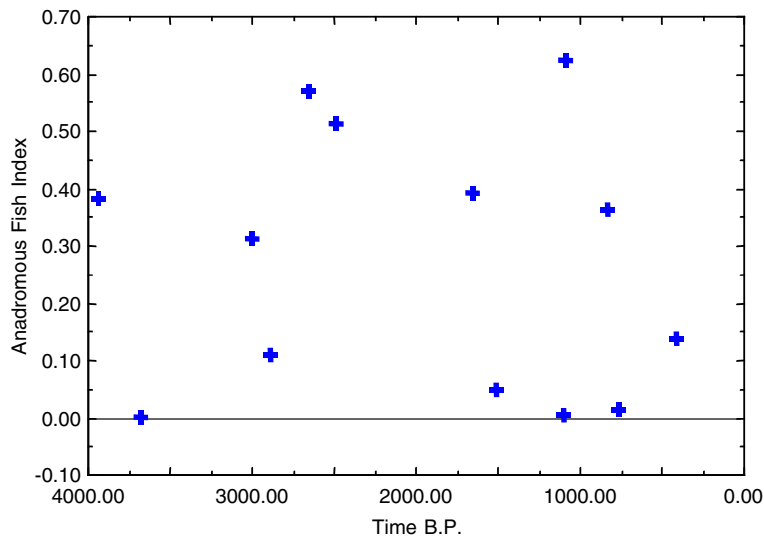


Fig. 7 Changing proportionate representation of large anadromous fishes compared to small resident fishes from the Sacramento Valley sites

Table 4 Chi-Square and Cochran's Test of Linear Trends for Sacramento Valley Sites with Occupational Midpoints Post-Dating 2800B.P.

Faunal pairing	Chi-square	<i>p</i> value	Chi-square linear trend	<i>p</i> value
Large-medium mammals: small resident fishes	2,422.06	0.000	668.49	0.000
Artiodactyls: lagomorphs	72.01	0.000	5.47	0.019
Artiodactyls: small resident fishes	1,623.05	0.000	441.67	0.000
Artiodactyls: rodents + lagomorphs	212.36	0.000	6.37	0.012
Large anadromous fishes: small resident fishes	2,804.53	0.000	116.28	0.000

The intensity of small seed utilization parallels that for acorns, with evidence for substantial use appearing first during the Middle Holocene. Still, seed resources appear at this time to have been exploited primarily during peak seasons of availability. A dramatic increase in small seed frequencies does not occur until 1200 and 500B.P. and appears to reflect bulk gathering and processing and an expansion of the gathering season to include lower return, green phase seeds. The intensified use of both acorns and small seeds continues from this point until Euro-American contact (Wohlgemuth 2004).

Summary of Sacramento Valley Subsistence Data

The dramatic Late Holocene declines in foraging efficiency implied by the intensified use of lower-return vertebrate and plant resources appear to be the result of anthropogenic depressions since they are uncorrelated with linear trends in paleoenvironmental conditions. Among faunal resources, the most dramatic change involves a decline in the proportionate use of larger terrestrial mammals, such as artiodactyls, relative to small resident freshwater fishes and lagomorphs over the last 3,000 years. Also evident, however, is a trend toward the increasing use of smaller resident fishes relative to larger anadromous forms such as salmon and sturgeon. These trends co-occur with substantial increases in the use of low-return plant resources, specifically acorns and small seeds. Similar trends have been documented in detail for many other regions of California, most notably the San Francisco Bay area (e.g., Broughton 1999; Broughton *et al.* 2007) and the Southern California coast (e.g., Porcasi *et al.* 2000; Rick *et al.* 2008). These trends have far-reaching implications for other aspects of human lifeways, including those related to human health, stature, and interpersonal violence.

Niche Construction and Human Skeletal Indicators of Health, Stature, and Violence

Our hypotheses described above suggest that this evidence for resource depression, broadening diets, and declining foraging efficiency should trigger both routes of niche construction: further cultural/behavioral responses can be predicted to occur involving increasing interpersonal violence (route 1), while changes in selective factors affecting the human genotype (route 2) are also expected.

Predictions involving changes in the degree of territoriality and interpersonal violence can be derived from EE models of territorial defense (Brown 1964;

Dyson-Hudson and Smith 1979) coupled with the distributional characteristics of the low-return resources that were increasingly utilized by Sacramento Valley foragers during the Late Holocene. Models of territorial defense attend to the ecological variables that influence the energetic costs and benefits of actively defending resource patches. One of the most critical such variables involves the density of resource distributions. Specifically, the cost of defending resources that occur in dense concentrations in stationary, spatially confined clumps is far lower than it is for more mobile dispersed ones. Hence, the degree of resource defense is predicted to be higher among foragers utilizing resources with those kinds of distributional characteristics (Broughton and O'Connell 1999; Brown 1964; Dyson-Hudson and Smith 1979).

Many of the important classes of lower-ranked resources that were subject to intensified use during the Late Holocene of the Sacramento Valley occur in dense seasonal concentrations at predictable locations (*e.g.*, resident fishes, acorns, grass seeds, freshwater mollusks). It follows that the niche of expanded diet breadth and low foraging efficiency created by generations of human foragers in this context should have been associated with higher levels of resource defense and territoriality. More investment in territorial defense should also entail substantial increases in the energetic costs of foraging, further exacerbating the declining returns resulting from resource depression alone. Insofar as the frequency of interpersonal violence is a proxy measure of the degree of resource defense and territoriality in these settings, skeletal evidence of such trauma should increase across the Late Holocene of the Sacramento Valley.

As noted above, broader diets and reduced foraging return rates imply greater foraging effort required to meet minimum caloric requirements and an increased risk of under- and malnutrition. Undernourished foragers should experience higher levels of morbidity and mortality, slower growth rates, and reduced adult body size. While we view these phenomena as predictable biological symptoms of resource depression here, we also observe that conditions constructed by the latter could further alter the selective environment on the human genotype, thereby producing route 2 effects (Fig. 1). Future work could explore, for instance, the anticipated effects of stronger selection on aspects of the immune/physiological response to disease and nutritional stresses, genetic-based reductions in adult body size, and aspects of life history (age at reproductive maturity) that are known to relate to changes in mortality rates in predictable ways (*e.g.*, Charnov 1993; O'Connell *et al.* 1999).

The Sacramento Valley Human Skeletal Assemblage Osteologically, declines in health in an archaeological context may be recognized through increased rates of pathological and developmental conditions, such as periosteal bone reactions, cribra orbitalia, reduced stature, and enamel hypoplasia defects. Here, we focus on three key stress indicators: tibial periosteal reactions, which are osseous lesions of the lower leg that are most often linked with nonspecific infection; cribra orbitalia, a condition that is most commonly attributed to anemic response in infancy and early childhood; and adult stature (using bicondylar femoral length as a proxy), which is linked to overall health status (Cohen 1989; Cohen and Armelagos 1984; Goodman *et al.* 1984; Goodman and Martin 2002; Larsen 1995, 1997, 2006; Steckel 1995;

Steckel *et al.* 2002). In addition to these conditions, we also consider skeletal indicators of violence.

The Late Holocene human skeletal series that we examine here includes 203 adult burials derived from five sites in the lower Sacramento Valley and from one site in the northern San Joaquin Valley (Fig. 2 and Table 5). Two of these sites (CA-SAC-43 and CA-SJO-68) provided faunal material utilized in the analyses above. Dating of these burials was achieved through the use of time-sensitive artifacts (*e.g.*, shell beads: Bennyhoff 1994; Bennyhoff and Hughes 1987), obsidian hydration, radiocarbon assays, and other contextual information. Burials were aggregated into five phases to increase sample size and to facilitate analysis, and a midpoint date was assigned to each phase based on the available chronological information (Table 5; see Bartelink 2006 for additional information).

Sex and age assignments were performed following guidelines summarized in Buikstra and Ubelaker (1994). Sex estimation included macroscopic analysis of sexually dimorphic features of the pelvis and cranium, supplemented by osteometric analysis (Dittrick and Suchey 1986). Age estimation involved the examination of epiphyseal union, tooth eruption, and dental development sequences, morphological assessment of degenerative changes in the pubic symphysis, auricular surface, and sternal rib end, and cranial suture closure (Brooks and Suchey 1990; Buikstra and Ubelaker 1994; Iscan *et al.* 1984, 1985; Katz and Suchey 1986; Lovejoy *et al.* 1985; Meindl and Lovejoy 1985; Scheuer and Black 2000). Only adult individuals of known sex are included in the present analysis. Males and females comprise 43.8% ($n=89$) and 56.2% ($n=114$) of the sample, respectively.

Tibial Periosteal Reactions

Periosteal bone reactions are among the most common lesions identified in human skeletal remains (Ortner 2003). Since the 1970s, these lesions have become commonly used indicators of general health status in prehistoric skeletons (Goodman and Martin 2002; Larsen 1995, 1997; Steckel *et al.* 2002). Although periosteal reactions can be caused by either infection or traumatic injury, paleopathologists

Table 5 Occupation Dates and References for the Sacramento Valley Human Skeletal Remains

Temporal phase	Occupation date (B.P.)	Midpoint	Sites	<i>n</i>	References
Late Period	1050–200	625	CA-SAC-06, -43, -60, CA-SJO-154	62	Hoffman (1987), Bennyhoff (1977), Bouey (1995), Lillard <i>et al.</i> (1939)
Middle/Late Period Transition	1250–1050	1150	CA-SAC-06, -43, -60, CA-SJO-154	5	Hoffman (1987), Bennyhoff (1977), Bouey (1995), Lillard <i>et al.</i> (1939)
Middle Period	2150–1250	1700	CA-SAC-06, -43, -60, CA-SJO-154	46	Hoffman (1987), Bennyhoff (1977), Lillard <i>et al.</i> (1939)
Early/Middle Period Transition	2450–2150	2300	CA-SJO-68, -142	2	Ragir 1972; Schulz 1981; Heizer (1949), Lillard <i>et al.</i> (1939)
Late Early Period	3050–2450	2750	CA-SJO-68, -142	52	Ragir (1972), Schulz (1981), Heizer (1949)
Early Early Period	4950–3050	4000	CA-SJO-68, -142	36	Ragir (1972), Schulz (1981), Heizer (1949)
Total				203	

generally interpret these lesions as a general measure of infectious disease (e.g., Bright and Loveland 1999; Lambert 1993, 1994, 1997; Lambert and Walker 1991; Larsen and Hutchinson 1999; Nelson 1999a; Roberts *et al.* 1998; Steckel *et al.* 2002). Active lesions are characterized by subperiosteal woven bone deposition that is laid down superficial to the cortex of the bone and may take on an “onion skin” appearance (Ortner 2003). Involvement may extend from isolated patches of new bone growth to large portions of the diaphysis (Ragsdale *et al.* 1981). In the healed state, lesions are often characterized by thick layers of striated bone that are contiguous with the unaffected cortex.

Individuals with weakened immune systems due to malnutrition or undernutrition are especially susceptible to infection, indicating synergistic effects between dietary quality and susceptibility to disease (Cohen 1989, 1997; Inhorn and Brown 1990; Larsen 1997). Furthermore, a higher prevalence of lesions is expected among more densely settled communities where conditions are conducive to long-term survival of infectious pathogens and water-borne parasites and with greater opportunity for person-to-person contact (Cohen 1989; Inhorn and Brown 1990). Involvement of the skeleton may occur through association with an open wound, adjacent affected tissues, or transmitted through the bloodstream from another part of the body (Ortner 2003). The tibia is the most sensitive element to record evidence of periosteal reaction, for reasons not well understood (Ortner 2003).

For this study, the tibiae from each burial were inventoried for completeness and scored for the presence or absence of periosteal reaction. Data recordation included the degree of involvement, stage of healing (active, mixed, healed), and the location of the lesion following recommendations in Buikstra and Ubelaker (1994). Only elements that were >60% complete were included in the analysis.

Cribræ Orbitalia

Cribræ orbitalia is a pathological condition that is characterized in the healed state by sieve-like lesions that occur in the superior roof of the eye orbit (Ortner 2003; Stuart-Macadam 1989). Although the specific causes of these lesions continue to be debated (see Walker *et al.* 2009), bioarchaeologists generally interpret the condition as evidence of osseous response to acquired anemia that is initiated in infancy or early childhood (Blom *et al.* 2005; El-Najjar *et al.* 1976; Grauer 1993; Kent 1986; Stuart-Macadam 1985, 1987a, b, 1989, 1992; Walker 1985, 1986; Wright and Chew 1998). However, the likely causes are multifactorial and have been attributed to iron-deficient diets, iron loss due to intestinal parasitism or diarrheal disease, or the sequestration of iron due to infection (Holland and O'Brien 1997; Kent 1986, 1992; Mensforth *et al.* 1978; Ortner 2003; Ryan 1997; Stuart-Macadam 1992). Acquired anemia is the result of below normal levels of red blood cells or the hemoglobin within them, which affects the efficiency of the transport of oxygen from the lungs to other bodily tissues (Stuart-Macadam 1992). Recent work by Walker *et al.* (2009) suggests that cribræ orbitalia lesions in New World populations more likely represent megaloblastic anemia due to insufficient intake or absorption of vitamin B₁₂ (cobalamin) and/or B₉ (folic acid), deficiencies that are passed on from mother to fetus. This suggests that cribræ orbitalia (or porotic hyperostosis in the cranial vault) may be the result of inadequate levels of animal protein consumption, the only source of vitamin B₁₂, which may be further exacerbated by the effects of intestinal parasites (Walker *et al.* 2009). Thus, temporal increases in the prevalence of these

lesions during the Late Holocene would be consistent with the increased consumption of vegetal plant staples (e.g., acorns, small seeds) relative to meat protein, an indication of declining foraging efficiency.

Our analysis included crania that had at least one superior orbital roof that was 50% complete. When both sides were present, the side with the most extreme expression of the lesion was recorded. Lesions were scored as present or absent and by the level of severity (Buikstra and Ubelaker 1994). Orbital roofs that were characterized only by pinprick porosity were not scored as present for the condition. Slight involvement included significant external porosity with no evidence of vault thickening, while moderate to severe involvement included evidence of vault thickening with or without coalescence of foraminae. Previous research indicated no sex differences in lesion prevalence, so both males and females are combined in our analysis (Bartelink 2006). We examine temporal patterns in the prevalence of cribra orbitalia for all levels of severity and also in a more restricted analysis that only includes moderate to severe lesions.

Stature

Adult stature is a commonly used indicator of population health status (Steckel 1995; Steckel *et al.* 2002). Because stature at the population level is linked to levels of malnutrition, undernutrition, and/or infectious disease, it serves as an excellent comparative measure of health status in both modern and prehistoric populations (Bogin 1999; Cameron and Demerath 2002; King and Ulijaszek 1999). During infancy and childhood, growth and development can be severely impacted by caloric and protein deficiency, as well as by infection, which may result in growth retardation and reduced adult stature (Bogin 1999; Cameron and Demerath 2002; Stinson 2002). Furthermore, individuals who experienced significant growth-related stress early in life tend to have higher levels of morbidity and die at a younger age (Cameron and Demerath 2002; Kemkes-Grottenthaler 2005). Factors such as poor maternal health, inadequate infant nutrition, and high pathogen load largely account for high rates of infant mortality in many underdeveloped nations and presumably in archaeological populations as well (Saunders and Hoppa 1993). To evaluate changes in health status in late Holocene populations from the Sacramento Valley, we use femoral bicondylar length as a proxy for stature (Lambert 1993, 1994). Femoral length accounts for approximately 27% of height (Lambert 1993); thus, this element provides a good proxy measure for stature comparison between samples. The sample is restricted to adult individuals with complete epiphyseal union, and only complete or fully reconstructed femora were included. The right femur was measured for each individual using an osteometric board (substituting the left side where necessary), and measurements were recorded to the nearest millimeter.

Temporal Patterns in Paleopathology

Cribra Orbitalia and Periosteal Lesions

The prevalence of paleopathological conditions from the Sacramento Valley sample is presented by major temporal phase in Table 6. Table 7 provides overall chi-square values and Cochran's test of linear trend results for the paleopathology indicators considered here, with skeletal samples arrayed over the temporal phase sequence described above. Figures 8 and 9 display the percentages of skeletons exhibiting cribra orbitalia and tibial periosteal lesions across the Late Holocene of

Table 6 Prevalence of Pathological Conditions in Human Skeletal Remains from the Sacramento Valley

Temporal phase	Occupation date (B.P.)	Midpoint	Left tibia% affected (<i>n</i>)	Right tibia% affected (<i>n</i>)	Cribrā orbitalia (all levels of severity)% affected (<i>n</i>)	Cribrā orbitalia (mod/sev severity)% affected (<i>n</i>)
Late Period	1050–200	625	13.1 (61)	9.8 (61)	38.6 (57)	12.9 (62)
Middle/Late Period Transition	1250–1050	1150	0 (4)	0 (4)	20 (5)	0 (6)
Middle Period	2150–1250	1700	15.6 (45)	10.9 (46)	24.4 (45)	12.8 (47)
Early/Middle Period Transition	2450–2150	2300	0 (2)	0 (1)	0 (2)	0 (2)
Late Early Period	3050–2450	2750	0 (46)	0 (47)	15.4 (52)	3.6 (56)
Early Early Period	4950–3050	4000	0 (31)	0 (32)	39.5 (43)	8.9 (45)

the Sacramento Valley. While the periosteal lesion data show consistent linear increases through time, the pattern of incidence for cribrā orbitalia is more complex. More specifically, the frequency of cases exhibiting any evidence of cribrā orbitalia shows no consistent trend through time, while those cases scored as “moderate or severe” show significant linear increases across the sequence. In addition, as Fig. 8 indicates, cases of cribrā orbitalia—irrespective of severity—decline dramatically between sites dating before 3000 B.P. (*i.e.*, the early Early Period) and sites dating to just before 2500 B.P. This pattern is fully consistent with the faunal data that provided evidence for low foraging efficiencies prior to about 2800 B.P., and for similar reasons, it suggests that detecting declining health status should be more easily accomplished using skeletons that post-date this time. Thus, Table 8 provides Cochran’s tests of linear trends in the health indicators exclusive of skeletons that date to the early Early Period. Trends in both indices of cribrā orbitalia increase in significance among this set of collections, while those for tibial periosteal lesions, for reasons unclear, decrease slightly. In any case, the overall trend indicates increases in the incidence of these markers of human health across the period that foraging efficiencies are declining.

Temporal Trends in Stature

Mean femur lengths are plotted through time for males and females in the Sacramento Valley skeletal sample (Table 9 and Figs. 10 and 11, respectively). For

Table 7 Chi-Square and Cochran’s Test of Linear Trends for the Sacramento Valley Paleopathology Data

Pathology	Chi-square	<i>p</i> value	Chi-square linear trend	<i>p</i> value
Cribrā orbitalia: <i>n</i> affected– <i>n</i> unaffected	12.978	0.011	1.05	0.305
Cribrā orbitalia: <i>n</i> mod/severe affected– <i>n</i> unaffected	9.58	0.048	2.84	0.092
Left tibia periosteal lesions: <i>n</i> affected– <i>n</i> unaffected	14.184	0.007	10.78	0.001
Right tibia periosteal lesions: <i>n</i> affected– <i>n</i> unaffected	7.329	0.119	5.66	0.017

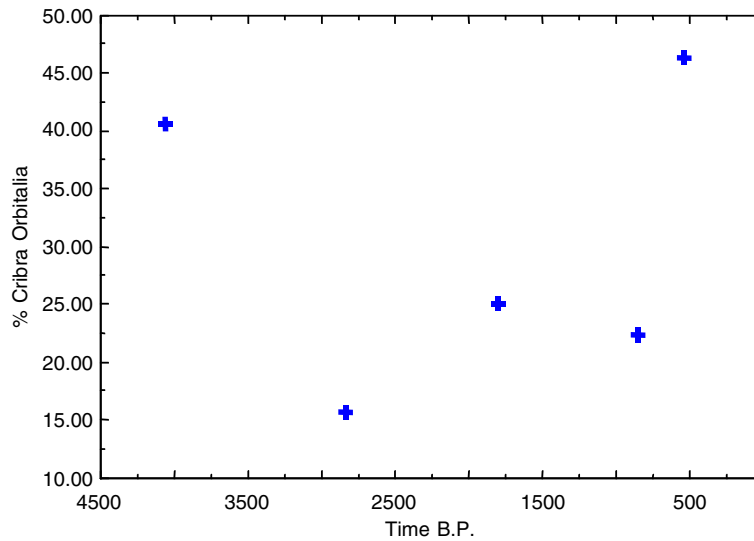


Fig. 8 Changes in the percentage of skeletons exhibiting cribra orbitalia from the lower Sacramento Valley sites

both sexes, temporal declines are suggested, although notable outliers are also present. For females, the decrease in size is marginally significant ($r^s=-0.50$, $p=0.05$; $r=-0.44$, $p=0.09$). For the male sample, significance is indicated if the lone outlier dating to 2500 B.P. is excluded from the analysis ($r^s=-0.52$, $p=0.06$; $r=-0.60$, $p=0.02$). The overall directional trends in these data are consistent with the subsistence data on foraging efficiency and the paleopathology summarized above.

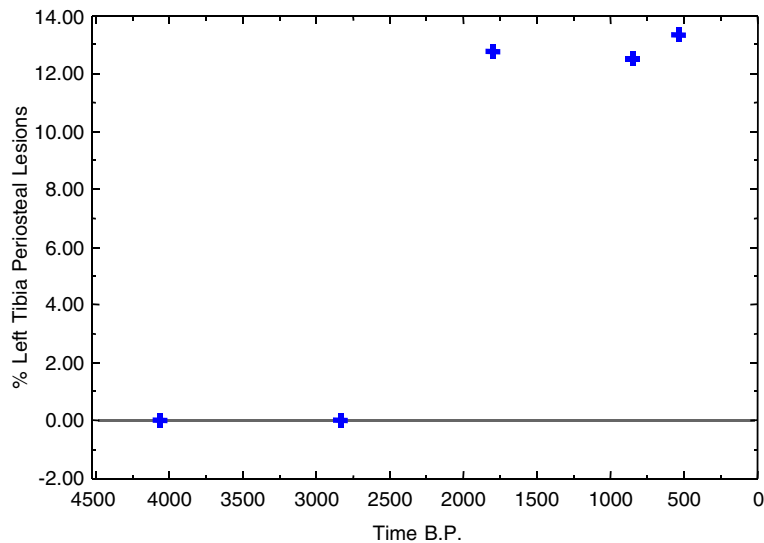


Fig. 9 Changes in the percentage of skeletons exhibiting periosteal lesions on the left tibia from the lower Sacramento Valley sites

Table 8 Chi-Square and Cochran's Test of Linear Trends for the Sacramento Valley Paleopathology Data Exclusive of Skeletons Dating to the Early Early Period

Pathology	Chi-square	<i>p</i> value	Chi-square linear trend	<i>p</i> value
Cribra orbitalia: <i>N</i> affected– <i>N</i> unaffected	10.788	0.013	9.40	0.002
Cribra orbitalia: <i>N</i> mod/severe affected– <i>N</i> unaffected	9.527	0.023	4.98	0.026
Left Tibia Periosteal lesions: <i>N</i> affected– <i>N</i> unaffected	5.737	0.125	3.24	0.072
Right Tibia Periosteal lesions: <i>N</i> affected– <i>N</i> unaffected	4.263	0.234	2.85	0.091

Interpersonal Violence

Direct evidence of interpersonal violence can be observed osteologically in human remains by the presence of craniofacial fractures, embedded projectile points, and, to a lesser extent, by forearm fractures (Judd 2008; Smith 1996) and trophy taking (Andrushko *et al.* 2005, 2010; Grady *et al.* 2001). More indirect but supporting evidence can be derived from the archaeological context, such as from multiple burials with projectile points recovered in positions suggesting they had been embedded in soft tissue. Most attention to these issues in California has been

Table 9 Bicondylar Femur Length (in mm) for Sacramento Valley Males and Females by Time Period

Period	Midpoint date	Females		Males	
		Mean	<i>n</i>	Mean	<i>n</i>
Late Period	300	432	6	448.5	2
	750	423	7	448	7
	950	395	1	–	–
Middle/Late Period Transition	1150	395	6	445	6
Middle Period	1350	409	3	456.5	2
	1550	414.75	12	437.5	12
	1650	410	1	–	–
	1750	422	1	452.5	2
	2000	415	1	438	5
	2300	417	2	–	–
	2500	435	3	457	3
Late Early Period	2650	426.25	4	455.5	14
	2850	427.33	3	443.5	8
	3000	435	2	–	–
	3500	–	–	452	1
	3650	–	–	455	5
Early Early Period	3850	416.7	3	464	5
	4450	432.6	5	468	4

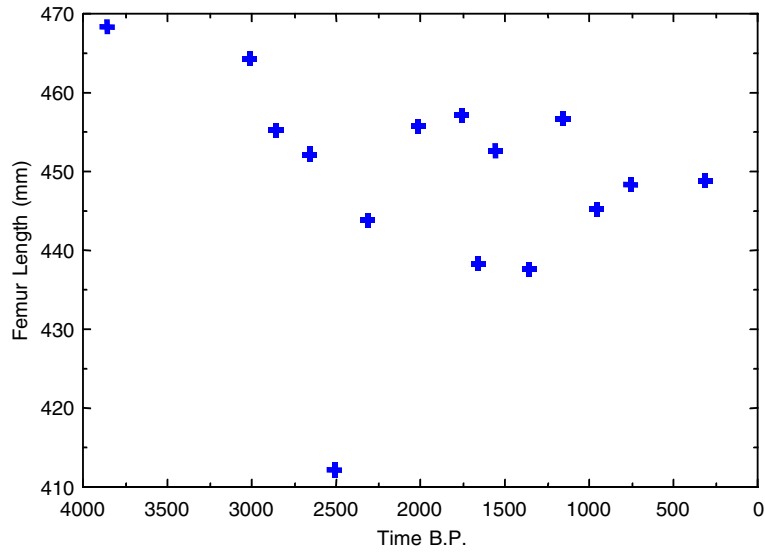


Fig. 10 Variation through time in mean male femur length from the lower Sacramento Valley sites

directed to populations from the Santa Barbara Channel area (Lambert 1994, 1997; Walker 1989, 1997) and the eastern margin of San Francisco Bay (Andrushko *et al.* 2005; Jurmain 1991, 2001; Jurmain and Bellifemine 1997; Jurmain *et al.* 2009), although some analyses have also been conducted with Central Valley samples (Nelson 1997; Newman 1957).

The prevalence of osteological indicators of violence in Southern California far surpasses that from any site or regional survey of skeletal trauma in North America,

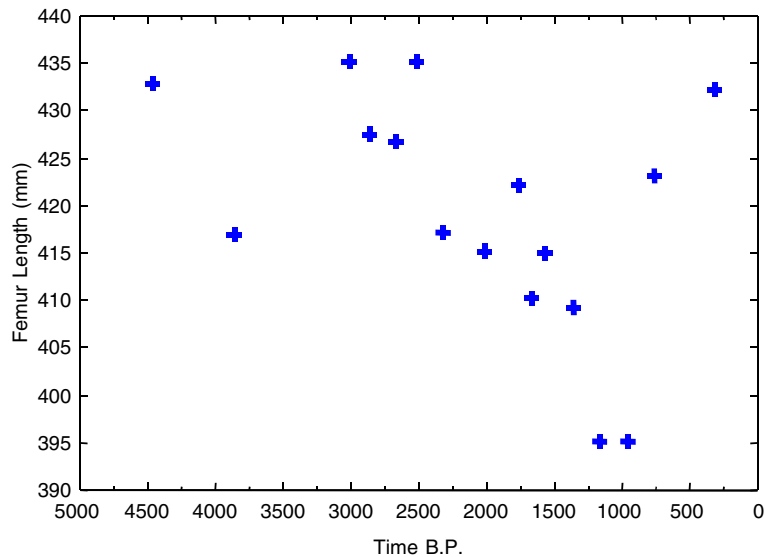


Fig. 11 Variation through time in mean female femur length from the lower Sacramento Valley sites

with rates of healed cranial trauma ranging from 7.5% to 18.5% in individuals from the Santa Barbara mainland and northern Channel Islands, respectively (Walker 1989). Males are affected twice as often as females (males = 24%; females = 10%), consistent with expectations of males participating more actively in warfare and territorial defense. Lambert's (1994, 1997) analysis found significant temporal increases in both cranial trauma and projectile point injuries (70% of which were lethal) throughout the Late Holocene (see also Jones and Schwitalla 2008; Lambert and Walker 1991).

Although prevalence rates of interpersonal violence in Central California are substantially lower than in Southern California, relatively high rates of craniofacial trauma and embedded projectile points have been noted in several studies (*e.g.*, Jurmain *et al.* 2009; Jurmain 2001; Jurmain and Bellifemine 1997). Systematic investigations of skeletal samples from single sites have reported prevalence rates of healed cranial trauma between about 2% and 4%, although one site from southeastern San Francisco Bay (CA-ALA-329) showed a craniofacial trauma rate of 9% (Jurmain *et al.* 2009). The prevalence of healed cranial vault lesions at CA-ALA-329 significantly increased between phase 1 and 2 of the Late Period (LP1=0.8%, LP2=6.8%, $p<0.05$). Four percent of the burials from this site also had evidence of embedded projectile points, a rate higher than that recorded for most regions of North America (Jurmain *et al.* 2009).

Similar trends are apparent from the more limited samples available from within the Sacramento Valley. Nelson (1997) examined the prevalence of craniofacial and forearm fractures in 205 human skeletons from seven sites in the northern Sacramento Valley (CA-BUT-233, -288, -294, -496; GLE-101; TEH-790, TEH-Butte Farms) and two sites from the mid-Central Valley (CA-SAC-127, CA-SJO-91), spanning the period from 4000 to 250 B.P. Cranial vault trauma affected 14.8% of the entire sample, while 9.3% of facial remains were affected (Nelson 1997:52). When grouped into three temporal periods, Nelson (1997:77) found a significant increase in the prevalence of cranial trauma from 4.3% between 4000 and 2500 B.P. to 17.2% between 2500 and 1200 B.P. and finally to 26.6% between 1250 and 250 B.P. Although the chronology of this study is coarse-grained due to limited dating information from the site components, the results are entirely consistent with expectations of increased interpersonal violence associated with late Holocene resource depression.

Resource Depression as Niche Construction in the Sacramento Valley: Summary

Sacramento Valley archaeofaunal collections provide quantitative evidence for Late Holocene resource depression. The human impacts on high-ranked faunal resources in this setting represent a clear case of niche construction that resulted in a cascading series of facultative behavioral adjustments and associated biological symptoms. The Sacramento Valley case thus illustrates the compatibility between EE and NCT: EE models provide testable hypotheses about behavioral and morphological changes that result from human-altered selective conditions and thereby constitute instances of niche construction.

We note that while we have focused on the niche construction factor of resource depression as it affected subsequent dietary changes and human health in the

Sacramento Valley, many other potential links could also be pursued in this setting. These include, among other things, the elaboration of hereditary inequalities and material display, as well as changes in technology and settlement (see Broughton and O'Connell 1999; Cannon and Broughton 2010). We explore changes in these latter two aspects of behavior in our next case study involving niche construction and agricultural intensification in the Mimbres region of Southwestern New Mexico.

Resource Depression and Agricultural Intensification Among the Mimbres-Mogollon

One of the most significant developments in human prehistory was certainly the emergence of agricultural economies, and agricultural landscapes represent at least the most obvious, if not also the most important, cases of human niche construction. EE has been used fruitfully to help understand the origins and spread of agriculture in a variety of settings, with many examples incorporating an important role for niche construction (e.g., Barlow 2002; Gremillion 1996; Hard and Roney 2005; Kennett and Winterhalder 2006). One such example comes from the Mimbres region of Southwestern New Mexico where a series of major socioeconomic changes occurred over several centuries beginning around A.D.400, including, among other developments, declines in residential mobility and large-scale population movements (e.g., Diehl 1997; LeBlanc 1989; Powell-Marti and Gilman 2006; Nelson and Anyon 1996; Nelson 1999a, b; Nelson *et al.* 2006). As an important component of this suite of changes, there is evidence that depression of large mammal prey occurred early on during the occupation of the region by agriculturalists and that this constituted an instance of niche construction somewhat analogous to the Sacramento Valley case just discussed, though involving intensification of agricultural production rather than of the use of low return wild resources (Cannon 2001a).

Allocating Time to Foraging and Farming

The Mimbres example can be understood as a case of human impacts on wild resources leading to the expansion of the agricultural niche and attendant changes in such things as settlement pattern. Recent work by Barlow (1997, 2002), which is directed at understanding the factors underlying variability in the importance of agriculture in the prehistoric American Southwest, provides a useful starting point for exploring this type of niche construction. Two aspects of Barlow's work are particularly relevant here.

First, Barlow (1997) considers how various models from foraging theory might be employed to help explain transitions from foraging to farming, and she concludes that a modified patch choice model, based on the marginal value theorem (Charnov 1976; Smith 1991; Stephens and Krebs 1986), is best suited for this purpose. This model is fundamentally the same as an opportunity cost model of time allocation (Hames 1992; Winterhalder 1983) that others have also applied to the relationship between foraging and farming (Cannon 2001a; Gremillion 1996). Making the reasonable assumption that considerations of resource harvesting efficiency are relevant to the economic decisions that people make (see, for example, Cannon and Broughton 2010; Smith 1991; Smith and Winterhalder 1992; Winterhalder and Goland 1997) and taking it as axiomatic that agriculturalists also subsist to some

degree on wild resources, this model predicts that individuals should increase the amount of time that they devote to farming, at the expense of less time spent foraging, if either of two things happens. One, they should do so if they experience an improvement in the efficiency of agricultural production (*i.e.*, in the caloric returns obtained from farming per unit time). Two, they should do so if they experience a decline in foraging efficiency, such as might result from depression of wild resources.

The second aspect of Barlow's work that is important here comes from her analysis of ethnographic and experimental data pertaining to the caloric return rates of corn farming or the amount of energy obtained from corn farming per unit of time allocated to it (Barlow 1997, 2002). She shows that due in large part to the high post-harvest processing costs of corn, the return rates that labor-intensive forms of maize agriculture provided in the past were probably comparable to the post-encounter return rates of relatively low-return wild resources such as small seeds. Moreover, she demonstrates that variability in the amount of time spent on agricultural tasks likely had a substantially greater effect on the return rates of farming than did variability in agricultural yields; that is, she shows that agricultural return rates are highly constrained by labor costs regardless of the absolute yields obtained.

This leads Barlow to conclude that the amount of time that people allocated to farming should in most cases have depended much less on the gross yields that they obtained from agriculture than on the rates at which they could harvest higher-return wild resources. In other words, reductions in wild resource foraging efficiency are more likely to have been responsible for agricultural intensification in the past than are improvements in agricultural efficiency. Or, as Barlow (1997:131) argues, "simply nominating factors that likely influenced expected harvest yields, including changes in climate, the development of new technology, or even higher-yielding varieties of corn, may be insufficient to explain transitions to corn farming" (also see Winterhalder and Goland 1997 on the importance of the distinction between gross agricultural yields and net return rates as these relate to economic decision making). The costs of agriculture must also be taken into account, and Barlow's work highlights the fact that it pays to accept those costs only when the returns provided by alternative subsistence pursuits are sufficiently low.

Barlow proposes that her ideas can be tested by examining a large geographic region and comparing data on variability in the importance of agriculture to data on variability in local resource availability: if she is correct, then we should see evidence of the greatest allocation of time to farming in places where rates of encounter with high-return wild resources were the lowest (*cf.* Hard 1986). Such a test would certainly be productive, but the core ideas here can also be tested by examining temporal variability in wild resource productivity and the importance of agriculture rather than solely spatial variability.

The temporal data necessary to do this are available from the Mimbres region. Variability in wild resource foraging efficiency in the Mimbres area can be measured using the methodology employed above that zooarchaeologists have developed for identifying cases of resource depression in the archaeological record, and several lines of evidence are available to track temporal changes in the importance of agriculture in the region. Together, these data can be used to test the hypothesis that

Mimbres farmers allocated increasing amounts of labor to agriculture in response to declines in foraging efficiency.

Environmental and Cultural Background

The Mimbres Valley is located in Southwestern New Mexico in a region of basin and range topography (Fig. 12). The Mimbres River is the only major waterway with perennial surface flow between the drainages of the Rio Grande and the Gila River, and its wide floodplain provides some of the best land for farming in the region (*e.g.*, Anyon and LeBlanc 1984; Minnis 1985). Outside of the riparian zone adjacent to the Mimbres River, there is a great deal of biotic variability within the region, with the semi-desert grasslands of lower elevations grading into pinyon–juniper woodland and then, at the highest elevations of mountain ranges, into forests dominated by ponderosa pine (*e.g.*, Brown 1994).

The culture history sequence for the Mimbres-Mogollon area is presented in Table 10. To maintain consistency with the Mimbres published literature, B.C./A.D. calendar year dates are used in this section rather than uncalibrated radiocarbon year dates as in the previous section.

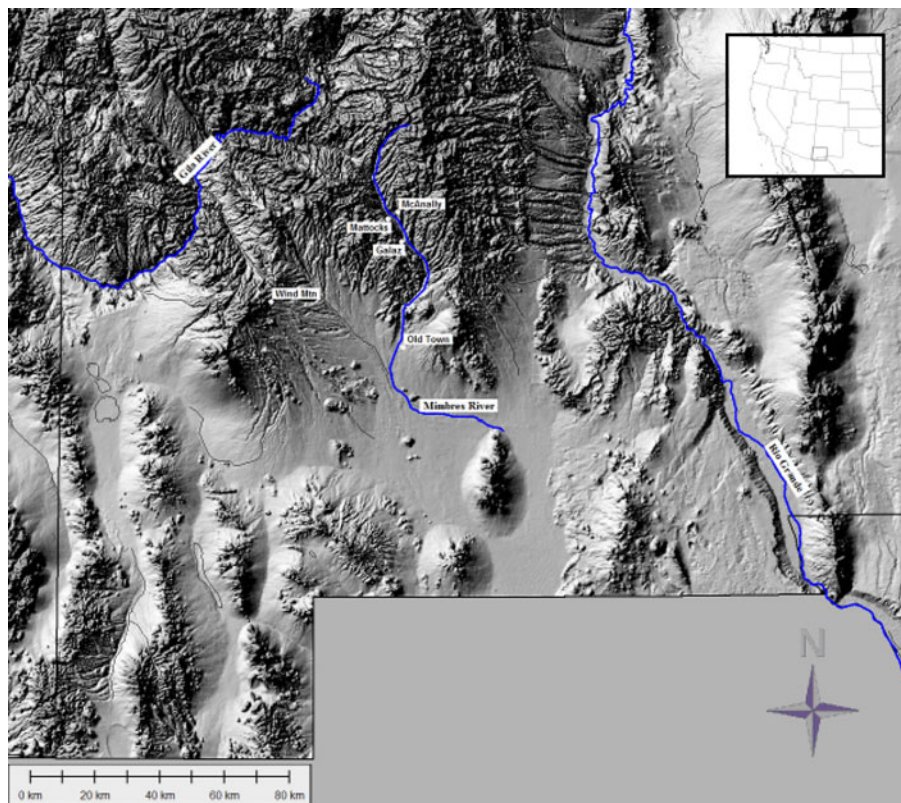


Fig. 12 Map of the Mimbres Valley showing the locations of sites mentioned in the text

Table 10 Mimbres-Mogollon Culture Historical Time Periods

Period	Phase	Abbreviation ^a	Dates (A.D.)
Early Pueblo	Terminal Classic	TCM	1130–1200
	Classic Mimbres	CM	1000–1130
Late Pithouse	Three Circle	TC	825/850–1000
	San Francisco	SF	700–825/850
	Georgetown	GT	600–700
Early Pithouse	Cumbre	EP	400–600

After Anyon *et al.* (1981), Diehl (1994), Diehl and LeBlanc (2001), Hegmon *et al.* (1999), Nelson and Anyon (1996), and Wills (1996)

^aUsed in subsequent tables and figures

Domesticates such as maize and squash were used by at least some groups in the region that is today the Southwestern USA and Northwestern Mexico prior to 1000 B.C. (*e.g.*, Hard and Roney 1998), but in the Mimbres area, there is no evidence of occupation by people who grew crops until well over a millennium later than this, during the Early Pithouse period (A.D.400–600). Sites in the Mimbres region that date to the Early Pithouse period contain pithouse depressions along with both ceramics and maize remains (*e.g.*, Anyon *et al.* 1981; Diehl and LeBlanc 2001; Minnis 1985). The Early Pithouse period is succeeded by the three phases of the Late Pithouse period (A.D.600–1000) and then by the Classic Mimbres phase (A.D.1000–1130), which follows a transition from pithouse to pueblo architecture that lasted about 100 years (*e.g.*, Shafer 1995). Though not accepted by all Mimbres researchers (*e.g.*, Anyon *et al.* 1981), some (*e.g.*, Lekson 1988; Woosley and McIntyre 1996) have delineated a pre-Classic Mimbres Mangas phase, beginning around A.D.950, that would correspond to this period of transition. The Classic Mimbres phase is followed by the Terminal Classic (A.D.1130–1200), the latest time period considered here, at the beginning of which new ceramic types appear in the region and during which many people seem to have emigrated from the Mimbres Valley to outlying areas (*e.g.*, Hegmon *et al.* 1999; Nelson 1999b). Most important for present purposes, there is evidence that the human population of the Mimbres region grew steadily from the Early Pithouse period through the Classic Mimbres phase (*e.g.*, Blake *et al.* 1986), and it is reasonable to expect that this led to the depression of prey through increased hunting offtakes. We also emphasize that regional paleoenvironmental records provide no suggestion that this interval was associated with climatic changes that would have caused reductions in artiodactyl herd sizes (Cannon 2001a).

Faunal Evidence for Resource Depression

Faunal assemblages that span the relevant period of time—specifically, from the Early Pithouse period through at least the Classic Mimbres phase—enable a test of the proposition that resource depression occurred in the Mimbres region. Such assemblages are available from the Old Town site, located in the relatively xeric Southern Mimbres Valley (Cannon 2001a), from a group of three sites—McAnally, Mattocks, and Galaz—located in the more wooded, higher elevation Central

Mimbres Valley (Cannon 2001a, 2003)—and from the Wind Mountain site, located in the Burro Mountains to the west of the Mimbres Valley (Cannon 2001a; Woosley and McIntyre 1996). All of these are residential sites with multiple, and in most cases large numbers of, pithouses and/or pueblo rooms.

By far, the most abundant vertebrate taxa in the assemblages from these sites are lagomorphs—*i.e.*, jackrabbits (*Lepus* spp.) and cottontails (*Sylvilagus* spp.)—followed by the artiodactyls deer (*Odocoileus* spp.) and pronghorn (*A. americana*). Using these taxa, a body size-based Artiodactyl Index, analogous to the abundance indices employed in the Sacramento Valley example, can be calculated. Because of spatial environmental differences that are reflected in faunal assemblages (see Cannon 2000, 2001a; Shaffer and Schick 1995), Artiodactyl Index values derived from different sub-areas of the Mimbres region are examined separately; these values are presented in Tables 11, 12, and 13.

Before discussing trends in these values, we first note that the data presented here from Old Town and the three Central Mimbres Valley sites incorporate faunal remains that come only from undisturbed, well-dated deposits that were screened through 0.25-in. mesh during excavation (see Cannon 2001a for further details). In addition, because there are systematic biases in artiodactyl relative abundance among different kinds of depositional contexts at these sites—for example, floor assemblages contain very low percentages of large mammal bones in comparison to trash fill deposits—we consider here only samples from intra-room trash fill contexts from which the largest samples of bones come (see Cannon 2001a:162–168; an exception to this is made in the case of McAnally due to the small size of the faunal sample from this site). Data are unfortunately not available from Wind Mountain that allow taphonomic factors to be controlled in the way that they can be for the other sites, though the consistency of patterns observed at Wind Mountain with those that occur at other sites in the region is encouraging.

We also point out that a variety of methods were used to date the faunal samples from Old Town and the three Central Mimbres Valley sites (see Cannon 2001a:75–142), the most useful of which involved quantitative analysis of ceramics from deposits that also produced faunal remains. Changes in ceramic design styles have been dated with considerable precision in the Mimbres region, and the ceramic types present in deposits can thus allow them to be dated precisely for the span of time

Table 11 Numbers of Identified Artiodactyl and Lagomorph Specimens, Aggregated by Time Period, in the Combined Samples from Mattocks, McAnally and Galaz

Phase	Artiodactyls	Lagomorphs	Total	Artiodactyl Index
TCM	16	52	68	0.235
CM	75	268	343	0.219
TC ^a	45	161	206	0.218
GT/SF	5	5	10	0.500
EP	17	1	18	0.944
Total	173	495	668	0.259

^a Most of the material in this sample likely dates to the Three Circle phase, though a small portion of it may date to the Classic Mimbres phase as well (see Cannon 2001a)

Table 12 Numbers of Identified Artiodactyl and Lagomorph Specimens, Aggregated by Time Period, from Old Town

Phase	Artiodactyls	Lagomorphs	Total	Artiodactyl Index
TCM	6	80	86	0.070
TC	107	1,287	1,394	0.077
EP/GT	2	16	18	0.111
Total	115	1,383	1,498	0.077

from the beginning of the Late Pithouse period onward (*e.g.*, Shafer and Brewington 1995; Stokes 2000). For the deposits from Old Town and the central valley sites that produced the faunal data used here, ceramic dating results are entirely consistent with all stratigraphic relationships and with all available radiocarbon and tree-ring dates (Cannon 2001a:100–140). Deposits at McAnally appear to date exclusively to the Early Pithouse period (*e.g.*, Cannon 2001a:140–142; Diehl and LeBlanc 2001), and the assignment of faunal samples from Wind Mountain to phases is discussed by Cannon (2001a:460).

Turning to the faunal data, declines in the Artiodactyl Index consistent with resource depression occur in each of the Mimbres region sub-areas for which data are available, though the details vary somewhat among the sub-areas, likely due to differences between them in environment and in human population trends. In the Central Mimbres Valley (Table 11), substantial reductions in the Artiodactyl Index occur between the Early Pithouse period and the early part of the Late Pithouse period, and then again in the Three Circle phase, the latest phase of the Late Pithouse period; subsequently, the Artiodactyl Index remains relatively unchanged through the Terminal Classic phase. Although the earliest two samples are small, the magnitude of the observed differences is large enough that these differences are highly significant ($\chi^2=53.23$, $p<0.001$; χ^2 trend=19.28, $p<0.001$).

At Old Town, the relative abundance of artiodactyls is much lower overall than is the case at the central valley sites—likely due to the site’s more arid, lower elevation setting—and temporal coverage is more intermittent (Table 12). Here, artiodactyl

Table 13 Numbers of Identified Artiodactyl and Lagomorph Specimens, Aggregated by Time Period, from Wind Mountain; Data are from Woosley and McIntyre (1996); also see Cannon (Cannon 2001a: Appendix E)

Phase	Artiodactyls	Lagomorphs	Total	Artiodactyl Index
CM	6	19	25	0.240
Mangas	161	861	1,022	0.158
TC	869	619	1,488	0.584
SF	117	125	242	0.483
GT	22	22	44	0.500
EP	68	16	84	0.810
Total	1,243	1,662	2,905	0.428

relative abundance declines by over 30% between the earliest sample—which dates to either the Early Pithouse period or the Georgetown phase—and the sample from the Three Circle phase, and it is then nearly identical in the Three Circle phase and Terminal Classic samples. Due to the small sizes of the earliest and the latest samples, none of the differences in artiodactyl relative abundance seen at Old Town are statistically significant ($\chi^2=0.36$, $p=0.836$; χ^2 trend=0.21, $p=0.648$). However, the consistency of the pattern that occurs here with that observed in the Central Mimbres Valley is noteworthy.

Wind Mountain, finally, is unique among excavated Mimbres sites in that it provides a faunal record that spans the entire period of time from the Early Pithouse period through the Classic Mimbres phase. It also provides the largest samples available for the earliest phases in the Mimbres culture history sequence. As is the case in the Central Mimbres Valley, the Early Pithouse period sample from Wind Mountain contains a very high abundance of artiodactyls relative to lagomorphs. This is followed by samples from the three phases of the Late Pithouse period in which artiodactyl relative abundance is moderately high, and these are followed in turn by Mangas and Classic Mimbres phase samples with much lower Artiodactyl Index values. The declining trend that occurs across these samples is highly significant ($\chi^2=510.86$, $p<0.001$; χ^2 trend=297.76, $p<0.001$).

To summarize these data, artiodactyl relative abundance declines dramatically, both at sites in the Mimbres Valley and at Wind Mountain, during the span of time represented by the Early Pithouse period and the early part of the Late Pithouse period. Artiodactyl relative abundance reaches its lowest point at Mimbres Valley sites by perhaps A.D.800, and it appears to do so somewhat later at Wind Mountain, by perhaps A.D.950. Once these nadirs are reached, there are no substantial changes in artiodactyl relative abundance anywhere in the Mimbres region through the Terminal Classic phase. As is discussed elsewhere (Cannon 2001a:207–256), the declines in artiodactyl relative abundance that occur at these sites probably cannot be explained by a reduction in rates of encounter with artiodactyls caused by a change in climate or by changes in the technologies or the strategies that Mimbres hunters used to procure artiodactyl and leporid prey: for example, increases in the frequency of rabbit drives (*e.g.*, Schmidt 1999; Shaffer and Gardner 1995; see also Grayson and Cannon 1999) or increases in the prevalence of “garden hunting” (*e.g.*, Linares 1976; Szuter 1991). They also cannot be explained by variability in the taphonomic processes to which samples have been subjected. This leaves resource depression as the best explanation for these declines.

Evidence of Agricultural Intensification

Just as resource depression and declining foraging efficiency in the Sacramento Valley appear to have produced a selective environment that favored the increased use of lower-return resources, not to mention one in which human health suffered greatly, in the Mimbres area, they appear to have produced a selective environment that favored agricultural intensification, which likely had momentous adaptive consequences of its own. As noted above, there is a strong theoretical foundation for expecting that reductions in wild resource foraging efficiency will lead individuals to allocate more time to agricultural pursuits. As is discussed here, three independent

lines of evidence suggest that agriculture did become increasingly important to people in the Mimbres Valley in concert with declines in foraging efficiency (see also Diehl 1996, 2001a). These lines of evidence, which are the best indicators of the amount of time that individuals allocated to agriculture that are currently available for the area, include settlement patterns, stable carbon isotopes in the bones of jackrabbits, and the size of the grinding tools that people used to process crops for consumption. Each of these is discussed here briefly in turn.

Settlement Patterns Among the primary criteria that have been used to differentiate the Mogollon Early and Late Pithouse periods is a shift in the location of residential sites from the tops of isolated knolls down to settings adjacent to floodplains in valley bottoms (e.g., Anyon *et al.* 1981). The explanation that is most commonly given for this often discussed, but rarely quantified, change in settlement pattern is that Early Pithouse period residences were built in inaccessible locations due to a need for defense from competing groups, which presumably was no longer necessary during later times (e.g., LeBlanc 1999:129–131, 186–189; see also LeBlanc 1980, 1983, 1989).

Linse (1999), however, has analyzed Pithouse Period settlement data from throughout Southwestern New Mexico, and she concludes that the available evidence does not support the proposition that a dramatic change in settlement location took place at the end of the Early Pithouse period. Instead, she argues that the shift was quite gradual, lasting well into the Late Pithouse period, and she also notes that at no time was any single type of landform used exclusively. In addition, Linse points out that little evidence independent of site location has been offered to support the hypothesis that conflict was common in the Mogollon area during the Early Pithouse period, and Diehl (2001b) has made a similar argument.

Given the lack of independent evidence to support the conflict hypothesis, an alternative explanation for the settlement shift must be sought, and EE can provide a firm foundation for developing one. Zeanah (2000, 2004) has developed a central place foraging model that shows that because of travel and transport costs, efficiency is maximized by locating residential sites nearest to the resources that provide the highest overall returns. In the one instance in which a detailed test of Zeanah's model has been conducted, involving Late Holocene hunter-gatherer archaeological data from the Carson Desert of Western Nevada (Zeanah 2004), model predictions were well supported. In light of this, it is reasonable to expect that shifts in settlement location in the Mimbres area would have occurred in response to changes in the relative returns of foraging and farming and that those shifts would therefore reflect changes in the proportion of time that individuals allocated to each activity (they may also have implications relevant to the sexual division of labor, though those are beyond the scope of this paper: see Zeanah 2004).

As noted above, irrigable alluvial floodplains, particularly that of the Mimbres River itself, provide the best land for farming in the Mimbres region, and all available evidence indicates that such settings were the focus of the most intensive agricultural efforts of the area's prehistoric occupants (e.g., Creel and Adams 1985; Sandor *et al.* 1990). On the other hand, the highest return wild resources available to them would have been such foods as deer, pinyon nuts, and juniper berries (e.g., Minnis 1985: Tables 5 and 8), which would have been most abundant in higher

elevation settings located away from floodplains. Because these types of wild resources certainly would have provided post-encounter return rates higher than the net return rates obtainable from most types of maize agriculture (*e.g.*, Barlow 2002: Fig. 5) and taking into account the cost of time required to travel to and from resource patches, it is likely that settlements would have been placed in upland settings as long as rates of encounter with high-return wild resources were sufficiently high. However, if people began to spend greater amounts of time working in agricultural fields in the floodplain—a predictable response to depression of high-return wild resources—then it is likely that they would have begun to move their residences closer to the fields where they were now spending more of their time.

The data that Linse (1999) has compiled enable a test of the proposition that the distribution of settlements on the landscape shifted in response to resource depression and a corresponding increase in time allocated to agriculture. The focus of Linse's analysis was a large portion of the greater Mogollon region, and the patterns that she observed across her entire study area may not hold for the more limited Mimbres area that is our focus here. We therefore use the subset of her data that comes from the Mimbres Valley; these data are from Linse (1999: Appendix C) and are used with modifications described by Cannon (2001a:266–269).

Linse classified sites as either “inaccessible” or “accessible” based on the landforms on which they sit (see Linse 1999 for details); in the Mimbres Valley, these two landform categories generally correspond to hilltops and locations adjacent to the floodplain, respectively. Table 14 shows the number of Mimbres Valley sites located in each type of setting that were occupied during each phase: four of the five sites in this sample that were inhabited during the Early Pithouse period are located in hilltop settings, one third of the sites that were occupied in the Georgetown phase occur in such settings, and much smaller percentages of the sites that were occupied during later phases are located in them. The declining trend observed here in the proportion of occupations located in inaccessible, hilltop settings is highly significant ($\chi^2=10.77$, $p=0.029$; χ^2 trend=7.41, $p=0.006$).

Importantly, this change in settlement pattern occurs in virtual lockstep with declines in wild resource foraging efficiency in the Mimbres Valley as indicated by trends in the Artiodactyl Index (*e.g.*, compare the values in Table 14 with those in Table 11). In light of the theoretical perspective on residential site location, discussed above, that EE can provide, this settlement shift toward locations adjacent to the floodplain may well indicate that people in the Mimbres Valley allocated more time

Table 14 Number of Mimbres Valley Sites Per Phase in Inaccessible (Hilltop) and Accessible (Adjacent to Floodplain) Locations

Location	EP	GT	SF	TC	CM
Inaccessible	4	2	1	2	1
Accessible	1	4	7	10	9
% Inaccessible	80	33	13	17	10

Data are from Linse (1999); also see Cannon (2001a)

to agriculture during the Georgetown phase than had been the case during the Early Pithouse period, and even more so during the San Francisco and succeeding phases.

Stable Carbon Isotopes Additional, independent evidence that the importance of agriculture in the Mimbres area increased over this span of time is provided by stable carbon isotope values taken from the bones of jackrabbits from the Old Town site (see Cannon 2001a for details). Stable carbon isotope ratios, of course, are a key archaeological measure of the importance of maize to past human societies (e.g., Hard *et al.* 1996; Pate 1994), and they have also been used by both archaeologists and ecologists to determine the contribution of maize to the diets of non-human animals such as deer and dogs (e.g., Cormie and Schwarcz 1994; Emery *et al.* 2000; Land *et al.* 1980; White *et al.* 1993, 2001). We use stable carbon isotope ratios here to explore whether jackrabbits, a noted agricultural pest (e.g., Dunn *et al.* 1982), consumed increasing quantities of maize or maize plants over time in the area surrounding Old Town. If maize became a significantly larger part of the diets of jackrabbits over this period, then we should observe an increase in the ratio of ^{13}C to ^{12}C in the bones of these animals. Such an increase would imply that ever greater amounts of land were placed into cultivation (e.g., Emery *et al.* 2000), which would imply, in turn, that people spent more time cultivating that land.

Table 15 presents $\delta^{13}\text{C}$ values (i.e., $^{13}\text{C}/^{12}\text{C}$ ratios relative to the PDB standard) that were obtained on bone collagen samples from ten adult jackrabbit specimens from Old Town; also given here are AMS radiocarbon dating results for these samples. As Fig. 13 shows, $\delta^{13}\text{C}$ values tend to be lower in older specimens than in younger ones, and this correlation between age and $\delta^{13}\text{C}$ is significant ($r=.66$, one-

Table 15 Stable Carbon Isotope Ratios and AMS Radiocarbon Dating Results for Old Town Jackrabbit Specimens

Laboratory number	$\delta^{13}\text{C}$ (‰)	Conventional radiocarbon age (B.P. \pm SD) ^a	Calibration intercept (A.D.) ^b	Calibrated 2-sigma age range (A.D.)	Phase
Beta-150688	-12.5	880 \pm 40	1180	1030–1250	BM ^c
Beta-150687	-17.0	980 \pm 40	1030	990–1160	CM
Beta-150684	-16.6	1000 \pm 40	1020	980–1150	CM
Beta-155846	-13.8	1060 \pm 40	990	900–1030	TC
Beta-150683	-14.5	1110 \pm 40	960	870–1010	TC
Beta-150685	-14.4	1130 \pm 40	900	790–1000	TC
Beta-150686	-16.4	1130 \pm 40	900	790–1000	TC
Beta-150682	-13.6	1140 \pm 40	900	790–990	TC
Beta-150689	-14.9	1260 \pm 40	770	670–880	SF
Beta-155847	-20.5	1480 \pm 40	600	530–650	EP/GT

^a Corrected for fractionation using the $\delta^{13}\text{C}$ values reported here

^b Calibrated using the INTCAL98 Radiocarbon Age Calibration program (Stuiver *et al.* 1998)

^c Black Mountain phase (A.D. 1200–1300). This specimen is from an architectural context that indicates a Black Mountain phase age, rather than a Terminal Classic age, and at 2-sigma its radiocarbon date is consistent with such a phase assignment

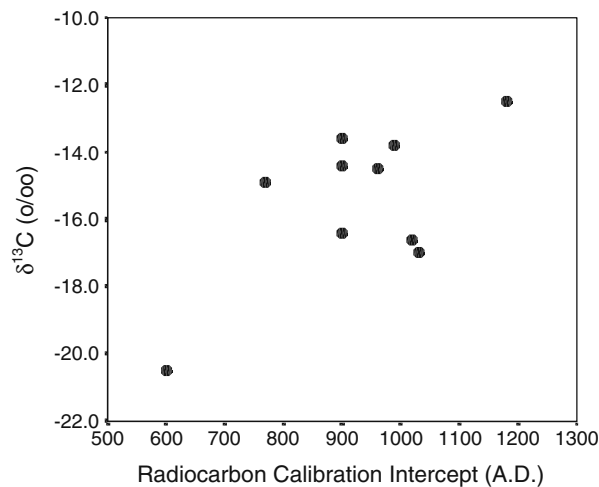


Fig. 13 Scatterplot of $\delta^{13}\text{C}$ value against radiocarbon calibration intercept for jackrabbit bone specimens from Old Town

tailed $p=.020$). Furthermore, the $\delta^{13}\text{C}$ value of the earliest specimen (-20.5‰), which based on its calibrated 2-sigma radiocarbon age range dates to either the Early Pithouse period or the Georgetown phase, is considerably lower than those of all later specimens (-17.0‰ to -12.5‰), which date to the San Francisco and succeeding phases and which do not vary greatly among themselves. As is illustrated in Fig. 14, aggregating these later specimens produces a distribution of $\delta^{13}\text{C}$ values that approximates normality, with a mean of -14.9‰ , while the early specimen falls significantly outside of this distribution ($t=3.51$, one-tailed $p=0.004$). Though this analysis is limited by the availability of only one early sample, at face value, it

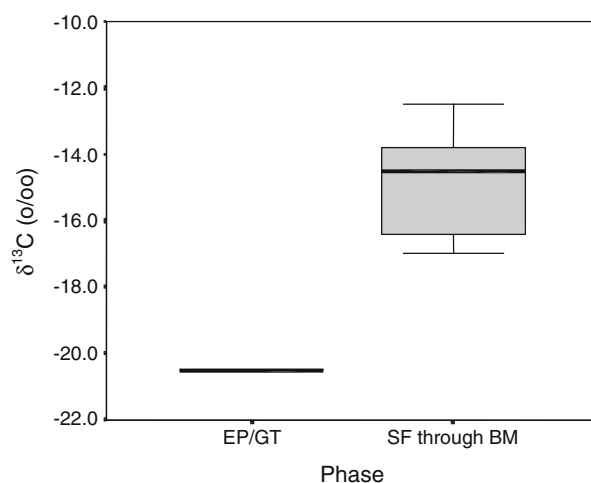


Fig. 14 Boxplot comparing the $\delta^{13}\text{C}$ value of the Old Town jackrabbit specimen dating to ca. A.D. 600 to the distribution of $\delta^{13}\text{C}$ values across all other specimens

appears that jackrabbit stable carbon isotope ratios increased substantially early on during the occupation of Old Town, with only relatively minor changes thereafter.

We are aware of no studies that have explored how dietary variability influences stable carbon isotope ratios in the bones of jackrabbits or any other lagomorph taxon, but such studies have been conducted for other North American herbivores. Cormie and Schwarcz (1994) have investigated the effects of variability in maize consumption on $\delta^{13}\text{C}$ values in the bones of modern deer (primarily white-tailed deer, *Odocoileus virginianus*), and Emery *et al.* (2000) have corrected the results of Cormie and Schwarcz to account for pre-industrial atmospheric carbon isotope values: they report average corrected values of -16.3‰ for deer that regularly consume maize and -21.8‰ for deer that feed entirely on plants that use the C3 photosynthetic pathway.

Assuming that stable carbon isotope ratios in the bones of jackrabbits and deer, both herbivores, respond to dietary variability in a similar manner, the results of this analysis of Mimbres Valley jackrabbit $^{13}\text{C}/^{12}\text{C}$ ratios suggest an initial absence of maize from the diets of these animals, followed by a substantial contribution of maize to their diets beginning during the San Francisco phase. This conclusion is strengthened when it is recognized that the $\delta^{13}\text{C}$ values observed in the Old Town jackrabbit specimens should be slightly higher than the corrected modern deer values reported by Emery *et al.* (2000) due to the presence of wild plants in the arid West that use the C4 and CAM photosynthetic pathways (*e.g.*, Hard *et al.* 1996). It therefore appears that maize plants became increasingly available to jackrabbits in the Mimbres Valley during more or less the same period when the shift in settlement locations suggests that the valley's human inhabitants spent increasing amounts of time working in agricultural fields.

Grinding Stone Size and Morphology A final measure that can be used to track changes in the amount of time that people in the Mimbres region devoted to agricultural tasks involves the tools that they used to grind maize. Archaeologists commonly employ both the size and the morphology of manos and metates as indicators of the degree to which people relied on agriculture (*e.g.*, Hard *et al.* 1996), and these variables have been used for this purpose particularly often in the Mogollon region (*e.g.*, Diehl 1996, 2001a; Hard 1986, 1990; Lancaster 1984, 1986; Mauldin 1993).

Such use of grinding stones as a measure of the importance of agriculture can be justified on both theoretical and empirical grounds (Diehl 1996, 2001a; Hard *et al.* 1996; Lancaster 1984; Mauldin 1993). Engineering studies show that the "capacity" of a grinding implement, or its output per unit time, is a function of its grinding surface area: larger tools can be used to grind more material to a given consistency in a given amount of time than can smaller tools. The use of larger grinding tools entails a trade-off, however, because they also require more physical effort on the part of the person doing the grinding. Given this trade-off between tool efficiency and the degree of effort required, it is to be expected that larger grinding tools will be used when more time is spent using them: when little time is spent grinding, the higher efficiency of larger tools will likely not be worth the additional physical effort that they require, but when several hours per day are spent grinding (*e.g.*, Hard *et al.* 1996:256–257), time constraints may make the increased efficiency of larger tools worth the added effort that they entail.

This theoretical justification for the use of grinding stones as an indicator of agricultural importance has considerable empirical support. Analyses of ethnographic data have documented correlations between mano size and “grinding intensity”, or the amount of time per day that people spend grinding plant foods, as well as between mano size and Murdock’s (1967) index of agricultural dependence, which reflects the percentage of the diet comprising domesticates (*e.g.*, Hard 1990; Hard *et al.* 1996; Mauldin 1993).

Diehl (1994, 1996, 2001a) has analyzed grinding stones from across the Mogollon region that date to the Early and Late Pithouse periods. He examined large manos that he argues were used for processing maize, an argument that he supports with a use-wear study (see also Lancaster 1984, 1986), and he found that the mean grinding surface area of these tools increased continuously from the Early Pithouse period through the Three Circle phase (*e.g.*, Diehl 1996: Fig. 4). As with Linse’s analysis of settlement patterns, however, Diehl’s study includes artifacts from a very large region, and the patterns that he observed may not hold for the more limited Mimbres area. We therefore present an analysis of mano size that is restricted to data from sites within the Mimbres Valley; these data, presented in Tables 16 and 17, come from Diehl (1994, 2001a: Table 60 and Table 6.3, respectively) for the Early and Late Pithouse periods and, since Diehl presents no data for the Classic Mimbres phase, from Lancaster (1983, cited in Hard 1986: Table 13) for this phase. We consider both mano grinding surface area and mano length, the former because only grinding surface area data are available for the Early Pithouse period and the latter because only length data are available for the Classic Mimbres phase; use of both variables together covers the entire span from Early Pithouse through Classic Mimbres.

Consistent with the expectation of increasing allocation of time to activities associated with agriculture, mano grinding surface area is somewhat larger during the San Francisco and Three Circle phases than during the preceding Georgetown phase (which is represented by only a single artifact) and Early Pithouse period (Table 16). It is not possible to treat these data statistically because the standard deviation of the Early Pithouse period sample is not available, but given the large standard deviations of the two latest samples relative to the amount of variability among the sample means, it is unlikely that the differences in mean grinding surface area that are apparent here would produce a significant result. The mano length data, which cover the Classic Mimbres phase but not the Early Pithouse period, likewise exhibit an increase between the Georgetown and San Francisco phases (Table 17). The differences observed here are not statistically significant (ANOVA: $F=0.12$, $p=0.995$), certainly

Table 16 Mean Grinding Surface Area of Mimbres Valley Manos

Phase	Mean Mano grinding surface area (cm ²)	<i>n</i>	SD
TC	249.3	27	87.2
SF	248.2	9	66.8
GT	203.0	1	–
EP	237.8	10	Unknown

Data are from Diehl (2001a: Table 6.3) for the Early Pithouse period and from Diehl (1994: Table 60) for the phases of the Late Pithouse period

Table 17 Mean Length of Mimbres Valley Manos

Phase	Mean mano length (cm)	<i>n</i>	SD
CM	20.6	146	5.3
TC	20.3	27	4.9
SF	20.6	9	4.9
GT	17.8	1	–

Data are from Diehl (1994: Table 60) for the phases of the Late Pithouse period and from Lancaster (1983, cited in Hard 1986: Table 13) for the Classic Mimbres phase

due in large part to the fact that only a single Georgetown phase mano has been analyzed. At the least, however, given that mean mano sizes are virtually identical from the San Francisco through Classic Mimbres phases, it would appear that people in the Mimbres Valley spent about as much time grinding corn, on average, during the San Francisco phase as during the later phases. And, since there is little question that a highly agricultural economy was in existence in the Mimbres Valley by the Classic Mimbres phase (*e.g.*, Holliday 1996), this would suggest that such an economy was well on its way to being established in the area by the San Francisco phase.

Finally, we note that metate data collected by both Lancaster (1986: Fig. 9.7) and Diehl (1994: Table 61) are also consistent with this conclusion. Through-trough metates, the morphological class of metate with the largest grinding surface area among the metate types that were used in the Mimbres Valley, are absent from the available Early Pithouse period metate sample from the valley, but they comprise 57% of the San Francisco phase sample, 26% of the Three Circle phase sample, and approximately 40% of the Classic Mimbres phase sample (no data are available for Mimbres Valley metates that date to the Georgetown phase). Again, these data cannot be treated statistically due to incomplete presentation of data in the primary sources (for further detail, see Cannon 2001a:282–286), but it is noteworthy that the trend in agricultural investment that can be inferred from the relative abundance of metate types is similar to the trend that can be reconstructed from mano sizes. Both lines of evidence imply that the amount of time that people spent grinding maize increased between the Early Pithouse period and the San Francisco phase, while neither provides a compelling reason to think that the amount of time allocated to this task increased from the San Francisco through Classic Mimbres phases.

In larger perspective, the ground stone evidence suggests that agriculture became more important to people in the Mimbres Valley over precisely the same span of time that is indicated by the settlement pattern and stable isotope data discussed above: all of these measures of the importance of agriculture point to increases during the period between about A.D.400 and the early 800s in the amount of time that individuals allocated to agricultural tasks such as working in fields and grinding corn.

Resource Depression and Niche Construction in the Mimbres Region: Summary

That all available indicators of the importance of agriculture in the Mimbres region change in a consistent direction over precisely the same span of time strongly

suggests that the amount of time that individuals in the region allocated to agriculture increased over this period. Moreover, that these changes happen in concert with declines in foraging efficiency, evidenced by the regional faunal record, strongly suggests that this increase in the allocation of time to agriculture occurred in response to reductions in the returns provided by wild resources.

The EE approach to modeling economic decision making provides the theoretical framework that links together these two developments—which involve such seemingly disparate components of the archaeological record as large mammal archaeofaunal relative abundance, settlement patterns, and attributes of food-processing tools—and makes one understandable as a consequence of the other (*cf.* Broughton and O’Connell 1999). In addition, by highlighting the role that humans can play in shaping their own selective environments, the Mimbres case study further exemplifies the compatibility between EE and NCT and shows how the combination of the two approaches can help archaeologists understand important developments such as agricultural intensification. And finally, we point out that though the discussion here focused on agricultural intensification and, to a lesser extent, settlement shifts, as consequences of resource depression, agricultural intensification in the Mimbres area may have led to consequences of its own, such as large-scale population movements (*e.g.*, Nelson 1999b), that are likely understandable as further instances of niche construction.

Conclusions

The Sacramento Valley and Mimbres-Mogollon case studies examined here suggest that the phenomenon of niche construction has likely played a fundamental role throughout human evolution and prehistory, and we thus fully concur that past human activities represent a potent cause of evolution (*e.g.*, Laland and Brown 2006). These examples also illustrate the inherent complementarity of EE and NCT. Indeed, archaeological applications of EE encompass the basic tenets of NCT to the extent that they view evolution as a continuous, cumulative, iterative process in which humans play a role in shaping their own selective environments.

Both approaches also have something to offer the other. For example, more explicit use of the theoretical tools of NCT—especially the framework that it provides for considering the evolutionary roles of genetic, cultural, and facultative proximate mechanisms—can only result in the further advancement of the EE approach in archaeology, which has largely ignored such issues thus far. There are two reasons, in particular why unpacking the black box of the phenotypic gambit could be productive.

First, both evolutionary ecologists working in biological disciplines (see Owens 2006) and archaeologists operating under different Darwinian approaches (*e.g.*, evolutionary archaeology, dual-inheritance theory; Mesoudi and O’Brien 2009; Henrich 2004; Lipo *et al.* 2006; Eerkens and Lipo 2005) have begun to explore how the details of the mechanisms of inheritance can have substantial effects on evolutionary outcomes. Mismatches between EE-derived predictions and the empirical record that might potentially result from such issues could be fruitfully explored using the framework of NCT.

Second, greater consideration of such issues might serve to strengthen the links between EE and these other Darwinian approaches in archaeology, which have traditionally placed more emphasis on the role that cultural transmission can play in the evolution and expression of the human phenotype. Because practitioners of all Darwinian approaches in archaeology share the goal of understanding the human past through the application of evolutionary logic and scientific methods, such integration of approaches, including the niche construction perspective, can only serve to strengthen the general Darwinian enterprise (see also Cannon and Broughton 2010; Bentley *et al.* 2007; Mesoudi and O'Brien 2009; Neff 2000).

At the same time, for advocates of the use of NCT in archaeology, the modeling tools of EE likewise have much to offer, and it can also be argued that EE is an effective vehicle through which to apply NCT to the archaeological record. Researchers using the EE approach have already made tremendous headway, both theoretical and empirical, in the study of human impacts on the environment, and to the extent that understanding such impacts is a necessary component of applying NCT, EE provides a ready-made means of doing so. More explicit use of formal EE models and of EE-inspired methods can only result in the further advancement of the NCT approach.

EE-based investigations into past human impacts on the environment have to date focused primarily on the issue of depression of large-bodied vertebrate resources. Likewise, though EE is in general applicable to—and, indeed, has been applied to—a wide range of issues of archaeological interest (see Broughton and Cannon 2010 for an overview), resource depression is undoubtedly the most thoroughly studied single topic in archaeological applications of EE. Accordingly, the examples presented here revolve around cases of resource depression, and these examples demonstrate how resource depression can constitute an important form of niche construction. While these examples involve the consequences of resource depression for such things as human health, violence, settlement patterns, and intensification of low-return wild and domesticated resources, we note that resource depression may also have similarly momentous consequences in other realms, such as technology (*e.g.*, Bright *et al.* 2002; Ugan *et al.* 2003), colonization or migration (*e.g.*, Kelly 1999), material display (*e.g.*, Kuhn *et al.* 2001), and hereditary inequalities (*e.g.*, Fitzhugh 2003; Kennett 2005). By providing a link between resource depression and these other issues, the combination of EE and NCT provides a powerful framework for developing an understanding of the human past that is firmly grounded in evolutionary theory. We are optimistic that further modeling and empirical applications that draw on both approaches will expand the synergies between them and advance our understanding of the human past even further.

Acknowledgments We thank Lydia Pyne and Julien Riel-Salvatore for organizing and chairing the symposium in which this paper was originally presented and for the work organizing the special JAMT volume. We also thank them and an anonymous reviewer for very helpful comments on the manuscript. EJB would like to acknowledge Tim D. White and the staff of the Phoebe Hearst Museum of Anthropology for their assistance with the human skeletal collections from the Sacramento Valley. He would also like to thank Randy Milliken who provided access to the burial seriation data from the personal note collection of the late James A. Bennyhoff. Funding for EJB's research summarized here was provided by a Wenner-Gren Foundation Dissertation Fieldwork Grant (no. 7163) and a National Science Foundation Doctoral Dissertation Improvement Grant (no. 0424292).

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