Late Holocene Resource Intensification in the Sacramento Valley, California: The Vertebrate Evidence

Jack M. Broughton

Department of Anthropology and Burke Memorial Museum (DB-10), University of Washington, Seattle, WA 98195, U.S.A.

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Late Holocene archaeological vertebrate faunas from the Sacramento Valley of north-central California document dramatic changes through time in the relative abundances of large- and small-sized species. The abundances of medium and large mammals decrease significantly through time relative to small resident fishes. When seasonal and spatial variability is held constant, significant decreases also exist in the abundances of large anadromous fishes relative to small resident fishes. These patterns support models of resource intensification posited for central California, which suggest that substantial decreases in foraging efficiency occurred during the late Holocene.

Keywords: RESOURCE INTENSIFICATION, LATE HOLOCENE, OPTIMAL FORAGING THEORY, CALIFORNIA, ARCHAEOLOGICAL FAUNAS.

Introduction

In recent years, several ecologically-oriented models have suggested that late prehistoric subsistence adaptations in California were characterized by a focus on high-cost resources and that significant decreases in foraging efficiency occurred during the late Holocene (Cohen, 1981; Basgall, 1987; Beaton, 1991; Bettinger, 1991a: 100). These models suggest that human population densities grew steadily during the late Holocene, causing decreases in the abundances of low-cost resources such as large terrestrial mammals. As a result, such smaller, higher-cost resources as molluscs, smaller fishes and acorns became the focus of intensive human exploitation. In short, such models suggest the occurrence of resource intensification, a process by which the total productivity per unit of land is increased at the expense of an overall decrease in foraging efficiency. In other words, more energy is harnessed from a given patch of land but individuals must expend more energy, per unit time, in the process (see Boserup, 1965). This basic argument has been suggested to account for such disparate phenomena as the late Holocene shift to intensive acorn use in the valleys and foothills (Basgall, 1987), and the intensive utilization of high-elevation alpine resources in the White Mountains (Bettinger, 1991b; Grayson, 1991). This perspective diverges widely from traditional views of aboriginal subsistence in California which have emphasized the unlimited supply of purported high-quality resources, such as acorns, salmon and deer, leading to its oft-cited depiction as the classic non-marginal environment (Kroeber, 1925; Baumann, 1963).

Because resource intensification models suggest that, overall, foraging efficiency decreased during the late Holocene, they allow for the prediction and evaluation of temporal changes in all classes of subsistence resources. However, no fine scale tests of these models have been conducted on the basis of archaeofaunal data. Here, such a test is conducted using archaeozoological vertebrate data from the Sacramento Valley in north-central California.

Resource Intensification, Foraging Efficiency and Archaeological Vertebrates

Intensification models predict decreases in foraging efficiency over time. Efficiency, in this context, refers to the overall net rate of return associated with particular strategies of resource use. As a result, measuring foraging efficiency requires attention to the relative abundances of resources with inherent differences in energetic returns. The fine-grained prey choice model, drawn from foraging theory, provides a framework for assessing the relative costs and benefits of different resources and how these variables interact with resource abundance and prey choice.

The prey choice model predicts that high-ranked prey will be taken whenever they are encountered, while low-ranked prey may or may not be selected, depending on the abundance of high-ranked prey. Prey ranks measure the profitability of various prey. These ranks are defined, in most formulations of the prey choice model, as a ratio of the net value gained by acquiring a prey item, on the one hand, to the time costs of pursuing and processing the prey once it has
been encountered, on the other. Prey ranks are, thus, established independent of encounter rates of prey taxa. Prey selection, however, is dependent on the encounter rates of prey. As the encounter rates of higher ranked prey decrease, prey are added to the diet sequentially in order of decreasing rank (see Stephens & Krebs, 1986: 17–24 and references therein).

From this, it follows that the relative abundances of high- and low-ranked prey in the diet can provide an index of foraging efficiency. A diet dominated by high-ranked prey indicates an overall higher energetic return per unit of foraging time relative to a diet dominated by low-ranked taxa (Bayham, 1979, 1982). Prey rank estimates are thus central to measuring foraging efficiency in archaeological faunas.

Prey ranks can be established empirically through actual measurement of pursuit and processing times and returns in actual tests of prey choice models. However, animal ecologists often rely on proxy measures of prey rank when actual return rates cannot be measured. The most common proxy measure of prey rank is the body size of prey items and the logic is straightforward.

In Figure 1, the hypothetical relationships between the critical variables that affect prey rank are graphically depicted (following Griffiths, 1975; Schoener, 1979; Bayham, 1982). As illustrated in Figure 1(a), the energetic value of an organism is more or less directly proportional to its weight. In conjunction with the energy value of an item, consideration must also be given to costs as a function of prey body size. Foraging theorists have proposed that pursuit and processing costs are at a minimum for certain intermediate body sizes, with increases incurred at the small and large end of the size spectrum (Figure 1(b)). In other words, there are upper and lower limits on the sizes of prey that a given predator species can efficiently capture and process for consumption: extremely large and small prey require higher pursuit and processing costs per item. The difference between the energy gain and cost curves represents the net energy gain per individual prey item (Figure 1(c)). The shape of this hypothetical curve is particularly important for it specifies the relative overall energetic returns of a prey item as a function of body size; consequently it may serve as an indication of prey rank. As depicted in Figure 1(c), for a large size range of prey species, the order of prey rank is the same as the order of prey size: large prey are high-ranked, while small prey are low-ranked.

While this simplified relationship between prey body size and prey profitability is strictly hypothetical, the basic relationship has strong support from empirical research on a diverse array of predatory species, including people (e.g. Mittelbach, 1981; Sutherland, 1982; Hill, Kaplan & Hurtado, 1987; Riechert, 1991). Table 1 provides correlation coefficients for the relationships between body size (kg) and return rates (calories/hour) for a variety of vertebrate species based on data obtained from human predators in a number of experimental and ethnographic settings. Significant positive relationships exist between body size and return rate for each independent data set, even in particular settings where different species are taken by different modes of capture (e.g. mass capture netting and single prey encounter hunting). This point is particularly germane since the logic specifying the relationship between body size and returns is based on the assumption that individual prey items are sequentially encountered.
Because it is certainly the case that prehistoric peoples captured many vertebrates not singly but in mass, such as with drives or nets, the return rates yielded in these settings could conceivably be as dependent on the density of the resource as they are on the body size of individual prey items. Unfortunately, it is also true that the means by which different classes of vertebrate prey were taken by prehistoric peoples at any particular setting is largely unknown and perhaps unknowable. Indeed, how prey are taken must surely vary with prey density, the latter reflecting inter- and intra-annual population dynamics of the particular prey species. For this reason, and because body size appears to be so strongly correlated with return rates among vertebrates, even among single groups of modern foragers using both encounter hunting and mass capture modes of prey acquisition (Table 1), body size would seem to be the only valid, context independent, proxy measure of prey rank currently available to archaeologists (see Bayham, 1979, 1982; Styles, 1981; Simms, 1987: 77; Broughton & Grayson, 1993; Broughton & Bayham, 1993; but see also Jones & Madsen, 1991; Madsen, 1993).

Insofar as body size is a valid measure of prey rank, a position which has been shown to have considerable theoretical and empirical support, changes in the relative efficiency of vertebrate prey selection, or "selective efficiency" (Bayham, 1982), can be measured in archaeological faunas by changes in the relative abundances of large- and small-sized prey items. Other things being equal, faunas dominated by large prey taxa represent a higher level of selective efficiency compared to faunas dominated by small-sized taxa.

The Sacramento Valley Archaeofaunas

To test the argument that resource intensification occurred in central California during the late Holocene, temporal patterns in selective efficiency as reflected in vertebrate faunas from nine archaeological sites from the Sacramento Valley, north-central California were examined (Figure 2). All nine sites are located on the valley floodplain near the Sacramento River or its major tributaries. These sites span the past 4000 years; all have been interpreted as representing prehistoric villages.

Minimally, the prehistoric inhabitants of these sites would have had access to the vertebrate faunas of four primary vegetational zones: freshwater marsh, grassland, oak woodland, and riparian forest. In addition, aquatic resources, especially fishes, could be taken in both lentic (warm oxbow and floodplain lakes, swamps and sloughs) and riverine (the swifter, cooler waters of the main channel of the Sacramento River and its larger tributaries) habitats.

Mammals and fishes overwhelmingly dominate all Sacramento Valley archaeological faunas and these classes are focused on here. Reptiles, especially western pond turtle (Clemmys marmorata), and birds, primarily ducks and geese (Anatidae), are also quite abundant in many assemblages. The relative abundances of archaeological mammals and fishes from the Sacramento Valley sites are provided in Table 2.

The number of identified specimens (NISP) is utilized as a measure of relative abundance whenever these data are available (see Grayson, 1984). However, only minimum numbers of individuals (MNI) are

**Table 1. Correlation coefficients for body size (kg) and return rate (calories/hour) for vertebrates taken in experimental and ethnographic settings**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>$r_s$</th>
<th>$P$</th>
<th>Capture method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gila bicolor</td>
<td>0.671</td>
<td>0.027</td>
<td>Mass capture</td>
<td>Raymond &amp; Sobel, 1990</td>
</tr>
<tr>
<td>Mammals</td>
<td>0.733</td>
<td>0.039</td>
<td>Single prey</td>
<td>Simms, 1987</td>
</tr>
<tr>
<td>Mammals/Birds/Fishes</td>
<td>0.900</td>
<td>0.072</td>
<td>Single prey, mass capture</td>
<td>Winterhalder, 1981</td>
</tr>
<tr>
<td>Mammals/Birds/Fishes</td>
<td>0.629</td>
<td>0.047</td>
<td>Single prey, mass capture</td>
<td>Smith, 1991</td>
</tr>
<tr>
<td>Mammals/Birds</td>
<td>0.599</td>
<td>0.066</td>
<td>Single prey</td>
<td>Ahvrd, 1993</td>
</tr>
<tr>
<td>Mammals/Birds</td>
<td>0.718</td>
<td>0.031</td>
<td>Single prey</td>
<td>Hill, Kaplan &amp; Hurtado, 1987</td>
</tr>
</tbody>
</table>

![Figure 2. Map of northern California and the Sacramento Valley indicating location of archaeological sites.](image-url)
Table 2. Numbers of identified specimens per taxon of fishes and mammals from Sacramento Valley assemblages (see Table 3 for source of faunal identifications and site abbreviations)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>68</td>
</tr>
<tr>
<td>Fishes</td>
<td></td>
</tr>
<tr>
<td>Aciplus sp.</td>
<td>1</td>
</tr>
<tr>
<td>Oncorhynchus sp.</td>
<td>1</td>
</tr>
<tr>
<td>Oncorhynchus tshawytscha</td>
<td></td>
</tr>
<tr>
<td>Oncorhynchus mykiss</td>
<td></td>
</tr>
<tr>
<td>Cyprinidae</td>
<td>5</td>
</tr>
<tr>
<td>Gila crassicauda</td>
<td>4</td>
</tr>
<tr>
<td>Lavinia exilicauda</td>
<td></td>
</tr>
<tr>
<td>Hesperoleucus symmetricus</td>
<td></td>
</tr>
<tr>
<td>Orthodontus macrolepidotus</td>
<td>2</td>
</tr>
<tr>
<td>Pogonichthys macrolepidotus</td>
<td></td>
</tr>
<tr>
<td>Mylopharodon monocophalus</td>
<td>3</td>
</tr>
<tr>
<td>Ichthyolichthys granulatus</td>
<td>3</td>
</tr>
<tr>
<td>Stizostedion oxias</td>
<td></td>
</tr>
<tr>
<td>Gasterosteus aculeatus</td>
<td>5</td>
</tr>
<tr>
<td>Archoplites interruptus</td>
<td></td>
</tr>
<tr>
<td>Hysterochirus traski</td>
<td></td>
</tr>
<tr>
<td>Cottus sp.</td>
<td></td>
</tr>
<tr>
<td>Total fish</td>
<td>7</td>
</tr>
<tr>
<td>Mammals</td>
<td></td>
</tr>
<tr>
<td>Scapanus latimanus</td>
<td></td>
</tr>
<tr>
<td>Didelphis virginiana</td>
<td></td>
</tr>
<tr>
<td>Leporidae</td>
<td></td>
</tr>
<tr>
<td>Sylvisagia sp.</td>
<td>7</td>
</tr>
<tr>
<td>Sylvisagia auduboni</td>
<td></td>
</tr>
<tr>
<td>Lepus californicus</td>
<td>31</td>
</tr>
<tr>
<td>Rodentia</td>
<td></td>
</tr>
<tr>
<td>Sciuridae</td>
<td></td>
</tr>
<tr>
<td>Eutamias spp.</td>
<td></td>
</tr>
<tr>
<td>Spermophilus beecheyi</td>
<td></td>
</tr>
<tr>
<td>Sciurus griseus</td>
<td>10</td>
</tr>
<tr>
<td>Thomomys sp.</td>
<td></td>
</tr>
<tr>
<td>Thomomys bottae</td>
<td>2</td>
</tr>
<tr>
<td>Perognathus sp.</td>
<td></td>
</tr>
<tr>
<td>Dipodomys heermanni</td>
<td>2</td>
</tr>
<tr>
<td>Castor canadensis</td>
<td>9</td>
</tr>
<tr>
<td>Reithrodonomys sp.</td>
<td></td>
</tr>
<tr>
<td>Peromyscus sp.</td>
<td></td>
</tr>
<tr>
<td>Cricetidae</td>
<td></td>
</tr>
<tr>
<td>Microtus californicus</td>
<td></td>
</tr>
<tr>
<td>Ondatra zibethicus</td>
<td>5</td>
</tr>
<tr>
<td>Erethison dorsatum</td>
<td></td>
</tr>
</tbody>
</table>

available for two of the assemblages, and these values are used here. Since the depositional agent(s) responsible for the presence of fossorial rodents and insectivores in these faunas is largely unknown, these taxa are not included in the following analyses.

With one exception, 1/4 in. (0.64 cm) or 1/8 in. (0.32 cm) screens were used to collect the vertebrate remains from these sites (Table 3). Screens were not used to recover the fauna from the Blossom Mound (SJO-68). However, the fact that both small mammals, such as Botta pocket gopher (Thomomys bottae) and Heerman’s kangaroo rat (Dipodomys heermanni), and small fishes, such as thick-failed chub (Gila crassicauda) and hardhead (Mylopharodon monocophalus), were identified from this assemblage suggests that the excavators were alert to the recovery of very small bones and teeth. Issues bearing on the effects of recovery methods on the composition of vertebrate faunas are discussed in the context of particular analyses below.

For several reasons, only a coarse-grained assessment of temporal trends in vertebrate utilization as represented in Sacramento Valley archaeofaunas is now possible. In particular, radiocarbon dates obtained from materials derived from Sacramento Valley middens are unevenly distributed within and between the deposits. In addition, the common practice of reporting faunal identifications for sites, rather than by stratigraphic subdivisions, makes it difficult to subdivide faunal materials temporally within given assemblages.

To deal with these circumstances, “mean dates” of accumulation were assigned to the faunas based on the span of time the sites were occupied as determined by
radiocarbon dating, obsidian hydration and artefact typologies. Using mean dates as a measure of time clearly eliminates variation in vertebrate use within the span of time individual sites were occupied, and allows an assessment of change only between occupations. Moreover, since the occupation spans of several assemblages were quite long, only the most general trends in selective efficiency can potentially be detected. It is also true, however, that given this extremely coarse-grained temporal control on vertebrate use, if significant changes in selective efficiency are indicated, they are likely to be adaptively meaningful. Dating and recovery methods for the Sacramento Valley assemblages are provided in Table 3.

**Temporal Patterns in Selective Efficiency**

There are a variety of ways to measure temporal patterns in the dietary contribution of different-sized prey animals in the Sacramento Valley. A multivariate measure incorporating the abundances and body sizes of all exploited vertebrates would be ideal. However, given the variability in the detail and breadth of vertebrate identifications available for the different assemblages, several simple taxonomic ratios based on NISP or MNI are used to explore these issues here. These ratios incorporate the substantial differences in body size both between and within the two vertebrate classes examined.

Sacramento Valley mammals, as a group, are considerably larger by weight than resident freshwater fishes. Resident fishes are represented by eight species of minnow (Cyprinidae; Table 1), Sacramento sucker (Catostomus occidentalis), Sacramento perch (Archoplites interruptus) and tule perch (Hypostomus traski). The average body size of the fishes exploited by prehistoric foragers of the Sacramento Valley typically did not exceed 500 g, to judge from live weight estimates calculated from archaeological fish remains in several sites (Schulz, 1976; Schulz, Wagner & Donning, 1976; Schulz, Wagner & Simons, n.d.). Even the smallest non-fossorial mammal exceeds the average weight of resident fishes (i.e. brush rabbit [Sylviagis bachmani] ~ 610 g). Artiodactyls such as tule elk (Cervus elaphus nannodes), black-tailed deer (Odocoileus hemionus) and...
Table 3. Occupation dates and screen size for the Sacramento Valley assemblages

<table>
<thead>
<tr>
<th>Site*</th>
<th>Screen size</th>
<th>Occupancy date (yr)</th>
<th>Fauna</th>
<th>Reference</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA-SJO-68 (68)</td>
<td>1/4&quot;</td>
<td>4350 2980 3665</td>
<td>Ragir, 1972</td>
<td>Ragir, 1972</td>
<td></td>
</tr>
<tr>
<td>CA-GLS-101 (101)</td>
<td>1/4&quot;</td>
<td>4250 1060 2650</td>
<td>Valente, 1990</td>
<td>Deal, 1988</td>
<td></td>
</tr>
<tr>
<td>CA-SAC-99 (99)</td>
<td>1/8&quot;</td>
<td>1890 1050 1470</td>
<td>Schulz, Wagner &amp; Simons, n.d.</td>
<td>Schulz, 1981; Breschini,</td>
<td></td>
</tr>
<tr>
<td>CA-BUT-12 (12)</td>
<td>1/8&quot;</td>
<td>550 250 400</td>
<td>Broughton, 1988; Martinez, unpublished data</td>
<td>Havensat &amp; Erlandson, 1990</td>
<td></td>
</tr>
<tr>
<td>CA-SHA-222 (222)</td>
<td>1/4&quot;</td>
<td>2330 1080 1705</td>
<td>Martinez &amp; Bayham, 1990</td>
<td>Sundahl, 1982</td>
<td></td>
</tr>
</tbody>
</table>

*The abbreviations in parentheses are those used in Table 2.

pronghorn (*Antilocapra americana*) are enormous by comparison.

A simple quantitative index of the relative abundances of freshwater fishes and non-fossorial mammals, the “mammal/fish index”, may be calculated as:

Σ Mammals / Σ (Mammals + Freshwater Fishes).

Values of the mammal/fish index which approach 1:0 indicate high frequencies of mammals relative to freshwater fishes, whereas values closer to 0:0 indicate lower frequencies of mammals relative to freshwater fishes.

Substantial differences in body size also exist within the mammal and fish classes. Among mammals, the starkest contrast in size is between lagomorphs and artiodactyls. The lagomorphs range in size from c. 612–2800 g, while artiodactyls range from 56–194 kg. The “artiodactyl index” summarizes the contribution of high-ranked artiodactyls within an assemblage:

Σ Artiodactyls / Σ (Artiodactyls + Lagomorphs).

Fishes of the Sacramento Valley can be separated into two broad groups based on pronounced differences in body size: the larger anadromous fishes and the smaller resident freshwater fishes.

While some resident freshwater species can exceed several kilograms [e.g. the largest Sacramento squawfish, *Psychotris grandis*, on record weighed 14.5 kg (Moyle, 1976: 192)], large individuals are the exception. For example, the average live weight for the Sacramento sucker (*Catostomus occidentalis*), one of the largest freshwater species, is only about 550 g (Villa, 1985). Indeed, live weight estimates reported for minnows and suckers from several of the lower Sacramento Valley assemblages indicate that individual freshwater fishes typically did not exceed 500 g (Schulz, 1976; Schulz, Wagner & Domning, 1976; Schulz, Wagner & Simon, n.d.).

Anadromous fishes are represented by three primary taxa: chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*) and white sturgeon (*Acipenser transmontanus*). Although sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), chum salmon (*O. keta*) and coho salmon (*O. kisutch*) have each been reported in the Sacramento River, they are extremely rare here. Individuals of these species represent either non-spawning strays or members of exceedingly small spawning runs (Hallack & Fry, 1967; Moyle, 1976: 117–125). None of these species have been identified from archaeological faunas in this region (Table 2), although species-level identifications for salmon are only available for two assemblages.

Spawning chinook salmon in the Sacramento–San Joaquin system typically weigh from 9–19 kg, though the largest on record from California weighed 38.6 kg (Moyle, 1976: 114). White sturgeon, formerly reaching lengths of up to 6.1 m and weights up to 816 kg, were the largest fish to occur in North American freshwater habitats (Moyle, 1976: 97). Since white sturgeon only move up the Sacramento River to spawn, and individuals do not reach sexual maturity until reaching lengths of about 1.1–1.5 m fork length (FL) (Skinner, 1962: 86; Eschmeyer, Herald & Hamann, 1985: 61), only large adult individuals would have been available to prehistoric people of this region.

The proportional contribution of large, high-ranked anadromous fishes in an assemblage may be calculated by the “fish index”:

Σ Anadromous Fishes / Σ (Anadromous Fishes + Freshwater Fishes).

Higher values of this ratio indicate higher proportions of anadromous fishes relative to the smaller freshwater taxa.

For each of these taxonomic ratios, higher values indicate proportionately higher frequencies of large-sized or high-ranked taxa in an assemblage. It follows that these ratios may be construed as indices of selective efficiency: high values represent high efficiency in vertebrate use, while low values represent low selective efficiency. Table 4 presents the values of these
Table 4. Indices of selective efficiency for the Sacramento Valley archaeological faunas

<table>
<thead>
<tr>
<th>Site</th>
<th>Mammal/fish index</th>
<th>Fish index</th>
<th>Artiodactyl index</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA-SJO-68</td>
<td>0.966</td>
<td>0.000</td>
<td>0.727</td>
</tr>
<tr>
<td>CA-GLE-105</td>
<td>0.919</td>
<td>0.105</td>
<td>0.813</td>
</tr>
<tr>
<td>CA-GLE-101</td>
<td>0.900</td>
<td>0.566</td>
<td>0.674</td>
</tr>
<tr>
<td>CA-BUT-288</td>
<td>0.587</td>
<td>0.392</td>
<td>0.632</td>
</tr>
<tr>
<td>CA-SAC-99</td>
<td>0.730</td>
<td>0.058</td>
<td>0.259</td>
</tr>
<tr>
<td>CA-BUT-12</td>
<td>0.028</td>
<td>0.153</td>
<td>0.625</td>
</tr>
<tr>
<td>CA-SAC-145</td>
<td>0.005</td>
<td>0.001</td>
<td>0.600</td>
</tr>
<tr>
<td>CA-SAC-329</td>
<td>0.016</td>
<td>0.010</td>
<td>0.833</td>
</tr>
<tr>
<td>CA-SHA-222</td>
<td>0.250</td>
<td>0.224</td>
<td>0.667</td>
</tr>
</tbody>
</table>

Figure 3 shows the relationship between the mammal/fish index and the mean occupation dates for the nine Sacramento Valley sites analysed here. This relationship is negative, linear, and highly significant ($r = -0.94$, $P<0.001$). The earliest occupations are dominated by medium- and large-sized mammals, while later assemblages are represented by significantly lower frequencies of mammals and higher frequencies of small freshwater fishes. The mammal/fish index is not correlated significantly with sample size ($r_s = -0.567$, $P=0.10$). However, since the bones of resident fishes are much smaller, on average, than those of mammals, and screen mesh size used to recover the faunas varied among the sites, it is possible that differential recovery may have affected these values.

Figure 4 displays the relationship between the mammal/fish index and mean occupation dates for those sites whose faunal materials were recovered with 1/4 in. screens or with no screens at all. The relationship between time and the mammal/fish index among this subset of assemblages is, again, linear and negative ($r = -0.85$, $P=0.07$), suggesting that variation in recovery methods does not underlie the temporal trend in the proportional representation of mammals and freshwater fishes.

Figure 4. The relationship between the mammal/fish index and time for Sacramento Valley sites excavated with 1/4 in. screens or none at all.

Figure 5 provides the relationship between the artiodactyl index and the mean occupation dates for the assemblages in the sample. Unlike the pattern in the mammal/fish index, no discernable trend through time is indicated in the proportional representation of high ranking artiodactyls relative to the smaller lagomorphs ($r = -0.246$, $P>0.50$). No relationship exists between sample size and the artiodactyl index ($r_s = -0.18$, $P>0.50$).

The relationship between the fish index and the mean occupation dates for the Sacramento Valley sites is presented in Figure 6. No temporal trend is indicated in the fish index ($r = -0.170$, $P>0.50$), nor is this ratio related significantly to sample size ($r_s = -0.120$, $P>0.50$). Freshwater fishes are far more abundant than anadromous species in all but one assemblage.

These indices suggest that mammals, as a group, decrease through time significantly relative to small resident fishes. This pattern, however, does not appear to be accompanied by changes in the relative abundances of different-sized taxa within the mammal or fish classes. Several variables that may be confounding
temporal trends in the relative abundances of large-sized species within these vertebrate classes are explored in more detail in the next section.

**Seasonal and Spatial Variation in Prey Availability**

Spatial and seasonal variation in the natural abundance and/or capturability of prey taxa can affect the spectrum of prey choices available to human foragers. Insofar as these variables are not held constant among the Sacramento Valley assemblages, temporal trends in vertebrate use may be obscured.

**Site seasonality**

Of the taxa whose abundances are included in the taxonomic indices, only anadromous fishes exhibit marked seasonal changes in availability. Lagomorphs, artiodactyls and freshwater fishes are available within the Sacramento Valley floodplain year-round (Orr, 1940; Longhurst, Leopold & Dasmann, 1952; McCullough, 1969; Moyle, 1976).

Anadromous species are present in the Sacramento River system only during spawning migrations. Chinook salmon move upriver in winter, spring, fall and late fall, though most fall-run fish spawn in the middle and lower reaches of the river (Healey, 1991; Williams & Williams, 1991). Spawning migrations of steelhead rainbow trout in the Sacramento River may occur in nearly every month of the year, but the vast majority of spawners enter the river from fall to spring (Shapovalov & Taft, 1954: 108; Skinner, 1962: 69). The enormous white sturgeon spend most of their lives in the San Francisco Bay estuary and move into the upper reaches of the Sacramento River between mid-March and early June to spawn (Moyle, 1976: 97).

As a result, human inhabitants of the lower and middle reaches of the Sacramento Valley floodplain would have had access to large runs of anadromous fishes during every season but summer, while groups inhabiting the upper main stem of the river would have had access to anadromous fishes primarily during winter and spring. Hence, sites that represent summer occupations in the lower and middle reaches of the river and summer-to-fall occupations in the upper main stem would be expected to contain low frequencies of anadromous fishes.

Estimates of the season(s) of occupation for the Sacramento Valley assemblages have been previously reported. Following the approach of Chatters (1987), analyses of annual growth rings of the freshwater mussels *Ma`aratifera*, *Anodonta* and *Gonidea* were recently conducted on two sites: CA-BUT-12 (Eugster, 1990) and CA-GLE-105 (Bayham & Broughton, 1990). For the other assemblages, a combination of the relative abundances of seasonally diagnostic waterfowl and mammal tooth eruption schedules were used to estimate site seasonality. In addition, Schulz, Wagner & Domning (1976) analysed the annular growth rings on the vertebrae of minnows, Sacramento sucker and Sacramento perch to refine seasonality estimates at CA-SAC-99. The results of these analyses are summarized in Table 5 (seasonality data are not available for SJO-68 and SHA-222).

Multi-seasonal or year-round occupations are indicated for all but one of these assemblages. Only GLE-105, located mid-way between the delta and the headwaters (Figure 2), represents a single season, summer occupation. As expected, the ichthyofauna from GLE-105 is heavily dominated by resident fishes. Since the fish index for the GLE-105 assemblage is constrained by the season that this site was occupied, this assemblage may be obscuring any temporal trend in the relative abundances of resident and anadromous fishes. The impact of this assemblage on the temporal

<table>
<thead>
<tr>
<th>Site</th>
<th>Season(s) occupied</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA-GLE-105</td>
<td>Summer</td>
<td>Bayham &amp; Broughton, 1990</td>
</tr>
<tr>
<td>CA-GLE-101</td>
<td>Fall-Spring (Summer?)</td>
<td>Valentine, 1990</td>
</tr>
<tr>
<td>CA-BUT-288</td>
<td>Year-round</td>
<td>Deal, 1988</td>
</tr>
<tr>
<td>CA-BUT-12</td>
<td>Year-round</td>
<td>Broughton, 1988; Eugster, 1990; Martinez, n.d.</td>
</tr>
<tr>
<td>CA-SAC-145</td>
<td>Year-round</td>
<td>Simons &amp; Schulz, 1972; Simons, Schulz &amp; Wagner, 1978</td>
</tr>
<tr>
<td>CA-SAC-329</td>
<td>Year-round</td>
<td>Schulz, Wagner &amp; Domning, 1976</td>
</tr>
</tbody>
</table>
Table 6. Correlation coefficients for indices of selective efficiency and latitude for Sacramento Valley assemblages

<table>
<thead>
<tr>
<th>Comparison</th>
<th>( r_s )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammal/fish index—latitude</td>
<td>0.842</td>
<td>&gt;0.50</td>
</tr>
<tr>
<td>Fish index—latitude</td>
<td>0.787</td>
<td>&lt;0.02</td>
</tr>
<tr>
<td>Artiodactyl index—latitude</td>
<td>-0.251</td>
<td>&gt;0.50</td>
</tr>
</tbody>
</table>

Pattern in fish utilization is assessed after examining the effect of spatial variation on prey availability.

**Spatial variation**

Although, in an attempt to reduce the effects of spatial variation on vertebrate use, the analysis was limited to sites located on the Sacramento Valley floodplain, the sites selected are nonetheless distributed across c. 275 linear kilometres. Hence, considerable latitudinal variation may have existed in the availability of different prey taxa. Since it is difficult to predict \textit{a priori} the effect that latitudinal variation may have had on vertebrate prey selection and the indices of selective efficiency, these relationships are explored inductively.

Table 6 provides correlation coefficients for the indices of selective efficiency and latitude among the Sacramento Valley assemblages. Only the relationship between latitude and the fish index is significant \((r_s = -0.787, P<0.02)\). As latitude increases in the Sacramento Valley, the fish index decreases. In other words, the relative abundance of large anadromous fishes in archaeological sites increases with latitude.

Prey choice models predict that whether or not a prey item is taken is independent of the abundance of that item but depends instead on the abundance of higher ranked prey. Hence, to gain insight into the cause(s) of the latitudinal pattern in the fish index, variables that may have affected the availability of the higher-ranked anadromous fishes across a north–south gradient are examined.

Presently, the majority of chinook salmon in the Sacramento River are full-run fish that enter the Sacramento River in September and October and spawn shortly after in the middle and lower reaches of the river. However, in the past, the Sacramento River supported large numbers of spring- and winter-run chinook. Winter-run and spring-run chinook spawn along the upper main-stem of the Sacramento River and its principal tributaries (Hallock & Fry, 1967; Healey, 1991: 319). While all spawners pass through the lower Sacramento River, the upper reaches of the river are visited only by winter- and spring-run fish. Hence, the absolute abundance of salmon in the Sacramento River declines with latitude or distance from the delta. Similar declines in salmon abundance with distance from the river mouth have been reported for the Columbia and Fraser Rivers (Fulton, 1968; Sneed, 1972; Schalk, 1977).

Variation in the natural abundance of salmon would not appear to underlie the latitudinal gradient in the fish index. That is, salmon are less abundant in archaeological sites closer to the river mouth where natural abundances are highest. Natural abundance is, however, only one aspect of availability. Of equal importance is accessibility or capturability.

Ethnographic data indicate that fish dams or weirs were an important means used to capture anadromous fishes in the main-channel of the Sacramento River (Baunhoff, 1963: 172). The latitudinal distribution of weirs along the Sacramento River during the ethnographic period provides insight into a possible source of variation in the capturability of salmon and sturgeon.

Kroeber & Barrett (1962: 261) indicate that the distribution of weirs along the stretch of river occupied by the River Patwin in the southern Sacramento Valley was limited by high flow levels of the Sacramento River. The weir built near the city of Grimes, c. 40 km north of the confluence of the Sacramento and Feather rivers (Figure 2), is specifically mentioned as the southernmost weir built on the Sacramento River (Kroeber, 1932: 261). "Farther down, especially after the Feather River came in, the Sacramento carried too much water to be weired" (Kroeber & Barrett, 1962: 28, my emphasis). While it is unknown how any particular prehistoric group captured salmon and sturgeon, the ethnographic pattern suggests that variation in flow may have had a major impact on the efficiency of extracting these fishes from the river, regardless of the particular technology used.

To explore the potential impacts of flow levels on salmon and sturgeon capturability and the prehistoric utilization of these fishes, the average annual discharge data (measured in cubic feet per second) from six localities along the Sacramento River was obtained (data from 1975 to 1985; U.S. Geological Survey, Water Resources Division, Redding, California, unpublished data). These modern flow data undoubtedly underestimate the degree of latitudinal variation in discharge during the prehistoric period, since the river has been extensively dammed and leveed during this century. However, the ordinal relationships between flow level and latitude almost certainly still hold today (Kahrl, 1979: 60–61).

Based on the modern latitudinal variation in discharge levels of the Sacramento River and the location of sites along this river, I scored the sites ordinantly, from 1 (low discharge) to 5 (high discharge). Figure 7 provides the relationship between the fish index and the Sacramento River discharge values for the various assemblages. The relationship between discharge and the fish index is negative and significant \((r_s = -0.82, P<0.05)\). As discharge decreases upstream, the relative abundance of anadromous fishes increases significantly relative to resident fishes.

These relationships suggest that variation in flow of the Sacramento River may have substantially
influenced the availability of large anadromous fishes to prehistoric peoples. This variation in availability may underlie the latitudinal gradient in the relative abundance of anadromous fishes in archaeological sites from this region. Whatever the precise causes, the fact that discharge and latitude are significantly correlated with the fish index suggests that these variables must be controlled in order to isolate temporal trends in the relative importance of freshwater and anadromous fishes.

Anadromous fishes comprise less than 1-0% of the identified fishes from sites located south of 39°N latitude, regardless of when they were occupied. Insofar as the anadromous fishery was far less accessible along the Sacramento River below 39°, such assemblages provide little information on the changing relative importance of anadromous and resident fishes through time.

Figure 8 provides the relationship between the fish index and time, excluding both (1) the assemblages south of 39°N latitude and (2) the summer-occupied GLE-105. Though the available sample is quite small, the relationship clearly indicates a trend toward and increasing emphasis on freshwater fishes use through time ($r = -0.90, p = 0.012$). Indeed, the differences in the relative abundance of anadromous and resident fishes between the earliest (GLE-101) and latest (BUT-12) assemblages in the northern Sacramento Valley are dramatically significant (chi-square=76.595, $P<0.0001$). Anadromous fishes are heavily overrepresented, and resident fishes heavily underrepresented, in the early assemblage. Differences in the relative abundances of these fishes across early and late assemblages remain significant when recovery method is held constant (GLE-101 versus SHA-222, chi-square=13.641, $P<0.0001$).

In sum, when spatial and seasonal variation in the availability of anadromous fishes is isolated and removed, the temporal pattern in the relative abundance of large and small fishes duplicates the pattern found between mammals and resident fishes: the relative abundance of large species decreases through time.

Conclusions

Resource intensification models of subsistence change during the late Holocene in central California predict decreases in selective efficiency through time (Cohen, 1981; Basgall, 1987; Beaton, 1991; Bettinger, 1991a: 100). Insofar as prey size is a valid proxy measure of prey rank, long-term patterns in vertebrate utilization in the Sacramento Valley provide evidence of resource intensification in this region. The relative abundances of large vertebrates, such as medium and large mammals, decrease through time relative to small resident fishes. In addition, when seasonal and spatial variation in the availability of large anadromous fishes is held constant, the abundances of these taxa decrease significantly through time relative to small resident fishes. The changes in proportional abundances of large- and small-sized prey are not correlated with sample sizes or the methods used to collect the faunas. I also note that these patterns are not correlated with environmental change (Adams & West, 1983; Moratto, 1984: 548), nor can they be readily accounted for by technological innovations.

Of all the tests of the intensification model for central California that I have applied, only one has failed: the relative abundance of lagomorphs compared to artiodactyls (the artiodactyl index) does not change through time. While medium and large mammals, as a group, clearly decrease in abundance through time relative to small resident fishes, no corresponding size shift is apparent within the mammal class; or at least between one group of large mammals—artiodactyls—and one group of medium mammals—lagomorphs. If the taphonomic issues regarding the depositional origin of the typically abundant small fossorial mammals in these assemblages, namely pocket gophers (Thomomys)
and ground squirrels (Spermophilus), can be resolved, it
would be interesting to examine the temporal patterns
in the relative abundances of these taxa in relation to
artiodactyls. Given that resolution, it could then be
asked whether the proportionate representation of
small mammals and artiodactyls changes through time.

If the prey body size measures I have used here are,
in fact, measuring foraging efficiency, then the failure
of the artiodactyl index may provide insight into the
measurement of efficiency in archaeological faunas in
general. Specifically, the pattern suggests that not all
simple indices that incorporate the relative abundances
of selected taxa with substantial differences in body size
will necessarily be sensitive to broad-scale changes in
vertebrate foraging efficiency. Indeed, overall changes
in vertebrate foraging efficiency can conceivably occur
in the absence of change in the proportionate abun-
dance of a particular species pair. In this case, dra-
matic, highly significant declines in efficiency were
indicated in the most species-inclusive index (the
mammal/fish index), while indices that incorporated
fewer species indicated variable results. While there is
a certain heuristic value in the less inclusive indices, in
that changing frequencies in particular species groups
can be monitored, this analysis suggests that for overall
changes in efficiency, pan-taxonomic measures that
incorporate the body sizes and abundances of all
represented vertebrates might be ideal. Bayham's
(1982; Szuter & Bayham, 1989) selective efficiency
index is one such measure.

Despite the present lack of resolution concerning the
dynamics of exploitation among Sacramento Valley
mammals, where I have detected significant changes in
selective efficiency among vertebrates, they are in the
direction predicted by intensification models. Indeed,
similar trends indicated from archaeological faunas in
other regions of California suggest that this pattern
may be a general one.

Along the Pit River, a tributary of the Sacramento
River in northeastern California (Figure 2), changes
through time in the relative abundance of large and
small vertebrates have been documented from archaeo-
logical faunas dating from 5000 BP to protohistoric
times. As in the Sacramento Valley, the relative abun-
dance of fishes, primarily resident minnows and
suckers, increases significantly through time compared
to large mammals (Greenspan, 1986; Broughton &
Bayham, 1993).

Chatters (1987) has shown that changes in the selec-
tive efficiency of vertebrate use in the Pit River region
are accompanied by changes in the intensity of pearl
mussel (Margaritifera margaritifera) exploitation.
Based on changes in age structure and growth rates, he
has argued that the pattern of mussel exploitation in
this region was "one of initial, relatively low exploita-
tion intensity, followed by increased intensity and then,
sharp decline" (Chatters, 1987: 20). The period of
"increased" exploitation intensity coincides with the
late prehistoric period, while the "sharp decline" oc-
curred after considerable Euro-American contact.
Chatters (1987) suggests that fluctuations in the inten-
sity of mussel exploitation are related to human popu-
lation growth and decline and the effects such changes
have on the abundances of high- and low-ranked
resources.

Analyses of archaeological vertebrate faunas from
San Francisco Bay shellmounds provide similar trends.
While large terrestrial mammals, namely black-tailed
deer and tule elk, dominate mammalian assemblages
during initial occupations of particular regions of the
Bayshore, their abundances decrease significantly
through time. The mammalian assemblages of late
period shellmounds are dominated by sea otters (En-
These changes do not occur synchronously throughout
the Bay region, but proceed at different rates and times
at different localities (Broughton, 1991).

In late Holocene high-elevation archaeological sites
in the White Mountains of eastern California, Grayson
(1991) has also documented dramatic changes through
time in the relative abundances of large and small
mammals. Specifically, the abundance of mountain
sheep (Ovis canadensis) decreases significantly through
time relative to yellow-bellied marmots (Marmota flai-
viventris). Grayson (1993) suggests "that the decreasing
relative abundances of mountain sheep through time in
the White Mountains assemblages reflect the local
depletion of these mammals."

While the species involved vary from context to context,
disperse archaeofaunal data sets from throughout California document an ever increasing reliance on smaller prey items during the late prehis-
toric. These data, coupled with the evidence for in-
creasing use of high-cost acorns during this time
(Basgall, 1987), provide strong support for resource
intensification models in California.

While the temporal patterns of change in taxonomic
composition are fully consistent with predictions de-
rived from intensification models, further analyses are
required to better assess the precise cause(s) of change.
Are the long-term changes documented in the relative
abundances of large and small vertebrates due simply
to per capita reductions in the densities of large taxa,
or are human populations actually depressing local
vertebrate prey populations, or both?

If direct harvesting of prey is the source of change in
the availability of different sized prey items and the
consequent changes in selective efficiency, then stress
or harvest pressure should track the observed trends in
relative abundances. That is, harvest pressure should
be initially evident on large taxa and thereafter along a
decreasing gradient of prey body size.

Harvest pressure on vertebrate populations causes
reductions in the mean and maximum ages of individu-
als. With increased harvest rates, individuals are cap-
tured well prior to reaching full growth potential, so
that overall longevity is decreased. This, in turn,
decreases intraspecific competition for resources, and
increases both growth rates and overall recruitment into a population. Demographic data from archaeological vertebrate faunas are thus critical to test hypotheses involving the impacts of human populations on prehistoric faunas.

Finally, I note that intensification models predict intensified use of smaller tracts of land and overall decreases in human mobility through time (Bassgall, 1987). Insofar as changes in land use and mobility patterns affect decisions in the dismemberment and transport of large mammal carcasses (e.g. Binford, 1981; O’Connell, Hawkes & Blurton Jones, 1990), intensification models entail predictions regarding temporal patterns in anatomical part representation of large mammals in archaeological faunas. Patterns in both demography and anatomical part representation from archaeological vertebrates will provide more definitive tests of resource intensification models in central California. My analysis, however, strongly supports the application of these models here.

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