# 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.

(Received 25 January 1993, revised manuscript accepted 7 June 1993)

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

n 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 areal 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; Baumhoff, 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 archaeological 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

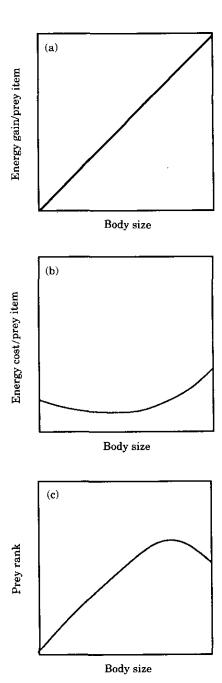


Figure 1. The hypothetical relationship between (a) prey body size and energy gain; (b) prey body size and energy cost; and (c) prey body size and prey rank (see text for explanation; adapted from Griffiths, 1975; Bayham, 1982).

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 germain since the logic specifying the relationship between body size and returns is based on the assumption that individual prey items are sequentially encountered.

Taxon	$r_s$	P	Capture method	Reference
Gila bicolor	0-671	0-027	Mass capture	Raymond & Sobel, 1990
Mammals	0-733	0.039	Single prey	Simms, 1987
Mammals/Birds/Fishes	0.900	0.072	Single prey, mass capture	Winterhalder, 1981
Mammals/Birds/Fishes	0.627	0.047	Single prey, mass capture	Smith, 1991
Mammals/Birds	0.650	0.066	Single prey	Alvard, 1993
Mammals/Birds	0.718	0.031	Single prey	Hill, Kaplan & Hurtado, 1987

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

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

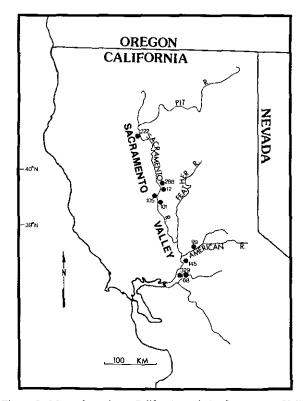


Figure 2. Map of northern California and the Sacramento Valley indicating location of archaeological sites.

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)

					S	ite				
Taxon	68	105	101	288	99	12	145*	329*	222	Σ
Fishes			<del>,,</del>		<del></del>					
Acipenser sp.		1	7	4	53	92	1	13		171
Oncorhynchus sp.		1	23	16	114	157			13	324
Oncorhynchus tshawytscha		_		_	39		2	4	_	45
Oncorhynchus mykiss	_			_	1	_		_	_	1
Cypriniformes	_	5	2	19	2467	1229	_	_	22	3744
Cyprinidae			8	2	236	106	_	_	2	354
Gila crassicauda	4			1	78	13	286	221	_	603
Lavinia exilicauda				1	33	22	460	100		616
Hesperoleucus symmetricus	_	_		_	6	_	_		_	6
Orthodon microlepidotus	_	2	3	1	23	31	29	50	1	140
Pogonichthyes macrolepidotus	_	_	1	1	19	44	143	50	_	258
Mylopharodon conocephalus	3	2	1	3	89	25	17	57	2	199
Ptychocheilus grandis	_	3	3	_	36	7	12	79	3	143
Rhinichthyes osculus	_	_		_	10	_		_	_	10
Catostomus occidentalis	_	5	2	3	263	67	91	103	14	548
Archoplites interruptus	_		2		231	56	1472	865	_	2626
Hysterocarpus traski	_	_	1		1		24	78	ì	105
Cottus sp.	_	_		_	_		1		_	1
Total fish	7	19	53	51	3699	1849	2538	1620	58	9894
Mammals										
Scapanus latimanus	_			_	23	1	_	_	_	24
Didelphis virginiana	_	11		_		_	_	_		11
Leporidae			2			_	_	_		2
Sylvilagus sp.		7	27	_	671	10	1	1	1	718
Sylvilagus auduboni	10	_	-	9	_			_		19
Lepus californicus	31	8	13	5	263	5	3	1	4	333
Rodentia	_	17	67	78		23	_		4	189
Sciuridae	_	3	15	20	_		_	_	7	45
Eutamias spp.	_	_	<del>-</del>		4		_	_	_	4
Spermophilus beecheyi	10	77	33	58	1405	6	3		1	1593
Sciuris griseus			2	10	24	_	_	1	_	37
Thomomys sp.	_	30					_	_	2	32
Thomomys bottae	2	_	115	174	547	21	25		_	884
Perognathus spp.	_		-115		2	5		_	_	7
Dipodomys heermanni	2	_	3	_	19	_	_			24
Castor canadensis	9	2	4	_	íź	_	ì	2	_	20
Reithrodontomys sp.	<u> </u>	_	<u>,</u>	_			6	ĩ	_	7
Peromyscus sp.		_	_	_	30		_	8	_	38
Cricetidae		_	_	_	2	_		_		2
Microtus californicus	_		_	_	33		36	73	_	142
Ondatra zibethicus	_		_	1				13	_	6
Erethizon dorsatum	_	_	_	<u> '</u>	1			_	_	1
					•			_	=	

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 heermani), and small fishes, such as thick-tailed chub (Gila crassicauda) and hardhead (Mylopharodon conocephalus), 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

Table 2. Continued

						Site				
Taxon	68	105	101	288	99	12	145*	329*	222	Σ
Mammals		_			<u></u>					
Carnivora	_	5	8	_		_	_	_	_	13
Canidae	_	_		_	4		_	_	_	4
Canis latranslfamiliaris	18	_	12			_		_	_	30
Canis latrans		1	31	4	309	1	1			347
Urocyon cinereoargenteus		_			21		-		_	21
Ursus sp.	1	_	1	1	_	_	_	_	_	3
Ursus cf. americanus	_	_	_	_	3	_	_	_	_	3
Procyon lotor	16	2	8	_	17	3	2	6	_	54
Mustelidae	_	2	1		1	_	_	_	_	4
Martes pennanti	_	_		_	1	_		_	_	1
Mustela sp.	_	_	_	_	3	_	_	_	_	3
Mustela frenata		_			2	_	_	_		2
Mustela vixon	_	_		_	4			1	_	5
Taxidea taxus	2	1	7	_	11	_	_	_	-	21
Spilogale putorius	_	_	_	_	2	_	_	1	_	3
Mephitis mephitis	1	_	2	_	12	_	_	1	_	16
Lutra canadensis	2		_	_	_	1	_	1	_	4
Lynx rufus	_		3	Ì	5	1	_		_	10
Equus caballus	_	_	_		_	_		I	_	1
Artiodactyla (indeterminate)	9	13	46	13	3	5	_	_	5	94
Artiodactyla (medium)	_	42	_	_	_	_	_	_		42
Artiodactyla (large)	_	4		_	_	_	_	_		4
Sus scrofa	_	_	_	_	2	_	_	_		2
Cervidae	6	1	2	_	_	_		_	_	9
Cervus elaphus		1	_		_	_		6		7
Cervus elaphus nannodes	43		4	1	43	_	1	_	_	92
Odocoileus sp.	24					_		_	_	24
Odocoileus hemionus	_	1	19	7	272	20	2	4	5	330
Antilocapra americana	27	3	16	1	6	_	3	_		29
Ovis sp.	_	_	_	_	1	_	_	_		i
Ovis cf. canadensis	_	_	_	2	1					3
Bos sp.	_	_		_	_	_	1	_	_	1
Total mammals	213	336	441	385	3749	102	85	108	29	5448
Total	220	355	494	436	7448	1951	2623	1728	87	15342

<sup>\*</sup>Values are Minimum Numbers of Individuals (MNI).

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 (Hysterocarpus 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 & Domning, 1976; Schulz, Wagner & Simons, n.d.). Even the smallest non-fossorial mammal exceeds the average weight of resident fishes (i.e. brush rabbit [Sylvilagus bachmani] = c. 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

	Occupation date (BP)			Reference			
Site*	Screen size	Initial	Terminal	Mean	Fauna	Date	
CA-SJO-68 (68)	_	4350	2980	3665	Ragir, 1972	Ragir, 1972	
CA-GLE-105 (105)	1/4"	3750	2000	2875	Bayham & Broughton, 1990	Bayham & Johnson, 1990	
CA-GLE-101 (101)	1/4"	4240	1060	2650	Valente, 1990	Bayham & Johnson, 1990	
CA-BUT-288 (288)	1/4"	3000	300	1650	Cole, 1986	Deal, 1988	
CA-SAC-99 (99)	1/8"	1890	1050	1470	Schulz, Wagner & Simons, n.d.	Schulz, 1981; Breschini, Haversat & Erlandson, 1990	
CA-BUT-12 (12)	1/8"	550	250	400	Broughton, 1988; Martinez, unpublished data	Chartkoff & Chartkoff, 1968	
CA-SAC-145 (145)	1/8"	2020	150	1085	Simons, Schulz & Wagner, 1978	Simons, Schulz & Wagner, 1978 Schulz, 1981	
CA-SAC-329 (329)	1/8"	1170	350	760	Schulz, Wagner & Domning, 1976	Soule, 1976	
CA-SHA-222 (222)	1/4"	2330	1080	1705	Martinez & Bayham, 1990	Sundahl, 1982	

<sup>\*</sup>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:

### $\Sigma$ Mammals $_i / \Sigma$ (Mammals $_i + Freshwater Fishes _i$ ).

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-ranking artiodactyls within an assemblage:

### $\Sigma$ Artiodactyls, $\Sigma$ (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, *Ptychocheilus 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 nonspawning strays or members of exceedingly small spawning runs (Hallock & 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 & Hammann, 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".

## $\Sigma$ Anadromous Fishes<sub>i</sub> / $\Sigma$ (Anadromous Fishes<sub>i</sub> + Freshwater Fishes<sub>i</sub>).

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

Site	Mammal/fish index	Fish index	Artiodactyl index	
CA-SJO-68	0-966	0.000	0.727	
CA-GLE-105	0.919	0.105	0.813	
CA-GLE-101	0.900	0.566	0.674	
CA-BUT-288	0.587	0.392	0.632	
CA-SAC-99	0.330	0.056	0.259	
CA-BUT-12	0.028	0.135	0.625	
CA-SAC-145	0.005	0.001	0.600	
CA-SAC-329	0.016	0.010	0.833	
CA-SHA-222	0.250	0-224	0.667	

three indices of selective efficiency for each of the Sacramento Valley assemblages.

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.

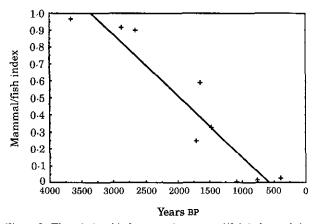


Figure 3. The relationship between the mammal/fish index and time for Sacramento Valley sites.

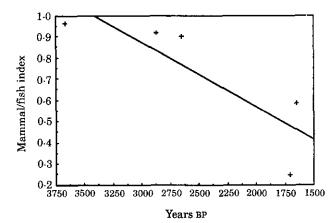


Figure 4. The relationship between the mammal/fish index and time for Sacramento Valley sites excavated with 1/4 in, screens or none at all

Figure 5 provides the relationship between the artio-dactyl 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

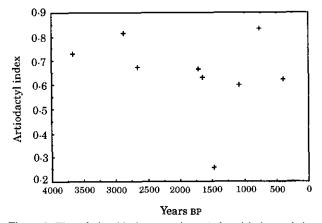


Figure 5. The relationship between the artiodactyl index and time for Sacramento Valley sites.

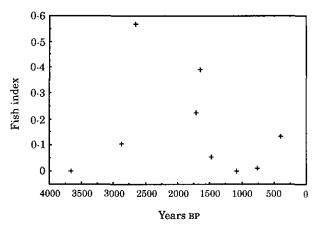


Figure 6. The relationship between the fish index and time for Sacramento Valley sites.

temporal trends in the relative abundances of largesized 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 Magaritifera, 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 5. Season of occupation for Sacramento Valley archaeological sites

Site	Season(s) occupied	Reference
CA-GLE-105	Summer	Bayham & Broughton, 1990
CA-GLE-101	Fall-Spring (Summer?)	Valente, 1990
CA-BUT-288	Fall-Spring (Summer?)	Deal, 1988
CA-SAC-99	Year-round	Schulz, Wagner & Simons, n.d.
CA-BUT-12	Year-round	Broughton, 1988; Eugster, 1990; Martinez, n.d.
CA-SAC-145	Year-round	Simons & Schulz, 1972; Simons, Schulz & Wagner, 1978
CA-SAC-329	Year-round	Schulz, Wagner & Domning, 1976

Table 6. Correlation coefficients for indices of selective efficiency and latitude for Sacramento Valley assemblages

Comparison	$r_s$	P
Mammal/fish index—latitude	0-042	>0.50
Fish index—latitude Artiodactyl index—latitude	0·787 0·251	<0.02 >0.50

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 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 fall-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 (Baumhoff, 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 ordinally, 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 upriver, 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

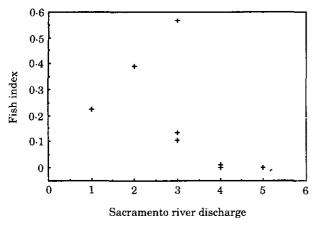


Figure 7. The relationship between the fish index and the discharge of the Sacramento River (converted to a ranked scale) adjacent to Sacramento Valley sites.

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

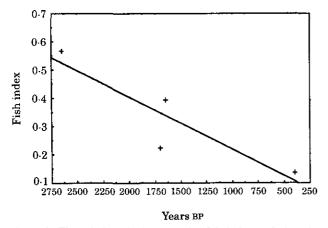


Figure 8. The relationship between the fish index and time for Sacramento Valley sites excluding GLE-105 and sites south of 39°N latitude.

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=0.102). 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 artio-dactyls (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 abundance of a particular species pair. In this case, dramatic, 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 archaeological faunas dating from 5000 BP to protohistoric times. As in the Sacramento Valley, the relative abundance 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 selective 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 exploitation 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 intensity of mussel exploitation are related to human population 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 (*Enhydra lutris*) (Simons, 1991, 1992; Broughton, 1991). 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 flaviventris). Grayson (1993) suggests "that the decreasing relative abundances of mountain sheep through time in the White Mountains assemblages reflect the local depletion of those mammals."

While the species involved vary from context to context, disparate archaeofaunal data sets from throughout California document an ever increasing reliance on smaller prey items during the late prehistoric. These data, coupled with the evidence for increasing 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 derived 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 individuals. With increased harvest rates, individuals are captured 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 (Basgall, 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.

### Acknowledgements

I thank F. E. Bayham and D. K. Grayson for extremely helpful comments on many earlier versions of this paper as well as for overall support and encouragement. I also thank V. L. Butler, K. Lightfoot, D. B. Madsen and P. D. Schulz for very helpful comments on the manuscript. I also appreciate the assistance provided by the Rohwer Lab group members, including N. Langston, M. Leu, S. A. Rohwer, G. Voelker, B., Young, and K. Zamudio, who provided insightful comments/discussion on this paper. P. B. Moyle provided many fish specimens and excellent advice on inland fishes. Helpful advice relevant to this paper was also provided by B. Dryer, M. Kowta, D. Simons, J. Williams, P. Maslin, and the late W. I. Follett, who set the standard for analyses of fish remains in California archaeological sites.

#### References

- Adams, D. P. & West, G. J. (1983). Temperature and precipitation estimates through the last glacial cycle from Clear Lake, California. Science 219, 168-170.
- Alvard, M. S. (1993). A test of the ecologically noble savage hypothesis: interspecific prey choice by Neotropical hunters. Human Ecology 21, 355–387.
- Basgall, M. E. (1987). Resource intensification among hunter-gatherers: acorn economies in prehistoric California. *Research in Economic Anthropology* 9, 21-52.
- Baumhoff, M. A. (1963). Ecological determinants of aboriginal California populations. University of California Publications in American Archaeology and Ethnology 49, 155-236.
- Bayham, F. E. (1979). Factors influencing the archaic pattern of animal utilization. Kiva 44, 219-235.
- Bayham, F. E. (1982). A diachronic analysis of prehistoric animal exploitation at Ventana Cave. Unpublished Ph. D dissertation, Department of Anthropology, Arizona State University, Tempe, AZ, U.S.A.
- Bayham, F. E. & Broughton, J. M. (1990). Animal utilization in the North Sacramento Valley. In (F. E. Bayham & K. Johnson, Eds)

- Archaeological investigations at CA-GLE-105: a multicomponent site along the Sacramento river, Glenn County, California. Reports of the Archaeological Research Program, California State University, Chico 90-109, 129-157.
- Bayham, F. E. & Johnson, K. (1990). Archaeological investigations at CA-GLE-105: a multicomponent site along the Sacramento river, Glenn County, California. Reports of the Archaeological Research Program, California State University, Chico 90-109.
- Beaton, J. M. (1991). Extensification and intensification in central California prehistory. *Antiquity* 65, 947–951.
- Bettinger, R. L. (1991a). Hunter-gatherers: archaeological and evolutionary theory. New York: Plenum.
- Bettinger, R. L. (1991b). Aboriginal occupation at high altitude: alpine villages in the White Mountains of eastern California. *American Anthropologist* 93, 656-679.
- Binford, L. R. (1981). Bones: ancient men and modern myths. London: Academic Press.
- Boserup, E. (1965). Conditions of agricultural growth: the economics of agrarian change under population pressure. Chicago, IL: Aldine.
- Breschini, G. S., Haversat, T. & Erlandson, J. (1990). California radiocarbon dates. Salinas, CA: Coyote Press.
- Broughton, J. M. (1988). Archaeological patterns of fish exploitation in the Sacramento Valley. Unpublished masters thesis, Department of Anthropology, California State University, Chico, California, U.S.A.
- Broughton, J. M. (1991). The evolution of prehistoric mammal predation around San Francisco Bay, California. In (E. Hattori, Ed.) *The archaeology of the Yerba Buena Shellmound*. Manuscript on file at Archeo-tec, consulting archaeologists, Oakland, CA, U.S.A.
- Broughton, J. M. & Bayman, F. E. (1993). Resource intensification in northern California: patterns in the archaeological vertebrate evidence. Paper presented at the 58th Annual Meeting of the Society for American Archaeology, St. Louis, MO, U.S.A.
- Broughton, J. M. & Grayson, D. K. (1993). Diet breadth, adaptive change, and the White Mountains faunas. *Journal of Archaeologi*cal Science 20, 331-336.
- Chartkoff, J. L. & Chartkoff, K. K. (1968). 1967 excavations at the Finch Site: research strategy and procedures. UCLA Archaeological Survey Annual Report 10.
- Chatters, J. (1987). Shell of Margaritifera margaritifera falcata as a source of paleoenvironmental and cultural data. In (M. Kelly, E. Nilsson & J. Cleland, Eds) Archaeological investigations at Lake Britton, California, Volume 2. San Diego, CA: Wirth Environmental Services.
- Cohen, M. N. (1981). Pacific Coast foragers: affluent or overcrowded? In (S. Koyama & D. H. Thomas, Eds) Affluent Foragers: Pacific Coasts East and West. Senri Ethnological Studies 9.
- Cole, L. (1986). Faunal analysis of the Cana Highway Site. Unpublished manuscript on file at the Zooarchaeology Laboratory, California State University, Chico, CA, U.S.A.
- Deal, K. (1988). The archaeology of the Cana Highway Site, CA-BUT-12, Butte County, California. Unpublished masters thesis, Department of Anthropology, California State University, Chico, CA, U.S.A.
- Eschmeyer, W. I., Herald, E. S. & Hammann, H. (1985). A Field Guide to Pacific Coast Fishes. Boston, MA: Houghton Mifflin.
- Eugster, S. E. (1990). Freshwater mussel utilization at a late prehistoric period archaeological site (CA-BUT-12) in the northern Sacramento Valley, California. Unpublished masters thesis, Department of Anthropology, California State University, Chico, CA, U.S.A.
- Fulton, L. A. (1968). Spawning areas and abundance of chinook salmon (Oncorhynchus tshawytscha) in the Columbia River: past and present. U.S. Fish and Wildlife Service Special Scientific Report No. 571, Washington, DC, U.S.A.
- Grayson, D. K. (1984). Quantitative Zooarchaeology. Orlando, FL: Academic Press.
- Grayson, D. K. (1991). Alpine faunas from the White Mountains, California: adaptive change in the Late Prehistoric Great Basin? Journal of Archaeological Science 18, 483-506.

- Grayson, D. K. (1993). The Alta Toquima vertebrate fauna. In (D. H. Thomas, Ed.) The Archaeology of Monitor Valley: 4. Alta Toquima and the Mt. Jefferson Complex. American Museum of Natural History Anthropological Papers, in press.
- Greenspan, R. (1986). Vertebrate faunal analysis. In (M. Kelley, E. Nilsson & J. Cleland, Eds) Archaeological Investigations at Lake Britton, California, Pit 3, 4, 5, Project, Archaeological Site Testing. San Diego, CA: Wirth Environmental Services.
- Griffiths, D. (1975). Prey availability and the food predators. Ecology 56, 1209-1214.
- Hallock, R. J. & Fry, D. H. (1967). Five species of salmon, Oncorhynchus, in the Sacramento River, California. California Fish and Game 53, 5-22.
- Healey, M. C. (1991). Life history of chinook salmon (Oncorhynchus tshawytscha). In (C. Groot & L. Marcolis, Eds) Pacific Salmon Life Histories. Vancouver: University of British Columbia Press, pp. 311-394.
- Hill, K. H., Kaplan, K. & Hurtado, A. M. (1987). Foraging decisions among the Achè Hunter-gatherers: new data and implications for optimal foraging theory. *Ethology and Sociobiology* 8, 1-36.
- optimal foraging theory. Ethology and Sociobiology 8, 1-36. Jones, K. T. & Madsen, D. B. (1991). Further experiments in native
- food procurement. *Utah Archaeology* 1991, 4, 68-77. Kahrl, W. L. (1979). *The California Water Atlas*. Sacramento, CA: State of California.
- Kroeber, A. L. (1925). Handbook of the California Indians. Smithsonian Institution, Bureau of American Ethnology Bulletin 78
- Kroeber, A. L. (1932). The Patwin and their neighbors. University of California Publications in American Archaeology and Ethnology 29, 253-423.
- Kroeber, A. L. & Barrett, S. (1962). Fishing among the Indians of northwestern California. *University of California Anthropological Records* 21, 1-211.
- Longhurst, W. A., Leopold, A. S. & Dasmann, R. F. (1952). A survey of California deer herds: their ranges and management problems. California Division of Fish and Game, Game Bulletin 6.
- Madsen, D. B. (1993). Testing diet breadth models: examining adaptive change in the late prehistoric Great Basin. *Journal of Archaeological Science* 20, 321-330.
- Martinez, A. & Bayham, F. E. (1990). Archaeofaunal remains from CA-SHA-222, Shasta County, California. Zooarchaeology Laboratory Report No. 90-3, Department of Anthropology, California State University, Chico, CA, U.S.A.
- McCullough, D. R. (1969). The Tule Elk: its history, behavior, and ecology. *University of California Publications in Zoology* 88.
- Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* **62**, 1370–1386.
- Moratto, M. J. (1984). California Archaeology. San Diego, CA: Academic Press.
- Moyle, P. B. (1976). Inland Fishes of California. Berkeley, CA: University of California Press.
- O'Connell, J. F., Hawkes, K. & Blurton Jones, N. (1990). Reanalysis of large mammal body part transport among the Hadza. *Journal* of Archaeological Science 17, 301-316.
- Otr, R. T. (1940). The rabbits of California. Occasional Papers of the California Academy of Sciences 19.
- Ragir, S. R. (1972). The Early Horizon in central California prehistory. Contributions of the University of California Archaeological Research Facility 15.
- Raymond, A. W. & Sobel, E. (1990). The use of tui chub as food by Indians of the western Great Basin. *Journal of California and Great Basin Anthropology* 12, 2-18.
- Riechert, S. E. (1991). Prey abundance vs diet breadth in a spider test system. Evolutionary Ecology 5, 327-338.
- Schalk, R. F. (1977). The structure of anadromous fish resource. In (L. Binford, Ed.) For Theory Building in Archaeology. New York: Academic Press, pp. 207-249.
- Schoener, T. W. (1979). Generality of the size-distance relation in models of optimal feeding. American Naturalist 114, 902-914.
- Schulz, P. D. (1976). Appendix C. Fish remains from the Blodgett Site (CA-SAC-267), Sacramento County, California. In (J. J.

- Johnson, Ed.) Archaeological Investigations at the Blodgett Site (CA-SAC-267) Sloughhouse Locality, California. Report submitted to National Park Service, Western Region, Sacramento, CA. Contract Report No. CX 8880-6-0002, U.S.A.
- Schulz, P. D. (1981). Osteoarchaeology and subsistence change in prchistoric central California. Unpublished Ph.D., dissertation, Department of Anthropology, University of California, Davis, CA, U.S.A.
- Schulz, P. D., Wagner, H. M. & Domning, D. (1976). Vertebrate fauna of site Ca-Sac-329, Sacramento County, California. In (W. E. Soule, Ed.) Archaeological excavations at SAC-329 near Walnut Grove, Sacramento County, California. Report submitted to the Army Corps of Engineers, Sacramento, CA. Contract No. DACW05-75-0082.
- Schulz, P. D., Wagner, H. M. & Simons, D. D. (n.d.). Vertebrate remains from the Deterding Site (CA-Sac-99), Sacramento County, California. Unpublished manuscript on file at the Archaeological Laboratory, California Department of Parks and Recreation, Sacramento, CA, U.S.A.
- Shapovalov, L. & Taft, A. C. (1954). The life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch). California Department of Fish and Game, Fish Bulletin 98.
- Simms, S. R. (1987). Behavioral ecology and hunter-gatherer foraging: An example from the Great Basin. Oxford: BAR International Series 381, 1-157.
- Simons, D. D. (1991). Prehistoric exploitation of mammals around San Francisco Bay. Paper presented at the 56th annual meeting of the Society for American Archaeology, New Orleans, Louisiana, U.S.A.
- Simons, D. D. (1992). Prehistoric mammal exploitation in the San Francisco Bay area. In (T. L. Jones, Ed.) Essays on the Prehistory of Maritime California. Center for Archaeological Research at Dayis, Publication 10, 73-103.
- Simons, D. D. & Schulz, P. D. (1972). Analysis of the vertebrate remains from the Stone Lake archaeological site (4-Sac-145). Unpublished manuscript on file at the Archaeological Laboratory, California Department of Parks and Recreation, Sacramento, CA, ILS A
- Simons, D. D., Schulz, P. D. & Wagner, H. M. (1978). Vertebrate remains from the Stone Lake Archaeological Site (CA-Sac-145). Unpublished manuscript on file at the Archaeological Laboratory, California Department of Parks and Recreation, Sacramento, CA, U.S.A.
- Skinner, J. E. (1962). An historical review of the fish and wildlife resources of the San Francisco Bay area. California Department of Fish and Game Water Projects Branch Report No. 1.
- Smith, E. A. (1991). Inujjuaniut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy. New York: Aldine De Gruyter.
- Sneed, P. G. (1972). Of salmon and men: an investigation of ecological determinants and aboriginal man in the Canadian Plateau. In (A. H. Stryd & R. A. Smith, Eds) Aboriginal Man and Environments on the Plateau of Northwest North America. Calgary: Students Press.
- Soule, W. E. (1976). Archeological excavations at SAC-329 near Walnut Grove, Sacramento County, California. Report submitted to the Army Corps of Engineers, Sacramento, CA. Contract No. DACW05-75-0082.
- Stephens, D. W. & Krebs, J. R. (1986). Foraging Theory. Princeton, NJ: Princeton University Press.
- Styles, B. W. (1981). Faunal Exploitation and Resource Selection: Early Late Woodland Subsistence in the Lower Illinois Valley. Evanston, IL: Northwestern University Archeological Program.
- Sundahl, E. (1982). The Shasta complex in the Redding area, California. Unpublished masters thesis, Department of Anthropology, California State University, Chico, CA, U.S.A.
- Sutherland, W. J. (1982). Do oystercatchers select the most profitable cockles? *Animal Behaviour* 30, 857-861.
- Szuter, C. R. & Bayham, F. E. (1989). Sedentism and prehistoric animal procurement among desert horticulturalists of the North

### 514 J. M. Broughton

American Southwest. In (S. Kent, Ed.) Farmers as Hunters: The Implications of Sedentism. Cambridge: Cambridge University Press, pp. 80–95.

California Fish and Game 71, 88-106.

Valente, N. (1990). Patterning of faunal assemblage from Glen-101 and its implication for determining season of habitation. Paper presented at the Annual meeting of the Society of California Archaeology.

presented at the Annual meeting of the Society of California Archaeology.

Villa, N. A. (1985). Life history of the Sacramento sucker, Catostomus occidentalis, in Thomes Creek, Tehama County, California.

Williams, J. E. & Williams, C. D. (1991). The Sacramento River winter chinook salmon: threatened with extinction. In (A. Lufkin, Ed.) California's Salmon and Steelhead: the Struggle to Restore an Imperiled Resource. Berkeley, CA: University of California Press,

pp. 105-115.
Winterhalder, B. (1981). Foraging strategies in the boreal forest: an analysis of Cree hunting and gathering. In (B. Winterhalder & E. A. Smith, Eds) Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses. Chicago, 1L: University of Chicago Press, pp. 66-98.