Declines in Mammalian Foraging Efficiency during the Late Holocene, San Francisco Bay, California

JACK M. BROUGHTON

Department of Anthropology and the Burke Museum DB-10, University of Washington, Seattle, Washington 98195

Resource intensification models that have been posited for prehistoric California predict decreases in foraging efficiency during the late Holocene. Using implications of the *fine-grained prey model* of optimal foraging theory, I derive an index of the efficiency of vertebrate prey choice from the relative abundances of large- and small-sized prey items. I then test the intensification models with late Holocene mammalian faunas from San Francisco Bay shellmounds. Dramatic linear decreases in the relative frequency of artiodactyls compared to the smaller sea otters (*Enhydra lutris*) throughout the occupational histories of particular localities strongly support the resource intensification models. The declines in artiodactyl abundances are not correlated with late Holocene climatic indices developed for this region, with changes in the seasonal use of shellmounds, or with technological innovations. An intra- and interregionally consistent pattern in declining abundances of large mammals in environmentally distinct regions throughout California suggests that resource depression driven by human predators may be the single most important cause of the declines. These patterns have far-reaching implications concerning the long-term human role in structuring prehistoric ecosystems. © 1994 Academic Press, Inc.

INTRODUCTION

The superabundance of large game in central California during the early historic period literally "taxed the descriptive powers" of the early explorers (McCullough 1969:15). Upon landing just north of San Francisco Bay in 1579, Sir Francis Drake was struck by the bounty of the land and the vast herds of "fat deer":

... a goodly country and fruitful soil, stored with many blessings fit for the use of man: infinite was the company of very large fat deer, which there we saw by the thousands as we supposed in a herd ... (in Bourne 1653).

In 1602, Sebastian Vizcaino (1891) also reported an abundance of deer "larger than cows" in the Monterey area. Drake's and Vizcaino's "fat deer," were, almost surely, tule elk (*Cervus elaphus nannodes*), which were later observed in abundance by others. During the 1830s, Wilkes (1845:113) was overwhelmed by the abundance of artiodactyls in the Central Valley: "the variety of game in this country almost exceeds

belief. The elk may be said to predominate." Newberry (1857) noted that during the 1850s, the large herds of game in the Central Valley rivaled the vast herds of bison that roamed the Great Plains. Pronghorn (*Antilocapra americana*) and black-tailed deer (*Odocoileus hemionus*) were abundant here as well. As one explorer noted, "At times we saw bands of elk, deer, and antelope in such numbers that they actually darkened the plains for miles, and looked in the distance like great herds of cattle" (Bosqui 1904).

Against this background, the paucity of deer, pronghorn, and tule elk in central California late prehistoric archaeological vertebrate faunas is striking. While the remains of artiodactyls are present in Late period faunas (ca. 1200 to 100 B.P.), in many settings they are greatly overshadowed by other vertebrates, such as sea otters (*Enhydra lutris*) in the San Francisco Bay area (Simons 1993) and small resident freshwater fishes in the Central Valley (Broughton 1994). In Early (ca. 4500 to 2800

B.P.) and Middle period (ca. 2800 to 1200 B.P.) assemblages, on the other hand, artiodactyls abound and are frequently the best represented taxa (see Simons 1993; Broughton 1994). These differences may indicate a decline in the natural abundance of artiodactyls throughout the late Holocene in central California, with the historic period superabundances reflecting a rebound after the collapse of Native American populations. If so, they tend to support several general ecological models of resource exploitation and subsistence change.

These ecological models suggest 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; Broughton 1994). As human population densities grew steadily during the late Holocene, it is argued, the abundances of such low-cost resources as large-bodied terrestrial herbivores decreased. As a result, such smaller, higher-cost resources as molluscs, smaller fishes, and acorns, became the focus of intensive human exploitation. In short, these particular models suggest the occurrence of *resource intensification*, classically defined as a process by which the total productivity per areal unit of land is increased at the expense of overall decreases in foraging efficiency (Boserup 1965; Beaton 1991). 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. In California, this basic argument has been suggested to account for a disparate set of archaeological phenomena, from the late Holocene shift to intensive acorn use in the valleys and foothills (Basgall 1987) to the intensive utilization of high-elevation alpine resources in the White Mountains (Bettinger 1991b; Grayson 1991).

Since these particular intensification models imply that foraging efficiency should covary with the relative densities of human populations and local resource abundances, spatial variation in the efficiency of resource procurement is predicted. However, because these models also specify *declines* in efficiency during the late Holocene of central California, they are amenable to archaeological tests involving all classes of subsistence resources throughout the region. Few empirical tests of these models have been conducted (but see Basgall 1987; Bouey 1987) and fewer still have tested the specific predictions they entail for animal prey choice (but see Broughton 1994; Broughton and Bayham 1993). I conduct such a test here, drawing upon taxonomic abundance data from archaeological mammal faunas of the San Francisco Bay shoreline. While my focus here is on deriving and testing specific predictions of these intensification models as they apply to taxonomic abundances of mammalian prey species, I emphasize that such models have far broader implications. These implications concern both other aspects of archaeological vertebrate remains (e.g., damage morphology, age structure, skeletal part representation) and other classes of archaeological data, from plant processing tools and storage technology to patterns of interhousehold and intergroup exchange.

RESOURCE INTENSIFICATION, FORAGING EFFICIENCY, AND ARCHAEOLOGICAL VERTEBRATES

As noted above, the particular resource intensification models posited for prehistoric California predict decreases in foraging efficiency over time. With respect to animal prey choice, efficiency refers to the overall net rate of return associated with a particular strategy of prey exploitation. As a result, measuring foraging efficiency requires consideration of the relative abundances of prey types with distinct 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 (Stephens and Krebs 1986).

The fine-grained prey choice model was designed to predict prey selection by predators within more-or-less homogeneous environments. Initially, the various prey types potentially exploited by a predator are ordinally ranked according to their profitability. The model predicts that the most profitable or highest-ranked prey will be taken whenever they are encountered, while prey of lower rank may or may not be selected, depending on the abundance of the highest-ranked prey. In most formulations of the prey model, prey ranks are defined 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* fully 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 and Krebs, 1986:17–24, and references therein). From this, it follows that the relative frequency with which high- and low-ranked prey are selected within a given resource patch can provide an index of foraging or predation efficiency. A diet dominated by high-ranked prey indicates higher energetic return per unit foraging time relative to a diet dominated by low-ranked prey.

One of the critical and often overlooked aspects of the prey model is that it assumes that different prey types are searched for simultaneously and that encountering a given prey type must not affect the chance of encountering another of that type. This assumption allows search time (time spent searching for prey items) to be disassociated from individual prey types and assigned to the set of resources as a whole (Smith 1991:206–207). More importantly, this feature provides the warrant for prey types to be added or dropped from the diet as a function of their postencounter return rate or rank. This assumption is generally referred to as the "fine-grained encounter" of prey, but as Smith (1991:228) notes "fine-grained search" is more accurate. If different prey types are distributed in discrete clumps or "patches" across the environment and different prey types are encountered nonrandomly, so that the predator is able to predict which prey type is likely to be encountered next, the fine-grained encounter assumption is violated and application of the prey model can lead to fallacious predictions (see Belovsky 1987:34–35; Smith 1991:206).

Applications of the prey model to archaeological settings would, thus, require that for any particular analysis all prey resources were sought simultaneously from within a single resource patch. On the surface, defining patches as units of analysis, difficult even among living foragers, would seem to be extremely problematic in the archaeological setting. Since human predators and some key prey types can quickly move across what might be considered discrete resource clumps, what appear today as spatially bounded areas or resource clumps need not have been "patches" to past human foragers. Indeed, the decision as to whether or not the approximation of simultaneous search is met requires "detailed knowledge of the foraging methods in a particular time and place" (Smith 1991:228). Such information is, of course, typically unavailable to archaeologists.

However, there are several fundamental differences between standard applications of the prey model among living foragers and archaeological contexts. In the modern setting, where strict applications of the

prey model are possible, the *predator* is modeled as a single individual, whether in fact it may or may not be. Since a single predator can search for prey in but one patch at a time, the simultaneous search restriction is linked to single resource patches, and application of the prey model must begin anew for analyses of prey choice in discrete patches.

In the analysis of bones and teeth from archaeological sites, prey remains clearly reflect the activities of multiple individual predators that have selected prey within multiple discrete patches in proximity to the site locality. At any particular point in time, different individual predators may be searching for prey in discrete patches adjacent to the site locality. Across the variable but typically long time periods of faunal accumulation represented in archaeological settings, it is probably accurate to assume that all resource patches are more or less continually searched by the site occupants. As a result, those occupants may be viewed as a *collective predator.* Insofar as the discrete resource patches adjacent to a residential occupation are continually monitored or searched by this collective predator, the site catchment, as a unit, may be properly viewed as the analytic resource patch. This conception of the archaeological vertebrate record preserves the stringent assumption of the prey model that encountering a given prey type does not affect what next prey type will be encountered.

Considering the site catchment as a single resource patch, and thereby assuming an approximation of fine-grained search of prey types, it follows that the relative frequency with which high- and low-ranked prey are selected can provide an index of foraging efficiency. A diet dominated by high-ranked prey indicates an overall higher energetic return per unit foraging time relative to a diet dominated by low-ranked prey. Prey rank estimates are, thus, a critical first step toward 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. The logic is straightforward.

In Fig. 1, I have graphically depicted the conceptual relationships between the critical variables that affect prey ranks. As il-
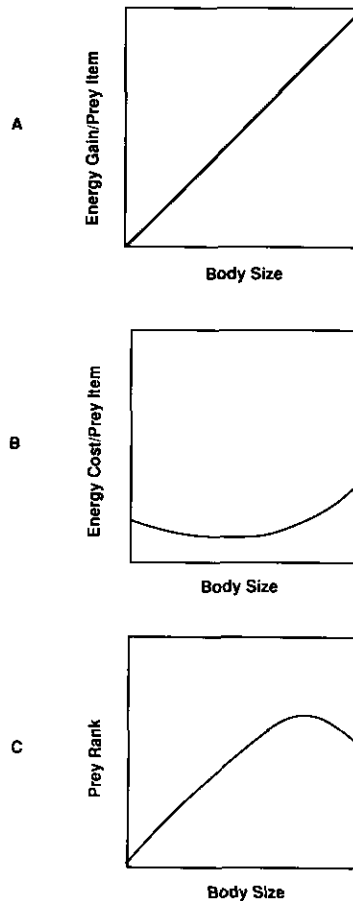

FIG. 1. The hypothetical relationship between (A) prey body size and energy gain, (B) prey body size and energy cost, and (C) prey body size and prey rank (see text for explanation; adapted from Griffiths 1975; Bayham 1979, 1982).

lustrated in Fig. 1A, the energetic *value* of an organism is more or less directly proportional to its weight. Larger prey items contain absolutely higher energetic values, both with respect to nutritional variables (i.e., energy, protein, fat) as well as raw materials for tools (hides, furs, bones). 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 body sizes, with increases incurred at the small and large ends of the size spectrum (Fig. 1B; see Griffiths 1975; Schoener 1979). 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. The difference between the energy gain and cost curves represents the net energy gain per individual prey item (Fig. 1C). The shape of this hypothetical curve is particularly important since it specifies the relative overall energetic returns of a prey item as a function of body size; consequently, the curve may serve as an indication of prey rank. As depicted in Fig. 1c, for a broad 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 (Griffiths 1975; Bayham 1979, 1982, Broughton 1994).

While this simplifying assumption has been employed in the past (see Bayham 1979; 1982; Szuter and Bayham 1989; Broughton 1994; Broughton and Bayham 1993), there is a rapidly accumulating body of empirical data from a great diversity of predatory species which supports the hypothesized relationship between prey size and prey profitability (e.g., Mittelbach, 1981; Sutherland, 1982; Hill et al., 1987; Simms, 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) in both terrestrial and aquatic habitats.

TABLE 1
Correlation Coefficients for Body Size (kg) and Return Rate (calories/hour) for Vertebrates Taken in
Experimental and Ethnographic Settings

Vertebrate class (no. of species)	r_s	P	Capture method	Reference	Notes
Fishes (1:12; see note)	.671	.027	Mass capture	Raymond and Sobel 1990	p. 13; Table 5. Twelve weight classes for one species.
Mammals (9)	.733	.039	Single prey	Simms 1987	p. 122; Table 4.
Mammals/birds/ fishes (6)	.900	.072	Single prey, mass capture	Winterhalder 1981	p. 82–83; Table 4.4. Seasons averaged.
Mammals/birds/ fishes (11)	.627	.047	Single prey, mass capture	Smith 1991	p. 234; Table 6.11; column 4 ("total time").
Mammals/birds[a] (9)	.650	.066	Single prey	Alvard 1993	Table 3.
Mammals/birds (7)	.718	.031	Single prey	Hill et al. 1987	p. 20; Table 2.

[a] Includes Brazilian tapir (*Tapirus terrestris*) and capybara (*Hydrochaeris hydrochaeris*).
Pursuit costs of these species were estimated from collared peccary (*Tayassu tajacu*).

Notwithstanding the potential importance of variation in procurement costs, in many diverse settings prey body size *alone* would appear to be the most important variable affecting both prey value as well as overall rank. This is fortunate, since prey body size is readily measurable from archaeological faunas. In any given setting, however, specific factors that may affect changes in procurement costs, in particular technological change, can and should be evaluated.

Insofar as body size is a valid proxy measure of prey profitability or rank, changes in the relative efficiency of mammal predation can be measured archaeologically by changes in the relative abundances of large- and small-sized mammals. Assuming the diet breadth of human predators continually expands and contracts across the time period of interest, with only the largest, highest ranked species always included in the diet, the relative abundances of smaller prey in a faunal assemblage may reflect the frequencies with which they entered the diet. Other things being equal (e.g., the seasonality of site occupation, taphonomic histories), archaeological faunas dominated by large mammals should represent a higher level of mammalian predation efficiency compared to faunas dominated by smaller-sized mammals (Bayham 1979, 1982; Jochim 1983; Broughton and Grayson 1993; Broughton 1994).

THE SAN FRANCISCO BAY ARCHAEOLOGICAL MAMMAL RECORD

As it applies to mammalian prey choice, the intensification model posited for central California predicts declines in predation efficiency during the late Holocene. To test this aspect of the model, I draw on archaeological mammal data gathered from San Francisco Bay shellmound sites over the past century. These sites represent a sample of the 425 shellmounds Nelson (1909) recorded in his turn-of-the-century survey of the San Francisco Bay shoreline and adjacent coast (the criteria of site selection for this analysis is discussed below). Many of these shellmounds were huge. The Emeryville Shellmound, for instance, covered an area roughly 100 × 300 m and was nearly 9.8 m deep (Schenck 1926). Radiocarbon dating has indicated that the earliest shellmounds began to form about 4000 B.P. and that the Bayshore was occupied continuously from that time to the historic period (Bickel 1978).

The large number of Bayshore shellmounds coupled with their often immense size inspired early attention by archaeologists. In fact, it was the work of turn-of-the-century San Francisco Bay shellmound archaeologists, including Nels Nelson and Max Uhle, that launched the long history of fine-scale stratigraphic excavations in American archaeology (Willey and Sabloff 1980:55–57). While Uhle, Nelson, and other early shellmound archaeologists were interested in examining evidence for culture change throughout the occupational history of shellmounds—hence the stratigraphic excavations—they were also interested in the age of the mounds, how large the human populations were that created them, and in the nature of the environments that existed during their formation. These latter interests led them to collect data that were otherwise atypical of the times, including large samples of vertebrate remains.

Though screens were not routinely used in the recovery of vertebrates in the field until the late 1960s, huge samples of remarkably well-preserved bones, teeth, and even fish scales, were nonetheless collected by the early workers, either by hand or within sediment samples (Uhle 1907; Gifford 1916; Greengo 1951; Gerow 1968). This allowed analyses of both vertebrates (Howard 1929) and molluscs (Gifford 1916) decades before such studies would become typical in American archaeology.

Since the late 1960s, many other shell-mounds have been excavated, providing vertebrates and other materials that were recovered with either 2- or 4-mm mesh screens and provenienced by arbitrary levels.

The long history of stratigraphic excavations and constituent analyses of numerous San Francisco Bay shellmounds have produced large samples of bones and teeth representing occupations that span the past 4000 years (e.g., Nelson 1909; Gifford 1916; Shenck 1926; Gerow 1968; Wallace and Lathrap 1975; Pastron and Walsh 1988a, 1988b; Hattori and Pastron 1991; Simons 1993). The archaeofaunal record of the San Francisco Bay is, thus, well suited for a diachronic analysis of mammalian foraging efficiency.

Although most San Francisco Bay shellmounds are represented by an impressive diversity of mammals, birds, and fishes, mammals have drawn the bulk of the attention (Simons 1993). Here, I draw on archaeological mammal data from 14 shellmound sites (Fig. 2). All 14 sites were located on the margin of San Francisco Bay, situated in a complex mosaic of terrestrial and aquatic habitat types, including open estuary, tidal mudflats, freshwater marsh, oak woodland, grassland, and redwood–fir forest.

At present, only a very coarse-grained assessment of temporal and spatial trends in mammal utilization as represented in those sites is possible. In particular, radiocarbon dates for Bayshore shellmounds are unevenly distributed throughout the deposits, with most dates derived from materials recovered from basal layers of middens. In addition, the common practice of presenting faunal identifications by site, rather than by stratigraphic subdivisions of those sites, often makes it difficult to subdivide faunal materials temporally within given shellmounds.

To deal with these circumstances, I have assigned shellmound faunas "mean dates" of accumulation based on the span of time the mounds were occupied, as determined by radiocarbon dating, obsidian hydration, and artifact typologies (dates are presented below). This means that each shellmound, or component thereof, was assigned a single date or point in time. All radiocarbon dates have been calibrated to calendar dates following Stuiver and Reimer (1993).

Using mean dates as a measure of time clearly eliminates variation in mammal use within the span of time that individual sites were occupied and allows an assessment of change only between occupations. I also note that since the occupation spans of several assemblages were quite long (see below), only the most general trends in mammalian predation efficiency can potentially be detected. However, should consistent, significant trends be indicated, they are likely to be adaptively meaningful.

TEMPORAL PATTERNS IN MAMMALIAN PREDATION EFFICIENCY

There are a variety of ways that spatial and temporal variation in the abundances of different-sized prey mammals from San Francisco Bay shellmound sites might be measured. A multivariate measure incorporating the abundances and body sizes of all exploited mammals would be ideal. However, given the uncertain depositional origin of the many smaller burrowing taxa, specifically, insectivores, lagomorphs, and rodents, I use a simple taxonomic ratio based on NISP (number of identified specimens) of several of the most abundant species whose depositional origin is clearly anthropogenic.

Table 2 provides the numbers of identified specimens for the San Francisco Bay shellmounds in the study sample, exclusive of fossorial insectivores, lagomorphs, and rodents. As indicated in Table 2, two
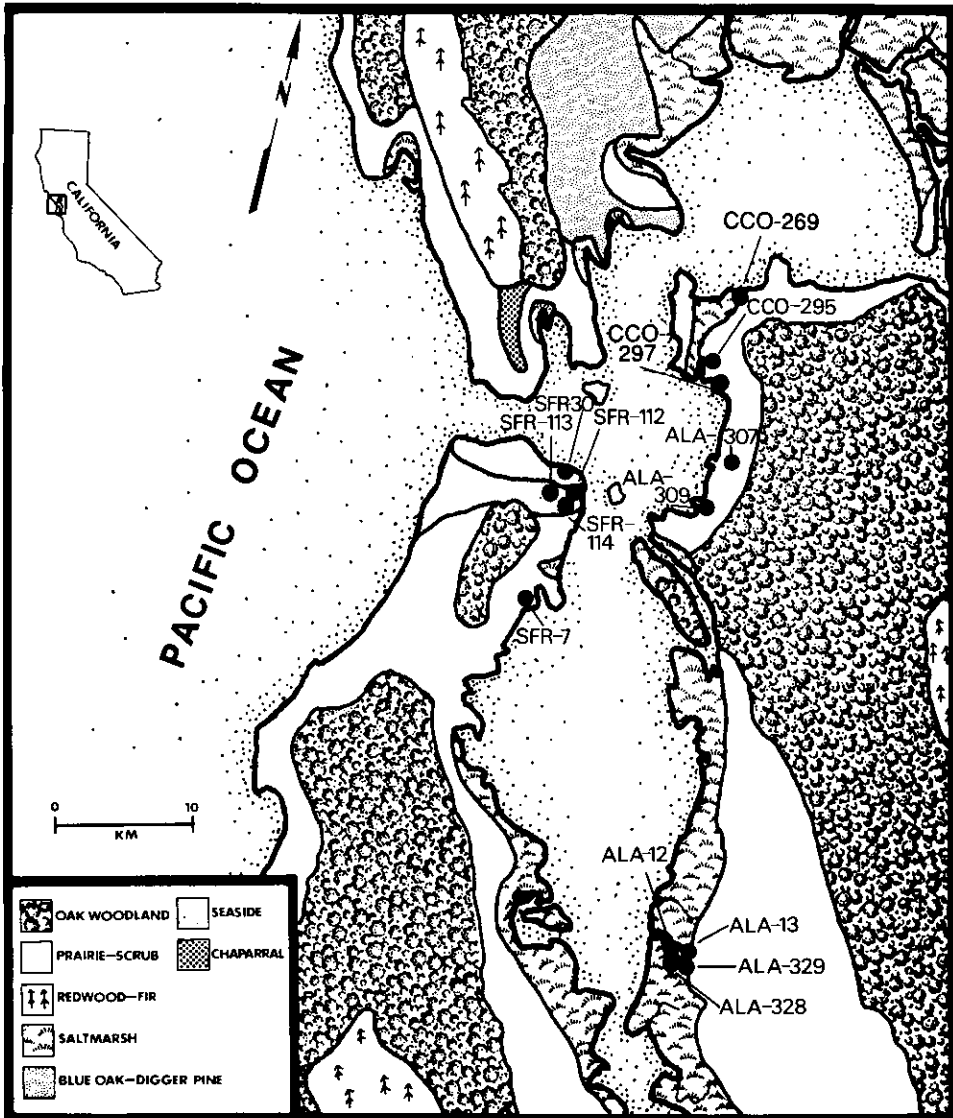
FIG. 2. Map of San Francisco Bay area indicating location of archaeological sites and historic-period vegetation (vegetation redrawn from Küchler 1977).

taxonomic groups overwhelmingly dominate the mammalian faunas of these assemblages: artiodactyls (including tule elk, black-tailed deer, and pronghorn) and sea otters. In fact, artiodacyls and sea otters, as a group, comprise 81.3% of the identified mammal specimens from these faunas (Table 2). Among the three artiodactyl species, black-tailed deer are by far the most abundant, representing 81.8% of the artiodactyl specimens that were identified to species.

Black-tailed deer are about twice the size, by weight (mean weight of 2.5- to 5.5-year males, 61.1 kg; females, 46.2 kg; Leopold et al. 1951), of sea otters (mean weight adult males, 29.5 kg; adult females, 19.5 kg; Riedman and Estes 1990:13), while

tule elk (mean weight adult males, 222 kg; adult females, 186 kg; McCullough 1969:5–6) are over six times as large.

A simple quantitative index of the relative abundances of sea otters and artiodactyls, the "artiodactyl index", may be calculated as

$$\Sigma \text{Artiodactyls }_i / \Sigma(\text{Artiodactyls }_i + \text{Sea Otters }_i).$$

Values of the artiodactyl index which approach 1.0 indicate high frequencies of artiodactyls relative to sea otters, whereas values closer to 0.0 indicate relatively few artiodactyls and higher numbers of sea otters. Moreover, given the numerical dominance of these two taxa in the mammalian faunas of this region, the artiodactyl index may be construed as a positive index of mammalian predation efficiency: higher values represent high efficiency in mammal procurement, while low values represent low efficiency. Temporal and spatial trends in the efficiency of mammal exploitation can then be revealed by plotting the artiodactyl index values calculated from dated shellmounds, or compounds thereof, against the occupation dates for these deposits.

While intensification models, in general, predict declines in mammalian foraging efficiency during the late Holocene, there are several key variables that might affect spatial variability in this trend. In particular, the artiodactyl index should vary according to the *local* relationship between population densities of human foragers and the natural abundance of artiodactyls. Specifically, localities adjacent to habitats that supported lower densities of artiodactyls should exhibit lower artiodactyl indices at any given point in time, other things being equal. Alternatively, localities represented by larger human population densities should also exhibit lower artiodactyl index values at any given time, given the potential effects that large aggregated human populations can have on local densities of high-ranked animal prey (see be-

low). To the extent that such variation exists within a defined region such as the San Francisco Bay area, a regional scale analysis of temporal patterns in the artiodactyl index may produce ambiguous results. That is, conflating multiple local sequences, all of which might independently signal dramatic declines in efficiency but at different rates and absolute times, would yield less than impressive temporal trends. Hence, tighter temporal trends are predicted to result as the spatial scale of analysis narrows.

The occupation dates, number of identified sea otters and artiodactyls, and artiodactyl index values for the 18 shellmound components are provided in Table 3. Only sites with total sea otter and artiodactyl sample sizes of greater than 50 specimens are considered in this analysis (i.e., NISP sea otters + artiodactyls > 50). Dating issues are discussed below.

Figure 3 shows the relationship between the artiodactyl index and the mean occupation dates for all of the San Francisco Bay assemblages in the study sample. A suggestive but fairly weak ($r = -.60$, $P = .01$) relationship is indicated between time and the artiodactyl index for the region as a whole. Though the artiodactyl index does appear to decrease through time, there is variability in this trend. At 1500 B.P., for example, this ratio varies from less than .20 at CA-SFR-114 (ET) to as great as .82 at CA-ALA-13 (lower). Do the relationships between time and the artiodactyl index increase in significance as the spatial scales of analysis are compressed?

Three localities or subregions within the Bay region hold promise in examining spatial variability in mammalian predation efficiency. These are the East Bay, the Coyote Hills (southeast Bay), and the San Francisco Peninsula (Fig. 2). Each of these localities are represented by several shellmounds that have had large samples of their mammalian faunas analyzed and reported.

TABLE 2

Numbers of Identified Mammal Specimens for the San Francisco Bay Shellmounds Exclusive of Insectivores, Lagomorphs, and Rodents (see Table 3 for Source of Faunal Identifications)

Taxon	ALA-328(U)	ALA-13(U)	ALA-329	ALA-13(L)	ALA-12	ALA-328(L)	CCO-297	ALA-309	CCO-295	CCO-269
Cetacean (whales and porpoises)	1	—	1	—	—	2	—	104	20	—
Canis familiaris/latrans (dog/coyote)	17	110	135	155	61	51	—	620	65	30
Canis lupus (gray wolf)	—	—	2	—	—	—	—	—	—	—
Urocyon cinereoargenteus (gray fox)	2	—	5	—	—	—	—	41	—	—
Ursus americanus (black bear)	—	—	—	—	—	—	—	26	—	—
Ursus arctos (grizzly bear)	—	—	—	—	—	—	—	7	—	—
Procyon lotor (raccoon)	1	11	30	13	1	2	—	73	12	4
Mustelidae (mustelids)	3	—	30	—	—	—	—	—	—	—
Mustela frenata (long-tailed weasel)	—	—	—	—	—	—	—	16	—	—
Taxidea taxus (badger)	7	24	43	7	4	5	—	18	12	1
Spilogale putorius (spotted skunk)	—	—	—	—	—	—	—	21	—	—
Mephitis mephitis (striped skunk)	3	6	18	26	1	3	5	42	8	1
Enhydra lutris (sea otter)	83	215	883	98	28	27	44	3,459	232	27
Felis concolor (mountain lion)	—	—	—	—	—	—	—	3	—	—
Lynx rufus (bobcat)	—	—	15	—	—	—	—	36	1	1
Pinniped (seals and sea lions)	—	—	1	—	—	3	—	—	—	—
Otaridae (eared seals)	—	—	—	—	—	—	—	—	31	2
Callorhinus ursinus (northern fur seal)	—	—	—	—	—	—	—	18	—	—
Eumetopias jubatus (Steller's sea lion)	—	—	—	—	—	—	—	231	—	—
Zalophus californianus (California sea lion)	—	—	—	—	—	—	—	317	—	—
Phoca vitulina (harbor seal)	8	—	95	1	1	6	2	203	64	10
Artiodactyla (artiodactyls)	38	—	603	—	—	45	—	—	—	—
Cervus elaphus (elk)	7	15	54	35	80	32	—	873	13	—
Odocoileus hemionus (black-tailed deer)	15	161	435	386	54	32	19	4,028	86	41
Antilocapra americana (pronghorn)	1	4	45	13	5	3	—	3	—	2
Total	186	546	2395	734	235	211	70	10,139	544	119

Taxon	ALA-307(U)	ALA-307(L)	SFR-114(W)	SFR-7	SFR-30	SFR-112	SFR-114(E)	SFR-113	Σ
Cetacean (whales and porpoises)	1	—	—	1	2	—	—	1	133
Canis familiaris/latrans (dog/coyote)	26	7	7	2	1	3	10	32	1,332
Canis lupus (gray wolf)	—	—	—	—	—	—	—	—	2
Urocyon cinereoargenteus (gray fox)	—	—	—	—	1	—	—	—	49
Ursus americanus (black bear)	—	—	—	—	—	—	—	—	26

TABLE 2—*Continued*

Taxon	ALA-307(U)	ALA-307(L)	SFR-114(W)	SFR-7	SFR-30	SFR-112	SFR-114(E)	SFR-113	Σ
Ursus arctos (grizzly bear)	—	—	—	—	1	—	—	—	8
Procyon lotor (raccoon)	2	—	1	9	2	3	1	—	165
Mustelidae (mustelids)	—	—	—	—	1	—	—	—	34
Mustela frenata (long-tailed weasel)	—	—	—	—	—	—	—	—	16
Taxidea taxus (badger)	1	—	—	5	—	—	—	—	127
Spilogale putorius (spotted skunk)	—	—	—	—	—	—	—	—	21
Mephitis mephitis (striped skunk)	—	—	—	1	—	—	1	—	115
Enhydra lutris (sea otter)	21	3	302	303	94	223	156	25	6,223
Felis concolor (mountain lion)	—	—	—	—	—	—	—	—	3
Lynx rufus (bobcat)	—	—	10	—	2	2	4	—	71
Pinniped (seals and sea lions)	—	—	—	—	1	—	—	—	5
Otaridae (eared seals)	6	3	1	—	9	—	—	2	54
Callorhinus ursinus (northern fur seal)	—	—	—	3	—	—	—	2	23
Eumetopias jubatus (Steller's sea lion)	—	—	—	—	—	—	—	—	231
Zalophus californianus (California sea lion)	—	—	—	11	32	7	—	—	367
Phoca vitulina (harbor seal)	6	8	1	3	26	11	—	2	447
Artiodactyla (artiodactyls)	—	—	24	—	13	—	23	—	746
Cervus elaphus (elk)	3	—	1	29	7	42	1	8	1,200
Odocoileus hemionus (black-tailed deer)	46	22	7	186	25	138	9	68	5,758
Antilocapra americana (pronghorn)	2	—	—	—	—	—	—	—	78
Total	114	43	354	553	217	429	205	140	17,234

Figures 4, 5, and 6 display the relationship between the artiodactyl index values and mean occupation dates for shellmound deposits in the East Bay, Coyote Hills, and the San Francisco Peninsula assemblages. In both the East Bay and Coyote Hills, highly significant, negative linear relationships exist between time and the artiodactyl index (East Bay, $r = -.86$, $P = .03$; Coyote Hills, $r = -.94$, $P = .006$), in contrast to the much weaker relationship between these variables for the region as a whole. For the Peninsula assemblages, on the other hand, this relationship, while in the same direction, is far less significant ($r = -.67$, $P = .15$). The artiodactyl index is not correlated significantly with the faunal sample sizes from any of the three subregions (East Bay, $r_s = -.41$, $P = .36$; Coyote Hills, $r_s = .09$, $P = .85$; Peninsula $r_s = -.14$, $P = .75$).

The temporal trend in the artiodactyl index indicated for the Coyote Hills subregion is straightforward and requires no further elaboration here. However, due to concerns involving the dating and occupation spans of the East Bay assemblages and the complicated nature of the temporal trend indicated on the Peninsula, these two subregions require further analysis and discussion.

The East Bay Subregion

Although a significant decline in the artiodactyl index was indicated for the East

TABLE 3

Occupation Dates, Numbers of Identified Sea Otters and Artiodactyls, and Artiodactyl Index Values for the San Francisco Bay Assemblages

Site	Subregion	Occupation date (B.P.)			NISP[a]	Artiodactyl index	Reference	
		Initial	Terminal	Mean			Fauna	Date
CA-ALA-328 (upper)	Coyote Hills	450	150	300	144	0.43	Watts 1984	Watts 1984
CA-ALA-13 (upper)	Coyote Hills	1150	500	825	395	0.46	Whelen 1967	Bickel 1981
CA-ALA-329	Coyote Hills	1205	501	853	2020	0.56	Watts 1984	Watts 1984
CA-ALA-13 (lower)	Coyote Hills	1880	1150	1515	532	0.82	Whelen 1967	Bickel 1981
CA-ALA-12	Coyote Hills	2500	1500	2000	167	0.83	Whelen 1967	Bickel 1981
CA-ALA-328 (lower)	Coyote Hills	2344	1927	2136	139	0.81	Watts 1984	Watts 1984
CA-CCO-297	East Bay	724	162	443	63	0.30	Simons 1981	Breschini et al. 1990
CA-ALA-309	East Bay	2717	850	1784	8363	0.59	Cope 1985	Breschini et al. 1990
CA-CCO-295	East Bay	3575	200	1886	331	0.30	Simons 1981	Beardsley 1954; Breschini et al. 1990
CA-CCO-269	East Bay	2769	1032	1900	70	0.61	Simons 1993	Breschini et al. 1990
CA-ALA-307 (upper)	East Bay	2776	2300	2538	72	0.71	Busby 1975	Wallace and Lathrap 1975; Breschini et al. 1990
CA-ALA-307 (lower)	East Bay	4264	2776	3520	25	0.88	Busby 1975	Wallace and Lathrap 1975; Breschini et al. 1990
CA-SFR-114 (WT)	Peninsula	1315	977	1146	334	0.10	Broughton 1991	Hattori and Pastron 1991
CA-SFR-7	Peninsula	1650	650	1150	518	0.42	McCrossin 1982	Rudo 1982
CA-SFR-30	Peninsula	1450	1250	1350	139	0.32	Eschmeyer and Shonewald 1981	Baker 1978; Breschini et al. 1990
CA-SFR-112	Peninsula	1706	1364	1535	403	0.45	Lieberson 1988	Pastron and Walsh 1988a
CA-SFR-114 (ET)	Peninsula	1878	1296	1587	189	0.18	Broughton 1991	Hattori and Pastron 1991
CA-SFR-113	Peninsula	2063	1728	1896	101	0.75	Hall and Simons 1988	Pastron and Walsh 1988b

[a] Sea otters + artiodactyls.
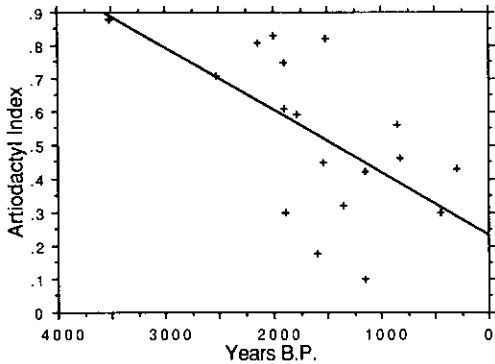
FIG. 3. The relationship between the artiodactyl index and time for the San Francisco Bay region (all sites included).

FIG. 5. The relationship between the artiodactyl index and time for the Coyote Hills assemblages.

Bay subregion, such a result was obtained by including several sites that were deposited over very long intervals of time. In addition, the dating of these shellmounds is presently very coarse-grained.

The East Bay assemblages include Emeryville (CA-ALA-309), Ellis Landing (CA-CCO-295), one of the Stege mounds (CA-CCO-297), CA-CCO-269, and the upper and lower components of the West Berkeley Shellmound (CA-ALA-307). The West Berkeley shellmound, the oldest assemblage in the study sample, was divided into "upper" (upper 6 feet) and "lower" (lower 6 feet) components by Wallace and Lathrap (1975), based on a visually evident stratigraphic break in the midden profile, as well as on differences in artifact types

between upper and lower excavation levels. As the West Berkeley mammal remains were reported by excavation level, I was able to split the West Berkeley faunal materials into these two components. Five calibrated radiocarbon dates for West Berkeley, ranging from 4264 to 2776 B.P., are available for the lower component. The age of deposition for the upper assemblage can be determined only on the basis of artifact types and cross dating. Based on the similarity of time-sensitive artifact types between the lower levels of Emeryville and the upper West Berkeley component, Wallace and Lathrap (1975) concluded that these occupations were more or less contemporaneous. This position is still accepted (Bennyhoff 1987). Two radiocarbon

FIG. 4. The relationship between the artiodactyl index and time for the East Bay assemblages.
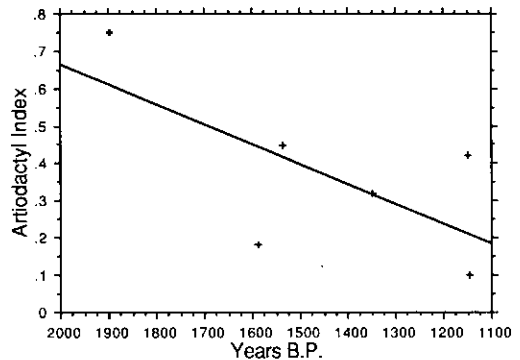
FIG. 6. The relationship between the artiodactyl index and time for the San Francisco Peninsula assemblages.

dates from composite charcoal are now available for the basal layers of the Emeryville shellmound; these fall at 2338 and 2717 B.P. (Bickel 1978; Bennyhoff 1987; Breschini et al. 1990). This is currently our best estimate for an approximate age of deposition for the upper component of West Berkeley.

Further complicating the apparent strong relationship between time and the artiodactyl index in the East Bay are the long occupation spans of Emeryville (2717 B.P. to Phase I, Late Horizon, ca. 850 B.P.) and Ellis Landing (3575 B.P. to Phase II, Late Horizon, ca. 200 B.P.) and the fact that the mammal faunas were reported for these shellmounds as units, rather than by the stratigraphic and arbitrary levels used in excavating the shellmounds. The dates for the initial occupations are determined by radiocarbon dates taken from the basal levels of the middens, whereas the terminal dates are derived from time diagnostic artifact types recovered from surficial levels of the sites (Beardsley 1954; Bennyhoff 1987).

In order to assess the effects of including these two sites in the analysis, I replotted the relationship between the artiodactyl index and time for the East Bay assemblages excluding Emeryville and Ellis Landing (Fig. 7). Without these sites, this relationship is again negative and linear, but the correlation is much stronger ($r = -.998$, $P = .002$). Including sites with long occupation spans simply appears to introduce noise by coarsening the temporal grain.

The San Francisco Peninsula Subregion

While the central concern of the East Bay subregion was the length of site occupation, in the Peninsula subregion of the Bay it is the complicated temporal pattern in the artiodactyl index that remains an issue. Though a general decline through time in the artiodactyl index is indicated for the
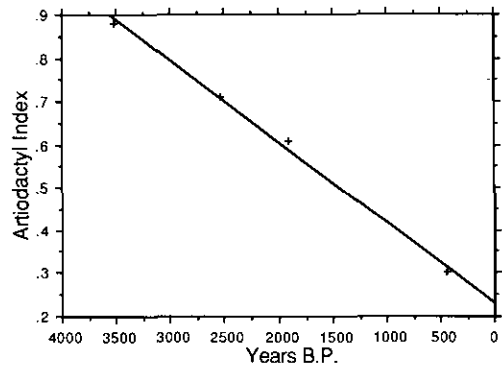
FIG. 7. The relationship between the artiodactyl index and time for the East Bay assemblages excluding Emeryville and Ellis Landing.

Peninsula assemblages in Fig. 6 ($r = -.67$, $P = .15$), smaller spatial scales may be required to sharpen the focus.

The mammalian fauna from the Yerba Buena Shellmound (CA-SFR-114) provides just such a scale. This recently excavated, well-dated shell midden is located beneath the streets of downtown San Francisco and provided a rich mammalian fauna. Separate artiodactyl index values were calculated for the West Trench and the East Trench at CA-SFR-114, as calibrated radiocarbon determinations indicated different occupation dates for these excavation units (West Trench = 1315 to 977 B.P.; East Trench = 1878 to 1296 B.P.; Hattori 1991). The artiodactyl index values from the two trenches were plotted separately in Fig. 6, with the earlier East Trench exhibiting an artiodactyl index of .18 and the later West Trench occupation indicating a value of .10 for this ratio. Is this trend toward a decline in mammalian predation efficiency replicated within the West and East Trench deposits individually?

The radiocarbon dates from the trenches confirm that antiquity increases with depth within these relatively undisturbed deposits (Hattori and Pastron 1991). Hence depth (level) is a reasonably accurate ordinal measure of time in this setting. When the artiodactyl index is plotted against

depth within the West and East Trenches, weak *positive* relationships are indicated (West Trench, $r = .60$, $P = .02$; East Trench, $r = .59$, $P = .08$). That is, the artiodactyl index appears to decrease with increasing depth (Figs. 8 and 9). This is the converse of the trend indicated by comparing the artiodactyl index values of the earlier East Trench and later West Trench, raising concerns about the validity of these apparent trends. However, inspection of the sample sizes of sea otters and artiodactyls represented per level within the trenches suggests that sample size may be related to the variability exhibited in the artiodactyl index.

Figures 10 and 11 display the relationship between the sample size of sea otters and artiodactyls per level for the West and East Trenches, arrayed against their respective artiodactyl index values. These figures indicate that in those levels with total artiodactyl and sea otter NISPs of less than 15, the artiodactyl index varies wildly. In those levels with specimen samples of 15 or greater, the artiodactyl index assumes greater stability. It would appear that levels with very few specimens, most of which occur in the surficial and basal levels of the deposits, may be obscuring any patterns in the artiodactyl index that may occur within the trenches.
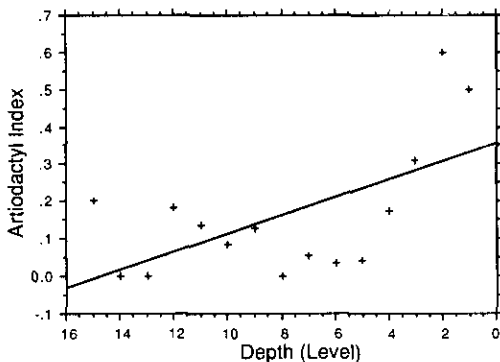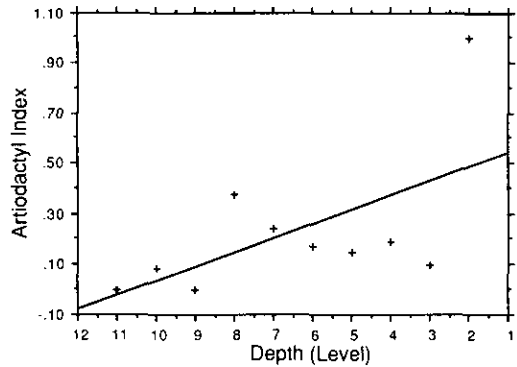
FIG. 9. The relationship between the artiodactyl index and depth (level) for the East Trench of the Yerba Buena Shellmound.

In the hopes of eliminating the noise created by levels with very small samples, I recalculated the artiodactyl index values for the West and East Trenches, excluding those levels represented by fewer than 15 specimens. The resulting relationships, displayed in Figs. 12 and 13, are both negative and significant at .10 (West Trench, $r = -.70$, $P = .08$ [does not include outlier]; East Trench, $r = -.82$, $P = .09$).

Either by comparing the artiodactyl index from the younger West Trench to the older East Trench, or by examining the index by depth within both trenches, a consistent pattern emerges. Sea otters steadily became a more important prey item, rela-

FIG. 8. The relationship between the artiodactyl index and depth (level) for the West Trench of the Yerba Buena Shellmound.
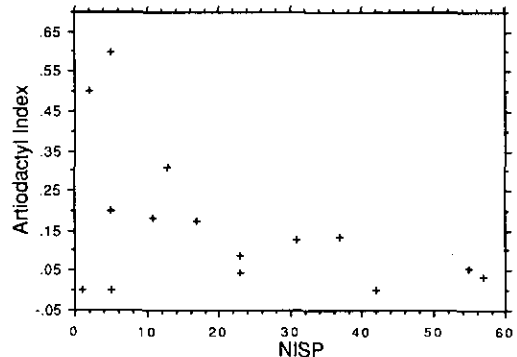

FIG. 10. The relationship between the number of identified sea otters and artiodactyls (NISP) per level and the artiodactyl index for the West Trench of the Yerba Buena Shellmound.
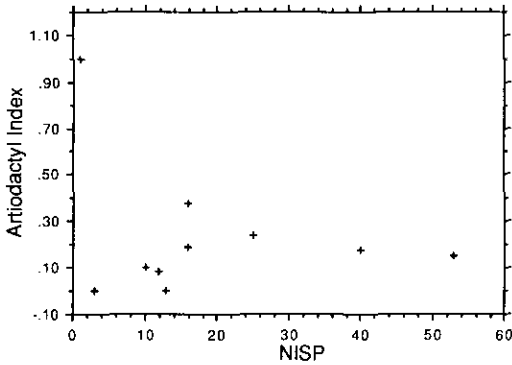
FIG. 11. The relationship between the number of identified sea otters and artiodactyls (NISP) per level and the artiodactyl index for the East Trench of the Yerba Buena Shellmound.
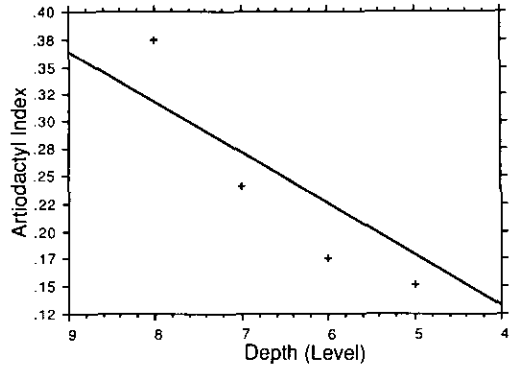

FIG. 13. The relationship between the artiodactyl index and depth (level) for the East Trench of the Yerba Buena Shellmound, excluding level samples less than 15 total NISP.

tive to artiodactyls, throughout the occupational history of the Yerba Buena Shellmound.

Summary

As predicted, the correlation between time and the artiodactyl index becomes increasingly stronger as the spatial scale of analysis is contracted. When analyzed on a regional scale, the relationship between time and the artiodactyl index was negative, but unimpressive. As subregions were extracted and analyzed individually, highly significant negative relationships
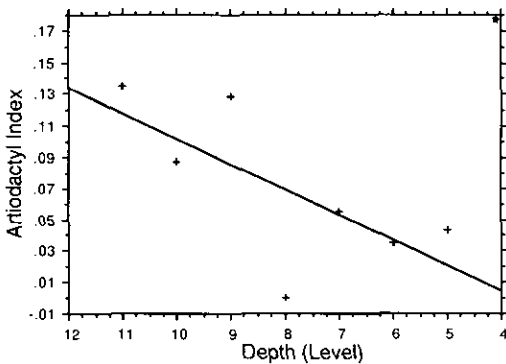

FIG. 12. The relationship between the artiodactyl index and depth (level) for the West Trench of the Yerba Buena Shellmound, excluding level samples less than 15 total NISP (outlier indicated by solid star).

between time and this index of mammalian foraging efficiency were indicated. Variation was also found to exist in the absolute size of the spatial scale sufficient to reveal significant declines in mammalian predation efficiency. On the San Francisco Peninsula, for example, a significant temporal trend in the artiodactyl index is only discernible within particular shellmounds. The rate or tempo of change in late Holocene mammalian foraging efficiency in the San Francisco Bay region is, thus, highly localized but it is unidirectional. That is, there is extensive spatial variability in the artiodactyl index between subregions at any point in time, but when change is discerned within subregions, this measure of mammalian predation efficiency invariably decreases with time. This pattern, fully consistent with intensification models, suggests that the precise cause or matrix of causes are linked to factors operating independently on localized spatial scales. I evaluate several such causes below.

LOCALIZED DECLINES IN EFFICIENCY: CHANGES IN ARTIODACTYL ENCOUNTER RATES

The fine-grained prey model specifies that whether or not a prey item is attacked

is independent of the encounter rate of that prey item, instead depending upon the encounter rate of higher-ranked prey (see Stephens and Krebs 1986:23). This prediction, often regarded as the most counterintuitive deduction from the prey model, suggests that fluctuations in the encounter rate of sea otters is irrelevant when considering the relative frequency that sea otters and artiodactyls were selected by prehistoric foragers. What is critical to prey selection is the encounter rate of the highest-ranked prey, in this case the artiodactyls.

A variety of factors could affect changes in the encounter rates of artiodactyls across the late Holocene occupation of the San Francisco Bay shoreline, including changes in their natural abundance via environmental change, seasonality of site occupation, resource depression, and/or competitive interactions with human foragers. I examine each of these variables below.

Environmental Change

The declining artiodactyl index may be reflecting reductions in the natural abundance of artiodactyls due to late Holocene changes in the distribution of terrestrial vegetation types. Figure 2 shows the vegetation of the San Francisco Bay area as it likely appeared when the Spanish first sailed the Golden Gate in 1775. Three general terrestrial vegetation types dominated the landscape: coastal prairie-scrub mosaic, mixed hardwood forest or oak woodland, and redwood–fir forest (Küchler 1977).

The prairie-scrub mosaic consists primarily of perennial grasses (e.g., *Danthonia* and *Festuca*) and coastal shrubs (e.g., coyote brush, *Baccaris pilularis*). This vegetation type forms a narrow (<10 km) margin around the perimeter of the bay.

The oak woodland represents the greatest areal coverage of any vegetation type in the region, extending from the prairie-scrub zone into higher elevations of the interior. The dominant trees of the oak woodland are coast live oak (*Quercus agrifolia*), madrone (*Arbutus menziesii*), and California bay (*Umbellularia californica*).

Patches of redwood–fir forest occur at higher elevations where coast redwood (*Sequoia sempervirens*) and Douglass fir (*Pseudotsuga menziesii*) are the key tree species. Douglass fir is also locally scattered within the oak woodland at higher elevations (Thomas 1961; McBride 1974; Küchler 1977).

The densities of black-tailed deer in coastal California are substantially higher in the oak woodland than in either the prairie-scrub or the redwood–fir forest (Longhurst et al. 1952:34–35; Dasmann and Dasmann 1963:12–15). Oak woodlands provide high concentrations of deer forage in both acorns and oak browse, as well as in other browse and grasses associated with the understory vegetation (Dixon 1934; Taber 1956; Menke and Fry 1980). By contrast, the availability of deer forage in coniferous forests and grasslands is much lower. Indeed, the encroachment of Douglass fir into oak woodlands is viewed as a serious issue in the management of habitats for black-tailed deer (Longhurst et al. 1952:35).

Though both tule elk and pronghorn were extirpated from central California and the Bay area soon after Euro-American settlement in the mid-19th century, historic records clearly indicate that both species inhabited open grassland or prairie-scrub habitats in this area (Burcham 1957: 108; McCullough 1969:15). Though tule elk did utilize oak woodlands, their occurrence in this habitat type depended upon the local presence of grasslands or prairie-scrub (McCullough 1969:15).

Late Holocene climatic fluctuations in the San Francisco Bay area could effect the local densities of these artiodactyl species by altering the distributions of the prairie-

scrub, oak woodland, and redwood–fir vegetation types. Specifically, given that the oak woodland supports the highest densities of deer, the expansion of oak woodland over prairie-scrub or redwood–fir forest should have a positive effect on deer densities. Conversely, climatic fluctuations favoring the invasion of prairie-scrub and/or redwood–fir forest into oak woodland should negatively affect deer densities. The densities of both tule elk and pronghorn should increase with the expansion of prairie-scrub into oak woodland.

Variation in late Holocene climatic parameters such as temperature and precipitation have clear implications for the distributional dynamics of these vegetation types. In particular, increasing effective precipitation and/or decreases in temperature might cause: (1) oak woodland to invade the prairie-scrub zone and (2) redwood–fir forest, especially Douglass fir, to encroach into oak woodland. However, prairie-scrub is fairly resilient to the invasion of oaks under a variety of environmental conditions over long time scales (see Williams et al. 1991). On the other hand, increasing effective precipitation and decreasing temperature should have dramatic positive effects on the encroachment of Douglass fir into oak woodland. The extremely rapid invasion of the fire-sensitive Douglass fir into oak woodland, chaparral, and grasslands, presently a critical forest management issue, has been linked to both fire suppression and increasing soil moisture (Barnhardt et al. 1987; Reed and Sugihara 1987).

To the extent that late Holocene environmental changes were of a scale sufficient to substantially alter the distribution of these vegetation types, the densities of artiodactyls in the San Francisco Bay area should, as a group, be negatively correlated with increasing precipitation and decreasing temperature. Conversely, decreases in precipitation and increases in temperature should be positively correlated with the natural abundance of artiodactyls. This is so because both prairie-scrub (tule elk and pronghorn habitat) and, particularly, oak woodland (deer habitat) should expand with increasing aridity. I emphasize that because deer numerically dominate Bay area artiodactyl assemblages throughout the late Holocene (Table 2), and because the prairie-scrub/oak woodland boundary is much more stable in the face of minor climatic fluctuations than is the redwood-fir/oak woodland boundary, increasing aridity should have the strongest impact on local artiodactyl densities by causing oak woodland invasion into redwood–fir forests and ultimately increasing the natural abundance of black-tailed deer. In other words, variation in artiodactyl encounters during the late Holocene should be driven primarily by variation in black-tailed deer encounters, since deer are by far the most abundant artiodactyl in the region during all time periods, and their habitat, oak woodland, is much more sensitive to minor climatic fluctuations than is the prairie-scrub zone.

These predicted effects of climate changes on the vegetational dynamics of the San Francisco Bay area could have been ameliorated, of course, by patterns of aboriginal burning (see Lewis 1973). By frequent burning, native Californians may have limited the expansion of Douglass fir into oak woodlands, offsetting any effects of local climatic changes on vegetational changes and, ultimately, artiodactyl densities.

The pollen record from Pearson's Pond provides evidence for several periods of increased and decreased precipitation and temperature during the late Holocene of the San Francisco Bay region (Adam 1975; Hattori 1991). Pearson's Pond, located at the southern end of the San Francisco Peninsula in the Santa Cruz Mountains, is a drainage basin that was formed within a

landslide feature at an elevation of about 365 m. Forty-nine pollen samples were collected from a 210-cm sediment core taken from the pond sediments. Three radiocarbon dates from the sediments were used to estimate the ages of the various samples (Adam 1975). Though the pollen record is complicated by the pond's sedimentary history, tectonic activity, and other factors, Adam (1975) suggests the core provides a sensitive record of local (i.e., San Francisco Bay area) climatic conditions between 3298 and 693 B.P. This time range encompasses all but two (CA-ALA-328, upper CA-CCO-297) of the archaeological assemblages examined here (see Table 3).

Following Adam's original analysis (1975) and Hattori's (1991) reassessment (1991), I use the relative abundances of four principal taxa in the Pearson's Pond pollen samples as indices of temperature and precipitation fluctuations. These taxa include TCT (Taxaceae–Cupressaceae–Taxodiaceae), oaks, cheno-ams (Chenopodiaceae and *Amaranthus*) and grasses (Gramineae).

I follow Adam (1975) in treating the TCT category as primarily representative of coast redwood, the expansion of which is linked to the prevalence of cool, summer, sea-fogs (Thomas 1961:11). TCT, then, is taken to represent an index of summer fog cover, or local summer temperature.

Oaks can adapt to a variety of stable climatic regimes but in this setting they are clearly indicators of increasing temperature and/or decreasing precipitation (see above). Hence, a positive index of temperature for a given pollen sample, *i*, may be calculated as

$$\Sigma \text{Oaks }_i / \Sigma(\text{Oaks} + \text{TCT }_i).$$

Although cheno-ams, as a group, are typically more drought tolerant than grasses, Adam (1975:728) suggests that the cheno-ams category at Pearson's Pond is mainly represented by *Amaranthus califor-* *nicus,* a species that colonizes ground recently exposed by receding pond waters (Thomas 1961:155). Adam (1975) argues that high proportions of cheno-ams reflect high pond levels and associated high effective precipitation.

The grasses, on the other hand, are viewed as a local indicator of decreased effective moisture. Grasses, which surround the margin of the pond, are flooded over in wet periods and expand as the pond retreats in dry periods (Hattori 1991:11). A positive index of effective precipitation may, thus, be calculated as

$$\Sigma \text{Cheno-ams }_i / \Sigma(\text{Cheno-ams} + \text{Grasses }_i).$$

I calculated both temperature and precipitation index values for each of the 49 pollen samples provided by Adam (1975: 726–727). Based on the dates assigned to these samples (Adam 1975:723) and the occupation spans of the San Francisco Bay archaeological sites (Table 3), I assigned each site a series of pollen samples with their associated temperature and precipitation index values (Table 4). From these samples, I calculated mean temperature and precipitation index values for each archaeological site (Table 4). (Sites CA-ALA-328 [upper] and CA-CCO-297 could not be included in this particular analysis because they postdate the Pearson's Pond pollen core).

Table 5 provides correlation coefficients for the paleoclimatic indices and the corresponding artiodactyl index values for the San Francisco Bay archaeological sites. None of these correlations are significant at $P = .05$ and only two, those for the Coyote Hill subregion, are significant at $P = .10$. I note, however, that with one exception, the results are directionally consistent. That is, for each geographic locality, temperature is positively, and precipitation negatively, correlated with the artiodactyl index. This is the relationship expected given the positive effects that aridity has on oak woodland expansion

TABLE 4
Temperature and Precipitation Index Values for San Francisco Bay Archaeological Sites

Site	Pollen sample nos.[a]	Temperature index	Precipitation index
CA-ALA-328 (upper)	—	—	—
CA-ALA-13 (upper)	12–19	0.045	0.593
CA-ALA-329	12–19	0.045	0.593
CA-ALA-13 (lower)	19–25	0.091	0.539
CA-ALA-12	23–31	0.130	0.541
CA-ALA-328 (lower)	25–29	0.110	0.552
CA-CCO-297	—	—	—
CA-ALA-309	14–38	0.145	0.618
CA-CCO-295	12–44	0.134	0.503
CA-CCO-269	17–37	0.154	0.633
CA-ALA-307 (upper)	29–38	0.241	0.708
CA-ALA-307 (lower)	38–44	0.140	0.084
CA-SFR-114 (WT)	16–21	0.062	0.637
CA-SFR-7	12–24	0.068	0.555
CA-SFR-30	20–22	0.080	0.617
CA-SFR-112	21–24	0.105	0.445
CA-SFR-114 (ET)	21–25	0.092	0.462
CA-SFR-113	24–27	0.075	0.495

[a] From Adam 1975.

and ultimately on the natural abundance of deer. The exception to this pattern is the relationship between precipitation and artiodactyl index values for the East Bay where absolutely no correlation exists.

As a whole, the relationships between the climatic and artiodactyl index values for the San Francisco Bay assemblages are suggestive but clearly unimpressive. Based on this analysis, I conclude that environmental change had a limited influence on the encounter rate of artiodactyls during the late Holocene of the San Francisco Bay.

Site Seasonality

Changing patterns in the seasonal use of Bayshore shellmounds could potentially influence the encounter rates of artiodactyls during the human occupation of the Bay margin environment. Artiodactyls would have been available year round in the Bay area. However, the fall rutting and winter congregations may have increased the local densities and, hence, encounter rates, of artiodactyls during these seasons. Additionally, artiodactyls carry their greatest levels of fat during the fall season (see

TABLE 5
Correlation Coefficients for Artiodactyl and Paleoclimatic Index Values for San Francisco Bay Assemblages

Comparison	Locality	r_s	P
Temperature index–Artiodactyl index	Coyote Hills	.870	.081
Temperature index–Artiodactyl index	East Bay	.400	.424
Temperature index–Artiodactyl index	Peninsula	.310	.482
Precipitation index–Artiodactyl index	Coyote Hills	−.870	.081
Precipitation index–Artiodactyl index	East Bay	.000	.999
Precipitation index–Artiodactyl index	Peninsula	−.540	.225

Speth and Spielmann 1983), increasing the energetic value per prey item during this season.

Sea otters mate and pup throughout the year and exhibit no predictable seasonal migrations or concentrations (Riedman and Estes 1990:49–56). In addition, sea otters do not exhibit pronounced seasonal variation in fat stores as do other marine mammals. (Sea otters do not possess a thick layer of subcutaneous fat as in other marine mammals, but, instead rely on a double-layer of extremely dense insulating fur for thermoregulation [Riedman and Estes 1990:20].) In sum, sea otters would have been abundant in San Francisco Bay year-round.

If changing seasonal use of Bayshore shellmounds can, in part, explain the variability in the artiodactyl index, earlier phases of the occupational sequences of particular subregions should have been more restricted to fall and winter occupations. More generally, the pattern in the artiodactyl index may be a function of a shift toward relative decreases in fall and winter occupations over time.

While a rigorous analysis of the seasonal occupation of San Francisco Bay shellmounds is not possible with existing data (fine scale seasonality studies using artiodactyl dentitions are presently underway and will be discussed later), I note that faunal material from the earliest occupations of both the San Francisco Peninsula and the East Bay suggest multiseasonal or year-round occupations and no decreases through time in fall occupations are apparent.

The relative abundances of several bird and fish taxa commonly exploited by prehistoric occupants of the San Francisco Bay vary dramatically across seasons. Bat rays (*Myliobatis californica*) and smoothhound sharks (Triakidae) move into shallow water estuaries during spring and summer to bear their young and move to deeper portions of estuaries and offshore during the

fall and winter (Ferguson and Cailliet 1990). Hence, both the natural abundance and the capturability of these fishes would have increased during the spring and summer in the San Francisco Bay. Large numbers of salmon (*Oncorhynchus* spp.)., primarily chinook salmon (*O. tshawytscha*), move through San Francisco Bay to upstream spawning localities from fall through spring, but reach peak abundances during the fall run in September and October (Hallock and Fry 1967; Healey 1991:319). With few exceptions, the myriad species of ducks and geese (Anatidae) that historically inhabited the San Francisco Bay area occurred there only during the winter months (Grinnell and Wythe 1927).

The fish and bird faunas from the earliest occupations on the East Bay (CA-ALA-307) and the San Francisco Peninsula (CA-SFR-113) are both represented by substantial numbers of smoothhound sharks, bat rays, salmon, and migratory waterfowl (Hall and Simons 1988; Gobalet 1988; Follett 1975; Brooks 1975). These data suggest multiseasonal occupations for these sites, rather than single-season fall occupations.

In addition, there are presently no indications that later occupations of the Bay shoreline were more concentrated during the spring and summer, relative to fall and winter. Late period occupations from throughout the Bay area are represented by substantial numbers of fall and winter indicator species, namely salmon and migratory waterfowl (Howard 1929; Simons 1981; Broughton 1991).

Artiodactyl Resource Depression

The foraging activities of predators commonly lead to the reduction in local densities and/or capturability of preferred prey within a given locality. This phenomena, termed *resource depression*, is due to direct harvesting of prey, to increased wariness of the prey species due to the continued presence of predators and/or to local

movements of prey species out of areas densely inhabited by predators (Hamilton and Watt 1970). Most vertebrate prey, which lack larger external pools from which lost individuals are replaced by immigration, are susceptible to depression (Charnov et al. 1976). Resource depression is particularly pronounced where relatively dense predator populations forage from a central base. The depression of prey around central places reduces the encounter rates of prey and requires foraging farther and farther from the central place. Where feeding territories are established and this is not possible, prey selection strategies are altered to include more abundant but less profitable prey (Hamilton and Watt 1970). In short, the depression of high-ranked prey around a central place can affect a decline through time in foraging efficiency throughout the occupational history of a particular locality (see Speth and Scott 1989; Vickers 1980 for modern examples).

The declining artiodactyl index over time around the San Francisco Bay may, in part, be symptomatic of localized reductions in the densities of artiodactyls through depression. Indeed, the unidirectional but temporally variable decline throughout the occupational sequences of Bay area subregions suggests just such localized causes of change.

If human harvest pressure caused absolute reductions in the densities of large, high-ranked prey items, the exploited populations represented archaeologically should exhibit indications of harvest pressure. Prey depression through overharvesting among vertebrates can be reflected in the demographic structure and size of individuals in a population.

An increase in harvest pressure on vertebrate populations typically causes reductions in the mean and maximum ages of individuals. With increased harvest rates, individual animals are captured well prior to reaching their full growth potential, so that overall longevity is decreased. This, in turn, decreases intraspecific competition for resources and increases overall recruitment of young individuals into a population (Caughley 1966, 1977). Since age is also correlated with size among species that continue to grow throughout life, a feature typical of both sea otters and male artiodactyls (Gashelis 1984; Leopold et al. 1951; McCullough 1969:4), increasing harvest rates are indicated by decreases in mean size. Selective exploitation of larger, older individuals, can further add to reductions in age and size. Reductions in mean and maximum age and size as a result of increasing harvest rates have been documented empirically in numerous wildlife management settings (e.g., Hesselton and Hesselton 1982; Mohler and Toweill 1982; Ricker 1980) and have been indicated in several archaeological settings (Koike and Ohtaishi 1985, 1987; Lyman 1987). I am now conducting systematic analyses of the ontogenetic age structure of San Francisco Bay artiodactyl and sea otter faunas to examine just this issue.

If change in mammalian predation efficiency resulted from decreasing densities of artiodactyls due to human harvest pressure, then evidence of depression should be evident initially on artiodactyls and thereafter on species along a decreasing gradient of prey body size. Hence, indications of harvest stress should be evident in artiodactyl populations by the time that there are significant decreases in the artiodactyl index. Only after artiodactyls decrease in abundance and the relative importance of sea otter exploitation increases should skeletal indications of hunting pressure be evident on archaeological sea otter populations.

Changes in the Subsistence System

While representing the dominant com-

ponent of exploited mammalian biomass, sea otters and artiodactyls obviously represented only one facet of the subsistence system. Bayshore shellmounds also contain an abundance of molluscs, waterbirds, and fishes; most also contain plant processing equipment, especially mortars and pestles. Changes in the relative importance of plant, mollusc, fish, and bird exploitation, while potentially signaling additional indications of intensification, could conceivably have indirectly caused declines in the encounter rates of artiodactyls. Acorn intensification provides an interesting example.

Although very little is known regarding the Holocene temporal trends in plant exploitation around San Francisco Bay, the inception of acorn exploitation appears to have begun much earlier in the Bay area than in other regions of California, at least to judge from the presence of mortars and pestles in Bay area assemblages dating to 4000 B.P. (Basgall 1987:32). Whether the intensity of acorn utilization in the Bay area steadily increased during the late Holocene, as it apparently did in most other regions of California (Basgall 1987; Bouey 1987), is unknown. If such were the case, Bay area peoples may have increasingly competed with black-tailed deer for acorns.

As indicated above, acorns provide very important forage for deer, being especially critical in fall and winter (Taber 1956; Menke and Fry 1980). Since deer are largely unable to exploit acorns until they fall to the ground, whereas native Californian's typically harvested acorns on the tree (see review in Baumhoff 1963), human foragers had a decided advantage in accessing this resource. Hence, an intensification of acorn exploitation during the late Holocene of the Bay area may have decreased the carrying capacity of oak woodland habitats for deer and ultimately caused deer densities and encounters to decline (see Gage 1979).

COSTS OF PROCUREMENT

Insofar as technological change affects handling times (i.e., pursuit and processing costs), the costs and ultimately the rank of artiodactyls and/or sea otters may have changed through time (see Alvard and Kaplan 1991). Artiodactyls, it is presumed, were taken with pointed bifaces or "projective points" recovered in Bayshore shellmounds. While changes in projectile point styles and material of manufacture have been well studied (e.g., Beardsley 1954; Bickel 1981), evidence of functional change is less clear. The widespread reduction in the size of projectile points in California at around 1500 B.P. (Moratto 1984:282), which many suggest indicates the introduction and adoption of the "bow and arrow," is the primary functional change recognized. It is unlikely, however, that this change in technology is causally related to the change in mammal exploitation since declines in the artiodactyl index are evident prior to, as well as after, the time this change occurred (Figs. 3, 4, and 5).

Perhaps the declining artiodactyl index is the result of a steadily improving means of capturing otters. Sea otters may have been taken with spears, darts, bow and arrow, and/or clubs while hauled out on shore, or with nets while in the water. No elaborate sea mammal harpoon technologies have been recovered archaeologically. Ethnographic accounts of California coastal groups indicate netting and clubbing from watercraft was the primary means of acquiring sea otters (see Ogden 1932, 1941). Evidence for a netting technology is well represented even in the earliest (ca 4000 to 3000 B.P.) Bay shellmounds, but only in the form of net weights or sinkers (Wallace and Lathrap 1975). Unfortunately, netting materials do not preserve in these contexts, and no archaeological evidence exists to evaluate changes in netting (or watercraft) technology. However,

the abundance of nestling cormorants (*Phalacrocorax* spp.), colonial island nesting birds, in the earliest assemblages indicates the presence of a watercraft technology at an early date in San Francisco Bay (However 1929; Brooks 1975).

If change in otter exploitation technology affected costs and ultimately change in the artiodactyl index, the critical technological change must have occurred at different times at different subregions in the Bay. This implies that functionally superior variation in sea otter predation technologies or tactics were not transmitted for hundreds of years among human populations residing only several miles apart. This seems unlikely, since a high frequency of interaction among Bayshore peoples is indicated by strong similarities in stylistic aspects of artifacts (shell bead types, bone whistles, etc.), during all time periods, involved here (Bennyhoff 1987; Elsasser 1978).

CONCLUSIONS

Highly significant declines in the abundance of artiodactyls, relative to sea otters, occurred throughout the occupational histories of particular San Francisco Bay localities. Insofar as the relative abundances of large- and small-sized mammals is a valid index of mammalian foraging efficiency, these data provide strong support for resource intensification models in this region of California. I emphasize that while absolute time is a poor predictor of the artiodactyl index around the Bay area as a whole, the temporal placement of a particular shellmound or component thereof within the occupational sequence of a particular locality allows the value of this ratio to be predicted with a good deal of precision.

This unidirectional, yet spatially variable, nature of change suggests the operation of localized causes, factors that were at work independently throughout the oc-

cupational histories of various shellmound localities. An assessment of the causes that would have altered the encounter rates of artiodactyls during the late Holocene suggests that environmental change played a limited role in the temporal decline in mammalian foraging efficiency. Factors such as changes in the seasonality of site occupation and technological innovations also do not appear to be causally related to this decline.

While there is presently no clear resolution concerning the precise matrix of causes that underlie the temporal trend in mammalian predation efficiency, I note that similar trends have been indicated from late Holocene archaeological faunas in many other regions of California. The temporal trend involving a decline in mammalian predation efficiency or a shift from an initial reliance on large prey items to an increasing emphasis on smaller ones may, indeed, be a general one.

Late Holocene archaeological faunas from the Sacramento Valley of north-central California document dramatic declines through time in the abundance of medium and large mammals relative to a small resident fishes, namely minnows (Cyprinidae), Sacramento suckers (*Catostomus occidentalis*), and Sacramento perch (*Archoplites interruptus*). In addition, when seasonal and spatial variation is held constant, significant decreases also exist in the abundances of large anadromous fishes relative to small resident fishes (Broughton 1994).

Along the Pit River, a tributary of the Sacramento River in northeastern California, changes through time in the relative abundance of large- and small-sized vertebrates have been documented from archaeological faunas dating from 5000 B.P. to contact. In a pattern identical to that found in the Sacramento Valley, the relative abundance of small resident freshwater fishes increase significantly through time compared to large- and medium-

sized mammals (Greenspan 1986; Broughton and Bayham 1993).

Chatters (1987) has shown that these indications of declines in the 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" occurred after considerable Euro-American contact and associated collapse of native human populations. Chatters (1987) argues that fluctuations in mussel use are related to human population growth and decline and the effects such changes have on the exploitation intensity of low-ranked prey, such as freshwater mussels.

Grayson (1991) has documented similarly dramatic changes through time in the relative abundance of large and small mammals from late Holocene high elevation archaeological sites in the White Mountains of eastern California. Specifically, the abundance of mountain sheep (*Ovis canadensis*) decrease significantly through time relative to yellow-bellied marmots (*Marmota flaviventris*). Grayson (1994) suggests "that the decreasing relative abundances of mountain sheep through time in the White Mountains assemblages reflect the local depletion of those mammals."

Finally, Hildebrant and Jones (1992) have indicated similar patterns among marine mammal faunas in coastal settings from both California and Oregon. They indicate that large-bodied pinnipeds such as Steller's sea lion (*Eumetopias jubatus*), California sea lion (*Zalophus californianus*), and northern fur seal (*Callorhinus ursinus*), decrease in abundance through time relative to the much smaller-sized harbor seal (*Phoca vitulina*) and sea otter. Human harvest pressure on the large species is suggested to be the critical variable driving this trend (Hildebrandt and Jones 1992).

While the species involved vary from context to context, disparate archaeofaunal data sets from environmentally distinct regions throughout California document an ever increasing reliance on smaller prey items during the late prehistoric. Given the ubiquitous evidence for human population growth throughout the late Holocene in California, this large-scale pattern of declining efficiency in mammal procurement may be linked, in part, to decreases in the encounter rates of large-bodied species through resource depression. While the herds of "fat deer" that darkened the California plains for miles and looked in the distance like great herds of cattle may have exceeded the belief and taxed the descriptive powers of the early explorers, my analysis suggests that they may have been far less a spectacle to native foragers of the late prehistoric.

This interregionally consistent pattern, strongly suggesting the depression of a variety of large-bodied mammal species in distinct environmental settings throughout prehistoric California, has far-reaching implications concerning the long-term human role in structuring both aquatic and terrestrial ecosystems. In the San Francisco Bay setting, the potential effects on the local estuarine ecosystem of artiodactyl declines and consequent increases in sea otter harvest pressure are particularly profound.

As "keystone predators" (*sensu* Paine and Vadas 1969), sea otters limit the size, density, and distribution of sea urchins (*Strongylocentrotus* spp.), which graze heavily on kelp. When the densities of sea otters are substantially reduced, urchin populations flourish and decimate local kelp forests (see many examples summa-

rized in Riedman and Estes 1990:29–30). Nearshore fisher which proliferate in kelp beds, decrease in abundance as do pinnipeds, whose densities are limited, in part, by the abundance of nearshore fishes. Simenstad et al. (1978) have identified precisely these patterns in archaeological assemblages from the Aleutian Islands, Alaska and have attributed them to intensive harvesting of sea otters by Aleut hunters.

A more thorough evaluation of the precise matrix of causes responsible for the declines in mammalian predation efficiency around San Francisco Bay, as well as the ultimate effects those declines had on both local ecosystems and on human adaptations to those ecosystems, requires currently unavailable or otherwise unsynthesized data. Most important are ontogenetic age and size data from the archaeological artiodactyl and sea otter populations coupled with finer scale chronological control. If deer, pronghorn, tule elk, and, later, sea otter populations were becoming locally depressed, this should be reflected in reductions in the mean age and size of individual animals represented in archaeological assemblages. Ripple effects resulting from increasing sea otter harvest pressure should also be evident in Bay area ichthyofaunas and other estuarine resources.

More generally, quantitative analyses involving other subsistence resources, such as acorns and other plant resources, could shed much light on this complex problem. In addition, if the taphonomic issues regarding the depositional origin of rodents and lagomorphs can be resolved, it would also be important to examine temporal and spatial patterns in the abundance of these taxa in relationship to larger terrestrial species. This information, as well as data bearing on other predictions from intensification models, can be gained through analyses of archaeological materials from existing collections.

REFERENCES CITED

Adam, D. P.
  1975   A late Holocene pollen record from Pearson's Pond, Weeks Creek Landslide, San Francisco Peninsula, California. *United States Geological Survey Journal of Research* 3:721–731.

Alvard, M. S.
  1993   A test of the ecologically noble savage hypothesis: interspecific prey choice by Neotropical hunters. *Human Ecology* 21:355–387.

Alvard, M. S., and H. Kaplan
  1991   Procurement technology and prey mortality among indigenous neotropical hunters. In *Human predators and prey mortality*, edited by M. C. Stiner, pp. 79–104. Westview, San Francisco.

Baker, S.
  1978   *Report on the Fort Mason archaeological test excavations.* Report to the U.S. Department of the Interior National Park Service, Western Region, San Francisco, CA.

Barnhardt, S. J., J. R. McBride, C. Cicero, P. de Silva, and P. Warner
  1987   Vegetation dynamics of the northern oak woodland. In *Proceedings of the symposium on multiple-use management of California's hardwood resources*, edited by T. R. Plumb and N. H. Pilsbury, pp. 53–58. USDA, Forest Service, General Technical Report PSW-100.

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 Cali-

fornia 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.
1982 *A diachronic analysis of prehistoric animal exploitation at Ventana Cave.* Unpublished Ph.D. dissertation, Department of Anthropology, Arizona State University, Tempe, AZ.

Beardsley, J. A.
1954 Temporal and areal relationships in central California archaeology. *Reports of the University of California Archaeological Survey* **24** and **25.**

Beaton, J. M.
1991 Extensification and intensification in central California prehistory. *Antiquity* **65**:947–951.

Belovsky, G. E.
1987 Hunter-gatherer foraging: A linear programming approach. *Journal of Anthropological Archaeology* **6**:29–76.

Bennyhoff, J. A.
1987 The Emeryville Site (ALA-309), viewed 93 years later. In A new look at some old sites, edited by F. Riddell, pp. 65–74. *Coyote Press Archives in California Prehistory* **6.**

Bettinger, R. L.
1991a *Hunter–gatherers: archaeological and evolutionary theory.* Plenum, New York.
1991b Aboriginal occupation at high altitude: Alpine villages in the White Mountains of eastern California. *American Anthropologist* **93**:656–679.

Bickel, P. McW.
1978 Changing sea levels along the California coast: Anthropological implications. *Journal of California Anthropology* **5**:6–20.
1981 San Francisco Bay archaeology: Sites Ala-328, Ala-13, and Ala-12. *Contributions of the University of California Archaeological Research Facility* **5**:6–20.

Boserup, E.
1965 *Conditions of agricultural growth: The economics of agrarian change under population pressure.* Aldine, Chicago.

Bosqui, E.
1904 *Memoirs, San Francisco.* Privately printed.

Bouey, P. D.
1987 The intensification of hunter-gatherer economies in the southern north coast ranges of California. *Research in Economic Anthropology* **9**:53–101.

Bourne, N.
1653 *Sir Francis Drake Revived.* London.

Breschini, G. S., T. Haversat, and J. Erlandson
1990 *California radiocarbon dates.* Coyote Press, Salinas, CA.

Brooks, R.
1975 Appendix D: Birds. In West Berkeley (CA-ALA-307): A culturally stratified shellmound on the east shore of San Francisco Bay, edited by W. J. Wallace and D. Lathrap, pp. 99–106. *Contributions of the University of California Archaeological Research Facility,* **29.**

Broughton, J. M.
1991 Vertebrate remains. In *The archaeology of the Yerba Buena Shellmound,* edited by E. Hattori and A. Pastron. Manuscript on file at Archeo-tec, Consulting Archaeologists, Oakland, CA.
1994 Lake Holocene resource intensification in the Sacramento Valley, California: The vertebrate evidence. *Journal of Archaeological Science* **21**:501–514.

Broughton, J. M., and F. E. Bayham
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, April 14–18, St. Louis, MO.

Broughton, J. M., and D. K. Grayson
1993 Diet breadth, adaptive change, and the White Mountains faunas. *Journal of Archaeological Science* **20**:331–336.

Burcham, L. T.
1957 *California rangeland.* California Department of Natural Resources, Sacramento.

Busby, C.
1975 Appendix C: A mammalian faunal analysis of CA-Ala-307. In West Berkeley˘ (CA-Ala-307): A culturally stratified shellmound on the east shore of San Francisco Bay, edited by W. J. Wallace and D. W. Lathrap, pp. 99–106. *Contributions of the University of California Archaeological Research Facility,* **29.**

Caughley, G.
1966 Mortality patterns in mammals. *Ecology* **47**:906–917.
1977 *Analysis of vertebrate populations.* Wiley, London.

Charnov, E. L., G. H. Orians, and K. Hyatt
1976 Ecological implications of resource depression. *American Naturalist* **110**:247–259.

Chatters, J.
1987 Shell of *Margaritifera margaritifera falcata* as a source of paleoenvironmental and cultural data. Archaeological Report 86-5. Pp. 1–31. Central Washington Archaeological Survey.

Central Washington University, Ellensburg, Washington.

Cohen, M. N.
1981 Pacific Coast foragers: affluent or over-crowded? In Affluent Foragers: Pacific Coasts East and West, edited by S. Koyama and D. H. Thomas. *Senri Ethnological Studies 9.*

Cope, C. R.
1985 *The mammalian fauna of the Emeryville Shellmound, CA-ALA-309.* Unpublished M.A. thesis, Special Major, Sonoma State University, Rohnert Park, CA.

Dasmann, W. P., and R. F. Dasmann
1963 Abundance and scarcity in California deer. *California Fish and Game* 49:4–15.

Dixon, J. S.
1934 A study of the life history and food habits of mule deer in California: Part II–Food habits. *California Fish and Game* 20:315–354.

Elsasser, A. B.
1978 Development of regional prehistoric cultures. In *Handbook of North American Indians: California*, edited by R. F. Heizer, Vol. 8, pp. 34–57. Smithsonian Institution, Washington, DC.

Eschmeyer, W. N., and J. Shonewald
1981 *Identification and analysis of Fort Mason osteological remains, archaeological sites SFR-29, 30, and 31, San Francisco, California.* A Report to the National Park Service.

Ferguson, A., and G. Cailliet
1990 *Sharks and rays of the Pacific Coast.* Monterey Bay Aquarium, Monterey, CA.

Follett, W. I.
1975 Appendix B: Fish remains from the West Berkeley Shellmound (Ca-Ala-307), Alameda County, California. In West Berkeley (Ca-Ala-307): A culturally stratified shellmound on the east shore of San Francisco Bay, edited by W. J. Wallace and D. W. Lathrap, pp. 71–98 *Contributions of the University of California Archaeological Research Facility, 29.*

Gage, T. B.
1979 The competitive interactions of man and deer in prehistoric California. *Human Ecology* 7:253–268.

Garshelis, D. L.
1984 Age estimation of living sea otters. *Journal of Wildlife Management* 48:456–463.

Gerow, B.
1968 *An analysis of the University Village complex: With a reappraisal of central California archaeology.* Board of Trustees, Leland Stanford Junior University, Stanford, CA.

Gifford, E. W.
1916 Composition of California shellmounds. *University of California Publications in American Archaeology and Ethnology* 12:1–29.

Gobalet, K. W.
1988 Appendix V: Piscatory fauna. In Archaeological excavations at CA-Sfr-113, the Market Street Shell Midden, edited by A. Pastron and M. Walsh, pp. 78–91. *Coyote Press Archives in California Prehistory 25.*

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.
1994 The Alta Toquima vertebrate fauna. In The archaeology of Monitor Valley: 4. Alta Toquima and the Mt. Jefferson complex, edited by D. H. Thomas, *American Museum of Natural History Anthropological Papers* (in press).

Greengo, R.
1951 Molluscan species in California shell middens. *University of California Archaeological Survey* 13.

Greenspan, R.
1986 Vertebrate faunal analysis. In *Archaeological Investigations at Lake Britton, California, Pit 3, 4, 5, Project, Archaeological Site Testing*, edited by M. Kelly, E. Nilsson, and J. Cleland. Wirth Environmental Services, San Diego, CA.

Griffiths, D.
1975 Prey availability and the food of predators. *Ecology* 56:1209–1214.

Grinnell, J., and M. W. Wythe
1927 Directory to the bird life of the San Francisco Bay region. *Cooper Ornithological Club Pacific Coast Avifauna* 27.

Hall, J. T., and D. D. Simons.
1988 Appendix IV: Ca-SFR-113 Fauna–Mammals and Birds. In Archaeological excavations at CA-SFR-113, the Market Street Shell Midden, San Francisco, California, edited by A. Pastron and M. Walsh, pp. 71–77. *Coyote Press Archives of California Prehistory 25.*

Hamilton, W. J., and K. E. F. Watt
1970 Refuging. *Annual Review of Ecology and Systematics* 1:263–286.

Hallock, R. J., and D. H. Fry
1967 Five species of salmon, *Oncorhynchus*, in the Sacramento River, California. *California Fish and Game* 53:5–22.

Hattori, E. M.
1991 Paleoenvironments. In *The archaeology of the Yerba Buena Shellmound*, edited by E. Hattori and A. Pastron. Manuscript on file at Ar-

cheo-tec, Consulting Archaeologists, Oakland, CA.

Hattori, E. M., and A. Pastron
1991   *The archaeology of the Yerba Buena Shellmound.* Manuscript on file at Archeo-tec, Consulting Archaeologists, Oakland, CA.

Healey, M. C.
1991   Life history of chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific salmon life histories,* edited by C. Groot and L. Marcolis, pp. 311–394. University of British Columbia Press, Vancouver, BC.

Hesselton, W. T., and R. M. Hesselton
1982   White-tailed deer (*Odocoileus virginianus*). In *Wild mammals of North America,* edited by J. A. Chapman and G. A. Feldmann, pp. 878–901. Johns Hopkins Univ. Press, Baltimore.

Hildebrandt, W. R., and T. L. Jones.
1992   Evolution of marine mammal hunting: A view from the California and Oregon coasts. *Journal of Anthropological Archaeology* 11:360–401.

Hill, K. H., K. Kaplan, and A. M. Hurtado
1987   Foraging decisions among the Ache hunter–gatherers: new data and implications for optimal foraging theory. *Ethology and Sociobiology* 8:1–36.

Howard, H.
1929   The avifauna of the Emeryville Shellmound. *University of California Publications in Zoology* 32:301–394.

Jochim, M. A.
1983   Optimization models in context. In *Archaeological Hammers and Theories,* edited by A. Keene and J. Moore, pp. 157–172. Academic Press, New York.

Koike, H., and N. Ohtaishi
1985   Prehistoric hunting pressure estimated by the age composition of excavated sika deer (*Cervus nippon*) using annual layer of tooth cement. *Journal of Archaeological Science* 12:443–456.
1987   Estimation of prehistoric hunting rates based on the age composition of sika deer (*Cervus nippon*). *Journal of Archaeological Science* 14:251–269.

Küchler, A. V.
1977   *Map of the natural vegetation of California.* University of Kansas, Lawrence, Kansas.

Leopold, A. S., R. McCain, and W. Longhurst
1951   The Jawbone deer herd. *California Division of Fish and Game, Game Bulletin* 4.

Lewis, H. T.
1973   Patterns of Indian burning in California: Ecology and ethnohistory. *Ballena Press Anthropological Papers* 1:1–101.

Longhurst, W. A., A. S. Leopold, and R. F. Dasmann
1952   A survey of California deer herds: their ranges and management problems. *California Division of Fish and Game, Game Bulletin* 6.

Lieberson, P.
1988   Appendix 4: Faunal analysis of CA-SFR-112. In Archaeological excavations at CA-SFR-112, The Stevenson Street Shellmound, San Francisco California, edited by A. Pastron and M. Walsh, pp. 117–129. *Coyote Press Archives of California Prehistory* 21.

Lyman, R. L.
1987   On the analysis of vertebrate mortality profiles: Sample size, mortality type, and hunting pressure. *American Antiquity* 52:125–142.

McCullough, D. R.
1969   The tule elk: Its history, behavior, and ecology. *University of California Publications in Zoology* 88.

McBride, J. R.
1974   Plant succession in the Berkeley Hills, California. *Madrono* 7:317–329.

McCrossin, M.
1982   Paleoecological inferences from a faunal analysis of CA-SFr-07. *Journal of California and Great Basin Anthropology* 4:138–141.

Menke, J. W., and M. E. Fry
1980   Trends in oak utilization: Fuelwood, mast production, animal use. In *Proceedings of the symposium on the ecology, management, and utilization of California oaks,* edited by T. R. Plumb, pp. 297–305. USDA, Forest Service, General Technical Report PSW-44.

Mittelbach, G. G.
1981   Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.

Mohler, L. L., and D. E. Toweill
1982   Regulated elk populations and hunter harvests. In *Elk of North America: Ecology and management,* edited by J. W. Thomas and D. E. Toweill, pp. 561–598. Stackpole Books, Harrisburg.

Moratto, M. J.
1984   *California archaeology.* Academic Press, San Diego, CA.

Nelson, N.
1909   Shellmounds of the San Francisco Bay region. *University of California Publications in American Archaeology and Ethnology* 7:309–356.

Newberry, J. S.
1857   Report upon the mammals. Reports of explorations and surveys to ascertain the most practical and economical route for a railroad

from the Mississippi River to the Pacific Ocean. *US War Department* **6**:35–72.

Ogden, A.
1932 The Californian's in Spain's Pacific otter trade, 1775–1795. *Pacific Historical Review* **1**:444–469.
1941 The California sea otter trade 1784–1848. *University of California Publications in History* **26**:1–251.

Paine, R. T., and R. L. Vadas
1969 The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* **14**:710–119.

Pastron, A. G., and M. R. Walsh
1988a Archaeological excavations at CA-Sfr-112, the Stevenson Street Shellmound, San Francisco, California. *Coyote Press Archives of California Prehistory* **21**.
1988b Archaeological excavations at CA-Sfr-113, the Market Street Shell Midden, San Francisco, California. *Coyote Press Archives in California Prehistory* **25**.

Raymond, A. W., and E. Sobel
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.

Reed, L. J., and N. G. Sugihara
1987 Northern oak woodlands: Ecosystem in jeopardy or is it already to late? In *Proceedings of the symposium on multiple-use management of California's hardwood resources*, edited by T. R. Plumb and N. H. Pilsbury, pp. 59–63. USDA, Forest Service, General Technical Report PSW-100.

Ricker, W. E.
1980 Causes of the decline in the age and size of Chinook salmon (*Oncorhynchus tshawytscha*). *Canada Technical Report of Fisheries and Aquatic Sciences* **944**.

Riechert, S. E.
1991 Prey abundance vs diet breadth in a spider test system. *Evolutionary Ecology* **5**:327–338.

Riedman, M. L., and J. A. Estes
1990 The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history. *United States Fish and Wildlife Service Biological Report* **90**:1–126.

Rudo, M. O.
1982 *The prehistory of San Francisco.* Unpublished M.A. thesis, Department of Anthropology, San Francisco State University, San Francisco.

Schenck, W. E.
1926 The Emeryville Shellmound final report. *University of California Publications in American Archaeology and Ethnology* **23**:150–282.

Schoener, T. W.
1979 Generality of the size-distance relation in models of optimal feeding. *American Naturalist* **114**:902–914.

Simenstad, C. A., J. A. Estes, and K. W. Kenyon
1978 Aleuts, sea otters, and alternate stable-state communities. *Science* **200**:403–411.

Simms, S. R.
1987 Behavioral ecology and hunter-gatherer foraging: An example from the Great Basin. *BAR International Series* **381**:1–157.

Simons, D. D.
1981 Appendix 1: Avian and mammalian remains from prehistoric sites in the Richmond Harbor area. In *Investigations of cultural resources within the Richmond Harbor redevelopment project 11-A*, edited by P. M. Banks and R. I. Orlins, pp. 12.1–12.73. California Archaeological Consulting. Submitted to the City of Richmond, CA [Copies available from Northwest Information Center, Department of Anthropology, Sonoma State University, Rohnert Park, CA]
1993 Prehistoric mammal exploitation in the San Francisco Bay Area. In *Essays on the Prehistory of Maritime California*, edited by T. L. Jones, pp. 73–103. Center for Archaeological Research at Davis Publications **10**.

Smith, E. A.
1991 *Inujjuamiut foraging strategies: Evolutionary ecology of an arctic hunting economy.* Aldine De Gruyter, New York, NY.

Speth, J. D., and S. L. Scott
1989 Horticulture and large-mammal hunting: the role of resource depletion and the constraints of time and labor. In *Farmers as hunters: The implications of sedentism*, edited by S. Kent, pp. 71–79. Cambridge Univ. Press, Cambridge.

Speth, J. D., and K. A. Spielmann
1983 Energy source, protein metabolism, and hunter–gatherer subsistence strategies. *Journal of Anthropological Archaeology* **2**:1–31.

Stephens, D. W., and J. R. Krebs.
1986 *Foraging theory.* Princeton University Press, Princeton.

Stuiver, M., and P. J. Reimer
1993 Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* **35**:215–230.

Sutherland, W. J.
1982 Do oystercatchers select the most profitable cockles? *Animal Behaviour* **30**:857–861.

Szuter, C. R., and F. E. Bayham
1989 Sedentism and prehistoric animal procurement among desert horticulturalists of the

North American Southwest. In *Farmers as Hunters: The Implications of Sedentism*, edited by S. Kent, pp. 80–95. Cambridge Univ. Press, Cambridge.

Taber, R. D.
1956 Deer nutrition and population dynamics in the North Coast Range of California. *Transactions, North American Wildlife Confederation* **21**:159–172.

Thomas, J. H.
1961 *Flora of the Santa Cruz Mountains of California: A manual of the vascular plants*. Stanford Univ. Press, Palo Alto, CA.

Uhle, M.
1907 The Emeryville Shellmound. *University of California Publications in American Archaeology and Ethnology 7*.

Vickers, W. T.
1980 An analysis of amazonian hunting yields as a function of settlement age. In *Working papers on South American Indians, volume 2*, edited by R. B. Hames, pp. 7–29. Bennington College, VT.

Vizcaino, S.
1891 Letter to King of Spain (1603). *Publications of the Historical Society Southern California* **2**:70–73.

Wallace, W. J., and D. W. Lathrap.
1975 West Berkeley (CA-Ala-307): A culturally stratified shellmound on the east shore of San Francisco Bay. *Contributions of the University of California Archaeological Research Facility*, **29**.

Watts, D. C.
1984 *Bones along the bayshore: A study of mammalian exploitation and cultural taphonomy of faunal assemblages from two bayshore shellmounds, CA-ALA-328 and CA-ALA-329*. Unpublished M.A. thesis, Department of Anthropology, California State University, Hayward, CA.

Whelan, J. P.
1967 A partial faunal analysis of 4-ALA-12 and 13, two San Francisco Bay shellmounds. *Department of Anthropology San Francisco State College Occasional Papers in Anthropology* **3**:1–24.

Wilkes, C.
1845 *Narrative of the United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842*. Lea and Blanchard, Philadelphia, PA.

Willey, G. R., and J. A. Sabloff
1980 *A history of American archaeology, second edition*. Freeman, San Francisco, CA.

Williams, K., S. D. Davis, B. L. Gartner, and S. Karlsson
1991 Factors limiting the establishment of a chaparral oak, *Quercus durata* Jeps, in grassland. In *Proceedings of the symposium on oak woodlands and hardwood rangeland management*, edited by R. B. Standiford, pp. 70–73. USDA, Forest Service, General Technical Report PSW-126.

Winterhalder, B.
1981 Foraging strategies in the boreal forest: An analysis of Cree hunting and gathering. In *Hunter–gatherer foraging strategies: Ethnographic and archaeological analyses*, edited by B. Winterhalder and E. A. Smith, pp. 66–98. Univ. of Chicago Press, Chicago, IL.