

# Prey spatial structure and behavior affect archaeological tests of optimal foraging models: examples from the Emeryville Shellmound vertebrate fauna

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## Abstract

Foraging theory is increasingly used as a framework to analyze prehistoric *resource depression*, or declines in prey capture rates that stem from the activities of foragers. Resource depression, with the resulting declines in foraging efficiency, appears to be an important variable underlying many behavioral transitions in human prehistory. And, while two of the primary lines of evidence used to document resource depression archaeologically are temporal declines in the relative abundances of 'high-return' species and the mean age of harvested prey, this phenomenon may also be reflected by *increases* in both high-ranked prey abundances and mean age. These divergent signals are linked to variation in the behavior and spatial distributions of different prey species and are illustrated with the Emeryville Shellmound faunal sequence. More detailed attention should be given to these variables in applications of foraging models to the archaeological record.

## Keywords

Age composition; Emeryville Shellmound; foraging theory; resource depression; relative abundance indices; zooarchaeology.

In the last decade, optimal foraging theory has increasingly been used as framework to analyze prehistoric *resource depression*, or declines in the capture rates of prey species that result from the activities of foragers (Charnov et al. 1976). These studies, based on analyses of archaeological vertebrate data, reflect a growing interest in understanding the details of how non-industrial peoples structured the environments in which they lived and many far-reaching implications for human prehistory have emerged from them (Alvard 1994; Steadman 1995; Redman 1999; Cannon 2000; Smith and Wishnie 2000; Grayson 2001; Kay and Simmons 2001).

In the late Holocene of California, for example, faunal evidence for resource depression and the associated declines in foraging efficiency has been causally linked to technological changes, increases in human violence and warfare, reduced stature, declining health and the emergence of social hierarchies (e.g. Hildebrandt and Jones 1992; Raab et al. 1995; Broughton and O'Connell 1999). Implications for modern wilderness conservation have also been derived from the evidence suggesting that late prehistoric faunal landscapes in this setting were fundamentally anthropogenic (Broughton 2001a; Grayson 2001).

Faunal resource depression and the resulting declines in foraging returns may be linked to many other important behavioral transitions in human prehistory. These range from late Pleistocene broad-spectrum transitions and the origins and adoption of agriculture (Hawkes and O'Connell 1992; Madsen and Simms 1998; Stiner et al. 2000) to changes in foraging behavior and material culture that occurred during hominid evolution (e.g. Marean and Assefa 1999).

So far, quantitative trends in relative taxonomic abundances and the age composition of exploited prey have been the primary measures of prehistoric resource depression. Based on implications of the fine-grained prey model of foraging theory (hereafter, simply the 'prey model'), quantitative indices summarizing the relative abundance of 'high-return' or large species in faunal samples have been used to measure hunting 'efficiency', or the overall caloric return rate derived from hunting. All other things being equal, such indices are commonly expected to *decline through time* in the context of increasing harvest rates and prey depression and in many cases they appear to do just that (e.g. Grayson 2001; Hildebrandt and Jones 1992; Broughton 1994a, 1994b, 1997, 1999; Janetski 1997; Butler 2000, 2001; Cannon 2000; Porcasi et al. 2000; Nagaoka 2000, 2001, this volume). But, in some settings, such trends have not been revealed where they are expected, leading some to suggest that the underlying foraging models may be flawed (McGuire and Hildebrandt 1994; Hildebrandt and McGuire 2000).

The ontogenetic age structure of harvested prey has also been used as a measure of human predation pressure to corroborate evidence for resource depression based on relative abundance indices. The standard prediction is that resource depression will drive a decline through time in the average age of a prey species and such trends have been empirically documented in many different prehistoric contexts as well (e.g. Anderson 1981; Klein and Cruz-Uribe 1984; Broughton 1997; Stiner et al. 2000; Butler 2001). But, again, increases in the average age of prey species, or no detectable changes at all, have appeared in several recent studies where all other data suggest the species were substantially depressed by intensive human harvesting (e.g. Broughton 1999; Butler 2001).

In this paper, I demonstrate with the Emeryville Shellmound faunal sequence how resource depression can produce different trends in large game relative abundances and prey age structure. This analysis suggests that variation in the spatial distribution and behavior of prey species are the important factors that influence the different trends and hence can be critical considerations in applying optimal foraging models to the archaeological record of ancient hunting behavior.

**Archaeological vertebrate measures of resource depression and foraging efficiency***Relative abundance indices*

In the late 1970s, Bayham (1979, 1982) pioneered a unique approach that used foraging theory to suggest how patterns in the relative abundances of different archaeological prey species could be used as measures of ancient hunting efficiency. The foundation for this approach came from two important papers in the ecological literature. The first was Wilson's (1976) application of the prey model to interpret patterns in insect prey derived from the stomach contents of birds. Wilson argued that the abundance of high- relative to low-ranked insect prey found in the stomach contents of birds could be used to measure the quality of their foraging environments. Since the prey types that yield the highest post-encounter return rates should always be pursued, their relative abundances measure both how frequently they were encountered and the amount of energy 'available in the environment'. Second, Griffiths (1975) contributed a detailed rationale for using prey body size as a proxy, positive measure of the 'post-encounter return rates' or ranks of prey species, an argument that is now supported by many empirical studies conducted among living foragers, both human and non-human (Broughton 1999; but see Madsen and Schmitt 1998; Lindstrom 1996 for interesting exceptions).

Adapting these arguments to the archaeological context, Bayham suggested that 'the relative abundance of small species in the diet should not only be a function of, but an indirect index to the availability of larger species or the higher ranking ones' (1979: 229). Ratios incorporating the numbers of archaeologically identified large and small prey species could thus be used as a measure of foraging efficiency: the more large, high-ranked prey in an assemblage, the higher the foraging efficiency.

Bayham discussed a variety of factors that could cause the abundances of high-ranking prey and, hence, foraging efficiency to decline and suggested that resource depression was likely one of the more ubiquitous among them. He also reasoned that the higher-ranked prey would exhibit depression prior to lower-ranking prey because the former should always be pursued upon encounter. Large prey should also be more sensitive to increased mortality because they typically have slower reproductive rates. Declines in large prey abundances could thus signal resource depression, if other causes, such as environmental change, could be ruled out (Bayham 1982: 63). This approach was applied to track variation in foraging efficiency through the Archaic and Hohokam periods in the American Southwest (Bayham 1979, 1982; Szuter and Bayham 1989).

It is important to note that this research strategy, as applied in either an ecological or archaeological context, does not actually test predictions of the prey model; it assumes them to be qualitatively true so as to 'use the behavior of the consumer' (Wilson 1976: 960) to measure inductively relative differences in encounter rates and foraging returns of foragers operating in different environments.

Recent archaeological applications, however, have adapted the Wilson-Bayham logic to a deductive research strategy by using regional archaeological data to leverage *predictions* about how foraging efficiency and relative abundance indices should have varied in the past. Quantitative analyses of archaeological vertebrate data are then conducted to decipher these trends. Insofar as the critical assumptions of the prey model apply, these

analyses thus constitute tests of its implications as they apply to prehistoric human foraging behavior.

One of those critical assumptions involves the spatial distribution of prey types and may be unrealistic in many archaeological contexts. This *fine-grained search assumption* stipulates that different prey types are searched for simultaneously and that the chance of encountering any prey type is independent of previous encounters with it or any other type. In other words, the model assumes prey types are encountered in a fine-grained manner. This assumption allows search time to be detached from individual prey types and assigned to the set of resources as a whole; it is also required for the relative abundances of high-ranked prey to be a valid measure of foraging efficiency. If, however, different prey types are spatially clumped across the environment surrounding a site, variation in the overall net caloric returns from those clumps or patches should dictate the extent to which they are used; patch use decisions, not just prey ranks, can thus determine prey choice (Smith 1991: 206).

An obvious strategy to deal with this constraint is to examine changes in differently ranked prey types within single 'patches' or 'hunt types'. These are defined as groups of prey taxa that were likely encountered in a fine-grained manner; that is, they are found in the same habitat types and were pursued and captured with similar technologies. Resource depression and declining foraging efficiency should still be signaled by declines in the relative abundances of high-ranked prey *within each patch*. In this approach, the fine-grained search assumption is analytically maintained.

The depression of prey within resource patches directly adjacent to a residential base has implications for changes in patch-use strategies in the wider environment surrounding a locality. Researchers investigating the effects of prehistoric resource depression on differential time allocation to resource patches have drawn on two separate models: Charnov's (1976) marginal value theorem and Orians and Pearson's (1979) central-place forager patch choice model (Broughton 1999; Cannon 2000; Nagaoka 2000). Both predict that more foraging time will be devoted to higher return patches but only the Orians and Pearson model explicitly considers the round-trip travel time between the resource patch and the central place. It is thus a more realistic model for the hunting behavior most commonly addressed in resource depression studies (Cannon 2000). Both models, however, can and have been used to derive the following prediction: as once high-return patches located closer to home become depleted, more use should be made of distant, less-depleted patches located farther away if such patches are available. Since the more distant patches were previously under-utilized, they should contain higher densities of high-ranked prey. Resource depression and overall reduced foraging efficiencies can thus be signaled by temporal *increases* in the abundances of high-ranked prey. Indeed, this phenomenon has been empirically documented in several ethnographic settings (see Hames 1989; Hames and Vickers 1982; Vickers 1980, 1988). Evaluating archaeologically whether or not increasing abundances of large prey are reflecting distant patch use will, however, require analyses of additional faunal data, as I discuss below.

Considered together, the prey and patch models suggest that the depression of high-ranked prey within local resource patches should lead to the selection of more abundant but lower-ranked prey species in those patches and/or increased foraging effort devoted to less-depleted patches located farther away from the central place. Both options entail

substantial declines in foraging efficiency. The transport models developed by Metcalfe and Barlow (Metcalfe and Barlow 1992; Barlow and Metcalfe 1996), for instance, indicate that even modest increases in round-trip travel times to resource patches for central-place foragers rapidly diminish the return rates of resource types exploited in those patches

### *Prey age composition*

Patterns in the age composition of archaeological prey species are one of the most frequently used (Broughton 1995, 1997, 1999; Stiner et al. 2000; Butler 2001) or suggested (Grayson and Cannon 1999; Cannon 2000; Wolverson 2001) means of corroborating evidence of resource depression derived from relative abundance indices. And, for several reasons, resource depression is commonly argued to cause declines in the mean and maximum ages of individuals in exploited populations. However, resource depression can also lead to *increases* in the mean age of harvested prey in certain contexts as well. Fortunately, these very different trends follow predictably from differences in the behavior and spatial characteristics of the particular prey species involved. This allows prey-specific predictions to be made regarding trends in age composition in analyses of resource depression.

A variety of factors can cause increasing harvest rates to produce declines in the mean and maximum ages of individuals in the harvested populations. First, for species that grow throughout their lives, older individuals can be substantially larger than younger ones and would likely represent higher-return prey items. In such cases, human predation should be biased towards older individuals, and increased harvest rates on species with indeterminate growth may thus be reflected by reductions in the proportion of adults in a population. Second, increasing mortality rates, even if they are unbiased with respect to age, can also produce this effect by reducing intra-specific competition and increasing recruitment rates (Caughley 1966, 1977). Third, increasing mortality rates may reduce the probability that individuals survive to enter older age classes so that average lifespans decrease and survivorship curves become steeper (Taber et al. 1982; Lyman 1987; Wolverson 2001). Finally, increased adult mortality rates may lead to the alteration of life-history schedules and the selection of phenotypes that mature early at the expense of later somatic growth (Charnov 1993).

While the reasons that suggest predation pressure should cause declines in mean age are sound in an abstract sense – making this the default prediction of resource depression – there are several factors that may overshadow their importance in certain zooarchaeological applications. In particular, these arguments do not account for the reality that archaeological faunas often result from foragers that encounter different-aged individuals within species in a coarse-grained manner. That is, some prey species occur in clumps or patches that are disproportionately comprised of juvenile or adult individuals. Differential use of such patches would thus have an important effect on the age composition of exploited prey.

The standard prediction also takes no accounting of the potential for prey ‘behavioral’ and ‘microhabitat’ depression. These phenomena refer collectively to behavioral responses prey species can make in response to increasing predation risk. Such responses may involve flocking behavior, greater alertness or shifting the time and duration of

particular activities (e.g. foraging, courtship) that place prey at high risks of predation. Prey species may also shift positions spatially as a response to an increased presence of predators such as, for example, by moving into denser vegetation cover, up steeper slopes or higher into the forest canopy (Charnov et al. 1976). Since individuals of different age and sex experience different trade-offs involving the use of habitat types that vary in predation risk and forage quality, there can be substantial variation in the degree to which individuals are sensitive to behavioral depression (e.g. Main and Coblentz 1996).

Pinnipeds and colonial waterbirds provide the best examples of taxa that are characterized both by patchy age-related spatial structure and the propensity to respond behaviorally to human hunting pressure. High-density, seasonally based, breeding colonies are typical components of the reproductive strategies of these animals. Such colonies are often quite sensitive to predation and even to the mere presence of predators. Sustained persecution will cause survivors to abandon colonies and form new ones in areas offering higher security – out of reach to human foragers (Boekelheide et al. 1990; Carney and Sydeman 1999; Gonzalez 1999). Regions that lose breeding colonies lose not only the highest return patches for the species but the major local source of sub-adult animals. In such cases, resource depression would cause relative increases in the encounter rates with adults and an increase in the mean age of exploited individuals.

A similar phenomenon may even occur for species that do not form spatially concentrated breeding colonies. For example, in many polygynous ungulates, the sexes are spatially segregated with female-young groups occupying habitats that provide greater security from predators (Bowyer 1984; Miquelle et al. 1992; Bowyer et al. 1996; Main and Coblentz 1996). Insofar as females with attendant young are more sensitive to predation risk or behavioral/microhabitat depression, areas subjected to elevated predator densities should be characterized by reductions in the relative frequencies of both females and sub-adult animals. For species with these characteristics, resource depression should again entail increases in the mean age of exploited animals.

### **Late Holocene resource depression in California: evidence from the Emeryville Shellmound fauna**

In the California setting, regional late Holocene archaeological data document both expanding human population densities and increasing use of lower-return plant resources, namely acorns (e.g. Bettinger and Baumhoff 1981: 499; Basgall 1987). These patterns have been read to suggest that overall foraging efficiencies were declining over this period of time. If so, evidence for resource depression and declining foraging efficiency, as described above, should be found among the vertebrate resources used by these foragers. The rich vertebrate record from the stratified Emeryville Shellmound provides an excellent test of this hypothesis since it reflects the activities of central-place human foragers using a single spot on the landscape for nearly 2000 years (Broughton 1999).

The Emeryville Shellmound was situated in a complex mosaic of terrestrial and aquatic habitat types on the east shore of San Francisco Bay before it was demolished in 1924 (Fig. 1 and Plate 1). The mound itself was huge, measuring 100 × 300m in area and extending to a depth of over 10m. Prior to its destruction, the mound was excavated on three

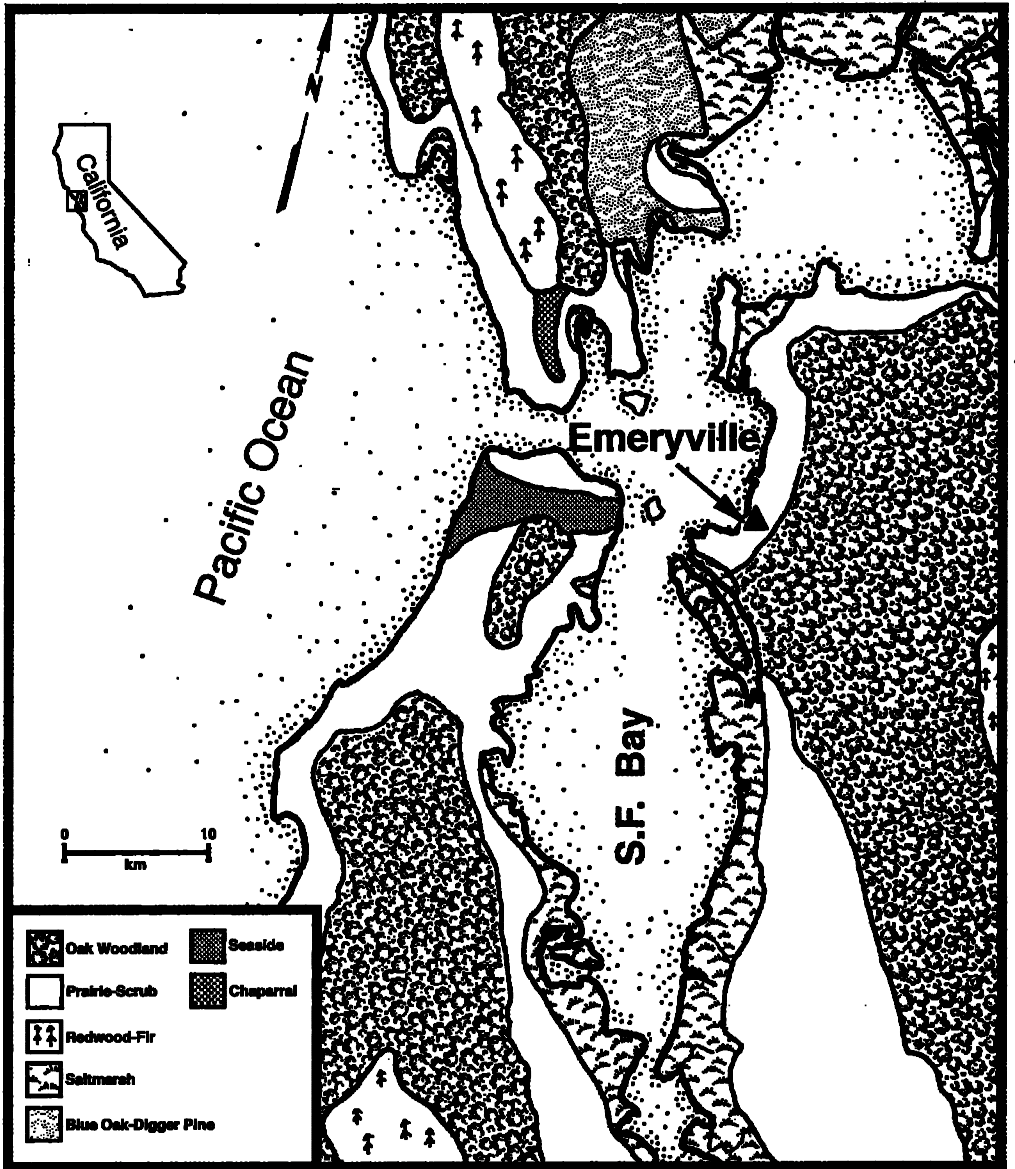


Figure 1 Map of the San Francisco Bay area indicating the location of the Emeryville Shellmound and historic period vegetation.

occasions, each time in a different location. Most of the sediments were excavated stratigraphically and sieved with coarse-mesh screens; ten primary strata were revealed during this work. Fourteen radiocarbon dates range from ~2600 to 700 <sup>14</sup>C year BP and exhibit no stratigraphic inconsistencies. On average, each stratum took about 200 years to accumulate.

During this time, the eastern San Francisco Bay region appears to have witnessed



Plate 1 Demolition of the Emeryville Shellmound by steam shovel, 1924. (Photo courtesy of the Phoebe A. Hearst Museum of Anthropology.)

significant human population growth, at least to judge from the increase through time in the number of dated site components (Broughton 1999). Thus the Emeryville region follows the more general California trend of expanding human population densities during the late Holocene.

The excavations at Emeryville provided seventeen faunal samples that could be placed into stratigraphic context. Collectively, about 24,000 fish, bird and mammal specimens, representing 102 different species, have been identified from these samples. The Emeryville deposits thus allow a fairly high-resolution, ordinal-scale analysis of change in human foraging behavior over much of the late Holocene. (For a full reporting of the mammal and fish data summarized below see Broughton 1995, 1999; for the birds see Broughton 2001b).

#### *Relative abundance indices from the Emeryville vertebrates*

##### Trends from local patches

As indicated above, the Emeryville site is surrounded by a number of distinct habitats so different that vertebrate prey species would have been spatially distributed in a patchy or coarse-grained manner. In order to satisfy the prey model's fine-grained search assumption, relative abundance indices should be constructed so as to include only taxa that were derived from the same patches or hunt types. Several of the more obvious resource patches surrounding the Emeryville locality are the terrestrial mammals patch, the estuarine fishes patch, and the waterfowl (*Anatidae*) patch. These different patches each



contain large and small-sized vertebrate prey types from which to derive relative abundance indices that can be analyzed separately for evidence of resource depression.

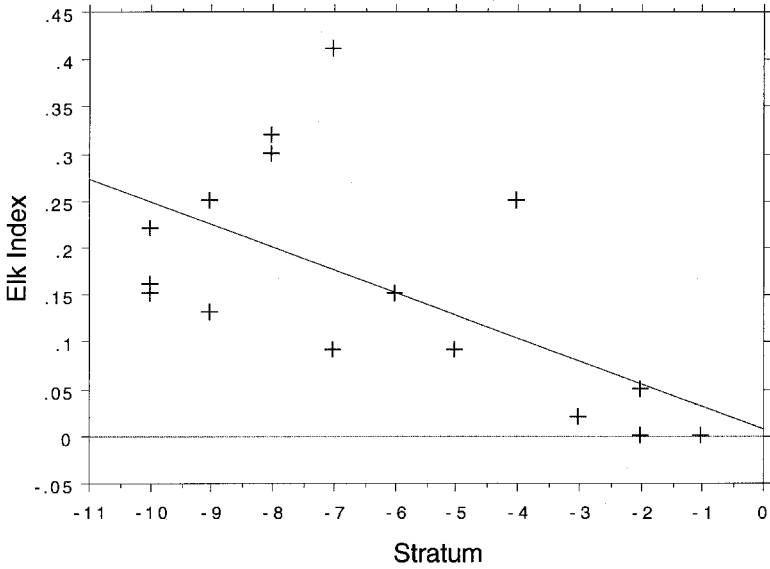


Figure 2 The distribution of the Elk Index ( $\Sigma$ NISP Elk / $\Sigma$ NISP Terrestrial Mammals]) by stratum at the Emeryville Shellmound ( $r_s = -0.658, p < 0.01$ ). Does not include the potentially intrusive rodents and lagomorphs. A least-squares regression line indicates the direction of the trend.

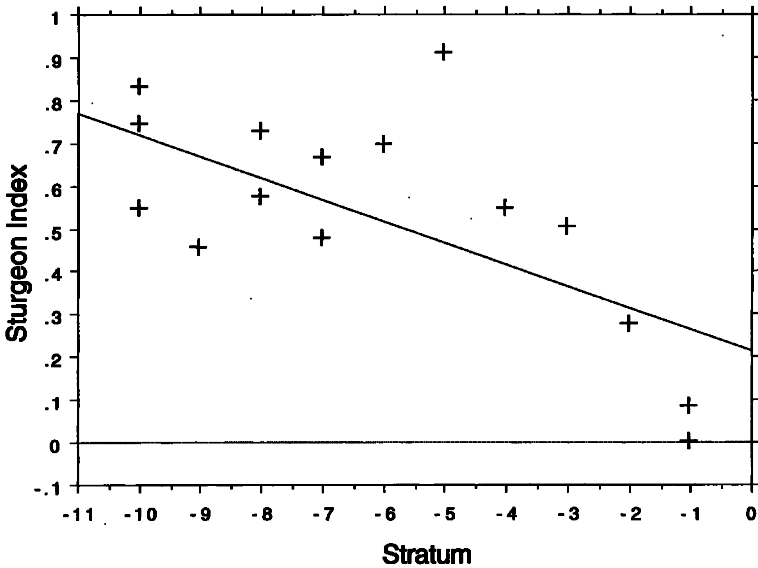


Figure 3 The distribution of the Sturgeon Index ( $\Sigma$ NISP Sturgeon / $\Sigma$ NISP Estuarine Fishes]) by stratum at the Emeryville Shellmound ( $r_s = -0.49, p = 0.05$ ). A least-squares regression line indicates the direction of the trend.

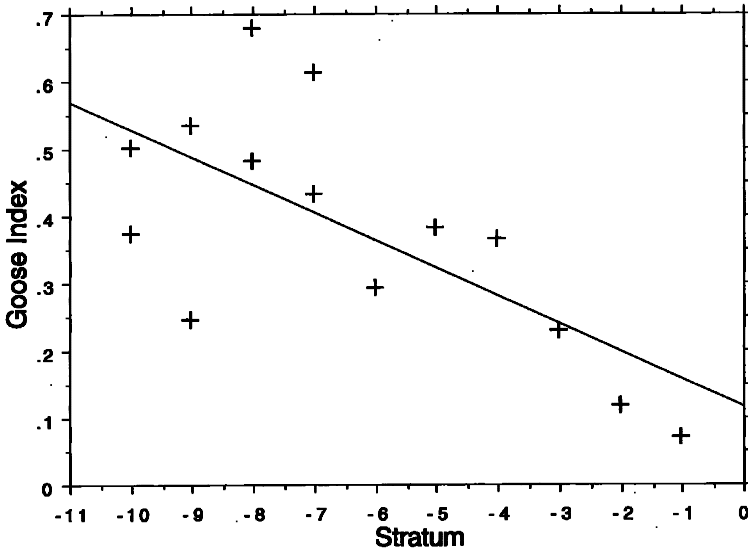


Figure 4 The distribution of the Goose Index ( $\Sigma$ NISP Medium + Large Geese/ $\Sigma$ NISP Anatids]) by stratum at the Emeryville Shellmound ( $r_s = -0.62$ ,  $p = 0.02$ ). A least-squares regression line indicates the direction of the trend.

The largest taxa, derived from the terrestrial mammals, estuarine fishes and waterfowl (Anatidae) patches, are tule elk (*Cervus elaphus*), white sturgeon (*Acipenser transmontanus*), and geese (*Anser*, *Branta*, *Chen*), respectively. If resource depression occurred across the occupational history of Emeryville, the abundances of these large-sized prey should decline through time relative to the smaller prey types that occurred in their respective patches. Figures 2–4 show that this is precisely what occurred at Emeryville. None of these changes appear to be caused by changes in the estuarine or terrestrial paleoenvironments (see Broughton 1999 for a detailed discussion of this issue). These patterns are also fully consistent with the data Gifford (1916) collected in his early twentieth-century study of the Emeryville molluscs. Specifically, the surface-dwelling molluscs of largest size (California oyster, *Ostrea lurida*, and bay mussel, *Mytilus edulis*) decline significantly ( $r_s = -.54$ ;  $p < .05$ ) across the Emeryville strata relative to smaller species (Broughton 1999: 71).

It is also important to emphasize that these resources occupied habitats that were, for the most part, confined to the region immediately surrounding the site. That is, sturgeon could have been found only within the San Francisco Bay estuary, geese would have been concentrated on the Bay itself or wetland areas on its flanks and tule elk were largely restricted to the marshlands and a narrow swath of grassland that surrounded the margin of the Bay (McCullough 1969; Broughton 1999). The molluscs, of course, are found only on the mudflats and the littoral zone of the estuary, just adjacent to the site. Travel times to and from these patches are thus not likely to have been important foraging costs. Collectively, these trends provide compelling evidence for resource depression in local patches over the period that Emeryville was occupied.

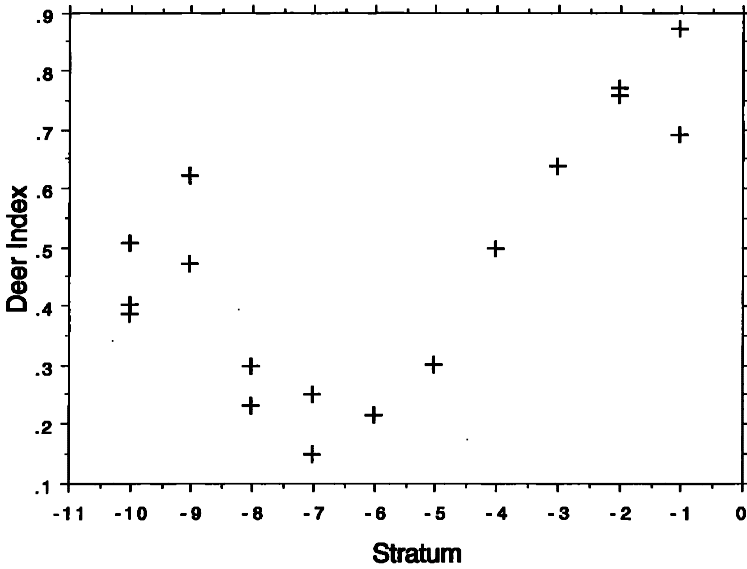


Figure 5 The distribution of the Deer Index ( $\Sigma$ NISP Deer /  $\Sigma$ NISP Mammals]) by stratum at the Emeryville Shellmound. Does not include the potentially intrusive rodents and lagomorphs. The Deer Index declines across the lower four strata (strata ten through seven:  $r_s = -0.721$ ,  $p = 0.04$ ) but increases over the upper six strata (strata six through one:  $r_s = 0.68$ ,  $p = 0.01$ ).

#### Increasing use of distant patches?

But these are not the only changes in vertebrate utilization that occurred across the Emeryville sequence. Against this background of steady declines in large prey from local patches, the relative abundance of black-tailed deer (*Odocoileus hemionus*), the second largest prey type from the terrestrial mammals patch, first declines over the four lower strata of the site but then increases across the upper six strata (Fig. 5). This resurgence in deer abundance is striking: no matter what set of mammalian taxa deer are arrayed against, deer overwhelmingly dominates the mammalian fauna of the upper-most strata of the mound. Given that all signals from local patches suggest foraging returns were declining across the entire occupational history of the mound, could the resurgence in deer use be reflecting the increasing use of less-depleted deer patches located in the oak woodlands that extend far to the east of the site? Such distant patches might have existed for a variety of reasons, including, for instance, buffer zones (Hickerson 1965; Mech 1977; Martin and Szuter 1999).

That the upper-strata deer were derived from distant patches has received support from patterns in skeletal part representation in relation to the economic utility of elements (Broughton 1999). Recent theoretical and ethnoarchaeological research (O'Connell et al. 1990; Metcalfe and Barlow 1992; Bird and Bliege Bird 2000) suggests that transport cost is one of the important variables that determine the degree to which low-utility body parts (those parts with minimal amounts of associated nutrition) are returned from kill sites to base camps, and transport distance is one of the most important components of transport

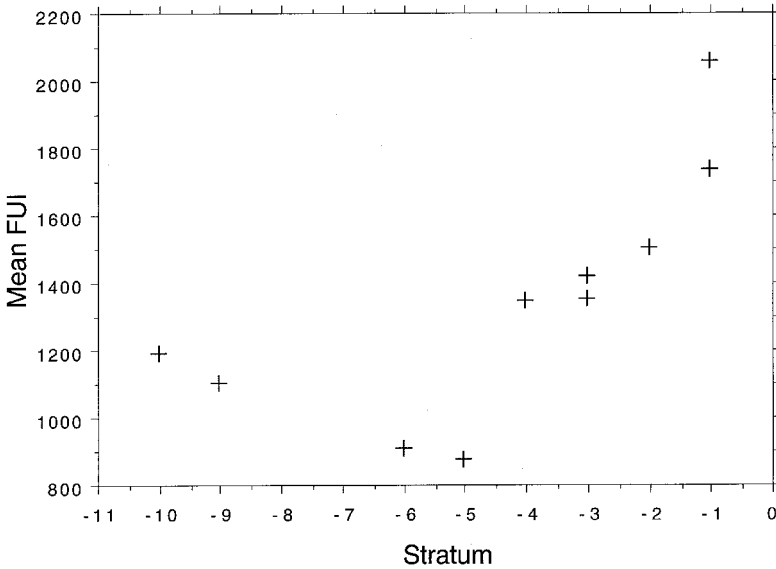


Figure 6 Mean utility of artiodactyl skeletal parts across the Emeryville strata. Samples showing a significant correlation between part density and part representation have been excluded (see Broughton 1999 for details). The Food Utility Index (FUI) is defined by Metcalfe and Jones (1988).

costs. Other things being equal, as the distance from kill site to home base increases, so should the degree of field processing to remove low-utility parts from the transported carcass. It follows that, if the resurgence in deer abundance documented across the upper strata at Emeryville is reflecting an ever-increasing use of distant, less-depleted deer patches, it should be associated with increasing relative frequencies of high-utility body parts, or an increase in the 'mean utility' of represented parts. Figure 6 shows that this is the pattern evident in the Emeryville fauna: mean utility increases significantly across the upper six strata ( $r_s = .96, p < .01$ ). Such a pattern was also revealed in an analysis of the anatomical part data based on the statistical method of maximum likelihood, although the trend could not be maintained when samples were pooled in order to produce acceptably narrow confidence intervals (Rogers and Broughton 2001).

### Conclusions

The increase in black-tailed deer use has yet to be revealed at any other site or sub-region in the San Francisco Bay area – settings that all show steady declines through time in the relative abundances of both elk and deer (Broughton 1994b) – and may have been conditioned by the availability of, and distance to, less-depleted deer patches. Emeryville sits just west of an extensive oak woodland zone – prime deer habitat – that reaches uninterrupted far to the east. This feature does not characterize other described sites in the region or other large taxa represented at Emeryville: elk, sturgeon and geese are, again, largely confined to the immediate area of the site locality. Once they are gone, there is no

other place to get them. Thus, the complex set of signals in relative abundance indices documented at Emeryville – all large prey from local patches steadily decline through time, but large prey with a more extensive regional distribution first decline and then increase – seems to be linked to the unique spatial structure of the available vertebrate species. Similar factors could possibly underlie the documented increases in large game in several other late Holocene contexts in California (McGuire and Hildebrandt 1994; Hildebrandt and McGuire 2000).

### *Trends in age composition for the Emeryville vertebrates*

As discussed in detail above, for prey species not susceptible to behavioral depression and not characterized by spatially discrete breeding colonies or rookeries, resource depression should lead to declines through time in both their relative abundances and the average age of exploited individuals. *Positive* correlations should thus be found between the relative abundance of a taxon and its mean age. Conversely, for species sensitive to predator disturbance and/or characterized by discrete breeding areas, resource depression should be reflected by *negative* correlations between relative abundance indices and mean age. That is, declining abundances of a species due to depression should correlate with increases in mean age. Several prey species well-represented in the Emeryville fauna exhibit these fundamental differences and clearly exemplify the distinctive demographic trends.

### Fish

The largest species derived from the estuarine fishes patch type is white sturgeon and, again, the relative abundance of this species declines steadily over the period that

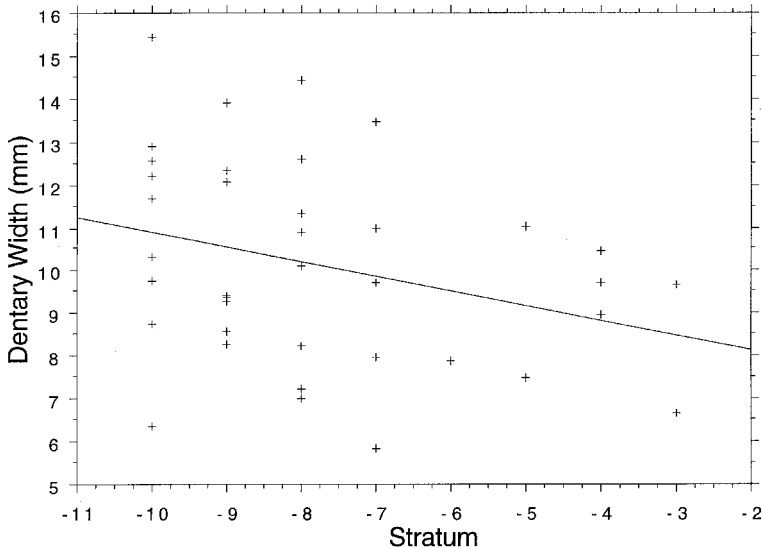


Figure 7 Dentary widths by stratum for the Emeryville Shellmound sturgeon (*Acipenser*).

Emeryville was occupied. This species does not form seasonal high-density breeding congregations and exhibits no detectable spatial structure by age/size within San Francisco Bay (David Kohlhurst pers. comm. 2001). It is also unlikely that sturgeon could perceive a human fishing threat in such a way that might lead them to abandon particular areas of the bay. White sturgeon then, probably like most fishes and molluscs, is a prey species for which resource depression should cause declines in mean age. As Figure 7 shows, both the mean and maximum size of measured sturgeon dentaries decline significantly with the relative abundance of this high-ranked fish across the occupational history of the site (maximum width by stratum:  $r_s = -0.833$ ,  $p < 0.03$ ; mean width by stratum:  $r_s = -0.76$ ,  $p < 0.05$ ).

#### Birds and mammals

Other well-represented vertebrate species in the Emeryville assemblage clearly form seasonal breeding congregations and are susceptible to behavioral/microhabitat depression. These include the cormorants, sea otters, tule elk and black-tailed deer. For these taxa, I assigned the identified specimens to three broad ontogenetic age classes – newborns (or chicks), sub-adults and adults – based primarily on bone size and development. More details on the criteria I used to make those assignments are described in Broughton (1999, 2001b).

Double-crested cormorants (*Phalacrocorax auritus*) and Brandt's cormorants (*P. penicillatus*) are the most abundant avian taxa in the Emeryville fauna, next to the winter visitant anatids. These birds form large rookeries during the spring and summer months in central California, typically on small islands within estuaries or off the coast. In no other contexts do chicks and sub-adult birds attain such high proportional abundances. Adult cormorants do not defend flightless young from large predators but cormorant colonies are well known for their sensitivity to disturbance: vandalized or disturbed colonies are routinely abandoned (Boekelheide et al. 1990: 165–6). Treasure Island, located 9km west of Emeryville, is the nearest location that may have supported cormorant rookeries in the past. Such colonies would have thus presented the highest-return patches for the cormorant resource.

The abundance of cormorants, relative to all other birds, increases steadily over the initial 800 years of site occupation (strata ten through seven; Figure 8), as elk, geese, sturgeon and deer decline. It is clear that cormorant rookeries were exploited here as the remains of baby chicks and subadults are extremely abundant in the collection (Broughton 2001b). Cormorant exploitation, however, then falls off dramatically to judge from the significant decline in the relative abundance of cormorant bones across the upper six strata of the mound. If this decline reflects resource depression and the loss of local breeding colonies it should be reflected by an increase in the proportion of adult birds. This is, in fact, the pattern revealed in the data: the relative abundances of cormorants is negatively correlated with the proportion of adults in the collection (Cormorant Index *versus* percentage adult cormorants:  $r_s = -0.72$ ,  $p = 0.01$ ; Figure 9). In other words, the average age of the harvested cormorants *increases* as the local population appears to decline through resource depression (Broughton 2001b).

Sea otters represent another taxon, well represented in the Emeryville fauna, that are characterized by 'rookery-like' breeding colonies and are very sensitive to human

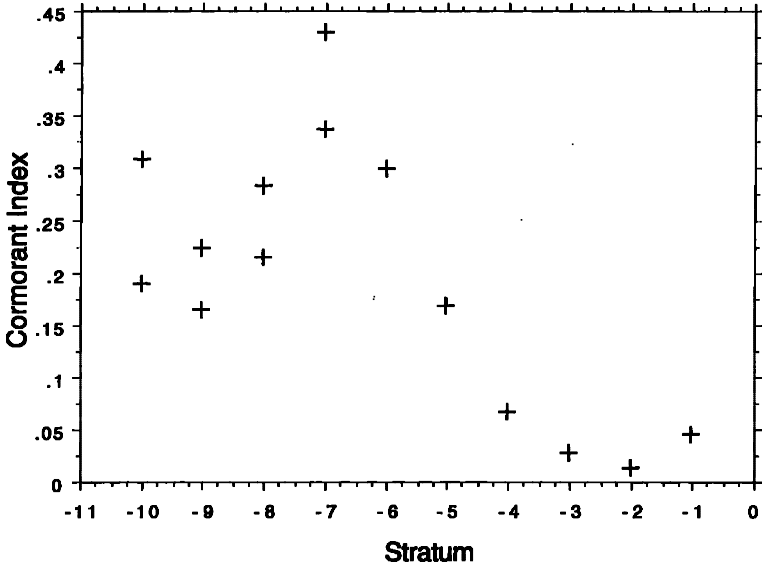


Figure 8 The distribution of the Cormorant Index ( $\Sigma$ NISP *Phalacrocorax* /  $\Sigma$ NISP Birds) by stratum at the Emeryville Shellmound. The Cormorant Index increases across the lower four strata (strata ten through seven:  $r_s = 0.595$ ,  $p = 0.11$ ) but declines over the upper six strata (strata six through one:  $r_s = -0.77$ ,  $p < 0.02$ ).

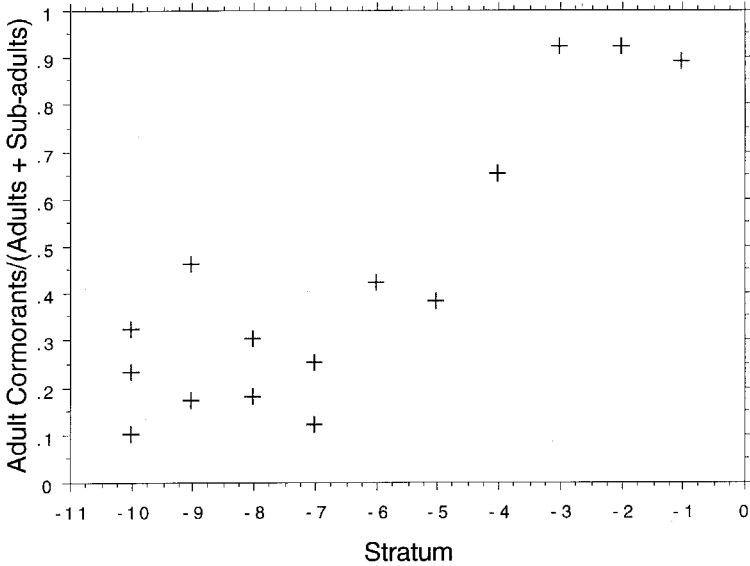


Figure 9 Changes in the proportional contribution of adult cormorants (Adult Cormorants / [Adults + Sub-adults]) across the Emeryville Shellmound strata. Sub-adults includes chicks. (Does not include stratum U1, that was represented by fewer than ten cormorant specimens for which age could be determined.)

persecution (Hall 1945; Riedman and Estes 1990). Sea-otter mother and pup pairs are known to congregate in extremely large nursery groups in sheltered bays (Riedman and Estes 1990: 68) and appear to have done so on land prior to their near-extinction at the hands of nineteenth-century fur trade hunters (Hall 1945; Broughton 1999). Depression of sea otters should thus be signaled by the local abandonment of these high-density nursery congregations and an increase in the relative encounter rate with adult animals.

As in the case of the cormorants, sea-otter use intensifies across the lower four Emeryville strata, but then declines dramatically over the upper strata. If this latter decline resulted from harvest pressure, it should thus be associated with the loss of breeding colonies, and an increase in the proportion of adult animals. Figures 10 and 11 show that pattern at Emeryville. As sea otters decrease in abundance, adults comprise a greater proportion of individuals in the samples; mean age thus *increases* significantly with declines in their abundances (Otter Index *versus* percentage adult otters:  $r_s = -0.68$ ,  $p = 0.01$ ).

As for many ungulates, spatial separation of the sexes outside the mating season is well documented for both of the cervids represented in the Emeryville fauna (Clutton-Brock et al. 1987; Bowyer et al. 1996; Main and Coblenz 1996). Although there are several competing hypotheses about why this occurs, evidence from black-tailed deer suggests it is driven at least in part by differential sensitivity to predation. In particular, females with young tend to occupy areas that offer greater protective cover and security for their offspring. Insofar as female-young groups are more sensitive to the presence of predators than males, resource depression may cause disproportionate local losses of such groups

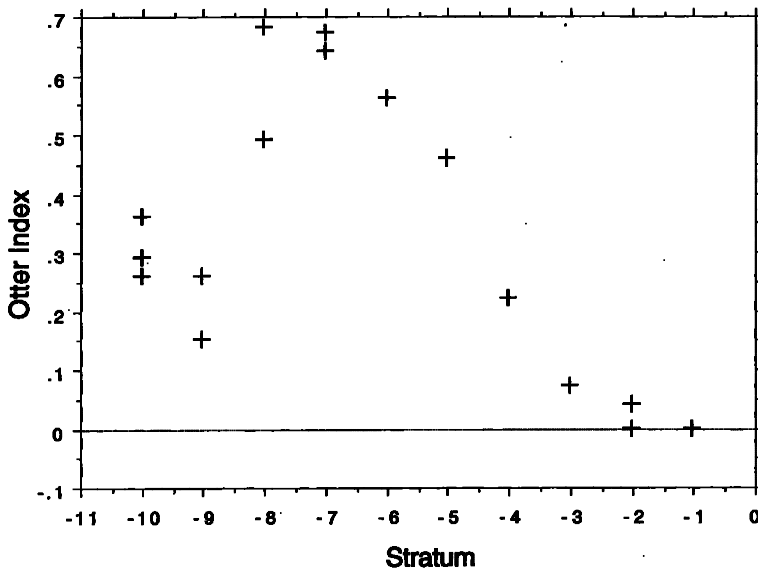


Figure 10 The distribution of the Otter Index ( $\Sigma \text{NISP } Enhydra lutris / [\Sigma \text{NISP Mammals}]$ ) by stratum at the Emeryville Shellmound. Does not include the potentially intrusive rodents and lagomorphs. The Otter Index increases across the lower four strata (strata ten through seven:  $r_s = 0.668$ ,  $p = 0.05$ ) but declines over the upper six strata (strata six through one:  $r_s = -0.73$ ,  $p < 0.01$ ).



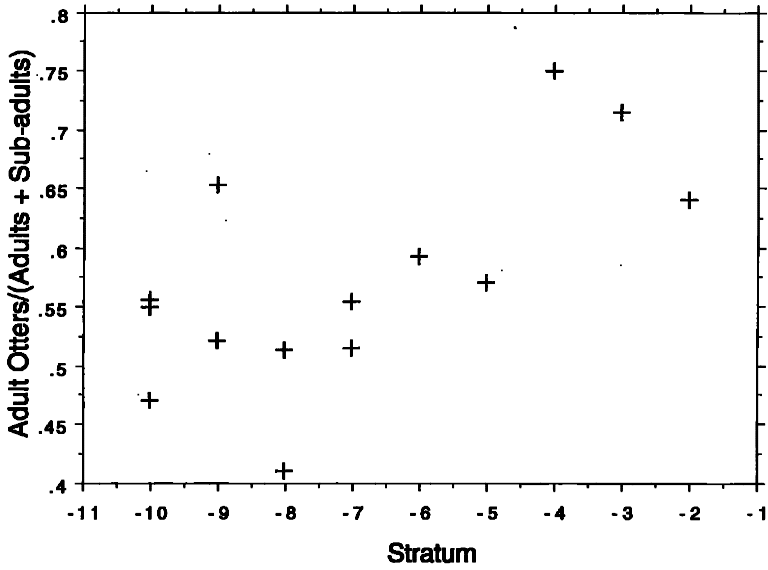


Figure 11 Changes in the proportional contribution of adult sea otters (Adult Sea Otters/ [Adults + Sub-adults]) across the Emeryville Shellmound strata. Sub-adults includes newborns. (Does not include stratum U1, that was represented by fewer than ten sea-otter specimens for which age could be determined.)

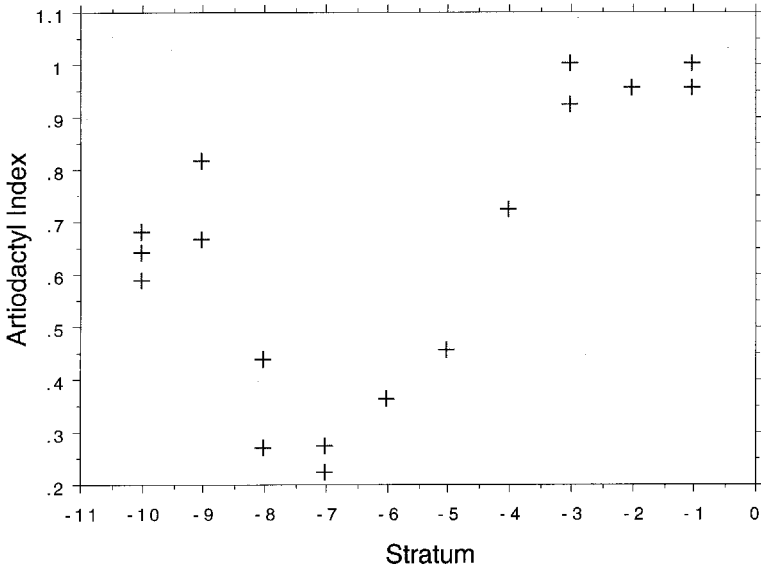


Figure 12 The distribution of the Artiodactyl Index ( $\Sigma$ NISP Artiodactyls /  $\Sigma$ NISP Artiodactyls + Sea otters]) by stratum at the Emeryville Shellmound.

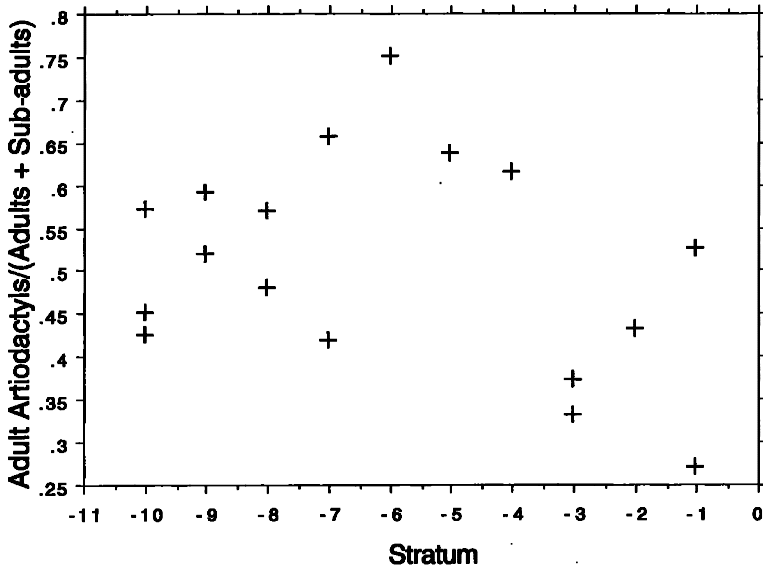


Figure 13 Changes in the proportional contribution of adult artiodactyls (Adult Artiodactyls/[Adults + Sub-adults]) across the Emeryville Shellmound strata. (The sub-adult category does not include foetal and newborn specimens; see Broughton 1999.)

and ultimately lead to an increase in the mean age of animals encountered in areas depressed from hunting.

As illustrated in Figures 2 and 5 above, both elk and deer decline significantly in abundance across strata ten through six or the initial 800 years of site occupation. And, while elk continue to decline in abundance, deer numbers steadily increase after that. Figure 12 shows the relative abundance of artiodactyls – the conjoined sample of elk and deer – compared to sea otter, the other most abundant mammal species in the Emeryville fauna. As a group, the relative abundance of artiodactyls follows the striking V-shaped pattern exhibited for deer.

As expected, changes in the proportions of adult artiodactyls mirror this trend precisely (Fig. 13). The initial decline in artiodactyl abundance is associated with an *increase* in adult animals and average age, while the upper strata increase in their abundance is associated with decreasing proportions of adults. Indeed, the abundance of artiodactyls is negatively correlated with the proportion of bones assigned as adults ( $r_s = -.50$ ;  $p < .05$ ). It appears that, as local artiodactyl populations first decline due to hunting pressure, fewer young are encountered. Later in the sequence, however, the proportion of young animal increases as more use is made of the less depleted herds located far away. This demographic signal is thus fully consistent with the proposed distant patch origin of the upper strata deer.

## Conclusions

Two of the most commonly used indicators of prehistoric resource depression are temporal declines in the relative abundances of high-ranked species and declines in the

mean age of harvested prey. However, resource depression may also be reflected by *increases* in both high-ranked prey abundances and mean age. The vertebrate sequence from Emeryville uniquely displays each of these different patterns that seem to reflect systematic differences in the behavior and spatial distributions of the represented prey species.

At Emeryville, the relative abundances of large-sized prey species more-or-less restricted to habitat types located near the site invariably exhibit significant declines through time. However, black-tailed deer, a large species whose preferred habitat extends far to the east of the mound, first declines in abundance but then steadily increases across the later period of site occupation. This resurgence in deer hunting seems to reflect continued resource depression from local patches and an ever-increasing use of distant, less-depleted patches located far away. That this resurgence in deer exploitation resulted from increasing distant patch use is supported by patterns in skeletal part abundances. An increase in large game use is thus one of the options rate-maximizing foragers can potentially take in response to a deteriorating local environment.

Temporal patterns in the age composition of the Emeryville vertebrates strongly support the evidence for prey depression based on relative abundance indices, but in ways that depart from standard expectations. White sturgeon show a significant decline in mean age/size through time in a pattern consistent with their demographically fine-grained spatial distribution and low susceptibility to behavioral depression. While this follows the commonly cited expectation, one that has been revealed in several other archaeological mollusc, fish, and turtle faunas, the well-represented resident bird and mammal taxa at Emeryville show just the opposite pattern.

Sea otters, cormorants, tule elk and black-tailed deer are taxa that exhibit pronounced age-related spatial structure and are responsive behaviorally to predation risk and human hunting activities. For these species, breeding colonies or microhabitats favored by females with young, may have been abandoned with increasing predation pressure. As the relative abundances of these prey species decrease, so does the proportion of specimens that represent sub-adult animals. For these species, resource depression thus appears to cause increases in the mean age of exploited animals.

Since increases or decreases in the mean age of harvested prey can follow from resource depression depending on the spatial structure and behavioral characteristics of the species involved, these features must be carefully evaluated *prior to* deriving expectations for prey response in any particular application. This is essential, of course, to maintain the deductive element of the enterprise. It will not be possible in most cases, however, to anticipate the contexts in which declining foraging returns will result in increasing distant patch use and increases in large game abundances. Detecting this phenomenon will require further tests involving other faunal data, such as, for example, anatomical part representation.

The documentation of resource depression and the associated declines in foraging efficiency and average fitness may entail predictions for variation in many other aspects of human behavior and morphology. Such features include, but are not limited to, technological changes associated with intensive processing of lower-ranked resources, increasing disease loads and declines in body size and stature, greater attention to resource defense with the development of more tightly circumscribed territories and

higher levels of interpersonal violence (Broughton and O'Connell 1999; Bright et al. this volume). These trends, in fact, characterize many regional sequences in world prehistory.

Perhaps of greater significance, we are starting to realize how knowledge of prehistoric human impacts on animal populations may have implications for the future conservation of species currently threatened by human influences (Broughton 2001a; Grayson 2001). For example, one of the fundamental goals of modern conservation biology has been to establish benchmarks for what the 'natural' or 'pristine' conditions of a region are so that management can be directed toward restoring and maintaining those conditions (Hunter 1996: 695). In the Americas, pristine is often equated with pre-European times, but archaeofaunal analyses of resource depression clearly show that this approach is aimed at a moving target (cf. Martin and Szuter 1999).

In California, for instance, many early historic records described a land of 'inexpressible fertility' (Margolin 1978) teeming with a wide variety of large, tame vertebrates. While these vast herds of elk and deer may have darkened the California landscape for miles during the early historic period, detailed records like Emeryville suggest that those taxa were anything but abundant during late prehistoric times. Prior to the disease-based near decimation of California Indians, beginning perhaps as early as the sixteenth century (Preston 1996), those peoples had reached extremely high densities and appear to have nearly eaten their way through many populations of large fishes, birds and mammals. The early European explorers, it now seems, had 'traversed an Edenic blip' on the California landscape (Grayson 2001: 8). The latest prehistoric and early historic benchmarks for California ecosystems, although separated in time by mere decades, would appear to be worlds apart. As I have discussed in detail elsewhere (Broughton 1997, 1999, 2001a), whether or not these very different benchmarks and the processes that created them are recognized has implications for how the restoration and maintenance of wilderness areas will be most effectively carried out.

These far-reaching implications suggest that there will be more riding on the accurate documentation of resource depression from archaeological faunas in the years to come. And it is clear from the Emeryville sequence that this task can be far more complex than many of us once thought. By giving more detailed attention to the spatial structure and behavioral characteristics of the prey resources involved, more robust applications of foraging theory to analyses of prehistoric resource depression can be made.

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