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Resource Intensification and Late Holocene Human Impacts on Pacific Coast Bird Populations: Evidence from the Emeryville Shellmound Avifauna

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INTRODUCTION

Anthropologists and conservation biologists have commonly assumed that the distributions and abundances of vertebrate resources recorded during the early historic period in North America reflected a "pristine" condition. This view follows from the perception that Native American population densities and technological capabilities were simply too low to deplete or extirpate vertebrate populations, or, alternatively, that native peoples were "children of nature" and the original conservationists (Alvard 1993, 1994; Kay 1994). In fact, these perceptions underlie modern wildlife management policies and practices. For example, because pre-Columbian environments are routinely viewed as "primordial wilderness" (Hewes 1973:150), restoring ecosystems to their "original condition" simply requires the elimination of European influences; this is the principle behind "hands-off" or "natural regulation" management (Kay 1994).

This traditional view has, however, been recently challenged on theoretical as well as empirical grounds in several contexts in western North America (e.g., Broughton 1994a, 1994b, 1995, 1997; Hildebrandt and Jones 1992; Jones and Hildebrandt 1995; Kay 1994). And since aboriginal human population densities were extremely high in prehistoric California (Cook 1976), it is not surprising that late Holocene California has been the focus of many of these recent challenges.

In the California setting, recent evidence for human impacts on prehistoric faunas has emerged from analyses of vertebrate remains from late Holocene archaeological sites. These analyses have documented steadily declining abundances of *large-sized* prey species from environmentally distinct regions throughout the state (see Broughton 1994a, 1994b, 1995, 1999; Grayson 1991; Hildebrandt and Jones 1992; Jones and Hildebrandt 1995). Most of these analyses have been conducted in the context of evaluating ecologically oriented models of subsistence change, and all have concluded that the documented declines in the archaeological abundances of large prey are a function of expanding prehistoric forager densities and game depletion.

The ecological models that underlie these analyses suggest that late prehistoric subsistence adaptations in California were characterized by a focus on low-return resources and that significant decreases in foraging efficiency occurred during the late Holocene (Basgall 1987; Beaton 1991; Bettinger 1991; Cohen 1981). As human population densities increased steadily during the late Holocene, some argue, the per capita and/or absolute abundances of such high-return resources as large-bodied terrestrial herbivores decreased. As a result, diets expanded to include higher frequencies of such smaller, lower-return resources as molluscs, smaller fishes, and acorns. These hypothetical 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 declines in return rates or foraging efficiency (Boserup 1965; Earle 1980). Insofar as declining per capita efficiencies in resource extraction implies decreases in average fitness among individuals in these populations, the widening of diet breadths can be seen to predict changes in other aspects of local human behavior and morphology. These range from higher levels of morbidity and mortality and smaller body size and stature, to changes in technology reflecting increasing investments in the processing of (as opposed to the search for) resources (see Hawkes and O'Connell 1992; Broughton and O'Connell 1999).

While recent analyses of archaeological vertebrate faunas from California have documented that late Holocene human populations of this region appear to have had substantial impacts on both terrestrial and marine fish and mammal populations, ultimately driving dramatic declines in foraging efficiency, evidence for harvest pressure on waterfowl and seabird populations in these settings has yet to be provided. Indeed, outside of oceanic island settings (see Steadman 1995 and references therein), there are as yet no well-described cases documenting that prehistoric foragers ever had substantial impacts on any avian population worldwide.

Through the integration of models drawn from evolutionary ecology and demography, I derive testable hypotheses that pertain to the nature of avian prey choice under conditions of expanding forager densities and declining foraging return rates. I propose that declining efficiencies in bird exploitation should be signaled by 1. decreasing abundances of large-sized prey types among sets of taxa occurring in the same local resource patches; and/or 2. increasing abundances of species that inhabit resource patches located far from a particular site locality. Additionally, harvest pressure on exploited avian populations should be indicated by declines in the mean age of individuals in a population. Analyses of the taxonomic composition and age structure of seabird and waterfowl materials from deeply stratified and well-dated late Holocene residential village sites, such as the Emeryville Shellmound of the San Francisco Bay, will thus allow fine-scale evaluations of the long-term dynamics of avian exploitation by populations of prehistoric human foragers. This research will have far-reaching implications not only for the management of resources and ecosystems currently threatened by human-caused habitat alteration, but for models involving the nature and causes of change in the behavior of prehistoric hunter-gatherers as well.

ARCHAEOLOGICAL VERTEBRATE MEASURES OF FORAGING EFFICIENCY AND HARVEST PRESSURE

Taxonomic Composition and Foraging Efficiency

Resource intensification models posited for California predict declines in foraging efficiency during the late Holocene. Efficiency refers to the overall net rate of return associated with a particular strategy of resource exploitation. Therefore, measuring foraging efficiency from archaeological faunas minimally requires consideration of the relative abundances of prey types with distinct differences in energetic returns. The prey and patch models of optimal foraging theory provide a framework for assessing the relative costs and benefits of exploiting different prey resources and patch types (see Stephens and Krebs 1986 and references therein) and, ultimately, the derivation of archaeological vertebrate measures of foraging efficiency.

The *fine-grained prey model*, or simply the prey model, was designed to predict prey selection by predators foraging within more or less homogeneous resource patches. The model assumes that foragers are designed by natural selection to maximize the long-term net rate of energy capture and that prey are encountered sequentially and taken one at a time. Initially, the various prey types potentially exploited by a predator are 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. 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). 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. Other things being equal (see below), a diet dominated by high-ranked prey indicates a higher energetic return per unit foraging time relative to a diet dominated by low-ranked prey.

However, for the relative abundances of differently ranked prey to be a measure of foraging efficiency, the stringent assumptions of the prey model must be met. The *fine-grained search* assumption is particularly important in this context. This assumption stipulates that all prey types must be sought simultaneously, and randomly encountered, within a more or less homogenous resource patch. This assumption is critical because it allows search, travel, and transport time to be detached from specific prey types and assigned to the set of resources as a whole. Thus, it is possible to predict that prey types will be added to or dropped from the optimal diet strictly as a function of their post-encounter return rates (Smith 1991:206; see also Cannon in press).

The fine-grained search assumption may seem to be particularly unrealistic for hunter-gatherers: Are all resources in the diet ever searched for simultaneously in the fine-grained manner required by the prey model? Clearly they are not. This issue, as Smith (1991:207) notes, has led to two mistakes. First, many researchers, and virtually all archaeologists, have completely ignored this assumption in testing implications of the prey model. Unfortunately, such an approach can easily lead to fallacious conclusions. Second, some researchers have found the limitations posed by this assumption insurmountable, suggesting the prey model cannot be applied when prey are distributed heterogeneously in a given environment (e.g., Belovsky 1987).

Smith (1991:207) reasons correctly that both approaches are inappropriate and provides a general strategy for applying the prey model among foragers utilizing a patchy environment:

the most useful approach is to define the foraging decision hierarchically, applying the fine-grained prey model only *within each patch* (where patches are defined so as to have fine-grained encounter patterns). And in cases in which foraging techniques and capabilities differ even within a patch, the model must be applied anew to each *hunt type*.

Applications of the prey model to archaeological settings would, thus, require that subsets of resources be assigned to discrete patches or *hunt types*. In practice, this will require separate analyses for prey types that occupied distinct habitat types and/or were likely pursued and captured with different methods and technologies. Addressing changes in the relative frequencies of prey resources that occurred in *different* hunt types or patches falls under the purview of patch-use models discussed below.

To the extent that an approximation of fine-grained search is met for prey resources handled singly with broadly similar methods, and taken within the same habitat type directly adjacent to a site locality, the relative abundances of high-and low-ranked prey types selected from such habitats can be a valid measure of foraging efficiency. Prey rank estimates are, thus, an important 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 foraging 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 (see Broughton 1994a, 1994b; 1995, 1997; Broughton and Grayson 1993). Figure 8.1 illustrates the hypothetical relationships between the critical variables that affect prey rank (following Bayham 1982; Griffiths 1975). Figure 8.1a depicts the energetic *value* of an organism as more or less directly proportional to its weight. In conjunction with the energy value of an item, consideration must also be given to absolute *costs* as a function of prey body size. Foraging theorists have proposed that pursuit and processing costs are at a minimum for certain intermediate body sizes, with increases incurred at the small and large end of the size spectrum (Figure 8.1b). In other words, there are upper and lower limits on the sizes of prey that a given predator species can efficiently capture and process for consumption: Extremely large and small prey require higher absolute pursuit and processing costs per item. The difference between the energy gain and cost curves represents the net energy gain per individual prey item (Figure 8.1c). The shape of this hypothetical curve is particularly important, for it specifies the relative overall energetic returns of a prey item as function of body size; consequently, it may serve as an indication of prey rank. As depicted in Figure 8.1c, for a large size range of prey species, the order of prey rank is the same as the order of prey size: large prey are high-ranked, while small prey are low-ranked.

While this simplified relationship between prey body size and prey profitability is strictly hypothetical, the basic relationship has strong support from empirical research on a diverse array of predatory species, including people (e.g., Alvard 1993; Bird 1996; Hill et al., 1987; Simms 1987; Smith 1991). At least among the size range of vertebrate species that occurred during the late Holocene in western North America, the larger the animal, the higher the post-encounter return rate (Broughton 1999).

While the extant data show that prey body mass and return rates are positively correlated, suggesting that prey size is probably the most important variable influencing profitability, some variation in return rates exists beyond that contained in body weight differences. That is, prey of the same body weight, whether from the same or different species, can potentially yield variable post-encounter return rates. This may be due to variation in either the handling costs or the energetic values of prey types. Variation in fat content, for example, has been shown to be especially critical in affecting differences in return rates for similarly sized prey items
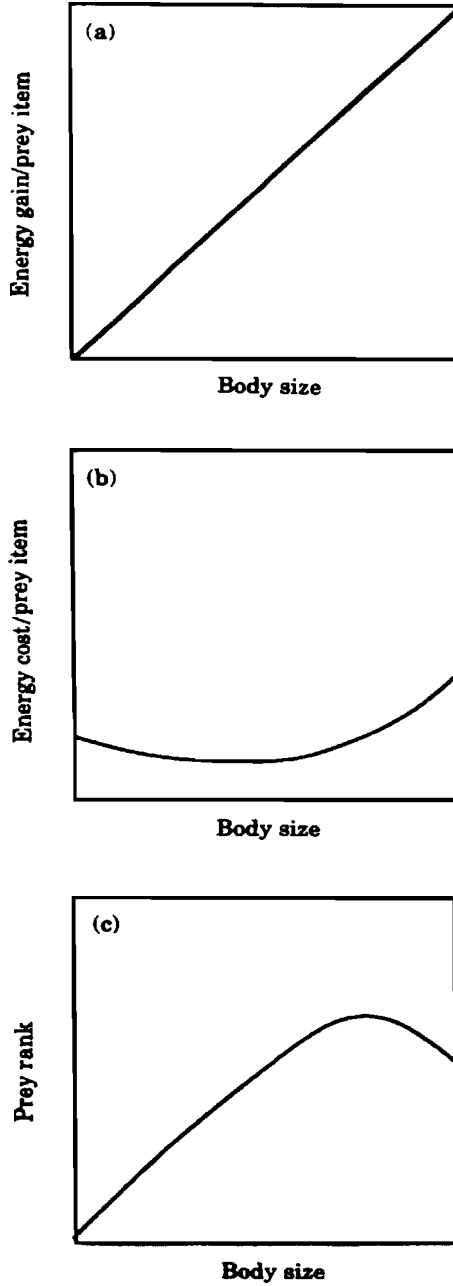
Figure 8.1. The hypothetical relationship between a) prey body size and energy gain; b) prey body size and energy cost; and c) prey body size and prey rank (see text for explanation; adapted from Griffiths 1975; Bayham 1982).

(see Hill et al. 1987; Kelly 1995; Smith 1991; see also Speth 1990; Speth and Spielmann 1983 for the nutritional importance of fat). Similarly, intra-annual variation in the flight or defense mechanisms of single prey species has been shown to affect substantial differences in their return rates across seasons. For instance, the handling times for Canada Geese *(Branta canadensis)* decline significantly during the summer molt when these birds temporarily become flightless (Smith 1991). As a result, the post-encounter returns for Canada Geese are substantially higher during the summer molt period than at other times of the year.

Handling costs for different prey types may also be differentially affected by changes in capture technologies. The introduction of netting or harpoon technologies, for example, might reduce handling times associated with the capture of specific aquatic and/or avian prey types (see Kelly 1995:80 for additional examples).

In sum, while body size is probably the best context-independent measure of prey rank available to archaeologists, this "rule of thumb" should be viewed with some caution. Indeed, in any particular setting, factors such as fat content and/or other peculiarities in the defense mechanisms of particular taxa can be examined and the body size-return rate generalization adjusted accordingly. Similarly, changes in archaeological tool assemblages can be monitored to evaluate changes in handling costs of specific prey resources.

Since the prey model predicts that the highest-ranked taxa should be attacked whenever they are encountered, large-sized prey species should be the most susceptible to population declines due to human foraging activities, other things being equal. A reduction in the densities and/or capturability of prey resources within patches is known as *resource depression* (Charnov et al. 1976; see also Cannon in press). This phenomenon 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. Resource depression is especially pronounced where dense, expanding predator populations forage from a central base (Charnov et al. 1976). 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.

Charnov's (1976) patch-use model, the *marginal value theorem*, addresses the decision of how long predators should forage in different resource patches within their range. The key prediction derived from this model is that a forager should depart a depleting patch when the return rate drops to the average return rate for all of the patches in the habitat as a whole. It follows that the depression of resource patches adjacent to a site locality should drive an increasing use of distant, less-depleted patches. Indeed, this phenomenon has been empirically documented in several ethnographic settings (Hames 1989; Hames and Vickers 1982; Vickers 1980, 1988).

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 in less-depleted patches located farther away from the central place. Both options entail substantial declines in foraging efficiency.[1]

Harvest Rates and Age Composition

Again, resource intensification models predict declines in foraging efficiency during the late Holocene of California due to absolute and/or per capita reductions in the encounter rates of high-ranked prey types. If increasing human harvest rates caused absolute reductions in the densities of particular prey types, the exploited populations represented archaeologically should exhibit demographic indications of harvest pressure. Specifically, the harvest rates of vertebrate populations are systematically reflected in the age composition of individuals in a population. An increase in the harvest rate of a population typically causes reductions in the mean and maximum ages of individuals. With increased harvest rates, individual animals are captured well before 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. Reductions in the mean and maximum ages of individuals in vertebrate populations as a result of increasing harvest rates have been documented empirically for a number of modern species including seabirds (e.g., Coulson et al. 1982; Duncan 1978). Hence, harvest pressure on prehistoric bird populations should be reflected in declines in the mean age of adult birds within archaeological samples.

The effects of increasing harvest rates on the population densities and age composition of different bird taxa should also vary according to certain life history parameters of the species involved. Specifically, *K-selected* species, those that produce smaller numbers of offspring, exhibit slower growth rates, a delayed onset of sexual maturity, and longer lifespans should be most susceptible to harvest pressure and the demographic effects of that pressure. By contrast, *r-selected* species, those that produce larger numbers of young, exhibit faster growth rates and attain reproductive maturity at a younger age, should be less susceptible to overharvesting and declines in mean age (see MacArthur and Wilson 1967:149).

Finally, the susceptibility of species to population declines due to harvest pressure should also vary according to their residence times within the predator's range. For example, prey species that migrate out of the predator's foraging range seasonally to breed would be less susceptible to depression than resident prey types (see Charnov et al. 1976:251).

Paleoclimatic Variables

The models outlined above focus on human-induced declines in foraging efficiency and the archaeological measures of those declines. Other factors can, of

course, cause changes in the natural abundances of vertebrate populations and ultimately declines in the efficiency of animal exploitation. In particular, abiotic or climatic factors can, through their effects on habitat structure, ultimately reduce the natural abundance and, hence, the encounter rates of prey taxa. Consequently, paleoenvironmental records are required to monitor potential climatically based effects on the encounter rates of specific avian taxa and foraging dynamics.

Summary

In sum, declining efficiencies in bird exploitation should be indicated by 1. decreasing abundances of large-sized species among a set of prey types that inhabit the same local resource patches; and/or 2. steadily increasing abundances of taxa that occur in resource patches located at distances far from the site locality. In addition, increasing harvest rates or harvest pressure on exploited avian populations should be signaled by declines in the mean age of individuals represented in archaeological samples, and human foraging activities should be most detrimental to resident species with *K-selected* life history characteristics. A background record of environmental change is critical to assess the potential effects of climatically driven environmental change on prey encounter rates and resource selection.

TESTING THE MODEL: THE EMERYVILLE SHELLMOUND

Since the focus of this research is on testing hypotheses concerning *diachronic* patterns in avian resource use during the late Holocene of northern California, a collection of archaeological avifaunal materials must be assembled from contexts that meet several specific criteria. First, since my primary predictions deal with temporal variation in avian foraging dynamics, and prey choice should be influenced by spatial variation in prey encounter rates that could confound temporal trends, it is advantageous to hold space constant. Hence, collections derived from a single site or set of sites at a single point on the landscape are ideal. The site must also represent substantial time depth and exhibit clear physical stratigraphy. In addition, the site must have been excavated by those natural strata and the vertebrate materials provenienced by those strata. Finally, the site must provide a rich collection of avifaunal remains. The Emeryville Shellmound (CA-ALA-309) of the San Francisco Bay meets these criteria and this research will focus on the enormous avifaunal collections from that site.

The Emeryville Shellmound is a deeply stratified, well-dated deposit that was once located on the east shore of San Francisco Bay, California, before it was destroyed in the early 20th century (Figure 8.2). The site was situated in a complex mosaic of terrestrial and aquatic habitat types, including open estuary, tidal mudflats, freshwater marsh, salt marsh, oak woodland, grassland, and redwood-fir forest.
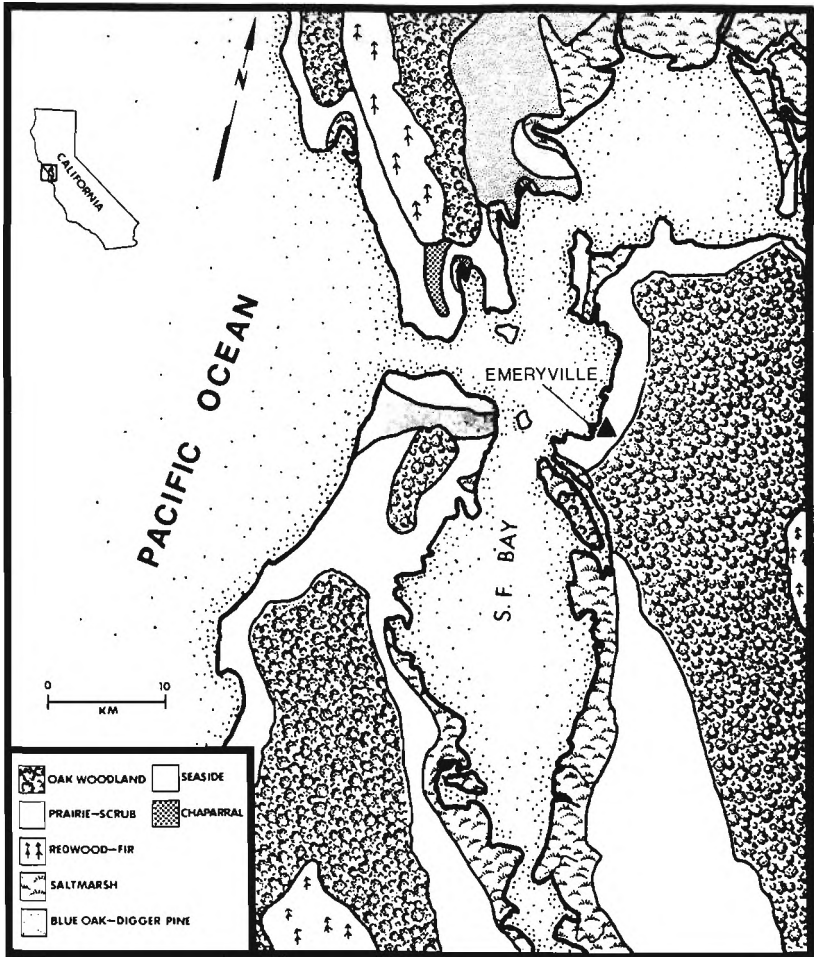
Figure 8.2. Map of the San Francisco Bay area indicating location of the Emeryville Shellmound and historic period vegetation (vegetation redrawn from Küchler 1977).

History of Excavations

Prior to its destruction in 1924, the Emeryville Shellmound was the site of three separate archaeological excavations. Max Uhle and John C. Merriam of the University of California, Berkeley, conducted the initial excavation of Emeryville in 1902. Uhle and Merriam excavated a lateral section on the west slope of the mound and a tunnel that extended into its center. In this work, they excavated over 200 cubic meters of midden and removed the sediments "stratum by stratum." In all, 10 distinct strata were encountered and all of the artifacts,

including a large sample of vertebrate remains, were collected and provenienced by these strata (Uhle 1907). The vertebrate materials as well as the other artifacts were collected with sieves of an unspecified mesh size (Schenck 1926:167; Uhle 1907:20). The nature of the vertebrate faunal collection is, however, consistent with moderate- to large-mesh (e.g., 1/4″ to 1/3″) screening (Broughton 1995).

In the spring of 1906, Nels C. Nelson led the second excavation at Emeryville; Nelson stratigraphically excavated a 6′ × 6′ unit in the east side of the mound. Nelson identified 11 natural strata in this work and collected and provenienced all of the artifacts, including vertebrate remains, by these natural strata (Broughton 1996; Nelson 1906).

The Emeryville Shellmound was leveled in 1924 to allow the construction of a paint factory. However, after the mound had been reduced to the level of the surrounding plain, W. E. Schenck excavated three 50′ × 6′ trenches in the base of the deposit near the center of the mound. These trenches, excavated in 1′ arbitrary levels to a depth of nearly 10′, produced a sizable faunal collection (Schenck 1926).

Chronology

Fourteen radiocarbon assays have been provided for bone and charcoal specimens recovered from various strata throughout the Emeryville deposit. Figure 8.3 shows a profile of the Uhle/Merriam excavation with the radiocarbon dates indicated in stratigraphic context. The dates range from 2620 ± 70 B.P. at the basal contact between midden and the alluvial clay upon which the mound sits, to 950 ± 50 B.P. for stratum 2. For the Nelson strata, the dates range from 2370 ± 70 B.P. for stratum 11, to 720 ± 60 B.P. for stratum 3. There are no inconsistencies in the stratigraphic ordering of the dates from either the Uhle/Merriam or Nelson excavations; within each excavation, the oldest dates are from the lowest strata, while the youngest dates are from the highest strata.

A single radiocarbon date was obtained near the top (the 1′–2′ level) of one of Schenck's trenches, while six dates were obtained for the base of the mound. Together, these dates serve to bracket the deposition of the Schenck trench sediments between 2600 and 1970 B.P. This time interval incorporates the period of the deposition for the basal four strata (stratum 10 through 7) from Uhle's excavation. Accordingly, I will aggregate the 1′-level samples from Schenck's three trenches into a total of four temporal-analytic units.

The ten Uhle strata, the three radiocarbon-dated Nelson strata[2], and the four Schenck trench levels together yield a total of 17 independent temporal-analytic units. I refer to these units collectively as the Emeryville "strata" below. These strata will allow a fairly fine-grained ordinal-scale analysis of change in the efficiency of bird exploitation and evidence for harvest pressure on local bird populations at a single point on northern California's late Holocene landscape between ca. 2600 and 700 B.P.[3]
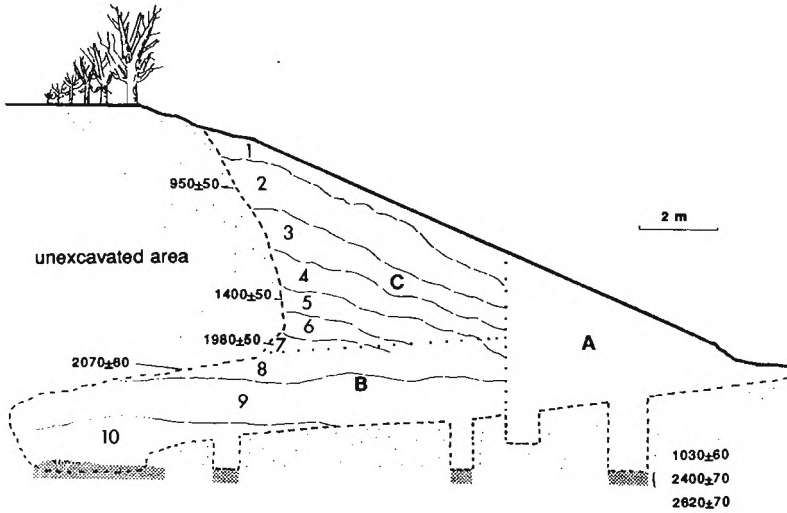
Figure 8.3. Profile of the Uhle/Merriam excavation showing radiocarbon dates placed into stratigraphic context (map redrawn from Uhle 1907: Plate 4).

THE EMERYVILLE SHELLMOUND MAMMAL AND FISH FAUNAS: EVIDENCE FOR DECLINING EFFICIENCIES AND HARVEST PRESSURE

My identification and analysis of some 18,000 fish and mammal specimens from the Emeryville Shellmound provide evidence for dramatic human-induced impacts on local populations of large-sized taxa, such as sturgeon (*Acipenser* spp.), tule elk (*Cervus elaphus*), and black-tailed deer (*Odocoileus hemionus*), across the occupational history of this site (Broughton 1995, 1997). To provide a broader context within which to understand patterns in the avifaunal data, I provide a brief summary of the results from the analyses of these other vertebrate classes.

Among the fishes, the abundance of sturgeon, by far the largest fish taxon represented in the Emeryville collection, declined significantly relative to the other smaller fishes from the oldest to the youngest strata (Figure 8.4; $r_s = -.49$, $P = .05$).[4] In addition, the mean age of the exploited sturgeon, as measured by dentary widths, also declined significantly across the history of mound occupation (Figure 8.5; $r_s = -.762$, $P < .05$). These changes are not correlated with late Holocene variation in estuarine salinity (Ingram et al. 1996), the most influential variable that currently limits the density of sturgeon in the central San Francisco Bay. The decrease in the relative abundance of sturgeon provides evidence for a significant decline in the efficiency of fish exploitation through time at Emeryville. The decreasing mean age supports the hypothesis that the decline in sturgeon abundances was due to an increasing harvest rate of this fish resource by the inhabitants of Emeryville, as well as other human groups occupying the San Francisco Bay margin.
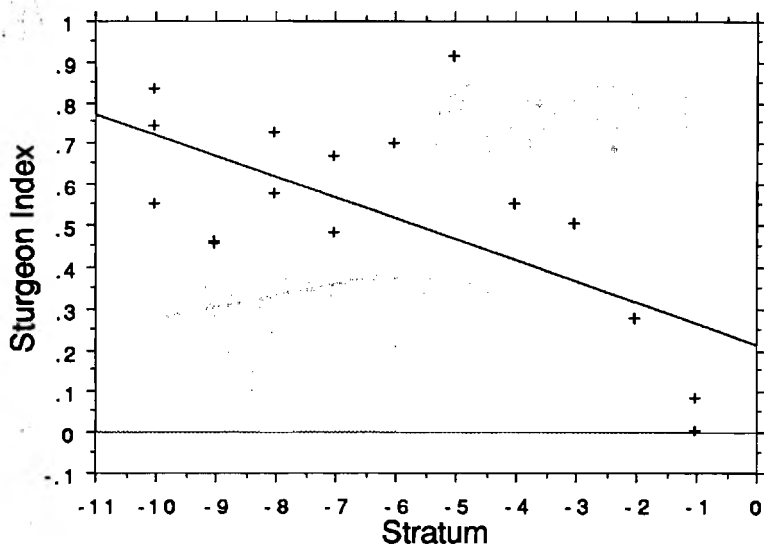
Figure 8.4. The distribution of sturgeon index (ΣNISP sturgeon/ΣNISP identified fishes) across the Emeryville strata.

Similar conclusions were reached from analyses of the mammal materials from this site. Among terrestrial mammals, for example, black-tailed deer and tule elk dominate the earliest strata, but decline relative to smaller mammals, namely small terrestrial carnivores (e.g., coyote, *Canis latrans;* raccoon, *Procyon lotor;* and striped skunk, *Mephitis mephitis*) across the initial 600 years of human occupation (Figure 8.6). While tule elk frequencies remain low throughout the remaining occupation of the mound, perhaps reflecting the limited available grassland habitat for elk in the region, deer numbers steadily increase in relative frequency throughout the remaining millennia of mound occupation. In my earlier work, I hypothesized that this resurgence in deer abundances reflected continuing depression of local resource patches and an ever-increasing use of distant, less-depleted deer patches in the oak woodland hinterlands of the Bay area. This hypothesis was strongly supported by changes in artiodactyl skeletal part frequencies across the Emeryville strata (Broughton 1999).

Recent theoretical and ethnoarchaeological research (Barlow and Metcalfe 1996; Binford 1978; Metcalfe and Barlow 1992; O'Connell et al. 1990) have made one point clear with respect to the economics of large mammal carcass transport: Transport costs determine the degree to which low-utility body parts are returned from kill sites to base camps, and transport distance is the single most important component of transport costs. It follows that if the resurgence in artiodactyl abundances 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. My analysis showed that after taphonomic biases in skeletal part representation were
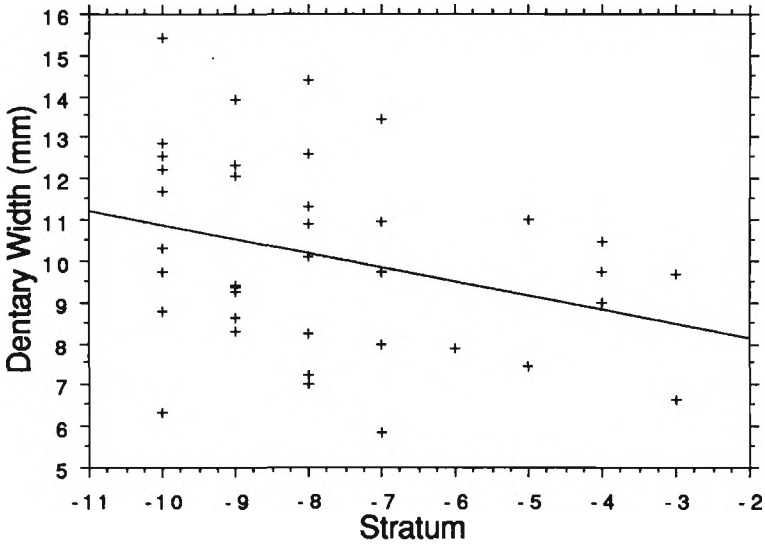
Figure 8.5. Dentary widths by stratum for the Emeryville sturgeon. (A least-squares regression line shows the direction of the trend.)

isolated and removed[5], the mean Food Utility Index (see Metcalfe and Jones 1987) of the represented anatomical parts increased significantly across the upper six strata of the Emeryville Shellmound (mean utility versus stratum r_s = .96, P < .02; see Broughton 1995:213–219). The skeletal part frequency data from the Emeryville artiodactyls, thus, strongly supports the local depression and distant patch use hypothesis. Many other aspects of the Emeryville mammal record—from change in the age structure of artiodactyls and marine mammals to cut-mark and bone fragmentation patterns—strongly support this hypothesis as well (Broughton 1999).

In sum, analyses of both the mammal and fish faunas from Emeryville provide support for the hypothesis that expanding forager densities depressed local vertebrate populations, ultimately driving declines in vertebrate foraging efficiencies. Is evidence of human impacts on prehistoric bird populations of San Francisco Bay indicated by patterns in the Emeryville Shellmound avifauna?

THE EMERYVILLE SHELLMOUND AVIFAUNA: EXPECTATIONS AND PRELIMINARY RESULTS

In her 1929 study of the Emeryville avifauna, Hildegarde Howard published what remains one of the premier paleontologically oriented analyses of avifaunal materials from a North American archaeological site (Howard 1929). In that work, Howard identified 4,155 bird specimens from a total of about 15,000 bird remains recovered from the Emeryville Shellmound. Howard, however, did not
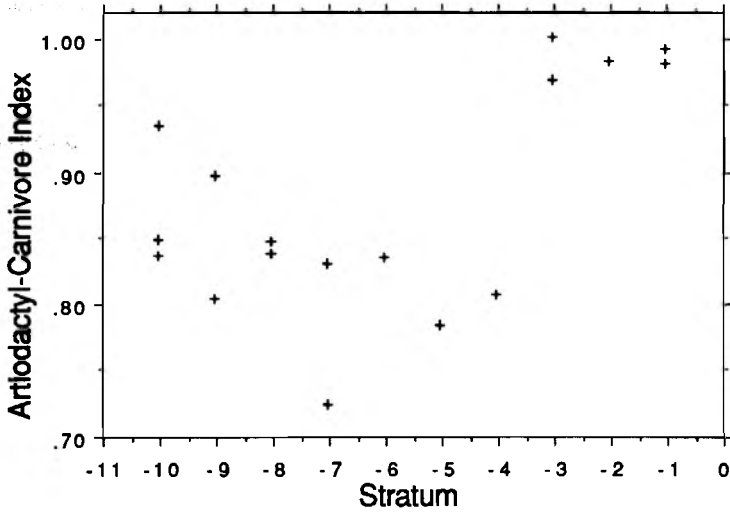
Figure 8.6. The distribution of the artiodactyl-carnivore index (ΣNISP artiodactyls/Σ NISP [artiodactyls + small carnivores]) across the Emeryville strata.

provide stratigraphic information for those identifications. From her unpublished laboratory catalog, on file with the vertebrate faunal collection at the Phoebe Hearst Museum of Anthropology, University of California, Berkeley, I was able to place 2,302 of her identifications into stratigraphic context (Broughton 1995:121–123). A preliminary analysis of this sample of identified bird speci-mens from Emeryville hints that local bird populations may have suffered sub-stantial impacts from late Holocene human foragers in this estuarine setting. Ducks and geese (Anatidae) and cormorants *(Phalacrocorax)* comprise 83.5% of the 2,302 identified bird specimens from the provenienced Emeryville avian assemblage, and I focus this preliminary analysis of the intensification of bird exploitation on these taxonomic groups.

Three species of cormorant were identified by Howard in the Emeryville Shellmound avifauna: Double-crested Cormorant *(Phalacrocorax auritis)*, Brandt's Cormorant *(P. penicillatus)*, and Pelagic Cormorant *(P pelagicus)*. Of the 491 identified cormorant specimens, Howard could securely identify 159 to species. Of this latter sample, 119, or 74.8%, were Double-crested Cormorant. To judge from the degree of bone ossification of the cormorant material, almost half (46.4%) of the specimens represented at Emeryville were fledgling-aged birds, indicating the exploitation of local breeding colonies (Howard 1929).

Adult Double-crested Cormorants range in weight from 1.75 to 2.75 kilograms. Brandt's and Pelagic Cormorants are slightly smaller, weighing between 1.4 and 2.6, and 1.4 and 2.4 kilograms, respectively (Johnsgard 1993:173, 202, 292).

All of these species are year-round residents of the San Francisco Bay area, and breed in colonies on islands, or virtually inaccessible rocky cliff faces on the

mainland coast. The nearest historically recorded colony to Emeryville was at Seal Rocks near the Golden Gate; exploiting cormorants on this island would require a 34-kilometer round-trip journey by water from Emeryville (Grinnell and Wythe 1927:47). The nearest island that may have supported cormorant nesting colonies in the past is Treasure Island, located 9 kilometers west of Emeryville.

Cormorant colonies are well known for their sensitivity to disturbance and vandalized or disturbed sites are routinely abandoned (e.g., Boekelheide et al. 1990:165–166). As a group, these cormorants begin to breed at about the age of three years, usually produce clutches of three to four eggs between April and June, and fledge two chicks per nest (Boekelheide et al 1990; Johnsgard 1993:202). Cormorants are piscivorous and use their excellent diving abilities to capture fish prey (Ainley et al. 1990:105–107).

In sum, the life history characteristics of cormorants are similar to the typical *K-selected* reproductive strategies of most seabirds. This adaptation includes relatively small clutches, slow growth rates, delayed sexual maturity, and long lifespans. Cormorants appear to be "geared" to maintain slow population turnover rates, and are unlikely to quickly rebound from intensive human exploitation (cf., Johnsgard 1993:125–126).

Howard identified 1,431 anatid specimens from the Emeryville strata. Most of those identifications were, however, only made to the family level. Only 78 specimens were identified to the genus or species level. The anatids are highly variable in size, from as large as 11 kilograms for Canada goose *(Branta canadensis),* to as small as 0.5 kilograms for teals *(Anas* spp.) (Palmer 1976:199, 488).

The anatid species that Howard identified in the Emeryville assemblage occur in the San Francisco Bay area only as winter visitants. These birds migrate to northern latitudes or the interior of the continent during spring to breed, where they produce relatively large broods of precocious chicks (geese 3–7 chicks; ducks 5–12). This characterizes the seasonal distribution of most of the anatid species, including all of the geese that occur in the San Francisco Bay area. In fact, of the 33 anatid species whose ranges include San Francisco Bay, only five duck species of the genus *Anas* are year-round residents here (Grinnell and Wythe 1927).

Diet is highly variable among the different species of anatids. Many anatid species routinely forage in terrestrial settings. In fact, all of the identified geese, including White-fronted Goose *(Anser albifrons),* Snow Goose *(Chen caerulescens),* Ross's Goose *(Chen rossii),* and Canada Goose are largely terrestrial vegetarians that prefer to forage in grassland or marshland settings. These species are generally quite gregarious, forming large impressive flocks, sometimes containing over 5,000 individuals in these settings (Palmer 1976).

According to ethnographic and ethnohistoric accounts, aboriginal foragers of this region used a wide variety of methods to capture waterfowl and seabirds, including the bow and arrow, bolas consisting of two pieces of bone or stone tied to each end of a string, snares or nooses hung by cords above the water's surface or within tule marshes, and nets used in association with stuffed skin decoys.

Cormorant rookeries on offshore islands were reached by small watercraft (tule balsas) (Beechey 1831:75; Johnson 1978:364; Levy 1978:491; Wallace 1978:450). Both watercraft and netting technologies were well established in the San Francisco Bay area well before the occupation of Emeryville (Broughton 1994b; Follet 1975; Howard 1929; Wallace and Lathrap 1975).

If expanding human forager densities drove declining foraging efficiencies across the occupational history of Emeryville, several predictions follow involving changes in the taxonomic composition and age structure of the Emeryville avian materials. First, since the different anatid species occur within the same resource patches, they should have been part of the same hunt type. And since the anatids share similar life history and antipredator adaptations, but differ substantially in body mass, declining efficiencies in anatid foraging should be signaled by declining abundances of geese relative to ducks across the history of mound occupation. In addition, since geese are larger in size than cormorants and occur in high densities in grassland and marshland settings close at hand to Emeryville, the abundances of geese relative to cormorants should also decline across the history of site occupation. That is, the relative abundances of cormorants in the Emeryville strata should signal the depression of *local* resource patches and the relative frequency that *distant* patches were exploited.

Cormorants should also be much more susceptible to absolute declines due to human harvest pressure than the anatids, since they are year-round residents of the Bay area, their breeding colonies can be directly exploited and disturbed, and they exhibit more *K-selected* life history strategies. Hence, if overall foraging returns declined enough to drive the intensive foraging of distant island-nesting cormorants, such exploitation may be relatively short-lived. Finally, if the resident populations of cormorants were depressed or extirpated from the region, indications of harvest pressure should be indicated by declines in the average age of the exploited cormorants from the Emeryville strata.

None of these predictions can be fully addressed with the very limited data now available. Because virtually all of the anatids were identified only to the family level, it is not possible to address the first two predictions at all. The present data do allow a cursory glance at the third prediction, that local cormorant populations could not sustain intensive long-term exploitation of breeding colonies.

The cormorant index:

$$\Sigma\text{NISP Cormorants}/\Sigma(\text{NISP Cormorants + Anatids})$$

summarizes the relative abundances of cormorants and anatids in the Emeryville Shellmound faunal assemblage, where NISP refers to the numbers of identified specimens per taxon. Figure 8.7 shows the relationship between the cormorant index and time as represented by selected Emeryville strata. Again, identified avian samples were lacking for many strata, hence it is not possible to reach any firm conclusions from these data. However, the data do suggest an increase in the exploitation of cormorants relative to ducks and geese across the lower four strata
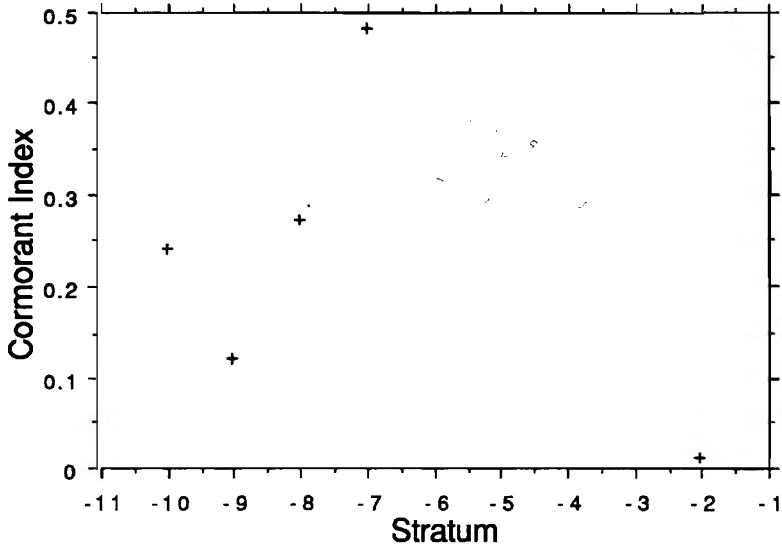
Figure 8.7. The distribution of the cormorant index (ΣNISP cormorants/ΣNISP [cormorants + anatids]) across selected Emeryville strata.

(i.e., 10 through 7). It is also intriguing that by stratum 2, the cormorant index has dropped to less than .01. Did declining foraging efficiencies drive a steadily increasing use of distant cormorant patches? And did this ultimately cause the extirpation of breeding populations of cormorants in San Francisco Bay? Addressing these and other questions requires a fine-scale analysis of the Emeryville Shellmound avifaunal collection.

DATA REQUIREMENTS

Taxonomic Composition

Identifications of the Emeryville Shellmound avian specimens are required to test the predictions concerning changes in taxonomic composition across the history of site occupation. These data will allow the calculation of taxonomic ratios, such as the cormorant index, that incorporate the abundances of differently ranked resources that occur in distinctive resource patches. These indices can then be plotted across the Emeryville strata to reveal temporal patterns in the energetics of avian prey choice and patch use.

Age Determination

The prediction concerning changes in age structure as a function of harvest pressure requires that estimates of the age of death be determined for the

Emeryville cormorant material. However, despite several little-known or other-wise unsuccessful attempts (Koubek and Hrabe 1984; Nelson and Bookhout 1980; Schaaf 1979; Stone and Morris 1981; van Soest and van Utrecht 1971), no well-documented, osteologically based methods for determining the age of adult birds have been fully developed. Hence, ornithologists, avian paleontologists, and archaeologists have been limited to assigning osteological bird remains to two broad age classes: subadults and adults. Finer-scale age assessments are required to measure harvest pressure and other demographic variables from archaeological avian faunas.

Fortunately, a recently described method of age determination for adult birds, based on analyses of annual rings registered in the circumferential lamellae of long bones, has produced very promising results. Specifically, Klomp and Furness (1992) use a sample of 12 known-aged birds of four species (Great Skua, *Catharacta skua*; Redshank, *Tringa totanus*; Northern Fulmar, *Fulmaris glacialis*; and European Shag, *Phalacrocorax aristotelis*) to demonstrate that the number of endosteal lamellae revealed in transverse thin sections of the tibiotar-sus corresponded tightly with age in years. Reading photographs of 1-millimeter thick, polished thin sections, taken through a transmitted light microscope at 100x, naive observers correctly determined the age of the birds within one year for specimens less than 12 years, and within two years for birds older than 12 years. The age of the single known-aged cormorant in the sample, the European Shag, was correctly determined *to the year* by each of the six observers.

In addition to demonstrating the annual nature of endosteal ring formation among small samples of individuals representing four bird species, Klomp and Furness (1992) also documented the *presence* of endosteal rings among individ-uals of three other species. Previous investigators have also documented the pres-ence of rings in the circumferential lamellae in either the periosteum or endosteum in a number of different skeletal elements from ten other species of bird (Koubek and Hrabe 1984; Nelson and Bookhout 1980; Schaaf 1979; Stone and Morris 1981; van Soest and van Utrecht 1971). Seasonal climatic changes, dietary shifts, and reproductive cycles have been proposed as possible factors resulting in the layered growth of avian bone, but further research is required to determine the precise biological basis of this phenomenon (Klomp and Furness 1992:134).

Applying this technique to archaeological specimens requires well-preserved incremental structures of avian long bone samples. And while the histological structures of bone, such as endosteal lamellae, are routinely preserved in archae-ological and paleontological contexts, including fossilized specimens (e.g., Grupe and Garland 1993; Reid 1981; de Ricqles 1986, 1993; Stout 1992), bone microstructure can be damaged or obscured by mechanical abrasion or diagenetic processes, such as fungal or bacterial invasion (see Hanson and Buikstra 1987).

Based on chemical and structural analyses of seven samples of mammal bone distributed across the Emeryville strata, the structural preservation of bone at this site appears to be excellent. Specifically, after demineralization, all but one of the

specimens retained original bone color and structure and provided high collagen yields (Broughton 1995:89–90). Hence, analyses of bone microstructure for age determination from the Emeryville osteological samples should provide fruitful results.

Prior to applying this age-determination technique to the Emeryville cormorant materials, it is necessary to establish experimentally the precise nature of the periodicity of ring formation in the circumferential lamellae of these birds. To this end, I will analyze a large sample (n = 54) of modern, known-aged Double-crested Cormorants to conduct these analyses.[6] With this sample, I will follow the protocol described by Klomp and Furness (1992) to verify the accuracy and precision of this technique for this species.

Finally, I have been granted permission by the Phoebe Hearst Museum, University of California, where the Emeryville materials are presently curated, to remove partial thin sections from 340 samples of cormorant long bones for the age determination analyses. This sample will allow an average of 20 specimens to be aged from each of the 17 temporal-analytic units of the site. Mean cormorant ages can then be determined for each Emeryville strata to evaluate diachronic patterns of harvest pressure on this resource.

Paleoenvironmental Data

In addition to human harvest pressure, environmental change can affect the densities, encounter rates, and ultimately the spectrum of avian prey choice options available to the prehistoric foragers that occupied particular localities on the landscape. Since the winter visitant anatid resources of San Francisco Bay are derived from multiple breeding populations from localities distributed across the continent, monitoring long-term environmentally based changes in the densities of these migrant populations is not feasible. However, regional late Holocene paleoenvironmental records will allow an assessment of environmentally based changes in the densities of the resident cormorant populations in this region.

Research on cormorant breeding colonies of the Farallon Islands, located 45 kilometers east of the Golden Gate, has indicated that interannual fluctuations in ocean water temperature influence the feeding ecology and, ultimately, the regional population densities of Pelagic, Brandt's, and Double-crested Cormorants. Specifically, during years with elevated sea surface temperatures associated with the El Nino Southern Oscillation (ENSO), the fish populations upon which cormorants feed are profoundly disrupted, foraging efficiencies decline, as does the number of pairs attempting to breed and the average number of chicks fledged per pair. As a result, Farallon cormorant populations during and immediately subsequent to ENSO years are substantially depressed (Ainley and Boekelheide 1990). Similar population declines among cormorant populations have been associated with warm-water years along the coasts of both South America and South Africa (Boekelheide et al. 1990; Crawford and Shelton 1978; Jordan 1967).

While cormorant populations gradually rebound from these short-term population declines associated with episodic, warm-water years, prolonged periods of elevated sea temperature in the past, on the scale of hundreds or thousands of years, might have produced significant long-term declines in cormorant populations or even local extirpation events. Evaluating the effect of ocean paleotemperature variation on the densities of San Francisco Bay cormorant populations and human exploitation of these resources requires fine-scale records of late Holocene fluctuations in ocean temperature in this region.

Several Holocene records of surface sea temperature have been provided for the California coast (e.g., Jones and Kennett 1999; Kennett and Ingram 1995; Pisias 1979). These records are based on a variety of paleoclimatic proxies derived from radiocarbon-dated ocean basin sediment cores. These proxies include $\delta^{18}O$ values from planktonic and benthic foraminifers, relative abundance changes of cold- and warm-water foraminifer and rodiolarian taxa, the morphology of foraminifer shell coils, and the degree of preservation of laminated ocean basin sediments. Variations in Holocene ocean temperature derived from these different proxies have provided internally consistent results and will allow a precise evaluation of correlation between late Holocene changes in eastern Pacific sea temperatures and the relative abundances of cormorants represented at the Emeryville Shellmound.

SIGNIFICANCE

Resource intensification models predict declines in foraging efficiency during the late Holocene of California due to expanding forager densities and declining encounter rates with certain especially profitable vertebrate resources. In many settings, it has been suggested that the declining encounter rate with high-ranked prey types was the result of depletion caused by human foraging activities. Through the integration of models drawn from evolutionary ecology and demography, I have deduced archaeological measures of foraging efficiency and harvest pressure that involve the taxonomic composition and age structure of the bird remains recovered from the famous, but long-since destroyed Emeryville Shellmound. The application of these measures in a fine-scale test of resource intensification models will have strong implications for 1. our knowledge of the specifics concerning the emergence of complex hunter-gatherers in late prehistoric California; 2. the causes of change in prehistoric hunter-gatherer behavior in general; as well as for 3. the long-term management of Pacific Coast bird populations currently threatened by human-caused habitat alteration.

Insofar as widening diet breadths imply lower average fitness within local populations, documenting declines in foraging efficiency entail predictions for variation in many other aspects of human behavior and morphology during the late Holocene of California. 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). Insofar as strong gradients develop in local resource densities and abundances as a consequence of the overall declines in foraging returns, opportunities would increasingly emerge for the growth of disparities in wealth and the exaggeration of social hierarchies.

Finally, informed ecosystem management clearly cannot be accomplished without detailed knowledge of the factors that structured pre-Columbian and historic period environments. Analyses of archaeological vertebrate faunas can provide a central avenue for attaining this knowledge and an objective means of evaluating the impact that people had on prehistoric environments. For many regions of the world, this knowledge resides untapped in museum collections that were derived from archaeological excavations conducted over the last century. Archaeology is in a unique position to contribute to modern management policies that will ultimately determine the nature of our planet's future environments.

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NOTES

1. Transport models developed by Metcalfe and Barlow (Barlow and Metcalfe 1996; Metcalfe and Barlow 1992), 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.

2. The Nelson excavation yielded a comparatively small sample of vertebrate specimens aside from the basal stratum 11. For this reason and because only two of the upper 10 strata were radiocarbon dated, I selected only the three dated strata (strata 3, 5, and 11) for the following analyses.

3. Given the coarse-grained recovery methods discussed above, there is undoubtedly a systematic recovery bias against the recovery of very small-sized vertebrate specimens. However, this bias should be internally consistent throughout the various strata of the deposit. Moreover, the bird taxa of primary interest here are of such substantial sizes that such a bias should be negligible.

4. Stratum 10 is at the base of the deposit; stratum 1 is at the top of the mound. The multiple points per stratum in Figure 8.4 and several figures to follow represent temporally equivalent stratigraphic units from the three different excavations conducted at three different horizontal locations of the mound.

5. Eight of the 17 strata exhibited positive Spearmann's rank order correlations between relative skeletal abundances and deer bone density values (from Lyman 1984). Fortunately, the positive correlations were concentrated (7 of the 8) in the lower strata of the deposit, so do not affect interpretations of skeletal part frequencies across the period of the artiodactyl resurgence in the upper strata of the deposit (Broughton 1995).

6. The known-aged cormorants are curated at the Museum of Zoology, University of Michigan, and have been made available for these analyses.

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