

Prehistoric Marine Mammal Overkill in the Northeastern Pacific: A Review of New Evidence

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A model of prehistoric marine mammal overexploitation advanced by Hildebrandt and Jones (1992) for the northeastern Pacific has been challenged by Colten (1995) and Colten and Arnold (1998) who argue that diachronic patterns in faunal remains from California's Channel Islands reflect climatically-induced decline in marine productivity and local socio-cultural developments not overpredation. In this paper, we point out that some Channel Islands faunal trends are consistent with overexploitation, while others reflect methodological variation between studies. Newly available paleoenvironmental data raise questions about previous characterizations of late Holocene marine productivity, while new zooarchaeological findings from Monterey Bay, San Miguel and San Clemente Islands provide strong support for overexploitation in ways not envisioned in the original model. Such findings show that linear optimal foraging constructs may not account for all local variation in faunal assemblages, but still provide powerful explanations for broad patterns over time and can further provide useful insights into prehistoric human ecology.

Prehistoric exploitation of marine mammals in the northeastern Pacific has been a subject of considerable attention since 1992 when Hildebrandt and Jones used an optimal foraging model to argue that when congregated in rookeries, seals and sea lions represent highly attractive resources vulnerable to overpredation. Using archaeofaunal data from sites along the Oregon and California coasts they pointed to many cases where the remains of terrestrially breeding species (elephant seals [*Mirounga angustirostris*], northern fur seals [*Callorhinus ursinus*], Guadalupe fur seals [*Arctocephalus townsendi*], California sea lions [*Zalophus californianus*] and Steller sea lions [*Eumetopias jubatus*]) decrease through time at the expense of smaller, more elusive, aquatic breeders (sea otters [*Enhydra lutris*] and harbor seals [*Phoca vitulina*]). These trends were argued to represent overexploitation of highly ranked taxa and their replacement by lower-ranked species pursued with sophisticated watercraft and maritime weaponry. Because such technologies are commonly associated with advanced socio-political organization, this model is closely tied to contentious, ongoing debate over the causes and chronology of emergent complexity among southern California coastal foragers (see Arnold 1992a, 1992b, 1997; Arnold et al. 1997; Kennett 1998; Kennett and Kennett 2000; Raab and Bradford 1997; Raab and Larsen 1997; Raab et al. 1995;). Marine mammal overexploitation is also one of a growing number of cases that illustrate the affects of prehistoric hunting on North American faunal populations. Increasing

recognition of these impacts is resulting in challenges to longstanding cultural ecological/functionalist portrayals of Native Americans as conservationists. Debate over this issue has expanded into the biological community, where wildlife biologists are showing increasing interest in the role of Native peoples in prehistoric ecosystems, and how this information can be used to manage national parks and other game reserves (Geist 1996; Kay 1990, 1994; McCann 1999; Truett 1996).

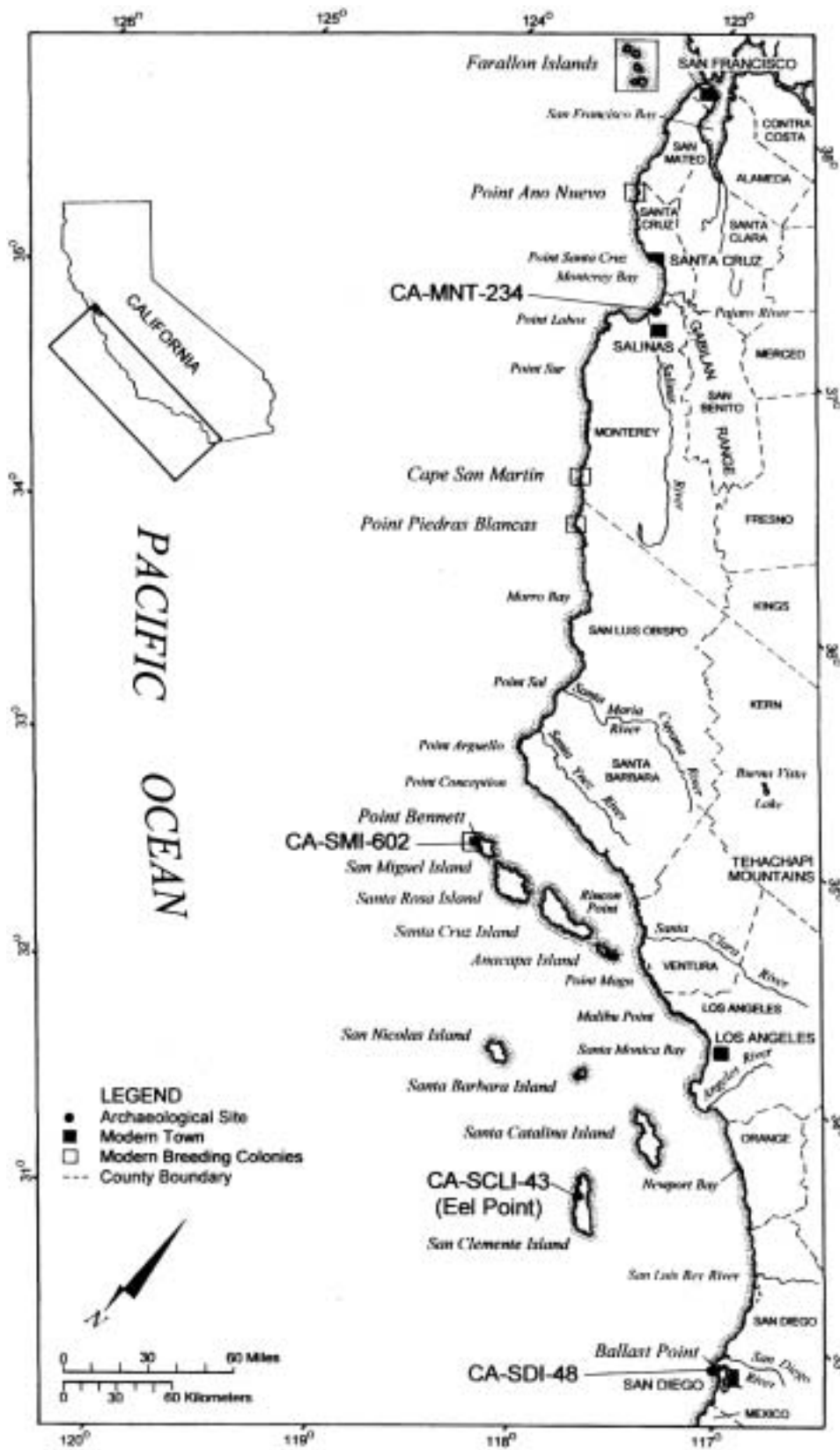
The marine mammal overpredation model has received attention both from those whose data show similar trends (Burton 2000; Porcasi 1995; Porcasi et al. 2000; Walker et al. 2000) and others who challenge the construct (e.g., Colten 1995; Lyman 1995). Recently, Colten and Arnold (1998) argued that variation through time in faunal remains from the Channel Islands off southern California does not conform with patterns and predictions outlined by Hildebrandt and Jones (1992) and Jones and Hildebrandt (1995), and reflects not predatory pressure and overexploitation but climatically-induced decline in marine productivity circa A.D. 1150-1250 in concert with local cultural developments. The purpose of this paper is to argue that there are still compelling reasons to suspect prehistoric overhunting in this area, and that the overall model has not been negated by Colten and Arnold's findings from Santa Cruz and Santa Miguel Islands. We begin by re-interpreting the Colten and Arnold findings and follow this with discussion of new data and perspectives on several key issues in the overhunting debate including: paleoclimatic influences, mainland rookeries, and sea mammal population ecology.

ALTERNATIVE PERSPECTIVES ON HUMAN PREDATION

For the purposes of archaeological debate, it is best to consider three possible scenarios for the relationship between human hunters and marine mammal populations: (1) hunting was so selective and infrequent that it had no significant affect on animal populations (no

affect); (2) hunting was actually beneficial to marine mammal populations as hunters enhanced the process of natural selection by targeting weak and/or sick animals (Lyman 1995) (positive affect); or (3) hunting of seals and sea lions caused animal numbers to decrease in a progression that correlates with the ranking of taxa by potential energy gains versus pursuit costs. The first two alternatives should be reflected by faunal assemblages that show conservation-oriented prey selection, including such things as higher frequency of males over females, old over young, and paleopathological evidence for disease among the exploited individuals. The third alternative, of course, envisions Native Americans as self-interested humans whose attempts to accomplish short-term subsistence goals efficiently resulted in impacts to prey populations. Hildebrandt and Jones (1992) argued that faunal assemblages from the coasts of Oregon and California reflect the third alternative of human overexploitation.

Colten and Arnold (1998), the most vocal critics of overexploitation, offered an alternative model of "no affect" that attributes variation in faunal assemblages to environmental change. They present a variety of macro and microfaunal data to support their contention that diachronic variability in faunal residues and inferred diet on Santa Cruz and San Miguel Islands during the late Holocene reflects not overexploitation but an ostensive decline in marine productivity ca A.D. 1150. The original Hildebrandt and Jones overexploitation model relied solely on marine mammal remains that were divided into two classes: terrestrial breeders (originally referred to as migratory breeders) and aquatic breeders (originally referred to as non-migratory, resident species). This provided a convenient predictive index for overexploitation, involving only one class of archaeological remains. Overexploitation of the former was argued to be reflected in increased frequency of the latter over time. In point of fact, of course, overhunting should be represented only by declining frequencies of bones from the larger more attractive prey (i.e.,



Archaeological sites and pinniped colonies mentioned in text.

terrestrial breeders), and their replacement in the diet with some other lower-ranked food source. While otters and harbor seals in some circumstances represent reasonable alternatives, it is equally clear that these animals were unimportant as food sources in many areas. Colten and Arnold employed faunal residues not only from marine mammals, but also from fish and invertebrates to evaluate possible variation in use of these alternative food sources. Comparisons were made by converting bone/shell weights into meat values via meat/weight ratios, which despite problems (see Casteel 1978; Mason et al. 1998), are useful for determining relative trends in diet through time. The dietary reconstructions reported by Colten and Arnold (1998:685) for Santa Cruz Island conform perfectly with the predictions of overexploitation: from the Middle (600 B.C.-A.D.1150) through Late (A.D.1300-1782) prehistoric periods, marine mammals decrease in dietary importance while fish increase. Faunal data recently reported from San Clemente Island (Porcasi et al 2000) show similar trends through time, as fish increased in dietary importance at the expense of terrestrially breeding pinnipeds through a 9000-year sequence. This again supports a model of overexploitation, albeit in a manner not envisioned in the original Hildebrandt/Jones model.

Colten and Arnold also assembled macrofaunal data that show trends different from those predicted by Hildebrandt and Jones (1992), but much of this deviance can be attributed to methodological variation. In the original model, Hildebrandt and Jones (1992) relied solely on faunal elements identified to genus and species¹. The bulk of the Colten and Arnold data, however, consists of elements identified only to the family level or higher, including such categories of otariid, fur seal, and cetacean. Since there are no comparable taxonomic categories for the lower-ranked sea otter and harbor seals, these categories increase the representation of larger taxa in the Colten and Arnold data tables. Future evaluations of overexploitation will need to advance beyond

this important methodological issue.

PALEOCLIMATIC INFLUENCES

Temporal fluctuations in marine conditions can potentially complicate the archaeological signature created by human predation. It is well known that warm sea-surface temperatures (SST) along the southern California coast suppress marine productivity (Ambrose et al. 1993; Dayton et al. 1992; Engle 1993, 1994; Ono et al. 1993; Stewart et al. 1993, Tegner and Dayton 1987, 1991). Historically, the warmest water conditions in California have been associated with the El Niño Southern Oscillation (ENSO) and increased SST in the eastern Pacific (Anderson 1992; Yarnal and Diaz 1986). Colten and Arnold (1998) (also see Colten 1993, 1994, 1995) correctly point out that decreased productivity associated with strong ENSO events can severely impact the reproduction, survival and foraging behavior of marine mammals (DeLong and Antonelis 1993; Ono et al. 1993; Stewart et al. 1993). Given this observation, Arnold and Colten (1998) have inferred the availability of marine mammals from a long-standing record of changing SST for the region (Pisias 1978, 1979). Pisias (1978, 1979) established this sequence with radiolaria assemblages from well-preserved marine deposits in the Santa Barbara Channel region (Core Y71-10-117P). Based on this record, Colten and Arnold (1998) argued that low marine productivity between approximately A.D. 1150 and 1250 caused a significant decline in the availability of sea mammals on Santa Cruz and San Miguel Islands. Increased SST and inferred low marine productivity during this interval is supported by three independent sources of archaeological data: black abalone growth patterns (Arnold and Tissot 1993), shellfish assemblages (Colten and Arnold 1998), and ichthyofaunal data suggesting warm and cold water species of fish during this interval (Colten 1994, 1995, Pletka 1996).

A new marine climate sequence has recently been established for the Santa Barbara Channel region based on oxygen isotopic

analysis of planktonic foraminifera from a sediment core from Santa Barbara Basin (ODP Hole 893A; Kennett and Ingram 1995; Kennett 1998; Kennett and Kennett 2000). This well-dated record spans the Holocene with 25-year resolution for the last 3,000 years and 50-year resolution for the remainder of the Holocene. It is clear from this recent work that Pisias overestimated the range of SST fluctuations during the Holocene and that chronological problems undermine its continued use by archaeologists in the region (Kennett and Kennett 2000). Furthermore, warm water conditions between A.D. 1150 and 1250 reported by Pisias (1978, 1979) are not evident in the new record, and it appears that this interval falls within one of the coldest, most unstable climatic periods in the Holocene (A.D. 450 and 1300) (Kennett and Kennett 2000). Oxygen isotopic analysis of California mussel (*Mytilus californianus*) shells from well-dated midden deposits on Santa Rosa Island provides independent evidence for cold water conditions and high marine productivity as suggested by increased fish density in midden deposits including samples that fall between A.D. 1150 and 1250 (Kennett 1998). At this point it is unclear why the archaeological data from Santa Cruz and Santa Rosa Islands are inconsistent for this interval, however methodological and chronological studies may resolve the issue in the future.

While most paleoenvironmental data from southern California do not suggest low marine productivity during the A.D. 1150-1250 interval, there is growing evidence for extended droughts and depressed terrestrial vitality during this time as part of a broader paleoclimatic phenomenon, the Medieval Climatic Anomaly (Stine 1994). Jones and Hildebrandt (1995:91-92) and others (e.g., Arnold 1992a, 1992b; Jones et al. 1999; Raab and Larson 1997) identified occupational hiatuses and settlement disruptions associated with the Medieval droughts in a variety of settings-including the southern California islands. Jones and Hildebrandt (1995) pointed out that drought-induced settlement shifts have subsistence implications different from those

associated with lowered marine productivity. Recent findings from San Clemente Island, for example, suggest temporary abatement of rookery exploitation during the Medieval Climatic Anomaly, which seems to have precipitated a rebound in formerly suppressed fur seal populations (Porcasi et al. 2000).

ROOKERIES AND SEA MAMMAL POPULATION ECOLOGY

A key feature in the original marine mammal overexploitation model was an assertion that, limited only by food resources, seal and sea lion populations have inherent potential to grow. In the absence of human predation, it was suggested that rookeries would have existed on the mainland, as populations expanded beyond the limits of island breeding space. The near exclusive restriction today of breeding sites to islands was argued to be the result of historic decimation that followed thousands of years of prehistoric hunting. The remarkable growth and expansion of northern elephant seal populations in the northern Pacific in last three decades, which has included expansion of rookeries from islands to the mainland (Le Bouef and Panken 1977) was seen as an analog for the potential growth and distribution of pinnipeds in the absence of human predation. From the standpoint of pinniped ecology, however, this portrayal underestimates the effects of non-human mainland predators, as well other factors that limit sea mammal population growth. Most marine mammal biologists (e.g., Le Bouef 1981:301) feel that non-human terrestrial predators (e.g., bears, mountain lions, coyotes, and wolves) would have always limited seal and sea lion populations on the mainland. Equally important are taxon-specific habitat requirements that render much of the North American mainland unsuitable for breeding (Le Bouef 1981:294). Elephant seals, for example, require sloping rocks and sandy beaches, and in historic times have established mainland breeding sites only on remote, windy points (e.g., Point Ano Nuevo and Piedras Blancas in California [Fig. 1]). The

sequence of colonization documented at these mainland locations shows that favorable sites were initially used as temporary haul outs and gradually grew into rookeries occupied for much of the year. The pressure to establish extra-island rookeries would probably always have been a feature of terrestrially-breeding sea mammals given their propensity for population growth, and it is possible that these pressures would have resulted in some mainland breeding sites- only in locations that meet the habitat requirements of the taxa and provide some protection from terrestrial predators.

Recent excavations at CA-MNT-234, a large multi-component site in the Monterey Bay area of central California (Fig. 1), have produced evidence for a prehistoric mainland breeding population of northern fur seals (Breschini and Haversat 1995; Milliken et al. 1999). Prior to the establishment of a small herd on San Miguel Island during the 1960s, this animal was known to breed only on islands along the coast of Alaska (Kenyon and Wilke 1953; Peterson et al. 1968). During the non-breeding season (largely fall and winter), immature males and females migrate south, many traveling as far as central California where they remain offshore unless they become sick or injured (Hanna 1951). In addition to an unusually high frequency of northern fur seal bones, Burton's (2000) recent analysis of the CA-MNT-234 materials shows a significant number of pups within the northern fur seal remains. Jaw length measurements from these specimens, when compared to reference samples with known age of death, showed that some of the pups were less than three months old when they died, clearly documenting the exploitation of a rookery (i.e., pups don't swim effectively at this age, ruling out a migration from another rookery)². Furthermore, analysis of stable isotope profiles showed that 90% of the adult individuals were consuming fish exclusively from the central California coast (i.e., no evidence for the consumption of Alaskan fauna was found), and analysis of the pup remains showed them to be feeding at one trophic level higher than that of the adults, indicating that they were nursing at the time of

death. It should also be emphasized that at the time the remains were deposited, the rookery was probably located on a sand spit separated by the Salinas River from the rest of the mainland (Jones et al. 1996:190) reducing its accessibility to mainland predators. This setting is very similar to that of Ballast Point in San Diego County, another mainland site that produced a substantial quantity of fur seal bones (Gallegos and Kyle 1998).

The abundance of northern fur seal bones at CA-MNT-234, as well as several other sites along the California coast (see Hildebrandt 1984), represents a classic example of prehistoric exploitation of terrestrial breeders in an area lacking offshore rocks or any historic evidence for a mainland rookery. As correctly noted by Lyman (1989, 1995), however, the simple presence of these animals does not necessarily represent the exploitation of a now extinct rookery, as the unqualified identification of a rookery requires evidence of pups within the archaeological assemblage. Data of this type are only slowly accumulating, but the findings from CA-MNT-234 suggest that mainland rookeries may be represented in archaeological collections- albeit only in localities with proper habitat.

Habitat must also be considered as a limiting factor in the distribution of island breeding colonies. Colten and Arnold (1998) argue that sea mammals played a minor dietary role throughout prehistory of Santa Cruz Island. Given the spatial distribution of sea mammals in the northern Channel Islands today it is not surprising that they played a minor dietary role on Santa Cruz Island. The only significant breeding colonies today are found on San Miguel Island, particularly on its windy, western end. Even the rapidly expanding elephant seal populations of today have failed to establish breeding sites on Santa Cruz Island, and it is fairly clear that these more sheltered islands do not meet the habitat requirements of terrestrial breeders. There are no rookeries there today, nor is it likely that they were widespread on these islands prehistorically. With regard to the San Miguel Island faunal data

that Colten and Arnold muster in opposition to the overexploitation model, Walker et al. (2000) recently reported compelling evidence for prehistoric predatory pressure on the San Miguel Island breeding colony (Fig. 1). The rookery there today includes breeding populations of northern fur seals, elephant seals, California sea lions and harbor seals. Breeding animals are found on the mainland of the island and on offshore islets and rocks. In the midst of the breeding colony, Walker et al. discovered a late prehistoric Chumash village site, complete with house features and a cemetery (CA-SMI-602). Radiocarbon dates define an occupation between cal A.D.1450 and 1850. Only preliminary findings from this deposit are currently available, but the occurrence of a large, permanent human settlement amidst a breeding colony represents an impossible contradiction, in that the two simply could not have occupied the same space at the same time. The site testifies to a significantly lower population of breeding animals during the period of its occupation and fosters the inescapable conclusion that the present-day marine mammal population on the island is larger than it was during the late Prehistoric Period (Walker et al. 2000). This scenario was not envisioned in the original model, but it clearly suggests overexploitation of prehistoric marine mammal populations.

A final set of data indicating non-conservative hunting of large marine mammals in the northeastern Pacific comes from Porcasi et al.'s (2000) study of the 9000-year sequence at San Clemente Island (Fig. 1). Among the most profound findings from Eel Point Site (CA-SCLI-43) was the discovery that very few pinniped bones represented adult males (19 bones or 5% of the pinniped collection). The vast majority of adult bones represented females, while 36.1% represented juveniles. Some of the bones were so poorly ossified that they were suspected to represent fetal or neonatal animals. The high incidence of females, young, and very young animals is consistent with exploitation of a rookery, while the low number of male elements suggested purposeful avoidance of large territorial bulls. Such a heavy focus on females and their young is antithetical to resource conservation (Porcasi et al. 2000).

SUMMARY AND DISCUSSION

While we appreciate the analytical rigor and new data brought to bear by Colten and Arnold (1998), we point out that many of their re-analyses have produced results that support rather than negate prehistoric marine mammal overexploitation in the northeastern Pacific. A growing number of other new studies from a range of geographic contexts employing a variety of methods have also produced compelling evidence for prehistoric overpredation of pinnipeds. Faunal residues and a greatly improved paleoenvironmental record suggest that the period ca. A.D.1150-1250 was a time of high marine productivity, but deterioration of terrestrial environments during droughts of the Medieval Climatic Anomaly probably explains some rebounds in highly-ranked taxa late in time. Breeding colonies were probably much less widespread prehistorically than implied in the original Hildebrandt/Jones overexploitation model, but evidence for at least one possible mainland rookery has recently come to light, albeit in a setting that offered nearly the same protection from mainland predators as an island. Findings from San Miguel Island indicate that the pinniped populations were lower prehistorically than they are today. Age-sex data from San Clemente Island show non-conservative hunting of females and juveniles over a 9000-year period.

While the overexploitation debate is certainly far from over, inasmuch as it has spread into the fields of biology and ecology, the findings described here show that the situation will undoubtedly prove to be more complex if not chaotic than originally envisioned. A linear optimal foraging construct applied to the entire northeastern Pacific for all of the Holocene is useful for identifying broad directional patterns in predation, but it will not account for all local variation in marine or other mammalian faunal assemblages, as correctly recognized by Colten and Arnold (1998). Nonetheless, when combined with evidence for historical contingencies (e.g., those created by anomalously prolonged droughts of the

Medieval Climatic Anomaly) and data obtained from increasingly powerful analytical techniques (e.g., isotopic studies as reported by Burton and Koch 1999 and Burton 2000) microeconomic models still show the potential to provide insightful portraits of prehistoric human ecology.

NOTES

¹ Colten and Arnold (1998) question why Hildebrandt and Jones (1992) and, later, Jones and Hildebrandt (1995) focused only on species-level identifications when reviewing the Channel Island database; i.e., why they did not incorporate more generalized data like marine versus terrestrial mammal, or eared seals (Otariidae) versus non-eared seals (Phocidae). They relied on species-level identifications for two reasons: (1) inter-specific differences in breeding behavior was a primary issue of their research; and (2) using data from a variety of sources required the species-level approach, because not all researchers report more generic-level identifications, and the ones that do, often do so differently, creating problems of inter-site comparability.

² This interpretation relies heavily upon precise estimation of the age of death of the pups. If the pups were greater than three months old at the time of death, the animals could have migrated from an island rookery, possibly on the Farallon Islands (Fig. 1).

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