The protracted Holocene extinction of California's flightless sea duck (*Chendytes lawi*) and its implications for the Pleistocene overkill hypothesis

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Edited by Dolores R. Piperno, Smithsonian Institution, Washington, DC, and Balboa, Panama, and approved December 26, 2007 (received for review November 25, 2007)

Bones of the flightless sea duck (*Chendytes lawi*) from 14 archaeological sites along the California coast indicate that humans hunted the species for at least 8,000 years before it was driven to extinction. Direct ^{14}C dates on *Chendytes* bones show that the duck was exploited on the southern California islands as early as ≈11,150–10,280 calendar years B.P., and on the mainland by at least 8,500 calendar years B.P. The youngest direct date of 2,720–2,350 calendar years B.P., combined with the absence of *Chendytes* bones from hundreds of late Holocene sites, suggests that the species was extinct by ≈2,400 years ago. Although the extinction of *Chendytes* clearly resulted from human overhunting, its demise raises questions about the Pleistocene overkill model, which suggests that megafauna were driven to extinction in a blitzkrieg fashion by Native Americans ≈13,000 years ago. That the extermination of *Chendytes* was so protracted and archaeologically visible suggests that, if the terminal Pleistocene megafauna extinctions were primarily the result of human exploitation, there should also be a long and readily detectable archaeological record of their demise. The brief window now attributed to the Clovis culture (≈13,300–12,900 B.P.) seems inconsistent with an overhunting event.

flightless birds | overhunting

The late Quaternary extinction of North America's large fauna has been a topic of intense scientific interest for decades, focused primarily on the Pleistocene overkill hypothesis, which suggests that 35 genera of megafauna were driven to extinction in a blitzkrieg fashion by Native Americans ≈13,000 years ago (1). This hypothesis has been challenged because of the paucity of supporting archaeological evidence for human hunting of most of the extinct taxa (2), while aspects of the extinctions have also been portrayed as inconsistent with climate change explanations (3). Added to this mix is a recent suggestion that an extraterrestrial impact ≈12,900 calendar years B.P. contributed to the megafauna extinctions (4). Here we challenge the overkill hypothesis based on the archaeological record of one of the few North American animals** demonstrably driven to extinction by Native Americans during the Holocene (6, 7)—the often overlooked flightless sea duck (*Chendytes lawi*).

Flightless birds are evolutionary oddities that developed almost exclusively in settings without major populations of terrestrial predators. On many Pacific islands, archaeological findings show that flightless birds were highly vulnerable to human hunting and were quickly decimated soon after humans arrived (8, 9). On the North American mainland many species of birds last disappear from the fossil record near the end of the Pleistocene, but their demise cannot be confidently attributed to human overhunting because their remains are absent from terminal Pleistocene archaeological sites (10). Indeed, a long-standing problem with the overhunting hypothesis is the fact that most genera that went extinct during the late Pleistocene have never been found in archaeological contexts that document their exploitation by humans (2).

Such is not the case with the flightless sea duck. Since at least the 1950s, *Chendytes* bones have been recognized in California archaeological sites where their co-occurrence with other subsistence remains has led to a general consensus that the species was exploited as a food source and was driven to extinction by prehistoric people. Most of the sites that produced these bones were clearly of Holocene age, but their exact chronology and the corresponding date of *Chendytes*' disappearance were not established. The bird's persistence into the Holocene was generally attributed to a relatively recent development of watercraft by Native Californians (10). Once good boats became available, California Indians were able to reach the islands, islets, and offshore rocks the birds used as breeding colonies—then exploit them into extinction.

Archaeological data from the last decade provide new insights into the antiquity of watercraft use along the California coast that have important implications for the chronology and duration of *Chendytes*' exploitation. Here we combine recent findings on the antiquity of seaworthy watercraft in prehistoric California with archaeological data on the chronology of *Chendytes* hunting, including ^{14}C dates obtained directly from *Chendytes* bones, to develop a most likely scenario for the species' extinction late in the Holocene. Key to this portrait is unequivocal evidence from the Channel Islands that Native Californians used watercraft at least 12,000 years ago (calendar years B.P.) and began exploiting flightless ducks soon thereafter. Together, the new dating for watercraft use and direct dates from *Chendytes* bones provide an absolute chronology for the extinction process. This new chronology relies on a highly visible record of human exploitation spanning at least 8,000 years before the species was completely exterminated.

Prehistoric California Watercraft

In the 1970s and 1980s, seaworthy boats were thought to be a relatively recent innovation in western North America. At European contact in A.D. 1542, three types of ocean-going vessels

Author contributions: T.L.J. and J.F.P. designed research; T.L.J., J.F.P., J.M.E., H.D., T.A.W., and R.S. performed research; T.L.J. analyzed data; and T.L.J., J.F.P., and J.M.E. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

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**The North American sea mink (*Mustela macrodon*) was exploited at least 5,100 years ago along the Gulf of Maine and was extinct at the time of European arrival, but the exact duration of species' exploitation has not been established (5).

This article contains supporting information online at www.pnas.org/cgi/content/full/0711140105/DC1.

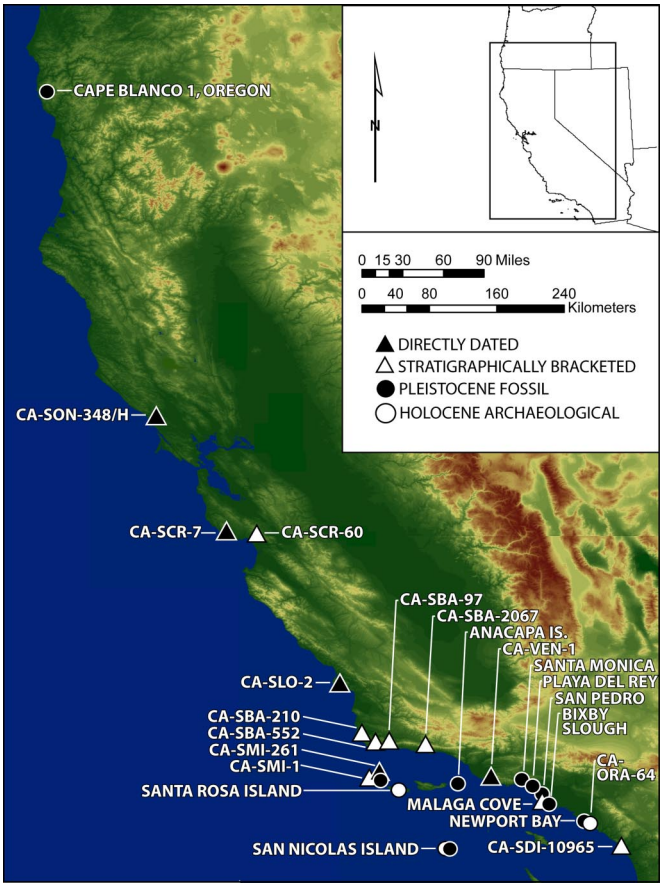

Fig. 1. Map showing location of archaeological and paleontological finds of *Chendytes lawi* along the California and Oregon coasts, highlighting locations of directly dated archaeological specimens. The figure was prepared by Brian F. Codding (Department of Anthropology, Stanford University, Stanford, CA).

were used by Native Californians: dugouts, tule balsas, and the sewn plank canoe (or *tomolo*, known only from the south coast and Channel Islands). The latter is a highly engineered craft that appears to have been developed more recently than the other vessels. Until the 1980s, the simpler craft [or possibly another composite vessel (11)] were thought to date no earlier than the early to middle Holocene, but it is now known that seaworthy boats were used to colonize the northern Channel Islands much earlier. Because these islands were never connected to the mainland even during the lowest global sea levels during the Last Glacial Maximum, the earliest archaeological evidence for human settlement also establishes a chronology for the use of watercraft. The earliest archaeological evidence for human presence on the islands is dated between 13,000 and 11,500 calendar years B.P. (12, 13). Similar findings from the western Pacific indicates that boats were used to settle islands at least ≈40,000 years ago, and there is growing evidence that western North America may have been colonized at least partially by maritime peoples arriving via a coastal route sometime before 13,000 calendar years B.P. (14).

Paleontology and Archaeology

Chendytes lawi was identified as an extinct species in 1925 (15) based on finds of Pleistocene age from coastal southern California. Subsequent finds established its presence in prehuman contexts as far north as southern Oregon (16). The greatest concentration of *Chendytes* bones comes from the northern and southern Channel Islands (Fig. 1), including Anacapa, San Nicolas, and particularly San Miguel, where ^{14}C dates on paleontological specimens establish a minimum antiquity of ≈40,000 years for the taxon (17). Hundreds of *Chendytes* bones and egg shells found in Pleistocene deposits on San Miguel Island have been interpreted as evidence that some of these island fossil localities were nesting colonies, one of which Guthrie (17) dated to ≈12,000 ^{14}C years (≈13,500–13,000 calendar years B.P.).

The concentration of *Chendytes* fossils on the Channel Islands is consistent with their vulnerability to terrestrial predators and the absence of such predators from the islands[††] (18). Pleistocene fossils have also been reported from at least four locations along southern California's mainland coast (Fig. 1), where offshore rocks and islets probably offered settings with comparable protection.

Results

Chendytes bones have been identified in archaeological assemblages from 14 coastal sites, including two on San Miguel Island and 12 in mainland localities. A directly dated specimen from the deepest cultural layer at Daisy Cave on San Miguel Island provides evidence for the earliest human exploitation of the species >10,000 years ago (11,150–10,280 calendar years B.P.) (Table 1). The oldest mainland date comes from Diablo Canyon on the central coast, where a *Chendytes* bone was dated to ≈8,500 calendar years B.P., and *Chendytes* contributes 19% of the identified bird and mammal remains associated with the earliest occupation [supporting information (SI) Fig. 2]. A direct date of ≈7,500 calendar years B.P. from Duncan's Point Cave on the north coast also indicates exploitation during the early Holocene, while a comparable age is suggested by stratigraphic associations to the south in San Diego County (SI Table 2). These dates suggest that, by at least 7,500 calendar years B.P., coastal peoples had a significant presence throughout the duck's California range and regularly exploited them by using watercraft to access nearshore rocks and islets. It seems likely that exploitation included the collection of eggs from offshore nesting sites, which may have contributed significantly to the eventual extinction of the species, although egg shells have not yet been identified in any archaeological site.

The youngest dates obtained for *Chendytes* bones from California archaeological sites fall between ≈3,500 and 2,350 calendar years B.P. The youngest direct date (2,720–2,350 calendar years B.P.) comes from the Little Sycamore site in Ventura County, with another specimen from the Laguna Creek site in Santa Cruz County dated to 3,550–3,320 calendar years B.P. These direct dates are consistent with a *Chendytes* bone found in a stratified shell midden stratum buried in canyon fill along the Santa Barbara coast dated between 4,360 and 3,750 calendar years B.P.

Overall, archaeological data from coastal California show a record of human exploitation of *Chendytes lawi* for at least 8,000 years. Findings from the trans-Holocene occupation at Diablo Canyon show that *Chendytes* exploitation declined after the mid-Holocene (SI Fig. 2), presumably in response to human population growth and the decreasing availability of the birds. The absence of *Chendytes* bones from the later strata at Diablo Canyon, and hundreds of other excavated late Holocene sites in coastal California, is consistent with region-wide extinction by ≈2,400–2,200 calendar years B.P.

[††]Today, the islands harbor only the diminutive Channel Islands fox (*Urocyon littoralis*)—which may have been introduced by Native Americans—and lack the coyote, bobcat, mountain lion, and bears common on the mainland. *Chendytes* may have been vulnerable to exploitation by bald eagles (17).

Table 1. Directly dated *Chendytes lawi* bones from California archaeological sites

Site no. and name	Laboratory no.	Skeletal element	Depth, cm	Measured ^{14}C age, years B.P.	^{13}C/^{12}C ratio,* ‰	Conventional ^{14}C age, years B.P.	Calendar age range (100% marine), calendar years B.P.
CA-SON-348/H, Duncan's Point Cave	Beta-204802	Right tarsometatarsus	170–180	7,040 ± 40	−11.8	7,260 ± 40	7,560–7,390
CA-SCR-7, Laguna Creek	Beta-204032	Left femur	Surface	3,670 ± 40	−15.3	3,830 ± 40	3,550–3,320
CA-SLO-2, Diablo Canyon	Beta-206363	Tibiotarsus	120–130	7,310 ± 40	−13.0	7,510 ± 40	7,720–7,630
CA-SLO-2, Diablo Canyon	SR-6833	Tarsometatarsus	290–300	—	−13.2	8,355 ± 25	8,580–8,440
CA-VEN-1, Little Sycamore	Beta-206734	Tibiotarsus	20–30	2,910 ± 40	−16.9	3,040 ± 40	2,720–2,350
CA-SMI-261, Daisy Cave	Beta-218492	Left femur	122–137	9,850 ± 70	−12.7	10,050 ± 70	11,150–10,280

*Measured ^{13}C/^{12}C ratios were calculated relative to the PDB-1 international standard.

Conclusions

Exploitation of *Chendytes lawi* colonies began soon after the earliest known human settlement of California's Channel Islands, as much as 11,500 calendar years B.P. By at least 7,500 years ago, the flightless duck was exploited by humans throughout its California range. Offshore rocks and islands that once served as refugia for *Chendytes* from terrestrial carnivores no longer provided safe haven from human predators with watercraft, as well as the dogs people brought with them. While human-induced resource suppression has been argued for other prehistoric marine resources in coastal California (19, 20), the vulnerability of *Chendytes* resulted in extinction between 3,000 and 2,000 years ago—after at least 8,000 years of human hunting.

Given the population densities and technological sophistication of native peoples along the California coast, as well as the record of rapid flightless bird extinctions elsewhere in the Pacific, it is noteworthy that this highly vulnerable species survived for so long along the Pacific Coast of North America. Although the extinction of *Chendytes* once may have been seen as a special case that required development of complex technology (e.g., seaworthy watercraft), it is now clear that such maritime technology existed along the California coast during the terminal Pleistocene (12–14). Thus, the *Chendytes* case sharply contrasts with the disappearance of late Pleistocene megafauna, none of which have produced an archaeological record comparable to the flightless duck. Few megafauna species have been recovered archaeologically, and those that are well represented (e.g., mammoths) must fit within the very narrow temporal window (13,250–12,800 calendar years B.P.) now associated with the Clovis culture (21). In addition, despite the presence of Paleoindian people throughout California, not a single well documented association of artifacts with the remains of mammoths or other Rancholabrean fauna has been found in the entire state.

There is nothing in the North American archaeological record indicating a span of exploitation for any megafaunal genera remotely as long as that of *Chendytes*. Flightless birds were eradicated relatively rapidly from many remote Pacific Islands by agricultural peoples in the late Holocene (8, 9), but these situations are not comparable to continents where animal populations would have been larger and less circumscribed. Our archaeological chronology for the extinction of *Chendytes* shows that exterminating even such a vulnerable species from continental settings took millennia of hunting by Native Americans. In contrast, Clovis peoples show no sign of such prolonged exploitation on a larger continental stage. Rapid extermination of species by humans in insular settings would have been much more feasible than on continents and is supported archaeologically by the remains of flightless birds in the Pacific (9) and inferentially by remnant populations of mammoths on islands in the Bering Sea (22). In those situations, vulnerable species persisted until mid-Holocene only because human arrival to these remote islands was delayed. Soon after humans arrived, the species disappeared, showing that island populations were uniquely vulnerable to overexploitation (23). Ground sloths on Caribbean islands, however, seem to have coexisted with humans for at least 1,000 (24) and possibly several thousand years (25), indicating that, even on islands, the process of rendering a species extinct was often prolonged. In Eurasia, megafauna extinctions were time-transgressive and overlaps with modern people lasted for tens of thousands of years (26). Along the continental mainland of North America, the protracted span of hunting that led to the extermination of *Chendytes lawi* contrasts with both the insular situations and megafaunal extinctions as envisioned in the Pleistocene overkill hypothesis. The *Chendytes* record is consistent with the Eurasian situation in suggesting that the extermination of entire populations from continents, particularly multiple species, should have been protracted and archaeologically visible if overhunting was the sole or primary cause.

Methods

Identification of *Chendytes* specimens was based on comparison with reference collections at the Los Angeles County Museum of Natural History. Radiocarbon dates were calibrated via CALIB 4, with calendar age ranges at two sigma, assuming a 100% marine diet for *Chendytes*. Sites north of Point Conception corrected with a ΔR of 290 ± 35, and sites south of Point Conception (CA-VEN-1 and CA-SMI-261) corrected with a ΔR of 225 ± 35 (27). All dates were obtained from bone collagen.

ACKNOWLEDGMENTS. We thank Dan Guthrie, David Wake, and James Kennett for reviewing earlier drafts of the manuscript. Dating and identifications for Diablo Canyon specimens were funded by California Sea Grant R/CZ-187. Dating of the CA-VEN-1 specimen was funded by the California Department of Parks and Recreation, and dating of the San Miguel Island specimen was funded by the University of Oregon.

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