Holocene underkill

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In this issue of PNAS, Jones *et al.* (1) address an issue that has been with us, in one way or another, for some 200 years. Around the year 1800, French paleontologist Georges Cuvier established the reality of vertebrate extinction by using animals so large that their future discovery on the hoof was highly unlikely (2). Included on the list were some now known to have been late Pleistocene in age, including mammoth and mastodon. As time went on, the list of extinct American and Eurasian mammals of this age grew hand in hand with our understanding of the geological deposits in which the fossils were embedded. As this happened, it became harder and harder to understand why all of these extinctions had occurred.

Things became even more complex in 1859, not because of the publication of Darwin's *On the Origin of Species*, but because that year also saw the recognition that the animals had actually coexisted with humans (3). Such coexistence raised the possibility that the extinctions had happened at least in part because of human hunting. Soon after 1860 many scientists agreed that people must have played some role in causing the losses.

Pleistocene Overkill

During the ensuing century, it was generally thought that the extinctions were most likely caused by a combination of human predation and climate change. All of that changed in 1967, with the publication of a powerful paper by paleoecologist Paul S. Martin (4). Martin observed that the North American extinctions seemed to coincide with the first arrival of people here, a phenenomen known as Clovis and dated to 11,000 ^{14}C (≈13,000 calibrated) years ago, plus or minus a few centuries (5). It was the sudden arrival of human predators in the Americas, he argued, that put an end to a diverse array of herbivores and the carnivores dependent on them, a process that became known as "Pleistocene overkill." He soon argued that all of this happened within a few hundred years, a "prehistoric blitzkrieg" (6).

The loss of some 35 genera of North American mammals toward the end of the Pleistocene continues to be hotly debated. Most of the mammals involved were huge: a ground sloth with the height of a giraffe and the bulk of an elephant (*Eremotherium*) and a beaver the size of a black bear (*Castoroides*). However, not all were large: the short-faced skunk (*Brachyprotoma*), the Aztlan hare (*Aztlanolagus*), and the diminutive pronghorn (*Capromeryx*) were small, the latter weighing no more than 15 kg. Although the timing of the losses is unclear, there is no reason to think that any lasted significantly after ≈10,500 ^{14}C years ago, whereas 16 of the mammals are known to have existed beyond 12,000 ^{14}C years ago. Some, however, cannot be shown to have survived the last glacial maximum, some 22,000 to 18,000 ^{14}C years ago (7).

From the beginning, the fate of species on islands has been critical to the overkill argument. Martin observed that

Island extinctions in the Pacific were associated with massive landscape modification.

in prehistoric island settings extinctions seemed to follow human colonization with great speed (moas in New Zealand, sloths in the Caribbean, flightless rails in Oceania); all seemed to have been quickly doomed by the arrival of humans. Human hunters and naïve prey could not, he argued, coexist in such settings: people arrived and extinction quickly followed.

Chendytes lawi

The extinct flightless sea duck *Chendytes lawi*, discussed by Jones *et al.* (1), provides an important counter-example.

Apparently most closely related to the eiders (*Somateria*) (8), *C. lawi* was defined by Loye Miller (9) in 1925 based on two specimens from late Pleistocene deposits near Santa Monica, California. He recognized it as a large species of extinct waterfowl but because only leg elements were known, he could not tell that it was flightless. That understanding came in 1947 when Hildegarde Howard (10) announced the discovery of wing bones that showed the bird could not fly.

For many years, it was widely assumed that *Chendytes* had been lost toward the end of the Pleistocene, even though there were early reports of material from archaeological contexts. Survival well into the Holocene became clear in 1976, when G. V. Morejohn (11) reported *C. lawi* bones in an archaeological site north of Santa Cruz, California dated to between 5,400 and 3,800 ^{14}C years ago. He estimated that the extinction of this bird had occurred between 2,500 and 3,000 years ago.

Jones *et al.* (1) now confirm that estimate, presenting new radiocarbon dates showing the survival of *Chendytes* to 3,000 ^{14}C, or ≈2,500 calibrated, years ago. Younger sites within what was once *Chendytes* territory do not contain *Chendytes* remains, suggesting that this date is likely to be very close to the time of extinction in this area.

The early literature on *C. lawi* understandably focused on its morphology and skeletal similarities and differences with other waterfowl and other flightless birds. Morejohn (11) speculated that the bird likely bred on offshore islands where it would be relatively immune to predation. This speculation was confirmed with Daniel Guthrie's report (12) of both immature individuals and eggshells in late Pleistocene sites on San Miguel Island, one of California's Channel Islands.

So we now know that the bird survived until 2,500 years ago and that it nested on islands. We also know that coastal California, including its islands, has an archaeological record that extends back into the latest Pleistocene (13). The simple presence of a *Chendytes* bone in the lowest level of Daisy Cave, on San Miguel Island, dated to 10,000 ^{14}C years ago, does not mean that it represents an animal hunted by people or even introduced into the site by them. However, it does show that people and the bird were at the same place at the same time. In addition, the fact that *Chendytes* remains have been found at so many island and mainland archaeological sites, sometimes in great number, strongly suggests that people were preying on them, although taphonomic analysis of all of this material would be helpful. As Jones *et al.* (1) note, even the specimens from mainland

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sites likely reflect hunting activities on nearby islands.

Holocene Underkill

This work establishes that people coexisted with, and fairly obviously preyed on, a flightless, ground-nesting bird for some 8,000 years. In the Greater Antilles, there is strong evidence that people coexisted with ground sloths for 1,000 years (14). We are thus now learning that rapid extinction is not the only possible outcome for such vulnerable species as flightless ducks and huge sloths, even if it is a common one. We are also learning that late Pleistocene species that became stranded on islands did not always require a human presence to end their existence. Mammoths became extinct on St. Paul Island in the Bering Sea after 5,700 ^{14}C years ago even though people did not arrive there until historic times (15, 16). A similar event occurred in Ireland and on the Isle of Man, where the giant deer *Megaloceros* was lost shortly after 11,000 ^{14}C years ago, again before people arrived (17).

It is all so much more complicated than we thought only a few years ago. What has made the difference is the construction of individual species histories. Rather than assuming that everything was lost at the same time and for the same reason, an assumption that is still routinely made for North America, focusing on the histories of individual species takes into explicit account the fact that, as Henry Gleason (18) once put it, every species ''is a law unto itself.'' Paleoecologists and ecologists alike now recognize that ''Gleasonian individualism'' is the general rule, not the exception. If that is the case, the knotty problem of understanding the North American extinctions is not likely to be solved until each species involved has been provided with its own history. This process is well under way in Eurasia, but has barely begun in North America (19).

The intellectual history of *Chendytes* shows the pattern well. Once thought to have been part of a wave of Pleistocene extinctions, it is now known to have lasted well into the Holocene. The same can be said for many other species, giant deer and muskox in Eurasia, for instance, and the North American vampire bat *Desmodus stocki*, all now known to have lasted into, and sometimes deep into, the Holocene (17, 20, 21). Although it is unlikely that any of the North American genera involved in the debate survived this long, it remains fully possible that substantial losses occurred long before the 11,000 year date that has been the focus of the debate (19).

But the history of *Chendytes* does far more than illustrate the benefits of building individual species histories. Given the rapidly achieved fate of so many island-breeding birds after prehistoric human arrival (22), how did this particular island breeder manage to last so many thousands of years alongside people?

The difference may have something to do with the multitude of impacts that people have on islands once they arrive. Jones *et al.* (1) suggest that in the Pacific the people involved were horticulturalists, but this is not quite true. Moas were lost on both South and North Island, New Zealand, but most of South Island was too cold to support the tropical food plants so important elsewhere in Oceania. However, island extinctions in the Pacific were associated with massive landscape modification, including burning and the introduction of exotic animals, most notably the Pacific rat (*Rattus exulans*) and dog. The human arrival on islands in other parts of the world was also routinely associated with significant habitat alteration. All agree that it was not just human hunting that contributed to species loss in island settings, but the many and varied impacts that people had on the landscape.

For breeding populations of *Chendytes* on the Channel Islands, one such additional impact is provided by the fox, *Urocyon littoralis*, seemingly introduced by people by at least the middle Holocene, before the bird's extinction (ref. 23 and T. Rick, personal communication). As Jones *et al.* (1) observe, dogs may have played a role as well, as might the postglacial loss of breeding islands as a result of rising sea levels.

The lesson seems to be that it is not necessarily hunting *per se* that has driven so many species to extinction so quickly on many islands. It is instead the interaction of the varied impacts, including hunting, that people had on the landscape, coupled with the ecology of each species, that determined the magnitude and speed of the losses. This is far from the requirements of the classic overkill argument, which sees islands as analogous to continents and requires rapid extinction in all settings.

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