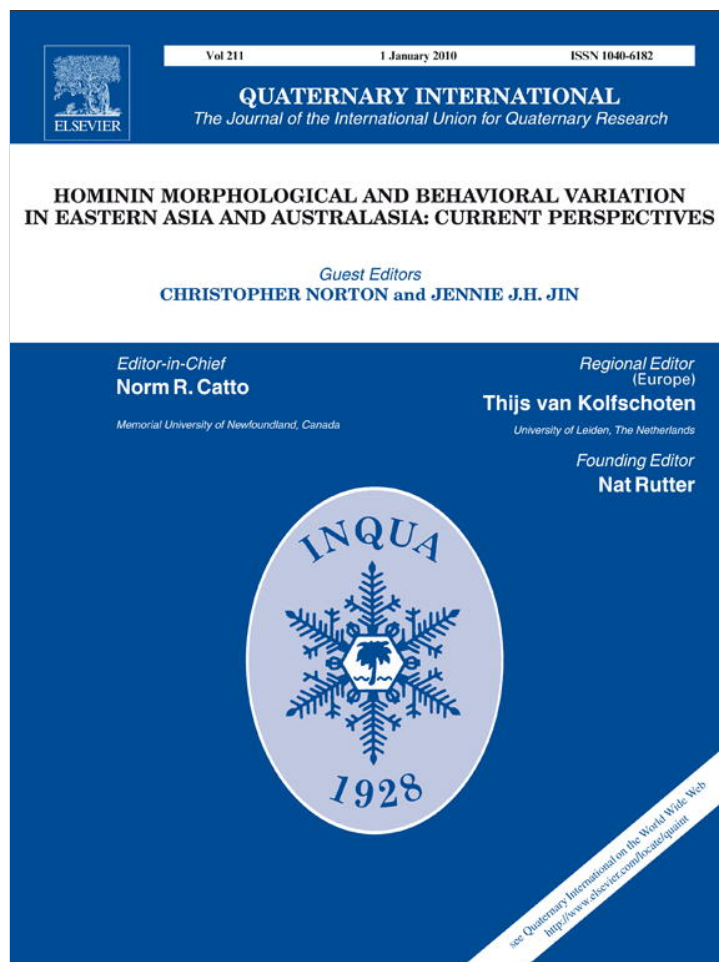


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The nature of megafaunal extinctions during the MIS 3–2 transition in Japan

Christopher J. Norton^{a,*}, Youichi Kondo^b, Akira Ono^c, Yingqi Zhang^d, Mark C. Diab^e^a Department of Anthropology, University of Hawaii at Manoa, 2424 Maile Way, Saunders Hall 346, Honolulu, HI 96822, USA^b Nojiriko Museum, 287-5, Nojiri, Shinano-machi Kamiminochi-gun, Nagano 389-1303, Japan^c Archaeology Laboratory, Tokyo Metropolitan University, Minami-Osawa 1-1, Hachioji City, Tokyo 192-0397, Japan^d Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Beijing 100044, The People's Republic of China^e Laboratory of Human Evolution, Department of Integrated Biosciences, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa 277-8562, Japan

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ABSTRACT

The nature of late Quaternary megafaunal extinctions has been the subject of intense debate since the 1960s. Traditionally, scientists cite either climatic changes or human predation as the primary reason for worldwide megafaunal extinctions. In many island cases (e.g., Madagascar, New Zealand), scientists have had a tendency to lean toward humans as being the direct or indirect dominant cause for the relatively quick extirpation of indigenous megafaunas. This study evaluates the record for megafaunal (e.g., *Palaeoloxodon*, *Mammuthus*, *Sinomegaceros*) extinctions in the Japanese islands and draw the tentative conclusion that: (1) humans directly and/or indirectly influenced the extinction of some large herbivores; and (2) the megafaunal extinctions likely began earlier than originally proposed; during the marine isotope stage (“MIS”) 3–2 transition (~30–20 ka) rather than during the MIS 2–1 (~15–10 ka) shift that roughly coincides with the advent of the Jomon period in Japan. However, we temper our findings due to the current paucity of sites in Japan that have associated archaeology and vertebrate paleontological materials that date to the MIS 3–2 transition.

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1. Introduction

The causal factors underlying Pleistocene megafaunal extinctions throughout the Old and New Worlds are one of the most debated topics in Quaternary research (Martin, 1984, 2005; Grayson, 2001; Haynes, 2002; Steadman and Martin, 2003; Barnosky et al., 2004; Meltzer, 2004; Burney and Flannery, 2005; Koch and Barnosky, 2006; Ugan and Byers, 2007; Surovell and Waguespack, 2008). At opposite ends of the spectrum, proposed primary reasons for megafaunal extirpations have ranged from climatic factors (e.g., Graham and Lundelius, 1984; Guthrie, 1984; Sher, 1997; Grayson and Meltzer, 2003; Wroe and Field, 2006; Ugan and Byers, 2007, 2008; Pushkina and Raia, 2008) to human predation and overkill (e.g., Martin, 1984, 2005; Fiedel and Haynes, 2004; Surovell et al., 2005). Recent reviews (e.g., Grayson, 2001; Barnosky et al., 2004; Burney and Flannery, 2005; Koch and Barnosky, 2006) suggest that megafaunal extinctions were likely multi-causal events and region-specific. As outlined by Barnosky et al. (2004), the megafaunal extirpations debate has been studied through computer simulations (e.g., Mithen, 1993; Alroy, 2001; Brook and Bowman, 2004), dating (e.g., MacPhee et al., 2002;

Kuzmin and Orlova, 2004; Ugan and Byers, 2007), stable isotope bone and tooth chemistry (e.g., Hoppe, 2004), and the archaeological and vertebrate paleontological (e.g., Grayson, 2001; Haynes, 2002; Steadman and Martin, 2003; Surovell and Waguespack, 2008) records. Not surprisingly, different approaches have drawn different conclusions.

Extinction is a fundamental part of nature. At its simplest explanation, extinction is the “flip side of speciation”, meaning a species' population size merely reaches a value of zero (Vincent and Brown, 2005: 233). MacPhee and Flemming (2001: 217) define it as the “... loss of all members of a minimally diagnosable evolutionary unit”. Extinction is multi-causal and complex, and is caused by habitat destruction/change, overexploitation, and competitive exclusion (Vincent and Brown, 2005; Koch and Barnosky, 2006). Additionally, there is a stochastic element to extinction that hinges on internal population demographics as well as environmental change (cf., Melbourne and Hastings, 2008). It has also been demonstrated that humans are essential components, creators, and destroyers of ecosystems (Birks et al., 1988; Smith and Wishnie, 2000; Grayson, 2001; Koch and Barnosky, 2006), and thus need to be factored into any discussions of faunal extirpations.

Perhaps the strongest support for human-influenced faunal extinctions comes from islands where human occupation occurred relatively late in prehistory followed by an almost immediate

* Corresponding author.

E-mail address: cnorton@hawaii.edu (C.J. Norton).

extirpation of many of the indigenous island faunas (Martin and Steadman, 1999; Grayson, 2001; Steadman and Martin, 2003). Indeed, even scholars who may be considered to lean toward climate-related explanations note that “there is no question that humans have caused extinctions in constrained environments such as islands” (Ugan and Byers, 2007: 3073; see also Grayson, 2001). Perhaps one of the strongest cases for human-induced faunal extirpations is the rapid extermination of moas (*Dinornis*), a flightless bird, on New Zealand (Worthy and Holdaway, 2002). Originally, moas had only one natural predator, the Haast's eagle (*Harpagornis moorei*). However, upon initial migration to New Zealand by the Maori before 1300 A.D., within 100 years the moas went extinct. It is argued that human hunting of the moas led directly to their extirpation (Holdaway and Jacomb, 2000; Worthy and Holdaway, 2002). Other examples include the extinction of many larger non-human primate taxa on Madagascar within 200 years of the appearance of humans (Burney et al., 2003), and the extermination of many flightless birds in the Hawaiian islands soon after the arrival of humans (Burney and Flannery, 2005; see also Steadman, 1995; Steadman et al., 2002; Steadman and Martin, 2003).

A substantial amount of research has been dedicated to megafaunal extinctions in North America (e.g., Grayson, 2001; Grayson and Meltzer, 2002, 2003; Haynes, 2002; Surovell and Waguespack, 2008), Australia (e.g., Miller et al., 1999; Roberts et al., 2001; Wroe et al., 2004; Wroe and Field, 2006), and broader Old World contexts (e.g., Martin, 1984, 2005; Surovell et al., 2005; Ugan and Byers, 2007, 2008; Pushkina and Raia, 2008). The purpose of this paper is to add the Japanese record to this debate, particularly because the factors underlying the disappearance of the megafauna on the Japanese archipelago during the Pleistocene have never been clearly understood or synthesized (but see Kawamura, 2007). In this paper, “megafauna” refers to large mammal and very large mammal taxa, particularly focusing on the Artiodactyla, Proboscidea, and Perissodactyla (>30 kg; see Norton and Gao (2008) taxon sizes 2–5).

2. Background

Japan is an archipelago comprised of four main islands (from north to south: Hokkaido, Honshu, Shikoku, Kyushu) and a series of smaller island chains further to the south (e.g., Ryukyu). Most Japanese Quaternary paleontologists (e.g., Kawamura et al., 1989; Kawamura, 2001, 2007; Takahashi et al., 2006) consider Hokkaido distinct from the Honshu-Shikoku-Kyushu (“HSK”) and Ryukyu faunal zones (Fig. 1). Kawamura (2007) notes that the Hokkaido fauna is more similar to the Asian mainland (indicating many land connections during the Pleistocene), the Ryukyu islands are dominated by endemic faunas, and HSK comprised a combination of both (see also Millien-Parra and Jaeger, 1999). The Mamiya Strait that separates the Asian mainland and Sakhalin is 12 m deep, while the Soya Strait that separates Sakhalin and Hokkaido is 55 m deep. During glacial periods Sakhalin and Hokkaido would have been connected to the Asian mainland. However, the Tsugaru Strait that separates Hokkaido and Honshu is about 130 m deep, which is similar to the Tsushima Strait that separates the Korean Peninsula and HSK (Fig. 1); thus, only during major glacial periods would a land connection exist between Hokkaido and Honshu. In this paper we concentrate our discussion on the HSK islands because most of the megafauna that disappeared during the Late Pleistocene and almost all current evidence for early hominin dispersals to Japan are restricted to that region.¹

For most of the Quaternary, Japan was separated from the Asian mainland (Millien-Parra and Jaeger, 1999; Ono, 2004; Matsufuji, in press). Vertebrate paleontological studies suggest that at least two times during the Middle Pleistocene land bridges connected the archipelago with the mainland (and possibly more, but of shorter durations: see Kawamura, 2001). During marine isotope stage (MIS) 16 (~0.63 Ma) *Stegodon orientalis* (*Stegodon* elephant) and during MIS 12 (~0.43 Ma) *Palaeoloxodon naumanni* made their appearance in Japan for the first time, likely through land connections between southern Korea and Japan (Konishi and Yoshikawa, 1999; see Table 1 for description of the marine isotope stages). *Sinomegaceros yabei* also appears for the first time in Japan during the Middle Pleistocene (Otsuka, 1987). During the Late Pleistocene [e.g., Last Glacial Maximum (~20–18 ka) when worldwide sea levels dropped an estimated 100–130 m], it is questionable whether a land bridge existed between Japan and the Asian mainland (for varying reconstructions see: Millien-Parra and Jaeger, 1999; Park, 2001; Ono, 2004; Kawamura, 2007; Norton, 2007; Lee et al., 2008; Pope and Terrell, 2008).

A number of hypotheses have been proposed to explain when the earliest peopling of Japan may have occurred. For example, Matsufuji (1999, in press) suggested that hominin occupation of the Japanese archipelago initially occurred sometime during MIS 6 (~186–127 ka). In support of this argument, Matsufuji (in press) considers Kanedori (located in northeastern Honshu; see Fig. 1) the “earliest” site in Japan with archaeological materials identified in the same horizon as an array of tephra (e.g., Aso-4, K-Tz) that range in age between 115 and 84 ka and falls within MIS 5 (~127–76 ka). Because MIS 5 is considered a generally warm climatic period with high sea levels, Matsufuji (in press) suggests MIS 6, being colder and with lower sea levels, would have been a more likely time for hominins to have reached the Japanese archipelago. Although evidence is present for hominins occupying the Korean Peninsula by the Middle Pleistocene (Norton, 2000; Norton et al., 2006; Norton and Bae, 2008; Bae, in press), there is currently no evidence to support the hypothesis that hominin dispersals reached Japan during MIS 6 or earlier. More detailed research should be designed to test the hypothesis that hominins reached Japan during the Middle Pleistocene.

Matsufuji's (in press) argument aside, currently there is no evidence for hominin occupation of the Japanese archipelago at any time prior to the advent of the Late Pleistocene and possibly not until MIS 3 (~59–24 ka; Ono, 2004). Only a handful of the more than 5400 reported Paleolithic sites in Japan are purported to be older than ~30 ka (Ono, 2004; Matsufuji, in press). The majority of the pre-30 ka sites have questions concerning their ages, contexts, and/or artifactual nature. For instance, questions exist about whether the Kanedori fractured stones from the lowest stratum are geofacts or artifacts. Aside from Kanedori, the earliest accepted archaeological site in Japan is Tategahana, Nojiriko with calibrated ¹⁴C dates ranging between 47 and 31 ka from different stratigraphic levels (Sawada et al., 1992; Nojiriko Excavation Research Group, 1994). Tategahana is an open-air lake-shore site that is best known for the presence of *Palaeoloxodon naumanni* and *Sinomegaceros yabei* fossils in association with archaeological traces (Kondo et al., 2001, 2007; Ono, 2004). Tategahana was interpreted as a kill and butchery site (Nojiriko Excavation Research Group, 1994; Kondo et al., 2001; Ono, 2001). The faunal materials from Tategahana are discussed in more detail below.

3. Megafaunal extinctions in Japan

As in other regions of the world, the nature of megafaunal extinctions in Japan is usually considered to be the result of a combination of environmental and cultural processes (e.g., Kawamura, 2007). We investigate the environmental and cultural influences that

¹ Not including the human fossil remains from Yamashita-cho, Okinawa that date to ~32 ka (Kobayashi et al., 1971).

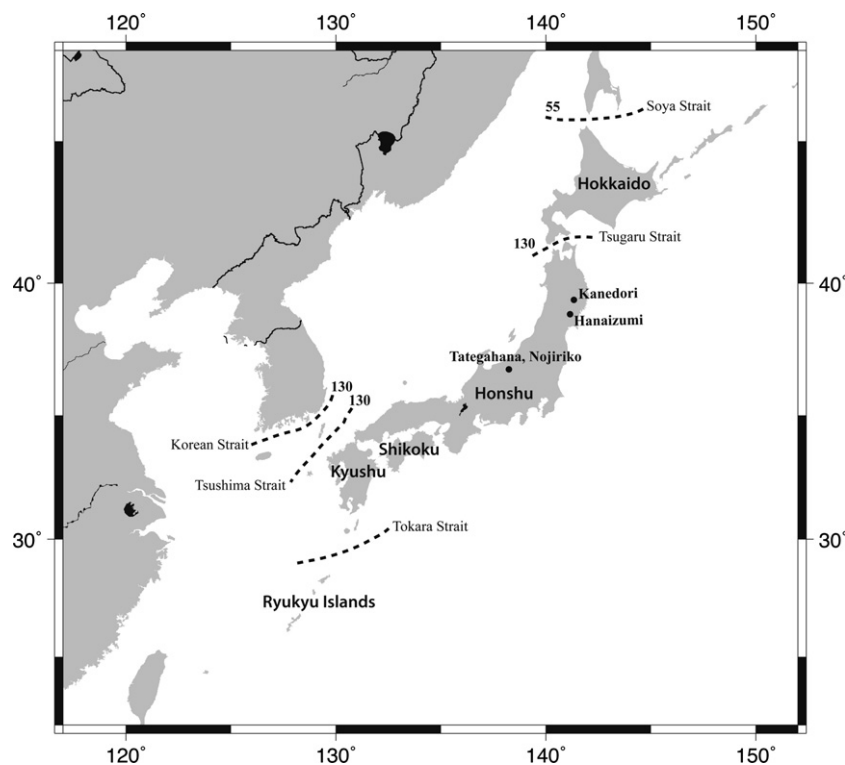


Fig. 1. Map of Japanese archipelago with biogeographic divisions and locations of sites discussed in text. See text for explanation of the biogeographic divisions and the meaning of the variation in paleobathymetry.

may have directly or indirectly caused the decimation and eventual extinction of many species of megafauna (e.g., *Palaeoloxodon*, *Sinomegaceros*) in Japan during the Late Pleistocene.

3.1. Environmental factors

Late Neogene and Quaternary environmental variation played a major role in affecting hominin evolution, particularly by influencing the patterning of dispersals and hominin behaviors (Vrba, 1995, 1996; Potts, 1996, 1998; Dennell and Roebroeks, 2005; Dennell, in press). A good example of this is the impact that cold climates had on hominin dispersals into more northerly latitudes. Current paleoanthropological evidence suggests that hominins did not arrive in northern Siberia until the latter part of the Late Pleistocene (Goebel, 1999; Goebel et al., 2008), but see evidence from Diring Yuriakh (Waters et al., 1997). In East Asia, *Mammuthus* migrated southward during colder periods (Wei et al., 2006) and reached latitude 36°N (Shandong Province) by c. 33 ka (Takahashi et al., 2007).² Typical Oriental biogeographic zone faunas (e.g., *Macaca*, *Bubalus*) appear further north at Zhoukoudian and Korea during interstadials (Norton, 2000; Norton et al., in press).

Faunal dispersals and extinctions in Japan during this time period would have been similarly affected. The environment during MIS 3 in Japan has been considered to be a warm, temperate climate with a mixed forest of conifer and deciduous trees (Yasuda, 1978; Ono, 2004; Norton et al., 2007). Takahashi et al. (2006) note that *Palaeoloxodon*, a temperate forest adapted taxon, temporarily displaced *Mammuthus primigenius* in Hokkaido during MIS 3, indicating a warmer environment in the region. However, with the onset of MIS 2, subarctic coniferous forests spread southward,

followed by the repopulation of Hokkaido by *Mammuthus* (Takahashi et al., 2004, 2006).

Extinction rates in Japan appear to have been at least partially influenced by environmental changes. For example, Kawamura et al. (1989) compiled a comprehensive faunal list from Middle and Late Pleistocene Japan. In examining the rate of extinction for Artiodactyla, Proboscidea, and Perissodactyla only, seven of the 10 taxa are present in both the Middle and Late Pleistocene (Table 2). This indicates that 30% of the larger faunas went extinct or were no longer present in the HSK region by the Late Pleistocene. Using data from Kawamura (2007), we note that during the Last Glacial Maximum (LGM) and Holocene only three out of 14 Artiodactyla and Proboscidea taxa are present (Table 3). This indicates that 78.6% of the larger faunas went extinct or were no longer present in HSK during the LGM–Holocene transition. The extinction rates between the Middle–Late Pleistocene and LGM–Early Holocene are significantly different ($\chi^2 = 5.562$, $df = 1$, $p = 0.017$). Of interest here, *Palaeoloxodon*, *Mammuthus*, and *Sinomegaceros* disappear some time during the latter period, but managed to survive the Middle–Late Pleistocene transition. We argue below that the extinction of these megafauna likely date to MIS 2 rather than the LGM–Early Holocene shift (MIS 2–1), and likely started during the end of MIS 3.³

The transition from the Middle to Late Pleistocene is correlated with the shift from MIS 6–5. The transition from the Last Glacial Maximum (c. 20–18 ka) to the Holocene is roughly correlated with

² It should be noted that *Mammuthus* continue to appear in many regions of Siberia through the Last Glacial Maximum (Kuzmin and Orlova, 2004).

³ The transition from MIS 6–5 is from cold to warm, while the shift from MIS 3–2 is from warm to cold. It might be suggested that the two are not comparable. However, we argue that we are observing the degree of climatic change broadly speaking that affected the megafauna, rather than trying to determine if moving from cold to warm or warm to cold impacted particular megafauna. Further justification for this is the fact that both *Palaeoloxodon* (more warm-adapted) and *Mammuthus* (more cold-adapted) megafauna both survive MIS 6–5, but appear to go extinct during MIS 3–2.

Table 1

Breakdown of marine isotope stages that are discussed in this paper and general characteristics of each period.

Marine isotope stage (MIS)	Years BP (ka)	General climatic setting	Culture	Megafauna
2–1	~15–10	Interglacial	Incipient/Early Jomon	Absent
2 (Last Glacial Maximum)	~20–18	Full glacial	Late Paleolithic	Absent ^a
3–2	~30–20	Cold	Late Paleolithic	Reduced megafauna
3	~59–24	Cold	Late Paleolithic	Reduced megafauna
6–5e	~130–120	Cold to warm	Absent	Full megafauna
6	~186–127	Full glacial	Absent	Full megafauna
12	~430–380	Full glacial	Absent	Full megafauna
16	~680–620	Full glacial	Absent	Full megafauna

^a We suggest that *Palaeoloxodon*, *Mammuthus*, and *Sinomegaceros* disappear by the onset of the Last Glacial Maximum (see text).

Table 2

Representative Artiodactyla, Proboscidea, and Perissodactyla faunas from the Honshu–Shikoku–Kyushu region that first appears during the Middle Pleistocene (after Kawamura et al., 1989; Takahashi et al., 2006).

Order	Genus/species	Common name	Middle Pleistocene	Late Pleistocene
ARTIODACTYLA	<i>Sus scrofa</i>	Wild boar	*	*
	<i>Moschus moschiferus</i>	Siberian musk deer	*	*
	<i>Sinomegaceros yabei</i>	Yabe's giant deer	*	*
	<i>Cervus kazusensis</i>	Kazusa deer	*	*
	<i>Cervus praenipponicus</i>	Ancient Sika deer	*	*
PROBOSCIDEA	<i>Stegodon akashiensis</i>	Akashi stegodont	*	*
	<i>Stegodon orientalis</i>	Oriental stegodont	*	*
	<i>Mammuthus parammonteus shigensis</i>	Mammoth	*	*
	<i>Palaeoloxodon naumanni</i>	Naumann's elephant	*	*
PERISSODACTYLA	<i>Rhinoceros sinensis</i>	Chinese rhinoceros	*	*

The list from Kawamura et al. (1989) is more extensive but we cut the list down to only include taxa that were present in the region during the Middle Pleistocene to determine how many of those taxa also appear during the Late Pleistocene. Note: In some cases, taxa were listed at the specific level (e.g., *Sus scrofa*) and at the generic level (e.g., *Sus* sp.). Because it may be possible that some or all of the bones identified to the generic level may actually represent already identified specific level taxa, we excluded the generic-only identified taxa (e.g., *Moschus* sp., *Cervus* sp., *Sus* sp.).

the MIS 2–1 shift (Gibbard et al., 2007). Marine isotope stage reconstructions suggest that the climatic transition from MIS 6–5 was as pronounced as, if not more pronounced than, the shift from MIS 2–1 (Gibbard et al., 2007). If extinctions were based primarily on climatic changes, we might expect there to be a higher extinction rate during MIS 6–5 than MIS 2–1 or at least a similar extinction rate. This does not appear to be the case for the Japanese HSK record. In fact, we find the opposite pattern where during the MIS 2–1 transition there is a significantly higher extinction rate.

3.2. Human factors

A diversity of anthropogenic influences (e.g., human hunting, expanding human home ranges, human modification of the environment) can directly or indirectly cause faunal extinctions (Grayson, 2001; Martin, 2005; Koch and Barnosky, 2006). Successful hunting by humans is often considered to be one of the primary factors leading to the extirpation of many large mammals (Barnosky et al., 2004; Burney and Flannery, 2005). The discovery of human-induced kill and butchery sites would be good evidence to support the hypothesis that humans played a direct role in the extinction of certain taxa through hunting (Haynes, 2002; Meltzer, 2004).⁴ Perhaps the best route to identify evidence for human predation of large game is through vertebrate taphonomic approaches. Currently there are only two faunal assemblages in

Japan that date to MIS 3–2 and are of sufficient size to conduct a viable taphonomic study: Hanaizumi and Tategahana.

Fieldwork at the open-air site of Hanaizumi since the 1950s revealed an extensive faunal assemblage dominated by *Bison priscus* [minimum number of individuals (MNI) = 11], with uncalibrated and calibrated ¹⁴C dates ranging between ~35–10 ka (Norton et al., 2007). Many Japanese archaeologists (e.g., Matsumoto et al., 1959a,b) have interpreted Hanaizumi as a bison kill site. Due to the absence of accepted stone artifacts at Hanaizumi, the excavators proposed that a diversity of bone tools were used to process the bison carcasses at the site (Matsumoto et al., 1959a,b). Nevertheless, a recent study of the Hanaizumi materials indicates that very little evidence for human involvement exists at the site (e.g., hearths, knapped stone), though some evidence of human butchery and processing of the bison carcasses is present (Norton et al., 2007). The Norton et al. (2007) taphonomic study found little support for the hypothesis that Hanaizumi served as a bison kill site, but rather more likely served as a fluvial-transported allochthonous accumulation.

The discovery of a *Palaeoloxodon naumanni* molar at Tategahana, Nojiriko in the early 1960s led to large scale excavations at the site that still continue (Kondo et al., 2007). Tategahana is an open-air, lake-shore site that is dominated by *Palaeoloxodon naumanni* (MNI = 25) and *Sinomegaceros yabei* (MNI = 12) (Kondo et al., 2001). A diversity of stone and possibly bone implements has been excavated from the same stratigraphic horizons as the faunal materials. Tategahana was originally interpreted to be an elephant and giant deer kill site based on mortality profiles and the associated archaeology (Kondo et al., 2001, 2007; Ono, 2001). We report here initial observations of our ongoing taphonomic study of the megafaunal remains from Tategahana.

Although data on bone surface modifications (e.g., cut marks, tooth marks, percussion marks, trampling) were not originally collected on the Tategahana faunal assemblage, our taphonomic

⁴ One point to keep in mind is that the earliest colonization of the Japanese archipelago was likely via watercraft. Production of such devices is often considered evidence for modern human behavior (Davidson and Noble, 1992). Because evidence of successful hunting is present in other regions of East Asia at sites associated with premodern *Homo sapiens* [e.g., Xujiaiyao, China (Norton and Gao, 2008)], we anticipate the modern *Homo sapiens* dispersals to Japan to have been by efficient hunters.

Table 3

Representative Proboscidea and Artiodactyla faunas from Honshu–Shikoku–Kyushu during the Last Glacial Maximum and the Holocene (after Kawamura, 2007).

Order	Genus/species	Common name	Last Glacial Maximum	Holocene
PROBOSCIDEA	<i>Palaeoloxodon naumanni</i>	Naumann's elephant	*	
ARTIODACTYLA	<i>Sus scrofa</i>	Wild boar	*	*
	<i>Sinomegaceros yabei</i>	Yabe's giant deer	*	
	<i>Alces alces</i>	Eurasian elk	*	
	<i>Cervus praenipponicus</i>	Ancient Sika deer	*	
	<i>Cervus nippon</i>	Sika deer	*	*
	<i>Capricornis crispus</i>	Japanese serow	*	*
	<i>Bison priscus</i>	Steppe bison	*	
	<i>Bos primigenius</i>	Aurochs	*	

analysis indicates that a variety of marks are present on the cortical surfaces of the bones. For instance, we note cut marks, which could suggest defleshing activities are present on at least one *Palaeoloxodon* rib fragment (Fig. 2). Other evidence of butchering is present in the form of cut marks on a proximal metatarsal from *Sinomegaceros*, that could indicate skinning or disarticulation based on its location (Fig. 3). When compared to cut marked bone from other Pleistocene localities in Japan [e.g., Hanaizumi (Norton et al., 2007)], the Tategahana modifications are shallower and more irregular. We are unsure if these morphologies are related to the edges of the stone flakes that were found in association with the faunal materials, the size of the animals that were processed, and/or diagenetic processes. We will be conducting a variety of taphonomic experiments to determine if we can replicate these marks.

Perhaps of most interest is a fractured *Palaeoloxodon* rib (Fig. 4). For this particular specimen, we identified a piece of stone deeply embedded in the bone at the point of fracture. Although we still need to conduct more detailed study of this specimen, the piece of stone appears to have broken off a larger stone flake that may have been embedded during the hunting and/or processing of the proboscidean carcass. An alternative explanation is that trampling

by other large animals could have caused the fracture and pushed the piece of stone into the elephant rib (see Haynes, 1991). However, the lack of trampling evidence and the fact that the embedded stone flake is at the point of fracture suggests humans may be the primary reason why the stone became embedded so deeply in the elephant's rib (e.g., human hunters either drove a spear into the live elephant or during the butchering process that followed). Unfortunately, in order to preserve the fragile proboscidean bone fragment, immediately following excavation the entire specimen was soaked overnight in a preservative which makes it very difficult to remove the stone flake from the bone. Although this Tategahana fractured rib is unusual, embedded stone flakes in animal bones from Paleolithic archaeological sites have been identified in other regions of the world. For instance, Milo (1998) identified a stone flake in a *Pelorovis antiquus* (giant cape buffalo) vertebra he examined from Klasies River Mouth, a Middle Stone Age locality in South Africa associated with modern *Homo sapiens*. Milo (1998) argued that the flake was part of a stone point that broke off during the hunting.

Indirect evidence that humans played a role in the extinction of certain megafaunas could be in the form of human range expansion,

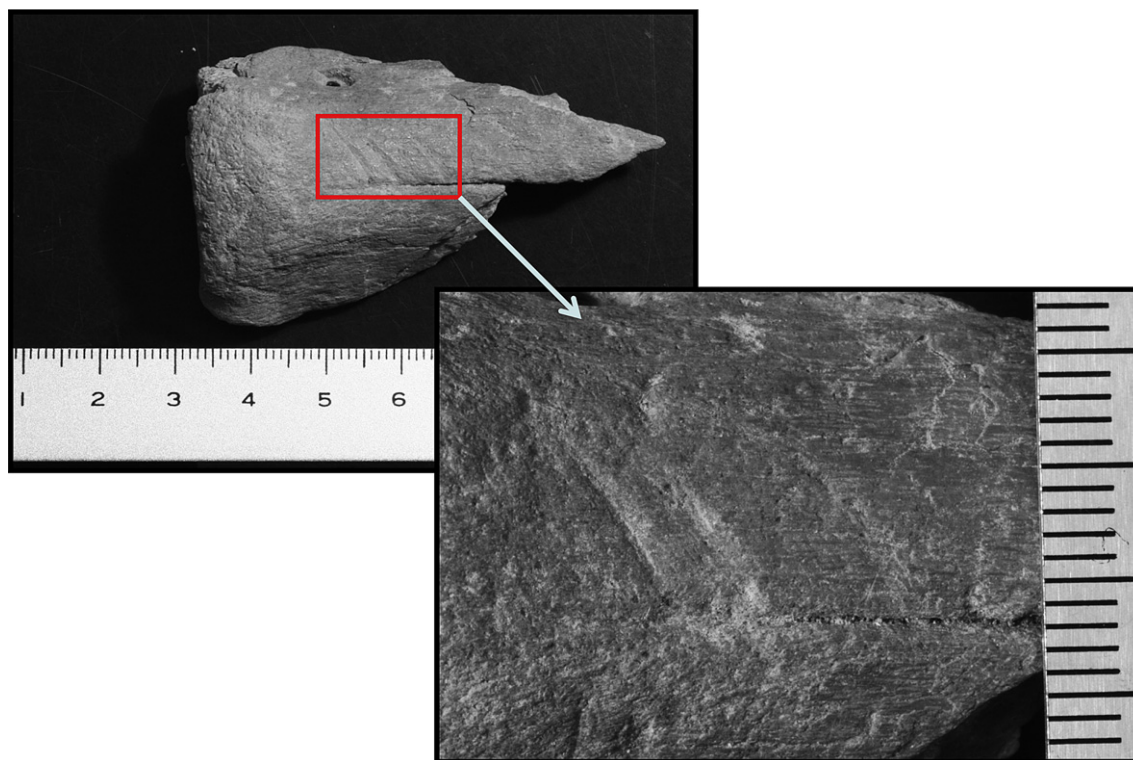


Fig. 2. *Sinomegaceros yabei* proximal metacarpal with parallel, linear striations (scale bar is in centimeters).

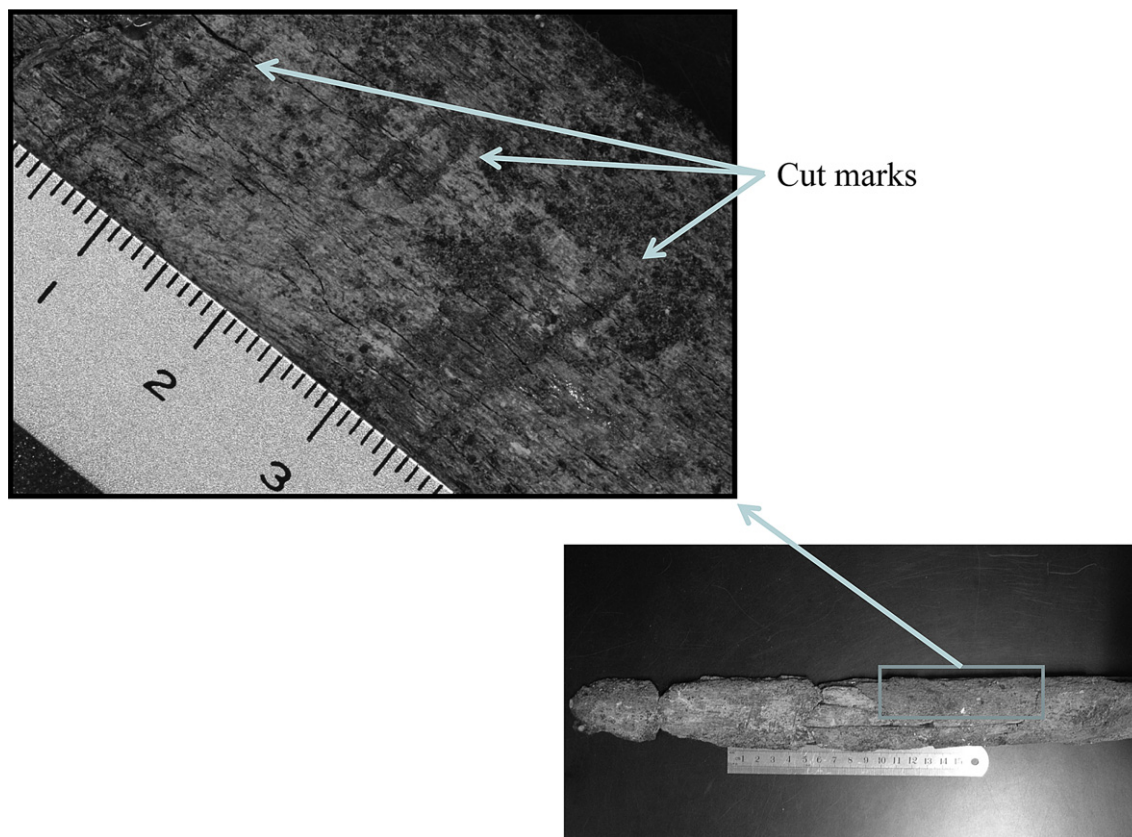


Fig. 3. *Palaeoloxodon naumanni* rib with parallel, linear striations (scale bar is in centimeters).

which could have served to push said taxa into less hospitable regions. For instance, Surovell et al. (2005) showed that as hominin range expanded during the Pleistocene throughout the Old and New Worlds, proboscideans went locally extinct (but see Ugan and Byers, 2007, 2008; Pushkina and Raia, 2008). In Japan, it is accepted that many megafauna (e.g., *Palaeoloxodon*, *Mammuthus*, *Sinomegaceros*) appeared during the Middle Pleistocene, survived the intense climatic transition between MIS 6–5, but went extinct during or by the end of MIS 2 or at the beginning of MIS 1 (Kawamura, 2007). Although direct human predation does not need to be cited as a cause for megafaunal extinctions in Japan, after 30 ka more than 5400 Paleolithic sites appear in Japan, which roughly coincides with the disappearance of the megafaunas. Indeed, if we tabulate and graph Ono et al.'s (2002) ^{14}C data, we find that after 30 ka the number of sites occupations increases, substantially after 25 ka (Fig. 5). We suggest that human population increase and range expansion in the Japanese islands particularly between 30 and 20 ka would have played a pivotal role in causing the local extinction of these megafaunas.

4. Discussion

The “Human Blitzkrieg” model, as originally proposed by Paul Martin (1973, 1984, 2005), argued that Paleoindians swept into North America during the terminal Pleistocene, carrying Clovis technologies, and wiped out the indigenous megafaunas. Martin (1984) suggested this was possible because the North American megafaunas and their natural predators coexisted for thousands of years without significantly impacting each other's reproductive cycles. However, when proficient human hunters entered North America the megafaunas were too naïve to protect themselves against this new threat. According to Martin (1984), these

megafaunas were wiped out too quickly for them to develop suitable defense mechanisms. The extirpation of these megafaunas occurred over the course of only a few centuries. Environmental factors played little or no role in the extermination of these North American megafaunas (Martin, 1973, 1984, 2005). Indeed, Paul Martin (2005: 116–117) recently reiterated this argument when he states “[t]he heart of the argument for me is that late Quaternary climatic change, while impressive, is essentially no different from what we see in many, many swings from cold-dry to warm-wet and dusty to dust-free climates in the last 700,000 years or so.” Nevertheless, as noted by Koch and Barnosky (2006: 240) “it is an oversimplification to say that an abrupt wave of hunting-induced extinctions swept continents right after first human contact.” We concur with Koch and Barnosky in that Martin's blitzkrieg model *sensu stricto* is not directly applicable at least to the Japanese case. However, we do propose that humans, either directly (through hunting) or indirectly (through home range expansion) still played a prominent role in causing the extirpation of *Palaeoloxodon*, *Mammuthus*, and *Sinomegaceros*. We do acknowledge that environmental fluctuations at least partially influenced the megafaunal extinctions in Japan.

Climatic changes likely would have influenced megafaunal lifeways during the MIS 6–5, MIS 3–2, and MIS 2–1 transitions. Because *Palaeoloxodon*, *Mammuthus*, and *Sinomegaceros* were able to survive the MIS 6–5 shift, they should have been able to survive the less severe MIS 2–1 transition just as readily. We need to search for possible causes for this.

Kawamura (2007) argued that a combination of climatic changes and influences by Jomon hunter-gatherers during the MIS 2–1 transition led to the extinction of *Sinomegaceros*, *Mammuthus*, and *Palaeoloxodon*. However, we propose that many of these megafaunal extinctions more readily date to the MIS 3–2 transition,

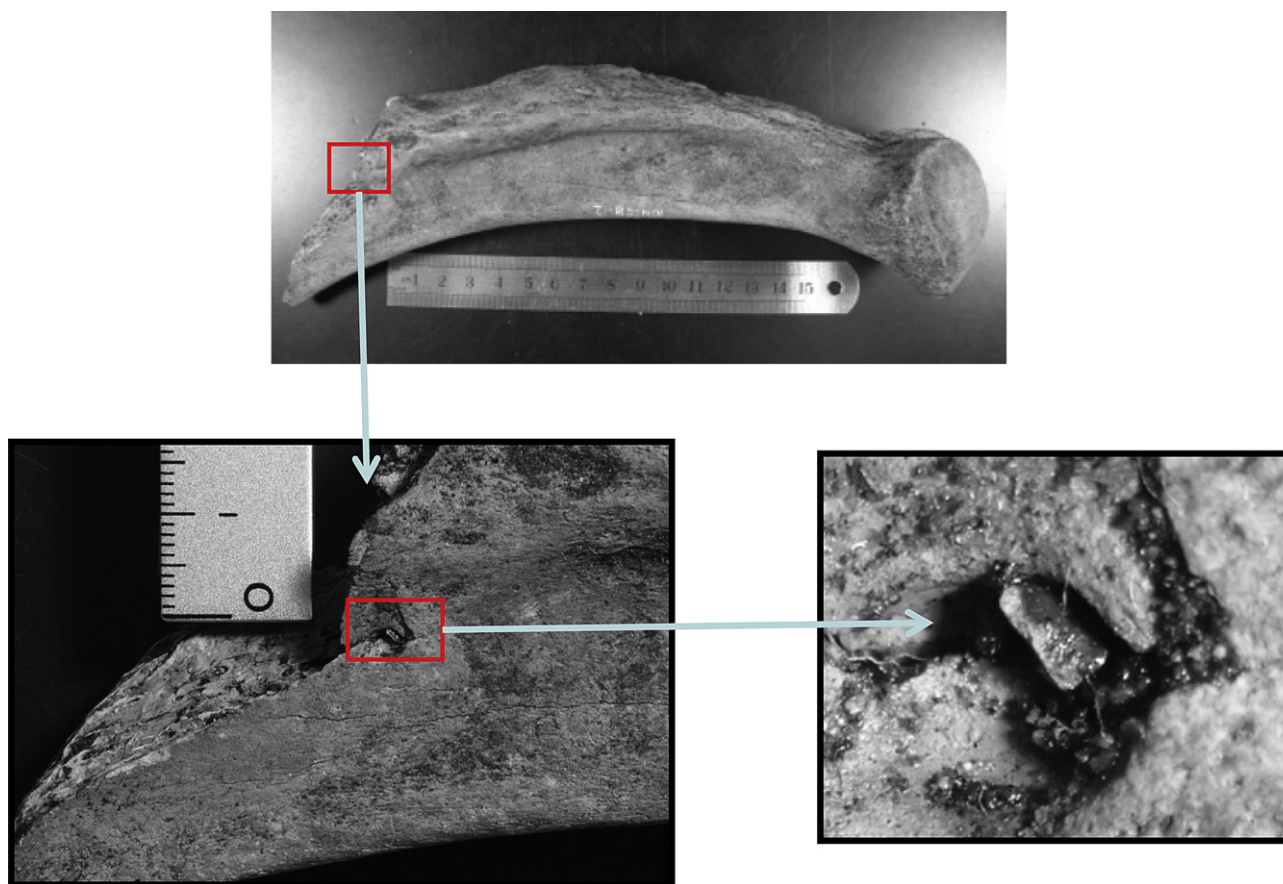


Fig. 4. Quartz stone flake embedded in *Palaeoloxodon naumanni* rib. Given the shape and angle, it may have broken off from either a spearpoint or hammerstone during hunting or butchering. Alternatively, it may have been the result of trampling by animals (scale bar is in centimeters).

particularly because the radiocarbon ages derived from many of the sites and materials that Kawamura (2007) presents could date more closely to this transition (see Ono et al., 2002; Ono, 2004). In particular, some of the ^{14}C dates used by Kawamura to support his argument are questionable. For instance, *Palaeoloxodon naumanni* was reported from Kumaishi-do Cave in Gifu Prefecture post-Last Glacial Maximum at $16,720 \pm 880$ years BP (GaK-7007; Okumura et al., 1982). However, this single uncalibrated ^{14}C date is based on an aggregate sample of bone fragments including not only *Palaeoloxodon*, but *Cervus praenipponicus* and *Sinomegaceros yabei* as well. Because the ^{14}C sample is comprised of mixed bone fragments, this age must be questioned. Further support for the argument for MIS 3–2 extinctions is the disappearance of *Mammuthus* from Hokkaido and *Palaeoloxodon* from HSK by 20 ka (Takahashi et al., 2006). Thus, we suggest it is unlikely that the early Jomon groups even saw live *Palaeoloxodon* or *Mammuthus*.⁵

Although substantial evidence for human hunting of the bison is not present at Hanaizumi, detailed taphonomic observations of the Tategahana faunal assemblage indicates that hominins were butchering at least some of the *Palaeoloxodon* and *Sinomegaceros* carcasses. We are still in the process of reconstructing the nature of hominin-megafaunal interactions at Tategahana. Nevertheless, as

discussed above, human interaction with these megafaunas could have contributed to the local extirpation and eventual extinction of these faunas. As such, we propose that:

1. The process of *Palaeoloxodon*, *Sinomegaceros*, and *Mammuthus* extinction in Japan was influenced by the initial human colonization of the Japanese archipelago after ~ 50 ka, particularly as evident from the human-megafaunal interactions at sites like Tategahana. However, the initial human dispersals into the archipelago were likely small-scale, as indicated by the low density of archaeological sites and the low density of behavioral traces at each of the sites purportedly dated between ~ 50 and 30 ka.
2. After ~ 30 ka more than 5400 Paleolithic archaeological sites appear in Japan. This directly reflects the significant increase in human population densities and proportion of the islands utilized, which would have directly or indirectly influenced megafaunal home ranges.
3. Many of the extinctions likely occurred soon after ~ 30 ka and during the MIS 3–2 transition (~ 30 – 20 ka), rather than during the MIS 2–1 transition (~ 15 – 10 ka) and before the advent of the Jomon period. In fact, there are currently no known Jomon sites that have yielded evidence of *Palaeoloxodon*, *Mammuthus*, or *Sinomegaceros* skeletal remains.

⁵ The Jomon culture appears in the archaeological record $\sim 15,000$ calibrated BP. It is beyond the scope of the current paper to evaluate the nature of the Paleolithic-Jomon transition; specifically, whether the Jomon is an indigenous development or due to colonization by foraging groups from the Asian mainland (see Imamura, 1996; Habu, 2004).

In general, *Palaeoloxodon*, *Mammuthus*, and *Sinomegaceros* are considered K-selected species, as opposed to r-selected taxa (e.g., shrews, rabbits, mice) (MacArthur and Wilson, 1967). K-selected taxa are slow reproducers and have slow birth rates, with the

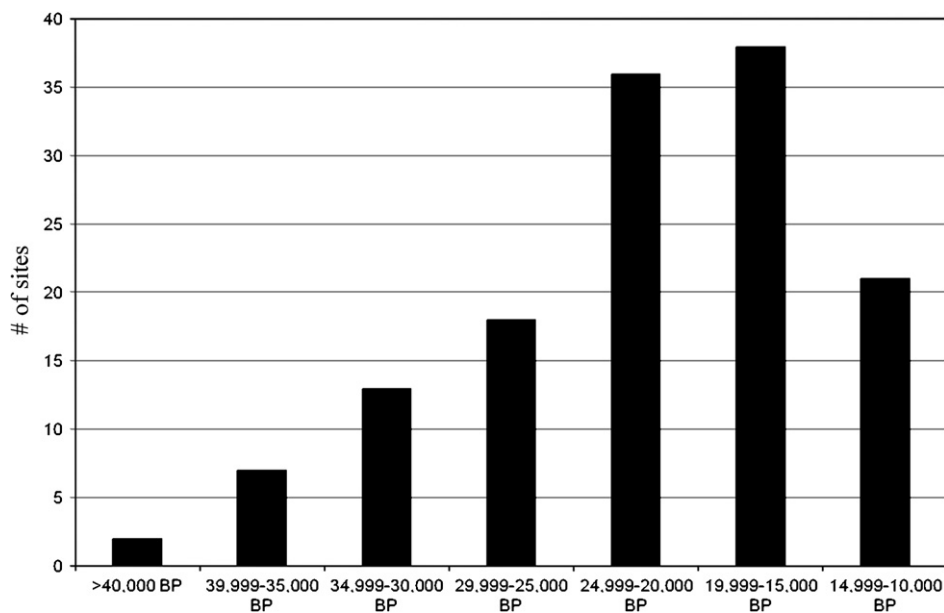


Fig. 5. Taking data from Ono et al. (2002: their Table 1), we find that the number of site occupations increases after 30 ka, particularly after 25 ka. We calculated the average ^{14}C age for sites that had multiple dates for the same stratigraphic level. For example, Tategahana stratigraphic level Upper Nojiri-ko Member I has 11 reported ^{14}C dates ranging between 42,540 and 30,580 BP. We took the average (36,699 BP) and counted it once. We counted as separate occupations ^{14}C dates for separate strata from the same site.

underlying evolutionary assumption that “by putting more energy into each offspring and producing fewer total offspring, overall individual fitness is increased” (Pianka, 1970: 592). It should be noted that “no organism is completely ‘r-selected’ or completely ‘K-selected’, but all must reach some compromise between the two extremes” (Pianka, 1970: 592). Nevertheless, K-selected species are very susceptible to even minor changes in the ecosystem (MacArthur and Wilson, 1967; Pianka, 1970, 1976). Indeed, Koch and Barnosky (2006: 226) note that “(b)ecause large body size is correlated with slow breeding, large animals would be more susceptible to extinction under any environmental or anthropogenic impact that targeted slow breeders.” Minor disruptions in their food sources or a shrinking of their home ranges could influence megafaunal rates of reproduction, thus contributing to their local extirpation and eventual extinction of the entire species (Haynes, 1991, 2002; Mithen, 1993).

The megafaunas of Japan were capable of surviving the harsher MIS 6–5 transition and not the more tolerable MIS 3–2 shift. We argue that the introduction of humans during MIS 3 disrupted the ecologies of these megafaunas; increasing human population densities caused the shrinking of the latter’s home ranges. In the face of increasing territorial circumscription, this resulted in a regular clustering into high-densities of prey species at predictable locations, whereby over time, the populations could have been more easily reduced by cursorial and/or ambush predators (see Klein and Cruz-Urbe, 1984; Stiner, 1990; Lyman, 1994 and references therein). Tategahana may be a case in point in that it appears to be a locality where *Palaeoloxodon* and *Sinomegaceros* clustered.

5. Conclusions

“There is a viewpoint among many prehistorians that if you don’t know everything, then you know nothing (paraphrased from R.J. Mason’s response to a critic [Mason, 1962]). Since no one knows “everything” about the Clovis era, owing to inadequate sampling or other reasons, does this mean that nothing should be said about it?” (Haynes, 2002: 264)

Haynes posed this question to scientists working on Clovis-related questions in North America. We suggest the same question could be posed to the Japanese megafaunal extinctions debate. The primary goal of this manuscript was to outline the nature of megafaunal extinctions in Japan and raise potential research questions that we feel could and should be asked.

Although we are still working on deciphering the disposition of megafaunal extinctions in Japan, we suggest that pre-Jomon foraging groups played a much greater role in the local extinction of *Sinomegaceros*, *Palaeoloxodon*, and *Mammuthus* than originally thought, and that the process was likely set in motion during MIS 3, culminating in the extinction of many megafaunas during MIS 2, rather than during the MIS 2–1 transition that coincides with the introduction of Jomon hunter-gatherers. An increase in secure calibrated accelerator mass spectrometry (AMS) radiocarbon samples from many of the sites and materials that date to the MIS 3–2 transition will facilitate reconstructions of the nature of these megafaunal extirpations (Ono et al., 2002; Ono, 2004).

Furthermore, it might be argued, and we would agree, that basing this megafaunal extinctions argument on taphonomic data primarily from one site is not a best case scenario. However, due to very acidic soils, bone preservation in Japan is very poor and within only a few hundred years, bones from archaeological sites disappear from almost all open-air localities. Although future fieldwork may prove otherwise, there is currently a paucity of sites in Japan that have megafaunal remains in association with cultural residues. This does not, however, mean that further studies of the nature of megafaunal extinctions in Japan are wasted energy. We do suggest that using other proxy data (e.g., stable isotope studies) can contribute to this debate in Japan.

The nature of megafaunal extinctions worldwide is still a matter of substantial debate as papers published just in the past decade illustrate (e.g., Grayson, 2001; Haynes, 2002; Steadman and Martin, 2003; Barnosky et al., 2004; Burney and Flannery, 2005; Martin, 2005; Surovell et al., 2005; Koch and Barnosky, 2006; Ugan and Byers, 2007, 2008; Surovell and Waguespack, 2008). What should be clear from this general debate, and from the discussion presented here, is that in many cases, hunter-gatherers could have directly (through hunting) or indirectly (through home range

expansion) caused the local eradication of many megafaunas. This is particularly evident in island populations, where geographic range expansion is usually restricted (e.g., New Zealand, Madagascar). The Japanese archipelago appears to be no different from the New Zealand and Madagascar cases, except that due to initial low hunter-gatherer population densities the megafaunal extinctions may have taken place over the course of a few thousand years, rather than a few centuries as what appears to have happened in the latter scenarios. Future hypothesis testing should serve to refine many of the observations presented here.

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