Abstract In the present study, we estimated age at death of extinct deer (*Cervus astylodon*) excavated from two Late Pleistocene sites in Okinawa Island (the Hananda-Gama Cave and Yamashita-cho Cave I sites) from degree of molar wear. This was done using a regression equation of extant sika deer of known age, and deriving an age estimation equation based on M3 crown height applicable to fossil specimens. We then reconstructed mortality profiles using 45 and 88 individuals of the Hananda-Gama and Yamashita-cho assemblages, respectively, and compared the profiles with those of extant and archaeological (Jomon period) sika deer (*C. nippon*) populations. The reconstructed age profiles of both sites were strikingly different from the living and hunted Jomon period profiles in relative abundance of old adults. They were more similar to the attritional mortality profiles of the extant sika deer that died by natural causes (i.e. not by human or animal predation), but showed a further shift towards older age. Combined with the fact that there is no fossil evidence of medium- to large-sized carnivores on Okinawa Island during the Late Pleistocene, our results suggest that *C. astylodon* populations had extended longevity because of low predatory pressure, including that by Paleolithic human hunters.

Key words: Pleistocene Okinawa, *Cervus astylodon*, mortality profiles, zooarchaeology, hunting

Introduction

In the Ryukyu Islands (Amami Islands, Okinawa Islands, and Sakishima Islands), there are numerous fossiliferous localities estimated to date from the end of the Pleistocene, which have yielded abundant vertebrate osseous remains. Among the excavated fossils of terrestrial vertebrates, an extinct deer species, *Cervus astylodon*, has drawn the attention of palaeontologists (Matsumoto, 1926; Tokunaga and Takai, 1939; Otsuka and Hasegawa, 1973; Takai, 1975; Hasegawa, 1978; Hasegawa et al., 1983; Ohshiro, 1994; Nohara et al., 1997; Matsumoto and Otsuka, 2000). These studies dealt with morphological description, taxonomy, and aspects of taphonomy of the deer remains, although the phylogenetic position of the extinct deer is not fully understood (Hasegawa, 1978). In the present study, we investigated the *C. astylodon* remains of two fossil-bearing sites of Okinawa Island (Okinawajima Island, the main island of the Okinawa Islands), the Hananda-Gama Cave and Yamashita-cho Cave I sites. From the excavated deer assemblages, we aim to reconstruct their mortality profiles, and examine the possibility of human hunting activity and/or life history patterns of the extinct deer.

The Hananda-Gama Cave site (26°8′7″N, 127°45′32″E) is located at the southern part of Okinawa Island. This site was excavated in 2006 and 2007, and more than 2500 identifiable vertebrate fossils were recovered (Yamasaki and Fujita, 2009). These animal remains are considered to have fallen into the cave through fissures or sink holes after decomposition. Most of the bones and teeth belong to two extinct deer species, *C. astylodon* and *Dicrocerus* sp. Only two isolated cheekteeth of boar were found; we cannot rule out the possibility that these are intrusive. The mammalian fauna of the Hananda-Gama Cave site contrasts with that of the Minatogawa fissure site in close vicinity (less than 1 km south of Hananda-Gama). At Minatogawa, deer fossils were confined to the lower levels of the fissure sediments, while boar fossils were less abundant in the lower levels but increased in number and became dominant in the upper levels. The dominance of deer at the Hananda-Gama Cave site implies that the geological age of the fossils may date back at least to that of the lower levels of the Minatogawa fissure site. Vertebrate fossils from the Minatogawa fissure site have been placed in the main part of the Last Glaciation to the end of the Pleistocene (see Matsu’ura, 1999), based primarily on two radiocarbon dates, 18250 ± 650 (TK-99) and 16600 ± 300 years BP (TK-142), of charcoal fragments from the lower levels of the site. A recent discussion on the geological age of the Minatogawa fissure sediments is available in Matsu’ura and Kondo (2011).

The Yamashita-cho Cave I site (26°11′52″N,
127°40'31"E) is also located at southern Okinawa Island, about 12.5 km northwest of Hananda-Gama. This cave is an important Pleistocene site of Japan because the earliest known human fossils of the present day Japanese archipelago, a child’s femur and tibia, were discovered there (Suzuki, 1975). This site consists of six stratigraphic layers summarized as follows. Layers I and II contained Holocene deposits, and layers III, IV, and V were considered to have been formed by Paleolithic inhabitants. The latter strata contained charcoal lens intercalations (layers III and V), a few possible stone implements (layer V) and relatively small amount of deer fossils (layer V). Layer VI contained a large number of deer fossils (Takamiya et al., 1975a, b). A radiocarbon date of $32,100 \pm 1000$ years BP (TK-78) was obtained on charcoal sampled from layer III (Takamiya et al., 1975a). The deer remains were assigned to Metacervus (Cervus) astylodon by Takai (1975), but some of them are Dicrocerus sp. according to our own observations. No boar fossils have been reported from either layers V or VI. Human skeletal remains (child’s femur and tibia) were excavated from layer VI just below its boundary with layer V. However, further research is necessary to ascertain contemporaneity of the human and deer fossils of layer VI. For example, given proximity with the layer V sediments, the possibility that the human remains are intrusive from layer V cannot be ruled out without further evaluations. Alternatively, the upper layer VI remains, including the human remains, might be temporally more closely associated with the layer V fossils than with the majority of the layer VI remains (see Matsu’ura, 1978). In any case, whereas the deer fossils from layer V might be anthropogenic, this is less certain for the layer VI remains.

Since both sites yielded considerable amounts of C. astylodon remains, it is possible to reconstruct mortality profiles of the extinct deer species, and compare them between the sites. Mortality profiles, or age-at-death distributions, reflect modes of accumulation of fossil assemblages, including human predation (Klein, 1978; Stiner, 1990). In palaeontological and zooarchaeological studies, two types of mortality profiles are recognized as fundamental to further interpretation: catastrophic and attritional (Klein, 1978; Stiner, 1990; Steele, 2003, 2005). If individuals of a population died near simultaneously by a catastrophic event, such as a flood or volcanic eruption, the mortality profile (the catastrophic mortality profile) of the assemblage would reflect the age profile of the living population, resulting in a high frequency of yearling and juvenile, gradual decrease of frequency of more aged individuals, and relatively rare occurrences of old-aged individuals. A mortality profile similar to the catastrophic profile may also result from accumulation of randomly (i.e., proportionally to the frequency of living populations) hunted animals. However, mortality profiles of prey animals hunted by Paleolithic and recent human hunters usually differ in that prime adults are more prominent due to the preference for economically rewarding prey (Stiner, 1990; Steele, 2003). The other type of mortality profile, the attritional mortality profile, reflects the number of individuals of each age class that die by natural causes, i.e., disease, starvation and non-human predation. Thus this is equivalent to a mathematical derivative of the age profile of the living population. Attritional mortality profiles are characterized by a high frequency of infants, fewer prime adults, and a rise of old age class frequencies because of the higher mortality rate of aged individuals. Thus attritional mortality profiles have two peaks and are described as “U-” or “J-shaped” (Caughley, 1966, 1977). Since medium- to large-sized carnivores are not known from the Late Pleistocene of Okinawa Island, an attritional profile might imply that the animals of the assemblages died of disease, injury, and senescence. Although other possible age distributions are possible, these two model mortality profiles offer useful guidelines for interpreting excavated assemblages.

Pioneer studies on mortality profiles of excavated animal assemblages were done by Klein and co-workers (e.g., Klein, 1978; Klein et al., 1981, 1983; Klein and Cruz-Uribe, 1984), who reconstructed mortality profiles by tooth wear for bovid assemblages from the Middle and Late Stone Age sites of South Africa. Klein (1978) found that prey mortality profiles did not differ significantly between sites but differed among species from the same site, inferring that hunting strategy varied according to prey species. Stiner (1990) provided information on mortality patterns of both non-human predation and human hunting in known modern settings, and compared them with reconstructed mortality patterns of bovids and cervids from the Middle and Upper Paleolithic sites in Italy, and more recently in fallow deer Dama cf. mesopotamica from the late Lower Paleolithic of Israel (Stiner et al., 2009). It was shown that a strategic change probably occurred through time from non-selective to prime-dominated hunting. Steele (2003, 2005) also reconstructed mortality profiles of red deer Cervus elaphus from the Middle and Upper Paleolithic sites in southwestern Europe, demonstrating prey selection for prime adults in the Middle Paleolithic. Compared to European and African regions, such studies in East Asia are so far limited. Zhang et al. (2009) reported mortality profiles of large herbivores from the Middle Paleolithic site in Henan Province, China, and indicated that the prime-dominated pattern had already established at that time also in East Asia. Among zooarchaeological studies in the Japanese archipelago, Koike and Ohtashi (1985, 1987) conducted analyses on mortality profiles of hunted sika deer C. nippon of archaeological sites of the Jomon period. Comparing the mortality profiles among sites from different time intervals, they observed a change from the “adult-abundant pattern” of the Initial and Early Jomon periods to the “juvenile-dominant pattern” of the Late Jomon and Yayoi periods, and suggested an increase in hunting pressure through time.

Age profile studies of palaeontological or archaeological assemblages of potential prey species in the Ryukyu Islands are so far limited. There is a single preliminary report on age estimation of an extinct deer species (Capreolus miyakoensis) from a non-archeological assemblage of Miyako Island, indicating a lower frequency of young adults (Zhen and Hasegawa, 1985). In the present study, we first estimated the ages of each C. astylodon specimen from degree of molar wear, and then reconstructed the mortality profiles of the deer assemblages of the two sites. With the Yamashita-cho Cave I site deer, we investigated age profiles separately for two stratigraphic intervals. This is because the fossils can be
segregated into two meaningful levels as detailed below. Finally we compared the mortality profiles of the Hananada-Gama Cave and Yamashita-cho Cave I assemblages with those of extant Japanese sika deer populations and Holocene archaeological sika deer remains. The latter were excavated from Jomon period shell midden deposits and reported in the literature.

There is some inconsistency in the descriptions of the C. astylodon bearing layers between Takai et al. (1975a) and Takai (1975). In Takai (1975), the deer specimens are reported as deriving from layers “5” and “6,” with a greater number of specimens attributed to layer “5.” This contradicts Takamiya et al. (1975a) (summarized after the second excavation in 1968–1969) who state that most of the deer fossils derive from layer VI. According to Takamiya (1967, 1968), there appears to have been some initial uncertainty in stratigraphy, with the earlier reports (of the first excavation conducted in 1962) recognizing only five layers. We suspect that much of Takai’s (1975) layer “5” deer fossils actually came from layer VI of the revised stratigraphy (Takamiya, 1968; Takamiya et al., 1975a). Therefore, we conducted an analysis of relative dating using bone fluorine content in order to clarify this uncertainty.

Materials and Methods

Materials

The specimens from the two sites that we used are listed in Appendix 1 and 2. The Hananada-Gama fossils are housed in Okinawa Prefectural Museum and Art Museum, and the Yamashita-cho Cave I collection is housed in the University Museum, The University of Tokyo. Of the fossils we identified in Appendix 1 and 2. The Hananada-Gama fossils are housed in Okinawa Prefectural Museum and Art Museum, and the Yamashita-cho Cave I collection is housed in the University Museum, The University of Tokyo. Of the fossils we identified as C. astylodon, we used all available specimens with measurable lower third molars (M3) isolated M3s and mandibles with M3s. The first and second molars were not used, because they are morphologically similar and potentially difficult to serially distinguish in ruminants.

After checking for obvious cases of antimeres, we used both right and left M3s, assuming that teeth from either sides were independent (i.e. they are not from the same individual) in order to maximize the number of specimens. We consider this procedure valid, because results of statistical comparisons of mortality profiles did not differ between sides or between the sides and the combined sample.

Fluorine dating of the Yamashita-cho samples

The Yamashita-cho Cave I materials derive from two excavations, the first in 1962 (Takamiya, 1967, 1968) and the second in 1968–1969. The stratigraphic context is outlined in Takamiya et al. (1975a), and the deer fossils are described in Takai (1975). Nearly two thirds of the Yamashita-cho sample (n = 58) were attributed by Takai (1975) to layer “5.” In contrast, Takamiya et al. (1975a) described the vast majority of deer fossils to derive from layer VI and few from layer V. We therefore consider it highly probable that Takai’s “layer “5” in part corresponds to layer VI of the revised stratigraphy. A subset of the Takai (1975) C. astylodon mandibular specimens (n = 38) was used in the fluorine analysis (Table 1).

In addition to the current University Museum, The University of Tokyo identification (ID) numbers, there is a set of previous ID numbers that accompany the specimens. These were published by Takai (1975), and appear to have been assigned in relation to an excavation code system; the first two or three digits seem to denote the excavated locus and the last two digits the order within a given locus (e.g. “4207” is the 7th specimen of locus “42”). Among Takai’s “5” specimens, 41 mandibles and five isolated molars have comparatively low locus numbers (42, 51, 58, 62, 67, 69, 77, 85, and 92) whereas the remaining 12 have higher numbers (142 and 148). We consider it probable that these sets of locus numbers correspond to the first and second excavations, respectively. Therefore, we compared bone fluorine content among three groups, i.e. layer “5” with lower number (n = 13), layer “5” with higher number (n = 12), and layer “6” (n = 13). We hypothesize that Takai’s (1975) layer “5” fossils with lower numbers and layer “6” fossils derive from layer VI of Takamiya et al. (1975a), while Takai’s (1975) layer “5” fossils with higher numbers may represent layer V of the revised stratigraphy.

About 0.03 g of powder was obtained using a dental drill from a representative portion of cortical bone of each bone specimen, after the surface at the drilling spot had been scraped away to eliminate possible contaminants such as soil particles. The powder was then subjected to fluorine content determination by the ion-sensitive electrode method, following the experimental procedure described in Matsu’ura and Kondo (2001). For a detailed description of the electrode method for fluorine analysis of bone, readers are referred to Matsu’ura (1991).

Age estimation

Although mortality patterns can be represented in histograms or box-plots of molar height (Steele, 2003, 2005), M3 height data are not necessarily available in the literature for both extant and archaeological sika deer comparative samples. In order to visualize mortality patterns of C. astylodon and to compare them with published age profiles of the sika deer, in the present study, we estimated the age of each fossil deer specimen from regression equations of age against M3 height. The regressions we used were derived from those of the modern sika deer populations for which skeletal assemblages with specimens of known age are available, and adjusted with unworn M3 crown height of C. astylodon. The latter adjustment is preferred because molar wear rates are intuitively independent of initial (unworn) crown height. The intercept adjustments correspond to increases in the regression-based age estimations of about 1–4 years, and do not significantly affect interpretations dependent on the re-constructed age patterns of the assemblages.

M3 measurement

On fully erupted molars (cervical line visible above the alveolus) we measured M3 height from the cervical line to the tip of the metaconid along the vertical axis using a digital caliper. When the molars were under eruption and could not be measured directly, we measured crown height by acquiring buccolingual cross-sectional images using the micro-computed tomography system of the University Museum, The University of Tokyo (TX225-ACTIS, TESCO
Corporation, Tokyo, Japan). The procedure of taking cross-sectional images and subsequent measuring of the molar heights is described in Ozaki et al. (2007).

$M_3$ wear rates in the modern sika deer

The age at death of each modern sika deer specimen was determined from the cementum growth layers of the I$_1$ root (methods outlined in Ohtaishi, 1980). The extant sika deer specimens we used originate from two populations of Honshu (the largest of the four main islands of Japan) region, the Izu Peninsula, and the Kinkazan Island populations. These are housed in the University Museum, The University of Tokyo. The Izu Peninsula population inhabits evergreen broad-leaved forests with some components of planted conifers, and are predominantly browsers (summarized in Ozaki et al., 2007). The vegetation of Kinkazan Island is deciduous broad-leaved forest with some open grasslands (Padmalal and Takatsuki, 1994; Takatsuki and Padmalal, 2009). The deer of this population consume leaves, twigs, and bark of woody plants, as well as significant amounts of graminoids (lawn-like grass). Because of this difference in food habits, molar wear rates differ significantly between the two populations: the Kinkazan population shows the fastest molar wear rates among the sika deer populations in Japan that we investigated, whereas the Izu population shows slower molar wear rates (Ozaki et al., 2010).

Several studies indicated that molar wear is faster in male than female deer (Loe et al., 2003; Carranza et al., 2004), but it was also shown that the difference in molar wear rates between the sexes is smaller than between species or populations with distinct food habits (Veiberg et al., 2007a, b). In the present study, only the female sika deer were used in estimation of wear rates, because available sample sizes of male sika deer were limited. If the molar wear rate of male C. asytodon was faster than female, as in the red deer male having a 1.12 times faster rate than female (Loe et al., 2003), applying female sika deer model to sex-combined fossil samples may result in slight (around 1–3 years, up to a

### Table 1. Deer mandibles from the Yamashita-cho Cave I site used for the fluorine dating

<table>
<thead>
<tr>
<th>ID</th>
<th>Layer in Takai (1975)</th>
<th>Previous ID</th>
<th>F (%)</th>
<th>Inferred source layer</th>
</tr>
</thead>
<tbody>
<tr>
<td>CV-13960</td>
<td>left mandible with M$_2$</td>
<td>“5”</td>
<td>4207</td>
<td>0.849</td>
</tr>
<tr>
<td>CV-13962</td>
<td>left mandible with M$_2$</td>
<td>“5”</td>
<td>4210</td>
<td>0.924</td>
</tr>
<tr>
<td>CV-13967</td>
<td>right mandible with P$_2$</td>
<td>“5”</td>
<td>4214</td>
<td>0.896</td>
</tr>
<tr>
<td>CV-13969</td>
<td>right mandible with M$_2$</td>
<td>“5”</td>
<td>4216</td>
<td>0.849</td>
</tr>
<tr>
<td>CV-13973</td>
<td>left mandible with P$_2$</td>
<td>“5”</td>
<td>5106</td>
<td>0.993</td>
</tr>
<tr>
<td>CV-13981</td>
<td>left mandible with M$_1$</td>
<td>“5”</td>
<td>5805</td>
<td>1.11</td>
</tr>
<tr>
<td>CV-13987</td>
<td>right mandible with M$_3$</td>
<td>“5”</td>
<td>6203</td>
<td>1.03</td>
</tr>
<tr>
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<td>right mandible with M$_3$</td>
<td>“5”</td>
<td>6204</td>
<td>0.873</td>
</tr>
<tr>
<td>CV-13993</td>
<td>right mandible with P$_3$</td>
<td>“5”</td>
<td>7704</td>
<td>1.01</td>
</tr>
<tr>
<td>CV-13994</td>
<td>right mandible with P$_3$</td>
<td>“5”</td>
<td>7705</td>
<td>1.03</td>
</tr>
<tr>
<td>CV-13998</td>
<td>left mandible with M$_1$</td>
<td>“5”</td>
<td>7709</td>
<td>0.758</td>
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<tr>
<td>CV-14006</td>
<td>left mandible with M$_1$</td>
<td>“5”</td>
<td>8505</td>
<td>1.01</td>
</tr>
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<td>“5”</td>
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</tr>
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<td>14207</td>
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<td>“5”</td>
<td>14208</td>
<td>0.583</td>
</tr>
<tr>
<td>CV-14020</td>
<td>right mandible with M$_3$</td>
<td>“5”</td>
<td>14209</td>
<td>0.621</td>
</tr>
<tr>
<td>CV-14021</td>
<td>right mandible with M$_3$</td>
<td>“5”</td>
<td>14210</td>
<td>0.707</td>
</tr>
<tr>
<td>CV-14022</td>
<td>right mandible with M$_3$</td>
<td>“5”</td>
<td>14211</td>
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</tr>
<tr>
<td>CV-14023</td>
<td>left mandible with M$_1$</td>
<td>“5”</td>
<td>14212</td>
<td>0.706</td>
</tr>
<tr>
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<td>14217</td>
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<td>14219</td>
<td>0.560</td>
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<tr>
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<td>14802</td>
<td>0.887</td>
</tr>
<tr>
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<td>“5”</td>
<td>14803</td>
<td>0.890</td>
</tr>
<tr>
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<td>left mandible with M$_3$</td>
<td>“5”</td>
<td>14804</td>
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<tr>
<td>CV-14035</td>
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<td>“5”</td>
<td>14806</td>
<td>0.707</td>
</tr>
<tr>
<td>CV-14038</td>
<td>right mandible with P$_3$</td>
<td>“6”</td>
<td>9804</td>
<td>0.925</td>
</tr>
<tr>
<td>CV-14039</td>
<td>right mandible with M$_3$</td>
<td>“6”</td>
<td>9805</td>
<td>1.09</td>
</tr>
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<td>“6”</td>
<td>9806</td>
<td>0.844</td>
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<tr>
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<td>“6”</td>
<td>11405</td>
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</tr>
<tr>
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<td>“6”</td>
<td>11406</td>
<td>0.830</td>
</tr>
<tr>
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<td>“6”</td>
<td>11407</td>
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</tr>
<tr>
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<td>“6”</td>
<td>11414</td>
<td>0.995</td>
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<tr>
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<td>left mandible with P$_3$</td>
<td>“6”</td>
<td>11418</td>
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</tr>
<tr>
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<td>left mandible with P$_3$</td>
<td>“6”</td>
<td>13006</td>
<td>0.873</td>
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<td>“6”</td>
<td>13015</td>
<td>1.16</td>
</tr>
<tr>
<td>CV-14073</td>
<td>left mandible with M$_3$</td>
<td>“6”</td>
<td>13705</td>
<td>0.721</td>
</tr>
</tbody>
</table>

Previous ID numbers are the specimen no. given in Takai (1975); F (%), fluorine content of bone samples. According to the layers reported in Takai (1975) and the previous IDs of the specimens, three groups (samples of layer “5” with low previous ID, those of layer “5” with high previous ID, and those of layer “6”) were compared for fluorine content (Figure 2).
maximum of 5 years in the Izu model using log-transformed M3 height, see below) overestimation of age for male C. astylodon individuals.

Reconstruction of mortality profiles

Because the palaeovegetation of Okinawa Islands during the last Glacial Maximum is considered to have been dominated by coniferous and evergreen broad-leaved forests (Kuroda, 1998), food habits of C. astylodon might have been similar to that of the sika deer of the Izu population, perhaps with similar molar wear rates. In the present study, however, we applied wear rate models of both Izu and Kinkazan sika deer populations in order to take into account possible variation of molar wear rates.

In the sika deer, the M3 starts occlusion at around 30 months (Ohtaishi, 1980), which is similar to the red deer (26–33 months; Brown and Chapman, 1991) and the fallow deer (26 months; Brown and Chapman, 1990). Thus we assigned an age of 30 months to unworn and slightly worn M3 of C. astylodon and considered them to represent the 2–3 year age group. Variation in age of M3 eruption (approximately 26–33 months) will not influence mortality profiles of this study because we only consider yearly frequencies after the age of 2.

For age estimation, previous studies used tooth wear stages (e.g. Brown and Chapman, 1991), the quadratic-crown height method (e.g. Klein et al., 1983; Gifford-Gonzalez, 1991), or regression equations based on known-age samples (e.g. Klein et al., 1981). Klein et al. (1981) compared regression equations based on raw measurements of molar crown height and those on natural logarithm (ln) of crown height, and showed that the log-transformation brought about a better fit of the regression for their data, assuming a rapid rate of molar wear for the initial periods of attrition and a slower rate near the end. For the sika deer populations used in the present study, nonlinearity of M3 wear was less pronounced and R² values were comparable between regressions based on raw M3 height and ln(M3 height) (Izu data, 0.81 compared to 0.76; Kinkazan data, 0.81 compared to 0.79). Thus we regressed age (in months) against both raw measurement and natural logarithm of M3 height in the two sika deer population samples. Since initial (unworn) M3 heights of the sika deer and that of C. astylodon were significantly different (mean unworn M3 height, Izu sika deer, 21.4 mm; Kinkazan sika deer, 20.8 mm; C. astylodon, 26.3 mm), we shifted the intercept so that the regression passes through the point of unworn C. astylodon M3 height (26.3 mm) at 30 months of age. Using these regression equations, the age for each C. astylodon specimen was estimated from worn M3 heights.

In order to cross-check the reliability of the above method of age estimation, we examined cementum growth layers at the M1 root (following Ohtaishi, 1980). We chose four C. astylodon mandibles with both M1 and M2 intact, so that we could compare the histologically based age estimate of the M1 with that derived from M3 wear. Following the methods described in Ohtaishi (1980) and other publications (Hachiya and Ohtaishi, 1994; Ohtaishi, 2003), we prepared thin sections (approximately 40 μm) of M1 at furcation of the roots, where thick cement is deposited (Figure 1). We carefully removed each M1 from the mandible with a dental saw and embedded it in epoxy resin. After sectioning (buccolingual direction) and grinding, we examined the section under a transmitted light microscope without staining, a method that is considered reliable for archaeological sika deer molars (Ohtaishi, 1980). A thin slice of M1 of the extant sika deer with known age (11 years old by cementum annuli of the I1) was also prepared for reference.

Mortality profiles of each fossil assemblage were expressed by yearly interval histograms starting from 2 years of age (since individuals before M3 eruption were not included). Mortality profiles of four extant sika deer populations were also constructed for comparison. Two of the populations (the eastern Hokkaido and Izu Peninsula populations) were regularly harvested. Their mortality profiles are based on randomly culled individuals, and are considered to correspond to the age histograms of living populations (i.e. equivalent to a catastrophic mortality profile). The other two populations (the Kinkazan Island and Nara Park populations) were not harvested and their age profiles are based on collected carcasses. Thus these mortality profiles are equivalent to attritional profiles. There are no sika deer predators in Kinkazan Island, whereas occasional attacks by feral dogs occur in Nara Park. The age data of the extant populations (Ohtaishi, 1975, 1976; Hokkaido Institute of Environmental Sciences, 1997; Takatsuki, 2006; Ozaki et al., 2010) and mortality profiles of the excavated Jomon sika deer (Koike and Ohtaishi, 1987) were obtained from the literature. For statistical comparisons of archaeological and extant deer mortality profiles, Kolmogorov–Smirnov tests were conducted (Sokal and Rohlf, 1995; Steele, 2003, 2005).

Results

Source bed identification of the Yamashita-cho specimens by fluorine analysis

Buried bone material takes up fluoride ions from the surrounding soil and groundwater at the cost of hydroxyl
ions in apatite crystals, and accumulates fluorine slowly with time. Analysis of this element thus provides relative dating information on bone remains from the same site or from similar sediments.

The results of fluorine analysis of the bone samples from the Yamashita-cho Cave I are given in Table 1 and shown in Figure 2. Statistical comparison by Mann–Whitney U-test among the three groups (see Figure 2) revealed that the fluorine content of samples from layer “5” with higher previous ID numbers is significantly lower than that of the others, i.e. the layer “5” with lower number, and the layer “6” samples. The box encloses the 25th and 75th percentiles, with the perpendicular line representing the median. The central 50% of the values fall within the interquartile range (the length of the box). The whiskers show the range of observed values that fall within 1.5× (the interquartile range) from the right and left edges of the box. The open circles represent values of individual specimens.

Figure 2. Box plots of comparison of fluorine content among three groups. The Yamashita-cho specimens are segregated into layer “5” with higher number, the layer “5” with lower number, and the layer “6” samples. The box encloses the 25th and 75th percentiles, with the perpendicular line representing the median. The central 50% of the values fall within the interquartile range (the length of the box). The whiskers show the range of observed values that fall within 1.5× (the interquartile range) from the right and left edges of the box. The open circles represent values of individual specimens.

Age estimation of *C. astylodon* by M₃ wear models and histological investigation

Based on the M₃ wear rate data of extant sika deer, four age estimation models were provided. Figure 3 illustrates how to obtain the age estimation equations from the original regression lines. The age estimation equations using raw M₃ height and ln(M₃ height) of the Izu data were:

\[
\text{Age} = 336.0 - 11.6 \times (M₃ \text{ height}) \quad (\text{Figure 3A})
\]

\[
\text{Age} = 630.3 - 183.6 \times \ln(M₃ \text{ height}) \quad (\text{Figure 3C}),
\]

whereas those based on the Kinkazan data were

\[
\text{Age} = 241.2 - 8.0 \times (M₃ \text{ height}) \quad (\text{Figure 3B})
\]

\[
\text{Age} = 361.4 - 101.3 \times \ln(M₃ \text{ height}) \quad (\text{Figure 3D}).
\]

The estimated ages of each *C. astylodon* specimen using these equations are shown in Appendix 1 and 2. Because the M₃ wear rate of the Izu population was slower than that of the Kinkazan population, the estimated age is older when applying the Izu model. The oldest ages obtained in the Yamashita-cho and Hananda-Gama assemblages were 26 and 25 years, respectively, by the Izu M₃ model, and 19 and 18 years, respectively, by the Kinkazan M₃ model. Application of ln(M₃) models yields younger and older estimates for individuals in the lower and higher age ranges respectively (see Appendix 1, 2). The latter effect (older age estimates of heavily worn molars) is exaggerated by the Izu model, most likely because of the truncated wear range of the reference sample.

Histological investigation of molar root cementum did correspond broadly to these estimates. In the control specimen (M₃) of extant sika deer (Figure 4A), we found clear cementum annuli (alternating opaque and translucent zones). These annuli were less clear in the thin slice preparation (Figure 4B), but the area with abundant cementocytes corresponds to the opaque layers and the area that contains fewer cementocytes is the translucent layers. Considering that the first translucent layer of the M₃ is formed during the autumn to winter season in 2 year old deer (Matsui et al., 1991), the number of annuli and the thick outermost opaque layer suggests an age of 11–11.5 years. This is comparable to its attributed age of 11 years from I₁ root cement.

In the four Hananda-Gama *C. astylodon* specimens that we examined, we could not observe such annuli, except in one specimen which showed partially preserved tissue structure. Three samples (Figure 5A–C) had dark-colored dentine and cementum regions, indicating probable diagenetic change (Burke and Castanet, 1995), and cementocytes were not identifiable. One specimen, HAN16 E13-9X (Figure 5D) exhibited clear dentinal tubules, implying better preservation of tissue structure. Cementocytes were also visible below the crown. However, the external region of the cementocyte-rich area lacks structure and is colored differently, possibly due to diagenesis. The disposition of the annuli structure was irregular and mesh-like compared to the extant sika deer example. However, a conservative count, made by omitting lines that seem to merge or disappear laterally, suggests at least seven layers, within a region of about two-thirds of the interradicular cementum thickness. This produces a minimum estimate of at least 9.5–12.5.
years, which does not contradict our estimates based on $M_3$ wear (10.5 or 13 years based on the Kinkazan model, and 17 or 18 years using the Izu model, see Appendix 1). However, our histological observations are presently limited and further analyses of better-preserved specimens are needed.

Comparisons of mortality profiles of extant and excavated deer samples

According to the results of the fluorine dating, we first compared mortality profiles of the Yamashita-cho Cave I samples of layers V (considered to be associated with human activity) and VI (association with human activity not certain). The layer V assemblage exhibited bias for older individuals, but given its small sample size, this was not statistically different from the layer VI profile (Kolmogorov–Smirnov Test, $P = 0.07$, Figure 6). In the following analyses, we used the mortality profile of the layer VI assemblage in comparisons with the extant sika deer and Hananda-Gama samples.

Figure 7 shows the mortality profiles of the extant sika deer populations (A–D) and representative archaeological sika deer assemblages from the Holocene Jomon period (E, Ishiyama, Initial Jomon; F, Fuyuki, Late Jomon). The eastern Hokkaido population exhibits a typical catastrophic profile, whereas that of the Izu population shows some irregular fluctuations from a similar catastrophic pattern. This may be due to a relatively small sample size. The Kinkazan population with a large sample size shows a representative attributional mortality profile, with the highest mortality rate at 7–8 years of age. The Nara Park population does not show such a clear peak. This difference may not only stem from smaller sample size but also from the fact that this population is under strong human influence (e.g., frequent feeding, treatment by veterinarians). The mortality profiles of the Jomon
sika deer were similar to the catastrophic profile of the Hokkaido population, although relative abundance of prime adults was higher in the Jomon assemblages.

The mortality profiles of the *C. astylodon* assemblages are shown in Figure 8. In both the Yamashita-cho (layer VI) and Hananda-Gama assemblages, the profiles obtained by the raw $M_3$ models (Figure 8A, B, E, and F) were strongly skewed to the old age class, whereas those by the ln($M_3$) models (Figure 8C, D, G, and F) showed a higher frequency of younger individuals. However, the dominance of post-prime-aged adults remained the same. Statistical comparisons of these profiles with those of the extant and Jomon sika deer revealed that the *C. astylodon* mortality profiles were significantly different from those of the sika deer populations (Kolmogorov–Smirnov Tests, $P < 0.01$ in any of the pairwise comparisons). On the other hand, there was no significant difference between the Yamashita-cho and the Hananda-Gama profiles ($P > 0.10$ in any comparisons of the same estimation models).

### Discussion and Conclusions

Using the $M_3$ wear models of modern sika deer populations, we showed that the oldest *C. astylodon* individuals of
Figure 5. Thin sections of *C. astylodon* M1 viewed under transmitted light for histological investigation of cementum growth layers. (A) HAN06 D13-6X (right M1). (B) HAN06 E13-9 (left M1). (C) HAN07 Y2 2–3 1016 (right M1). (D) HAN06 E13-9X (right M1). Microscopic structures of dentine and cementum are not observed in three specimens (A–C), probably from diagenesis. One specimen (D) shows relatively better preservation, with dentinal tubules (DT) and cementocytes (Cc) clearly visible. There are more than seven possible translucent layers of the cementum. Considering the thick outer region of cementum that lacks visible tissue structure (from diagenetic alteration), this cementum count does not contradict the age estimated from M3 wear (see text for further discussion). Abbreviations: En, enamel; Dn, dentine; Rt, root; Cm, cementum; DT, dentinal tubules; Cc, cementocytes. Scale bars are 1 mm.
the Yamashita-cho and Hananda-Gama assemblages probably reached an age of around 25 years (by the Izu models), or 18 years (by the Kinkazan models). These age estimates are equivalent to or older than the oldest individuals documented in the Kinkazan sika deer population under human protection. There are two possible explanations for these observations: (1) C. astylodon actually lived long until the M₃ were worn extremely heavily; (2) they had a much faster M₃ wear rate than even the Kinkazan sika deer, so that their age at death has been overestimated.

Although it is difficult to analytically evaluate possible differences in molar wear rates between a certain fossil and modern reference populations, we note the following circumstances that suggest that C. astylodon was actually long-lived. Firstly, the wear rate of the Kinkazan deer is the highest documented among the modern sika deer populations (Ozaki et al., 2010). The high wear rate is probably due to the Kinkazan deer habitually foraging in an open grassland, resulting in increased ingestion of soil particles and grit when they eat lawn-like grass and/or tough plant materials such as bark or twigs during food-scarce winter seasons (Takatsuki and Padmalal, 2009). On the contrary, since the vegetation of Okinawa Island during the last Glacial Maximum was characterized by coniferous and broad-leaved evergreen forests (Kuroda, 1998), the C. astylodon populations probably faced a less abrasive feeding habitat than that of modern Kinkazan Island.

As outlined above, it is possible that sexual difference in molar wear rates has biased the results somewhat towards older age. However, the magnitude of known sexual differences in modern deer molar wear rates is slight (reviewed above), and for most of the age range, such estimation bias should be within around 1–3 years. In any case, the wide range of size variation (M₁ breadth) seen in our C. astylodon samples suggest that both sexes are represented in the heavily worn individuals.

Another potential factor that might influence wear rate is the balance between tooth and body size. With other factors being equal, a species with larger teeth relative to body size could have slower wear rates. Therefore, relative tooth size of C. astylodon is of interest. Body length (back length, from withers to base of tail) is around 70 cm for the Kinkazan sika deer (Takatsuki, 2006) and 52 cm for C. astylodon (obtained from the reconstructed skeleton of Hasegawa et al., 1983); M₁ occlusal area (M₁ buccolingual breadth × M₁ anteroposterior length) is 2.5 and 1.6 cm², respectively. Thus the square root of M₁ area (79% smaller in C. astylodon) relative to body length (74% smaller in C. astylodon) is approximately isometric or slightly larger in C. astylodon. Hence there is no indication from relative tooth size that C. astylodon might have had higher wear rates than the sika deer used as analogues.

Regardless of the actual degree of longevity in C. astylodon, the mortality profiles of C. astylodon, underlain by the presence of numerous individuals with very worn M₃s (Figure 9), are skewed towards older age. When a simple ratio of relative M₃ height (M₃ height/mean unworn M₃ height) is compared, the degree of M₃ wear in C. astylodon is shown to be significantly more extreme than in the Kinkazan deer which shows the most rapid M₃ wear among the Japanese sika deer (Mann–Whitney U-tests, P < 0.01 for both cases, Figure 9A). Such heavily worn M₃s (Figure 9B) are not seen among the sika deer of extant wild populations.

This age profile of the C. astylodon assemblages differ profoundly from the catastrophic mortality profile of the extant sika deer (Figure 7A) and the hunted Jomon sika deer profiles (Figure 7E and F) in that a young adult mortality peak is lacking. The C. astylodon profile is more similar to the attritional mortality profiles of the extant sika deer populations (Figure 7C), especially when we applied ln (M₃ height) models (Figure 8C, D, G, and H), but appear to have an even older peak than that of the Kinkazan sika deer. This may reflect natural deaths in a C. astylodon population characterized by prolonged longevity, or alternatively, hunting or scavenging of older animals by humans. The latter explanation is unlikely because a human hunting strategy that focuses on the more rewarding prime adult is known as early or earlier than the late Lower Paleolithic of Eurasia and the Middle Stone Age of Africa (see Introduction), and because profiles skewed towards old age are rare in archaeological assemblages (e.g. Stiner, 1990; Steele, 2003, 2004). In addition, in the Hananda-Gama Cave assemblage, there are no obvious cutmarks or percussion marks on the postcranial bones (Yamasaki and Fujita, 2009). A taphonomical analysis of the Yamashita-cho Cave I assemblages has not yet been undertaken, but the layer V materials, considered to be associated with anthropogenic sediments, also exhibit dominance of older-aged individuals. Ecological studies of ruminant populations indicate that, under human hunting pressure, observed maximum longevity decreased because of increment of a chance to be harvested for long-living animals, and that maximum longevity increased when the populations became free from hunting pressure (Langvatn and Loison, 1999; Koizumi, 2006). This supports the idea that humans faced a less abrasive feeding habitat than that of the Kinkazan sika deer.
that the prolonged longevity of *C. astylodon* was associated with lack of significant hunting pressure from humans. In conclusion, although further evaluations are needed from a taphonomic perspective, especially regarding bone breakage and mark patterns, the present results do not support active hunting of this extinct deer species by Late Pleistocene humans. Rather, we infer that *C. astylodon* was probably under very low predatory pressure from both carnivores and humans, which might have resulted in extended longevity. Investigations of mortality profiles of other fossil assemblages in Pleistocene Okinawa and other Ryukyu Islands will elucidate whether such a life history pattern was universal to these island populations, or if there was geographical or temporal changes perhaps related to climatic induced environmental factors and/or differential human influences.

Acknowledgments

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remains. We thank the Okinawa Prefectural Archaeological Center, the Educational Board of Yaese-cho, the Educational Board of Okinawa-shi, and especially Dr. Itsuro Ohshiro, Mr. Yoshio Aragaki, Mr. Kiyoshi Miyagi, and Mr. Seiko Oyama for their kind support to our research. We thank all the people who participated in the field at Hananda-Gama and later laboratory work. Dr. Takenori Sasaki is acknowledged for access to the Yamashita-cho materials in his care.

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Figure 8. Age profiles of *C. astylodon* from the Yamashita-cho Cave I site (the layer VI specimens) and the Hananda-Gama Cave site. The upper row is based on the Izu models and the lower row by the Kinkazan models. The left two columns are using raw $M_3$ height regressions and the right two are $\ln(M_3)$ height regressions. Both assemblages lack distinct young mortality peaks and differ from the catastrophic mortality profile of the Hokkaido population (Figure 7A) or the Jomon sika deer assemblages (Figure 7E and F). These profiles are closer to the attritional mortality profile of the Kinkazan population (Figure 7C).

Figure 9. (A) Box plot of worn relative molar height. An extant sika deer population (Kinkazan) and two fossil *C. astylodon* assemblages (the Yamashita-cho Cave I and Hananda-Gama Cave sites) are compared. The y-axis is relative $M_3$ height (height/mean unworn height). See Figure 2 for the basic format of the box plot. Outliers ranged over the whiskers are presented as asterisks. The $M_3$ of both fossil assemblages are significantly more worn than in the Kinkazan sika deer. (B) Progression of $M_3$ wear in *C. astylodon* of the Hananda-Gama Cave site. Left, unworn (HAN06 D11-3); middle, well-worn (relative $M_3$ height = 0.20, HAN06 D12-3); right, extremely worn (relative $M_3$ height = 0.09, HAN06 Y48–9).
References


### MORTALITY PROFILES OF FOSSIL DEER IN OKINAWA

#### Vol. 119, 2011

**Appendix 1. *Cervus astylodon* from the Hananda-Gama Cave site, M₃ height and estimated age in month**

<table>
<thead>
<tr>
<th>ID</th>
<th>Element</th>
<th>M₃ height</th>
<th>Relative M₃ height</th>
<th>Age (95% PL) by Izu models</th>
<th>Age (95% PL) by Kinkazan models</th>
</tr>
</thead>
<tbody>
<tr>
<td>HAN06 D11-1</td>
<td>left M₃</td>
<td>13.79</td>
<td>0.52</td>
<td>176 (116–235)</td>
<td>131 (102–159)</td>
</tr>
<tr>
<td>HAN06 D11-3</td>
<td>left M₃</td>
<td>25.89¹²</td>
<td>0.98</td>
<td>274 (204–343)</td>
<td>198 (167–229)</td>
</tr>
<tr>
<td>HAN06 D12-3</td>
<td>left M₃</td>
<td>5.37</td>
<td>0.20</td>
<td>322 (255–388)</td>
<td>191 (158–224)</td>
</tr>
<tr>
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<td>left M₃</td>
<td>5.54</td>
<td>0.21</td>
<td>272 (202–341)</td>
<td>197 (166–228)</td>
</tr>
<tr>
<td>HAN06 E12-7</td>
<td>left M₃</td>
<td>17.95</td>
<td>0.68</td>
<td>316 (250–382)</td>
<td>188 (155–221)</td>
</tr>
<tr>
<td>HAN06 G6-1X</td>
<td>left M₃</td>
<td>9.73</td>
<td>0.37</td>
<td>122 (95–198)</td>
<td>95 (65–126)</td>
</tr>
<tr>
<td>HAN06 Y4 1–2</td>
<td>left M₃</td>
<td>21.03</td>
<td>0.80</td>
<td>213 (158–267)</td>
<td>131 (100–161)</td>
</tr>
<tr>
<td>HAN06 Y4 8–9</td>
<td>left M₃</td>
<td>2.37</td>
<td>0.09</td>
<td>308 (234–383)</td>
<td>222 (189–255)</td>
</tr>
<tr>
<td>HAN06 Y4 9–10</td>
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</tr>
<tr>
<td>HAN06 D11-3</td>
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<td>7.00</td>
<td>0.27</td>
<td>255 (188–322)</td>
<td>185 (154–216)</td>
</tr>
<tr>
<td>HAN06 E11-1</td>
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<td>18.42</td>
<td>0.70</td>
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<td>93 (65–122)</td>
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<tr>
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<td>left mandible with M₃</td>
<td>11.73</td>
<td>0.45</td>
<td>200 (138–261)</td>
<td>178 (147–208)</td>
</tr>
<tr>
<td>HAN06 E13-5 L</td>
<td>right M₃</td>
<td>25.42¹²</td>
<td>0.97</td>
<td>244 (178–310)</td>
<td>221 (193–255)</td>
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<tr>
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<td>left mandible with M₃</td>
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<td>0.65</td>
<td>138 (81–196)</td>
<td>112 (82–142)</td>
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<td>left M₃</td>
<td>21.07</td>
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<td>227 (172–283)</td>
<td>139 (108–170)</td>
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<td>HAN06 E13-9X</td>
<td>right mandible with Pₑ-M₃³</td>
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<td>HAN06 E13-5 S</td>
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<td>205 (174–237)</td>
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<td>58 (30–87)</td>
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<td>0.45</td>
<td>200 (138–261)</td>
<td>178 (147–208)</td>
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<td>0.34</td>
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<td>169 (139–199)</td>
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<td>0.16</td>
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<td>206 (175–238)</td>
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<td>361 (290–433)</td>
<td>213 (178–247)</td>
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<tr>
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<td>194 (163–226)</td>
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<td>305 (232–379)</td>
<td>220 (187–253)</td>
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<td>138 (81–196)</td>
<td>105 (76–133)</td>
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<td>180 (150–210)</td>
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Appendix 1. (continued)

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<th>Relative $M_3$ height</th>
<th>Age (95% PL) by Izu models</th>
<th>Age (95% PL) by Kinkazan models</th>
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Relative $M_3$ height is $M_3$ height divided by mean unworn $M_3$ height. Estimated age in months with 95% prediction limits were shown for each of the estimation models. The age estimates in the upper row are using raw $M_3$ height regression and those in the lower row are ln($M_3$ height) regression.

1 Unworn and slightly worn $M_3$s were considered to be 30 months of age (see text for further explanations).

2 $M_3$ heights were obtained by the micro-CT system.

3 Cementum annuli of $M_3$ roots were histologically investigated.
### Appendix 2. *Cervus astylodon* from the Yamashita-cho Cave I site, M₃ height, estimated age in month, and source layer

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<th>ID</th>
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<th>M₃ height</th>
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<th>Age (95% PL) by Izu model</th>
<th>Age (95% PL) by Kinkazan model</th>
<th>Layer in Takai (1975)</th>
<th>Inferred source layer</th>
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<td>191 (160–222)</td>
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<td>1.02</td>
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<td>0.44</td>
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<td>58 (30–87)</td>
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### Appendix 2. (continued)

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<th>ID</th>
<th>Elements</th>
<th>M₃ height</th>
<th>Relative M₃ height</th>
<th>Age (95% PL) by Izu model</th>
<th>Age (95% PL) by Kinkazan model</th>
<th>Layer in Takai (1975)</th>
<th>Inferred source layer</th>
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<td>CV-14042</td>
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<td>2.00</td>
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<td>177 (147–207)</td>
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<td>192 (131–253)</td>
<td>142 (113–171)</td>
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</table>

Layer in Takai (1975) and inferred source layer assigned by the fluorine dating are also shown (see text and Table 1). The age estimates in the upper row are using raw M₃ height regression and those in the lower row are ln(M₃ height) regression.

¹ Unworn M₃ were considered to be 30 months of age (see text for further explanations).
² M₃ heights were obtained by the micro-CT system.