

1 Title:

2 **Variation and mechanisms of life history evolution in insular dwarfism as revealed**
3 **by a natural experiment**

4

5 Author affiliation:

6 Shoji Hayashi^{1,2,*,**}, Mugino O. Kubo^{3,*,**}, Marcelo R. Sánchez-Villagra⁴, Hiroyuki
7 Taruno⁵, Masako Izawa⁶, Tsunehiro Shiroma⁶, Takayoshi Nakano², Masaki Fujita⁷

8

9 ¹ Faculty of Biosphere-Geosphere Science, Okayama University of Science, Kita-ku
10 Ridaicho 1-1, Okayama, 700-0005, Japan; ² Division of Materials and Manufacturing
11 Science, Graduate School of Engineering, Osaka University, Yamada-Oka, Suita, Osaka,
12 565-0871, Japan; ³ Department of Natural Environmental Studies, Graduate School of
13 Frontier Sciences, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-
14 8563, Japan; ⁴ Paläontologisches Institut und Museum der Universität Zürich, Karl
15 Schmid-Strasse 4, CH-8006 Zürich, Switzerland; ⁵ Osaka Museum of Natural History,
16 Nagai Park 1-23, Higashi-Sumiyoshi-ku, Osaka, 546-0034, Japan; ⁶ Faculty of Science,
17 University of the Ryukyus, Okinawa 903-0213, Japan; ⁷ Department of Anthropology,
18 National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba-shi, Ibaraki 305-
19 0005, Japan

20 * Both authors contributed equally to this work.

21 ** *Authors for correspondence*: Shoji Hayashi e-mail: hayashi@big.ous.ac.jp, Mugino
22 O. Kubo e-mail: mugino@k.u-tokyo.ac.jp

23

24 Keywords: Growth, longevity, Deer, bone histology, life history, Japan

25 **Abstract**

26 **Islands offer a classic topic for evolutionary studies. Few other subjects have**
27 **historically raised as much fascination as the island large mammals that having**
28 **evolved into dwarfs. Consensus has been gained that multivariate ecological causes**
29 **are behind those changes, but what remains largely unexplored are the**
30 **mechanisms behind them: how life history (age of reproduction, growth rate,**
31 **longevity) change with insular dwarfism. Previous studies produced contrasting**
32 **results difficult to compare, as they concerned different species in single islands.**
33 **The Japanese Archipelago offers worldwide a unique natural experiment, as in its**
34 **numerous islands of different sizes the same group of organisms, deer, have**
35 **evolved into different sizes. Using an extensive examination of bone**
36 **microstructure, statistical modelling of growth rate and demography, we**
37 **demonstrate different degrees of change in life history in different islands. We**
38 **discovered how different life parameters amount to a new, *K*-strategy contrasting**
39 **to that of the parent population.**

40

41 **Introduction**

42 Among the most iconic examples of visible evolutionary change are island mammals
43 that dramatically changed in body size (Foster 1964, Sander et al. 2006, van der Geer et
44 al. 2010). Elephants, hippos and deer in islands across the world became very small,
45 whereas small mammals became larger (van der Geer et al. 2010), what led to the
46 suggestion of an ‘island rule’ (Foster 1964). A classic example is the pigmy elephant
47 (*Elephas falconeri*) of Sicily, which had a body mass of only 1% of its mainland
48 ancestor (Larramendi and Palombo 2015).

49 Several factors have been proposed to be associated with these extreme changes in
50 body size, such as ecological release due to a lack of predators and competitors,
51 resource limitation on islands, founder effects of island immigrants, and the remoteness
52 and duration of isolation, all of which interact in a complex way to establish or obscure
53 the pattern of body size change in focal taxa (Lomolino et al. 2012, Lomolino et al.
54 2013, Raia and Meiri 2006, van der Geer et al. 2010, van der Geer et al. 2013).
55 Consensus has been gained that what remains largely unexplored are the mechanisms
56 behind those size changes, how life history – age of reproduction, growth rate, longevity
57 – evolves. As these animals are mostly extinct, their bones have been the source of
58 information, via studies of bone microstructure.

59 The few studies available produced contrasting results, and they were difficult to
60 compare, as they concern different species in single islands. Some studied taxa show a
61 distinctly slower growth rate and delayed somatic maturity compared with continental
62 taxa (Köhler and Moyà-Solà 2009), whereas others do not show extreme modifications
63 in their life histories (Kolb, Scheyer, Lister, et al. 2015, Kolb, Scheyer, Veitschegger, et
64 al. 2015). What is clear is that the reduction of body size in large mammals appears to
65 be associated with modification of the growth trajectory (Long et al. 2019, Palkovacs
66 2003), indicating that comparisons of trajectories of insular taxa and their mainland
67 relatives would shed light on the process of body size reduction. To achieve this, studies
68 of mainland and insular populations of a single species are particularly useful because
69 they allow confounding factors other than living on islands to be controlled.

70 The Japanese Archipelago offers worldwide a unique natural experiment, as in its
71 numerous islands of different sizes the same group of organisms, deer, have evolved
72 into different sizes. Using an extensive examination of bone microstructure, CT

73 imaging, statistical modelling of growth rate and demography, we demonstrate different
74 degrees of change in life history parameters in different islands. We discovered how
75 different life parameters amount to a new, *K*-strategy contrasting to that of the parent
76 population.

77 Extant Japanese sika deer (*Cervus nippon*) populations inhabit both the mainland and
78 islands, providing a perfect setting for testing insular effects on the growth rate and life
79 history of a species. Body size of sika deer shows considerable variation among the
80 populations, with deer in the northernmost population showing the largest body size
81 (adult male body mass of ca. 126 kg) whereas those in the southernmost insular
82 population the smallest (adult male body mass of ca. 35 kg) for the species (Kubo and
83 Takatsuki 2015, Ohtaishi 1986). We analyzed and body growth rates and life histories of
84 extant mainland and insular populations of sika deer in Japan using long bone
85 histological and demographic analyses (Figure 1).

86 To further test the predictions of the model generated by the study of extant forms, we
87 investigated the life history traits of two insular and one gigantic mainland deer that
88 became extinct in the Late Pleistocene (Figure 1). The insular deer (*Cervus astylodon*
89 and Muntiacini gen. et. sp. indet., hereafter referred to as “the Ryukyu muntjac”)
90 considered to have migrated to the Okinawa Islands during the Early Pleistocene
91 (Otsuka and Takahashi 2000). *Cervus astylodon* exhibits morphological characteristics
92 that are considered typical of insular dwarfs, e.g., a small body size, shortened limbs,
93 and hypsodont molars (Kubo et al. 2015, van der Geer et al. 2010). By contrast, the
94 gigantic mainland deer (*Sinomegaceros yabei*), from the Late Pleistocene deposits on
95 Honshu mainland, had a comparable body size to the largest extant deer, the moose
96 (*Alces alces*) (Taruno et al. 2017), which has been shown to have the highest growth

97 rate among deer (Kolb, Scheyer, Veitschegger, et al. 2015). Therefore, we expected to
98 observe significant variation in the growth rates and life histories among the extant and
99 fossil mainland and insular populations of Japanese cervids, reflecting varying levels of
100 insular effects.

101

102 **Results**

103 **Variation in bone tissue among insular cervids in Japan**

104 There were clear differences in the cortical bone tissues between extant and extinct
105 deer. The cortical bone tissues of *C. astylodon* and the Ryukyu muntjac from Okinawa
106 Island show similar features, having primary parallel-fibered bone tissue with multiple
107 LAGs, which are comparable to the features of an extinct dwarf bovid *Myotragus*
108 (Köhler and Moyà-Solà 2009) and typical extant reptiles ^{e.g.} (Woodward, Horner, and
109 Farlow 2014). The LAGs are spaced evenly throughout the cortex (Figure 2A–C; SI
110 Appendix, Figures S1A–C and S3A–F) but become closer together as they approach the
111 periosteal surface in older individuals, indicating a decrease in growth rate with age.
112 Only a few areas of the innermost cortex show a prevalence of fibro-lamellar bone
113 tissue with primary osteons, which alternates with nonvascular parallel-fibered bone
114 tissue with flattened osteocytes and LAGs. There is relatively little vascularization
115 showing the longitudinal orientation of the channels compared with other cervids and
116 large mammals (Klevezal 1996, Kolb, Scheyer, Lister, et al. 2015). Haversian bones are
117 seen only at the inner medullary surface and the part of the cortex where the ligaments
118 are strongly attached (e.g., the labium laterale in the femur) in adults.

119 In contrast, all of the extant deer populations [i.e., the four extant sika deer
120 populations, the extant Reeves's muntjac (*Muntiacus reevesi*)] and the gigantic fossil *S.*

121 *yabei* exhibit a similar bone tissue structure to continental cervids (Calderon et al. 2019,
122 Jordana et al. 2016, Kolb, Scheyer, Lister, et al. 2015), consisting of a fibro-lamellar
123 bone with a high level of laminar to plexiform vascularization and plumped osteocytes
124 in most of the cortex and parallel-fibered bone tissue in the outer cortex (Figure 2G–L;
125 SI Appendix, Figures S2A–I, S3G–I, and S4A–O). Notably, the parallel-fibered bone
126 tissue is more extensively developed and the LAGs at the inner to middle cortex are
127 tighter in the two insular populations (sika deer from Yakushima and Kerama islands)
128 compared with the mainland deer (Figure 2D–F), suggesting a slower growth rate
129 among the insular populations.

130 Figure 2 summarizes the main histological features of the cervids we examined (also
131 see SI Appendix, Tables S1–S4).

132

133 **Growth curve models and growth rate comparisons**

134 The LAGs in the long bones of both the extant and fossil deer were well preserved,
135 allowing us to depict a growth curve for each individual (SI Appendix, Figure S7–S14).
136 We then averaged each of three growth curve parameters (the asymptote, growth rate,
137 and inflection point) for each species/population to deduce a representative growth
138 curve for each (Figure 3A, SI Appendix, Figure S15).

139 The two fossil insular deer (*C. astylodon* and the Ryukyu muntjac) showed remarkably
140 slow and prolonged growth compared to the other cervids, while the two extant insular
141 deer (sika deer from Yakushima and Kerama islands) were intermediate between the
142 fossil insular deer and the extant sika deer from the two mainland areas (Honshu and
143 Hokkaido mainland). The extant Reeves's muntjac showed the fastest growth,
144 corresponding with its early sexual maturity at ca. 6 months (Chiba Prefecture and Deer

145 Research Group on Boso 2007). The Pleistocene giant deer *S. yabei* also showed fast
146 growth, suggesting a similar growth pattern to other extant large deer, such as moose
147 (Sand, Cederlund, and Danell 1995). Statistical comparisons of the growth parameters
148 revealed that both the fossil and extant insular deer had significantly slower growth
149 rates than Reeves's muntjac and *S. yabei* (SI Appendix, Tables S9–S11), supporting the
150 results of the bone histological analyses. However, the growth rates of the four extant
151 sika deer populations and the fossil insular deer were not significantly different from
152 each other (SI Appendix, Tables S9–S11), due to the transitional position of the extant
153 insular deer, although the limited numbers of possible samples may also play a role. The
154 inflection point, which marks the transition from the initial phase of exponential growth
155 to the subsequent phase of asymptotic growth, is known to be associated with the timing
156 of sexual maturity (Monteiro and Falconer 1966) and was greatest in *C. astylodon* (SI
157 Appendix, Tables S9 and S11), implying that sexual maturity may be delayed in this
158 species. However, the differences were not always statistically significant, reflecting
159 high levels of variation within species/populations.

160

161 **Survivorship curve comparisons among extant and fossil cervids.**

162 There was variation in the survivorship curves of *C. astylodon* and the three extant sika
163 deer populations on the Hokkaido and Honshu mainland and Yakushima Island (Figure
164 3B). The survivorship curve of *C. astylodon* was characterized by very low mortality
165 from the juvenile through to the prime age period, followed by an increase in mortality
166 during senescence, appearing like an inversed L, which is categorized as a type I
167 survivorship curve (Pianka 1978). At the other extreme, extant sika deer from Hokkaido
168 mainland showed high mortality in the younger age class, followed by a more gradual

169 decrease in the number of survivors from the prime age to senescence, which is
170 characteristic of a type III survivorship curve. The survivorship curves of sika deer from
171 Honshu mainland and Yakushima Island lay between those of *C. astylodon* and
172 Hokkaido sika deer, being characterized by a steady decrease in survivorship until the
173 prime age (i.e., a type II survivorship curve), though the Honshu population showed an
174 increased mortality rate after the prime age. The maximum longevity of *C. astylodon*
175 was 25 years (Kubo et al. 2011), which was much greater than that of the extant sika
176 deer (17, 19, and 17 years for the Honshu, Hokkaido, and Yakushima Island
177 populations, respectively). Finally, the Ryukyu muntjac had a type I survivorship curve,
178 like *C. astylodon* (Figure 3B), indicating that its mortality rate also did not increase until
179 senescence.

180

181 **Discussion**

182 The examination of life history and metabolic features in a phylogenetically controlled
183 set of species, based on bone microstructure and other hard tissue markers, reveals the
184 processes associated with dwarfism in the evolution of large herbivorous mammals in
185 islands. There is a common mechanism involved, but the historical background of the
186 populations and the nature of the new environments may result in different evolutionary
187 transformations.

188 The bone histological analysis showed that the bone tissues of the mainland
189 species/populations are characterized by azonal bone with few LAGs in the outermost
190 cortex, whereas those of the insular populations are characterized by zonal bone with
191 multiple LAGs through the entire cortex, as occurs in the bone tissues of ectotherms
192 (Köhler and Moyà-Solà 2009), indicating that mainland and insular populations may

193 have different metabolic rates. Notably, two fossil cervids from Okinawa Island (*C.*
194 *astylodon* and the Ryukyu muntjac) were found to have zonal bones consisting of
195 parallel-fibered bone, which is unusual for endotherms and indicates a drastic decrease
196 in the bone deposition rate (de Margerie, J. Cubo, and Castanet 2002). We hypothesize
197 this is associated with a lower metabolic rate, comparable to what has been reported for
198 the fossil insular bovid *Myotragus* (Köhler and Moyà-Solà 2009). By contrast, extant
199 sika deer from Yakushima and Kerama islands showed intermediate histological
200 features between the mainland sika deer and the fossil insular cervids, with the retention
201 of fibro-lamellar bone (which is a typical mammalian bone tissue (Kolb, Scheyer,
202 Veitschegger, et al. 2015)), parallel-fibered bone, and multiple LAGs, showing similar
203 histological features to the fossil insular cervid *Candiacervus* (Kolb, Scheyer, Lister, et
204 al. 2015).

205 Alongside this change in metabolic rate, there was a large difference in relative growth
206 rate among the mainland and insular forms (Figure 3A). Among the extant sika deer
207 populations, we observed a transitional change in growth rate from fast-growing
208 mainland populations (Hokkaido and Honshu) to slow-growing insular populations
209 (Yakushima and Kerama islands). Furthermore, the magnitude of the decrease in growth
210 among the insular deer was related to island size, with a slower rate of growth and a
211 more shrunken body size being observed on the smaller island (Kerama Islands). Sika
212 deer on Kerama Islands are the smallest sika deer in Japan and showed the slowest
213 growth rate among the four studied populations. These deer were introduced to Kerama
214 Islands from the Kyushu mainland ca. 400 years ago by humans (Okinawa Prefectural
215 Board of Education 1996). Although fast change on body size in less than six thousand
216 years have been previously documented in red deer in other islands (Lister 1989), it is

217 surprising that this drastic change in growth trajectory could have occurred over such a
218 short period of time, which equates to ca. 80 generations (assuming a generation time of
219 5 years for the sika deer). This change in growth trajectory was brought about by
220 phenotypic plasticity rather than genetic modification in response to the less abundant
221 understory vegetation in the subtropical evergreen-broadleaved forest and thus the poor
222 nutritional status of Kerama deer (Shiroma and Ohta 1996), which was supported by the
223 observation of a possible malnourished individual (URB-MAM-55; see SI Appendix for
224 details). By contrast, the slower growth rate of Yakushima deer compared with the
225 mainland deer may have a genetic basis because 1) Yakushima deer are not
226 malnourished and have enjoyed a recent population increase (Tsujino, Noma, and
227 Yumoto 2004) and 2) some of their macromorphological features have a genetic basis
228 (Terada and Saitoh 2018, Terada, Tatsuzawa, and Saitoh 2012).

229 It was not surprising that the fossil gigantic deer *S. yabei* showed fast growth, as this
230 has been reported in a previous study (Kolb, Scheyer, Veitschegger, et al. 2015).
231 However, it is notable that the extant Reeves's muntjac had the highest growth rate
232 among the studied cervids, which fits the expectation given the early sexual maturity of
233 this species (Sand, Cederlund, and Danell 1995), and that this growth rate was
234 statistically equivalent to that of *S. yabei* despite the immense difference in body size
235 between these species. The lowest growth rate was identified for *C. astylodon* followed
236 by the Ryukyu muntjac in the present study (SI Appendix, Table S8). Although the
237 mature body size is similar between Reeves's muntjac and fossil Ryukyu muntjac, their
238 growth rate is different from each other, suggesting the importance of the slow growth
239 rate as an adaptation to the resource-limited island environment. In the study of island
240 adaptation of mammals, it is important to examine not only the body size, proportion,

241 and morphology, but also consider growth rate and life history. The histological
242 research is an important method for this purpose.

243 As with Kerama deer, it is possible that phenotypic plasticity influenced the growth
244 trajectories of the extinct insular deer we studied. We do not currently have any reliable
245 sources of information on the nutritional status of fossil deer, except that they were C₃
246 plant feeders (Kubo et al. 2015). However, reports of healed bone fractures on a number
247 of leg bones from a museum collection of fossil insular deer of Okinawa Island
248 (Okinawa Prefectural Museum and Art Museum 2009) implies that these deer survived
249 long enough to recover from serious leg injuries, refuting the possibility that fossil
250 Okinawa deer were malnourished and their body growth was suppressed due to a lack
251 of resources.

252 Comparison of the growth trajectories showed that the extant sika deer populations
253 exhibit a transitional change in somatic maturity from mainland deer (less than 3 years
254 for the Hokkaido and Honshu populations) to insular deer (more than 5 and 7 years for
255 the Yakushima and Kerama Island populations, respectively) (Figure 3A), and these
256 observations have been independently supported by investigations of culled individuals
257 (Ochiai and Asada 1995, Suzuki et al. 2001) and by long-term field observations of wild
258 deer (Agetsuma and Agetsuma-Yanagihara, personal communication). Surprisingly, the
259 two fossil Okinawa deer (*C. astylodon* and the Ryukyu muntjac) were expected to attain
260 somatic maturity at 14 and 7 years old, respectively. Examination of the sexual maturity
261 data for the extant sika deer and Reeves's muntjac populations indicated that the female
262 age at first pregnancy matches or is slightly before the age of somatic maturity
263 (Hokkaido sika deer, 2 years old (Hokkaido Institute of Environmental Sciences 1997);
264 Honshu sika deer, 2 years old (Ochiai and Asada 1995); Yakushima sika deer, 4 years

265 old, Agetsuma and Agetsuma-Yanagihara pers. comm.; Reeves's muntjac, 1 year old
266 (Chiba Prefecture and Deer Research Group on Boso 2007)). Thus, it can be predicted
267 that *C. astylodon* and the Ryukyu muntjac would have become sexually mature at 14
268 and 7 years of age, respectively, indicating that both somatic and sexual maturity were
269 delayed in the insular forms compared with the mainland forms.

270 Analysis of the survivorship curves also produced intriguing results. The two fossil
271 insular deer showed inversed L-shaped (type I) survivorship curves, indicating lower
272 mortality during the juvenile through prime age periods and increased mortality during
273 senescence. Together with the body growth patterns, this implies that these fossil deer
274 had similar life histories to *K*-strategists (Pianka 1978), such as large anthropoids or
275 elephants. Similar findings have been reported for *Myotragus* (Köhler and Moyà-Solà
276 2009, Marin-Moratalla, Jordana, and Köhler 2013), implying the commonality of this
277 life history change on predator-free islands. The previous report on dwarfed
278 deer *Candiacervus* having a slower growth from the continental relatives but not as
279 extreme like *Myotragus* (Kolb, Scheyer, Lister, et al. 2015) may result from Crete Island
280 not being such a small island, even in times in which it may have been partitioned (van
281 der Geer et al. 2010). Indeed, all cervids from the mainland of Japan do not show any
282 modifications of life history traits compared with the continental relatives. Furthermore,
283 our study is the first to demonstrate a gradual, transitional shift toward a 'slow life
284 history' from mainland to insular populations, underlying the move toward insular
285 dwarfism. To further test the complete scenario of life history evolution we hypothesize
286 here, it would be relevant to obtain reliable mortality data for Kerama deer, which
287 showed the slowest growth rate among the extant sika deer populations.

288 We obtained strong evidence that the fossil deer of Okinawa Island had a distinct life

289 history based on their growth and mortality patterns. These deer were isolated for a very
290 long time (over 1.5 Ma), and during it they evolved their life history strategy in a small
291 insular environment, including a lower extrinsic mortality due to a lack of predators but
292 limited food resources (Köhler and Moyà-Solà 2009). This process may have started
293 after their initial settlement on Okinawa Island in part through phenotypic plasticity due
294 to a lack of sufficient foods, as possibly occurred in Kerama deer. The life history
295 change would then have become genetically fixed through the natural selection of more
296 *K*-shifted individuals, as appears to have occurred in Yakushima Island deer. The final
297 outcome will have been the development of extreme *K*-strategists, despite their small
298 body size. Unfortunately, this life history trait will have made these species vulnerable
299 to human exploitation, because animals with a *K*-strategy have lower population
300 recruitment (Pianka 1978). Consequently, the two Okinawa deer became extinct at the
301 time of or soon after Paleolithic human arrival to the Okinawa Islands (Fujita et al.
302 2016, Fujita et al. 2014), possibly due to hunting.

303 These findings explain the growth variation of insular mammals previously
304 documented (Figure 4). Okinawa deer and *Myotragus*, which dwelt on small islands and
305 underwent exceptionally long time of evolution in predator-free insular environments
306 (over 1.5Ma and 5.2 Ma respectively), showed a dramatic decrease in bone growth rate
307 and an evolution towards a slow life history. On the other hand, other Japanese deer do
308 not show extreme life modifications from the continental relatives, the condition similar
309 to previously reported cases (e.g., a fossil hippo *Hippopotamus minor* from Cyprus, a
310 living cervid *Odocoileus hemionus* from Blakley island and a fossil cervid
311 *Candiacervus* from Crete (Kolb, Scheyer, Lister, et al. 2015, Kolb, Scheyer,
312 Veitschegger, et al. 2015)). These results suggest that the degree of modification in life

313 history is strongly affected by both island size and duration of isolation, with smaller
314 islands and longer isolations resulting in life history changes into *K*-strategists. This
315 idea is also supported by an ecological study on a recent insular rabbit *Pentalagus*
316 *furnessi* in the Ryukyu Archipelago of Japan, having *K*-strategy (Hamada and Mizuta
317 2020). A report on the Sicilian pigmy elephant *Elephas falconeri*, may represent an
318 exception to this pattern, as the age distribution of the fossil assemblage with an
319 exceptionally high number of calves and immature individuals was interpreted as
320 reflective of a *r*-strategy (Raia, Barbera, and Conte 2003). However, a histological study
321 suggested that this pigmy elephant had a much slower growth rate than its mainland
322 relatives, and sexual maturity was within the range of extant elephants (Köhler et al.
323 2013). These observations further tempt us to expect an evolutionary optimum of body
324 mass and life history in small predator-free islands, which would be *K*-strategists with
325 body size within small to medium-sized range. Further accumulation of life history
326 information clarified from bone histology should shed light on the generality of life
327 history evolution on islands.

328

329 **Conclusion**

330 Extant Japanese sika deer are able to modify their life history traits through a
331 combination of phenotypic plasticity and natural selection. This ability likely underlies
332 the process of insular dwarfism also recorded in fossil deer (*C. astylodon* and the
333 Ryukyu muntjac) from Okinawa Island, showing lower mortality during the juvenile
334 through prime age periods and increased mortality during senescence. Together with the
335 body growth patterns, this implies that these fossil deer had a *K*-strategy life history
336 (Pianka 1978). Combining the results of the present and previous studies on life

337 histories of insular mammals, we conclude that the degree of modification in life history
338 is strongly affected by both island size and duration of isolation, with longer isolations
339 on smaller islands resulting in more prominent life history changes. We demonstrate the
340 evolution of a gradual, transitional shift toward a ‘slow life history’ in large tetrapods
341 from mainland to insular populations as the main life history change accompanying
342 insular dwarfism.

343

344 **Material and methods**

345 **Materials**

346 Samples of extant sika deer were obtained from two mainland populations (Hokkaido
347 and Honshu) and two insular populations (Yakushima Island and Kerama Islands)
348 (Figure 1). The four populations had different properties of their habitat environments
349 and showed considerable differences in body size (Table 1). Samples of extant Reeve’s
350 muntjac were obtained from the Honshu mainland (Figure 1). This analysis included
351 two mainland populations of sika deer in the Japanese Archipelago (Hokkaido and
352 Honshu mainland) that differ in their maximum body size, with Hokkaido deer being
353 the largest population of Japanese sika deer, and two insular populations (Yakushima
354 and Kerama islands), both of which inhabit subtropical forests but differ in the habitat
355 area (island size = 505 km² and 36 km², respectively) and isolation period (ca. 100,000–
356 20,000 years and 400 years, respectively). All extant samples were obtained from wild
357 individuals.

358 Fossils of the following taxa were examined: *Cervus astylodon* and Muntiacini gen. et
359 sp. indet. (the Ryukyu muntjac), collected from the Hananda-Gama Cave site of the
360 Late Pleistocene (>20 ka (Okinawa Prefectural Museum and Art Museum 2009)) on

361 Okinawa Island, Japan; and *Sinomegaceros yabei*, collected from the Kumaishi-do Cave
362 of the Late Pleistocene (16–23 ka (Okumura et al. 2016)) on Honshu mainland, Japan.

363 Detailed information on the extant and fossil specimens is provided in the SI Appendix
364 and is listed in Table 1 and SI Appendix, Tables S1–S4.

365

366 **Thin sectioning and X-ray computed tomography (CT) scanning**

367 Life history traits, including growth trajectories, longevity, and sexual maturity can be
368 examined by long bone histology counting the lines of arrested growth (LAGs) ^{e.g.}
369 (Amson et al. 2015, Klevezal 1996, Köhler et al. 2012, Köhler and Moyà-Solà 2009,
370 Kolb, Scheyer, Lister, et al. 2015, Kolb, Scheyer, Veitschegger, et al. 2015, Marin-
371 Moratalla, Jordana, and Köhler 2013) We used in total 62 extant and 21 fossil long
372 bones for histological analyses (Table 1). All of the specimens were photographed and
373 standard measurements were taken, following which thin sections of the midshaft of the
374 long bones were made based on the methodology described in Chinsamy & Raath
375 (Chinsamy and Raath 1992) and Sander (Sander 2000). For the extant species, we
376 sampled both femur and tibia from the same individual, whereas we used either femur
377 or tibia for fossil specimens, as their skeletal remains were not associated. The thin
378 sections were photographed with a digital film scanner (Pixus Mp 800, Canon) and
379 analyzed using an Optiphot2-pol microscope (Nikon). Microscopic photographs were
380 taken with a Nikon Df camera.

381 Neonatal specimens of sika deer (Honshu mainland: CBM-ZZ-757) and Reeves's
382 muntjac (CBM-ZZ-4974) were scanned using an experimental animal X-ray CT scanner
383 (Latheta LCT-200, Aloka; 24- μ m resolution, 80 kV, 0.2 mA) at the Okayama
384 University of Science, Okayama, Japan, to determine the initial diameter of the cortical

385 bone and an open medullary cavity in these species. Image segmentation and
386 visualization were performed using VG-Studio Max (Volume Graphics) version 3.1.

387 The nomenclature and definitions of the bone microstructures included in the
388 following descriptions are based on Francillon-Vieillot et al. (Francillon-Vieillot et al.
389 1989) and Castanet et al. (Castanet et al. 1993).

390

391 **Age assessment**

392 For most of the extant deer samples, age at death was assessed by tooth eruption or the
393 number of dental cementum annuli in the tooth root (SI Appendix, Table S3 and S4). In
394 the case of fossil deer samples, the long bones were not associated with skulls and
395 mandibles, therefore it was required to estimate the age at death from the number of
396 LAGs found in the long bones. Several previous studies have reported a good
397 correlation between the number of LAGs and the age at death in a range of vertebrate
398 groups ^{e.g.} (Castanet et al. 2004). However, only one study has examined this correlation
399 in an extant deer species [red deer (*Cervus elaphus*)], which reported that the number of
400 LAGs in the tibia corresponds to the actual age but the number in the femur corresponds
401 to the age before the deposition of the external fundamental system (EFS) (Calderon et
402 al. 2019). Therefore, the relationship between the actual age at death and the number of
403 LAGs in the bones of the extant cervids sampled was examined first. This showed that
404 the estimated age of the extant deer based on the number of LAGs in both the femur and
405 tibia was highly correlated with the actual age determined by tooth cementum annuli (SI
406 Appendix, Figure S5 and Table S5). While some old adults that were over 8 years of age
407 (HOUMVC-00037, CBM-ZZ-412, and URB-MAM-193) had fewer LAGs in their long
408 bones than their actual age, the diameters of their expanded medullary cavities were

409 identical or even larger than the bone diameters observed in neonates and fawns (<1
410 year old), indicating that the first (and also second in URB-MAM-193) LAG is likely
411 eliminated in old individuals (SI Appendix, Table S5). Thus, since the number of LAGs
412 matched the actual age in extant Japanese cervids, the age of individuals of fossil taxa
413 was also estimated by counting the number of LAGs in their long bones (SI Appendix,
414 Table S6).

415

416 **Body mass estimation**

417 The body mass during ontogeny was estimated from the bone diameters at the LAGs
418 (Lehman and Woodward 2008). Body mass estimation formulas for both the femora and
419 tibiae were obtained from Scott (Scott 1990) and the formula that uses the mediolateral
420 diameter (MLD) of the femora and tibiae was selected for use in this study (see SI
421 Appendix for details). In addition to the diameters at the LAGs, the external diaphysial
422 measurements [anteroposterior diameter (APD) and MLD] were collected and used to
423 estimate the body mass at death. Raw measurement data of diameters at the LAGs
424 together with the estimated body mass used for growth curve modeling are presented in
425 Supplementary Table S14.

426

427 **Comparison of growth patterns**

428 Growth curves of body mass were constructed for each individual specimen that were
429 older than yearlings (i.e., those that had more than one LAG). The exception to this was
430 the extant Reeves's muntjac, for which a fawn and yearling were included in the growth
431 curve fitting because this species is known to have rapid growth (Chiba Prefecture and
432 Deer Research Group on Boso 2007). Before fitting the growth curves, neonatal body

433 mass data were obtained for both the extant and fossil taxa as a starting point (SI
434 Appendix, Table S7, and Figure S6).

435 To fit growth curves to the obtained data, the number of LAGs was first transformed
436 into age in years. For each specimen, the body mass (W , in kg) was then formulated
437 with age (x , in years) using the Gompertz curve, which is described as:

$$438 \quad W = a\text{Exp}(-\text{Exp}(-b(x - c)))$$

439 where a , b , and c represent the asymptote (i.e., the body mass when body growth
440 ceases), growth rate, and inflection point, respectively. The growth curve parameters
441 were then averaged for each population/species to produce a representative growth
442 curve for each group, and the growth rate (b) and inflection point (c) were statistically
443 compared among species/populations using the Tukey–Kramer method. These analyses
444 were conducted separately for the femora and tibiae, and all statistical analyses were
445 conducted in JMP Pro 14.2.0 (SAS Institute Inc.).

446

447 **Comparison of survivorship curves**

448 Kubo et al. (Kubo et al. 2011) estimated the age at death for *C. astylodon* based on the
449 height of the lower third molar by applying the molar wear rate of extant sika deer.

450 Here, the same age data ($n = 45$) were used to depict survivorship curves following the
451 method of Caughley (Caughley 1977). In addition, age data were collected from three

452 sika deer populations that were used to investigate the long bone histology (Hokkaido,

453 Honshu, and Yakushima Island populations). These data were collected from the

454 literature (Hokkaido Institute of Environmental Sciences 1997, Kubo et al. 2011) for the

455 Hokkaido and Honshu mainland populations. However, no reliable published age data

456 were available for the Yakushima Island population, so instead histological analysis of

457 the cementum layers of the lower first incisors was performed on museum specimens
458 housed in the University Museum of the University of Tokyo, the Tochigi Prefectural
459 Museum, and the Hokkaido University Museum to identify their age at death. Age data
460 were collected from 1060, 594, and 74 individual deer in the Hokkaido, Honshu, and
461 Yakushima Island populations, respectively.

462 The age at death of the fossil Ryukyu muntjac was also estimated by evaluating the
463 wear score of the lower third molars. Ozaki (Ozaki 2009) previously estimated the age
464 at death of the Ryukyu muntjac by applying the molar wear scoring method developed
465 by Chapman et al. (Chapman, Brown, and Rothery 2005) for extant Reeves's muntjac.
466 While no age data of extant Reeves's muntjac from Honshu mainland have been
467 reported to date, despite their ecology being well investigated for management purposes
468 (Chiba Prefecture and Deer Research Group on Boso 2007), age data have been
469 reported for extant Reeves's muntjac from England (Chapman, Brown, and Rothery
470 2005). Therefore, these age data were used to depict the survivorship curve of extant
471 Reeves's muntjac. Fossil *S. yabei* and extant Kerama Islands deer were not included in
472 these survivorship curve comparisons due to a lack of reliable age data.

473

474 For more details on the materials and methods used in this study, see the SI Appendix.

475

476 **Acknowledgments**

477 We thank the following curators for the access to the museum collections under their
478 care: Shimoinaba, S. (Natural History Museum and Institute, Chiba, Japan), Hayashi, T.
479 (Tochigi Prefectural Museum), Eda, M. (The Hokkaido University Museum), Usami, K.
480 (Okinawa Prefectural Museum and Art Museum). Oshiro I. is acknowledged for his

481 advice on the fossil Okinawa deer and support for this study. We also thank Ochiai, K.
482 and Shimoinaba, S. for providing ecological data of sika deer and Reeves's muntjac in
483 Honshu. Agetsuma, N. and Agetsuma-Yanagihara, Y. are appreciated for sharing data
484 of their long-term field survey of Yakushima deer. We are grateful to Nakamura, K. and
485 Nomura, H. for technical assistance for thin-sectioning; Kodaira, S. and Kodama, R. for
486 CT scanning; Kawada, S. (National Museum of Nature and Science, Tokyo), van der
487 Geer, A. (Naturalis Biodiversity Center), Köhler, M. (ICP), Takakuwa, Y. (Gunma
488 Museum of Natural History), Kikuchi, H. and Umemura, Y. for providing photos of
489 *Odocoileus hemionus*, *Hippopotamus minor* and *Candiacervus* spp., *Myotragus*
490 *baleanicus*, *Sinomegaceros yabei*, *Elephas falconeri*, and sika deer (Yakushima Island
491 and Hokkaido mainland, respectively).

492

493 **Additional information**

494 **Funding**

495 This work was supported by grants from the Sanyo Broadcasting Foundation (to SH and
496 MOK) and JSPS KAKENHI Grant Numbers JP16K18615 (to MOK) and JP19K04060
497 (to SH and MOK). MRSV is supported by Swiss SNF 31003A_169395.

498

499 **Competing interest**

500 We have no competing interests to declare.

501

502 **Additional files**

503 **Supplementary files**

504 ● Supplementary file 1. Supplementary information including additional text, figures

505 and data set.

506 ● Supplementary file 2. Raw data of measurements (Table S14).

507

508 **Data accessibility**

509 All data not presented in the manuscript are available as electronic supplementary

510 information and uploaded to Dryad Digital Repository

511 (<https://doi.org/10.5061/dryad.wdbrv15n8>).

512

513 **References**

514 Amson, Eli, Christian Kolb, Torsten M. Scheyer, and Marcelo R. Sánchez-Villagra.

515 2015. "Growth and life history of Middle Miocene deer (Mammalia, Cervidae)

516 based on bone histology." *Comptes Rendus Palevol* 14 (8):637-645. doi:

517 10.1016/j.crpv.2015.07.001.

518 Calderon, T., D. DeMiguel, W. Arnold, G. Stalder, and M. Köhler. 2019. "Calibration of

519 life history traits with epiphyseal closure, dental eruption and bone histology in

520 captive and wild red deer." *J Anat* 235 (2):205-216. doi: 10.1111/joa.13016.

521 Castanet, J., S. Croci, F. Aujard, M. Perret, J. Cubo, and E. de Margerie. 2004. "Lines of

522 arrested growth in bone and age estimation in a small primate: *Microcebus*

523 *murinus*." *Journal of Zoology* 263 (1):31-39. doi:

524 10.1017/s0952836904004844.

525 Castanet, J., H. Francillon-Vieillot, F.J. Meunier, and A. de Ricqlès. 1993. "Bone and

526 individual aging." In *Bone. Vol. 7: Bone Growth*, edited by B. K. Hall, 245–283.

527 Boca Raton: CRC Press.

528 Caughley, G. 1977. *Analysis of Vertebrate Populations*. New York: John Wiley & Sons

529 Inc.

530 Chapman, Norma G., W. A. B. Brown, and P. Rothery. 2005. "Assessing the age of

531 Reeves' muntjac (*Muntiacus reevesi*) by scoring wear of the mandibular molars."

532 *Journal of Zoology* 267 (03). doi: 10.1017/s0952836905007405.

533 Chiba Prefecture, and Deer Research Group on Boso. 2007. *Science report on emergent*

534 *survey of invasive alien species (Reeves's muntjac) in Boso*. Chiba: Chiba

535 Prefecture.

536 Chinsamy, Anusuya, and Michael A Raath. 1992. "Preparation of fossil bone for

- 537 histological examination." *Palaeontologia Africana* 29:39-44.
- 538 de Margerie, E., J. Cubo, and J. Castanet. 2002. "Bone typology and growth rate: testing
539 and quantifying 'Amprino's rule' in the mallard (*Anas platyrhynchos*)."
540 *Comptes Rendus Biologies* 325:221-230.
- 541 Foster, J. B. 1964. "Evolution of Mammals on Islands." *Nature* 202 (492):234-235.
- 542 Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Géraudie, F.J. Meunier, J. Y. Sire,
543 L. Zylberberg, and A. de Ricqlès. 1989. "Microstructure and Mineralization of
544 Vertebrate Skeletal Tissues." In *Skeletal Biomineralization: Patterns, Processes
545 and Evolutionary Trends*, edited by J. G. Carter, 471-530. New York: Van
546 Nostrand Reinhold.
- 547 Fujita, M., S. Yamasaki, C. Katagiri, I. Oshiro, K. Sano, T. Kurozumi, H. Sugawara, D.
548 Kunikita, H. Matsuzaki, A. Kano, T. Okumura, T. Sone, H. Fujita, S. Kobayashi,
549 T. Naruse, M. Kondo, S. Matsu'ura, G. Suwa, and Y. Kaifu. 2016. "Advanced
550 maritime adaptation in the western Pacific coastal region extends back to
551 35,000-30,000 years before present." *Proc Natl Acad Sci U S A* 113
552 (40):11184-11189. doi: 10.1073/pnas.1607857113.
- 553 Fujita, Masaki, Shinji Yamasaki, Hiroshi Sugawara, and Masaki Eda. 2014. "Body size
554 reduction in wild boar (*Sus scrofa*) from the late Pleistocene Maehira Fissure
555 Site in Okinawa-jima Island, Japan, with relevance to human arrival."
556 *Quaternary International* 339:289-299. doi: 10.1016/j.quaint.2014.04.043.
- 557 Hamada, Futoshi, and Taku Mizuta. 2020. "Unique reproductive traits of the Amami
558 rabbit *Pentalagus furnessi*: an endangered endemic species from southwestern
559 Japan." *Mammal Research* 65 (4):805-813. doi: 10.1007/s13364-020-00497-9.
- 560 Hokkaido Institute of Environmental Sciences. 1997. Results of a survey related to sika
561 deer and brown bear sighting on Hokkaido. Sapporo: Hokkaido Institute of
562 Environmental Sciences (in Japanese).
- 563 Jordana, Xavier, Nekane Marín-Moratalla, Blanca Moncunill-Solè, Carmen Nacarino-
564 Meneses, and Meike Köhler. 2016. "Ontogenetic changes in the histological
565 features of zonal bone tissue of ruminants: A quantitative approach." *Comptes
566 Rendus Palevol* 15 (1-2):255-266. doi: 10.1016/j.crpv.2015.03.008.
- 567 Kawamura, Y. 2009. "Fossil record of sika deer in Japan." In *Sika Deer: Biology and
568 Management of Native and Introduced Populations*, edited by D.R. McCullough,
569 S. Takatsuki and K. Kaji, 11-25. Tokyo: Springer.
- 570 Klevezal, G. A. 1996. *Recording Structures of Mammals. Determination of Age and
571 Reconstruction of Life History*. Rotterdam: A. A. Balkema.
- 572 Köhler, M., N. Marin-Moratalla, X. Jordana, and R. Aanes. 2012. "Seasonal bone

- 573 growth and physiology in endotherms shed light on dinosaur physiology."
574 *Nature* 487 (7407):358-361. doi: 10.1038/nature11264.
- 575 Köhler, M., and S. Moyà-Solà. 2009. "Physiological and life history strategies of a
576 fossil large mammal in a resource-limited environment." *Proceedings of the*
577 *National Academy of Sciences of the United States of America* 106 (48):20354-
578 20358.
- 579 Köhler, M., M. R. Palombo, J. Ll. Pretus, X. Jordana, B. Moncunill-Solé, J. Madurell-
580 Malapeira, N. Marín-Moratalla, and T. G. Bromage. 2013. "Bone histology of
581 the dwarf elephant *Palaeoloxodon falconeri* from Sicily." The Second
582 International Symposium on Paleohistology ISPH 2013, Bozeman, Montana,
583 USA.
- 584 Kolb, C., T. M. Scheyer, A. M. Lister, C. Azorit, J. de Vos, M. A. Schlingemann, G. E.
585 Rossner, N. T. Monaghan, and M. R. Sanchez-Villagra. 2015. "Growth in fossil
586 and extant deer and implications for body size and life history evolution."
587 *BMC Evol Biol* 15:19. doi: 10.1186/s12862-015-0295-3.
- 588 Kolb, C., T. M. Scheyer, K. Veitschegger, A. M. Forasiepi, E. Amson, A. A. Van der
589 Geer, L. W. Van den Hoek Ostende, S. Hayashi, and M. R. Sanchez-Villagra.
590 2015. "Mammalian bone palaeohistology: a survey and new data with emphasis
591 on island forms." *PeerJ* 3:e1358. doi: 10.7717/peerj.1358.
- 592 Kubo, Mugino O., Masaki Fujita, Shuji Matsu'ura, Megumi Kondo, and G. Suwa. 2011.
593 "Mortality profiles of late Pleistocene deer remains of Okinawa Island: evidence
594 from the Hananda-Gama cave and Yamashita-cho cave I sites."
595 *Anthropological Science* 119 (2):183-201. doi: 10.1537/ase.091215.
- 596 Kubo, Mugino O., and Seiki Takatsuki. 2015. "Geographical body size clines in sika
597 deer: path analysis to discern amongst environmental influences."
598 *Evolutionary Biology* 42 (1):115-127. doi: 10.1007/s11692-015-9303-1.
- 599 Kubo, Mugino Ozaki, Eisuke Yamada, Masaki Fujita, and Ituro Oshiro. 2015.
600 "Paleoecological reconstruction of Late Pleistocene deer from the Ryukyu
601 Islands, Japan: combined evidence of mesowear and stable isotope analyses."
602 *Palaeogeography, Palaeoclimatology, Palaeoecology* 435:159-166. doi:
603 10.1016/j.palaeo.2015.06.001.
- 604 Larramendi, A., and M. R. Palombo. 2015. "Body Size, biology and encephalization
605 quotient of *Palaeoloxodon* ex gr. *P. falconeri* from Spinagallo Cave (Hyblean
606 plateau, Sicily)." *Hystrix-Italian Journal of Mammalogy* 26 (2):102-109. doi:
607 10.4404/hystrix-26.2-11478.
- 608 Lehman, Thomas M., and Holly N. Woodward. 2008. "Modeling growth rates for

- 609 sauropod dinosaurs." *Paleobiology* 34 (2):264-281. doi: 10.1666/0094-
610 8373(2008)034[0264:Mgrfsd]2.0.Co;2.
- 611 Lister, A. M. 1989. "Rapid dwarfing of red deer on Jersey in the Last Interglacial."
612 *Nature* 342:539-542.
- 613 Lomolino, M. V., A. A. van der Geer, G. A. Lyras, M. R. Palombo, D. F. Sax, and R.
614 Rozzi. 2013. "Of mice and mammoths: generality and antiquity of the island
615 rule." *Journal of Biogeography* 40 (8):1427-1439. doi: 10.1111/jbi.12096.
- 616 Lomolino, Mark V., Dov F. Sax, Maria Rita Palombo, and Alexandra A. van der Geer.
617 2012. "Of mice and mammoths: evaluations of causal explanations for body size
618 evolution in insular mammals." *Journal of Biogeography* 39 (5):842-854. doi:
619 10.1111/j.1365-2699.2011.02656.x.
- 620 Long, E. S., K. L. Courtney, J. C. Lippert, and C. M. Wall-Scheffler. 2019. "Reduced
621 body size of insular black-tailed deer is caused by slowed development."
622 *Oecologia* 189 (3):675-685. doi: 10.1007/s00442-019-04367-3.
- 623 Marin-Moratalla, N., X. Jordana, and M. Köhler. 2013. "Bone histology as an approach
624 to providing data on certain key life history traits in mammals: implications for
625 conservation biology." *Mammalian Biology* 78 (6):422-429. doi:
626 10.1016/j.mambio.2013.07.079.
- 627 Monteiro, L. S., and D. S. Falconer. 1966. "Compensatory growth and sexual maturity
628 in mice." *Animal Science* 8 (2):179-192. doi: 10.1017/S0003356100034565.
- 629 Ochiai, Keiji, and Masahiko Asada. 1995. "Growth in the body size of sika deer (*Cervus*
630 *nippon*) on the Boso Peninsula, central Japan." *Journal of the Natural History*
631 *Museum and Institute, Chiba* 3 (2):223-232 (in Japanese with English abstract).
- 632 Ohtaishi, N. 1986. "Preliminary memorandum of classification, distribution and
633 geographic variation on Sika deer." *Honyurui Kagaku (Mammalian Science)*
634 53:13-17 (in Japanese with English abstract).
- 635 Okinawa Prefectural Board of Education. 1996. *A report of conservation and*
636 *management of sika deer in Kerama Islands*. Okinawa: Okinawa Prefectural
637 Board of Education.
- 638 Okinawa Prefectural Museum and Art Museum, ed. 2009. *Excavation of the Hananda-*
639 *Gama Cave site, Okinawa*. Naha: Kokusai-insatsu Co.
- 640 Okumura, K., S. Ishida, H. Taruno, and Y. Kawamura. 2016. "Yabe's giant deer and elk
641 remains from the Late Pleistocene of Kumaishi-do Cave, Gifu Prefecture (Part
642 1): Antlers, a skull, mandibles, and teeth." *Bulletin of the Osaka Museum of*
643 *Natural History* 70:1-82 (in Japanese with English abstract).
- 644 Otsuka, H., and A. Takahashi. 2000. "Pleistocene vertebrate faunas in the Ryukyu

- 645 Islands: their migration and extinction." *Tropics* 10:25-40.
- 646 Ozaki, M. 2009. "Estimation of age at death from tooth wear of lower molars of
647 excavated deer and comparison of age structures with modern deer populations."
648 In *Excavation of the Hananda-Gama Cave site, Okinawa*, edited by Okinawa
649 Prefectural Museum and Art Museum, 24-34 (in Japanese). Naha: Kokusai-
650 insatsu Co.
- 651 Palkovacs, Eric P. 2003. "Explaining adaptive shifts in body size on islands: a life
652 history approach." *Oikos* 103 (1):37-44. doi: [https://doi.org/10.1034/j.1600-
653 0706.2003.12502.x](https://doi.org/10.1034/j.1600-0706.2003.12502.x).
- 654 Palombo, M. R. 2001. "Endemic elephants of the Mediterranean Islands: knowledge,
655 problems and perspectives." *The World of Elephants - International Congress*,
656 Rome 2001, Rome.
- 657 Pianka, E. R. 1978. *Evolutionary Ecology*. New York: Harper & Row.
- 658 Raia, P., C. Barbera, and M. Conte. 2003. "The fast life of a dwarfed giant."
659 *Evolutionary Ecology* 17:293-312.
- 660 Raia, P., and S. Meiri. 2006. "The island rule in large mammals: paleontology meets
661 ecology." *Evolution* 60 (8):1731-1742.
- 662 Sand, Håkan, Göran Cederlund, and Kjell Danell. 1995. "Geographical and latitudinal
663 variation in growth patterns and adult body size of Swedish moose (*Alces
664 alces*)." *Oecologia* 102:433-442.
- 665 Sander, P. M., O. Mateus, T. Laven, and N. Knotschke. 2006. "Bone histology indicates
666 insular dwarfism in a new Late Jurassic sauropod dinosaur." *Nature* 441
667 (7094):739-41. doi: 10.1038/nature04633.
- 668 Sander, P. Martin. 2000. "Longbone histology of the Tendaguru sauropods: implications
669 for growth and biology." *Paleobiology* 26 (3):466-488. doi: 10.1666/0094-
670 8373(2000)026<0466:LHOTT>2.0.CO;2.
- 671 Scott, K. M. 1990. "Postcranial dimensions of ungulates as predictors of body mass." In
672 *Body size in mammalian paleontology: estimation and biological implications*,
673 edited by John Damuth and Bruce J. MacFadden, 301-335. Cambridge:
674 Cambridge University Press.
- 675 Shiroma, T., and H. Ohta. 1996. "Geographical variation in cranial morphology in sika
676 deer with a special reference on Kerama deer " In *A report of conservation and
677 management of sika deer in Kerama Islands*, edited by Okinawa Prefectural
678 Board of Education, 13-55 (in Japanese). Okinawa: Okinawa Prefectural Board
679 of Education.
- 680 Suzuki, M., M. Onuma, M. Yokoyama, K. Kaji, M. Yamanaka, and N. Ohtaishi. 2001.

- 681 "Body size, sexual dimorphism, and seasonal mass fluctuations in a larger sika
682 deer subspecies, the Hokkaido sika deer (*Cervus nippon yesoensis* Heude,
683 1884)." *Canadian Journal of Zoology* 79 (1):154-159.
- 684 Taruno, H., Y. Kawamura, S. Ishida, and K. Okumura. 2017. "Yabe's giant deer and elk
685 remains from the Late Pleistocene of Kumaishi-do Cave, Gifu Prefecture, central
686 Japan (Part 2): Postcranial bones." *Bulletin of the Osaka Museum of Natural
687 History* 71:17-142.
- 688 Terada, Chisato, and Takashi Saitoh. 2018. "Phenotypic and genetic divergence among
689 island populations of sika deer (*Cervus nippon*) in southern Japan: a test of the
690 local adaptation hypothesis." *Population Ecology* 60 (3):211-221. doi:
691 10.1007/s10144-018-0607-8.
- 692 Terada, Chisato, Shirow Tatsuzawa, and Takashi Saitoh. 2012. "Ecological correlates
693 and determinants in the geographical variation of deer morphology."
694 *Oecologia* 169 (4):981-994. doi: 10.1007/s00442-012-2270-7.
- 695 Tsujino, R., N. Noma, and T. Yumoto. 2004. "Growth in sika deer (*Cervus nippon
696 yakushimae*) population in the western lowland forest on Yakushima Island,
697 Japan." *Mammal Study* 29:105-111.
- 698 van der Geer, A. A., G. A. Lyras, M. V. Lomolino, M. R. Palombo, and D. F. Sax. 2013.
699 "Body size evolution of palaeo-insular mammals: temporal variations and
700 interspecific interactions." *Journal of Biogeography* 40 (8):1440-1450. doi:
701 10.1111/jbi.12119.
- 702 van der Geer, A., G. Lyras, J. de Vos, and M. Dermitzakis. 2010. *Evolution of Island
703 Mammals: Adaptation and Extinction of Placental Mammals on Island*. West
704 Sussex: John Wiley & Sons Ltd.
- 705 Woodward, H. N., J. R. Horner, and J. O. Farlow. 2014. "Quantification of intraskeletal
706 histovariability in *Alligator mississippiensis* and implications for vertebrate
707 osteohistology." *PeerJ* 2:e422. doi: 10.7717/peerj.422.
- 708

Figures

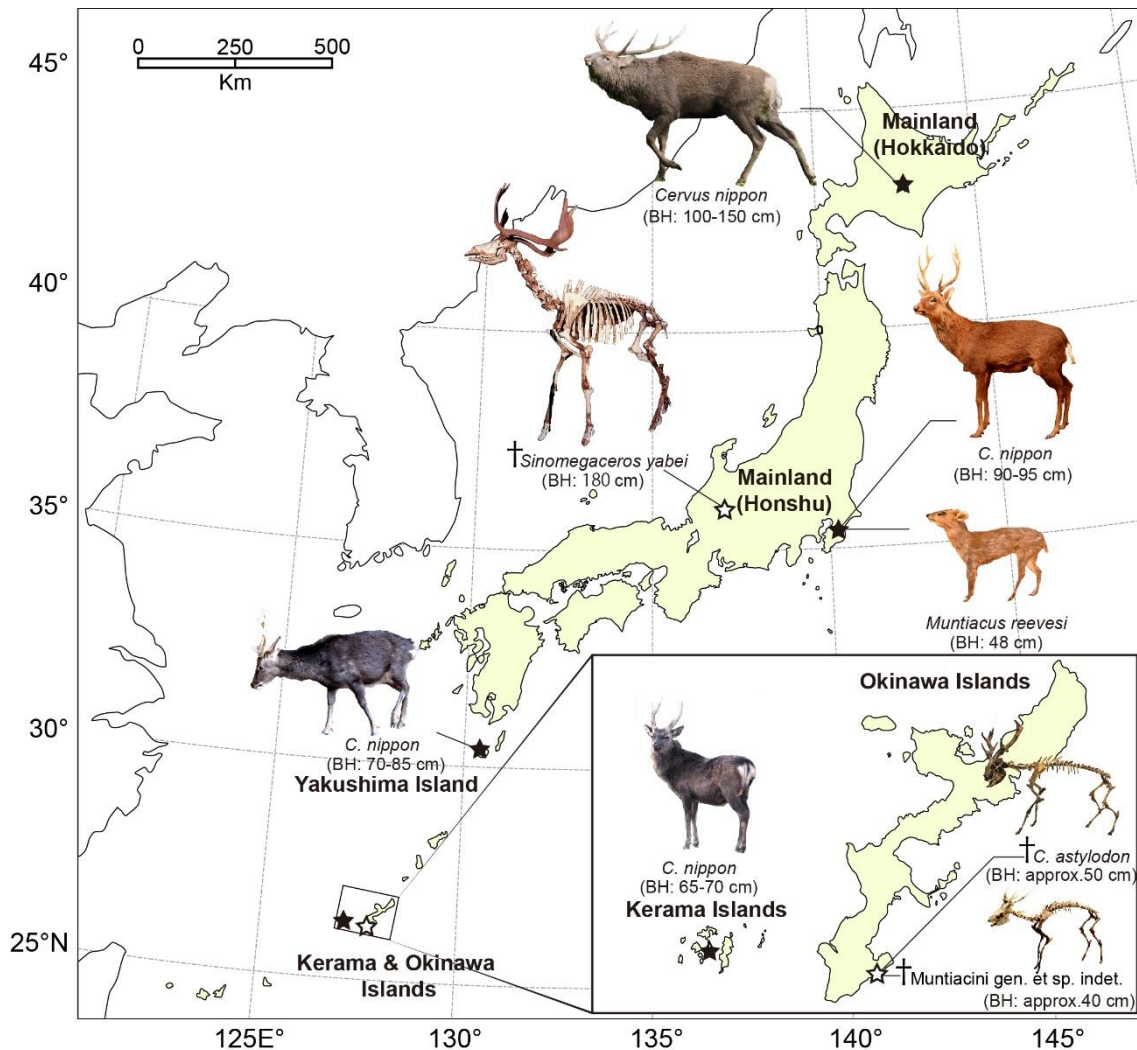
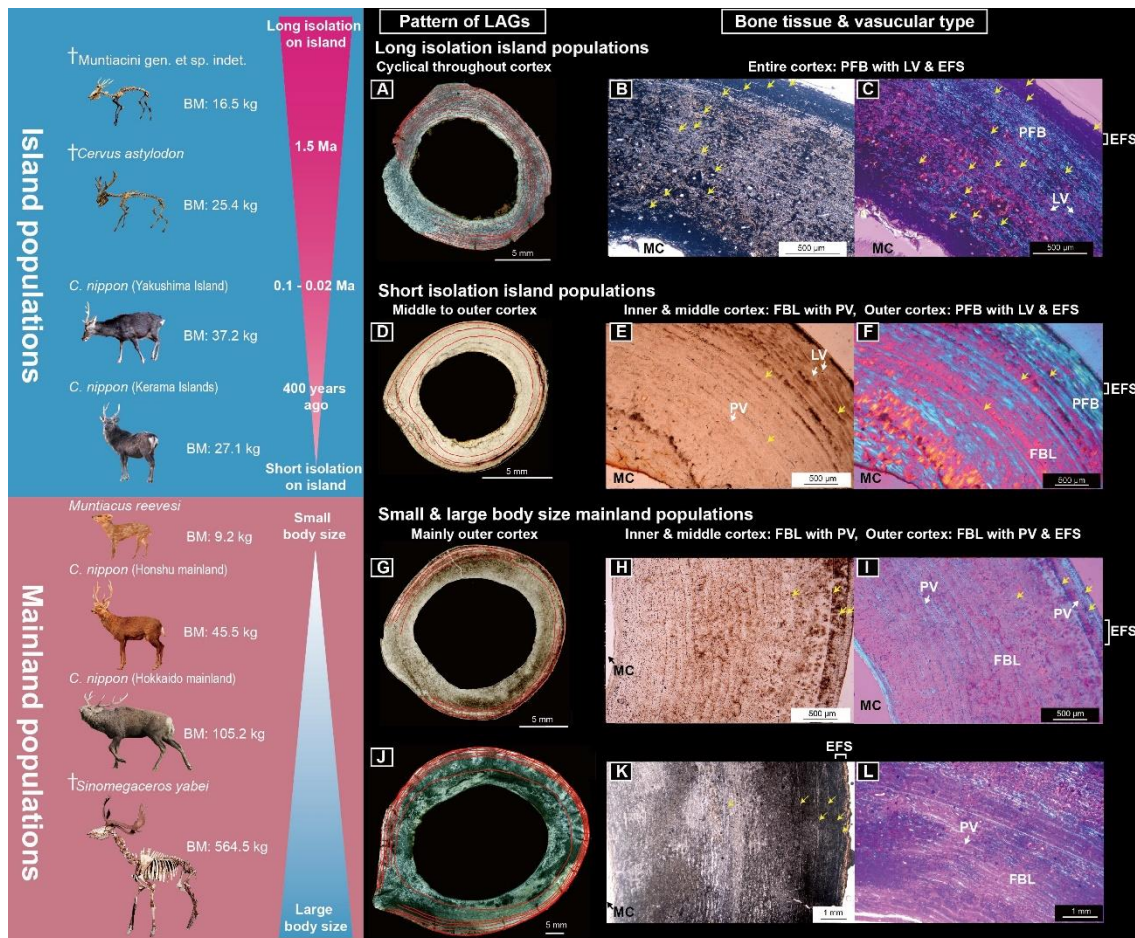


Figure 1. Locations of the sampled cervids in Japan. † indicates fossils excavated from Late Pleistocene deposits. The localities of extant taxa are shown in closed stars and those of extinct taxa are in open stars. The approximate body height (BH) is indicated for each species/population. Photography of fossil cervids courtesy of Gunma Museum of Natural History (*Sinomegaceros yabei*) and Okinawa Prefectural Museum & Art Museum (*Cervus astylodon* and *Muntiacini gen. et sp. indet.*).



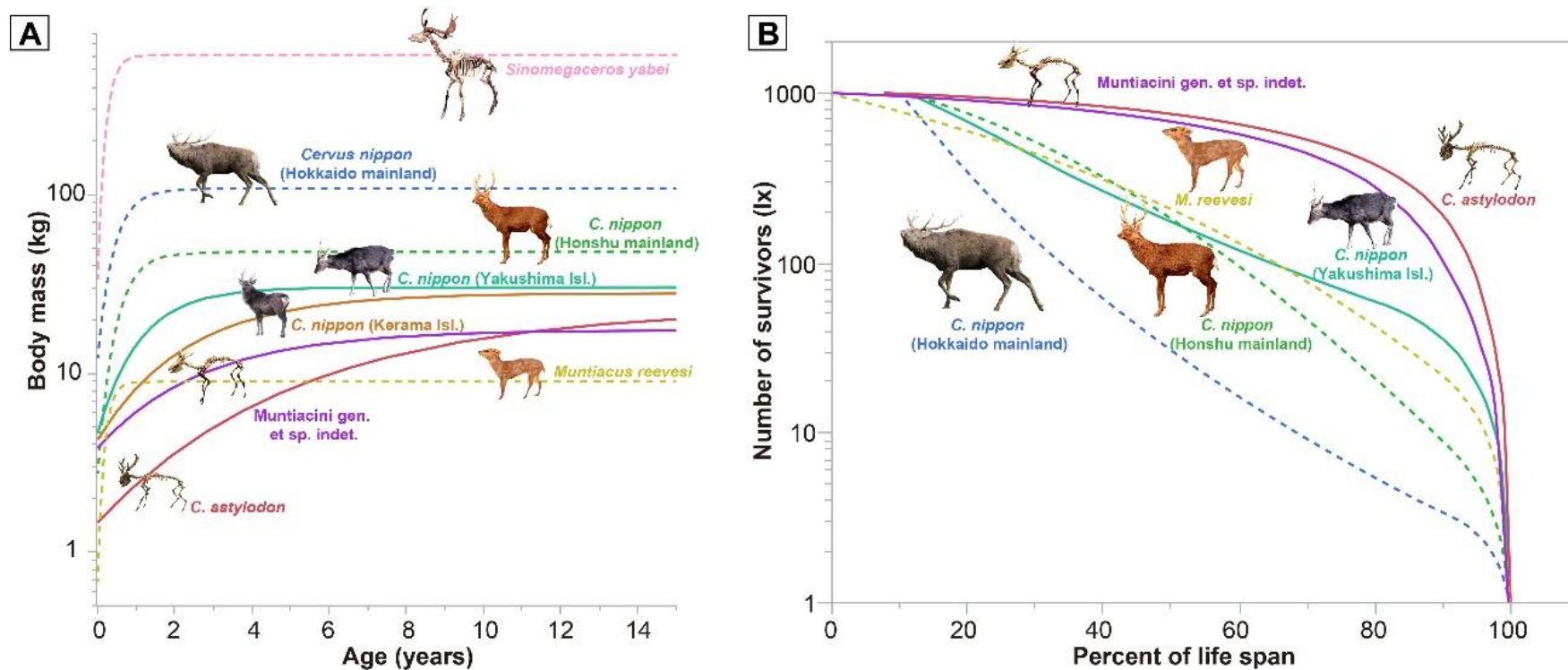


Figure 3. (A) Growth and (B) survivorship curves for Japanese cervids. Insular deer have a significantly slower growth rate and a delayed growth plateau (somatic maturity) compared with mainland deer (A), and there is an ecological shift from the *r*- to *K*-strategy between the insular and mainland deer (B). Growth and survivorship curves of insular cervids are solid lines and those of mainland cervids are dashed-lines.

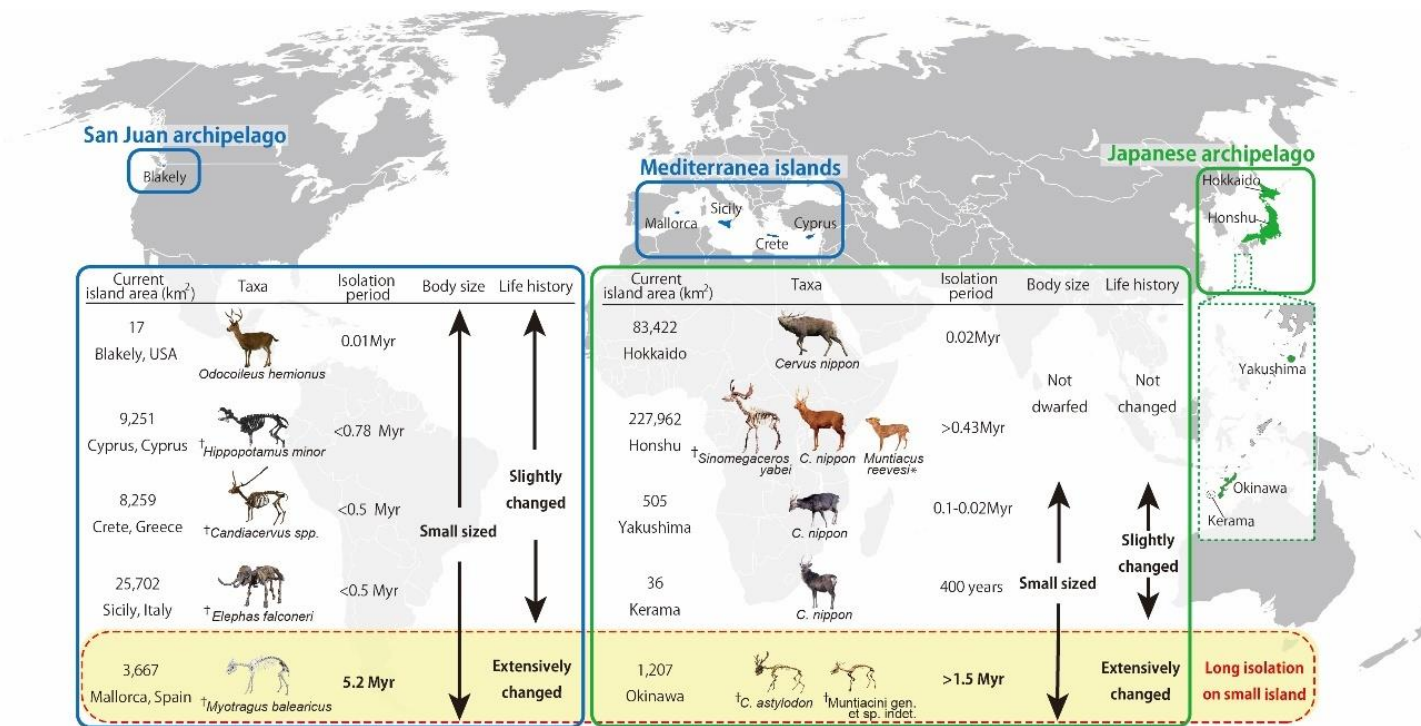


Figure 4. Summary of the relationship between insularity, body size and life history found in extant and fossil large mammals.

The cervid species/populations of Japanese Archipelago were investigated in the present study and information of animals in other islands were obtained from references: *Odocoileus hemionus* (Long et al. 2019), *Hippopotamus minor* (van der Geer et al. 2010), *Candiacervus* spp. (van der Geer et al. 2010), *Elephas falconeri* (Palombo 2001, van der Geer et al. 2010), *Myotragus balearicus* (Köhler and Moyà-Solà 2009). Photographs of fossil mammals of Mediterranean islands courtesy of Gunma Museum of Natural History (*Elephas falconeri*), Alexandra van der Geer (*Hippopotamus minor* and *Candiacervus* spp.), and Meike Köhler (*Myotragus balearicus*).

* *Muntiacus reevesi* is an artificially introduced animal in 1980's, therefore the isolation period of > 0.43 Myr is not applicable to it (Chiba Prefecture and Deer Research Group on Boso 2007).

Table 1. Summary of the general information of sampled Japanese insular cervids.

Species/Population	Locality (island size)	Timing of immigration/isolation (reference)	Habitat type	EBM (kg) ‡	N of histological samples (Femur, Tibia)	N of demographic analysis samples (reference of data)
Extant species/population						
<i>Cervus nippon</i> (Hokkaido mainland)	Hokkaido (83,424 km ²)	Separation from Honshu mainland population: Late Pleistocene (ca. 0.02 Ma) (Kawamura 2009)	Subarctic coniferous forests or mixed forests	105.2	F: 7, T: 7	1060 (Hokkaido Institute of Environmental Sciences 1997)
<i>Cervus nippon</i> (Honshu mainland)	Honshu (227,962 km ²)	Middle Pleistocene (0.43 Ma) (Kawamura 2009)	Temperate evergreen broadleaved forests	45.5	F: 8, T: 8	594 (Kubo et al. 2011)
<i>Muntiacus reevesi</i>		Recent introduction (1960–1980) (Chiba Prefecture and Deer Research Group on Boso 2007)				84 (Chapman, Brown, and Rothery 2005)
<i>Cervus nippon</i> (Yakushima Island)	Yakushima Island (505 km ²)	Isolation from Kyushu mainland: Late Pleistocene (ca. 0.1–0.02 Ma; see SI Appendix for details and references there in)	Subtropical evergreen broadleaved forests	37.2	F: 4, T: 4	74 (this study)
<i>Cervus nippon</i> (Kerama Islands)	Kerama Islands (36 km ²)	Historic introduction (ca. 400 years ago) (Shiroma and Ohta 1996)	Subtropical evergreen broadleaved forests	27.1	F: 7, T: 7	NA
Fossil species						
† <i>Sinomegaceros yabei</i>	Honshu (227,962 km ²)	Middle Pleistocene (> 0.43 Ma) (Taruno et al. 2017)	NA	564.5	F: 2, T: 2	NA
† <i>Cervus astylodon</i>	Okinawa Island (1,207 km ²)	Early Pleistocene (ca. 1.5 Ma) (Otsuka and Takahashi 2000)	NA	25.4	F: 6, T: 5	45 (Kubo et al. 2011)
† Muntiacini gen. et sp. indet.						65 (Ozaki 2009)

† Fossil cervids.

‡ The estimated body mass (EBM) was obtained from fitted growth curves (SI Appendix, Fig. S7–S14) by averaging asymptotes for each species/population.

Supplementary information

Variation and mechanisms of life history evolution in insular dwarfism as revealed by a natural experiment

by Hayashi and Kubo et al.

Shoji Hayashi^{1,2,*,**}, Mugino O. Kubo^{3,*,**}, Marcelo R. Sánchez-Villagra⁴, Hiroyuki Taruno⁵, Masako Izawa⁶, Tsunehiro Shiroma⁶, Takayoshi Nakano², Masaki Fujita⁷

¹ Faculty of Biosphere-Geosphere Science, Okayama University of Science, Kita-ku Ridaicho 1-1, Okayama, 700-0005, Japan; ² Division of Materials and Manufacturing Science, Graduate School of Engineering, Osaka University, Yamada-Oka, Suita, Osaka, 565-0871, Japan; ³ Department of Natural Environmental Studies, Graduate School of Frontier Sciences, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8563, Japan; ⁴ Paläontologisches Institut und Museum der Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland; ⁵ Osaka Museum of Natural History, Nagai Park 1-23, Higashi-Sumiyoshi-ku, Osaka, 546-0034, Japan; ⁶ Faculty of Science, University of the Ryukyus, Okinawa 903-0213, Japan; ⁷ Department of Anthropology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba-shi, Ibaraki 305-0005, Japan

* Both authors contributed equally to this work.

** *Authors for correspondence*: Shoji Hayashi e-mail: hayashi@big.ous.ac.jp, Mugino O. Kubo e-mail: mugino@k.u-tokyo.ac.jp

Supplementary text

1. Locality and specimen information for the sampled cervids used in the histological analyses

A summary of the sampled taxa is provided in Tables S1–S4.

1-1. Extant taxa

Sika deer (*Cervus nippon*) from Hokkaido mainland. All individuals were wild and were hunted in Hokkaido Prefecture (43°N, 143°E), northern Japan (Figure 1). Hokkaido is one of the four main islands constituting the Japanese archipelago and was considered “mainland” for the purposes of this study. Hokkaido sika deer inhabit subarctic coniferous forests mixed with cool temperate deciduous trees and are known to be the largest subspecies [*C. nippon yesoensis* (Groves 2006, Ohtaishi 1986)]. The complete skeleton of each individual is now housed in the Hokkaido University Museum (HOUMVC), Sapporo, Japan. The age at death was assessed based on tooth eruption for fawns and yearlings and the tooth cementum annuli formed at the roots of the incisors for adults.

Sika deer and Reeves’s muntjac (*Muntiacus reevesi*) from Honshu mainland. All individuals were wild and were hunted or collected in Chiba Prefecture (35°N, 140°E), which is in the central region of Honshu (Figure 1). Honshu is one of the four main islands constituting the Japanese archipelago and was considered “mainland” for the purposes of this study. Both of these species inhabit evergreen broadleaved forests in the temperate zone. Reeves’s muntjac was introduced to Chiba Prefecture ca. 1960–1980 following an escape from a private park (Chiba Prefecture and Deer Research Group on Boso 2007). The source population is unknown, but the body size of these deer is closer to that of the Taiwanese population. The complete skeletons of these individuals are stored at the Natural History Museum and Institute, Chiba (CBM), Japan. The age at death was assessed based on tooth eruption or the cementum annuli for the Honshu sika deer and from tooth eruption and the molar wear condition for Reeves’s muntjac.

Sika deer from Yakushima island. All individuals were wild and were hunted or collected on Yakushima Island (30°18'N, 130°30'E) in Kagoshima Prefecture, Japan, where they inhabit subtropical evergreen broadleaved forests. The sika deer on Yakushima Island are considered to be the subspecies *C. nippon yakushimae* (Ohtaishi 1986) and exhibit considerable phenotypic differences from the mainland populations, such as a small body size, simplified antlers, and shortened limbs (Ohtaishi 1986,

Terada, Tatsuzawa, and Saitoh 2012). The sika deer of Yakushima Island diverged from the population on Kyushu Island (one of the four main islands constituting the Japanese archipelago) ca. 0.1 Mya when the Ohsumi Strait was formed between the two islands (Ohshima 1990). Yakushima Island was possibly connected to Kyushu Island by a land bridge during the Last Glacial Maximum (ca. 25,000 ya), but the genetic differentiation between the two populations implies a much longer period of isolation for Yakushima deer (Nagata et al. 1999, Terada and Saitoh 2018). The complete skeleton of each individual has been stored at Tochigi Prefectural Museum (TPM), Utsunomiya, Japan. The age at death was assessed based on tooth eruption for fawns and yearlings and the tooth cementum annuli of the incisors and molars for adults.

Sika deer from Kerama islands. All individuals were wild and were collected as carcasses resulting from natural deaths on Kerama Islands (26°12'N, 127°24'E) in Okinawa Prefecture, Japan, by two of the authors (MI and TS) during their fieldwork. Sika deer were introduced to Kerama Islands from Kyushu ca. 400 years ago (Okinawa Prefectural Board of Education 1996) and inhabit subtropical evergreen broadleaved forests. These deer exhibit the phenotypic characteristics of insular dwarf deer (similar to Yakushima Island deer) and so are also regarded as a subspecies of sika deer (*C. nippon keramae*) (Ohtaishi 1986). Most individuals were complete skeletons, but some bone elements were lost at the time of collection in the field for some individuals. All of the specimens have been stored at the Faculty of Science, University of the Ryukyus (URB), Nishihara, Japan. The age at death was assessed based on tooth eruption for fawns and yearlings and the tooth cementum annuli for adults. However, no reliable age at death was obtained for URB-MAM-34.

1-2. Fossil taxa

***Cervus astylodon* and *Muntiacini* gen. et sp. indet. (the Ryukyu Muntjac).** Both of these fossil deer species were excavated from the Hananda-Gama Cave site (26°8'7"N, 127°45'32"E) in the southern part of Okinawa Island (Okinawa Prefectural Museum and Art Museum 2009). These animal remains are mainly isolated materials consisting of limb bones and teeth and are considered to have fallen into the cave through fissures or sinkholes following decomposition of the carcasses (Okinawa Prefectural Museum and Art Museum 2009). The detailed geological age of these fossils is not clear due to a lack of suitable specimens for radiocarbon dating. However, based on radiocarbon dating at other sites that have yielded fossils of these species, the geological age of both species has been estimated as the Latest Pleistocene (Okinawa Prefectural Museum and Art

Museum 2009). *Cervus astylodon* has been recognized as a typical insular dwarf due to its very small body size and shortened limbs (van der Geer et al. 2010). The Ryukyu muntjac used to be referred to as *Dicrocerus* sp. (van der Geer et al. 2010), which is a genus that is known mostly from Miocene Europe. However, the finding that the antlers have a clear burr and grow from the posterior parts of the frontals oriented backward clearly indicates that it does not belong to this genus (Gertrud Rößner, personal communication to MOK). Rather, it appears to be closely related to *Muntiacus* based on the presence of tusk-like canines and a lack of antlers in the females, neither of which is found in *Dicrocerus* (Azanza et al. 2011). Full revision of this species is required, including a detailed description and comparisons with other fossil and extant taxa. Therefore, in this paper, we present it as *Muntiacini* gen. et sp. indet. and refer to it as “the Ryukyu muntjac.” All of the specimens that were examined are stored at Okinawa Prefectural Museum and Art Museum (OPM), Naha, Japan.

***Sinomegaceros yabei*.** This fossil deer had a gigantic body size that was comparable to that of Irish elk (*Megaloceros giganteus*) (Okumura et al. 2016, Taruno et al. 2017). The skeletal remains were excavated from the Kumaishi-do Cave site (35°45’N, 137°00’E) in Hachiman-cho, Gujo city, Gifu Prefecture, central Japan. Most of the animal remains obtained from this site are isolated materials, but an incomplete skeleton that includes the skull has also been discovered (Okumura et al. 2016). The geological age of these fossils is the Late Pleistocene based on radiocarbon dating of the bones of cervids and proboscideans (Okumura et al. 1982). All of the specimens we sampled are stored at the Osaka Museum of Natural History (OMNH), Osaka, Japan.

2. Growth curve modeling using the femora and tibiae

2-1. Validity of using the number of lines of arrested growth (LAGs) to estimate

Age. We first checked the correlation between the numbers of LAGs observed in the long bones and the actual ages at death assessed by the numbers of dental cementum annuli formed in the tooth roots using 20 extant sika deer from both mainland and island localities (Table S5). Since the date or season of death had been recorded for all of these samples together with the age at death, we counted how many times deer experienced winter (i.e., the season when LAGs are usually formed) and compared this with the number of LAGs. The scatter plot clearly showed that, with the exception of four individuals, the number of LAGs equaled the number of winter seasons the deer experienced in their lifetime (Figure S5). The exceptions to this were one sika deer from

Hokkaido mainland (HOUMVC00037), one sika deer from Honshu mainland (CBM-ZZ-412), and two sika deer from Kerama Islands (URB-MAM-55 and -193). HOUMVC00037, CBM-ZZ-412, and URB-MAM-193 had fewer LAGs (7, 7, and 8, respectively) than their actual age at death (8, 8, and 10, respectively). Based on the expansion of the medullary cavity in these old individuals, it seemed likely that the first (and also second in URB-MAM-193) LAG had been eliminated, and this was supported by the estimated body mass at the first LAG, which was greater than that of younger deer of the same population and sex (based on a comparison of HOUMVC00037 with HOUMVC00033, CBM-ZZ-412 with CBM-ZZ-218, and URB-MAM-193 with URB-MAM-211). Therefore, we considered that these three individuals had lost their initial growth information. In the case of URB-MAM-55, the number of LAGs (7) was greater than the actual age at death (4). This individual had limb bones without epiphyseal fusion, indicating that the bones were still actively growing in a longitudinal direction. However, observation of the long bone histology showed that appositional growth was decelerated and marked with many LAGs. Therefore, it is possible that this deer was malnourished and its growth was arrested intermittently even during the growing season. Consequently, we excluded this individual from the following growth curve analysis.

For the extant Reeves's muntjac specimens, the age at death was estimated based on tooth eruption and the molar wear condition. Assessment of the correspondence between the number of LAGs and the age assessed by tooth eruption and wear for Reeves's muntjac showed that the two were perfectly matched. Therefore, for this species, we considered the age assessed by tooth eruption and wear to be the actual age at death.

2-2. Age assessment. We estimated the age at death of the fossil specimens from the number of LAGs. However, several specimens showed explicit expansion of the medullary cavity, which may have erased the record of early growth. Therefore, we also estimated the number of lost LAGs due to bone remodeling. Several estimation methods have been proposed in paleo-histological studies (Cooper et al. 2008, Erickson 2014, Kolb et al. 2015). Here, we applied a simple method that uses a reference specimen with no apparent bone remodeling or expansion of the medullary cavity and compares this with specimens with possible dissipation of the initial LAGs. We chose this method because backward estimation from fitted growth curves (Cooper et al. 2008) resulted in overestimation of the number of lost LAGs, generating a slower growth rate for the fossil taxa. Therefore, to yield a more conservative comparison with extant taxa, we

estimated the number of lost LAGs through comparisons with younger specimens of the same taxa that were well preserved. Table S6 summarizes the estimation of lost LAGs based on comparisons with the reference specimens. The number of lost LAGs was small in all cases except for the femora of *C. astylodon*, which exhibited a more obvious expansion of the medullary cavity, resulting in up to seven LAGs potentially being lost (in OPM-HAN06-155).

Among the extant specimens we analyzed, only one sika deer (Kerama Islands, URB-MAM-34) did not have a reliable age based on the tooth cementum annuli. This specimen had eight LAGs in both the femur and tibia with completely fused epiphyses. Comparison of this specimen with other Kerama deer specimens indicated that one LAG had been erased by bone remodeling. Therefore, the age at death of this specimen was estimated to be 9 years old.

Raw data of LAG and external diaphysial measurements of specimens used in the histological analyses, together with estimated body mass is presented in Table S14 (Separate Excel file).

2-3. Body mass estimation. In addition to measuring the bone diameters at the LAGs, we measured the external diaphysial measurements [anteroposterior diameter (APD) and mediolateral diameter (MLD)] and used these to estimate the body mass at death. The body mass estimation formulae for both the femur and tibia were obtained from Scott (1990), who presented the following linear regression equations of body mass against limb bone metrics for extant artiodactyls:

$$\text{Log}_{10}(\text{body mass in kg}) = 0.8737 + 2.7585 * \text{log}_{10}(\text{femur APD in cm})$$

$$\text{Log}_{10}(\text{body mass in kg}) = 0.8915 + 2.8771 * \text{log}_{10}(\text{femur MLD in cm})$$

$$\text{Log}_{10}(\text{body mass in kg}) = 0.9834 + 2.9356 * \text{log}_{10}(\text{tibia APD in cm})$$

$$\text{Log}_{10}(\text{body mass in kg}) = 0.8689 + 2.7672 * \text{log}_{10}(\text{tibia MLD in cm})$$

We compared the two formulae for each of the femur and tibia and selected those that produced the least discrepancy in estimated body mass with the femur and tibia metrics of extant cervids. This resulted in the formulae using MLD being selected for both bones.

Accurate fitting of a growth curve requires knowledge of the starting point (i.e., the neonatal body mass). For extant sika deer (Honshu and Hokkaido mainland, Yakushima Island) and Reeves's muntjac, we collected neonatal or perinatal body mass data from the literature (Suzuki and Ohtaishi 1993) or zoo reports. However, the neonatal body mass was not known for sika deer from Kerama Islands. Therefore, we used the value of sika deer from Yakushima Island for this population because of their similar body sizes

as adults. For the fossil taxa, we estimated the neonatal body mass using the following adult–neonate body mass regression equation based on data from 121 extant artiodactyls in the PanTHERIA database [Jones et al. (2009);

<http://esapubs.org/archive/ecol/E090/184/>] (Figure S6):

$$\text{Log}_{10}(\text{neonatal body mass in g}) = -0.3009 + 0.806 * \text{log}_{10}(\text{adult body mass in g})$$

The adult body masses of the fossil cervids, which were obtained from the external diaphysial measurements of the femora and tibiae, were averaged for each species and substituted into the regression equation to predict the neonatal body mass. The estimated neonatal body masses of the fossil cervids are presented in Table S7.

2-4. Growth curve modeling and statistical comparisons of the growth curve parameters. For both the extant and fossil samples, all individuals that were older than yearlings were used for growth curve fitting. In addition, we included a fawn and a yearling in the growth curve fitting for extant Reeves’s muntjac. A Gompertz curve was fitted to the longitudinal body mass data for each individual using the formula:

$$W = a \text{Exp}(-\text{Exp}(-b(x - c)))$$

where W is the body mass in kg, x is the age in years, and the parameters a , b , and c represent the asymptote, growth rate, and inflection point, respectively. We then obtained growth curves for each species/population and each leg bone (femur or tibia) (Figure S7–S14) and compared two of the parameters (growth rate and inflection point) statistically among the extant and fossil cervids. Two-way analysis of variance (ANOVA) showed that bone type (i.e., femur or tibia) had no significant effect on the growth curve parameters (Table S8). Therefore, we combined the data from the femur and tibia and conducted multiple comparisons using the Tukey-Kramer method to examine differences in the growth parameters among the eight species/populations (Table S9), averaging the growth curve parameters from the femur and tibia for the extant species to avoid repeated sampling from the same individual. In addition, we conducted multiple comparisons using the uncombined femur and tibia datasets (Tables S10 and S11). A comparison of the growth curves is presented in Figure 3A for the femur and Figure S15 for the tibia.

3. Reconstruction of survivorship curves using age data of extant and fossil cervids. We obtained age data for the three extant sika deer populations that were used in the histological investigations either from published papers or through investigation of the cementum annuli of the incisor roots: Hokkaido mainland [$n = 1,060$ (Hokkaido Institute of Environmental Sciences 1997)], Honshu mainland [$n = 594$ (Ozaki et al.

2010)], and Yakushima Island (n = 74, cementum annuli of museum specimens). These age data were based on randomly culled individuals and so were considered to be indicative of actual extant populations. To depict the survivorship curves, we constructed life tables following the method described in Caughley (1977), assuming stationary age distributions, and applied probit regression to smooth the age distributions. The survivorship curves were presented with an initial value of 1,000 individuals.

The age data for extant Reeves's muntjac from England and fossil insular cervids from Okinawa Island were obtained from published references [Reeves's muntjac: n = 84 (Chapman, Brown, and Rothery 2005); *C. astylodon*: n = 45 (Kubo et al. 2011); the Ryukyu muntjac: n = 65 (Ozaki 2009)]. Since the age data for these populations were based on natural deaths, the age class frequency was divided by the sample size to obtain a multiple of the frequency of mortality (dx). Life tables were then derived from this mortality frequency (Caughley 1977).

The observed age class frequencies and derived life tables for each deer population are shown in Tables S12 and S13, and the survivorship curves are presented in Figure 3B.

Supplementary figures

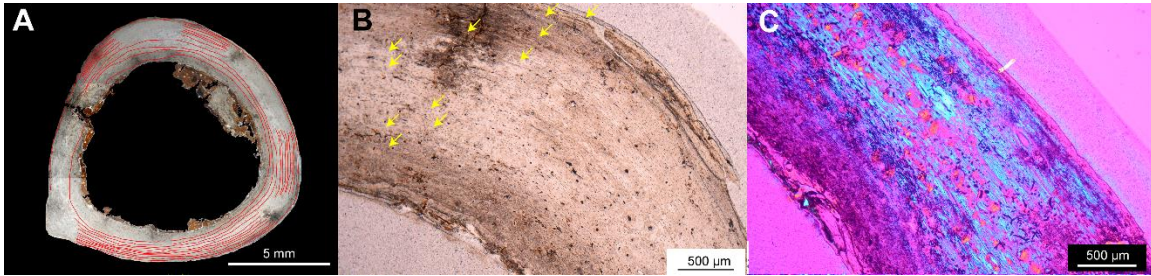


Figure S1. Bone histologies of the femora of fossil Ryukyu muntjac. (A–C) Midshaft cross section in normal light (A), cortex in normal light (B), and cortex in polarized light (C) of femora of the Ryukyu muntjac (*Muntiacini* gen. et sp. indet.; A and B: OPM-HAN06-163; C: OPM-HAN07-1618). The red lines in A and the yellow arrows in B indicate lines of arrested growth (LAGs). The outer cortex is in the upper right in B and C. Note: LAGs appear at narrow intervals in the inner cortex in the Ryukyu muntjac, which also has an abundance of parallel-fibered bone tissue (blue tissues in C).

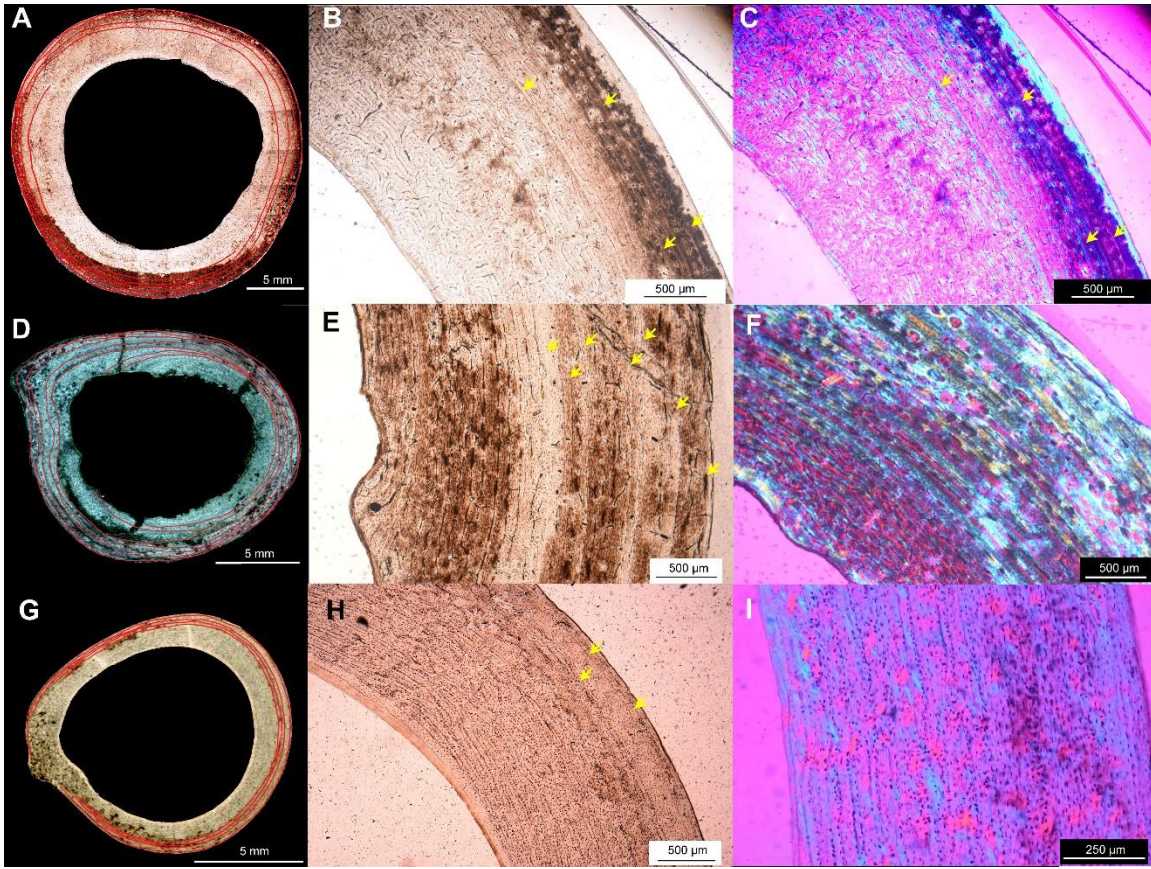


Figure S2. Bone histologies of the femora of extant Japanese cervids. (A–C) Midshaft cross section in normal light (A), cortex in normal light (B), and cortex in polarized light (C) of a femur of sika deer (*Cervus nippon*) from Hokkaido mainland (HOUMVC00035). (D–F) Midshaft cross section in normal light (D), cortex in normal light (E), and cortex in polarized light (F) of a femur of sika deer from Kerama Islands (URB-MAM-183). (G–I) Midshaft cross section in normal light (G), cortex in normal light (H), and cortex in polarized light (I) of a femur of Reeves’s muntjac (*Muntiacus reevesi*) from Honshu mainland (CBM-ZZ-2646). The red lines in A, D, and G and the yellow arrows in B, E, and H indicate lines of arrested growth (LAGs). The outer cortex is on the right in E and I and in the upper right in B, C, F, and H.

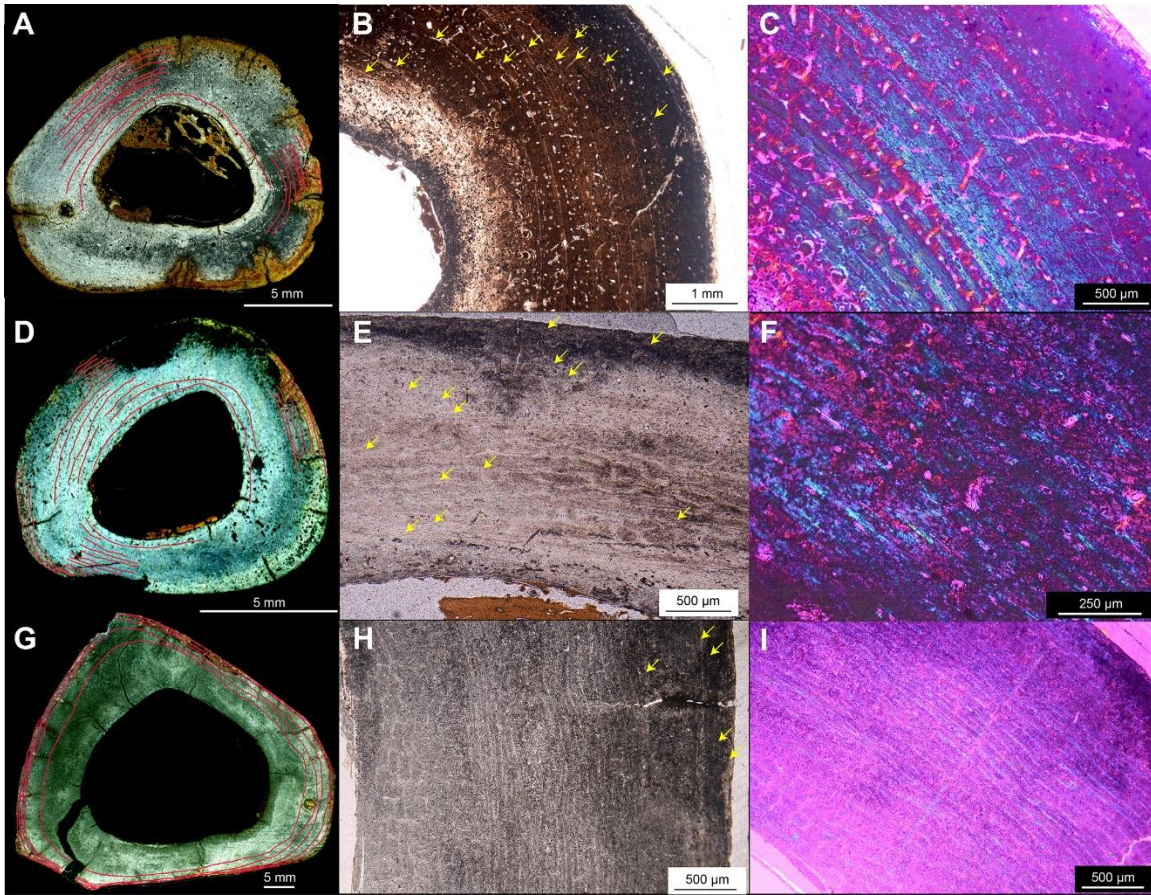


Figure S3. Bone histologies of the tibiae of fossil Japanese cervids. (A–C) Midshaft cross section in normal light (A), cortex in normal light (B), and magnified view of the cortex in polarized light (C) of a tibia of *Cervus astylodon* (OPM-HAN07-1585). (D–F) Midshaft cross section in normal light (D), cortex in normal light (E), and magnified view of the cortex in polarized light (F) of a tibia of the Ryukyu muntjac (*Muntiacini* gen. et sp. indet.; OPM-HAN07-1599). (G–I) Midshaft cross section in normal light (G), cortex in normal light (H), and cortex in polarized light (I) of a tibia of *Sinomegaceros yabei* (OMNH-QV-4068). The outer cortex is in the upper right in B, C, F, and I, at the top in E, and on the right in H.

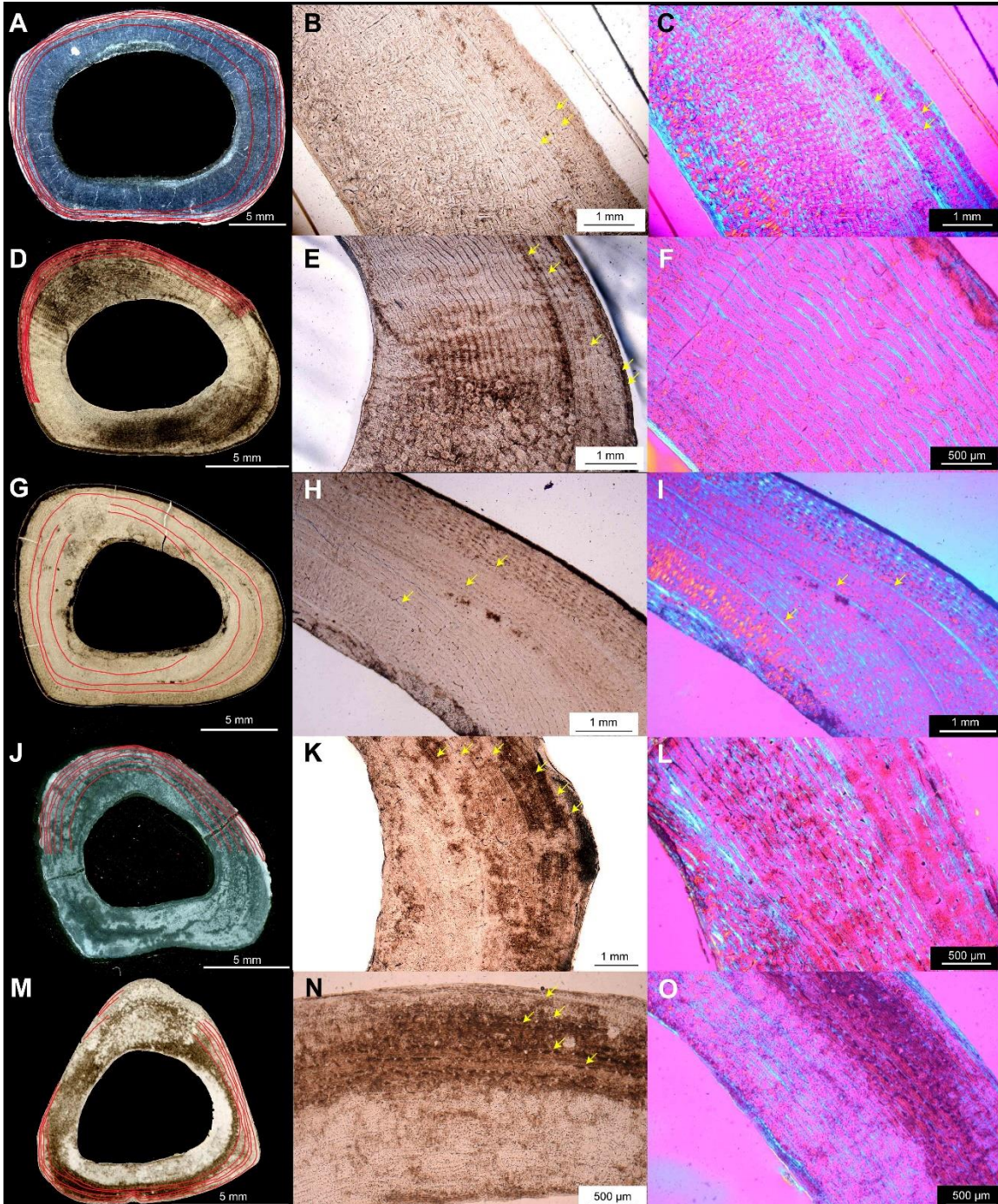


Figure S4. Bone histologies of the tibiae of extant Japanese cervids. (A–C) Midshaft cross section in normal light (A), cortex in normal light (B), and cortex in polarized light (C) of a tibia of sika deer (*Cervus nippon*) from Hokkaido mainland (HOUMVC00035). (D–F) Midshaft cross section in normal light (D), cortex in normal light (E), and cortex in polarized light (F) of a tibia of sika deer from Honshu mainland (CBM-ZZ-412). (G–I) Midshaft cross section in normal light (G), cortex in normal light (H), and cortex in polarized light (I) of a tibia of sika deer from Yakushima Island (TPM-M-313). (J–L) Midshaft cross section in normal light (J), cortex in normal light (K), and cortex in polarized light (L) of a tibia of sika deer from Kerama Islands (URB-MAM-183). (M–O)

Midshaft cross section in normal light (M), cortex in normal light (N), and cortex in polarized light (O) of a tibia of Reeves's muntjac (*Muntiacus reevesi*) from Honshu mainland (CBM-ZZ-2646). The outer cortex is in the upper right in B, C, E, F, H, I, K, L, and O at the top in N.

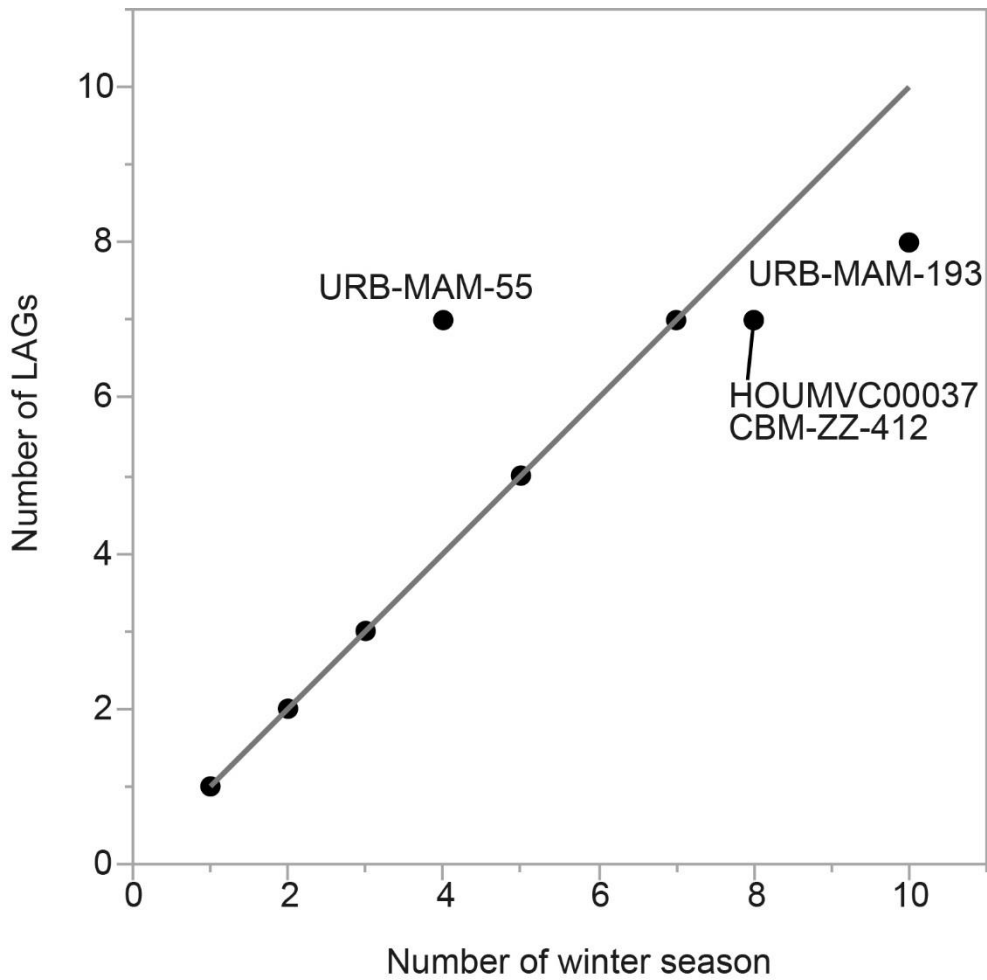


Figure S5. Scatter plot showing the correlation between the number of winter seasons a deer experienced during its lifetime and the number of lines of arrested growth (LAGs). The raw data are presented in Table S5. There was a perfect match between the two variables in extant sika deer (*Cervus nippon*) of known age, with the exception of four individuals (HOUMVC00037, CBM-ZZ-412, URB-MAM-55, and URB-MAM-193). The solid line represents $x = y$.

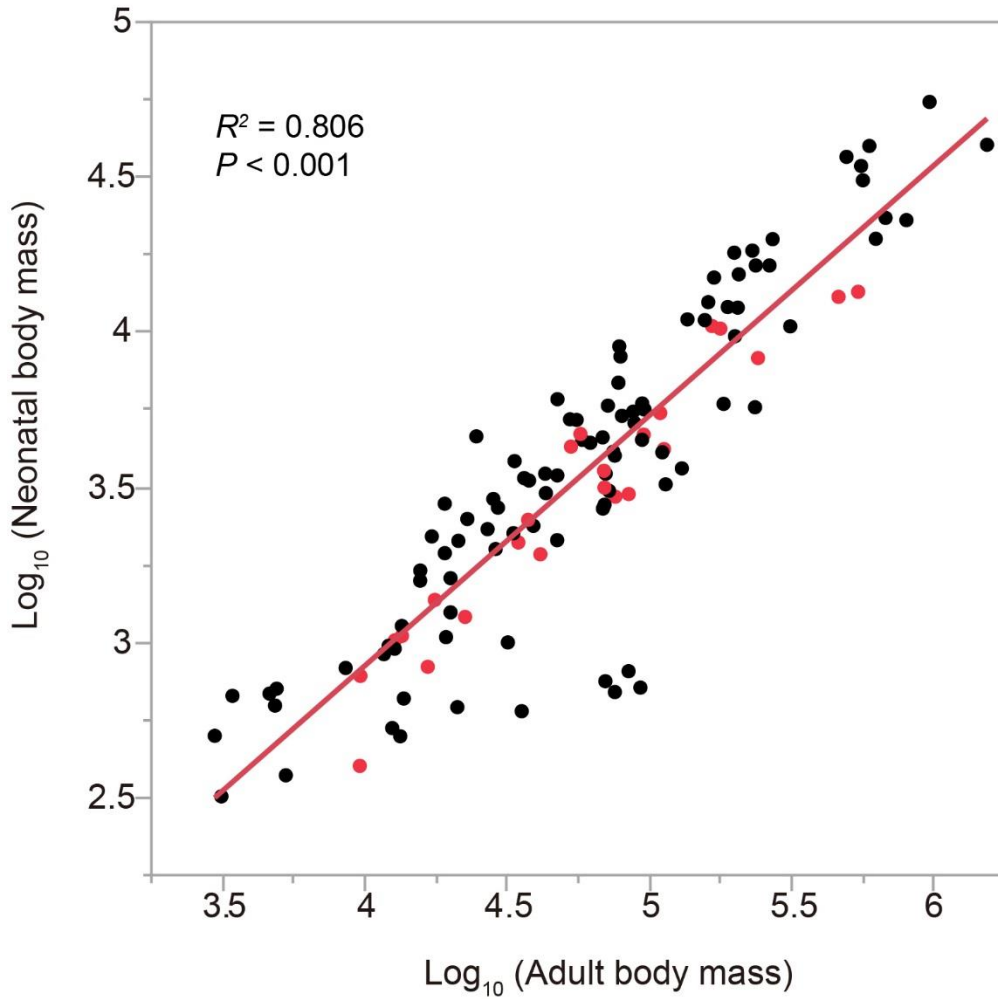
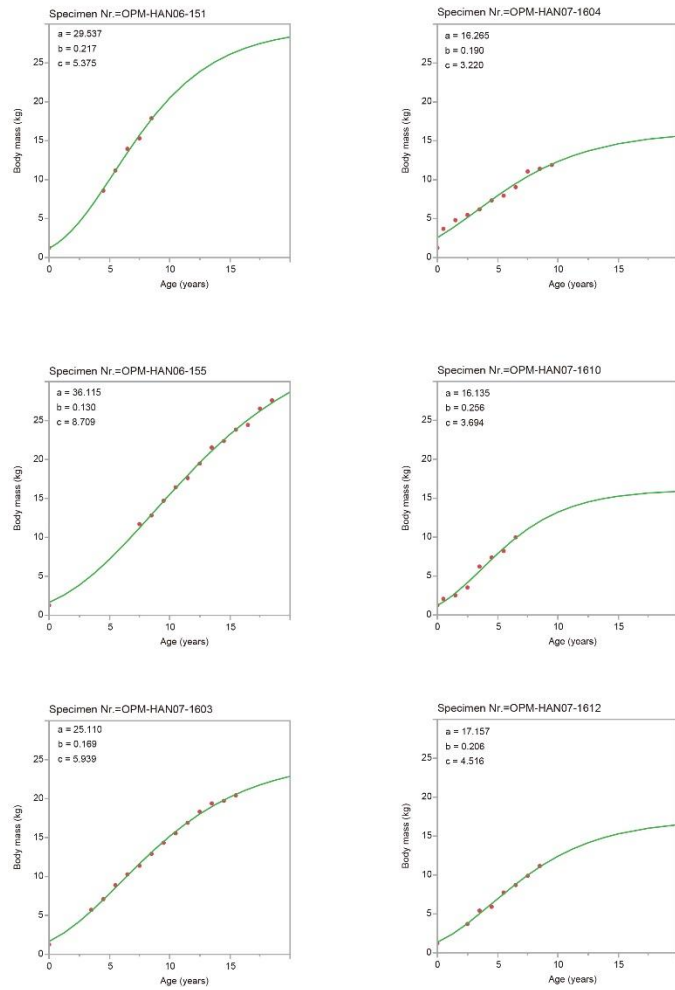


Figure S6. Scatter plot showing the correlation between adult and neonatal body mass in extant artiodactyls ($n = 121$). The solid line represents the linear regression line. The red dots indicate Cervidae species. Data were obtained from PanTHERIA [(Jones et al. 2009); <http://esapubs.org/archive/ecol/E090/184/>]. The regression equation was then used to estimate the neonatal body mass of three fossil cervids (see Table S7).

Growth curves of *Cervus astylodon* based on femora



Growth curves of *Cervus astylodon* based on tibia

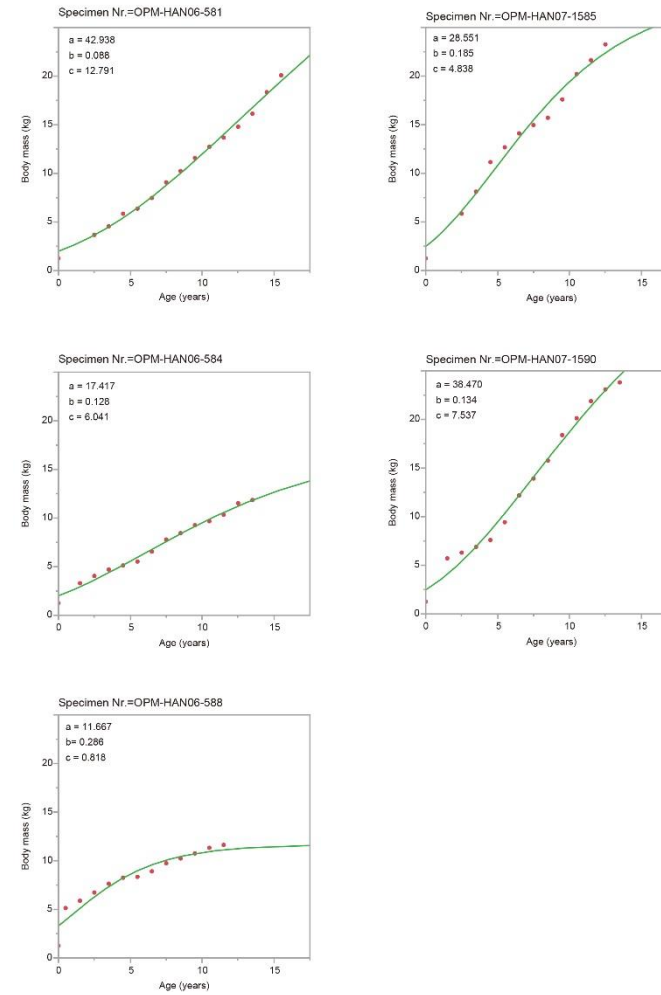
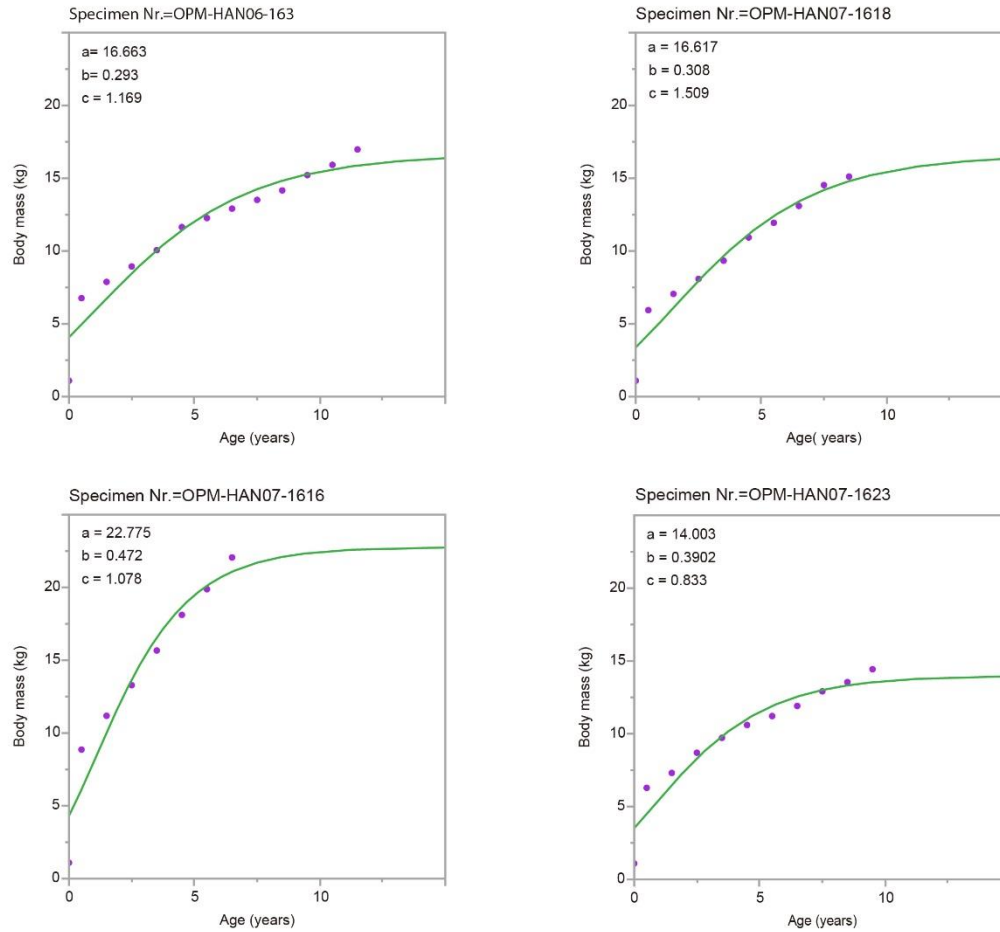


Figure S7. Growth curves of body mass for fossil *Cervus astylodon*. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of Muntiacini genus et sp. indet. (Ryukyu muntjac) based on femora



Growth curve of Muntiacini genus et sp. indet. (Ryukyu muntjac) based on tibia

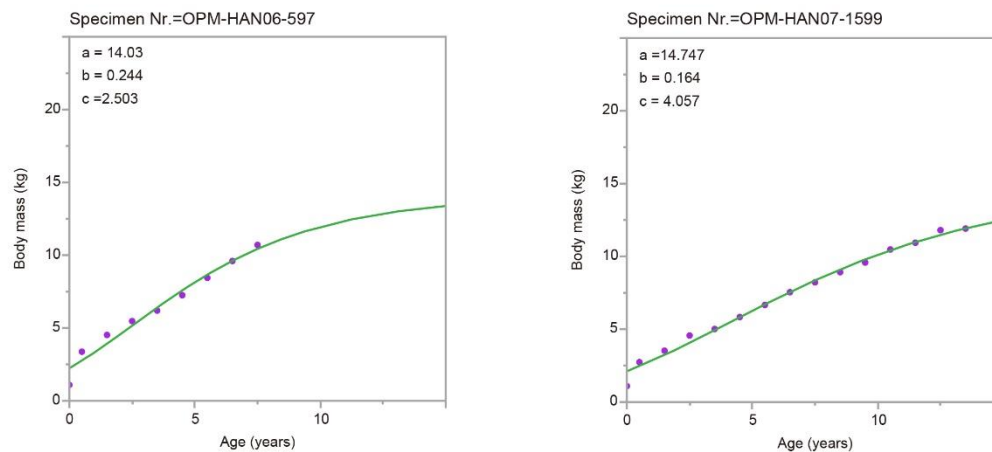


Figure S8. Growth curves of body mass for fossil Ryukyu muntjac (Muntiacini gen. et sp. indet.). Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of sika deer (Hokkaido mainland)

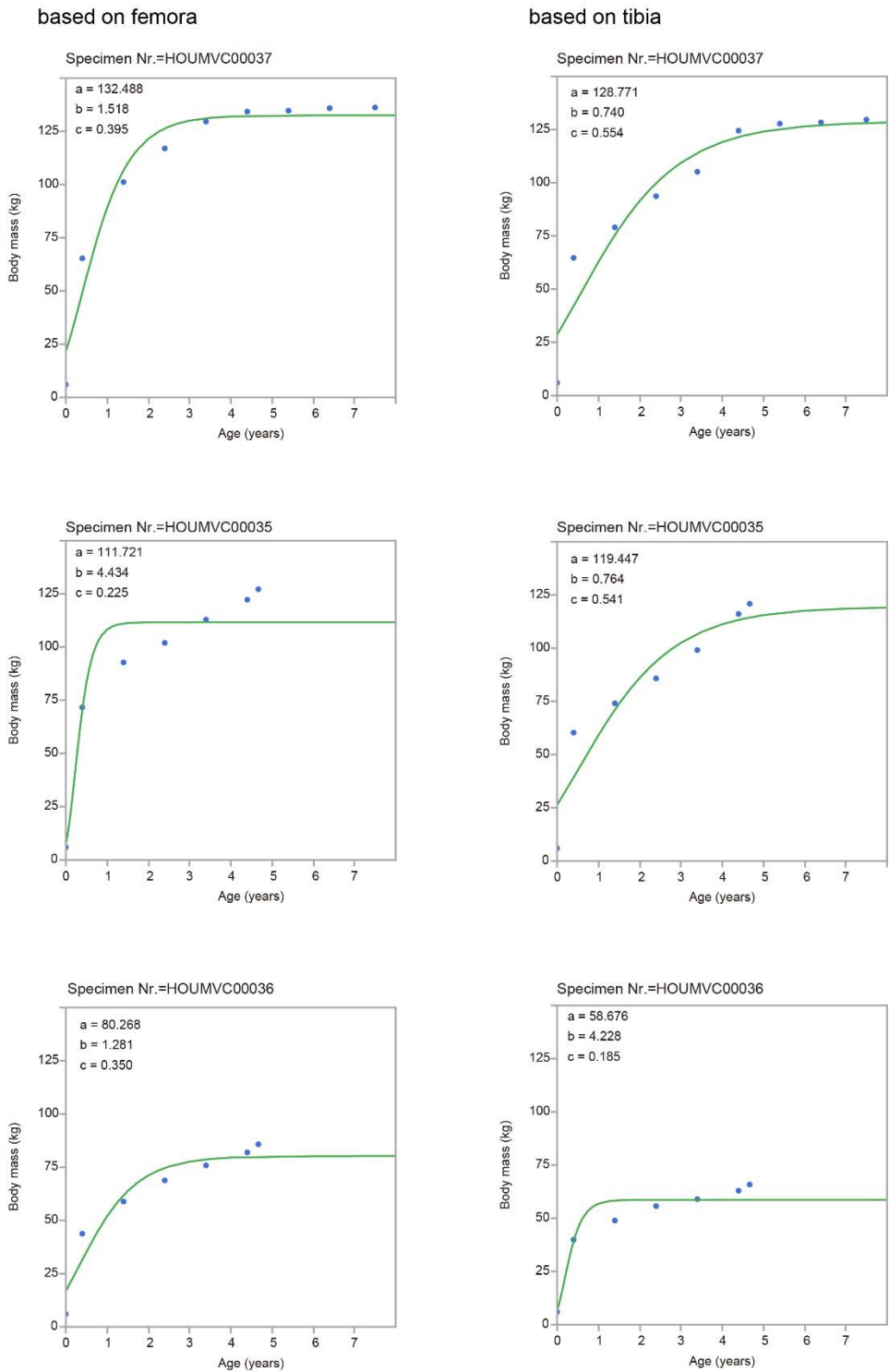


Figure S9. Growth curves of body mass for extant sika deer (*Cervus nippon*) from Hokkaido mainland. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of sika deer (Honshu mainland)

based on femora

based on tibia

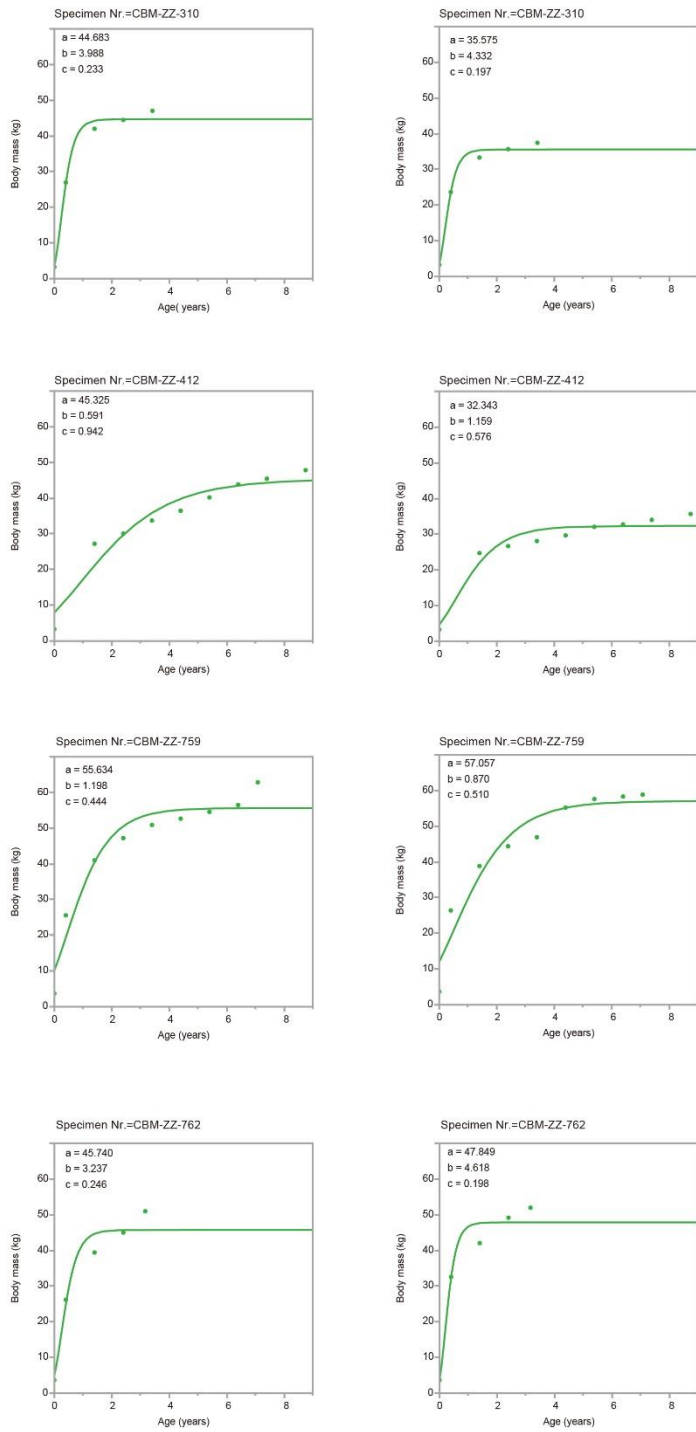
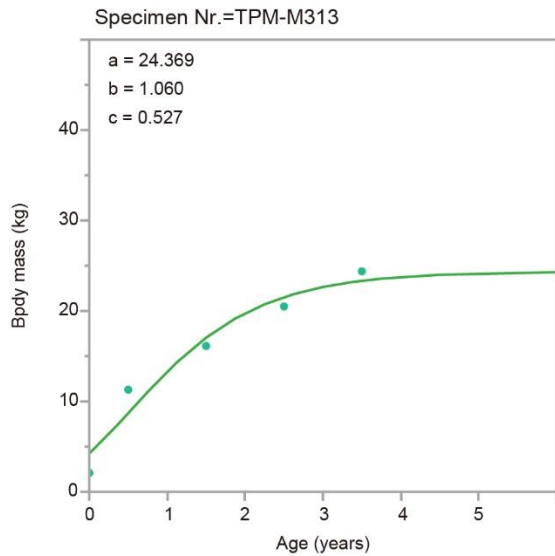


Figure S10. Growth curves of body mass for extant sika deer (*Cervus nippon*) from Honshu mainland. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of sika deer (Yakushima Island)

based on femora



based on tibia

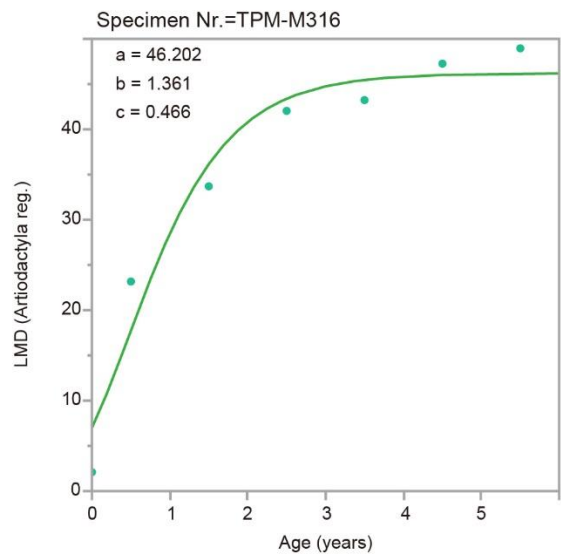
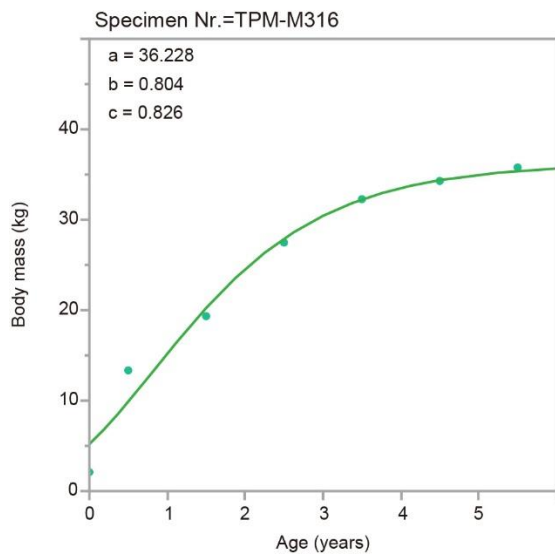
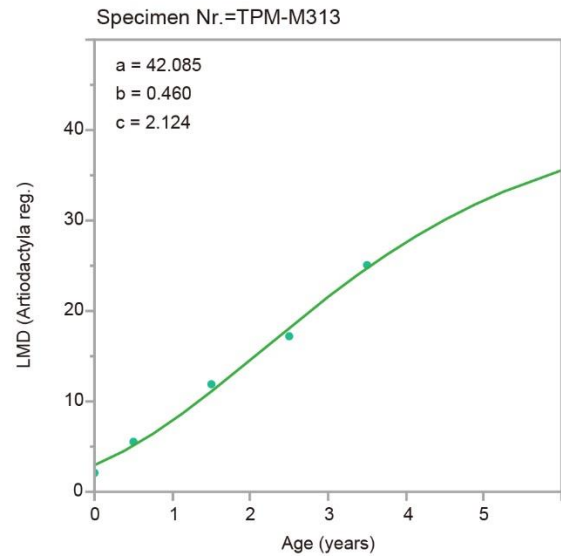


Figure S11. Growth curves of body mass for extant sika deer (*Cervus nippon*) from Yakushima Island. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of sika deer (Kerama Islands)

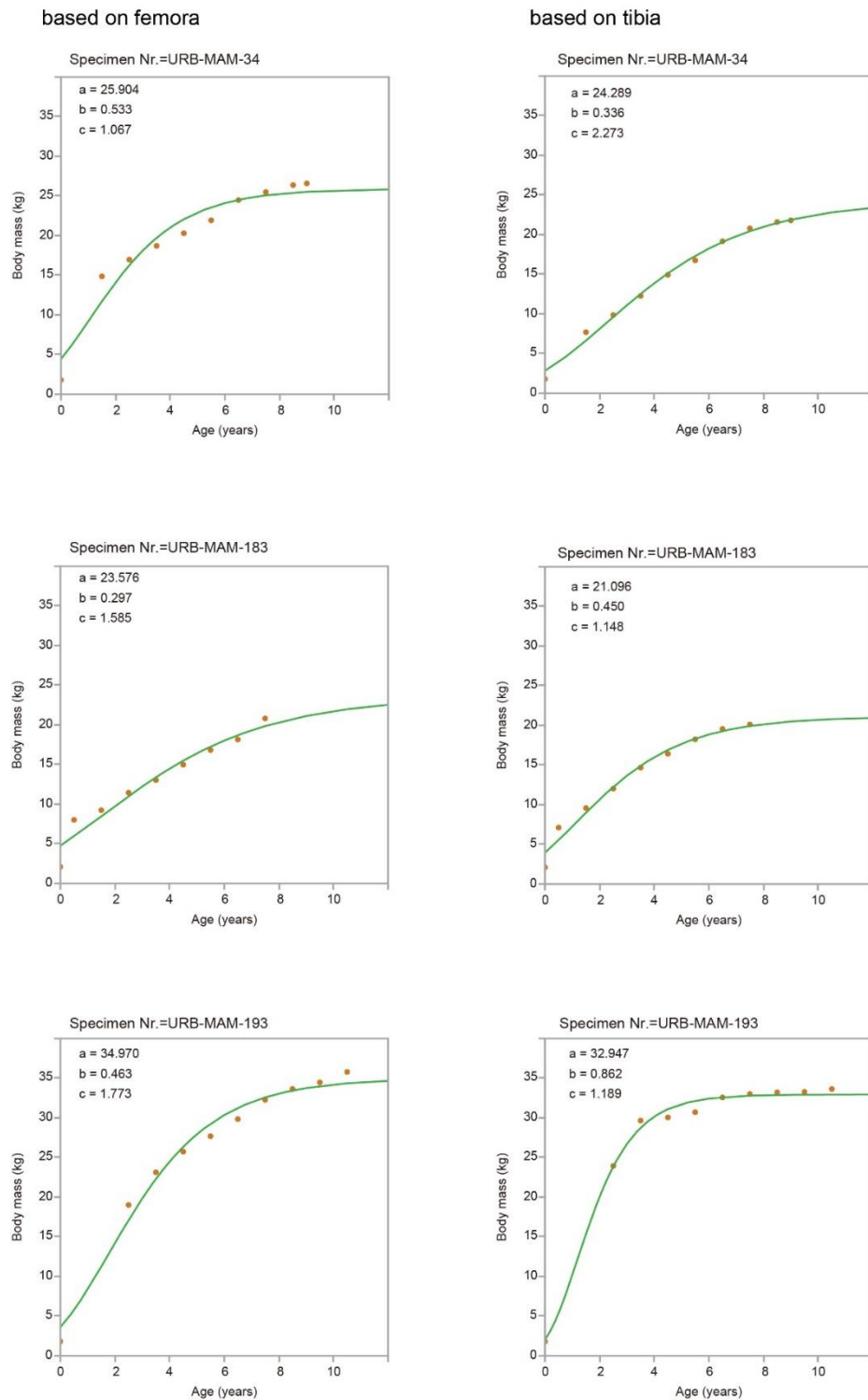


Figure S12. Growth curves of body mass for extant sika deer (*Cervus nippon*) from the Kerama Islands. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

Growth curve of Reeves's muntjac

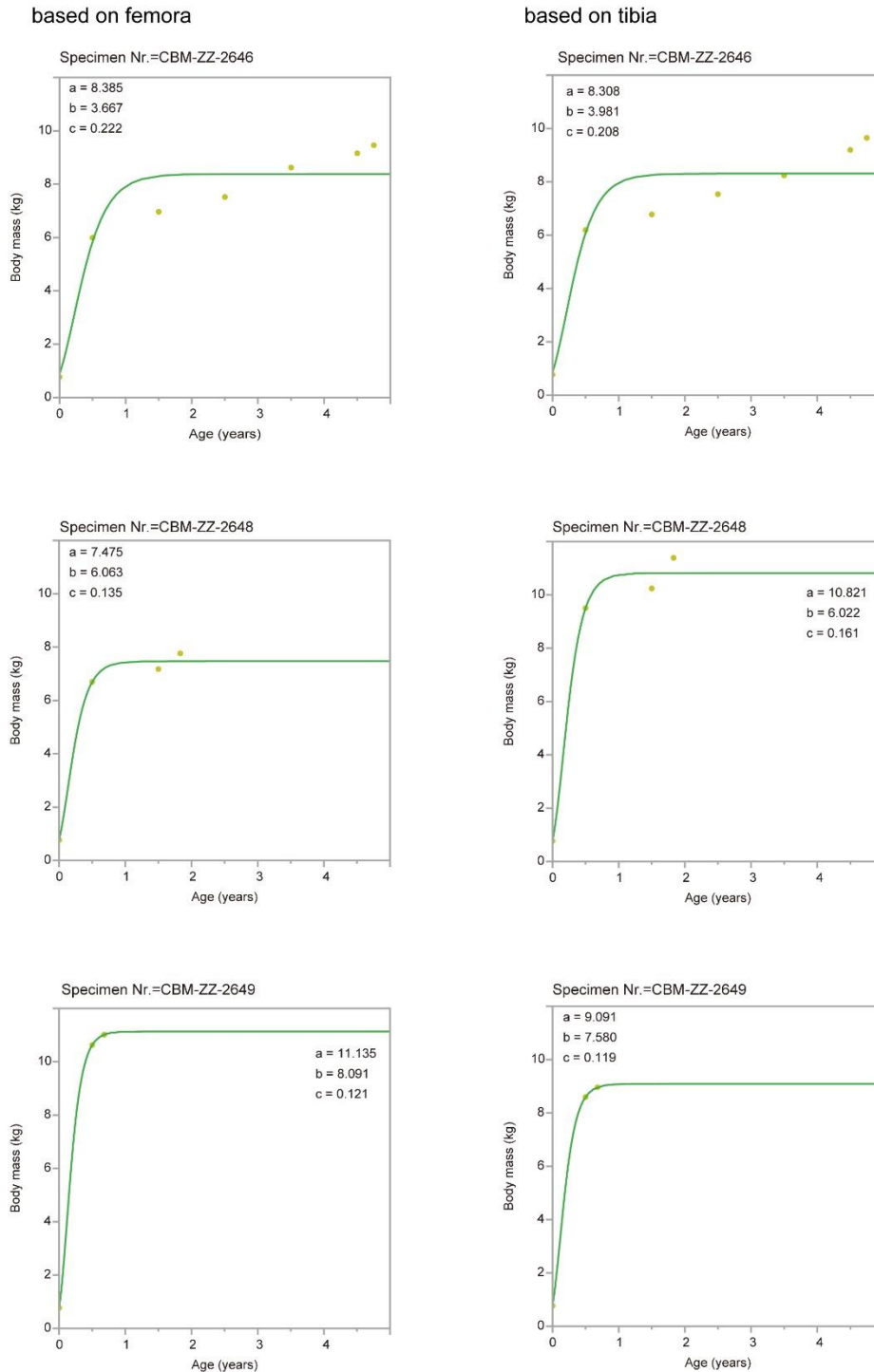


Figure S13. Growth curves of body mass for extant Reeves's muntjac (*Muntiacus reevesi*). Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote, b: growth rate and c: inflection point) are shown on the plot for each individual.

Growth curve of *Sinomegaceros yabei*

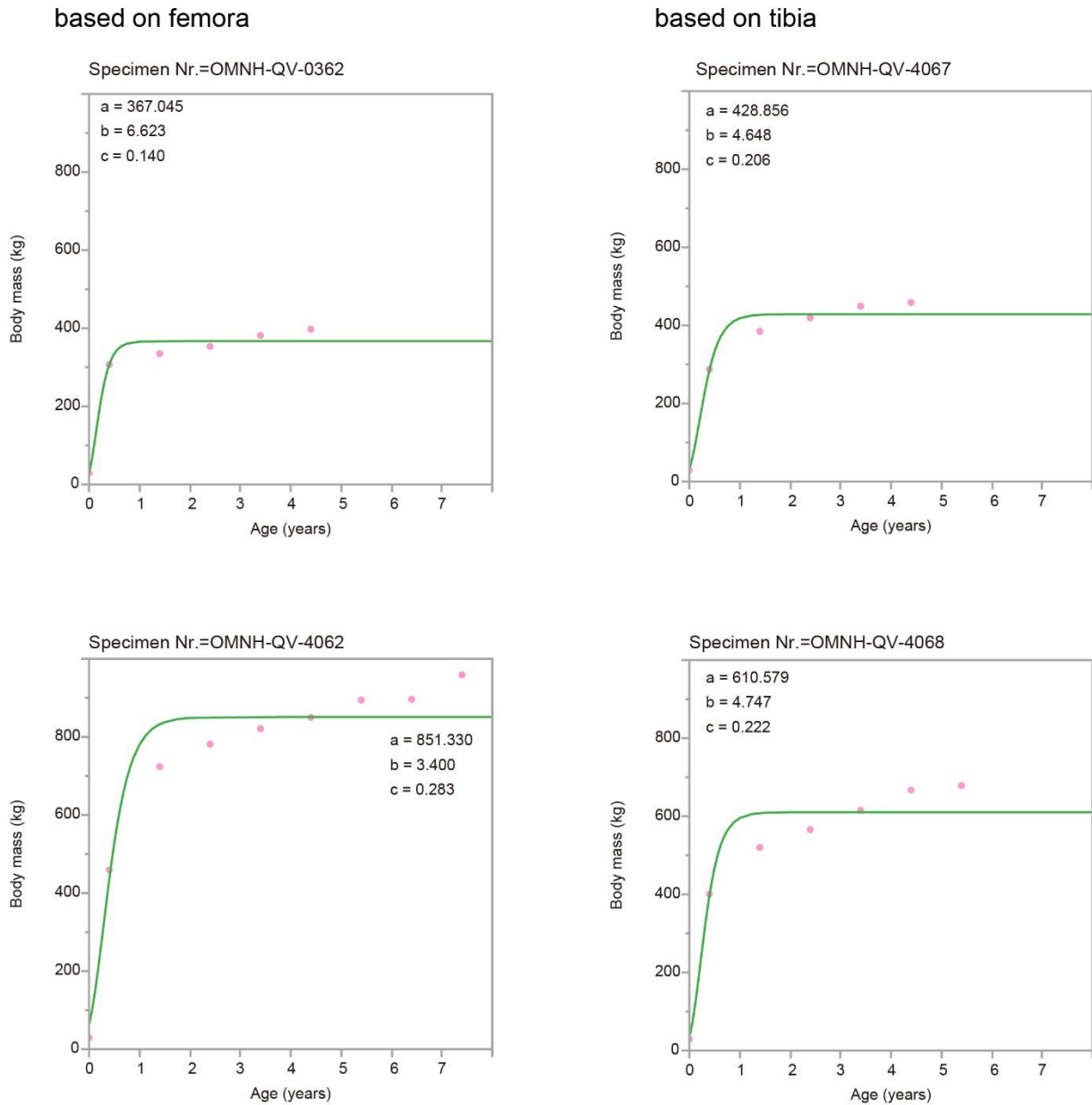


Figure S14. Growth curves of body mass for fossil *Sinomegaceros yabei*. Body mass was estimated from the femur or tibia mediolateral diameter (MLD). Green solid lines represent the fitted Gompertz curves, the parameters for which (a: asymptote; b: growth rate; and c: inflection point) are shown on the plot for each individual.

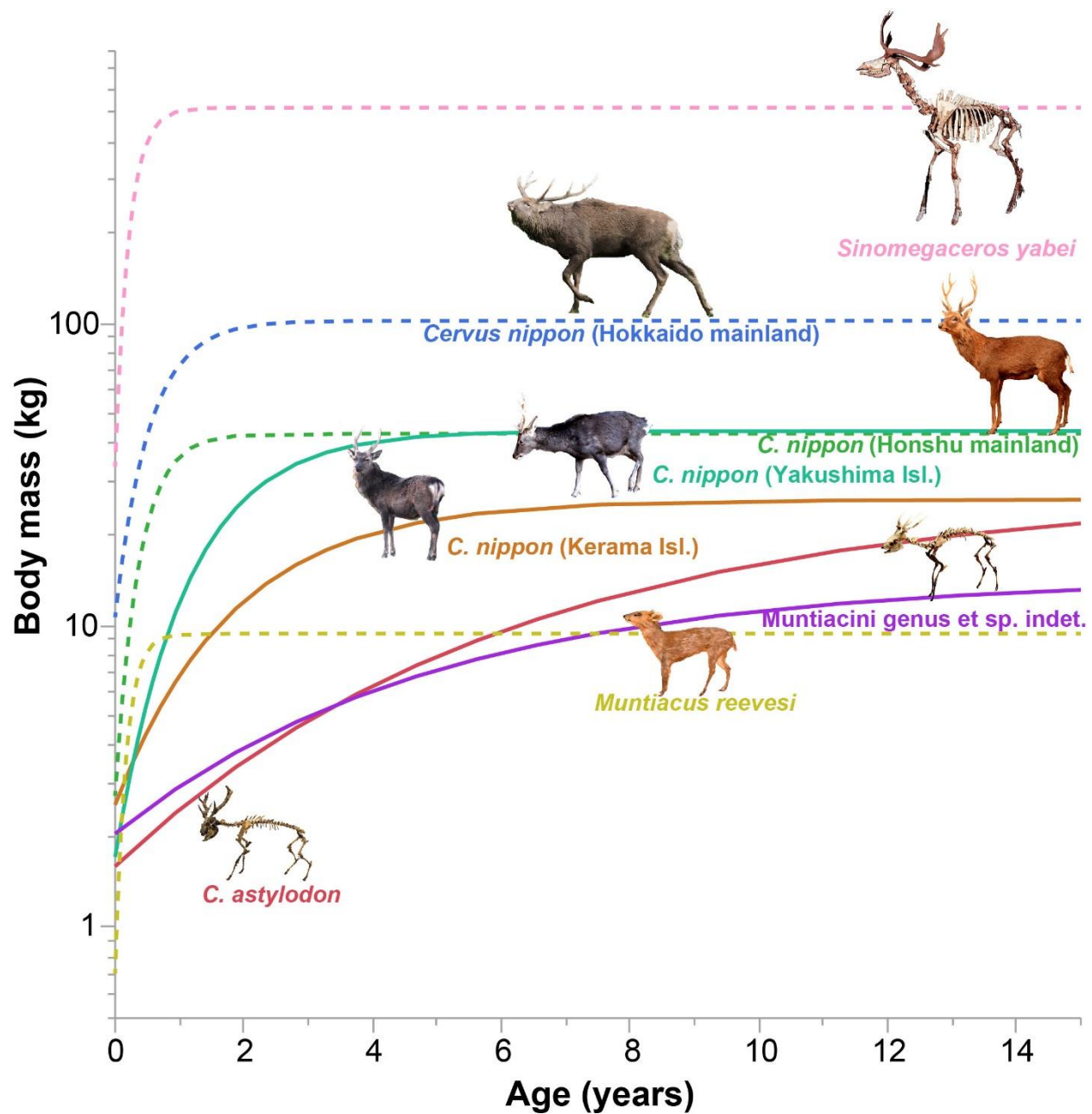


Figure S15. Growth curves of insular cervids in Japan based on lines of arrested growth (LAGs) in the tibiae. Mainland cervids show rapid growth, attaining their maximum body size within 2 years, whereas two fossil Okinawa cervids exhibited an extremely slow growth rate, reaching their maximum body size at ca. 14 years for *Cervus astylodon* and 10 years for the Ryukyu muntjac (Muntiacini gen. et. sp. indet.). Sika deer (*Cervus nippon*) from Yakushima and Kerama islands have an intermediate growth rate, attaining their maximum body size at around 5 years of age. Growth curves of insular cervids are solid lines and those of mainland cervids are dashed-lines.

Supplementary tables

Table S1. Measurements and histological features of the femora of the fossil cervids that were sampled. Note that the presence of EFS is correlated with epiphyseal fusions, suggesting the somatic maturity of the animals [see also Erickson (2007)].

Taxon	Collection no.	GL (mm)	EBM (kg) [†]	Epiphyseal fusion	Number of LAGs	Bone tissue type	Degree of remodeling
<i>Cervus astylodon</i>	OPM-HAN07-1610	101.3 ^a	10.0	Prox: broken Dis: broken	6	PFB	Poor (only inner cortex)
	OPM-HAN07-1612	104.3 ^a	11.2	Prox: broken Dis: unfused	6	PFB	Poor (only inner cortex)
	OPM-HAN07-1604	112.1 ^a	11.9	Prox: fused Dis: broken	9	PFB	Poor (only inner cortex)
	OPM-HAN06-151	124.1 ^a	17.9	Prox: broken Dis: fused	4	PFB, EFS	Extensive (PBTs are present only in the outer cortex)
	OPM-HAN06-155	129.5 ^a	27.6	Prox: broken Dis: broken	11	PFB	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1603	130.4 ^a	20.4	Prox: broken Dis: broken	12	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
<i>Muntiacini gen. et sp. indet. (Ryukyu muntjac)</i>	OPM-HAN06-163	112.9 ^a	17.0	Prox: fused Dis: broken	11	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1618	121.4 ^a	15.1	Prox: broken Dis: broken	8	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1623	134.3 ^a	14.4	Prox: broken Dis: broken	9	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1616	144.4 ^a	22.1	Prox: fused Dis: broken	6	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
<i>Sinomegaceros yabei</i>	OMNH-QV-0362	391.7 ^a	959.2	Prox: unfused Dis: broken	5	FBL	Moderate (only posterior side of the cortex)
	OMNH-QV-4062	465.0	397.6	Prox: fused Dis: broken	7	FBL, EFS	Moderate (only posterior side of the cortex)

Dis, distal epiphysis; EBM, estimated body mass; EFS, external fundamental system; FBL, fibro-lamellar bone tissue; GL, greatest length of femur; LAG, line of arrested growth; PBT, primary bone tissue; PFB, parallel-fibered bone tissue; Prox, proximal epiphysis; SO, secondary osteon.

Collection acronyms: OPM, Okinawa Prefectural Museum and Art Museum, Okinawa, Japan; OMNH, Osaka Museum of Natural History, Osaka, Japan.

[†] The estimated body mass (EBM) was obtained from the estimation equation based on femur mediolateral diameter. ^a The estimated greatest length of the bone based on measurements of the complete femora of other individuals.

Table S2. Measurements and histological features of the tibiae of the fossil cervids from Late Pleistocene deposits that were sampled. See Table S1 for an explanation of the abbreviations. Note that the presence of EFS is correlated with epiphyseal fusions.

Taxon	Collection no.	GL (mm)	EBM (kg) [†]	Epiphyseal fusion	Number of LAGs	Bone tissue type	Degree of remodeling
<i>Cervus astylodon</i>	OPM-HAN06-588	118.9 ^a	11.6	Prox: broken Dis: fused	11	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN06-584	122.5 ^a	11.9	Prox: broken Dis: fused	12	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN06-581	146.0 ^a	20.1	Prox: broken Dis: fused	13	FBL (from perimedullary region to 3 rd LAGs), PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1585	147.0 ^a	23.3	Prox: broken Dis: broken	10	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1590	148.1 ^a	23.8	Prox: broken Dis: broken	12	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
Muntiacini gen. et sp. indet. (Ryukyu muntjac)	OPM-HAN06-597	112.2 ^a	10.7	Prox: broken Dis: fused	7	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
	OPM-HAN07-1599	117.2 ^a	11.9	Prox: broken Dis: broken	13	PFB, EFS	Moderate (scattered SOs are present throughout the entire cortex)
<i>Sinomegaceros yabei</i>	OMNH-QV-4067	406.7 ^a	458.6	Prox: broken Dis: broken	4	FBL, EFS	Moderate (only anterior side of the cortex)
	OMNH-QV-4068	444.9 ^a	678.6	Prox: fused Dis: broken	5	FBL, EFS	Moderate (only anterior side of the cortex)

[†] The estimated body mass (EBM) was obtained from the estimation equation based on tibia mediolateral diameter.

^a The estimated greatest length of the bone based on measurements of the complete femora of other individuals.

Table S3. Measurements and histological features of the femora of the extant cervids that were sampled.

Taxon	Collection no.	Age [†]	Sex	GL (mm)	EBM (kg) [‡]	Epiphyseal fusion	Number of LAGs	Bone tissue type	Degree of remodeling
Sika deer (<i>Cervus nippon</i>) (Hokkaido, mainland)	HOU MVC 00039	8M	♂	235	56.2	Prox: unfused Dis: unfused	1	FBL	Poor (only posterior side of the cortex)
	HOU MVC 00038	8M	♀	218	38.0	Prox: unfused Dis: unfused	1	FBL	Poor (only posterior side of the cortex)
	HOU MVC 00033	1Y8M	♂	284	94.5	Prox: unfused Dis: unfused	2	FBL	Poor (only posterior side of the cortex)
	HOU MVC 00034	1Y9M	♀	271	96.7	Prox: unfused Dis: unfused	2	FBL	Moderate (only posterior side of the cortex)
	HOU MVC 00035	4Y8M	♂	299	127.2	Prox: fused Dis: unfused	5	FBL	Extensive (only posterior side of the cortex)
	HOU MVC 00036	4Y8M	♀	243	85.8	Prox: fused Dis: fused	5	FBL, EFS	Extensive (only posterior side of the cortex)
	HOU MVC 00037	7Y6M	♂	300	175.5 ^b	Prox: fused Dis: fused	7	FBL, EFS	Extensive (only posterior side of the cortex)
Sika deer (Honshu, mainland)	CBM-ZZ-757	0 D	NA	104.3	3.5	Prox: unfused Dis: unfused	0	WB	None
	CBM-ZZ-671	6M	♀	170.5 ^a	22.2	Prox: unfused Dis: broken	1	FBL	Poor (only a few erosion cavities)
	CBM-ZZ-218	1Y2M	♀	191.4	28.2	Prox: unfused Dis: unfused	1	FBL	Poor (only a few erosion cavities)
	CBM-ZZ-761	1Y2M	♂	203.4	35.6	Prox: unfused Dis: unfused	1	FBL	Poor (only a few erosion cavities)
	CBM-ZZ-310	3Y5M	♀	217.4	47.0	Prox: fused Dis: fused	2	FBL, EFS	Extensive (only posterior side of the cortex)
	CBM-ZZ-762	3Y2M	♂	252	51.0	Prox: partially fused Dis: unfused	3	FBL	Extensive (only posterior side of the cortex)
	CBM-ZZ-759	7Y1M	♂	237.6	62.8	Prox: fused Dis: fused	7	FBL, EFS	Extensive (only posterior side of the cortex)
CBM-ZZ-412	8Y9M	♀	218.6	47.8	Prox: fused Dis: fused	7	FBL, EFS	Extensive (only posterior side of the cortex)	
Sika deer (Yakushima Island)	TPM-M-312	0Y	NA	142 ^a	13.5	Prox: unfused Dis: unfused	0	FBL	None
	TPM-M-314	1Y6M	♂	174.9 ^a	30.8	Prox: unfused Dis: unfused	1	FBL	Poor (only a few erosion cavities)
	TPM-M-313	3Y6M	♂	179	24.4	Prox: unfused Dis: unfused	3	FBL	Extensive (only posterior side of the cortex)
	TPM-M-316	5Y6M	♂	216.6	35.8	Prox: fused Dis: fused	5	FBL, EFS	Extensive (only posterior side of the cortex)

Sika deer (Kerama Islands)	URB-MAM-80	4M	NA	120.1	7.2	Prox: unfused Dis: unfused	0	FBL	None
	URB-MAM-211	1Y	♀	167.8	13.8	Prox: unfused Dis: unfused	1	FBL	None
	URB-MAM-194	1Y	♂	168.3	18.4	Prox: unfused Dis: unfused	1	FBL	None
	URB-MAM-34	NA	♀	182.7	26.6	Prox: fused Dis: fused	8	FBL, PFB, EFS	Extensive (only inner cortex)
	URB-MAM-183	7Y6M	♂	184.3	20.8	Prox: fused Dis: fused	7	FBL, PFB, EFS	Moderate (only inner cortex)
	URB-MAM-55	4Y6M	♂	185.5	21.6	Prox: unfused Dis: unfused	7	FBL, PFB, EFS	Extensive (only posterior side of the cortex)
	URB-MAM-193	10Y6M	♀	198.4	35.8	Prox: fused Dis: fused	8	FBL, PFB, EFS	Extensive (only posterior side of the cortex)
Reeves's muntjac (<i>Muntiacus reevesi</i>)	CBM-ZZ-4974	0D	NA	34.3	0.8	Prox: unfused Dis: unfused	0	WB	None
	CBM-ZZ-2687	5M	♂	110.7	4.9 ^b	Prox: unfused Dis: unfused	0	FBL	Poor (scattered erosion cavities on posterior side of the cortex)
	CBM-ZZ-2649	10M	♀	124.6	6.8 ^b	Prox: unfused Dis: unfused	1	FBL	Poor (scattered erosion cavities on posterior side of the cortex)
	CBM-ZZ-2648	1Y10M	♀	127.5	8.5 ^b	Prox: fused Dis: fused	2	FBL, EFS	Extensive (only posterior side of the cortex)
	CBM-ZZ-2646	4Y9M	♀	126.4	7.2 ^b	Prox: fused Dis: fused	5	FBL, EFS	Extensive (only posterior side of the cortex)

D, days old; M, months old; NA, unknown; WB, woven bone; Y, years old. See Table S1 for explanations of all other abbreviations.

Collection acronyms: CBM-ZZ, Natural History Museum and Institute, Chiba, Japan; TPM, Tochigi Prefectural Museum, Tochigi, Japan; HOUMVC, the Hokkaido University Museum, Sapporo, Japan; URB, University of the Ryukyus, Okinawa, Japan.

[†] Age at death was determined through analyses of tooth eruption and the cementum annuli for sika deer and tooth eruption and the molar wear score for Reeves's muntjac.

[‡] The estimated body mass (EBM) was obtained from the estimation equation based on femur mediolateral diameter.

^a The estimated greatest length of the bone based on measurements of the complete femora of other individuals.

^b The actual body mass measurement.

Table S4. Measurements and histological features of the tibiae of the extant cervids that were sampled.

Taxon	Collection No.	Age [†]	Sex	GL (mm)	EBM (kg) [‡]	Epiphyseal fusion	Number of LAGs	Bone tissue Type	Degree of Remodeling
Sika deer (<i>Cervus nippon</i>) (Hokkaido, mainland)	HOU MVC 00039	8M	♂	282	41.9	Prox: unfused Dis: unfused	1	FBL	Poor (only innermost cortex)
	HOU MVC 00038	8M	♀	270	39.0	Prox: unfused Dis: unfused	1	FBL	None
	HOU MVC 00033	1Y8M	♂	337	69.3	Prox: unfused Dis: fused	2	FBL	Extensive (only anterior side of the cortex)
	HOU MVC 00034	1Y9M	♀	319	76.1	Prox: unfused Dis: unfused	2	FBL	None
	HOU MVC 00035	4Y8M	♂	356	120.9	Prox: unfused Dis: fused	5	FBL	Extensive (only anterior side of the cortex)
	HOU MVC 00036	4Y8M	♀	295	65.9	Prox: fused Dis: fused	5	FBL, EFS	Poor (only innermost cortex)
	HOU MVC 00037	7Y6M	♂	346	175.5 ^b	Prox: fused Dis: fused	7	FBL, EFS	Poor (only innermost cortex)
Sika deer (Honshu, mainland)	CBM-ZZ-757	0 D	NA	128.1	3.5	Prox: unfused Dis: unfused	0	WB	None
	CBM-ZZ-671	6M	♀	202	24.3	Prox: unfused Dis: unfused	1	FBL	None
	CBM-ZZ-218	1Y2M	♀	212.6	36.4	Prox: unfused Dis: unfused	1	FBL	Moderate (only anterior side of the cortex)
	CBM-ZZ-761	1Y2M	♂	239.4	38.2	Prox: unfused Dis: unfused	1	FBL	Poor (only a few erosion cavities)
	CBM-ZZ-310	3Y5M	♀	253	37.4	Prox: fused Dis: fused	2	FBL, EFS	Extensive (only anterior side of the cortex)
	CBM-ZZ-762	3Y2M	♂	292.4	52.0	Prox: partially fused Dis: fused	3	FBL	Moderate (scattered SOs are present throughout the entire cortex)
	CBM-ZZ-759	7Y1M	♂	277.6	58.8	Prox: fused Dis: fused	7	FBL, EFS	Extensive (only anterior side of the cortex)
Sika deer (Yakushima Island)	CBM-ZZ-412	8Y9M	♀	258.8	35.7	Prox: fused Dis: fused	7	FBL, EFS	Extensive (only anterior side of the cortex)
	TPM-M-312	0Y	NA	160.8 ^a	12.4	Prox: unfused Dis: unfused	0	FBL	None
	TPM-M-314	1Y6M	♂	213.2 ^a	36.4	Prox: unfused Dis: fused	1	FBL	Poor (only a few erosion cavities)
	TPM-M-313	3Y6M	♂	207.4	25.1	Prox: unfused Dis: fused	3	FBL	Extensive (only anterior side of the cortex)

Sika deer (Kerama Islands)	TPM-M-316	5Y6M	♂	249.6	49.0	Prox: fused Dis: fused	5	FBL, EFS	Extensive (only anterior side of the cortex)
	URB-MAM-80	4M	NA	147.7	4.5	Prox: unfused Dis: unfused	0	FBL	None
	URB-MAM-211	1Y	♀	195	20.8	Prox: unfused Dis: unfused	1	FBL	None
	URB-MAM-194	1Y	♂	198	23.2	Prox: unfused Dis: unfused	1	FBL	None
	URB-MAM-34	NA	♀	218	21.8	Prox: fused Dis: fused	8	FBL, PFB, EFS	Moderate (only inner cortex)
	URB-MAM-183	7Y6M	♂	215	20.1	Prox: fused Dis: fused	7	FBL, PFB, EFS	Extensive (only anterior side of the cortex)
	URB-MAM-55	4Y6M	♂	229	19.6	Prox: unfused Dis: unfused	7	FBL, PFB, EFS	Extensive (only anterior side of the cortex)
	URB-MAM-193	10Y6M	♀	224	33.6	Prox: fused Dis: fused	8	FBL, PFB, EFS	Extensive (only anterior side of the cortex)
Reeves's muntjac (<i>Muntiacus reevesi</i>)	CBM-ZZ-4974	0D	NA	40.6	0.8	Prox: unfused Dis: unfused	0	WB	None
	CBM-ZZ-2687	5M	♂	116.9	4.9 ^b	Prox: unfused Dis: unfused	0	FBL	Poor (scattered erosion cavities on posterior side of the cortex)
	CBM-ZZ-2649	10M	♀	126.4	6.8 ^b	Prox: unfused Dis: fused	1	FBL	Poor (scattered erosion cavities on posterior side of the cortex)
	CBM-ZZ-2648	1Y10M	♀	135	8.5 ^b	Prox: fused Dis: fused	2	FBL	Extensive (only posterior side of the cortex)
	CBM-ZZ-2646	4Y9M	♀	135	7.2 ^b	Prox: fused Dis: fused	5	FBL, EFS	Extensive (only posterior side of the cortex)

See Tables S1 and S3 for explanations of the abbreviations.

[†] Age at death was determined through analyses of tooth eruption and the cementum annuli for sika deer and tooth eruption and the molar wear score for Reeves's muntjac.

[‡] The estimated body mass (EBM) was obtained from the estimation equation based on tibia mediolateral diameter.

^a The estimated greatest length of the bone based on measurements of the complete tibiae of other individuals.

^b The actual body mass measurement.

Table S5. List of the extant sika deer (*Cervus nippon*) samples that were used to check the validity of using lines of arrested growth (LAGs) to estimate age. Since LAGs form during winter, we compared the number of LAGs with the number of winter seasons a deer had experienced during its lifetime (See also Figure S5).

Taxon	Specimen no.	Sex	Age assessment method	Age at death	Date or season of death	No. of winter seasons	No. of LAGs
Sika deer (Hokkaido mainland)	HOU MVC 00039	♂	Tooth eruption	8 months	1977/2/20	1	1
	HOU MVC 00038	♀	Tooth eruption	8 months	1977/2/23	1	1
	HOU MVC 00033	♂	Tooth eruption	1 year 8 months	1976/2/29	2	2
	HOU MVC 00034	♀	Tooth eruption	1 year 9 months	1976/2/29	2	2
	HOU MVC 00035	♂	Cementum annuli	4 years 8 months	1976/2/26	5	5
	HOU MVC 00036	♀	Cementum annuli	4 years 8 months	1977/2/20	5	5
	HOU MVC 00037	♂	Cementum annuli	7 years 6 months	1955/12/19	8	7
Sika deer (Honshu mainland)	CMB-ZZ-671	♀	Tooth eruption	6 months	1987/12/19	1	1
	CBM-ZZ-218	♀	Tooth eruption	1 year 2 months	1986/8/9	1	1
	CBM-ZZ-761	♂	Tooth eruption	1 year 2 months	1988/8/8	1	1
	CBM-ZZ-310	♀	Cementum annuli	3 years 5 months	1986/11/19	3	3
	CBM-ZZ-762	♂	Cementum annuli	3 years 2 months	1988/8/9	3	3
	CBM-ZZ-759	♂	Cementum annuli	7 years 1 month	1988/7/4	7	7
	CBM-ZZ-412	♀	Cementum annuli	8 years 9 months	1987/3/12	8	7
Sika deer (Yakushima Island)	TPM-M314	♂	Tooth eruption	1 year 6 months	Autumn–winter	1	1
	TPM-M313	♂	Cementum annuli	3 years 6 months	Autumn–winter	3	3
	TPM-M316	♂	Cementum annuli	5 years 6 months	Autumn–winter	5	5
Sika deer (Kerama Islands)	URB-MAM-55	♂	Cementum annuli	4 years 6 months	Autumn–winter?	4	7
	URB-MAM-183	♂	Cementum annuli	7 years 6 months	Autumn–winter?	7	7
	URB-MAM-193	♀	Cementum annuli	10 years 6 months	Autumn–winter?	11	8

Table S6. Estimation of the number of lines of arrested growth (LAGs) that were lost through bone remodeling in fossil specimens.

Taxon	Bone	Specimen no.	No. observed LAGs	Reference specimen	Expansion of medullary cavity	Estimated LAGs lost	Estimated age at death (years)		
<i>Cervus astylodon</i>	Femur	OPM-HAN07-1610	6	NA	NA	NA	6		
		OPM-HAN07-1612	6	OPM-HAN07-1610	Yes (2 LAGs)	2	8		
		OPM-HAN07-1604	9	OPM-HAN07-1610	No	0	9		
		OPM-HAN07-1603	12	OPM-HAN07-1610	Yes (3 LAGs)	3	15		
		OPM-HAN06-155	11	OPM-HAN07-1610	Yes (7 LAGs)	7	18		
		OPM-HAN06-151	4	OPM-HAN07-1610	Yes (4 LAGs)	4	8		
	Tibia	OPM-HAN06-588	11	NA	NA	0	11		
		OPM-HAN06-584	12	OPM-HAN06-588	Yes (1 LAG)	1	13		
		OPM-HAN07-1585	10	OPM-HAN06-588	Yes (2 LAGs)	2	12		
		OPM-HAN06-581	13	OPM-HAN06-588	Yes (2 LAGs)	2	15		
		OPM-HAN07-1590	12	OPM-HAN06-588	Yes (1 LAG)	1	13		
		Muntiacini gen. et. sp. indet. (Ryukyu muntjac)	Femur	OPM-HAN07-1618	8	NA	NA	0	8
				OPM-HAN07-1623	9	OPM-HAN07-1618	No	0	9
OPM-HAN07-1616	6			OPM-HAN07-1618	No	0	6		
OPM-HAN06-163	11			OPM-HAN07-1618	No	0	11		
Tibia	OPM-HAN06-597		7	NA	NA	0	7		
	OPM-HAN07-1599		13	OPM-HAN06-597	No	0	13		

<i>Sinomegaceros yabei</i>	Femur	OMNH-QV-0362	4	NA	NA	0	4
		OMNH-QV-4062	7	OMNH-QV-0362	No	0	7
	Tibia	OMNH-QV-4067	4	NA	NA	0	4
		OMNH-QV-4068	5	OMNH-QV-4067	No	0	5

Table S7. Estimation of the neonatal body mass of the fossil cervids. Estimates were made using the regression equation of neonatal body mass against adult body mass for 121 extant artiodactyls (see also Figure S6).

Species	Estimated adult body mass (kg)			Estimated neonatal body mass (kg)
	Femur MLD	Tibia MLD	Average	
<i>Cervus astylodon</i>	15.531	17.424	16.477	1.2588
Muntiacini gen. et. sp. indet. (Ryukyu muntjac)	16.273	11.307	13.790	1.0905
<i>Sinomegaceros yabei</i>	959.175	678.566	818.870	29.378

MLD, mediolateral diameter.

Table S8. Results of a two-way analysis of variance testing the effects of species and bone type (femur or tibia) on the Gompertz growth curve parameters.

Parameter	Factor	d.f.	Sum of square	F-value	P-value
Growth rate	Species	7	197.234	20.634	<0.0001
	Bone type	1	0.009	0.007	0.934
Inflection point	Species	7	231.866	13.059	<0.0001
	Bone type	1	3.571	1.408	0.242

Table S9. Statistical comparisons of the growth curve parameters (growth rate and inflection point) among eight extant and fossil cervids. Since bone type (femur or tibia) did not have a statistically significant effect on the growth curve parameters (see Table S8), the femur and tibia data were combined.

Taxon	Growth rate					Inflection point						
		95% CI		Statistical tests			95% CI		Statistical tests			
Reeves's muntjac (<i>Muntiacus reevesi</i>)	3	5.901	0.543	4.788	7.013	A	3	0.161	1.129	-2.152	2.474	A
<i>Sinomegaceros yabei</i>	4	4.854	0.470	3.891	5.818	A	4	0.213	0.978	-1.790	2.216	A
Sika deer (<i>Cervus nippon</i>) (Honshu mainland)	4	2.499	0.470	1.536	3.462	B	4	0.418	0.978	-1.585	2.422	A
Sika deer (Hokkaido mainland)	3	2.161	0.543	1.049	3.273	B C	3	0.375	1.129	-1.938	2.688	A
Sika deer (Yakushima Island)	2	0.921	0.665	-0.441	2.283	B C	2	0.986	1.383	-1.847	3.819	A B
Sika deer (Kerama Islands)	3	0.490	0.543	-0.622	1.603	B C	3	1.506	1.129	-0.807	3.819	A
Ryukyu muntjac (<i>Muntiacini</i> gen. et. sp. indet.)	6	0.312	0.384	-0.474	1.098	C	6	1.858	0.799	0.222	3.494	A
<i>Cervus astylodon</i>	11	0.181	0.284	-0.400	0.761	C	11	5.771	0.590	4.563	6.979	B

CI, confidence interval; SE, standard error. Taxa with different letters in the “Statistical tests” columns are significantly different (Tukey–Kramer method, $P < 0.05$).

Table S10. Statistical comparisons of the growth rates of extant and fossil cervids based on measurements of the femora and tibiae.

Taxon	Growth rate estimated from femur MLD					Growth rate estimated from tibia MLD						
		95% CI		Statistical tests			95% CI		Statistical tests			
Reeves's muntjac (<i>Muntiacus reevesi</i>)	3	5.940	0.715	4.444	7.436	A	3	5.861	0.753	4.264	7.457	A
<i>Sinomegaceros yabei</i>	2	5.011	0.875	3.179	6.844	A B	2	4.697	0.922	2.742	6.653	A B
Sika deer (<i>Cervus nippon</i>) (Honshu mainland)	4	2.254	0.619	0.958	3.549	B C	4	2.745	0.652	1.362	4.128	A B C
Sika deer (Hokkaido mainland)	3	2.411	0.715	0.915	3.907	B C	3	1.911	0.753	0.314	3.507	B C
Sika deer (Yakushima Island)	2	0.932	0.875	-0.900	2.764	B C	2	0.910	0.922	-1.045	2.866	B C
Sika deer (Kerama Islands)	3	0.431	0.715	-1.065	1.927	C	3	0.550	0.753	-1.047	2.146	C
Ryukyu muntjac (<i>Muntiacini</i> gen. et. sp. indet.)	4	0.366	0.619	-0.930	1.661	C	2	0.204	0.922	-1.751	2.159	B C
<i>Cervus astylodon</i>	6	0.195	0.505	-0.863	1.252	C	5	0.164	0.583	-1.073	1.401	C

CI, confidence interval; MLD, mediolateral diameter; SE, standard error.

Taxa with different letters in the "Statistical tests" columns are significantly different (Tukey-Kramer method, $P < 0.05$).

Table S11. Statistical comparison of the inflection point for extant and fossil cervids based on measurements of the femora and tibiae.

Taxon	Inflection point estimated from femur MLD						Inflection point estimated from tibia MLD					
		95% CI			Statistical tests			95% CI			Statistical tests	
<i>Cervus astylodon</i>	6	5.242	0.424	4.356	6.129	A	5	6.405	0.997	4.292	8.518	A
Ryukyu muntjac (Muntiacini gen. et. sp. indet.)	4	1.147	0.519	0.062	2.233	B	2	3.280	1.576	-0.061	6.621	A B
Sika deer (<i>Cervus nippon</i>) (Kerama Islands)	3	1.475	0.599	0.221	2.728	B	3	1.537	1.287	-1.191	4.265	A B
Sika deer (Yakushima Island)	2	0.677	0.734	-0.859	2.212	B	2	1.295	1.576	-2.046	4.636	A B
Sika deer (Honshu mainland)	4	0.466	0.519	-0.619	1.552	B	4	0.370	1.114	-1.992	2.733	B
Sika deer (Hokkaido mainland)	3	0.323	0.599	-0.930	1.577		3	0.427	1.287	-2.301	3.155	B
<i>Sinomegaceros yabei</i>	2	0.212	0.734	-1.324	1.747	B	2	0.214	1.576	-3.127	3.555	A B
Reeves's muntjac (<i>Muntiacus reevesi</i>)	3	0.160	0.599	-1.094	1.413	B	3	0.163	1.287	-2.565	2.891	B

CI, confidence interval; MLD, mediolateral diameter; SE, standard error.

Taxa with different letters in the “Statistical tests” columns are significantly different (Tukey-Kramer method, $P < 0.05$).

Table S12. Life tables for three extant sika deer (*Cervus nippon*) populations based on age data from randomly culled individuals.

Population	Age (years)	Age (% of maximum observed age)	Sampled fx	Fx (Probit smoothing)	lx	lx*1000
Sika deer (Hokkaido mainland)	2	10	450	409	1.000	1000
	3	15	242	236	0.577	577
	4	20	113	141	0.345	345
	5	25	63	88	0.214	214
	6	30	46	56	0.138	138
	7	35	34	37	0.091	91
	8	40	37	25	0.062	62
	9	45	24	18	0.043	43
	10	50	14	13	0.031	31
	11	55	15	9	0.022	22
	12	60	6	7	0.016	16
	13	65	6	5	0.012	12
	14	70	3	4	0.009	9
	15	75	2	3	0.007	7
	16	80	2	2	0.005	5
	17	85	2	2	0.004	4
	18	90	0	1	0.003	3
	19	95	1	1	0.003	3
				Total: 1060		
Sika deer (Honshu mainland)	2	11	132	126	1.000	1000
	3	17	108	108	0.853	853
	4	22	78	89	0.708	708
	5	28	70	72	0.571	571
	6	33	51	56	0.448	448
	7	39	42	43	0.342	342
	8	44	34	32	0.254	254
	9	50	24	23	0.184	184
	10	56	25	16	0.130	130
	11	61	14	11	0.089	89
	12	67	7	8	0.060	60
	13	72	7	5	0.040	40
	14	78	1	3	0.026	26

	15	83	0	2	0.016	16
	16	89	0	1	0.010	10
	17	94	1	1	0.006	6
			Total: 594			
Sika deer (Yakushima Island)	2	11	18	18	1.000	1000
	3	17	16	14	0.776	776
	4	22	10	11	0.595	595
	5	28	6	8	0.457	457
	6	33	8	6	0.354	354
	7	39	4	5	0.277	277
	8	44	3	4	0.219	219
	9	50	0	3	0.175	175
	10	56	3	3	0.141	141
	11	61	2	2	0.114	114
	12	67	2	2	0.093	93
	13	72	1	1	0.077	77
	14	78	0	1	0.064	64
	15	83	0	1	0.053	53
	16	89	0	1	0.045	45
	17	94	1	1	0.038	38
			Total: 74			

Table S13. Life tables for extant Reeves's muntjac (*Muntiacus reevesi*) and two fossil insular deer based on age data from individuals that died naturally.

Population	Age (years)	Age (% of maximum observed age)	Sampled fx	dx	lx	lx (Probit smoothing)	lx*1000
<i>Cervus astylodon</i>	2	8	3	0.067	1.000	0.952	1000
	3	12	0	0.000	0.933	0.938	986
	4	15	0	0.000	0.933	0.923	970
	5	19	2	0.044	0.933	0.907	953
	6	23	1	0.022	0.889	0.889	934
	7	27	3	0.067	0.867	0.870	914
	8	31	0	0.000	0.800	0.849	893
	9	35	0	0.000	0.800	0.827	869
	10	38	3	0.067	0.800	0.803	843
	11	42	2	0.044	0.733	0.776	815
	12	46	0	0.000	0.689	0.747	785
	13	50	0	0.000	0.689	0.716	752
	14	54	1	0.022	0.689	0.682	717
	15	58	0	0.000	0.667	0.645	678
	16	62	2	0.044	0.667	0.605	636
	17	65	2	0.044	0.622	0.562	591
	18	69	4	0.089	0.578	0.515	541
	19	73	5	0.111	0.489	0.464	487
	20	77	3	0.067	0.378	0.408	429
	21	81	2	0.044	0.311	0.348	366
	22	85	4	0.089	0.267	0.283	297
	23	88	3	0.067	0.178	0.212	223
	24	92	3	0.067	0.111	0.135	142
	25	96	2	0.044	0.044	0.051	54
	Total: 45						
Muntiacini gen. et sp. indet. (Ryukyu muntjac)	0	0	5	0.077	1.000	0.996	1000
	1	9	2	0.031	0.923	0.958	961
	2	18	6	0.092	0.892	0.912	915
	3	27	1	0.015	0.800	0.858	861
	4	36	0	0.000	0.785	0.794	797
	5	45	2	0.031	0.785	0.719	722
	6	55	3	0.046	0.754	0.630	632
	7	64	27	0.415	0.708	0.525	527
	8	73	16	0.246	0.292	0.400	402
	9	82	2	0.031	0.046	0.254	254

	10	91	1	0.015	0.015	0.080	80
			Total: 65				
Extant Reeves's muntjac	0	0	12	0.143	1.000	0.920	1000
	1	6	21	0.250	0.857	0.798	868
	2	13	9	0.107	0.607	0.684	744
	3	19	7	0.083	0.500	0.578	629
	4	25	3	0.036	0.417	0.482	524
	5	31	8	0.095	0.381	0.395	429
	6	38	2	0.024	0.286	0.318	346
	7	44	3	0.036	0.262	0.251	273
	8	50	4	0.048	0.226	0.194	211
	9	56	5	0.060	0.179	0.147	160
	10	63	1	0.012	0.119	0.109	118
	11	69	0	0.000	0.107	0.078	85
	12	75	1	0.012	0.107	0.054	59
	13	81	2	0.024	0.095	0.037	40
	14	88	2	0.024	0.071	0.024	26
	15	94	4	0.048	0.048	0.015	16
			Total: 84				

Supplementary references

- Azanza, B., D. DeMiguel, D. DeMiguel, M. Andrés, and M. Andrés. 2011. "The antler-like appendages of the primitive deer *Dicrocerus elegans*: morphology, growth cycle, ontogeny, and sexual dimorphism." *Estudios Geológicos* 67 (2):579-602. doi: 10.3989/egeol.40559.207.
- Caughley, G. 1977. *Analysis of Vertebrate Populations*. New York: John Wiley & Sons Inc.
- Chapman, Norma G., W. A. B. Brown, and P. Rothery. 2005. "Assessing the age of Reeves' muntjac (*Muntiacus reevesi*) by scoring wear of the mandibular molars." *Journal of Zoology* 267 (03). doi: 10.1017/s0952836905007405.
- Chiba Prefecture, and Deer Research Group on Boso. 2007. *Science report on emergent survey of invasive alien species (Reeves's muntjac) in Boso*. Chiba: Chiba Prefecture.
- Cooper, L. N., A. H. Lee, M. L. Taper, and J. R. Horner. 2008. "Relative growth rates of predator and prey dinosaurs reflect effects of predation." *Proc Biol Sci* 275 (1651):2609-15. doi: 10.1098/rspb.2008.0912.
- Erickson, G M. 2007. "Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition." *Biology Letters* 3:558-561.
- Erickson, Gregory M. 2014. "On Dinosaur Growth." *Annual Review of Earth and Planetary Sciences* 42 (1):675-697. doi: 10.1146/annurev-earth-060313-054858.
- Groves, C. 2006. "The genus *Cervus* in eastern Eurasia." *European Journal of Wildlife Research* 52 (1):14-22.
- Hokkaido Institute of Environmental Sciences. 1997. Results of a survey related to sika deer and brown bear sighting on Hokkaido. Sapporo: Hokkaido Institute of Environmental Sciences (in Japanese).
- Jones, Kate E., Jon Bielby, Marcel Cardillo, Susanne A. Fritz, Justin O'Dell, C. David L. Orme, Kamran Safi, Wes Sechrest, Elizabeth H. Boakes, Chris Carbone, Christina Connolly, Michael J. Cutts, Janine K. Foster, Richard Grenyer, Michael Habib, Christopher A. Plaster, Samantha A. Price, Elizabeth A. Rigby, Janna Rist, Amber Teacher, Olaf R. P. Bininda-Emonds, John L. Gittleman, Georgina M. Mace, and Andy Purvis. 2009. "PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals." *Ecology* 90 (9):2648-2648. doi: 10.1890/08-1494.1.
- Kolb, C., T. M. Scheyer, K. Veitschegger, A. M. Forasiepi, E. Amson, A. A. Van der Geer, L. W. Van den Hoek Ostende, S. Hayashi, and M. R. Sanchez-Villagra. 2015. "Mammalian bone palaeohistology: a survey and new data with emphasis on island forms." *PeerJ* 3:e1358. doi: 10.7717/peerj.1358.
- Kubo, Mugino O., Masaki Fujita, Shuji Matsu'ura, Megumi Kondo, and G. Suwa. 2011. "Mortality profiles of late Pleistocene deer remains of Okinawa Island: evidence from the Hananda-Gama cave and Yamashita-cho cave I sites." *Anthropological Science* 119 (2):183-201. doi: 10.1537/ase.091215.
- Nagata, J., R. Masuda, H. B. Tamate, S. Hamasaki, K. Ochiai, M. Asada, S. Tatsuzawa, K. Suda, H. Tado, and M. C. Yoshida. 1999. "Two genetically distinct lineages of

- the sika deer, *Cervus nippon*, in Japanese islands: comparison of mitochondrial D-loop region sequences." *Molecular Phylogenetics and Evolution* 13 (3):511-519.
- Ohshima, K. 1990. "The history of straits around the Japanese Islands in the Late-Quaternary." *The Quaternary Research* 29:193-208 (in Japanese with English abstract).
- Ohtaishi, N. 1986. "Preliminary memorandum of classification, distribution and geographic variation on Sika deer." *Honyurui Kagaku (Mammalian Science)* 53:13-17 (in Japanese with English abstract).
- Okinawa Prefectural Board of Education. 1996. *A report of conservation and management of sika deer in Kerama Islands*. Okinawa: Okinawa Prefectural Board of Education.
- Okinawa Prefectural Museum and Art Museum, ed. 2009. *Excavation of the Hananda-Gama Cave site, Okinawa*. Naha: Kokusai-insatsu Co.
- Okumura, K., S. Ishida, Y. Kawamura, M. Kumada, and S. Tamiya. 1982. "Latest Pleistocene Mammalian assemblage of Kumaishi-do Cave, Gifu Prefecture and the significance of its ¹⁴C age." *Earth Science (Chikyu Kagaku)* 36:214-218 (in Japanese with English abstract).
- Okumura, K., S. Ishida, H. Taruno, and Y. Kawamura. 2016. "Yabe's giant deer and elk remains from the Late Pleistocene of Kumaishi-do Cave, Gifu Prefecture (Part 1): Antlers, a skull, mandibles, and teeth." *Bulletin of the Osaka Museum of Natural History* 70:1-82 (in Japanese with English abstract).
- Ozaki, M. 2009. "Estimation of age at death from tooth wear of lower molars of excavated deer and comparison of age structures with modern deer populations." In *Excavation of the Hananda-Gama Cave site, Okinawa*, edited by Okinawa Prefectural Museum and Art Museum, 24-34 (in Japanese). Naha: Kokusai-insatsu Co.
- Ozaki, M., K. Kaji, N. Matsuda, K. Ochiai, M. Asada, T. Ohba, E. Hosoi, H. Tado, T. Koizumi, G. Suwa, and S. Takatsuki. 2010. "The relationship between food habits, molar wear and life expectancy in wild sika deer populations." *Journal of Zoology* 280 (2):202-212. doi: 10.1111/j.1469-7998.2009.00653.x.
- Scott, K. M. 1990. "Postcranial dimensions of ungulates as predictors of body mass." In *Body size in mammalian paleontology: estimation and biological implications*, edited by John Damuth and Bruce J. MacFadden, 301-335. Cambridge: Cambridge University Press.
- Suzuki, M., and N. Ohtaishi. 1993. "Reproduction of female Sika deer (*Cervus nippon yesoensis* Heude, 1884) in Ashoro District, Hokkaido." *Journal of Veterinary Medical Science* 55:833-836.
- Taruno, H., Y. Kawamura, S. Ishida, and K. Okumura. 2017. "Yabe's giant deer and elk remains from the Late Pleistocene of Kumaishi-do Cave, Gifu Prefecture, central Japan (Part 2): Postcranial bones." *Bulletin of the Osaka Museum of Natural History* 71:17-142.
- Terada, Chisato, and Takashi Saitoh. 2018. "Phenotypic and genetic divergence among island populations of sika deer (*Cervus nippon*) in southern Japan: a test of the local adaptation hypothesis." *Population Ecology* 60 (3):211-221. doi: 10.1007/s10144-018-0607-8.

- Terada, Chisato, Shirow Tatsuzawa, and Takashi Saitoh. 2012. "Ecological correlates and determinants in the geographical variation of deer morphology." *Oecologia* 169 (4):981-994. doi: 10.1007/s00442-012-2270-7.
- van der Geer, A., G. Lyras, J. de Vos, and M. Dermitzakis. 2010. *Evolution of Island Mammals: Adaptation and Extinction of Placental Mammals on Island*. West Sussex: John Wiley & Sons Ltd.