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Source: Mammal Study, 48(4) : 231-244

Published By: Mammal Society of Japan

URL: https://doi.org/10.3106/ms2022-0034

Mammal Study 48: 231–244 (2023) DOI: 10.3106/ms2022-0034

Original paper

Demographic parameters of Asian black bears in central Japan

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Published online 21 July, 2023; Print publication 31 October, 2023

Abstract. Currently, fundamental demographic data for wild Asian black bears (*Ursus thibetanus*) in Japan are lacking. As a first step toward science-based management, we must improve our understanding of life history characteristics such as reproduction and mortality. This study aimed to quantify the demographic parameters of Asian black bears in central Japan. (1) By measuring the cementum annuli width of the teeth of females, age at first reproduction was estimated to be 5.44 ± 0.22 (mean ± *SE*) years and reproductive interval 2.38 ± 0.48 years. (2) By counting placental scars in uteri sampled from recovered bear carcasses, we estimated litter size to be 1.58 ± 0.09 cubs and minimum age at primiparity to be two years. (3) We clarified the annual rates of natural mortality (0.108, 95% *CI*: 0.064–0.174) and human-caused mortality (0.005, 95% *CI*: 0.002–0.021) by using capture–recapture records for subadult and adult bears. We used observation data from the first six months after birth to estimate cub mortality rate (0.235, 95% *CI*: 0.080–0.465). Further research will allow us to identify which endogenous and exogenous factors affect demographic parameters and to use these parameters to estimate population dynamics as a next step.

Key words: age at first reproduction, life history, mortality, reproductive parameters, *Ursus thibetanus.*

Understanding the life history and demographic parameters of animals is important for making conservation and management decisions for target populations (Williams et al. 2002). Among various demographic parameters, reproduction and survival rates are essential for determining population growth, size, and fluctuation (Oli and Dobson 2003; Mitchell et al. 2009). Demographic parameters vary greatly among populations, primarily because of variations in resource availability (Nawaz et al. 2008), and therefore the demographic parameters of other populations or closely related species cannot necessarily be applied to analyses of specific populations. For long-lived animals that occur at low densities, such as large carnivores, collecting demographic data is challenging (Karanth and Chellam 2009). Long-term and individual-based monitoring is essential to estimate or document life history parameters of a species or population (Clutton-Brock and Sheldon 2010). However, such information is currently lacking for many, if not most, wildlife species and populations.

Given their potential for aggressive conflict with humans and livestock, overlap in habitat, and broad food

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habits, ursids are particularly vulnerable to human-caused disturbance, exploitation, and persecution (Ripple et al. 2014). In many regions of their distribution range, Asian black bears (*Ursus thibetanus*) have conflicts with humans, as they can come close to human residences, cause agricultural damage, and may attack and potentially injure humans (Krofel et al. 2020). For example, Asian black bears have expanded their range in most regions of Japan, excluding some small isolated populations (Kozakai et al. 2020). Consequently, each year in Japan a large number of bears are killed as nuisance animals (ranging from 975 to 6085 bears per year from 2008 to 2021; Ministry of the Environment 2022). However, our current knowledge on the population ecology of this species remains inadequate and it is unknown whether these culling operations have an impact on demographic parameters, and ultimately population growth, size, and fluctuations.

Given these concerns regarding Asian black bear conservation and management, appropriate population management based on an analysis of population dynamics is needed across most of the species' distribution range. Some data on demographic parameters, such as age at primiparity and litter size, have been reported for nuisance Asian black bears in Japan (Katayama et al. 1996; Iibuchi et al. 2009; Nakamura et al. 2011; Yamanaka et al. 2011b). However, these parameters have been estimated from small sample sizes or fragmentary samples, or both (i.e., they are not based on population-scale data). When population analyses are performed for bear management, the demographic parameters of the target population—and not that from another population—must be applied. Therefore, as a first step towards science-based management of Asian black bears in Japan, we must advance our understanding of population-based life history parameters, such as reproduction and mortality.

Here, we aimed to quantify the demographic parameters of female Asian black bears in central Japan, namely age at first reproduction, reproductive interval, litter size, age at primiparity, and natural and human-caused mortality rates. We used cementum annuli width, number of placental scars, and observational data to estimate key demographic parameters for our study population. We focused on the Echigo–Mikuni population, because the government and our research team have collected various data from this population for a prolonged period of time.

Materials and methods

Study area

In Japan, the Asian black bear is managed through 18 policy-based management units (Fig. 1a; Ministry of the Environment 2010). The Ministry of the Environment defined the management units based on the distribution of bears, geographical factors (e.g., the presence of large rivers), and land use (e.g., agricultural land, built-up areas, and roads). We focused on the Echigo–Mikuni management unit (hereafter, Echigo–Mikuni population) for the sampling of teeth and uteri. The Echigo–Mikuni population is continuously distributed across five prefectures: northeastern Nagano, central Niigata, western Fukushima, northern Gunma, and western Tochigi (approximately 13 800 km^2; 36.30°–37.90°N, 138.14°–140.30°E). Elevation ranges between 0 and 2600 m a.s.l. (Fig. 1a). The population is located in a mountainous area covered by a cool-temperate forest, and part of the area is managed as a national park (Ministry of the Environment 2010). The borders of the management area are located along the Ban'etsu West railway line and the Agano River in the north, the Tōhoku Main railway line in the east, the Tone and Shinano rivers in the south, and the Echigo Plains in the west.

We have conducted 20 years of continuous field research on Asian black bears in the study area (inset square in Fig. 1b; approximately 460 km^2; 36.54°–36.80°N, 139.22°–139.49°E), which is located in the Ashio–Nikko Mountains in central Honshu Island, within the borders of the Echigo–Mikuni management unit. Here, elevation ranges between 400 and 2400 m a.s.l.

In the Nagano, Gunma, and Tochigi prefecture areas of the Echigo–Mikuni population, bears have been captured for sport hunting (winter), control kills (throughout the year), and as part of our research project (mark and release; summer). There are no restrictions on sport hunting or nuisance kills with regard to bear reproductive status or age (Tochigi Prefecture 2020; Gunma Prefecture 2022; Nagano Prefecture 2022).

Definition of reproduction

We defined the term "reproduction" used in "age at first reproduction" and "reproductive interval" as the successful raising of cubs-of-the-year until at least August. We selected August as the cut-off month, because the primary mating season of Asian black bears takes place during June and July, when males sometimes commit infanticide and cub survival is low (Yamazaki 2017; Naganuma et al.

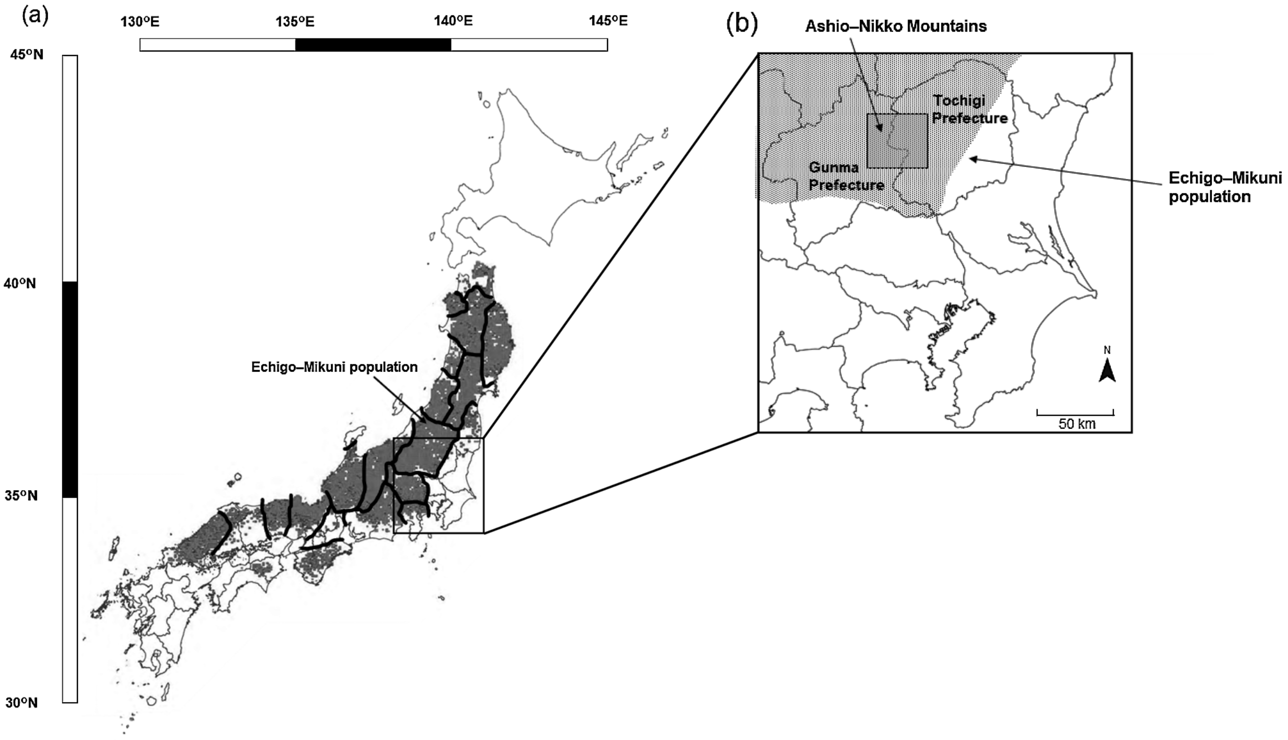

Fig. 1. (a) Distribution of Asian black bears in Japan (redrawn from the Japan Bear Network 2014). Shaded areas represent the 2014 distribution of Asian black bears, based on the Ministry of the Environment (2004) and the Japan Bear Network (2014). The black lines indicate the borders of 18 policy-based management units. (b) Map of the study area for our long-term bear research in the Ashio–Nikko Mountains in Tochigi and Gunma prefectures, central Japan.

2021). Therefore, we determined age at first reproduction as the first year in which each mother successfully raised cubs-of-the-year with a high probability until at least August (Fig. 2). We also defined reproductive interval as the time interval (year) between the years each female succeeded in raising cubs-of-the-year with a high probability until at least August (Fig. 2). Moreover, we defined age at primiparity as the age at which females gave birth for the first time, regardless of whether females subsequently lost their offspring. Because in this study we estimated the lowest age at which females possibly gave birth, our data must be interpreted as the "minimum" age at primiparity.

Collection of teeth and uteri from culled female bears

To estimate the age of individuals, age at reproduction, and litter size, we collected tooth and uterus samples from culled female bears. These bears were culled because they were suspected to have displayed nuisance behaviors, such as intruding into human settlements in the Nagano (2005–2017), Gunma (2009–2019), and Tochigi (2007–2014) prefectures in central Japan. However, we suspect that many of these individuals only used the mid-mountainous areas as their habitat, and may not have caused any damage, because local hunters and managers could not confirm whether the bears captured close to the damaged areas were actually the ones causing the damages.

Controlled killing of bears was conducted under permits obtained by municipalities or hunters from each prefectural government and in accordance with the "Wildlife Protection, Control, and Hunting Management Act" of 2005–2019 (Ministry of the Environment 2015) and the "Category 2 Specified Wildlife Protection Plan" of each prefectures (Nagano Prefecture: 2005–2017, Nagano Prefecture 2022, Gunma Prefecture: 2009–2019, Gunma Prefecture 2022, Tochigi Prefecture: 2007–2014, Tochigi Prefecture 2020). In our study area, the bears were euthanized as soon as possible after capture in box traps. They were shot, ensuring that the cerebral hemispheres and brainstem were sufficiently disrupted by the projectile to induce immediate loss of consciousness and subsequent death (American Veterinary Medical Association 2013).

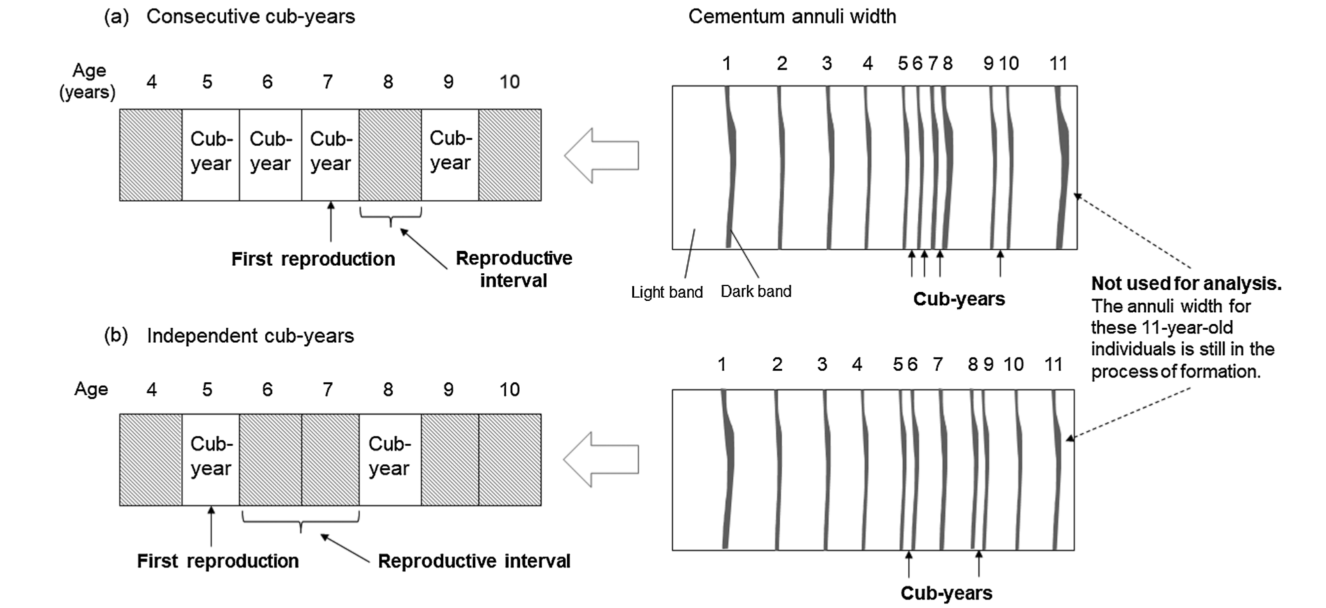

Fig. 2. Definition of first reproduction and reproductive interval, based on (a) a case of consecutive cub-years case and (b) a case of independent cub-years. The two diagrams on the right side show how the cementum annulus width was used to determine a cub-year (i.e., a year when a female bear probably had cubs until at least August), and the two age scales on the left side illustrate how the diagrams on the right were interpreted to define which cub-years were reproduction years.

Preservation of teeth and uteri

In each prefecture, capture, sampling, and sample storage were performed by hunters and by wildlife personnel employed by the municipality. Samples were stored in the following facilities: Nagano Environment Conservation Research Institute, Gunma Museum of Natural History, and Tochigi Prefectural Forestry Research Center.

Municipalities were requested to provide the skull, internal organs, reproductive organs, and muscles from the culled bear, but some municipalities submitted the entire body. Tooth samples were submitted together with the skull, mandible, or maxilla collected at the capture site. When the entire body was submitted, teeth were collected at the time of autopsy by using a knife or a similar tool. The uterine sample was submitted either as a single sample obtained at the capture site or together with the digestive tract and other organs that were also collected at the capture site. If the entire body of the individual was delivered, then the uterus was collected at the time of autopsy.

For each tooth sample, we decalcified, sliced, mounted on a glass slide, and stained the tooth sections in accordance with the method of Ohtaishi et al. (1990). The uteri were frozen and stored at –20°C or fixed in 70% ethanol or 10% buffered formalin before examination.

Calculation of the cementum annuli width index

We used the first premolar teeth from culled female bears in Nagano, Gunma, and Tochigi prefectures. After counting the cementum annuli to determine age, we measured cementum annuli width (μm) with the imaging software (cellSens, Olympus). Sectioning, counting of annual layers, and measuring of layer widths were conducted by the authors and by municipal wildlife managers (Nagano: M. Kuroe, R. and K. Tochigi; Gunma: T. Anezaki, K. Takayama, and K. Tochigi; Tochigi: S. Fujino and K. Tochigi). The proportional width index (PWI; Medill et al. 2009) was calculated as follows:

i : age
x_i : cementum annulus width (μm)

$$PW_i = \frac{x_i}{\sum_0^i x_i}$$

$$PWI_i = \log_{10}\left(\frac{PW_i}{\overline{PW_i}} + 1\right)$$

The PWI was calculated for each individual and each age. PWI can be compared between individuals and different ages, because the effect of decreased cementum width with increasing age is corrected for during the calculation (Medill et al. 2009).

Counting of placental scars

To estimate litter size, we inspected the uteri from female Asian black bears culled in Gunma Prefecture from 2009 to 2019. The uterine horns were cut longitudinally to reveal the endometrium. The endometrium of both uterine horns was observed macroscopically to determine the presence or absence of placental scars. When placental scars were observed in the uteri, we summed the number of placental scars in the left and right uterine horns for each individual. We determined the age of female bears by counting the cementum annuli of teeth that were collected along with the uteri. Placental scars persist for one or two years after giving birth (Tsubota et al. 1990), and they remain even if the litter is lost. Therefore, their existence indicates that the female was pregnant and gave birth at the latest during the winter of the capture year and at the earliest during the winter of the year before the capture year.

Collection of cub survival records through long-term research

To assess cub survival, we used two sources of information: bears identified during capture and bears identified through direct observation during fieldwork. During 2003–2021, we captured bears with handmade barrel traps baited with honey, setting a maximum of nine traps per year within a 35-km^2 area. We immobilized the trapped bears with a mixture of tiletamine hydrochloride and zolazepam hydrochloride (Virbac, Carros, France). After being subjected to basic body measurements and premolar extraction for age determination, the bears were equipped with a microchip, and a GPS collar was fitted to bears of sufficient size. Some bears were marked with colored ear tags too. All bears were released at their capture sites. Bear capture and handling were performed in accordance with the guidelines for animal research established by the Mammal Society of Japan (http://www.mammalogy.jp/guideline.html) and the Animal Care and Use Committee (1998). Mortality was recorded when the identified individuals were hunted or culled, and individual identity was confirmed with DNA sequence data from muscle samples or introduced microchip IDs.

Direct observation was performed during parallel fieldwork (e.g., Fujiwara et al. 2013; Furusaka et al. 2017), such as when hiking towards trap sites for bear handling, and during field visits at GPS cluster sites (e.g., Furusaka et al. 2017). The observed bears were identified from information obtained from GPS collars and ear tags, if present. We also used photograph or video data from infrared-triggered sensor cameras set at the study sites. Photographically captured bears were identified based on the information obtained from GPS collars, ear tags, chest mark patterns, and DNA sequence data from hair-snare traps that were placed with the camera traps. Details on the methods used for identifying individuals based on DNA can be found in Takayama et al. (2023). For identified female bears, we recorded whether they were accompanied by cubs-of-the-year. If so, the number of cubs was determined from at least two independent observations or at least two independent photographs or videos. We defined cub survival as the direct or image-based confirmation that the female bears were accompanied by cubs in or after August or by yearlings in the subsequent year. We defined cub loss as the direct or image-based confirmation that the females became solitary during the year when they had been accompanied by cubs.

Estimation of reproductive parameters

We used PWI data of bears that were at least five years old to estimate age at first reproduction and reproductive interval. Although female bears are sexually mature and able to reproduce from four years old (Katayama et al. 1996; Yamanaka et al. 2011b), PWI for four-year-old females can be obtained from the annulus width only between the ages of three and four, because the annulus width from four to five years old is still in the process of formation (Tochigi et al. 2019). Therefore, we used the PWI of female bears ≥ five years old. Previous studies indicated that the PWI was significantly smaller in years when female bears gave birth successfully and raised cubs until at least August (Tochigi et al. 2018; Tochigi et al. 2019). We used the threshold reported by Tochigi et al. (2018); a PWI < 0.25 indicated that the bear probably had a cub or cubs until at least August (i.e., a "cub-year"). If two or more consecutive "cub-years" were detected, then female bears were possibly accompanied by cubs during all the consecutive cub-years. Consecutive litter production occurs largely when a female loses her cubs-of-the-year (Garrison et al. 2007) and then produces another litter in the subsequent year. Therefore, detection of consecutive cub-years likely indicates that the female lost her cubs-of-the-year before the end of the mating season (Medill et al. 2010). Furthermore, there was a low chance that females lost cubs-of-the-year before the end of the mating season during the final year of consecutive cub-years (Fig. 2). We defined a non-consecutive cub-year or the final year of consecutive cub-years as a reproduction year (Fig. 2). For example, in Fig. 2a, where the PWI indicated three consecutive cub-years from age five to age seven, we assumed that the bear lost the cubs that she gave birth to at ages five and six, making year seven her "first reproduction."

We estimated the age at first reproduction by recording the minimum age during a cub-year for each female bear. We determined the reproductive interval by tallying the number of years between a cub-year and the next cub-year for each female bear. The 95% confidence intervals (*CI*) for the age at first reproduction and the reproductive interval were generated from bootstrapping (2000 resamplings) by using the simpleboot (Peng 2019) and boot packages (Canty and Ripley 2021) in R software v. 4.0.3 (R Core Team 2022).

To estimate litter size at birth, we tallied the placental scars for each female bear. This method is widely used (e.g., Helle and Kauhala 1995; Wooding and Bukata 1996), because the number of placental scars corresponds to the number of blastocysts that implant in the uterine wall (Tsubota et al. 1990) and is positively correlated with observed litter size (Strand et al. 1995). In addition, we defined the minimum age at which placental scars were detected as minimum age at primiparity. The 95% *CI* for the litter size was also generated from bootstrapping (2000 resamplings).

Estimation of mortality rates

To estimate the mortality rates of subadult and adult female bears (one to 21 years old), we used the mark–recapture–recovery (MRR) model based on the Cormack–Jolly–Seber process (Langrock and King 2013), which can estimate both natural and human-caused mortality separately. An individual bear has three possible fates in any given year: remaining alive, dying of natural causes, and being killed by humans. The process model of MRR was described by a multinomial distribution that determines the transition of an individual's fate. For simplicity, natural mortality and human-caused mortality were assumed to be additive; this is a good approximation for animals with low mortality rates such as ursids (Hebblewhite et al. 2003; Beston 2011; Bischof et al. 2018). To impose a sum-to-one constraint on the multinomial probabilities, we implemented the following vector of probabilities of survival rate, natural mortality rate, and human-caused mortality rate:

$$\mathbf{\Phi} = ((1 - p_n)(1 - p_h),\ p_n(p_n + p_h - p_n p_h) / (p_n + p_h),\ p_h(p_n + p_h - p_n p_h) / (p_n + p_h)),$$

where p_n and p_h are parameters of the natural mortality rate and human-caused mortality rate, respectively. When p_n and p_h are small enough (say, $p_n p_h < 0.01$), $\mathbf{\Phi} \approx (1 - p_n - p_h, p_n, p_h)$. The detection of an individual by trapping can be regarded as a Bernoulli trial in which the observation probability depends on the trapping effort in year t. A simple Poisson catchability model (Fukasawa et al. 2020) was assumed for the detection probability $q_t = 1 - \exp(-cE_t)$, where c is the detectability coefficient (i.e., detection probability per unit effort) and E_t is the trapping effort in year t. Tags of individuals killed by humans were assumed to be recovered with certainty. We defined the structure of our MRR model as natural or human-caused mortality with a certain probability per unit time step; living individuals are captured with a probability corresponding to the trapping effort and then released alive, and individuals killed by humans are recovered with a probability of 1. As the dataset for model estimation, we constructed detection histories of each female bear in each year and used the histories as input data to fit models containing parameters for natural mortality, human-caused mortality, and detectability over the year. To ensure the identifiability of the model, we assumed that human-caused mortality was constant over the study period. We defined the trapping effort as a product of the total number of traps and number of nights. Because the maximum value of effort was more than 300 000, we divided the detectability by 1000 to avoid numerical overflow in the parameter estimation. The model fit was conducted by using a non-linear optimization function, nlm(), with a self-written log-likelihood function in R (Supplementary Material S1). The 95% *CI* was calculated by using profile likelihood methods.

We used a generalized linear model with binomial error and a logit link function to estimate cub mortality. Although we considered the possibility of variance across mothers, the sample size was too small to be used as a random effect. Therefore, we set the number of cubs that survived until at least August and the number of cubs first observed with a particular female (i.e., immediately after the mother had given birth) as the response variable, with only the intercept as the predictor term.

Results

Reproductive parameters

We gathered cementum annuli data from 132 adult female bears (five to 17 years old), of which 55 were esti-

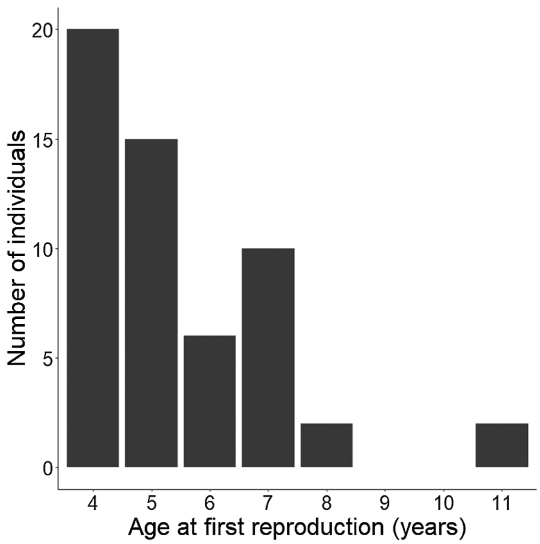

Fig. 3. Distribution of age at first reproduction of culled female Asian black bears (2005–2019) of the Echigo–Mikuni population in Japan.

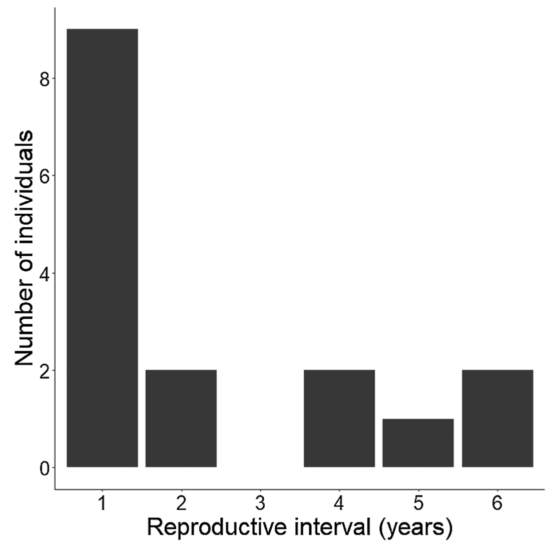

Fig. 4. Frequency distribution of time intervals between documented reproduction in individual female Asian black bears that were culled (2005–2019) from the Echigo–Mikuni population in Japan.

mated to have reproduced at least once (Nagano = 25, Gunma = 18, and Tochigi = 12). We were unable to obtain first reproduction records for more than half (77 of 132) of the bears. Although we used cementum annuli data from culled individuals older than four years, the majority of the bears for which we used cementum annuli data were young (7.16 ± 0.19 [mean ± *SE*] years). Moreover, the individuals whose cementum annuli data were not used because they were under the age of five accounted for 50.2% of all the culled female bears from the Echigo–Mikuni population whose tooth samples were collected. The mean age at first reproduction was 5.44 ± 0.22 years old (range: 4–11; 95% *CI*: 5.02–5.87). The age of first reproduction tended to be concentrated around four or five years old (four years old = 19/54, five years old = 15/54; Fig. 3).

The mean reproductive interval was 2.38 ± 0.48 years (range: 1–6; 95% *CI*: 1.50–3.37). More than half of the individuals were estimated to have reproduced every other year (one year interval = 9/16; Fig. 4).

We obtained the uteri of 88 female bears (zero to 20 years old) and observed placental scars in 36 (Appendix 1). The mean litter size was 1.58 ± 0.09 cubs (range: 1–3; 95% *CI*: 1.40–1.76). Most litters consisted of one or two cubs (one cub = 16/36, 44.4%; two cubs = 19/36, 52.8%; Fig. 5), and exceptionally three cubs (one case, 2.8%). For females with placental scars, the minimum and maximum ages were two years and 20 years, respectively (Fig. 5). The mean litter size, based on data collected in the Ashio–Nikko Mountains, was 1.80 ± 0.10 cubs from April to July, soon after birth (range: 1–2; 95% *CI*: 1.43–1.93; Table 1), and 1.70 ± 0.15 cubs from August to November, for cubs surviving into autumn (range: 1–2; 95% *CI*: 1.26–1.80; Table 1).

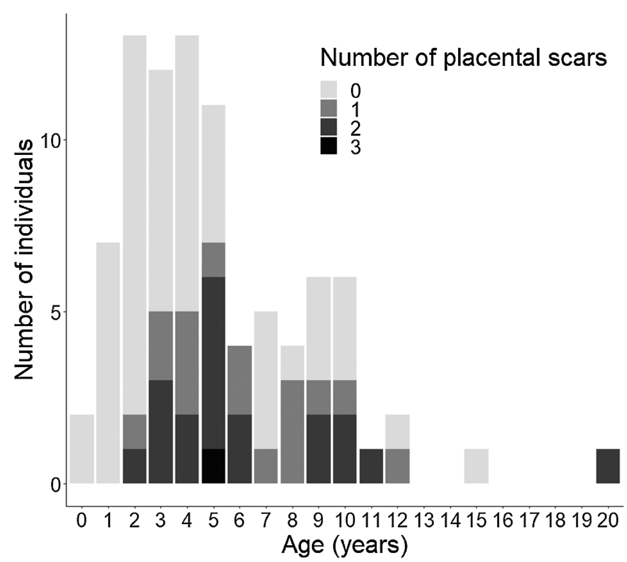

Fig. 5. Stacked histogram of ages of female Asian black bears with different numbers of placental scars. The samples were obtained from individuals culled (2009–2019) in Gunma Prefecture in Japan.

Mortality parameters

We used capture–recapture data from 43 female bears;

Table 1. Direct observation records of female bears accompanied by cubs from 2003 to 2019 in the Ashio–Nikko Mountains

Bear ID	Latest observed date	No. of cubs	No. of surviving cubs*	Yearling observed	Cub-year	Mother age
AF07	**2009/3/27**	**1**	**1**	**1**	**2008**	**8**
AF09	**2008/6/17**	**1**	**0**		**2008**	**4**
AF09	2018/9/26		1		2018	14
AF18	2014/5/1	2			2014	8
AF18	**2015/5/1**	**2**	**0**		**2015**	**9**
AF18	**2016/5/1**	**2**	**0**		**2016**	**10**
AF19	**2012/8/20**	**2**	**2**		**2012**	**5**
AF19	2014/6/23	2			2014	7
AF23	2010/6/2		1	1	2009	12
AF24	**2009/7/15**	**2**	**2**	**1**	**2008**	**7**
AF45	**2019/8/28**	**2**	**2**		**2019**	**11**
AF46	2015/5/12	2			2015	9
AF55	**2019/6/9**	**2**	**2**	**1**	**2018**	**9**
AF64	2017/7/15	2	2		2017	10
FB70	**2004/7/21**	**2**	**2**	**1**	**2003**	**9**
FB70	**2006/10/20**	**1**	**0**		**2006**	**11**
FB70	**2009/6/2**	**2**	**2**	**1**	**2008**	**14**

* Cubs that were observed to be with their mother in or after August of their birth year. Bold characters show the records that we used for the analysis of cub mortality.

these bears were captured or recaptured a total of 112 times, and four dead bears were recovered from 2003 to 2021 (Fig. 6). All recovery records (i.e., human-caused mortality) were related to nuisance kills. Analysis of the MRR model results revealed that the mean natural mortality rate of subadults and adults was 0.108 (95% *CI*: 0.064–0.174) and the mean human-caused mortality rate was 0.005 (95% *CI*: 0.002–0.021). The estimated detectability (per 1000 trap nights) was 0.004 (95% *CI*: 0.003–0.005), and the estimated annual capture probability was 0.005 (95% *CI*: 0.002–0.021).

We observed 11 female bears accompanied by cubs a total of 16 times from 2003 to 2019 (Table 1). We confirmed cub survival in 11 cases, for eight female bears (Table 1). From the generalized linear model results, the mean cub mortality rate was estimated to be 0.235 (95% *CI*: 0.080–0.465).

Discussion

Reproductive parameters

The mean age at first reproduction (5.44 years old; range four to seven years) of our study population was in the range of previously reported ages of sexual maturity (Katayama et al. 1996; Nakamura et al. 2011; Yamanaka et al. 2011b). Additionally, more than half of the female bears had a successful first reproduction at age four or five years. This finding also indicates that several primiparous mothers that had given birth as soon as they reached sexual maturity were able to successfully raise cubs through the first summer.

Along with age at first reproduction, reproductive interval duration in Asian black bears was previously unknown. The reproductive interval observed here (2.38 years) indicates that female Asian black bears take two years or more before their next reproduction. In several American black bear (*U. americanus*) and brown bear (*U. arctos*) populations, offspring separate from their mother at one–two years of age (Rogers 1987; Steyaert et al. 2012). This might indicate that mothers are unable to raise cubs the year after separation, even if they separate from their yearlings (i.e., the cubs survive to the following year) and have the opportunity to mate with males during the mating season. Alternatively, mothers might not separate from their yearlings and might therefore continue to raise their two-year-old cubs (i.e., the yearlings survive to the following year). However, we did not observe female bears caring for two-year-old cubs at our

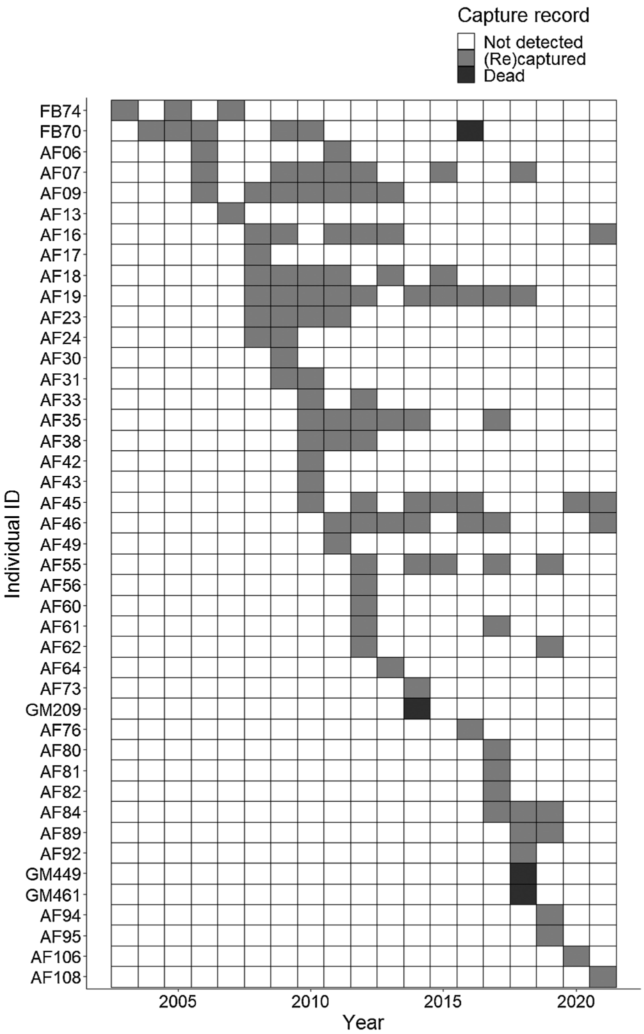

Fig. 6. Mark–recapture–recovery records of female Asian black bears from 2003 to 2021 in the Ashio–Nikko Mountains.

long-term study site; we therefore infer that females may not be able to give birth to another litter immediately after separation. We expect that limiting factors such as low food availability may delay the next chance of successful reproduction (Costello et al. 2003). We think it possible that Asian black bears depend on pulsed resources—that is, resources whose availability changes in space and time with a low frequency, a large magnitude, and a short duration (Yang et al. 2008). Alternatively, since related female Asian black bears form matrilineal assemblages and have overlapping home ranges (Kozakai et al. 2017), the reproductive intervals of daughters may become longer if they stay close to their mothers even after natal dispersal (Støen et al. 2005; Ordiz et al. 2008). In addition, longer intervals may be a consequence of estimating reproductive interval duration for primiparous females only; the reproductive intervals of these females can be longer than those of multiparous females, as documented in brown bears (Zedrosser et al. 2009). We removed consecutive cub-years from our calculations because females would likely have lost their cubs during such years. Thus, our reproductive interval represents the time interval between two litters of cubs that have a high chance of surviving until at least August of their birth year. Therefore, our "reproductive interval" is most certainly longer than the interbirth interval (i.e., the time interval between the birth of a female's litter and the birth of her next litter; Stringham 1990), which is one of the key representations of the reproductive interval.

Although we did not perform a statistical analysis, the mean litter size in this study (1.58 ± 0.09), as determined by observation of placental scars, appears to have been smaller than that in previous studies (2.00 ± 0.00 in Katayama et al. 1996; 1.8 in Nakamura et al. 2011; and 1.88 ± 0.12 in Yamanaka et al. 2011b). This may be explained by the average age of bears or the duration of the sampling period in our study. Our sample contained younger females (6.45 ± 0.57 years for individuals with placental scars) and covered a longer period (11 years) than in previous studies (female age 10.6 ± 1.22 years and study period over three years in Katayama et al. [1996]; about 10.8 ± 0.63 years and over one year in Nakamura et al. [2011]; and 10.6 ± 0.50 years and over nine years in Yamanaka et al. [2011b]). It is possible that younger females have smaller litter sizes because of a lack of reproductive experience (Zedrosser et al. 2009). In addition, good environmental conditions, such as high food availability, could lead to larger litter sizes (Czetwertynski et al. 2007; Johnson et al. 2020). If the samples had been collected over a short period of time, then the litter size might have been either under- or overestimated, because it is difficult to account for changes in food availability over time. However, our sample spanned 11 years, enabling us to determine the litter size over many years, during which time food availability fluctuated. Additionally, had we checked both the placental scars and the corpus albicans, we could have determined whether the cubs had been born during the current or the previous year (Yamanaka et al. 2011b). However, given the difficulty of sectioning and staining our samples for microscopic examination, uncertainty exists regarding whether the estimated litter was born during the year in which the female was captured or the year before.

Moreover, the mean litter size based on the number of placental scars (1.58) was lower than the mean litter size observed in the core distribution area (number of cubs first observed = 1.80; number of cubs surviving after the mating season = 1.70). In general, the number of cubs observed would be smaller than the number of placental scars because of partial litter loss (Katayama et al. 1996; Yamanaka et al. 2011b), but our litter size estimates showed an opposite relationship. Our litter size estimates based on placental scars may have been biased because our sample contained younger females, or because our estimation was based on individuals culled at the periphery of the distribution, or both.

We confirmed that placental scars could be formed in relatively young bears (two years old), which is younger than the previously reported age of sexual maturity (four years old; Katayama et al. 1996). The inference that bears may give birth at two years old does not contradict the results from previous studies suggesting that ovulation may occur in females one–three years old (Katayama et al. 1996) or at least two years of age (Yamanaka et al. 2011b). The maximum observed age of females with placental scars was 20 years. Because placental scars persist for one or two years after giving birth (Tsubota et al. 1990), it is likely that the maximum reproductive age was 19. The possibility that bears 19 or 20 years old might still be of reproductive age is concordant with previous reports or observations of 16–18-year-old mothers with cubs (Katayama et al. 1996; Yamanaka et al. 2011b). Nakamura et al. (2009) also documented ovulation in a 22-year-old female. Our results and those of these previous studies suggest that Asian black bears produce cubs until their 20s.

In general, reproductive parameters (age at first reproduction, reproductive interval, litter size, and minimum age at primiparity) are affected by external factors such as habitat condition, population density, and magnitude of conflict with humans (e.g., Bischof et al. 2018; van de Walle et al. 2018). In addition, internal factors such as nutritional condition and the length of maternal care would affect reproductive parameters (van de Walle et al. 2018). Therefore, the reproductive parameters of the Echigo–Mikuni population may differ from those of other populations of Asian black bears, because females in other populations may live in habitats with different nutritional conditions or exhibit a different age structure from that of the Echigo–Mikuni population. Additionally, we should be cautious about interpreting the reproductive parameters from our study, because our data included those on nuisance bears. Nevertheless, Asian black bears culled as nuisances in mast failure condition of hard mast in Japan do not differ substantially from nuisance bears in better masting condition with regard to stored body fat, indicating that poor nutritional condition is not directly related to nuisance behavior (Yamanaka et al. 2011a). Given that nutritional condition, which could affect reproductive parameters, possibly does not significantly differ between culled bears and free-ranging bears, the reproductive parameters observed here may be similar to those of free-ranging Asian black bears.

Mortality parameters

Human-caused mortality, such as from sport hunting and culling, was relatively low (0.005, 95% *CI*: 0.002–0.021) compared with natural mortality (0.101, 95% *CI*: 0.059–0.167). The Ashio–Nikko Mountains are located in an area where nuisance killing and sport hunting are conducted (Tochigi Prefecture 2021; Gunma Prefecture 2022). In both prefectures, most bears were killed during control operations (more than 50%; Tochigi Prefecture 2021; Gunma Prefecture 2022). Our recovery records, which are all for nuisance kills, reflect this situation (Fig. 6). However, human access is controlled in most of our study area. Thus, culling pressure and human–bear conflicts are lower in our study area than in other areas inhabited by the Echigo–Mikuni population. If future population size estimates or population trend estimates are conducted by using our data for human-caused mortality, it may lead to overestimation of population size. Therefore, estimating specific human-caused mortality before population analysis is critical.

Mortality and survival rates vary by season, year, age class, reproductive status, and other factors in brown bears, American black bears, and polar bears (*U. maritimus*) (Hebblewhite et al. 2003; Regehr et al. 2010; Krofel et al. 2012; Bischof et al. 2018). Here, we estimated the average natural mortality across a 19-year period for individuals ranging in age from one to 21 years, thereby smoothing variation in age structure and over time. The mortality rates for each age group and season must be confirmed in order to estimate how each parameter contributes to population dynamics. However, for ursids, adult survival rate is an essential parameter affecting population growth and fluctuation (Hebblewhite et al. 2003; Mitchell et al. 2009). Considering the absence of reports on the mortality rate of Asian black bears, our finding is important and constitutes fundamental biological data.

In Japan, the number of Asian black bears that are culled fluctuates among seasons and years (Echigo–

Mikuni population: Tochigi Prefecture 2020; Gunma Prefecture 2022; Nagano Prefecture 2022; Japan: Oka 2006; Ministry of the Environment 2022). Although there may be seasonal and annual variations in human-caused mortality in our study area, we were unable to account for fluctuations, because our sample size was small and there was no annual change in culling pressure. In the future, we should conduct an analysis using more samples across a wider area to take temporal fluctuations into account and estimate general human-caused mortality. This would help us understand the bear-culling situation in Japan and the impact of culling on bear population dynamics.

Cub mortality (0.235) during the first half year after birth was higher than natural mortality (0.108) and human-caused mortality (0.005) in subadult and adult female bears. We expect that sexually selected infanticide (the killing of dependent offspring by adult males to generate mating opportunities) (Steyaert et al. 2014) may have an impact on cub survival rates in our study system. Factors affecting cub mortality remain unclear for Asian black bear so far, but a previous study showed evidence for male infanticide during the mating season in our study area (Yamazaki 2017) and in another population in Japan (Naganuma et al. 2021). We suggest that more observations and field verifications are needed to clarify the main causes of cub mortality and the occurrence of sexually selected infanticide in our study system. Cub mortality also varies with mother-related factors: age, nutritional condition, and the length of maternal care, as is for example the case in brown bears (Zedrosser et al. 2009; van de Walle et al. 2018). This finding indicates that reproductive experience may also affect cub mortality, and it may also apply to Asian black bears. We need more samples to evaluate the factors that impact cub mortality and to reduce uncertainty in future studies.

Conclusion

We estimated some reproductive parameters (i.e., age at first reproduction and reproductive interval) for the first time in female Asian black bears and updated others (i.e., litter size and minimum age at primiparity). The reproductive history of female Asian black bears from birth until death is reflected in their teeth, and litter size is recorded in the uterus. By long-term collection of samples from culled and captured individuals, combined with field observation data, we clarified fundamental reproductive parameters of Asian black bears that are difficult to observe visually and repeatedly during their lifespan. Moreover, long-term monitoring data (~20 years) provided us with mortality rates for two age classes. Further research will allow us to identify factors that affect demographic parameters and how these factors impact population dynamics. This will help to improve the conservation and management of Asian black bears.

Supplementary data

Supplementary data are available at *Mammal Study* online.
Supplementary Material S1. R script of the mark–recapture–recovery model based on the Cormack–Jolly–Seber process for estimating natural and human-caused mortality.

Acknowledgments: We thank the members of the Asian Black Bear Research Group for supporting the field work and study design. We also thank Mr. Shinichi Haneo for providing information on the study area. We thank the Gunma and Nagano, and Tochigi Prefecture, officers of the municipality of each prefecture, and hunters belonging to the local Hunters' Association for treatment of bears at capture sites and cooperation in collecting and submitting samples of culled bears. We are grateful to Ms. Kozue Kigure for preparing, organizing, and preserving bear samples of Gunma Prefecture. We are also grateful to Mr. Tetsuya Maruyama of Tochigi Prefectural Forestry Research Center for providing bear samples of Tochigi Prefecture. We also thank Nikko City for granting permission to capture bears for academic research purpose. We thank the Nikko District Forest Office of the Forestry Agency for permission to set traps in the national forest. This work was partially supported by JSPS KAKENHI (grant numbers 20J21115 and 19H02990) and the Institute of Global Innovation Research at the Tokyo University of Agriculture and Technology.

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Received 17 July 2022. Accepted 18 May 2023.
Editor was Emmanuel Do Linh San.

Appendix 1.

Number of placental scars for culled female Asian black bears (2010–2019) of the Echigo–Mikuni population in Japan

Bear ID	Capture date	Age* (years)	No. of placental scars
VM10-175	2010/07/28	3	0
VM10-259	2010/08/29	5	0
VM10-266	2010/08/05	15	0
VM10-270	2010/08/09	2	2
VM10-288	2010/09/17	12	1
VM10-290	2010/09/25	10	0
VM10-331	2010/10/19	4	0
VM10-362	2010/08/18	5	2
VM10-402	2010/11/08	11	2
VM10-74	2010/05/31	2	0
VM11-111	2011/08/10	9	2
VM11-120	2011/08/24	3	1
VM11-162	2011/10/04	1	0
VM12-107	2012/07/21	3	0
VM12-163	2012/07/30	5	2
VM12-167	2012/08/11	10	0
VM12-182	2012/08/25	2	0
VM12-208	2012/09/01	10	0
VM12-219	2012/09/14	10	2
VM12-221	2012/09/13	4	1
VM12-238	2012/09/18	5	2
VM12-251	2012/09/28	5	1
VM12-252	2012/09/27	3	2
VM12-303	2012/11/04	8	1
VM12-80	2012/06/05	3	0
VM12-94	2012/06/20	1	0
VM13-102	2013/07/03	6	2
VM13-111	2013/07/07	4	2
VM13-151	2013/08/12	5	0
VM13-157	2013/08/23	6	2
VM13-167	2013/08/20	2	1
VM13-168	2013/08/18	9	1
VM14-204	2014/06/04	1	0
VM14-208	2014/07/05	4	0
VM14-241	2014/08/07	1	0
VM14-254	2014/08/12	4	1
VM14-271	2014/08/16	5	0
VM14-289	2014/08/27	4	0
VM14-299	2014/08/29	7	0
VM14-308	2014/08/24	8	1
VM14-309	2014/09/06	6	1
VM14-315	2014/08/28	2	0
VM14-328	2014/09/09	9	0
VM14-334	2014/09/09	0	0
VM14-336	2014/09/09	2	0
VM14-337	2014/09/09	8	1
VM14-341	2014/09/07	3	0
VM14-362	2014/09/13	7	0
VM14-390	2014/09/29	2	0
VM15-108	2015/07/04	3	2
VM15-135	2015/08/28	4	0
VM15-145	2015/09/04	4	0
VM15-55	2015/05/20	5	2
VM15-90	2015/06/10	3	0
VM16-102	2016/05/20	0	0
VM16-105	2016/05/13	3	0
VM16-135	2016/06/07	2	0
VM16-147/180	2016/07/09	1	0
VM16-153	2016/07/11	3	0
VM16-173	2016/08/11	5	2
VM16-179	2016/07/25	2	0
VM16-195	2016/08/17	4	0
VM16-199	2016/06/08	5	0
VM16-221	2016/07/20	7	0
VM16-232	2016/08/28	2	0
VM16-247	2016/08/31	12	0
VM16-257	2016/07/07	1	0
VM16-277	2016/09/18	9	2
VM16-295	2016/08/28	9	0
VM16-308	2016/10/11	3	1
VM16-312	2016/10/18	6	1
VM16-317	2016/10/31	20	2
VM16-373	2016/11/11	9	0
VM16-376	2016/11/17	5	3
VM16-439	2016/11/03	7	0
VM16-707	2016/11/07	4	2
VM16-92	2016/05/15	3	2
VM17-217	2017/07/24	1	0
VM17-287	2017/06/20	2	0
VM17-294	2017/09/03	2	0
VM17-301	2017/09/11	8	0
VM17-346	2017/09/17	2	0
VM18-69	2018/05/23	4	0
VM18-70	2018/06/06	4	0
VM19-151	2019/07/02	4	1
VM19-172	2019/07/09	10	2
VM19-251	2019/09/25	7	1
VM19-256	2019/09/10	10	1

* Age at capture year. Age was estimated by counting tooth cementum annuli.