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Reproductive characteristics of Japanese monkeys on Shimokita Peninsula, Japan, the northernmost habitat of wild primates in the world

Shin-ichi HAYAMA[1)]*, Yuki KAWABATA[1)], Aoi OCHI[1)], Setsuko NAKANISHI[1)], Yoshi KAWAMOTO[1)] and Hideharu YAMAZAKI[2)]

[1)]Laboratory of Wildlife Medicine, Nippon Veterinary and Life Science University, 1-7-1 Kyonan-cho, Musashino, Tokyo 180-8602, Japan

[2)]Shimokita Peninsula Municipal Liaison Conference for Damage Control by Wild Monkeys, Wakinosawa, Mutsu, Aomori 039-5323, Japan

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ABSTRACT. The Shimokita Peninsula in Aomori Prefecture, Japan, which is inhabited by Japanese monkeys (*Macaca fuscata*), is the northernmost habitat for wild primates in the world. This study was the first to determine the conception dates of specific individuals and estimate the pregnancy rate of wild populations in this region. The pregnancy rate of animals aged 5 years or more at delivery was estimated to be 40.9% (27/66). Conception dates of each fetus were also estimated using a regression line of Pig-tail monkeys (*Macaca nemestrina*), which are taxonomically related to Japanese monkeys and have a similar physique. The conception dates were distributed across 90 days between September 24th and December 23rd, with a mean conception date of November 4th (SD=22.3 days, n=53). Using these findings, the mean birth date was estimated as April 25th, more than two weeks earlier than the mean birth date in previous research determined using direct observations carried out over the past 20 years ago. Global warming due to climate change is thought to be one of the main causes of this difference.

KEY WORDS: climate change, conception date, Japanese monkey, *Macaca fuscata*, pregnancy rate

The Shimokita Peninsula in Aomori Prefecture, Japan, which is inhabited by Japanese monkeys (*Macaca fuscata*), is the northernmost habitat for wild primates in the world (Fig. 1). Ancestral populations were isolated within refugia along the southern coast of the Japanese archipelago during the Last Glacial Maximum or possibly a former glacial period [13]. During subsequent warming, the distribution front of Japanese monkeys moved north again, and approximately 5,000–10,000 years ago, Shimokita Peninsula became largely isolated from the mainland [30]. The first ancestral population bottleneck and considerable genetic differentiation from surrounding populations is therefore thought to have occurred in this region as a result [17].

In the latter half of the 19th century and the first half of the 20th century, Japanese monkeys on Shimokita Peninsula became endangered due to overhunting [24]. Meanwhile, a separate troop was discovered in Wakinosawa district in 1963, and despite causing crop damage, provisions were provided to feed the monkeys and conserve population numbers. In 1970, Japanese monkeys inhabiting the Shimokita Peninsula were subsequently designated a national natural monument, with the number of populations at this time estimated at around 200 to 240 in seven troops [3, 16]. With subsequent increases in population sizes, fission troops and habitat expansion followed [1] resulting in 1081 populations (27 troops) by 2002. However, due to increasing disturbance, the government of Aomori Prefecture formulated a management plan for Japanese monkeys in the region, allowing for the capture of individuals that have attacked people or invaded local homes. Some municipalities also assigned professionals to help carry out damage control. However, in 2008, with the number of populations continuing to increase, the government decided to capture all individuals causing damage to crops [1] (Fig. 2).

Meanwhile, in 2012, a new management plan of systematic population control was implemented in order to both curb damage and prevent further increases in populations (Fig. 2). Because Japanese monkeys on Shimokita Peninsula are classified as a national natural monument, capture is based on monitoring results of population and breeding dynamics, with euthanasia carried out by professionals according to the guidelines of the Wildlife Conservation and Management Law, Japan.

*Correspondence to: Hayama, S.: hayama@nvlu.ac.jp

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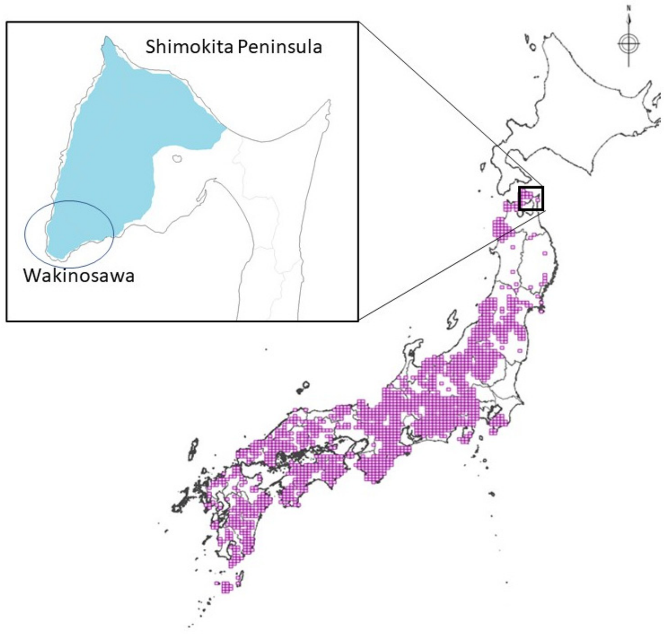

Fig. 1. Habitat distribution of Japanese monkeys in Japan (main map; pink meshes) and on Shimokita Peninsula (inset map; light blue area). The circled area in the Shimokita Peninsula map represents Wakinosawa district. The main map was created from distribution surveys of Japanese animals (mammals) conducted by the Biodiversity Center of Japan, Nature Conservation Bureau, Ministry of the Environment (http://gis.biodic.go.jp/webgis/).

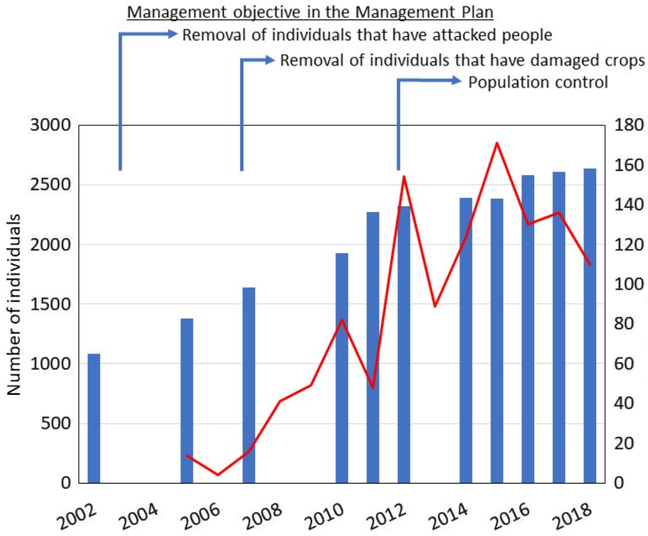

Fig. 2. Annual changes in population numbers and captures on Shimokita Peninsula, and the transition in management objectives over time. Blue bars indicate the number of individuals (left vertical axis) and the red line indicates the number of captures (right vertical axis).

The reproductive characteristics of Japanese monkeys, including pregnancy rate and birth season, have changed along with population status and these characteristics are used as assessments for population management in wildlife [21]. For example, the rate of population increase is estimated from the pregnancy rate, and the result is reflected in the appropriate number of permitted captures. A number of detailed studies have examined the reproductive characteristics of provisioned troops of Japanese monkeys. However, due to the effects of artificial feeding in provisioned troops mainly for tourism purposes, the nutritional status of individual monkeys has improved, significantly impacting their reproductive characteristics and leading to increased birth rates [19, 32]. To clarify the reproductive characteristics of wild troops, direct observation of specific individuals over a long period of time is also required, resulting in limited reports to date [8, 18, 35]. Maruhashi [22] investigated the birth rates of multiple adjacent troops on Yakushima Island and discovered that birth rates differed by troop even in the same year. On Shimokita Peninsula, the birth rates and dates of birth have been examined via direct observation since the 1960s [2, 7, 20]; however, the observation targets are limited to only a few troops inhabiting Wakinosawa district.

Research on the reproductive characteristics of regional populations consisting of dozens of troops is difficult due to the labor intensity of direct observations. Therefore, in this study, we aimed to clarify the reproductive characteristics (the pregnancy rate, and dates of conception and birth) of populations in the region using monkey carcasses provided by the local government in order to support the appropriate protection and management of Japanese monkey populations on Shimokita Peninsula. Anatomical observations of the culled individuals were used to determine both conception dates and pregnancy rates [11].

MATERIALS AND METHODS

Culled individuals of a local population of wild Japanese monkeys inhabiting Shimokita Peninsula were the subject of this study. The population consists of 70 troops, with an estimated 2,400 individuals [1].

Carcasses from 37 troops were provided by the city of Mutsu, the town of Ohma, and the villages of Sai and Kazamaura on Shimokita Peninsula. Monkeys were killed by shooting or with the use of CO_2 in a chamber immediately after being captured in a box trap; these procedures were carried out by management staff with the permission of the governor of Aomori Prefecture and in accordance with the Aomori Japanese Monkey (Shimokita Peninsula) Management Plan, which was established based on the Wildlife Protection and Hunting Management Law. Capture and euthanasia were carried out in accordance with the guidelines of the above management plan in an ethical manner, and in accordance with the guidelines of the Primate Research Institute, Kyoto University. The Japanese monkeys inhabiting this study area are not listed as endangered on the Japanese Red List, as revised by the Ministry of the Environment in 2012.

The study was carried out from August 2012 to July 2018, during which time a total of 199 females aged 4 years or older considered to have reproductive potential were included in the analyses. All carcasses were subjected to necropsy to determine their pregnancy status, and any fetuses were removed from pregnant individuals and measured for crown–rump length (CRL) and body weight. The ages of the captured animals were estimated from dental eruption according to the method of Iwamoto *et al*. [15] and classified as subadult (4–5 years) or adult (6 years and older). Pregnant sub-adults and adults were considered 5–6 and 7 years old or older at delivery, respectively. The exact ages of pregnant females were determined from annual layers in the cementum of the first upper incisor in order to clarify the relationship between age and conception date, following the method of Wada *et al*. [38].

Conception dates were estimated from the fetal age. Hayama *et al*. [11] previously used the fetal growth curve of rhesus monkeys (*Macaca mulata*) [37] to determine fetal age, given that there are no studies on fetal age and fetal growth in Japanese monkeys. However, Japanese monkeys on Shimokita Peninsula are relatively large [10]. The body size (head and body length) of adult females in taxonomically related *Macaca* species were reported to be 470–531 mm for rhesus monkeys, 467–564 mm for pig-tailed monkeys (*Macaca nemestrina*), and 472–601 mm for Japanese monkeys, respectively [27]. Therefore, the relational expression between fetal CRL and fetal age in the larger pig-tailed monkeys [28] was used in this study. The relational expression was calculated as follows:

Gestation age (days)=53.064 + 0.00282 × CRL (mm)^2

The pregnancy rate was estimated based on the proportion of pregnant individuals during the period from the latest conception date to the earliest birth date in the population. Birth dates were estimated from the conception date using the mean gestation period of Japanese monkeys of 173 days [29]. The difference between the mean values of the two groups was analyzed using the *t*-test. We tested differences in pregnancy rate between age classes by using Fisher's exact test. Pearson's correlation coefficient was used to examine correlations between age at delivery and estimated conception date.

RESULTS

Dissection of 199 female Japanese monkeys revealed 53 fetuses, all of which were singletons. The ages of the pregnant females at delivery ranged from 5 to 20 years. Figure 3 shows the fetal CRL by capture date. Conception dates estimated from the results of fetal age were spread across 90 days from September 24th to December 23rd, with a mean conception date of November 4th (SD=22.3, median: the same date). Comparisons of the mean conception dates by age class revealed that sub-adults conceived on November 13th (median: November 12th) and adults on November 2nd (median: the same date), with no significant differences between the two groups. Estimated dates of birth date ranged from March 16th to June 14th, with a mean date of April 25th. A significant negative correlation was found between the conception date and age at delivery (P=0.029); however, the correlation coefficient was −0.303, suggesting a weak correlation (Fig. 4).

Between the latest estimated conception date (December 23rd) and earliest birth date (March 16th), 66 animals were captured, with a pregnancy rate of 40.9% (27/66). Pregnancy rates were subsequently compared by age class, revealing no significant differences between sub-adults (41.7%, 5/12) and adults (40.0%, 22/54).

DISCUSSION

Birth rates in Japanese monkeys have been studied extensively in provisioned troops and are thought to have increased due to the improved nutritional status resulting from feeding. In Arashiyama, Kyoto Prefecture, the birth rate was found to be 80–90% in 6–19-year-olds [34], whereas in Ryozen, Shiga Prefecture, a rate of 59.26% was revealed in adults [32]. Meanwhile, in Takasakiyama, Oita Prefecture, the birth rate of adult females was estimated at 58.9% (1,190/2,020) in 1974–1977, at the beginning of provision, whereas in 1980–1983, following a reduction in feeding, the rate decreased to 46.9% (1,014/2,164), representing a significant reduction in line with the nutritional status [19]. Takahata *et al*. [34] also investigated the annual birth rate (births per female aged 5 years or more) in wild troops not dependent on agricultural provision, reporting a rate of 35.3% in two troops on Kinkasan, Miyagi Prefecture and 27% in three troops on Yakushima Island, Kagoshima Prefecture. In addition, Azuma [2] observed three wild troops inhabiting Wakinosawa district on Shimokita Peninsula from 1965 to 1974 and reported a birth rate of 28%.

Mastuoka [20] reported birth records of the A2-85 and A87 troops inhabiting Wakinosawa district from 1987 to 1998, revealing birth rates of 58% and 46%, respectively (Table 1). In the present study, the pregnancy rate was estimated to be 40.9% from 2012 to 2018. Assuming that all pregnant individuals gave birth, this birth rate was slightly higher than those of the wild troops mentioned above but was lower than those of the provisioned troops. Muroyama [26] reviewed previous studies and found that the birth rates of the crop-damaging wild troops were similar to that of the provisioned troops. The management plan had yet to be formulated during this previous study, and the monkeys may have been more dependent on crops than they are today (Fig. 2). The individuals in our study were captured from mainly crop-damaging troops, suggesting that they were relatively dependent on crops. It is therefore possible that the pregnancy rate decreased due to crop-damage countermeasures implemented via the population management plan.

In this study, the dates of conception were estimated in a population of Japanese monkey inhabiting Shimokita Peninsula. Although there was no significant difference in the mean conception date between adults and sub-adults, younger individuals tended to have a later conception date (Fig. 4). A similar tendency was also reported in the birth dates of the Shiga A troop in Nagano Prefecture, which was provisioned [36]. In addition, in the Katsuyama troop in Okayama Prefecture, which is also

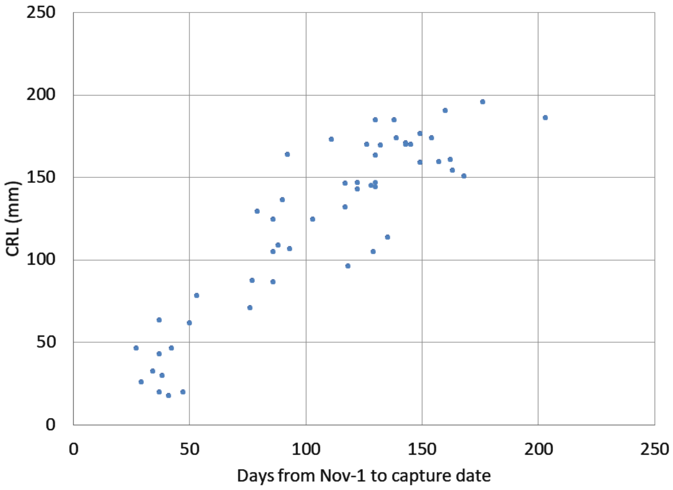

Fig. 3. Relationship between the capture date and fetal crown rump length (CRL).

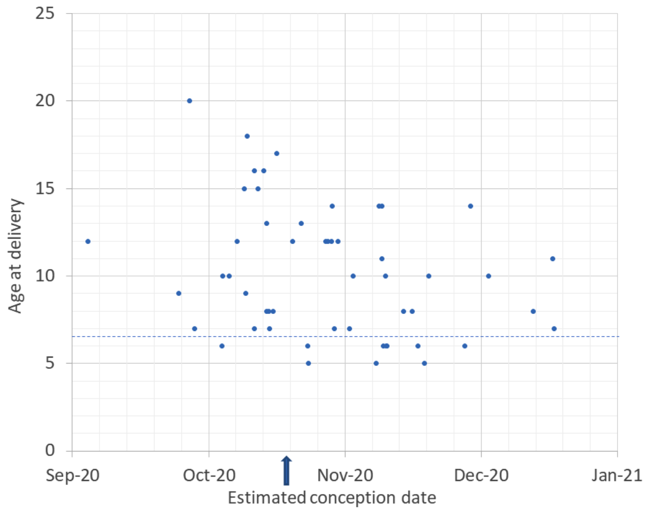

Fig. 4. Relationship between age at delivery and estimated conception date. The horizontal dotted line in the graph indicates the age-class boundary, and the arrow under the X-axis indicates the mean conception date (November 4th).

Table 1. Reported mean birth dates and birth rates reported in Japanese monkeys on Shimokita Peninsula

Region (Troop)	Survey period	Estimated mean birth date (N; SD)	Birth rate (%) (babies/mature females)	Source
Wakinosawa (A, O, B)	1965–1974	—	28 (10/32)	Azuma (1985) [2]
Wakinosawa (A2-85)	1987–1998	—	58 (52/90)	Calculated using the troop family tree in Matsuoka (2000) [20]
Wakinosawa (A87)	1987–1998	—	46 (19/41)	
Wakinosawa	1965–1966, 1987–2001	13 May (109; 22.0)	—	Fooden & Aimi (2003)* [7]
Shimokita Peninsula	2012–2018	25 Apr (53; 22.3)	40.9** (27/66)	Present study

*Data from Koford 1969, p. 12; Azuma 1985, p. 3; Dr. Shirou Matsuoka, Working Group for Monkeys in the Shimokita Peninsula, 101 unpublished records; cf. Kawai *et al*. 1967, p. 39. **Pregnancy rate to be exact (fetus/mature females).

provisioned, primiparous individuals aged 5 to 8 years were found to give birth significantly later, whereas multiparous individuals aged 20 to 24 years gave birth significantly earlier, although there was no significant difference in the dates of birth of parous individuals [14]. Also, the infant mortality rate was higher for primiparous mothers than for multiparous mothers in both this troop and the Ryozen troop [32]. These findings suggest that there may be competition among older multiparous individuals to conceive earlier in the breeding season for reproductive success.

According to the birth dates calculated in this study from the results of conception date and the mean gestation period of Japanese monkeys of 173 days [28], the mean birth date was estimated to be April 25th, with a range from March 16th to June 14th. Fooden and Aimi [7] calculated the mean birth date as May 13th based on birth records observed between 1965 and 1966 and between 1987 and 2001 in the Wakinosawa district of Shimokita Peninsula. In comparison, the estimated value in this study was about two weeks earlier. One reason for this is that, in this study, the fetal growth curve used to estimate the conception date was not that of Japanese monkeys, and the gestation period used was the mean value obtained in the laboratory (n=17, mean: 173 days, SD: 6.9 days, range: 161–188 days; [28]). Fujita *et al*. [8] estimated the ovulation date from changes in fecal hormones in wild Japanese monkeys and then calculated the gestation period from the difference between the birth date and ovulation date as 176.3 days (n=9, SD: 7.1 days, range: 170–188 days). In both the results of this study and those of Fooden and Aimi [7], the longest gestation period was 188 days, suggesting no difference between the results of the two studies. However, it would be unrealistic to assume that all individuals on Shimokita Peninsula undergo this maximum gestation period.

Another possible reason for the accelerated birth date observed here is global warming. In Shimokita Peninsula, the annual average temperature has risen by more than 1°C in the last half century according to transitional changes in annual average temperatures reported by Mutsu Meteorological Observatory of the Japan Meteorological Agency (Supplementary Fig. 1). This is thought to be due to the effects of global climate change.

In recent years, the flowering of plants [23] and the timing of egg laying in birds [5, 6, 12] have gradually accelerated worldwide. Meanwhile, in mammals, a few reports have also reported accelerated birth dates. For example, Moyes *et al*. [25]

revealed a significant advance in the parturition date (0.42 ± 0.08 days per year between 1980 and 2007) of wild red deer (*Cervus elaphus*) populations on the Isle of Rum, Scotland. Renaud *et al*. [31] revealed that the median parturition date advanced by approximately 15.7 days in bighorn sheep (*Ovis canadensis*) across 26 years on Alberta, Canada. In this area, autumn temperatures during the mating season have increased by 2.9°C, suggesting an effect on the birthing period.

Similarly, Graham *et al*. [9] reviewed the diverse effects of global warming on primates, citing reduced fertility and increased neonatal mortality due to more frequent droughts and high temperatures. Beehner *et al*. [4] also reported that drought reduced reproductive success in baboons (*Papio cynocephalus*) in Kenya. In addition, Wiederholt and Post [39] studied the relationship between reproduction and climate change in woolly spider monkeys (*Brachyteles hypoxanthus*) in Brazil and woolly monkeys (*Lagothrix lagotricha*) in Colombia, suggesting that drought and the El Niño phenomenon could limit reproductive output by delaying the birthing period. However, most of these studies focused on the effects on primates in the tropics and subtropics, with no documented findings in high latitudes and more temperate regions such as that in the present study.

Although the results of this study suggest that the Japanese monkey population on Shimokita Peninsula has experienced an accelerated birthing period during the past two decades, the results are not definitive and further long-term continuous analysis is required. Future analysis via direct observations and continued surveys of individuals in the same region are therefore necessary.

In conclusion, this study revealed the reproductive characteristics of a local population of Japanese monkeys on Shimokita Peninsula using culled individuals from a wild population. Accordingly, predictions of the approximate growth rate of the population are also possible. The findings suggest that the birthing period is gradually accelerating, which may put individuals at greater risk of giving birth during periods of particularly heavy snow [33] or cold waves, thereby increasing the mortality rate of babies born at this time. To ensure appropriate management of Japanese monkey populations in the Shimokita Peninsula region, continued monitoring is necessary, with careful evaluation of the population control plan based on analytical results.

CONFLICT OF INTEREST. The authors declare no conflict of interest.

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