Characteristics of Female Reproductive Success in a High-Density Population of the Japanese Serow, Capricornis crispus, in Akita, Northern Honshu, Japan

Authors: Kishimoto, Ryosuke, and Kuroe, Misako

Source: Mammal Study, 49(2) : 117-124

Published By: Mammal Society of Japan

URL: https://doi.org/10.3106/ms2023-0009

Mammal Study 49: 117–124 (2024) DOI: 10.3106/ms2023-0009

Original paper

Characteristics of female reproductive success in a high-density population of the Japanese serow, *Capricornis crispus*, in Akita, northern Honshu, Japan

Ryosuke Kishimoto[1,*] and Misako Kuroe[2]

[1] *Shinshu University Institute of Mountain Science, 8304 Minami-minowa, Kamiina, Nagano 399-4598, Japan*
[2] *Nagano Environment Conservation Research Institute, Nagano, 2054-120 Kitago, Nagano 391-0075, Japan*

Published online 13 March, 2024; Print publication 30 April, 2024

Abstract. There have been few field studies to date on female reproductive success in the Japanese serow, *Capricornis crispus*. Data were collected on female reproduction and kid mortality in a high-density population in Akita City, Japan, for seven years from 1979 to 1985. The parturition rate from 1979 to 1984 was at least 81.1%, and the annual variation (73.3–85.7%) was not significant. Each adult female usually gave birth to a single kid in successive years and may have intermittently had 1- or 2-year interruptions of parturition. In the seven females observed from zero or one year of age, four (57.1%) and three females (42.9%) first gave birth at three and four years of age, respectively. The kid mortality rate from 1979 to 1984 was 54.7%, and the annual variation (27.3–88.9%) was significant. Compared with the pregnancy rates of culled serows in low-density local populations, parturition rates were remarkably high in the study area, perhaps because of good nutritional conditions. In low-density populations such as red-listed areas, it is necessary to monitor fertility rates as well as population densities to avoid local extinction.

Key words: age at first reproduction, kid mortality, parturition rate, population density.

In large and long-lived mammals with low reproductive rates and high female parental care, information on female reproductive success is fundamental for species conservation. Especially in solitary territorial ungulates, female reproduction is considered to directly influence the condition of local populations because population densities are inherently kept low by their territoriality.

The Japanese serow *Capricornis crispus* is a forest-dweller that is usually solitary, defends intrasexual territories in both sexes, and exhibits monogamy as overlapping territories between sexes (Ochiai 1983a, 1983b; Kishimoto and Kawamichi 1996; Ochiai and Susaki 2002). It has been strictly protected as a "Special Natural Monument", because of its endemic status and academic value since 1955. It currently has a Red List status of Least Concern according to IUCN criteria (Tokida 2020). However, forestry damage by serows has gradually become conspicuous since the 1970s as a result of population recovery, and serow culling started with legal permission in two prefectures, Gifu and Nagano, in 1979. More recently, culling has been approved in six prefectures, including the former two, to reduce agricultural and forestry damage (Tokida 2007).

On the other hand, it was recently reported that population densities have been decreasing in the 15 designated montane serow conservation areas throughout Japan, including two presently undeclared but proposed areas, perhaps because of increases in sika deer (*Cervus nippon*) populations and a decrease in clear-cut and newly planted areas, in which the dense understories provide plenty of food for serows (Agency for Cultural Affairs 2013). Therefore, an investigation of the female reproductive success of serows is indispensable for management and conservation.

Several methods can be used to investigate the fertility of serows. One is an anatomical check of an embryo in the uteri of culled serows. Another is the measurement of annual horn growth increments, by which the reproductive history of females can be traced using the width between horn annuli (Miura et al. 1987), which can be

*To whom correspondence should be addressed. E-mail: capri_crisp350@yahoo.co.jp

used as an age criterion (Miura 1985). However, in these methods, it is necessary to kill or at least capture the individual to make these determinations, and culling itself may affect female reproduction due to such as mate loss and decreasing population density.

In contrast, direct observation can be made to collect natural information on parturition and also young mortality in the field without culling. Adult female serows give birth to single kids, mostly between May and June, and are accompanied by their offspring for around one year (Kishimoto 1989; Ochiai and Susaki 2007; Ochiai 2016). The young start to be independent around one year of age, but still stay within their mother's home ranges up to about two to four years of age (Kishimoto 1987; Ochiai and Susaki 2007). Therefore, in a field study, it is possible to estimate the reproductive success of females by observing their surviving young. However, it is difficult to accurately estimate the parturition rate by direct observation of adult females with or without kids because observers might not locate kids due to their relatively high mortality rate (Kishimoto 1994; Ochiai et al. 2010). Between the late 1970s and the 1990s, many behavioral studies of serows were conducted because it was easy to observe serows in clear-cut and newly planted areas due to the open habitat and high serow densities (e.g., Forest Technology Association 1979). Nevertheless, no studies estimated the parturition rates of serows by direct observation in the field. Furthermore, it has recently become increasingly difficult to study serows in the field by direct observations because clear-cut areas and densities of serows have tended to decrease throughout Japan (Agency for Cultural Affairs 2013).

Kishimoto and Kawamichi (1996) conducted field observations of serows in a high-density population in Akita City, northern Honshu, Japan, for seven years from 1979 to 1985 to study their social organization. During the study period, if at all possible, data were also collected on female reproductive success, such as parturition rates, individual reproductive histories and mortality rates of their offspring within the first year of birth. In this paper, the characteristics of reproductive success in adult female serows are described from data collected in the Akita study area observed around 40 years ago, compared with the fertility rates of culled serows in other prefectures in recent years.

Materials and methods

The study area (39°N, 140°E; 150–574 m above sea level) covers montane areas of 320 ha in Nibetsu, Akita City, Japan. Valleys surrounded approximately two-thirds of the study area in the southeast, south, and northwest peripheries, and forest roads ran nearly along the valleys. The vegetation mainly consisted of natural mixed forests of Japanese cedar (*Cryptomeria japonica*) and Japanese beech (*Fagus crenata*) (43% of the study area) and mature forests of planted Japanese cedar (28%). The clear-cut and newly planted areas were patchily distributed (19%). The annual mean temperatures ranged from 14.2°C to 15.7°C, and the annual rainfall from 1459 mm to 2128 mm in the Akita Local Meteorological Station, located about 18 km south-west of the study area, between 1979 and 1985 (Japan Meteorological Agency, Tokyo, https://www.data.jma.go.jp/obd/stats/etrn/index.php, Accessed 8 June 2023). The snow cover, at most 1 m in depth, remained usually from mid-December to early April.

Field observations were conducted for 1057 days between 1979 and 1985: 144 days from June to December 1979; 220 days from late February to November 1980; 212 days from March to December 1981; 184 days from April to December 1982; 61 days from late February to March, and from May to July 1983; 133 days from May to December 1984; 103 days from March to early July, and from November to December 1985. A random route throughout the study area was walked to search for serows. When found, their behavior was observed using binoculars (12 × 40) and a zoom spotting scope (25–50 × 60). Because the serows in the study area were relatively tame, they could be tracked at distances of 20–30 m in the forests without apparently disturbing their natural behavior. In the clear-cut areas, observation distances were 50 to over 100 m. In total, 159 individual serows (one year old or older) and 119 kids (less than one year old) were identified, with variations in natural features such as the shapes of their horns, torn ears, facial scars, and body colors, although the identities of mothers were of particular help in identifying their offspring. Sexing was mainly by observations of the external genitalia, and the individuals were classified by horn shape into four age classes (Kishimoto 1988): kids, yearlings, subadults (two years old), and adults (three years old or more). Both male and female serows become sexually mature at about 2.5–3 years of age (Sugimura et al. 1981; Tiba et al. 1988).

The mean (± *SE*) annual density of serows in the study area was 19.4 ± 1.0 individuals/km^2 (range: 17.1–24.3, n = 7 years) (Kishimoto and Kawamichi 1996). This population density is very high compared to the mean (± *SD*) densities across Japan (2.6 ± 0.2 individuals/km^2 in both

1977 and 1983; Agency for Cultural Affairs 2013), perhaps because clear-cut and newly planted areas which provided plenty of food for serows in the undergrowth (Ochiai et al. 1993a, 1993b; Ochiai 1996) were patchily distributed in about 20% of the study area.

All possible effort was put into determining whether females were accompanied by their kids, to measure parturition rates and kid mortality rates. Analyses were based on 24 adult females and their 95 kids that were resident in the main part of the study area, i.e., excluding the periphery. The absolute ages of seven of the 24 adult females were known, because they were observed from zero or one years of age. Exceptionally, one of the 95 kids was found dead at the first observation, and the adult female whose home range included the dead spot was defined as its mother. Because there still exists the possibility that some kids were not found because of mortality soon after birth, the parturition rates should be considered as underestimated values. Especially in 1985, it was presumed that the failure to find a number of kids may be because no observations were undertaken during the four months immediately after the parturition season. Therefore, data from 1985 were omitted from the calculation of parturition rates. Because offspring accompanied their mothers for about one year after birth, the disappearance of kids before the next birth season was considered to be due to their death.

The generalized linear mixed model (GLMM) was used to analyze annual or individual variation in parturition rates and kid mortality rates. To analyze annual variation in parturition rates, parturition status was set as response variable, and the explanatory variables were year as a categorical variable, and the female ID was set as the random effect. To analyze the effect of year and individual (mother) on kid mortality rates, the GLMM was also used; the response variable was kid mortality status and the explanatory variables were year, and the female ID was set as the random effect. The both GLMMs were estimated with binomial distribution and logit link function by using statistical package "lme4" in free statistical software R. *P*-value of both GLMMs were estimated by using "lmerTest" package (Kuznetsova et al. 2017) in R. A *t*-test was conducted using Satterthwaite's method to determine the degrees of freedom, and explanatory variables with a risk rate less than 0.05 were judged to be variables that significantly affected the response variable. To identify the years with higher kid mortality, Turkey's honestly significant difference (HSD) test was performed as a post-hoc test comparing the intercepts for each observed year using the "multcomp" package in R. The binomial test was used to analyze sex ratio of kids at birth. The test was conducted with the "binom.test" function in the R. The all analyses were conducted using the R version 4.3.0 statistical software (R Core Team 2023).

Results

Parturition rate

Figure 1 shows the residential and reproductive histories of the 24 adult females observed. All seven females whose absolute ages were known were three or four years old in each first year, as shown with "3y" or "4y" in Fig. 1. All 24 females were territory holders, although five females (F21, F26, F111, F114, and F123) were not territorial yet, staying in their mothers' home ranges up to three or four years of age. Six females (the above five and F19) established their own territories in their native areas by taking over a part of their mother's territory or the whole territory of their mother who disappeared (Kishimoto 1987). The other female (F41) was observed in the periphery of the study area at 1–3 years of age and intruded into the main study area and established her own territory at four years of age. During the study period, 24 females had 122 breeding seasons, and 95 kids were confirmed to be born. In 1978, the year prior to the study, at least six females gave birth, judging from the fact that their 1-year-old offspring stayed in their mother's home range in 1979.

At 27 of the 122 breeding seasons, females were not accompanied by kids. At least two females showed indications of a birth, as shown with "?" in Fig. 1, even though their kids were not found. Udder development of F111 was observed despite the absence of her newborn kid while she was three years old in June 1982, perhaps because her kid was stillborn or died soon after parturition. Serow mothers use a characteristic call to contact their lost newborn kids (Ochiai 2016). In June 1983, F12 exhibited the behavior of using this call, although her kid was not observed that year. However, because of uncertainty regarding these two cases, they were treated as cases of no parturition. Consequently, the parturition rate from 1979 to 1984 was at least 81.1% (n = 106), and the annual variation (73.3–85.7%) was not significant (GLMM, P = 0.655; Table 1 and 2).

Birth histories of individuals

Individual adult females usually gave birth to a kid

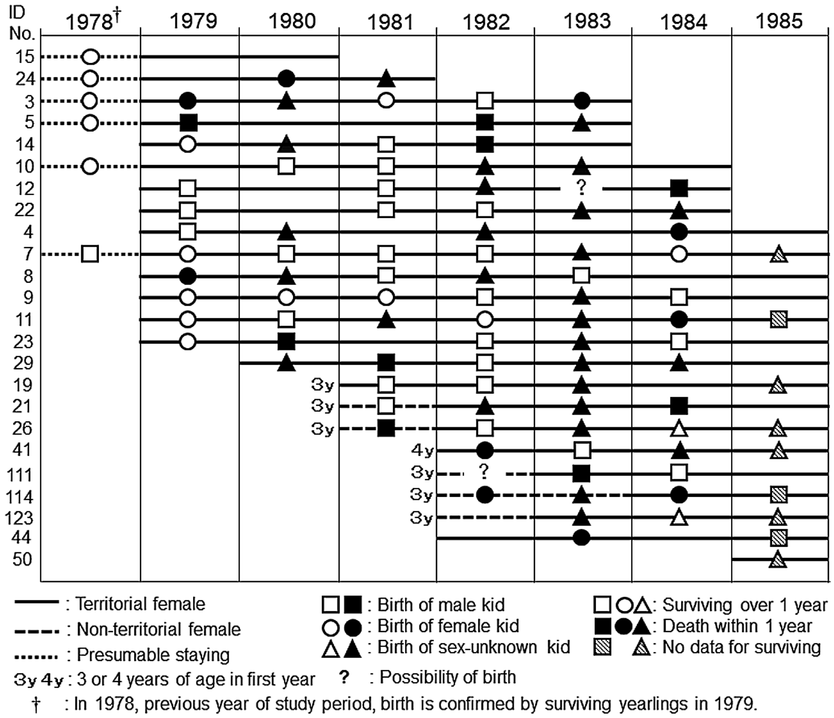

Fig. 1. Individual birth histories of adult female Japanese serow.

Table 1. Parturition rates of adult female serows, mortality rates of their kids within year and kid sex ratio

Year	*n* of adult females	*n* of born kids (parturition rate)	*n* of dead kids (mortality rate)	Kid sex ratio			
				♂:♀:Unknown	♂	♀	*P* [a]
1979	14	11 (78.6%)	3 (27.3%)	0.6:1:0.0	4	7	0.549
1980	15	11 (73.3%)	7 (63.6%)	2.0:1:2.5	4	2	0.688
1981	17	14 (82.4%)	4 (28.6%)	5.0:1:1.0	10	2	0.039*
1982	21	18 (85.7%)	9 (50.0%)	3.3:1:1.7	10	3	0.092
1983	21	18 (85.7%)	16 (88.9%)	1.5:1:6.5	3	2	1.000
1984	18	14 (77.8%)	8 (57.1%)	1.3:1:1.3	5	3	0.727
Total	106	86 (81.1%)	47 (54.7%)	2.3:1:2.2	39[b]	19[b]	0.012*

[a] *P*-value in binomial test of kid sex ratio.
[b] Three males and no females in 1985 are included.
*: $P < 0.05$.

Table 2. Generalized linear mixed model (GLMM) estimates of effect of observed year on parturition probability

		Estimated parameters			
		Average	Standard	*z*-value	*P*
Intercept		1.299	0.651	1.995	0.046*
Observed year	1980	–0.288	0.875	–0.329	0.742
	1981	0.241	0.911	0.265	0.791
	1982	0.492	0.902	0.546	0.585
	1983	0.492	0.902	0.546	0.585
	1984	–0.047	0.854	–0.054	0.957

Estimated parameters in 1979 are included in intercept.
*: $P < 0.05$.

in successive years, and intermittently had 1- or 2-year interruptions of parturition, although some births may have been overlooked, as explained above (Fig. 1). The highest number of annually successive births was eight kids by F7 from 1978 to 1985 and seven kids by F11 from 1979 to 1985 throughout the study period.

Age at first reproduction

Among the seven age-known females, at least four (57.1%) first gave birth at three years of age. The other three females (42.9%) gave birth at four years of age, although F111 was presumed to have been pregnant or

Table 3. Generalized linear mixed model (GLMM) estimates of effect of observed year on kid mortality probability

		Estimated parameters			
		Average	Standard	*z*-value	*P*
Intercept		0.988	0.692	1.429	0.153
Observed year	1980	–1.573	0.945	–1.664	0.096
	1981	–0.061	0.912	–0.067	0.946
	1982	–0.990	0.837	–1.182	0.237
	1983	–3.123	1.051	–2.970	0.003*
	1984	–1.302	0.890	–1.437	0.144

Estimated parameters in 1979 are included in intercept.
*: $P < 0.01$.

Table 4. *P*-values of post-hoc test (Tukey's HSD) for observed year in GLMM estimating kid mortality

	1979	1980	1981	1982	1983	1984
1979						
1980	0.031*					
1981	ns	0.032*				
1982	ns	ns	ns			
1983	0.010*	ns	0.011*	0.043*		
1984	ns	ns	ns	ns	0.047*	

*: $P < 0.05$, ns: non-significant.

may have given birth at three years of age, as described above. All seven females gave birth to a kid when four and five years of age.

Sex ratio of kids

The sex ratio of newborn kids was presumed to be female-biased in 1978, the year prior to the beginning of the study, because five of six surviving yearlings were female in 1979 (Fig. 1) and was estimated at 0.6 male to one female in 1979 (Table 1), although it was not significantly biased in both years (binomial test, $P = 0.219$ and 0.349, respectively). In contrast, it was male-biased in 1981 and 1982, when the male ratio was 2.5 and 1.2 times a total of female and sex-unknown ratio, respectively, although it was significantly biased as excluding sex-unknown ratio only in 1981 ($P < 0.05$; Table 1). Throughout the 7-year study period, the male-biased sex ratio was significant as excluding sex-unknown ratio ($P < 0.05$; Table 1).

Mortality rate of kids and female reproductive rate

The mortality rate of kids from 1979 to 1984 was 54.7% ($n = 86$), and the annual variation (27.3–88.9%) was significant (GLMM, $P < 0.001$; Table 1 and 3). The highest kid mortality rate (1983) was significantly different from all other rates except for the second highest rate (1980), and the rate in 1980 was significantly different from the two lowest rates (1979 and 1981) (Tukey's HSD; Table 1 and 4). The female reproductive rate considering the number of offspring surviving more than one year was 36.8% ($n = 106$).

Discussion

Adult females of the Japanese serow produce offspring almost every year in the study area. Even though some newborn kids may not have been found due to their early mortality, at least 81% of adult females were confirmed to produce offspring throughout the six years. At least four (57.1%) of the seven age-known females gave birth to a kid at three years of age, and all seven females were reproductive at four and five years of age. These results indicate that Japanese serows have the ability to breed every year from three or four years of age, and they may intermittently have 1-year or rarely 2-year interruptions in reproductive activity for reasons unknown. For example, aged females may have 2-year or more birth intervals due to reproductive senescence (Clutton-Brock et al. 1984; Bérubé et al. 1999; Côté and Festa-Bianchet 2001), and some females may miss the timing of insemination, possibly during mate changes, although the precise cause was not identified in the present study.

Recently, serows have been culled in six prefectures based on a "Specified Wildlife Management Plan", which is legally established by each prefectural office. In five of these prefectures, the pregnancy rates of culled female serows (more than three years of age) were investigated by anatomically checking an embryo in utero (Table 5). The average pregnancy rate was approximately 60% in each prefecture. Miura et al. (1987) also reported a fertility rate of 71.5% by measuring the annual horn growth increments in the Gifu and Nagano Prefectures. Compared with these rates, the fertility rates in the Akita study area were high (at least 81%). While the mean population density was also high (19.4/km^2) in the study area, it was 0.5–2.2/km^2 in each prefecture where serows were culled, although the counting methods differed between the study area and the prefectures (Table 5). Perhaps, in the study area, good nutritional conditions in clear-cut and newly planted areas directly increase the fertility rate as well as the population density.

Ochiai et al. (2010) reported that female reproductive rates with the number of surviving offspring over one

Table 5. Pregnancy rates of culled adult female serows in each prefecture

Prefecture	Pregnancy rate (%)[a]	Min–Max (%)	Period	Population density (n/km^2)[b]	Reference
Nagano	Ave. 61.1	43.3–73.0	1985–2017	Ave. 0.8 in 2018	Nagano Pre. (2018, 2020)
Gifu	Ca. 65	50.5–75.0	1982–2014	Ave. 1.3 in 2015	Gifu Pre. (2017)
	Ca. 50	Min. 40.7	2015–2020	Ave. 1.7 in 2020	Gifu Pre. (2022)
Aichi	Ave. 52.7	12.5–87.5	1989–2020	Ave. 0.9–1.6 in 2015	Aichi Pre. (2017, 2022)
Gunma	Ave. 63.3	50.0–83.3	2007–2014	Ave. 0.5–1.7 in 2006–2015	Gunma Pre. (2016)
Shizuoka	Ave. 59.6	46.3–84.6	2001–2015	Ave. 1.8 in 2020	Shizuoka Pre. (2022)

[a] by anatomical method of checking an embryo in utero.
[b] by methods of block counting and partially pellet group counting.

year were 37.0% in Shimokita, 26.9% in Asahi, and 12.0% in Kamikochi; the values in these three study areas were positively correlated with winter food availability and population density. In the Akita study area, the female reproductive rate (36.8%) and the annual mean population density (19.4/km^2) were similar to those in Shimokita (37.0% and 14.2/km^2, respectively), unlike the lower values in Asahi and Kamikochi, which may indicate that habitat conditions such as food supply were similar between Akita and Shimokita.

In the Gifu and Nagano Prefectures, the age at first reproduction of culled serows determined through anatomical checks of embryos was 2–6 years of age, and the mean age was 3.7 years (Miura and Tokida 1993). In the Gifu Prefecture, Kita et al. (1983) also stated that ovulation and pregnancy rates were approximately 10% and 1.5% in 1.5-year-old females, and about 30% and 23.1% in 2.5-year-old females, respectively. Miura et al. (1987) reported the age at first reproduction using the horn annuli method in the Gifu and Nagano Prefectures: 172 females, 14.5% at two years, 27.9% at three years, 39.4% at four years, and 18.0% at five years. In the Akita study area, the age at first reproduction of seven females was three (at least 57.1%) or four years (at most 42.9%). While no females gave birth at two years of age in the study area, the rate of first reproduction up to three years was higher than that in the other two prefectures, although the sample size was small.

While Miura and Tokida (1993) reported that the sex ratio of fetuses of pregnant females culled in Gifu and Nagano Prefectures between 1979 and 1992 was approximately 1:1 (294 males to 307 females), Miura (1998) also reported that the annual sex ratio in Gifu Prefecture was female-biased between 1980 and 1985 and male-biased between 1988 and 1993, and suggested that the sex ratio which was female-biased in good nutritional conditions with many clear-cut and newly planted forests became male-biased in the process of deteriorating nutritional conditions due to growth of the planted forests. In the Akita study area, the sex ratio of newborn kids excluding sex-unknown kids was significantly male-biased during the 7-year study period, although the annual ratio was significantly male-biased only in 1981. The male-biased sex ratio could have shown only a partial period of long-term changes of biased sex ratio as seen in Gifu Prefecture, although the reason for the male-biased ratio was unknown.

The annual mortality rates of kids significantly varied, probably because their mortality factors depended on the particular year. In 1983, the highest kid mortality rate (88.9%) was probably caused by record-setting heavy snow cover during winter from late 1983 to early 1984. In that winter, a sharp drop in the population density of the sika deer occurred on Kinkazan Island, which is nearly at the same latitude as the study area (Ito 1986; Takatsuki et al. 1994). In 1980, epidemic dermatitis caused by parapoxvirus, whose symptoms are severe for wild Japanese serows (Inoshima and Ishiguro 2010), spread to the study area, with a disease incidence rate of 22% (n = 63) compared to 0 to 6% (n = 51–79) in the other years (unpublished data). This was suspected to be the cause of the second highest mortality rate (63.6%), although some offspring survived the grave symptoms of the disease. However, the causes of death were not determined, except for one kid that accidentally died after falling over a steep road slope face in August 1982.

Recently, the population densities of Japanese serows have tended to decrease in and presumably even outside the serow conservation areas throughout Japan (Agency for Cultural Affairs 2013). While the serow population is widely and continuously distributed throughout the central and northern mountainous areas of Honshu, several local populations in the western part of Japan are generally isolated in limited ranges (Agency for Cultural

Affairs 2013). In particular, local populations in the Kyushu and Shikoku Islands and in the Kii and Suzuka Mountains are designated as endangered local populations in the Red List of Japan (Ministry of the Environment 2020). Results in the Akita study area and the prefectures culling serows show that fertility rates of female serows tend to be low in low density populations. According to the latest investigations, the mean population density was 0.3–1.4/km^2 in the serow conservation areas of western local populations including Kyushu, Shikoku, Kii, Suzuka, and Ibuki-Hira Mountains (Agency for Cultural Affairs 2013). Therefore, fertility rates of female serows are presumed to be low also in the red-listed local populations. In these areas, it is necessary to monitor fertility rates as well as population densities to take measures to avoid local extinction.

Acknowledgments: I would like to thank Dr. Takeo Kawamichi for his advice during the course of this field study, and Prof. Shigeyuki Izumiyama for providing the opportunity to write papers with the reorganization of previous data at the Mountain Science Research Institute of Shinshu University. I also would like to thank anonymous reviewers for constructive comments to improve the manuscript.

References

Agency for Cultural Affairs. 2013. Management of the Japanese Serow as a Special Natural Monument and Its Conservation Areas. Monument and Sites Division, Cultural Properties Department, Agency for Cultural Affairs, Tokyo, 130 pp. (in Japanese).

Aichi Prefecture. 2017. Class II Specified Wildlife Management Plan (the Japanese Serow Management Plan for the 5th Term). Natural Environment Division, Environment Policy Department, Environment Bureau, Aichi Prefecture, Nagoya, Text 24 pp. + Appendix 16 pp. (in Japanese).

Aichi Prefecture. 2022. Class II Specified Wildlife Management Plan (the Japanese Serow Management Plan for the 6th Term). Natural Environment Division, Environment Policy Department, Environment Bureau, Aichi Prefecture, Nagoya, Text 29 pp. + Appendix 26 pp. (in Japanese).

Bérubé, C. H., Festa-Bianchet, M. and Jorgenson, J. T. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology 80: 2555–2565.

Clutton-Brock, T. H., Albon, S. D. and Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308: 358–360.

Côté, S. D. and Festa-Bianchet, M. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62: 173–181.

Forest Technology Association. 1979. The Japanese Serow – Research Report of Habitats. Nagano Regional Forest Office, Nagano, 219 pp. (in Japanese).

Gifu Prefecture. 2017. Class II Specific Wildlife Management Plan (the Japanese Serow) for the 2nd Term. Gifu Prefecture, Gifu, 27 pp. (in Japanese).

Gifu Prefecture. 2022. Class II Specific Wildlife Management Plan (the Japanese Serow) for the 3rd Term. Gifu Prefecture, Gifu, 30 pp. (in Japanese).

Gunma Prefecture. 2016. Gunma Proper Management Plan for the Japanese Serow (Class II Specified Wildlife Management Plan for the 3rd Term). Gunma Prefecture, Maebashi, 46 pp. (in Japanese).

Inoshima, Y. and Ishiguro, N. 2010. Molecular and biological characterization of vascular endothelial growth factor of parapoxviruses isolated from wild Japanese serows (*Capricornis crispus*). Veterinary Microbiology 140: 63–71.

Ito, T. 1986. Population trend of sika deer on Kinkazan Island. Honyurui Kagaku (Mammalian Science) 53: 29–31 (in Japanese with English abstract).

Kishimoto, R. 1987. Family break-up in Japanese serow, *Capricornis crispus*. In (Soma, H., ed.) The Biology and Management of *Capricornis* and Related Mountain Antelopes, pp. 104–109. Croom Helm, London.

Kishimoto, R. 1988. Age and sex determination of the Japanese serow *Capricornis crispus* in the field. Journal of the Mammalogical Society of Japan 13: 51–58.

Kishimoto, R. 1989. Early mother and kid behavior of a typical "follower", Japanese serow *Capricornis crispus*. Mammalia 53: 165–176.

Kishimoto, R. 1994. Social organization of the Japanese serow and its forest damage problems. Shinrin Kagaku (Journal of Forest Research) 11: 26–32 (in Japanese).

Kishimoto, R. and Kawamichi, T. 1996. Territoriality and monogamous pairs in a solitary ungulate, the Japanese serow, *Capricornis crispus*. Animal Behaviour 52: 673–682.

Kita, I., Sugimura, M., Suzuki, Y. and Tiba, T. 1983. Reproduction of female Japanese serows, *Capricornis crispus*, based on pregnancy and macroscopical ovarian findings. Research Bulletin of the Faculty College of Agriculture Gifu University 48: 137–146 (in Japanese with English abstract).

Kuznetsova, S., Brockhoff, P. B. and Christense, R. H. B. 2017. *lmerTest* package: tests in linear mixed effects models. Journal of Statistical Software 82: 1–26.

Ministry of the Environment. 2020. Red Data Book / Red List. Available at https://www.env.go.jp/content/900515981.pdf (Accessed 18 Jan 2023).

Miura, M. 1985. Horn and cementum annulation as age criteria in Japanese serow. Journal of Wildlife Management 49: 152–156.

Miura, S. 1998. Behavior and Social Organization of the Mammals (Biology of the Mammals 4). University of Tokyo Press, Tokyo, 156 pp. (in Japanese).

Miura, S., Kita, I. and Sugimura, M. 1987. Horn growth and reproductive history in female Japanese serow. Journal of Mammalogy 68: 826–836.

Miura, S. and Tokida, K. 1993. A review of management techniques for Japanese serow (*Capricornis crispus*) population. Journal of the Mammalogical Society of Japan 32: 149–157 (in Japanese).

Nagano Prefecture. 2018. Monitoring Report 2017 of Culled Samples in a Special Natural Monument, the Japanese Serow. Nagano Prefecture, Nagano, 23 pp. (in Japanese).

Nagano Prefecture. 2020. Class II Specific Wildlife Management Plan (for the 5th Term of the Japanese Serow). Nagano Prefecture, Nagano, 62 pp. (in Japanese).

Ochiai, K. 1983a. Pair-bond and mother-offspring relationships of Japanese serow in Kusoudomari, Wakinosawa Village. Journal of the Mammalogical Society of Japan 9: 192–203 (in Japanese with English abstract).

Ochiai, K. 1983b. Territorial behavior of the Japanese serow in Kusoudomari, Wakinosawa Village. Journal of Mammalogical Society of Japan 9: 253–259 (in Japanese with English abstract).

Ochiai, K. 1996. Effects of forest management on Japanese serow populations – in relation to habitat conservation for serows. Journal of the Mammalogical Society of Japan 36: 79–87 (in Japanese).

Ochiai, K. 2016. The Japanese Serow: Behavior and Ecology of a Solitary Ungulate. University of Tokyo Press, Tokyo, 276 pp. (in Japanese).

Ochiai, K., Nakama, S., Hanawa, S. and Amagasa, T. 1993a. Population dynamics of Japanese serow in relation to social organization and habitat conditions. I. Stability of Japanese serow density in stable habitat conditions. Ecological Research 8: 11–18.

Ochiai, K., Nakama, S., Hanawa, S. and Amagasa, T. 1993b. Population dynamics of Japanese serow in relation to social organization and habitat conditions. II. Effects of clear-cutting and planted tree growth on Japanese serow populations. Ecological Research 8: 19–25.

Ochiai, K. and Susaki, K. 2002. Effects of territoriality on population density in the Japanese serow (*Capricornis crispus*). Journal of Mammalogy 83: 964–972.

Ochiai, K. and Susaki, K. 2007. Causes of natal dispersal in a monogamous ungulate, the Japanese serow, *Capricornis crispus*. Animal Behaviour 73: 125–131.

Ochiai, K., Susaki, K., Mochizuki, T., Okasaka, Y. and Yamada, Y. 2010. Relationships among habitat quality, home range size, reproductive performance and population density: comparison of three populations of the Japanese serow (*Capricornis crispus*). Mammal Study 35: 265–276.

R Core Team. 2023. R: A language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at www.R-project.org/ (Accessed 16 May 2023).

Shizuoka Prefecture. 2022. Class II Specific Wildlife Management Plan (for the 6th Term of the Japanese Serow). Shizuoka Prefecture, Shizuoka, 31 pp. (in Japanese).

Sugimura, M., Suzuki, Y., Kamiya, S. and Fujita, T. 1981. Reproduction and prenatal growth in the wild Japanese serow, *Capricornis crispus*. Japanese Journal of Veterinary Science 43: 553–555.

Takatsuki, S., Suzuki, K. and Suzuki, I. 1994. A mass-mortality of Sika deer on Kinkazan Island, northern Japan. Ecological Research 9: 215–223.

Tiba, T., Sato, M., Hirano, T., Kita, I., Sugimura, M. and Suzuki, Y. 1988. An annual rhythm in reproductive activities and sexual maturation in male Japanese serows (*Capricornis crispus*). Zeitschrift für Säugetierkunde 53: 178–187.

Tokida, K. 2007. A Report on the Public Symposium Part 2 “The present status of and perspectives on the Specified Wildlife Conservation and Management Plans” at the annual meeting of the Mammalogical Society of Japan (2006): Improvement in Japanese serow management over the last twenty-five years. Journal of the Mammalogical Society of Japan 47: 139–142 (in Japanese).

Tokida, K. 2020. *Capricornis crispus*. The IUCN Red List of Threatened Species 2020: e.T3811A22151909. https://www.iucnredlist.org/species/3811/22151909 (Accessed 18 January 2023).

Received 9 February 2023. Accepted 27 November 2023.
Editor was Hayato Iijima.