

Evaluation of the effect of culling on browse damage by the Japanese serow in Gifu Prefecture, Japan

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Abstract: The Japanese serow (*Capricornis crispus*; serow) is a protected territorial ungulate native to Japan. However, locally overabundant serow populations can damage forest plantations and agriculture through browsing. Despite government permitted annual culling of serows on forest lands of Gifu Prefecture, Japan, browse damage continues to be reported in hinoki cypress (*Chamaecyparis obtusa*; cypress) plantations. Sika deer (*Cervus nippon*; deer), which are co-located with serows can also browse cypress, but their impacts have never been evaluated. The objective of our research was to evaluate the involvement of each species in browse damage and to establish the damage-causing mechanisms after serow culling at selected study sites (T1 [0.3 ha], T2 [0.2 ha], and T3 [1.1 ha]) in 3 cypress plantations in Takayama City, Gifu Prefecture, where serow culling was conducted. In 2019 and 2020, 2 and 2 serows were culled in T1, 3 and 0 in T2, and 1 and 1 in T3, respectively. Forestry workers also applied a chemical repellent (ziram-based fungicide) to some stands in T3 in October 2019 and May 2020. Between December 2018 and September 2020, we used camera traps to monitor activity patterns of serows and deer and the replacement of territorial serows before and after culling. We also investigated seasonal browsing impacts between August 2019 and June 2020 by thoroughly checking for browsing marks on the terminal shoot. Serows and deer accounted for 79% and 21% of camera-trap videos, respectively. Despite annual culling, serows were recorded at all browsed sites before the next growing season. Browse damage was higher in autumn and winter, but in T3 it was reduced when the repellent was applied. Management of ungulate browse damage to cypress will require accurate identification of species causing the damage, monitoring serow activity before and after culling, and a using repellent immediately before browsing seasons.

Key words: browse damage, *Capricornis crispus*, *Cervus nippon*, *Chamaecyparis obtusa*, culling, hinoki cypress, Japan, Japanese serow, repellents, sika deer

The Japanese serow (*Capricornis crispus*; serow) is an endemic solitary-dwelling ungulate that inhabits the forests of Honshu, Shikoku, and Kyushu in Japan (Figure 1). Adults of both sexes have intrasexually exclusive territories of approximately 10 to several dozen ha (Ochiai 2015, 2016). Serows are generally monogamous and occasionally polygynous; mating pairs and their offspring overlap their home ranges (Ochiai 1993). The offspring disperse from their natal areas and establish their own territories at 2–4 years of age (Ochiai 1993).

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Figure 1. Japanese serow (*Capricornis crispus*) in Gifu Prefecture, Japan (photo courtesy of N. Kuninaga).

The serow is a browser that feeds primarily on the leaves and twigs of deciduous broad-leaved trees (Ochiai 1999) but occasionally consumes conifers, evergreen broad-leaved shrubs, and dwarf bamboos (*Sasa* spp.; Takatsuki et al. 1995, Jiang et al. 2008). Due to its food habits, serows are often considered nuisance animals responsible for forestry and agricultural damage.

The serow was designated as a special natural monument of Japan by the Agency for Cultural Affairs in 1955 (Agency for Cultural Affairs 2020) and has been protected ever since. Expansive afforestation during the mid-1950s to early 1970s provided serows with new food resources, resulting in increased serow populations and browse damage reported by forest hinoki cypress (*Chamaecyparis obtusa*; cypress) plantation owners (Tokida 2019).

In 1979, to address the complaints of forest owners, the Japanese government implemented a serow management program that included culling, despite opposition from some stakeholders to the lethal control of a special natural monument (Tokida 2019). The government also established serow conservation areas in mountainous regions where culling was not permitted. Serow hunting was not permitted in any area.

Although the area of browsed land is decreasing due to recent reductions in newly afforested areas, the culling of serows, targeted at removing individuals causing damage, continues in browsed land located in 6 prefectures. Annual culling has been conducted for >40 years in Gifu Prefecture, Japan, where it first began. Despite serow culling measures, damage to plantation areas continues to occur.

Evaluating management intervention is criti-

cal to the adaptive management process to determine whether an intervention has achieved the desired result (Organ et al. 2012). Post-evaluation of the effect of predator and disease management programs is routinely completed (Wolfe et al. 2018, Porteus et al. 2019). However, the effectiveness of culling serows to prevent browse damage has not been scientifically evaluated.

Accurate identification of the species responsible for causing damage is important for implementing appropriate management strategies (Messmer 2000, Humberg et al. 2007). If serows and sika deer (*Cervus nippon*; deer) were sympatrically distributed, it would be difficult to identify the species responsible for the damage only from browsing marks or other field signs (e.g., fecal pellets), as these signs are similar in both species (Aikawa 2018). Although deer have been shown to cause severe browse damage to forestry (Takatsuki 2009), evidence regarding whether deer activity is related to the damage in forest plantations where the serow has been identified as the pest species is insufficient.

Theoretically, removing territorial serows from browsed land would be a direct solution for reducing browse damage because serows form territories and inhabit them in low-density populations. However, because browse damage continues to occur after culling operations, it is important to identify the factors contributing to the damage to propose effective control measures. To better inform this management discussion, we conducted a pilot study to elucidate the ecology of serows and deer at the browsed sites and evaluate the effectiveness of serow culling and the subsequent use of a repellent to mitigate browse damage. Specifically, we focused on the ungulate frequency of appearance at browsed study sites, species diel activity patterns, temporal overlap of serows and deer with human activities, and serow presence before and after culling. We also investigated seasonal variations and factors associated with browsing. We provide recommendations to improve the efficacy of serow culling programs and methods to reduce damage.

Study area

We conducted our study between 2018 and 2020 on 3 cypress plantations in Takayama City, northern Gifu Prefecture, central Honshu, Japan (Figure 2; Table 1). The plantations were

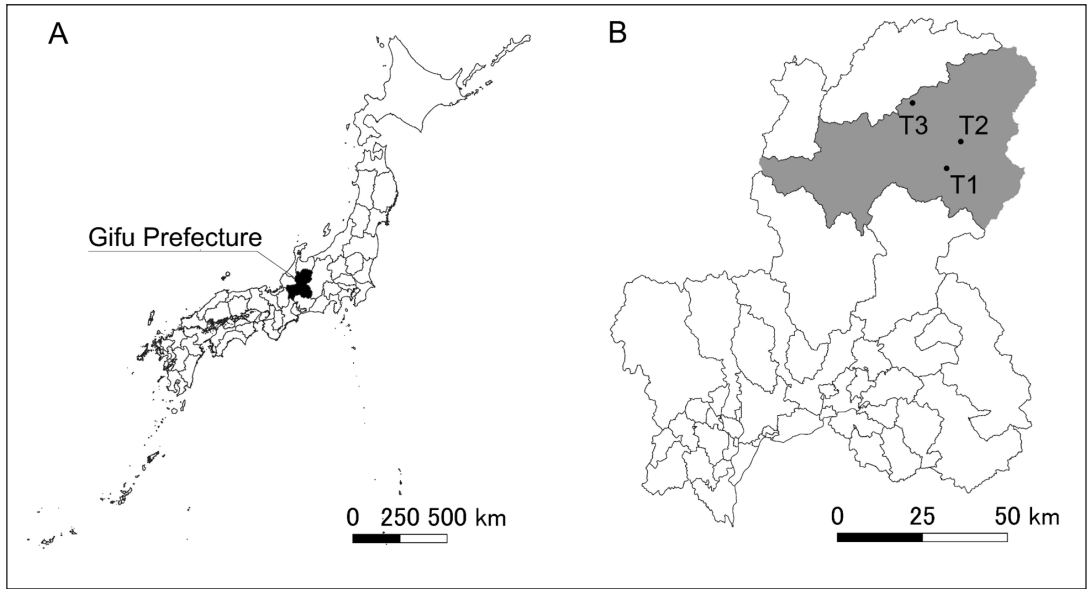


Figure 2. (A) Location of Gifu Prefecture, and (B) location of 3 study sites (T1, T2, and T3) in Takayama City (gray shaded area), Gifu Prefecture, Japan, 2018–2020.

Table 1. Overview of the study sites in a hinoki cypress (*Chamaecyparis obtusa*) plantation located in Takayama City, Gifu Prefecture, Japan.

Site	Planted year	Height of saplings (cm)	Elevation (m)	Area of investigation (ha)	Camera-trap survey	Browse damage survey	
					No. of cameras	No. of saplings monitored	Survey dates
T1	2015	24–115	850	0.3	3	94–108	Aug. 22 and Oct. 31, 2019; Jan. 9, Mar. 17, and Jun. 2, 2020
T2	2017	17–92	1,130	0.2	2	88–104	Aug. 21 and Nov. 1, 2019; Jan. 9, Mar. 18, and Jun. 2, 2020
T3	2015	30–220	910	1.1	3	178–182	Aug. 21 and Nov. 1, 2019; Jan. 10, Mar. 18, and Jun. 3, 2020

created after clear-cutting sloping forest. Within each plantation, we selected 3 study sites (T1, T2, and T3). Cypress saplings were planted in 2015 (T1 and T3) and 2017 (T2). The study sites were 0.3 ha (T1), 0.2 ha (T2), and 1.1 ha (T3) in size and situated at elevations of 850 m (T1), 1,130 m (T2), and 910 m (T3), respectively, above sea level. Browsing by serows was previously reported at these sites (Figure 3). The plantations were surrounded by natural forests consisting of broad-leaved deciduous trees such

as Japanese oak (*Quercus crispula*) or Japanese beech (*Fagus crenata*), or coniferous plantations consisting of Japanese cedar (*Cryptomeria japonica*) and cypress. The mean annual precipitation and temperature in Takayama City are 1,699.5 mm and 11.0°C, respectively (Gifu Local Meteorological Office 2020). Forested land (200,500 ha) occupies almost 92% of the Takayama City area (217,800 ha), of which plantations occupy 37% (74,200 ha; Gifu Prefecture 2018b). Broad-leaved and coniferous forest, including planta-



Figure 3. Browsing mark on the terminal shoot of hinoki cypress (*Chamaecyparis obtusa*) in site T3 in Takayama City, Gifu Prefecture, Japan (photo courtesy of S. Ikushima).

tions, cover 42% (84,600 ha) and 50% (99,300 ha) of the total forested area, respectively.

The culling of serows requires permission from both the Agency for Cultural Affairs, Government of Japan and the prefectural government. The culling program was performed within the framework of the Specified Wildlife Conservation and Management Plan (Gifu Prefecture 2017), which is implemented in wildlife management in each prefectural unit. The Gifu Prefectural Government oversees the entire culling program in Gifu Prefecture. The Specified Wildlife Conservation and Management Plan of Gifu Prefecture states that the goal of the culling program is to reduce damage to an acceptable level in each browsed plantation while sustaining a stable serow population.

Each municipality performs culling under the supervision of the Gifu Prefectural Government. The amount of browse damage is investigated in spring by a municipal officer or landowner, and the number of serows that can be culled during the following winter is determined based on this result. Local people provide information on serow sightings around the browsed land. The culling is completed by private hunters and is only allowed within 10–150 ha of the browsed plantation: the “culling area.” Culling area size is based on the browsed area, and the number of animals that can be culled differs according to the culling area extent (<50 ha: 1 serow; ≥50 ha and <100 ha: 2 serows; and ≥100 ha: 3 serows).

We verified the culling dates and age of serows culled at each study site using administrative documents provided by the Gifu Prefectural Government. During the camera-trap survey period, culling was performed in the winters of 2019 (including December 2018) and 2020 (Table 2).

Methods

Camera-trapping

Depending on the size of each study site, we deployed 2 (T2) or 3 (T1 and T3) infrared-triggered cameras (Ltl Acorn 6210MC; LTL Acorn Outdoors, Green Bay, Wisconsin, USA) for a camera-trap survey between December 7, 2018, and September 5, 2020. We attached the cameras to a tree at the height of 1.2–1.5 m above the ground using a mounting strap and oriented it toward the planted area (Figure 4). The cameras were set to be active for 24 hours per day to ensure the motion sensor triggered immediately when any movement was detected. We programmed the cameras to record a video for 15 seconds with an interval of 1 second. We checked the cameras once every 2 months to replace SD cards and batteries.

The cameras recorded the date and time in all videos captured. Using these data, we identified serows, deer, and humans and recorded the number of serows and deer in each video. All videos were used for evaluating diel activity patterns following Ikeda et al. (2016).

For other analyses, following Watts et al. (2008) and Yamashiro et al. (2019), we defined videos of the same species (serows and deer) at a site as 2 independent events if separated by >60 minutes to avoid overestimation of species abundance by double counting. We used the maximum number of individuals in each independent event for the analyses. The total number of serows and deer captured by the cameras were reported for each site. We calculated the abundance indices of serows and deer between November 1 (October 31 in T1) and January 9 (January 10 in T3) for each site, for logistic-regression analysis, as the total number of animals divided by the sampling effort (the total number of camera-trap-nights at each site).

Damage assessment

We assessed browse damage once every 2–3 months between August 2019 and June 2020. We completed 5 surveys at each site (August, November [October in T1], January, March, and June; Table 1).

In Takayama, the spring-growth flush of cypress, when the shoots begin to elongate, occurs from spring to summer. As the trees were planted linearly traversing the slope, we selected several planted lanes from the top to the

Table 2. The last date of appearance before culling, date of culling (A), first date of appearance after the last culling (B), and length of period between date of culling (A) and first date of appearance after the last culling (B) of Japanese serow (*Capricornis crispus*) in 3 study sites in Takayama City, Gifu Prefecture, Japan, during winter 2019 (include December 2018) and 2020.

Year	Site	Last date of appearance before culling	Date of culling (A)*	First date of appearance after the last culling (B)	Length of period between A*** and B (days)
2019	T1	No appearance at site	Dec. 16, 2018 and Jan. 2, 2019	Apr. 7, 2019	95
2019	T2	Dec. 16, 2018	Dec. 22, 2018** and Jan. 2, 2019	Mar. 25, 2019	82
2019	T3	Dec. 26, 2018	Jan. 13, 2019	Feb. 22, 2019	40
2020	T1	Jan. 1, 2020	Jan 11. and Feb. 5, 2020	Feb. 7, 2020	2
2020	T2		Culling not conducted		
2020	T3	Jan. 9, 2020	Jan. 12, 2020	Jan. 25, 2020	13

* The number of culled serow per day was 1 unless annotation was added.

** Culled 2 animals.

*** The latter date if culling was conducted twice.



Figure 4. Camera trapping in site T2 in Takayama City, Gifu Prefecture, Japan, 2018–2020. Left: distant view (white arrow). Right: close-up view of the camera attachment (photos courtesy of N. Kuninaga).

bottom of the slope at regular intervals for damage assessment. At the start of the survey, we monitored 108 (T1), 104 (T2), and 182 (T3) cypress saplings, respectively. We measured the tree height at the time of shoot elongation and tagged each sapling with a number for individual identification. Browsing on the terminal shoot is a better indicator of damage than feed-

ing on the lateral shoot because repeated annual browsing of the terminal shoot causes stunted trees or distorts growth (Nolte and Dykzeul 2000). Therefore, we recorded the presence of browsing marks on terminal shoots. We then calculated the percentages of newly browsed stands for each survey. We did not count the damage assumed to be caused by the Japanese

hare (*Lepus brachyurus*), which showed clean-angled clipping. We also excluded trees with no value, which had died or been cut accidentally during weeding.

Forestry workers applied a ziram-based fungicide chemical repellent, which has irritant properties and deters browsing, to some of the stands in T3. Of the 178 stands in T3, 143 stands were treated with the repellent on October 27, 2019. A second treatment with the repellent was performed on 171 of the 178 stands on May 11 and 12, 2020.

Data analysis

Using pooled data from all study sites, we analyzed the activity patterns of serows, deer, and humans by kernel density estimation using von Mises distribution (Ridout and Linkie 2009). The clock time was converted to the sunrise time (or sunset time if it was a night record) of a specific day to mitigate the differences in activity patterns across site or time period (Nouvellet et al. 2011), and sunrise and sunset were adjusted to $\pi/2$ and $3\pi/2$ in radians, respectively. In executing the conversion process, we determined the sunrise and sunset times based on dates and coordinates. The degree of agreement of kernel density curves was calculated in 2 pairs: serows and humans, and deer and humans. We estimated the coefficient of overlapping (\overline{OVL}_4), which ranged from 0 (no overlap) to 1 (identical activity patterns; Schmid and Schmidt 2006). We calculated the 95% confidence intervals (CI) using a smoothed bootstrap of 10,000 resamples.

Following the criterion of Gómez et al. (2005), we classified serows and deer as diurnal (<10% of observations at night), mostly diurnal (between 10% and 30% of observations at night), mostly nocturnal (between 70% and 90% of observations at night), nocturnal (>90% of observations at night), and crepuscular if >50% of activity was observed during twilight (1 hour before and after sunset or sunrise). The remaining cases were considered cathemeral.

Following the conventional method used in field observation (Sakurai 1981, Kishimoto and Kawamichi 1996), we identified the serows photographed at each study site based on variations in natural features such as horn shape, facial or body scars, facial patterns, and body colors. The camera traps also allowed for

the individual identification of serows based on these features (Yasuda 2015, Faiznur et al. 2020). However, we did not use the videos that were recorded at night unless the distinguishing features of an individual (e.g., horn deficiency) were clearly detected. Furthermore, we also excluded the data from analysis if the images lacked sharpness, the serow was far from the camera, and no characteristic features of an animal were displayed.

For the serows that were identified, we reported their presence before and after culling at each site. No serows were photographed in T1 before the culling in 2019; therefore, we only examined that site for the culling in 2020. In T2, the composition of serows was only analyzed for the culling of 2019 because culling was not performed in 2020. In T3, we conducted the analysis for both years. As 0- or 1-year-old kids usually follow their mothers (Ochiai 1993), an adult–kid pair was considered to be a mother and her offspring.

We prepared a multivariable logistic-regression model to estimate the factors associated with browsing on terminal shoots (response variable), including the explanatory variables of sapling height (cm), abundance index of serow and deer, application of chemical repellent (presence or absence), and distance from forest edge (m). The selection of explanatory variables was based on existing knowledge of factors associated with the browsing incidence of deer (Williamson and Hirth 1985, Okamoto et al. 2008, Ward and Williams 2010, Enoki et al. 2016). Considering the maximum duration of the effectiveness of the repellent (approximately 3–6 months; Nagano Prefecture Forestry Research Center 1993, Koizumi 2003), we used the January browsing data for logistic-regression analysis, because November (October in T1) to January was the only period throughout which the repellent was working. Multicollinearity was assessed using the variance inflation factor (VIF; Zuur et al. 2010), and we removed the explanatory variable of deer due to $VIF \geq 3$ between serow and deer. Then, we selected the minimum adequate model ($\Delta AIC \leq 2$) using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We conducted all statistical analyses using R 3.6.1 (R Development Core Team 2018) with the "overlap" package (Ridout and Linkie 2009) for analyzing the diel activity patterns.

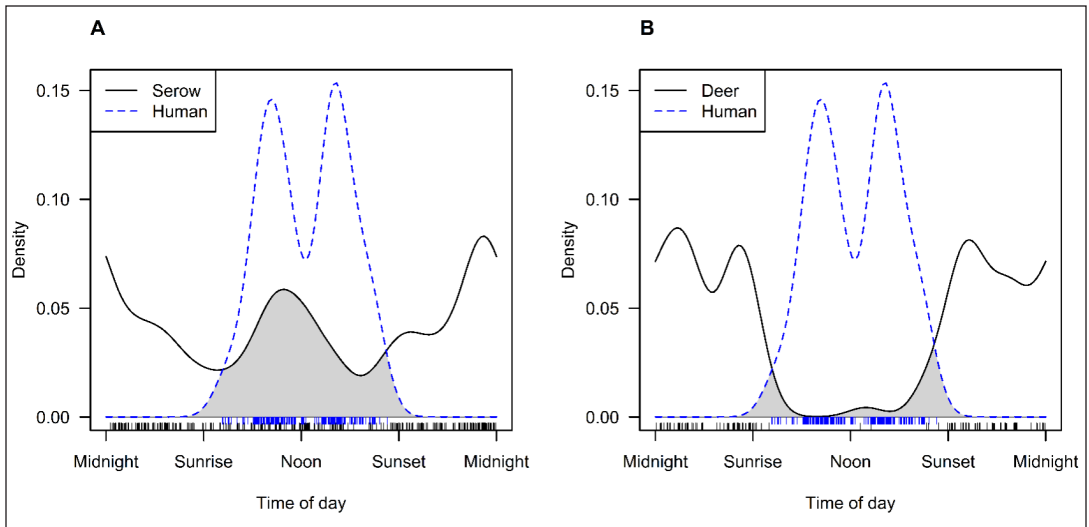


Figure 5. Diel activity patterns of (A) Japanese serow (*Capricornis crispus*) and (B) sika deer (*Cervus nippon*) and temporal overlap with human activity in 3 hinoki cypress (*Chamaecyparis obtusa*) plantation study sites in Takayama City, Gifu Prefecture, Japan, from December 2018 to September 2020. Solid lines (A: Japanese serow; B: sika deer) and the dashed line (humans) indicate kernel density estimates. The overlap area is shown in gray. The rugs in the upper (humans) and lower (A: Japanese serow; B: sika deer) rows are daily video records.

Results

Species activity pattern

We obtained 436, 174, and 337 videos of serows, deer, and humans over 4,887 trap nights, respectively. Serows and deer accounted for 79% (262 serows) and 21% (69 deer) of captured images, respectively, throughout the study period. The percentage of deer differed by study site: 35% (120 serows and 64 deer) in T1, 9% (32 serows and 3 deer) in T2, and 2% (110 serows and 2 deer) in T3. The mean group size per independent event was 1.1 in both species.

Serows were cathemeral (58% in the night-time and 12% in the twilight-time observations) with a bimodal type of activity in the late morning and before midnight (Figure 5A). On the other hand, deer exhibited nocturnal activity patterns (91% in the night-time and 26% in the twilight-time observations; Figure 5B). Humans were only observed in the study sites during the diurnal period (no observation in the night-time). The (\overline{OVL}_4) of serow and deer with humans were 0.38 (CI = 0.330.42) and 0.065 (CI = 0.0280.11), respectively.

Serow appearance patterns relative to culling

Cameras captured images of adult serows 2 days (shortest period) and 95 days (longest peri-

od) after culling (Table 2). In 2019 and 2020, 2 and 2 serows were culled in T1, 3 and 0 in T2, and 1 and 1 in T3, respectively; all of them were adults.

Serow presence at study sites consisted of multiple individuals, not singles (Table 3). There were 8, 3, and 7 serows identified at site T1, T2, and T3, respectively. In T1, 4 serows (numbers 2, 3, 5, and 7) were identical before and after the cull of 2020, indicating that they escaped culling. On the other hand, serow numbers 1, 4, and 8 were never photographed after the 2020 cull. Serow number 6 was detected after the 2020 cull. In T2, serow number 9, who was identified before the cull of 2019, was never subsequently photographed. Cameras captured images of serow number 10 on a long-term basis from March 2019 to August 2020. In T3, 1 serow (number 17) was only photographed once before the cull of 2019. Four serows (numbers 12, 13, 14, and 18; numbers 13 and 18 were adult female and offspring) were identified in the period between the culling events of each year. However, they were not re-sighted after the cull of 2020; 2 newcomers (numbers 15 and 16) were detected instead.

Seasonal variations and factors associated with browsing

The seasonal variations in the browsing rate were similar among study sites. The percentages

Table 3. Identification of Japanese serows (*Capricornis crispus*) photographed at 3 study sites in Takayama City, Gifu Prefecture, Japan, from December 2018 to September 2020. S = the months when serows were photographed. C = the months when culling was conducted.

Site	Serow no.	Adult/offspring	2019												2020											
			Dec. (C)	Jan. (C)	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan. (C)	Feb. (C)	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.		
T1	1	Adult								S	S															
	2	Adult								S	S											S	S			
	3	Adult									S												S			
	4	Adult										S														
	5	Adult											S*	S*												
	6	Adult																						S		
	7	Adult										S												S		
	8	Offspring																						S		
T2	9	Adult																								
	10	Adult												S	S									S	S	
	11	Adult																						S		
T3	12	Adult																								
	13**	Adult																								
	14	Adult																								
	15	Adult																								
	16	Adult																						S	S	
	17	Offspring																							S	
	18***	Offspring																							S	

* Serow was photographed after the cull event of this month.
 ** Serow was photographed before the cull event of this month.
 *** Mother and offspring.

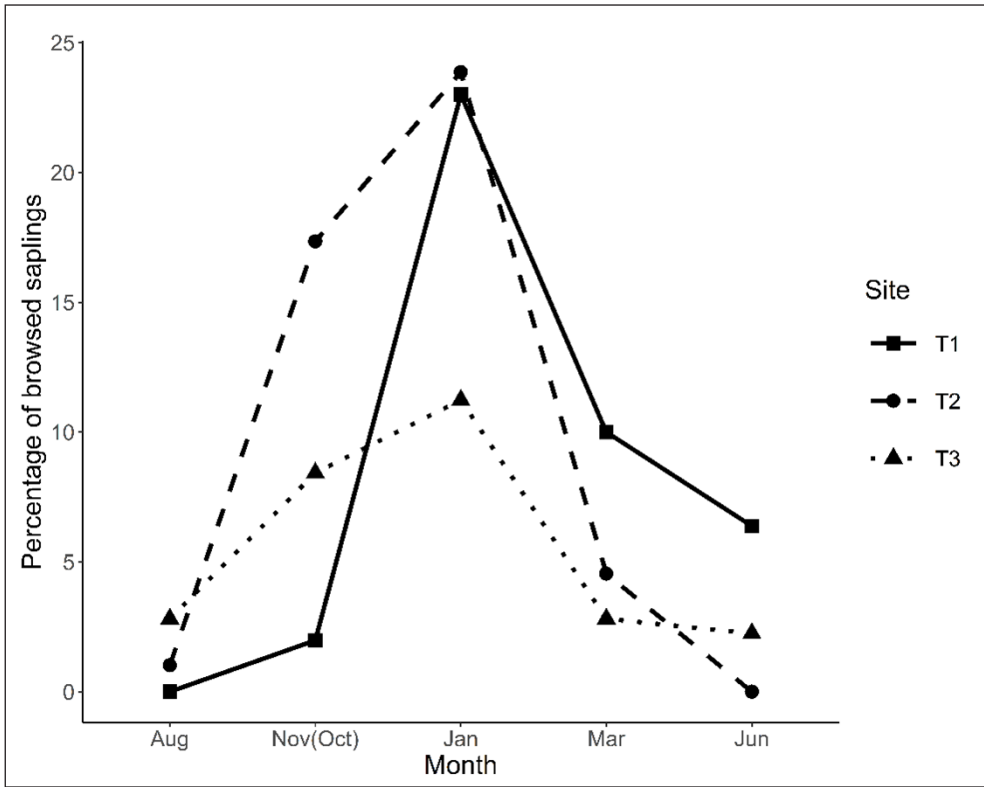


Figure 6. Seasonal variation in the browsing rate on terminal shoots of hinoki cypress (*Chamaecyparis obtusa*) in 3 study sites in Takayama City, Gifu Prefecture, Japan, from August 2019 to June 2020. The percentage of newly browsed saplings was calculated for each survey occasion (August, November [October in T1], January, March, and June). The filled squares with a solid line, filled circles with a dashed line, and filled triangles with a dotted line represent the T1, T2, and T3 study sites, respectively.

Table 4. Model structure, degrees of freedom (df), log likelihood (logLik), Akaike's Information Criterion (AIC) values, Δ AIC values, and Akaike weight for the final logistic-regression models (Δ AIC ≤ 2) assessing the application of chemical repellent (repellent), the height of sapling (height), abundance index of Japanese serow (*Capricornis crispus*; serow), and distance from forest edge (distance) data on the probability of browsing in 3 study sites in Takayama City, Gifu Prefecture, Japan, from November (October in study site T1) 2019 to January 2020.

Model structure	df	logLik	AIC	Δ AIC	Akaike weight
Repellent + height	3	-158.67	323.33	0	0.264
Repellent	2	-159.69	323.37	0.04	0.259
Repellent + distance	3	-159.62	325.23	1.90	0.102
Repellent + height + serow	4	-158.65	325.29	1.96	0.099
Repellent + height + distance	4	-158.67	325.33	2.0	0.097

of saplings newly browsed ranged from 0–3% in August, increased to 11–24% by January, and declined to 0–6% in June (Figure 6). Browsing occurred mostly from autumn to winter.

Five models were selected as the final models (Δ AIC ≤ 2 ; Table 4). In the most parsimonious

model, browsing incidence was explained only by repellent application (repellent: $\hat{\beta} = -1.28$, CI = -1.66 to 0.90, $P < 0.001$; height: $\hat{\beta} = -0.0078$, CI = -0.013 to -0.0022, $P = 0.17$). The odds ratio of browsing when repellent was present compared to that when absent was 0.28 (CI = 0.19 to 0.41).

Discussion

Species damage

Although primarily serows were believed to damage saplings, serows and deer occurred sympatrically at browsed sites. This suggests that deer could also be responsible for the observed browse damage. Japanese farmers, when asked to identify browse damage based on field signs, misidentified serows and deer with considerable frequency (Sugawara and Seki 2015). Human perceptions of vertebrate pest species may be biased depending on the visual impact of damage such as destroying and scattering plants (Can-Hernández et al. 2019) or high visibility of species due to large body size, gregariousness, and diurnal activity pattern (Gabrey et al. 1993). However, in this study, serows and deer had similar body sizes and field signs as well as the same mean group sizes. Thus, the higher degree of temporal overlap of activity patterns (frequency of encounter) with humans would explain the perceptions of the serow as the dominant pest species.

Deer were recorded less frequently than serows in this study. This also may explain why humans did not recognize the deer as a potential pest species. Deer distribution and their subsequent browsing on the forest ecosystem only started to expand northward of Gifu Prefecture over the last 10–15 years (Tsunoda et al. 2017). Additionally, sighting per unit effort by hunters, which is the deer density indicator used, was low around the study sites (Gifu Prefecture 2018a, 2021). Considering these factors, local communities would be less likely to perceive the presence of the deer. Furthermore, the annual serow culling program may have convinced people that the serow, and not deer, was a pest species.

The accurate identification of pest species causing damage requires rigorous evidence (Messmer 2000). For instance, the molecular biological diagnostic method for discriminating between serows and deer is applicable for environmental DNA remaining on the browsing mark (Nichols et al. 2012) or in feces on the ground (Aikawa et al. 2015). The contribution of each species to browse damage can be better understood through the analysis of food habits using fecal pellets after identifying the species from which the pellets originated, or by determining how much cypress foliage was

consumed based on gut analysis (Wardlaw and Burton 2008).

In the areas sympatrically inhabited by serows and deer, the people involved in the culling program may have been misidentifying the culprit species and culling serows, which were not responsible for all the damage. Therefore, the culling protocol should be modified to include mandatory camera trapping or DNA analysis to ensure the accurate identification of the culprit species before culling begins.

Effect of culling

After the culling of territorial serows, other adults appeared at the study sites within a short period, the longest time being before the spring growth flush of cypress. This suggests that serows can browse shoots throughout the growing season even though culling was conducted. Indeed, browse damage to terminal shoots had occurred in the growing season after the cull of 2019 (Figure 6). During the damage assessment period, 0 and 1 deer were photographed at T2 and T3, respectively, indicating that serows caused almost all of the damage that occurred in these plantations.

Our findings showed that there were 2 patterns in the composition of territory holders before and after culling. The first pattern was that some animals were not culled and continued to inhabit the browsed sites. This was true in T1 because some individually identified serows were photographically captured before and after culling. Although some serows identified before culling were not detected after culling, serows likely escaped culling in T3 because the single culled animal was an adult in 2019, indicating that the offspring identified before the 2019 cull was not culled, and the number of culled serows was lower than the number of serows identified before culling in 2020. In other words, the number of animals that disappeared after culling was greater than the number of animals culled. Territorial serows naturally disappear in serow society (e.g., death or change of territory), and this could explain the non-detection of identified serows after culling. Furthermore, because identification by camera traps is challenging, especially at night, the apparent disappearance of individuals could also be attributed to failure in identification.

The second pattern was that individuals at

a browsed site that had been culled were replaced by other serows. In Japanese serows, if a territory dweller dies or disappears, a neighboring serow expands their range to cover the range of the previous dweller, or a newcomer is recruited to occupy empty territory within a short period (Kishimoto 1989). Thus, the serows that appeared after culling for the first time might have been new inhabitants of emptied territories in the study sites. Comparing the serows before and after the 2020 cull, this pattern was possible in T1 and T3 because serows not detected before the cull were identified after it. However, in 2019, the survey period prior to culling was too short to verify this assumption.

The results of this study are limited in that not all serows captured by cameras could be identified, and therefore the result might underestimate the number of individuals that appeared at the sites or overlook the appearance of each identified individual. Further research using Global Positioning System tracking or direct observation of serows could compensate for any shortcomings of our study.

Browse damage

Our results showed seasonal variation in the occurrence of browsing on cypress with high levels in autumn and winter. This finding is supported by previous studies on the Japanese serow's food habits, which suggested that they feed more on conifers in autumn and winter than in other seasons when abundant broad-leaved trees or forbs are available (Koganezawa 1999, Asakura et al. 2014). As cypress dominated the winter diet of serows (Takatsuki and Suzuki 1984), the young plantation was subjected to browse damage during this season. Deer also reportedly browse on young cypress in the autumn and winter, which could be attributed to the relative quality and palatability of food vegetation available within such habitats (Ueda et al. 2003).

Regardless of the abundance of animals, height of saplings, and distance from the forest edge, browse damage was negatively correlated with the chemical repellent application. When a repellent was applied, browsing was 3.6 ($1/0.28 = 3.6$) times less likely to occur than if no repellent was applied. Although the application of repellent is not a mandatory measure to attain institutional permission for culling, owing to

the seasonality of browsing, the application of repellent immediately before the high-risk season (November to January) is labor-saving and effective in mitigating damage.

Removal of the animal causing the damage is the most direct method for preventing browse damage. Our results suggest that damage could occur even after a culling program due to animals that escaped the culling or new territory holders entering the empty space. Additionally, we found that deer were also potential culprits. In these situations, the repellent application, which is effective in mitigating both serow and deer browsing, is a more appropriate approach for damage control. Fencing is also effective for preventing browse damage in Japan (Takayanagi and Yoshimura 1988), although it is sometimes difficult to maintain in the snowy and steep mountainous serow habitat. Wire nets are more effective than plastic nets but are costly. Wrapping saplings with plastic or wire mesh are other good options (Takatsuki 2009). Balancing cost and effectiveness for an appropriate combination of nonlethal prevention measures would enable us to manage damage more efficiently.

It is important to establish specific goals of the culling program at each browsed site based on the required level of damage reduction. Without a goal, it will be difficult to evaluate the effectiveness of culling, and culling operations would be conventionalized. Furthermore, it is essential to maintain realistic expectations for damage reduction and not to expect complete damage elimination. Tolerance of the negative aspects of wildlife presence depends on perceived cost and benefit formed by personal experiences (Kansky et al. 2016) or on socio-demographic factors such as age, gender, or education (Kimmig et al. 2020). Therefore, in setting the goals of a culling program at each browsed site, studies on this topic will hold the key to a long-term solution for human-wildlife conflicts. Adequate communication between government and local residents, such as providing problem-prevention information and opportunities to voice residents' concerns, could increase confidence in their ability to control a problem and tolerate wildlife (Sakurai et al. 2013). Education programs explaining the information obtained in this study could also help improve people's awareness about the

culprit species and aid in conducting adequate prevention measures.

In summary, we recommend the following measures to improve the management plan: (1) identify species before culling serows using camera traps or DNA identification methods; (2) evaluate the effect of serow culling in mitigating damage by monitoring the appearance of serows before and after culling; and (3) give higher priority to the use of a repellent immediately before the high-risk browsing season than to serow culling. A feasible and sustainable management plan based on scientific evidence would allow us to ameliorate conflict and conserve the Japanese serow.

Management implications

Based on evidence of the immediate appearance of serows after culling and the existence of another threat, deer, our study demonstrated that serow culling alone, as currently practiced here, is not sufficient to prevent browse damage. The culling program should require municipal officers or landowners who investigate browse damage to identify the responsible species using camera traps or molecular biological diagnostic methods. Before and after culling, the replacement of territorial serows should be monitored. The effect of culling in mitigating browse damage should be evaluated after every culling program. If it appears that serow culling only has a minor damage-prevention effect, managers should consider prevention methods such as fencing or repellents.

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