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Original paper

Trends in habitat use between sympatric sika deer and Japanese serow as revealed by camera traps

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Abstract. In response to severe vegetation degradation caused by sika deer in Japan, it is important to understand the habitat use trends of the sika deer and sympatric Japanese serows to promote the management and conservation of both species and their habitats. This study used camera traps to examine the trends of habitat use of the two sympatric ungulates in the Kuraiyama Experimental Forest (KEF) at Gifu University. We set camera traps at 20 sites and evaluated the number of individuals photographed for three years. Additionally, we surveyed several environmental factors around the camera trap sites to determine the relationship between species prevalence and habitat features. Both species were photographed at all sites, and some habitat use trends were observed. The deer used the west side of the valley, whereas the serows used the east, with clearer trends further observed in summer. Both ungulates avoided snow cover in winter and used steeper slopes and ridges in several seasons. With the current increase in the deer population, niche overlap between the two species may occur in the common place preferred by both species; therefore, careful monitoring of their relationships and their changes should be continued in the future.

Key words: camera trap survey, *Capricornis crispus*, *Cervus nippon*, environmental factors, sympatric ungulates.

The growing cervid populations can affect ecosystems directly via effects on foraged plant species; additionally, they can have cascading effects on a wide range of organisms within their habitat via vegetation modification (Rooney and Waller 2003; Côté et al. 2004). Damage to agriculture and forestry as well as vegetation degradation caused by sika deer (*Cervus nippon*) is severe in Japan (Ohashi et al. 2014; Ministry of the Environment, Japan 2016), especially in several national parks and conserved forests (Yumoto and Matsuda 2006). Moreover, invertebrates, birds, and mammals are affected by the degrading vegetation (Shibata and Hino 2009). When multiple species of herbivorous ungulates occur sympatrically and resources are limited, interspecific competition occurs due to overlapping niches (Fraser 1996; Putman 1996; Kalb et al. 2018). There are two large herbivorous ungulates, sika deer and Japanese serow (*Capricornis crispus*), in Japan. Monitoring the population increase and expansion of sika deer is important for the management of both species because of their niche overlap which can change interspecies relationships although not yet observed in Japan. Therefore, the conservation and management of both species and their habitats should be thoroughly investigated.

The basic ecology of sika deer and Japanese serow habitats has been reported in previous studies. Sika deer are gregarious (Maruyama 1981), and some populations seasonally migrate to habitats with better foraging chances during early summer and autumn, and to habitats with less snow cover during winter (Igota et al. 2004; Izumiyama and Mochizuki 2008; Takii et al. 2012). Previous studies have reported that in snowy areas, where the food availability for sika deer is severely limited in winter, they use mixed or coniferous forests with less snow cover (Sakuragi et al. 2003). Even in areas with no snow cover and no seasonal migration, sika deer change their habitat use depending on the productivity of vegetation (Ito and Takatsuki 2009). These studies suggest that environmental factors, such as snow cover and vegetation related to food availability, affect the habitat use of

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sika deer. In contrast, Japanese serows are almost solitary and maintain the same territory year-round (Kishimoto and Kawamichi 1996; Ochiai and Susaki 2002; Takada and Minami 2019; Takada et al. 2020a). Furthermore, they prefer steep slopes and low-visibility shrub thickets, which provide greater security against predators (Takada et al. 2019; Takada 2020). Therefore, environmental factors, such as topography and vegetation, affect the habitat use of Japanese serows.

However, few studies have investigated sympatric sika deer and Japanese serows. In the Chichibu Mountains, central Japan, Ishida et al. (1993) found Japanese serows from the north to southeastern slopes and steeper slopes, whereas sika deer were observed at higher altitudes and on southeastern slopes. Both species were also often observed near valley-like terrains. Nowicki and Koganezawa (2001) observed Japanese serows on steep slopes close to roads and at high or low elevations, where sika deer were not often found. Yamashiro et al. (2019) conducted a camera trap survey and found that Japanese serows were found on steep rocky slopes, whereas sika deer appeared more frequently in grasslands. Takada et al. (2020b) reported that sika deer frequently occupied dwarf bamboo-rich communities in autumn and winter but did not have topographic preferences. In contrast, Takada et al. (2020b) also reported that Japanese serows frequently occupied deciduous broadleaf shrub communities and steep terrain throughout the year.

Few studies have examined the interspecific competition between the two species. Koganezawa (1999) reported that the number of Japanese serows declined as sika deer increased at Mt. Ashio, where both species inhabit sympatrically. Nowicki and Koganezawa (2002) observed that among 43 encounters on Mt. Ashio, Japanese serows often avoided sika deer while sika deer ignored the presence of Japanese serows. They hypothesized that interference competition was asymmetrical and disadvantageous only for the Japanese serow. Takada et al. (2020b) indicated that Japanese serows with smaller niche breadths would be more vulnerable to habitat alteration than sika deer and would be at a disadvantage compared to sika deer during exploitative competition. Takada et al. (2020b) also mentioned that sika deer tended to be habitat generalist and the Japanese serows habitat specialist.

As sika deer populations increase in Japan, the Japanese serow may be negatively affected by the vegetation degradation caused by sika deer. Currently, four local populations of Japanese serow are listed as threatened local populations on the red list of the Ministry of the Environment, Government of Japan (Ministry of the Environment, Japan 2020a). Two of these four populations were newly listed in 2020. The impact of vegetation modification of habitats by sika deer is suspected to be the cause of the population decline that led to the listing of the Japanese serow (Ministry of the Environment, Japan 2020b) as a threatened species. To clarify the interspecific relationships between sika deer and Japanese serow in the future, it is necessary to understand the habitat uses of the two species in the areas where they live sympatrically. Furthermore, it is important to collect reliable and robust habitat use data to manage and conserve both species and their habitats.

In this study, we monitored the habitat use of sika deer and Japanese serows for three years using camera traps in Gifu Prefecture, central Japan. We aimed to understand the trends in habitat use and the differences and similarities between the two sympatric ungulates.

Materials and methods

Study area

This study was conducted at the Kuraiyama Experimental Forest (KEF) of Gifu University in Gero City, Gifu Prefecture, central Japan (36°00'N, 137°13'E). The forest covers an area of 553 ha and its elevation ranges from 830 to 1210 m. The Shinnomata Valley lies from the northeast to the southwest in the center of the survey area (Fig. 1). This site consists of various forest types, including natural broad-leaved forests dominated by Japanese beech (*Fagus crenata*), Jolcham oak (*Quercus serrata*), and Japanese oak (*Q. crispula*); natural coniferous forests dominated by cypress (*Chamaecyparis obtusa*) and Asunaro (*Thujopsis dolabrata*); and coniferous plantations of cedar (*Cryptomeria japonica*), cypress, and larch (*Larix kaempferi*). The understory vegetation is dominated by dwarf bamboo (*Sasa senanensis*). Sedge (*Carex* spp.), ferns, and saplings of coniferous species (i.e., *C. pisifera*) also appeared, but their cover was insignificant. Many mammal species, including sika deer, Japanese serows, Asiatic black bears (*Ursus thibetanus*), and wild boars (*Sus scrofa*), inhabit the area. In the Gifu Prefecture, the increase and expansion of sika deer population and the subsequent degradation of shrub layer vegetation have become problematic (Tsunoda et al. 2017; Gifu Prefecture 2021). A substantial disappearance of understory vegetation has not yet been identified in the KEF. However, partial declines in dwarf bamboo cover and disap-

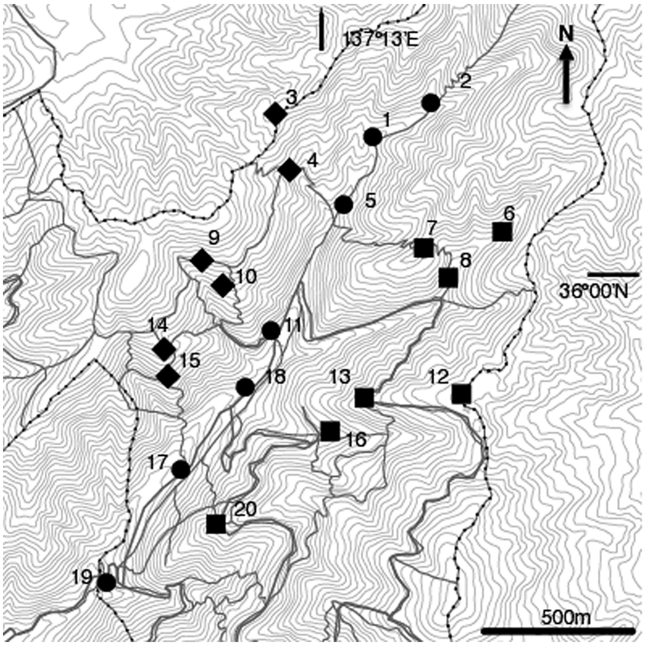

Fig. 1. The Kuraiyama Experimental Forest (KEF) of Gifu University. The black filled symbols indicate the camera trap sites, and the number indicates the designated site number. The environmental parameters of each site can be obtained from Table 1. The same symbols indicate the same location category in the KEF: circles indicate the bottom of the Shinnomata Valley, squares indicate the east side, and diamonds indicate the west side. The thick grey lines indicate roads open to vehicles, the thin grey lines indicate work trails, and the dotted lines indicate the KEF boundaries.

pearance of *Cephalotaxus harringtonia* var. *nana* communities have been observed (presumably due to sika deer foraging in winter, field observations by the authors). Since the KEF is located close to the central part of Gifu Prefecture, where the impact of sika deer on vegetation is heavy (Tsunoda et al. 2017), knowledge of the KEF is important to assess the status of the sika deer and Japanese serow for future management in the Gifu Prefecture.

Camera trap surveys

To measure the habitat use of the sika deer and Japanese serow, passive infrared-triggered camera traps (Ltl Acorn 5210a, Oldboys Outdoors, USA) were installed at 20 sites on November 22, 2013. Since most of the forest floor in the KEF was covered with dwarf bamboo, operating the camera traps stably for a long time was difficult in the dwarf bamboo bushes. Thus, all camera traps were installed along the human/animal trails: at the bottom of the Shinnomata valley (n = 7), east side (n = 7), and west side (n = 6) (Fig. 1). As the KEF is a protected area (hunting prohibited) with few tourists, human disturbance was relatively less. In May 2015, all camera traps were replaced with cameras of another model (HykeCam SP108-J, Hyke Co. Ltd., Japan). Data from December 1, 2013, to November 30, 2016 (three years, 1096 days) were used in our analyses. The number of times each species was photographed at each site was used as a proxy for habitat use frequency for each species. To facilitate the identification of the photographed animals, the camera traps were set to take three consecutive digital photographs each time the camera was triggered. When the photographed object was unclear (e.g., because of triggering due to wind, rain, or an unknown animal), the trigger was determined based on the plant conditions and weather. Photographs taken by a trigger test or broken photo data (unreadable files) by apparatus failure were treated as invalid and excluded from the analyses. All other photographs were treated as valid triggers and were used to identify the photographed animals.

Environmental surveys

At each camera trap site, environmental factors related to vegetation, including the coverage of dwarf bamboo (% cover in ~1 ha around camera trap by visual survey); forest type (categorical: broad-leaved, coniferous, and mixed); physical environmental factors, such as slope (mean degree around camera trap), topography (categorical: hillside, ridge, and valley), and snow depth (cm, average of five measurements at each site taken in late February of 2014–2016); and environmental factors indicating the area within the KEF, elevation (m) and location in the KEF (categorical: east side, the bottom of the Shinnomata Valley, and west side) were recorded or calculated. The values of slope (mean degree) around the camera trap were calculated from a 10-m digital elevation model distributed from the Geospatial Information Authority of Japan and averaged within a 25-m radius (ca. equal to the camera sensing distance) from the camera site, using R 4.0.3 (R Development Core Team 2020).

Data analyses

To examine the trends in habitat use of sika deer and Japanese serow, a generalized linear mixed model (GLMM) was used. Models were constructed for each species in four periods: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). The number of sika deer and Japanese serows photographed were set as response variables, whereas the coverage of dwarf bamboo, forest type, slope, topography, snow depth (winter models only), elevation, and location in the KEF were set as explanatory variables. Each camera trap site was set as a random effect. In all models, the error distribution of the response variables was set as a Poisson distribution with a logarithmic link function, and the camera active days at each site were set as the offset term. Each forest type was estimated as a fixed term, with broad-leaved forests set at zero. Similarly, topography was estimated, with the hillside set as zero, and the location in the KEF was estimated, with the east side set as zero.

Burton et al. (2015) indicated that sampling error because of imperfect detection due to the detection zone, sensitivity, and specific placement; ambient and animal temperatures; and animal density and behavior in the landscape, etc., was problematic in wildlife surveys using camera traps. To address these issues, we designed our analysis as follows: (1) Instead of applying statistical models that require strong assumptions (estimating density, relative density, occupancy, etc.), we applied a simple model that regressed the number of ungulates photographed from multiple environmental factors. (2) To exclude the effects of seasonal changes on animal behavior and camera detection, the data aggregation unit was set as a season (three months), and analysis was conducted for each season. (3) There is a possibility that the differences in the detection rates of the hardware of each camera affected the analysis results. However, the camera hardware used during the same period was the same for all sites. Ltl Acorn 5210a was installed at all sites until late May 2015, after which the hardware was simultaneously switched to Hyke SP108-J. Consequently, we could ignore the differences in camera detection rates that occurred between camera sites owing to differences in the camera hardware.

All possible model combinations of response and explanatory variables were calculated. The total number of built models was 64 in spring, summer, and autumn for each species, and 128 in winter. All models were ranked according to their Akaike Information Criteria (AIC) values in ascending order. Differences in the AIC values between each model and the model with the minimum AIC were calculated as the Delta-AIC in each model. Delta-AIC values < 2 indicate an approximately equal fit of the models (Burnham and Anderson 2002). Thus, models with a Delta-AIC < 2 were selected as the best model group. In this study, we selected the best model from the best model group based on the following criteria: (1) the model(s) with the fewest non-significant explanatory variables in the model, (2) the model(s) with the fewest explanatory variables consisting of the model, and (3) the model with the lowest AIC as the best model.

Bolker et al. (2009) reported that discussing statistical inferences based on results from the complex GLMMs is challenging because of the boundary effect and the difficulty in calculating the degree of freedom. Therefore, to verify the reliability of the results of the best model selected in the aforementioned procedure, we reviewed the trends in the model structure (adoption of explanatory variables) and trends of coefficient estimates in models with the highest ten Delta-AIC values (referring to the fact that the maximum number of models in the best model group was nine). Subsequently, we evaluated the robustness of the model structure and coefficient trends in the best model.

Multicollinearity affects the coefficient estimates in multivariate regression models, and when multicollinearity exists, coefficient estimates can easily change their trend when the explanatory variables adopted in the model are switched. By overviewing the aforementioned trends of coefficient estimates in models with the top ten Delta-AIC, we determined that the multicollinearity problem did not arise when the coefficient trends of the explanatory variables in the best models were robust.

R 4.0.3 (R Development Core Team 2020) and the "lme4" package (Bates et al. 2015) were used for all analyses.

Results

The camera trap sites consisted of various environmental conditions in the KEF (Table 1). The snow depth (mean ± *SD*) in the KEF was 66 ± 20 cm in February 2014, 132 ± 27 cm in February 2015, and 4 ± 8 cm in February 2016.

The total number of camera triggers was 39 960 (invalid triggers = 485, valid triggers = 39 475). The number of triggers at each site differed widely, with the maximum triggers observed at Site 14 (n = 5568) and the least triggers observed at Site 17 (n = 396). Both species were documented at all sites. The number of camera triggers caused by sika deer (n = 6481) was higher than that caused by the Japanese serow (n = 1602).

The trends of explanatory variables in the Delta-AIC top ten models are summarized in Appendices 1 and 2. After reviewing the top ten models for each season for each species, the trend of the coefficient estimates of the environmental factors selected in the best model was stable, indicating that the model selection was appropriate and that problems of multicollinearity were minor.

Table 1. Environmental parameters in 20 camera trap sites in the Kuraiyama Experimental Forest (KEF), central Japan

Site	The coverage of dwarf bamboo (%)	Forest type	Slope (°)	Topography	Snow depth (cm)			Elevation (m)	Location in the KEF
					Feb. 2014	Feb. 2015	Feb. 2016		
1	61	Broad-leaved	25.9	Valley	95.4	144.0	0.0	1080	Bottom of the valley
2	52	Mixed	22.3	Valley	81.8	183.0	0.0	1120	Bottom of the valley
3	91	Mixed	13.7	Ridge	52.4	142.6	5.4	1200	West side
4	85	Broad-leaved	33.6	Hillside	62.8	141.2	0.0	1115	West side
5	64	Mixed	23.9	Valley	75.4	148.6	0.0	1040	Bottom of the valley
6	74	Coniferous	23.8	Valley	31.8	185.6	33.4	1170	East side
7	100	Coniferous	23.7	Ridge	106.2	132.2	6.6	1170	East side
8	66	Broad-leaved	30.6	Valley	84.6	166.0	18.6	1095	East side
9	91	Broad-leaved	33.0	Hillside	65.8	131.4	0.0	1140	West side
10	100	Coniferous	28.0	Hillside	67.4	149.8	8.2	1110	West side
11	21	Broad-leaved	32.3	Valley	61.2	105.6	0.0	990	Bottom of the valley
12	85	Mixed	7.4	Ridge	65.8	113.0	0.0	1215	East side
13	89	Mixed	26.3	Ridge	57.4	113.6	0.0	1140	East side
14	99	Coniferous	18.1	Ridge	39.4	99.4	0.0	1105	West side
15	97	Coniferous	33.8	Hillside	40.4	112.2	0.0	1055	West side
16	55	Coniferous	21.7	Hillside	82.4	153.0	0.0	1050	East side
17	5	Mixed	23.9	Hillside	45.6	108.4	0.0	900	Bottom of the valley
18	77	Broad-leaved	14.5	Valley	78.8	114.6	0.0	950	Bottom of the valley
19	27	Broad-leaved	15.3	Valley	46.0	81.6	0.0	835	Bottom of the valley
20	87	Coniferous	27.4	Ridge	78.8	122.0	0.0	1040	East side

The coverage of dwarf bamboo is a continuous variable representing the dwarf bamboo coverage per hectare (%). Forest type is a categorical variable representing the forest type (Broad-leaved, Coniferous, and Mixed) around the site. Slope is a continuous variable representing the slope around the site within a 25-m radius (°). Topography is a categorical variable representing the topography (Hillside, Ridge, and Valley) around the site. Snow depth is a continuous variable measured five times and averaged in each site from late February of 2014 to 2016 for each year (cm). Elevation is a continuous variable representing the elevation around the site obtained from a 1/25 000 scale map (m). Location in the KEF is a categorical variable that indicates the location (East side, the Bottom of the Shinnomata Valley, and West side) of the site in the KEF.

The results of the best models in the GLMM analyses are summarized in Tables 2 and 3. The results showed that the estimates of snow depth in winter for both species were negative. According to the trends in other explanatory variables, sika deer used higher elevations in spring, whereas Japanese serows used lower elevations in spring, summer, and autumn. Regarding the KEF location, sika deer were found frequently on the west side in summer and winter. In winter, sika deer also used the bottom of the valley. In contrast, Japanese serows were more frequently observed on the east side in summer and autumn than on the west side. In addition, Japanese serows did not use the bottom of the valley in spring and autumn. The slope was used in the best model of sika deer in autumn and winter, and the trend was positive. Slope was adopted in all seasons in the best models of the Japanese serow, and the trends were all positive. Regarding the trends of habitat use in topography, sika deer used ridges in autumn and winter, and valleys in winter. Japanese serows frequently used ridges in all seasons and used valleys in the spring. The coverage of dwarf bamboo was not included in the best models for either species. Regarding the forest type, sika deer did not use coniferous forests during summer, whereas Japanese serows frequently used coniferous forests during winter along with mixed forests in spring.

Discussion

Because both species were documented at all camera trap sites, the results of this study were not biased due to the absence of each species at specific sites. In addition, the results of our analyses were reliable and robust because of sufficient data of the number of photographs of each species obtained through three years of monitoring.

Previous studies have shown that habitat use by sika deer is affected by understory and forest vegetation (Sakuragi et al. 2003; Ito and Takatsuki 2009). Our results showed that sika deer inhabited broad-leaved and

Table 2. Estimated coefficients adopted in the best model in each season by generalized linear mixed model analysis for habitat use of sika deer

Season	Adopted explanatory variables		Estimate	*SE*	*z* value	*P* value
Spring	(Intercept)		–8.156	2.364	–3.450	< 0.001
	Elevation		0.506×10^{-2}	0.218×10^{-2}	2.323	< 0.05
Summer	(Intercept)		–1.819	0.287	–6.336	< 0.001
	Location in the KEF	East side	(Set as 0)	—	—	—
		Bottom of the valley	–0.604	0.408	–1.481	0.14
		West side	1.030	0.417	2.469	< 0.05
Autumn	(Intercept)		–2.424	0.810	–2.990	< 0.01
	Forest type	Broad-leaved	(Set as 0)	—	—	—
		Coniferous	–0.837	0.387	–2.166	< 0.05
		Mixed	0.311×10^{-1}	0.404	0.770×10^{-1}	0.94
	Slope		0.637×10^{-1}	0.241×10^{-1}	2.639	< 0.01
	Topography	Hillside	(Set as 0)			
		Ridge	0.925	0.427	2.165	< 0.05
		Valley	0.500	0.379	1.319	0.19
Winter	(Intercept)		–5.446	0.906	–6.009	< 0.001
	Slope		0.896×10^{-1}	0.247×10^{-1}	3.621	< 0.001
	Topography	Hillside	(Set as 0)	—	—	—
		Ridge	1.610	0.510	3.156	< 0.01
		Valley	1.381	0.488	2.831	< 0.01
	Snow depth		-0.274×10^{-1}	0.114×10^{-2}	-2.410×10	< 0.001
	Location in the KEF	East side	(Set as 0)	—	—	—
		Bottom of the valley	1.398	0.461	3.033	< 0.01
		West side	1.854	0.418	4.435	< 0.001

Forest type is a categorical variable representing the forest type (Broad-leaved, Coniferous, and Mixed) around the site. Slope is a continuous variable representing the slope around the site within a 25-m radius (°). Topography is a categorical variable representing the topography (Hillside, Ridge, and Valley) around the site. Snow depth is a continuous variable measured five times and averaged in each site from late February of 2014 to 2016 for each year (cm). Elevation is a continuous variable representing the elevation around the site obtained from a 1/25 000 scale map (m). Location in the KEF is a categorical variable that indicates the location (East side, the Bottom of the Shinnomata Valley, and West side) of the site in the KEF.

mixed forests more than they did coniferous forests in autumn (Table 2). Sika deer in the Yamaguchi Prefecture foraged heavily on the acorns of Japanese Chinquapin (*Castanopsis sieboldii*), sawtooth oak (*Q. acutissima*), and Jolcham oak in November (Weerasinghe and Takatsuki 1999). Compared with the surrounding forests dominated by coniferous plantations, the KEF included deciduous broad-leaved forests with Japanese beech, Jolcham oak, and Japanese oak, which are acorn trees (field observation by authors). This trend suggested that sika deer inhabiting the KEF might preferentially use broad-leaved and mixed forests, where the availability of acorns is high in autumn. Additionally, our results showed that Japanese serows used coniferous forests in winter and mixed forests in spring (Table 3). Previous studies on fecal pellet surveys have reported that Japanese serows often use coniferous forests as defecation sites (Haneda et al. 1966; Haneda and Yamada 1967; Hirata et al. 1973; Miyazawa et al. 2005). Furthermore, previous studies on radio telemetry tracking have shown that Japanese serows often use coniferous forests in winter to avoid wind and snow (Okumura 1989; Tano et al. 1994; Otsuki and Ito 1996). The results of the trends of winter habitat use by the Japanese serow in this study were consistent with previous studies. However, the reason for using mixed forest frequently in spring remains unknown.

Japanese serows use steep terrain and low-visibility sites (Takada et al. 2019; Takada 2020), while sika deer use relatively gentle slopes compared to sympatric Japanese serows (Takada et al. 2020b). Our results suggested that Japanese serows used steeper slopes in all seasons (Table 3), as reported in previous studies. In contrast, Takii et al. (2012) described that sika deer used steeper slopes in winter than in summer to avoid hunting distur-

Table 3. Estimated coefficients adopted in the best model in each season by generalized linear mixed model analysis for habitat use of Japanese serow

Season	Adopted explanatory variables		Estimate	*SE*	*z* value	*P* value
Spring	(Intercept)		2.065	1.169	1.766	0.08
	Forest type	Broad-leaved	(Set as 0)	—	—	—
		Coniferous	0.292	0.249	1.173	0.24
		Mixed	0.860	0.284	3.024	< 0.01
	Slope		0.496×10^{-1}	0.143×10^{-1}	3.455	< 0.001
	Topography	Hillside	(Set as 0)	—	—	—
		Ridge	1.098	0.262	4.184	< 0.001
		Valley	0.648	0.305	2.124	< 0.05
	Elevation		-0.595×10^{-2}	0.101×10^{-2}	–5.891	< 0.001
	Location in the KEF	East side	(Set as 0)	—	—	—
		Bottom of the valley	–1.438	0.333	–4.319	< 0.001
		West side	–0.469	0.245	–1.912	0.06
Summer	(Intercept)		0.821	2.267	0.362	0.72
	Slope		0.521×10^{-1}	0.218×10^{-1}	2.393	< 0.05
	Topography	Hillside	(Set as 0)	—	—	—
		Ridge	0.974	0.321	3.032	< 0.01
		Valley	0.348×10^{-1}	0.338	0.103	0.92
	Elevation		-0.378×10^{-2}	0.170×10^{-2}	–2.231	< 0.05
	Location in the KEF	East side	(Set as 0)	—	—	—
		Bottom of the valley	–0.713	0.436	–1.636	0.10
		West side	–1.221	0.297	–4.112	< 0.001
Autumn	(Intercept)		–0.605	1.090	–0.555	0.58
	Slope		0.418×10^{-1}	0.140×10^{-1}	2.986	< 0.01
	Topography	Hillside	(Set as 0)	—	—	—
		Ridge	0.893	0.276	3.239	< 0.01
		Valley	0.362	0.277	1.305	0.19
	Elevation		-0.269×10^{-2}	-0.927×10^{-3}	–2.902	< 0.01
	Location in the KEF	East side	(Set as 0)	—	—	—
		Bottom of the valley	–0.893	0.285	–3.131	< 0.01
		West side	–1.016	0.243	–4.173	< 0.001
Winter	(Intercept)		–6.148	0.856	–7.183	< 0.001
	Forest type	Broad-leaved	(Set as 0)	—	—	—
		Coniferous	1.252	0.403	3.109	< 0.01
		Mixed	0.637	0.449	1.420	0.16
	Slope		0.613×10^{-1}	0.239×10^{-1}	2.571	< 0.05
	Topography	Hillside	(Set as 0)	—	—	—
		Ridge	1.019	0.318	3.208	< 0.01
		Valley	0.781×10^{-1}	0.383	0.204	0.84
	Snow depth		-0.163×10^{-1}	0.266×10^{-2}	–6.134	< 0.001

Forest type is a categorical variable representing the forest type (Broad-leaved, Coniferous, and Mixed) around the site. Slope is a continuous variable representing the slope around the site within a 25-m radius (°). Topography is a categorical variable representing the topography (Hillside, Ridge, and Valley) around the site. Snow depth is a continuous variable measured five times and averaged in each site from late February of 2014 to 2016 for each year (cm). Elevation is a continuous variable representing the elevation around the site obtained from a 1/25 000 scale map (m). Location in the KEF is a categorical variable that indicates the location (East side, the Bottom of the Shinnomata Valley, and West side) of the site in the KEF.

bance. Sika deer in the KEF also frequently use steeper slopes in winter. In addition, the hunting season has been initiated on November 1 in recent years in Gifu Prefecture, and in our study, November was included in autumn. Although our study site is a protected area where hunting is prohibited, hunting was previously permitted in the forests surrounding our study site. Therefore, the trend of using steeper slopes in autumn and winter by sika deer may also be a response to hunting pressure.

Few previous studies have observed trends in habitat use by sika deer and Japanese serows in terms of topographic factors, such as ridges and valleys. Ishida et al. (1993) reported that both species were often observed near valley-like terrain through a helicopter survey in December 1987, 1988, and 1989, but they mentioned that the reasons for such trends in habitat use were unclear. Our results differed from those of previous studies, indicating that Japanese serows used ridges in all seasons and valleys in spring (Table 3). Our results also indicated that sika deer used ridges in autumn and valleys in winter (Table 2). However, the explanations for this trend are unclear, and thus, other survey methods (i.e., GPS telemetry) would be required to understand the environmental factors of their territories and the effect of these factors on the species.

The coefficients of snow depth for models of both species were negative (Tables 2 and 3), indicating that both species avoided snow during winter. Sakuragi et al. (2003) reported that sika deer used areas with less snow cover during winter. Seto et al. (2015) found that when deep snow prevented sika deer from accessing the understory, snow depth affected the proportion of dwarf bamboo and graminoids negatively and bark and twigs positively in the rumen content of sika deer. Regarding the Japanese serow, Takatsuki et al. (1995) indicated that snow cover decreased forage availability. Our results supported the trends shown in previous studies that occurred possibly because of a decline in food availability due to snow cover.

Regarding the location in the KEF, the east side of the valley primarily consisted of westward- and northward-facing slopes (Fig. 1), and it is expected that snow does not melt readily due to limited daylight; therefore, obtaining food in winter may be more difficult than it is on the west side of the valley. As sika deer utilize suitable environments depending on the season (Izumiyama and Mochizuki 2008), they likely tend not to use the east side of the valley due to low food availability in winter (Table 2). However, the reasons for the presence of sika deer in high elevation areas in spring and on the west side in summer are still unclear. In contrast, Japanese serows used the east side of the valley in summer and autumn, and lower elevation areas in all seasons, except winter (Table 3). Several previous studies showed that the Japanese serows remained in their territories with no seasonal movements (Kishimoto and Kawamichi 1996; Ochiai and Susaki 2002; Takada et al. 2020a), but one study reported that they changed their habitat use trends in winter due to changes in food availability (Nagaki 2000). The reasons why Japanese serows frequently inhabited the east side in summer and autumn and did not use the bottom of the valley in spring and autumn are unclear. However, the reason why Japanese serows did not show such a trend in winter may be the same as that for the sika deer mentioned above. Further studies on food resource availability and its relationships with topological factors (i.e., relationships among elevation, slope facing, and forage biomass) are needed to confirm these trends.

When overviewing the habitat use trends of both species throughout the year, elevation (sika deer: higher in spring, Japanese serow: lower from spring to autumn) and location in the KEF (sika deer: west side in summer and winter, Japanese serow: east side in summer and autumn) showed differences between the two species. On the contrary, both species showed positive steeper slopes and ridge trends (sika deer in autumn and winter, while Japanese serow in all seasons) and negative snow depth trends. Contrasting trends may indicate partitioning of spatial resources, while similar trends may indicate overlapping of resource use, but further studies with adequate analyses (i.e., niche breadth calculations) are needed to discuss interspecific relationships.

In this study, we clarified the habitat use trends of the sika deer and Japanese serow in the KEF, and it was clear that most trends were similar to those reported in previous studies. We focused on describing the habitat use trends of both species and did not analyze or refer to the interspecific relationships between them. However, several previous studies have discussed the interspecific relationships. These studies suggested that Japanese serows might be at a disadvantage during competition for food and space resources (Nowicki and Koganezawa 2002; Takada et al. 2020b; Takada et al. 2021). Our results revealed that snow depth, slope, and ridges showed similar trends in habitat use by both species. They avoided snow cover in winter and used steeper slopes and ridges in several seasons. With the current increase in the deer population, niche overlap in space between the two species may occur in places preferred by the two sympatric ungulates. In the future, long-term data collection and appropriate analyses of their interspecific relationships and their changes should be promoted in all areas where both species live sympatrically.

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Appendix 1. Results of Delta-AIC top 10 model (model structure, AIC, Delta-AIC, Number of explanatory variables in each model, and the trends of explanatory variables adopted in each model) for sika deer

Season	Model structure	AIC	Delta-AIC	Number of explanatory variables	Best model	The coverage of dwarf bamboo	Forest type (Broad-leaved: set as 0)		Slope	Topography (Hillside: set as 0)		Snow depth	Elevation	Location in the KEF (East side: set as 0)		Intercept
							Coniferous	Mixed		Ridge	Valley			Bottom of the valley	West side	
Spring	**Elevation + 1**	**413.50**	**0.00**	**1**	○								+			–
	Forest type + Topography + Location in the KEF + 1	414.66	1.16	3			(–)	(+)		+	(+)			–	(+)	–
	Topography + Elevation + 1	415.18	1.68	2						(+)	(+)		(+)			–
	Slope + Elevation + 1	415.33	1.82	2					(–)				+			–
	Topography + Location in the KEF + 1	415.44	1.94	2						+	(+)			(–)	(+)	–
	Topography + 1	415.44	1.94	1						+	(+)					–
	The coverage of dwarf bamboo + Elevation + 1	415.50	1.99	3		(+)							(+)			–
	The coverage of dwarf bamboo + 1	415.87	2.37	1		(+)										–
	Forest type + Elevation + 1	415.91	2.41	2			(–)	(+)					+			–
	Forest type + Location in the KEF + 1	415.92	2.41	2			(–)	(+)						–	(+)	–
Summer	Slope + Topography + Location in the KEF + 1	696.49	0.00	3					(+)	+	(–)			(+)	+	–
	Topography + Location in the KEF + 1	696.55	0.06	2						(+)	(–)			(+)	+	–
	Slope + Topography + Elevation + Location in the KEF + 1	697.50	1.01	4					(+)	(+)	(–)		(+)	(+)	+	–
	Location in the KEF + 1	**697.60**	**1.11**	**1**	○									(–)	+	–
	Topography + Elevation + Location in the KEF + 1	697.71	1.22	3						(+)	(–)		(+)	(+)	+	(–)
	Forest type + Location in the KEF + 1	698.46	1.97	2			(+)	(+)						(–)	+	–
	The coverage of dwarf bamboo + Slope + Topography + Location in the KEF + 1	698.47	1.98	4		(–)			(+)	+	(–)			(+)	+	–
	Slope + Topography + 1	698.54	2.05	2					(+)	(+)	–					–
	The coverage of dwarf bamboo + Topography + Location in the KEF + 1	698.55	2.06	3		(–)				(+)	(–)			(+)	+	–
	Elevation + Location in the KEF + 1	698.61	2.12	2									(+)	(–)	+	(–)
Autumn	Forest type + Slope + Topography + Location in the KEF + 1	903.41	0.00	4			(–)	(+)	+	+	+			(+)	+	–
	The coverage of dwarf bamboo + Slope + Topography + Elevation + Location in the KEF + 1	903.98	0.57	5		(–)			+	+	+		+	(+)	+	–
	Forest type + Slope + Topography + Elevation + Location in the KEF + 1	904.52	1.11	4			–	(+)	+	+	(+)		(+)	(+)	+	–
	Forest type + Slope + Elevation + 1	904.65	1.24	3			–	(–)	(+)				(+)			–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Elevation + Location in the KEF + 1	904.68	1.27	6		(–)	(–)	(–)	+	+	+		(+)	(+)	+	–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Location in the KEF + 1	904.81	1.40	5		(–)	(–)	(+)	+	+	+			(–)	+	–
	Forest type + Elevation + 1	905.05	1.64	2			–	(–)					(+)			–
	Forest type + Slope + Topography + 1	**905.18**	**1.77**	**3**	○		–	(+)	+	+	(+)					–
	Slope + Topography + Elevation + Location in the KEF + 1	905.26	1.84	4					+	+	(+)		(+)	+	+	–
	Forest type + Slope + 1	905.44	2.03	2			–	(+)	(+)							–
Winter	**Slope + Topography + Snow depth + Location in the KEF + 1**	**434.14**	**0.00**	**4**	○				+	+	+	–		+	+	–
	The coverage of dwarf bamboo + Slope + Topography + Snow depth + Location in the KEF + 1	435.30	1.16	5		(+)			+	+	+	–		+	+	–
	Slope + Topography + Snow depth + Elevation + Location in the KEF + 1	436.13	1.99	5					+	+	+	–	(+)	+	+	–
	The coverage of dwarf bamboo + Slope + Topography + Snow depth + Elevation + Location in the KEF + 1	437.25	3.11	6		(+)			+	+	+	–	(–)	+	+	–
	Forest type + Slope + Topography + Snow depth + Location in the KEF + 1	437.35	3.21	5			(+)	(+)	+	+	+	–		+	+	–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + Location in the KEF + 1	438.64	4.50	6		(+)	(+)	(+)	+	+	+	–		+	+	–
	The coverage of dwarf bamboo + Slope + Snow depth + Location in the KEF + 1	439.25	5.11	4		+			+			–		+	+	–
	Forest type + Slope + Topography + Snow depth + Elevation + Location in the KEF + 1	439.27	5.13	6			(+)	(+)	+	+	+	–	(–)	+	+	–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + Elevation + Location in the KEF + 1	440.07	5.93	7		(+)	(+)	(+)	+	+	+	–	(–)	+	+	–
	The coverage of dwarf bamboo + Slope + Snow depth + Elevation + Location in the KEF + 1	441.08	6.94	5		(+)			+			–	(+)	+	+	–

Models with bold, gray shading and a "○" in the column of Best model are the best models for that season. Models described with gray text indicate that the model is not included in the best model group (Delta-AIC > 2). "1" in model structure means Intercept. "+" indicates positive, and "–" indicates a negative trend of estimated coefficient. Parentheses indicate that the estimated coefficient is not significant.
The coverage of dwarf bamboo is a continuous variable representing the dwarf bamboo coverage per hectare (%). Forest type is a categorical variable representing the forest type (Broad-leaved, Coniferous, and Mixed) around the site. Slope is a continuous variable representing the slope around the site within a 25-m radius (°). Topography is a categorical variable representing the topography (Hillside, Ridge, and Valley) around the site. Snow depth is a continuous variable measured five times and averaged in each site from late February of 2014 to 2016 for each year (cm). Elevation is a continuous variable representing the elevation around the site obtained from a 1/25 000 scale map (m). Location in the KEF is a categorical variable that indicates the location (East side, the Bottom of the Shinnomata Valley, and Eest side) of the site in the KEF.

Appendix 2. Results of Delta-AIC top 10 model (model structure, AIC, Delta-AIC, Number of explanatory variables in each model, and the trends of explanatory variables adopted in each model) for Japanese serow

Season	Model structure	AIC	Delta-AIC	Number of explanatory variables	Best model	The coverage of dwarf bamboo	Forest type (Broad-leaved: set as 0)		Slope	Topography (Hillside: set as 0)		Snow depth	Elevation	Location in the KEF (East side: set as 0)		Intercept
							Coniferous	Mixed		Ridge	Valley			Bottom of the valley	West side	
Spring	**Forest type + Slope + Topography + Elevation + Location in the KEF + 1**	**346.70**	**0.00**	**5**	○		(+)	+	+	+	+		–	–	(–)	(+)
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Elevation + Location in the KEF + 1	348.48	1.78	6		(+)	(+)	+	+	+	(+)		–	–	(–)	(+)
	Slope + Topography + Elevation + Location in the KEF + 1	348.78	2.08	4					+	+	(+)		–	–	–	(+)
	The coverage of dwarf bamboo + Slope + Topography + Elevation + Location in the KEF + 1	350.77	4.07	5		(+)			+	+	(+)		–	–	–	(+)
	Slope + Topography + Location in the KEF + 1	351.52	4.82	3					+	+	(–)			(–)	–	–
	Topography + Elevation + Location in the KEF + 1	351.57	4.87	3						+	(+)		–	–	–	(+)
	Elevation + Location in the KEF + 1	351.71	5.01	2									–	–	–	(+)
	Location in the KEF + 1	352.19	5.49	1										–	–	–
	The coverage of dwarf bamboo + Forest type + Slope + Elevation + Location in the KEF + 1	352.73	6.03	5		(+)	(+)	+	(+)				–	–	–	(+)
	The coverage of dwarf bamboo + Elevation + Location in the KEF + 1	353.02	6.32	3		(+)							–	–	–	(+)
Summer	**Slope + Topography + Elevation + Location in the KEF + 1**	**463.76**	**0.00**	**4**	○				+	+	(+)		–	(–)	–	(+)
	The coverage of dwarf bamboo + Slope + Topography + Elevation + Location in the KEF + 1	465.55	1.80	5		(+)			+	+	(–)		–	(–)	–	(+)
	Slope + Topography + Location in the KEF + 1	467.15	3.40	3					+	(+)	(–)			(–)	–	–
	Forest type + Slope + Topography + Elevation + Location in the KEF + 1	467.58	3.82	4			(+)	(+)	+	+	(+)		–	(–)	–	(+)
	Slope + Elevation + Location in the KEF + 1	467.83	4.07	3					(+)				(–)	–	–	(+)
	Elevation + Location in the KEF + 1	467.99	4.23	2									–	–	–	(+)
	The coverage of dwarf bamboo + Slope + Elevation + Location in the KEF + 1	468.54	4.79	4		(+)			(+)				–	–	–	(+)
	Slope + Location in the KEF + 1	468.56	4.80	2					(+)					–	–	–
	The coverage of dwarf bamboo + Slope + Topography + Location in the KEF + 1	469.06	5.30	4		(–)			+	(+)	(–)			(–)	–	–
	Location in the KEF + 1	469.13	5.38	1										–	–	–
Autumn	**Slope + Topography + Elevation + Location in the KEF + 1**	**350.72**	**0.00**	**4**	○				+	+	(+)		–	–	–	(–)
	The coverage of dwarf bamboo + Slope + Topography + Elevation + Location in the KEF + 1	351.92	1.20	5		(+)			+	+	(+)		–	–	–	(–)
	Slope + Topography + Location in the KEF + 1	352.88	2.16	3					+	+	(+)			(–)	–	–
	The coverage of dwarf bamboo + Slope + Elevation + Location in the KEF + 1	353.60	2.88	4		+			(+)				–	–	–	(–)
	Forest type + Slope + Topography + Elevation + Location in the KEF + 1	354.11	3.39	5			(–)	(–)	+	+	(+)		–	–	–	(–)
	Slope + Location in the KEF + 1	354.30	3.58	2					(+)					–	–	–
	Location in the KEF + 1	354.76	4.04	1										–	–	–
	Slope + Elevation + Location in the KEF + 1	354.84	4.12	3					(+)				(–)	–	–	(–)
	The coverage of dwarf bamboo + Elevation + Location in the KEF + 1	354.84	4.12	3		(+)							–	–	–	(+)
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Elevation + Location in the KEF + 1	354.86	4.14	6		(+)	(–)	(–)	+	+	(+)		–	–	–	(–)
Winter	**Forest type + Slope + Topography + Snow depth + Elevation + Location in the KEF + 1**	169.53	0.00	5			+	(+)	+	+	(–)	–	(+)	(+)	–	–
	Forest type + Slope + Topography + Snow depth + 1	**169.58**	**0.05**	**4**	○		+	(+)	+	+	(+)	–				–
	Forest type + Slope + Topography + Snow depth + Location in the KEF + 1	169.68	0.16	5			+	(+)	+	+	(–)	–		(+)	(–)	–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + Location in the KEF + 1	170.70	1.17	6		(+)	+	(+)	+	(+)	(–)	–		(+)	–	–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + 1	171.02	1.49	5		(–)	+	(+)	+	+	(+)	–				–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + Elevation + Location in the KEF + 1	171.47	1.94	7		(+)	+	(+)	+	(+)	(–)	–	(+)	(+)	(–)	–
	Forest type + Slope + Topography + Snow depth + Elevation + 1	171.57	2.05	5			+	(+)	+	+	(+)	–	(+)			–
	The coverage of dwarf bamboo + Forest type + Slope + Topography + Snow depth + Elevation + 1	171.84	2.32	6		(–)	+	(+)	+	+	(–)	–	(+)			–
	The coverage of dwarf bamboo + Forest type + Topography + Snow depth + Location in the KEF + 1	173.75	4.22	5		(+)	+	(+)		(+)	(–)	–		(+)	–	–
	Forest type + Topography + Snow depth + Location in the KEF + 1	173.95	4.42	4			+	(+)		(+)	(–)	–		(+)	–	–

Models with bold, gray shading and a "○" in the column of Best model are the best models for that season. Models described with gray text indicate that the model is not included in the best model group (Delta-AIC > 2). "1" in model structure means Intercept. "+" indicates positive, and "–" indicates a negative trend of estimated coefficient. Parentheses indicate that the estimated coefficient is not significant.
The coverage of dwarf bamboo is a continuous variable representing the dwarf bamboo coverage per hectare (%). Forest type is a categorical variable representing the forest type (Broad-leaved, Coniferous, and Mixed) around the site. Slope is a continuous variable representing the slope around the site within a 25-m radius (°). Topography is a categorical variable representing the topography (Hillside, Ridge, and Valley) around the site. Snow depth is a continuous variable measured five times and averaged in each site from late February of 2014 to 2016 for each year (cm). Elevation is a continuous variable representing the elevation around the site obtained from a 1/25 000 scale map (m). Location in the KEF is a categorical variable that indicates the location (East side, the Bottom of the Shinnomata Valley, and Eest side) of the site in the KEF.