Diets of sika deer invading Mt Yatsugatake and the Japanese South Alps in the alpine zone of central Japan

Authors: Kagamiuchi, Yasunori, and Takatsuki, Seiki

Source: Wildlife Biology, 2020(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00710

Wildlife Biology 2020: wlb.00710
doi: 10.2981/wlb.00710

Subject Editor: Jennifer Forbey. Editor-in-Chief: Ilse Storch. Accepted 13 July 2020

Diets of sika deer invading Mt Yatsugatake and the Japanese South Alps in the alpine zone of central Japan

Yasunori Kagamiuchi and Seiki Takatsuki

Y. Kagamiuchi and S. Takatsuki (https://orcid.org/0000-0002-3108-6420) ✉ (takatuki@azabu-u.ac.jp), Veterinary Medicine, Azabu Univ., Fuchinobe, 1-1-71 Chuo-ku, Kanagawa, JP-229-850 Sagamihara, Japan.

Sika deer *Cervus nippon* populations have been increasing on the Japanese archipelago. Their range is expanding to include the alpine zone in central Japan, where they stay during summer before descending to the lower areas during winter. No studies on dietary habits of alpine deer in mainland Japan have been conducted. This study assessed the composition of sika deer diets and compared nutritional quality between the low montane, subalpine and alpine zones. We analyzed sika deer fecal samples from Mt Yatsugatake (YT) and the Japanese South Alps (SA). In the lower mountain in YT, dwarf bamboo comprised 40–55% of the plant compositions in fecal samples, whereas dicots were mostly found in SA samples. In subalpine zones in YT, grasses are an important food item, comprising about 50% of the samples. In SA, monocots (10–20%) and dicots (10–20%) were both prevalent. In the alpine zone of both YT and SA, grasses were present the fecal samples (50% and 10–20%, respectively). Crude protein contents were higher at higher zones (15–20%) than at lower zones (8–12%) in both study areas.

Keywords: Alpine, elevation, food, Japan, sika deer

In the last three decades, sika deer *Cervus nippon* populations have been increasing and expanding their range in Japan (Nakajima 2007), thus exerting an impact on vegetation (Akashi and Terazawa 2005, Ohashi et al. 2007, Takatsuki 2009a, Otsu et al. 2011, Tamura 2013). The effect of sika deer on alpine vegetation has become more prominent since 2000, specifically on Mt Yatsugatake (YT) and the Japanese South Alps (SA; Chubu Forest Management Office 2007, 2008, 2010). The plants that incur damage from sika deer include the endangered *Viola crassa yatsugatakeana*, *Cypripedium yatabeanum* and *Coeloglossum viride* var. *akaishimontanum*. Sika deer not only excert effects on plants but also on abundance of birds (Okuda et al. 2012), mammals (Seki and Koganezawa 2012), insects (Iida et al. 2016) and soil erosion (Yamada and Takatsuki 2015) through vegetational changes.

Some populations of sika deer are seasonal migrants (Takatsuki et al. 2000, Igota et al. 2004, Sakuragi et al. 2004). In central Japan, they inhabit subalpine and alpine zones from June to November, and then descend to lower elevations during the winter (Izumiyama and Mochizuki 2008, Izumiyama et al. 2009). Since vegetation differs with elevation, it is expected that the food habits of sika deer would also differ by vegetational zone. There have been two case studies on the variation in sika deer diet with elevation. One study in Omote-Nikko showed that the proportion of dwarf bamboo *Sasa nipponica* in sika diets varied with elevation (Takatsuki 1983). Another study on Yakushima Island, southern Japan, found that sika deer at low elevation ate more dicot leaves, while those in the alpine zone mainly ate *Pseudosasa owatarii* bamboo (Takatsuki 1990b). Since the alpine zones in central Japan have not yet been inhabited by deer until the late 1990s, no study has been done on the food habits of alpine sika deer. The objective of this study was to characterize the botanical compositions and crude protein contents of the feces of sika deer according to elevation in central Japan.

Material and methods

Study sites

We chose Mt Yatsugatake (YT) and the Japan South Alps (SA) as the study sites (Fig. 1). YT (the summit: 36°00′N, 138°22′E), situated in the eastern part of Nagano Prefecture, is 15 km wide and 25 km long. The mean temperature in November at the foothill of YT ranges from −0.1°C in February to 24.8°C in August, and the mean annual

---

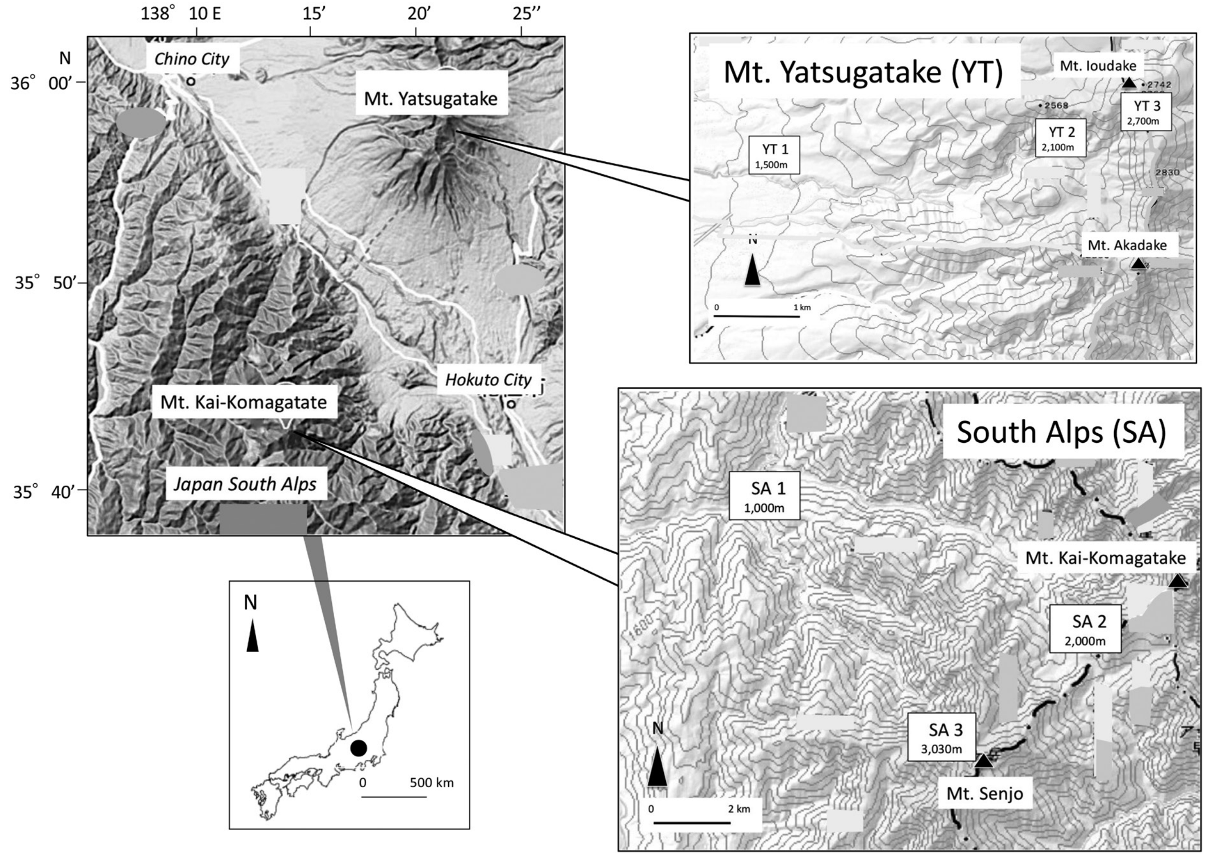

Figure 1. Location map of Mt Yatsugatake (YT) and the Japanese South Alps (SA). Fecal samples of sika deer were collected from the low montane (YT 1, SA 1), the subalpine (YT 2, SA 2) and the alpine zones (YT 3, SA 3).

precipitation is 1440 mm. The vegetation of YT is a primarily *Betula ermanii*- and *Larix kaempferi*-dominated forest with *Sasa borealis*, a dwarf bamboo, in the understory at YT 1 in the montane zone (Fig. 2), a coniferous *Tsuga diversifolia* and *Abies veitchii* forest with *T. diversifolia*, *Picea jezoensis*, *A. veitchii* and *Betula ermanii* at YT 2 in the subalpine zone, and Siberian dwarf pine *Pinus pumila* shrubs and alpine meadows dominated by *Calamagrostis hakonensis, Veratrum album* and *Potentilla matsumurae* at YT 3 in the alpine zone (Chubu Forest Management Office 2010). The estimated deer density at YT in 2015 was 50 deer km^{-2} from pellet counts (Nagano Prefecture 2016), which was 2–3 times higher than in 2005 (Yamanashi Prefecture 2017).

SA (the summit: 35°45′N, 138°14′E) is situated in the southeastern part of Nagano Prefecture, bordering the Yamanashi and Shizuoka Prefectures (Fig. 1). It is 100 km long and 50 km wide. The mean temperature ranges from −1.6°C in February to 22.5°C in August, and the mean annual precipitation is 1499 mm at Minami-arupusu Town at a foothill of SA. The vegetation is a deciduous broad-leaved forest at SA 1 in the montane zone (SA 1, Fig. 2), with a coniferous *Abies veitchii–Abies mariesi* forest at SA 2 in the subalpine zone, and dwarf pine shrubs and alpine meadows at SA 3 in the alpine zone (Chubu Forest Management Office 2007). The estimated deer density of SA in 2015 was 13 deer km^{-2} from pellet counts (Nagano Prefecture 2016), which was three times higher than in 2005 (Yamanashi Prefecture 2017).

Fecal collection and analyses

We collected sika deer fecal pellets from three vegetational zones: the montane zone (YT 1, SA 1), the subalpine zone (YT 2, SA 2) and the alpine zone (YT 3, SA 3) in YT and SA (Table 1) in August and November 2011, and in March 2012. We randomly walked in the forests and shrubs, and collected fresh pellets (n = 20) from fecal piles (n = 10). The March collection was only possible at low elevations (YT 1 and SA 1) because snow was present at higher elevations (YT 2, 3, SA 2, 3). It took 7 days and 8 days for collection at YT and SA, respectively.

We analyzed the feces using a micro-histological method (Stewart 1967). Fecal samples were washed over a 0.5 mm aperture sieve, and the remaining material was microscopically analyzed using the point-frame method (Chamrad and Box 1964, Takatsuki 1978). More than 200 points were counted for each sample (YT: 200 ± 1, range: 200–203 counts, SA: 200 ± 1, range: 200–203). Plant fragments were spread over a glass slide (1 mm grid size) and categorized into 11 groups: dwarf bamboo, grasses, sedges, other monocots, dicots, coniferous leaves, dicots, ferns, culms and sheaths, fiber, fruits and seeds, and others.

Since ruminants are often protein-deficient (Robbins 1992), the protein content of forage is important. Since the crude protein content of sika deer feces is relative to that within their rumen (Watanabe and Takatsuki 1993), we used fecal crude protein as an index for food quality. Fecal

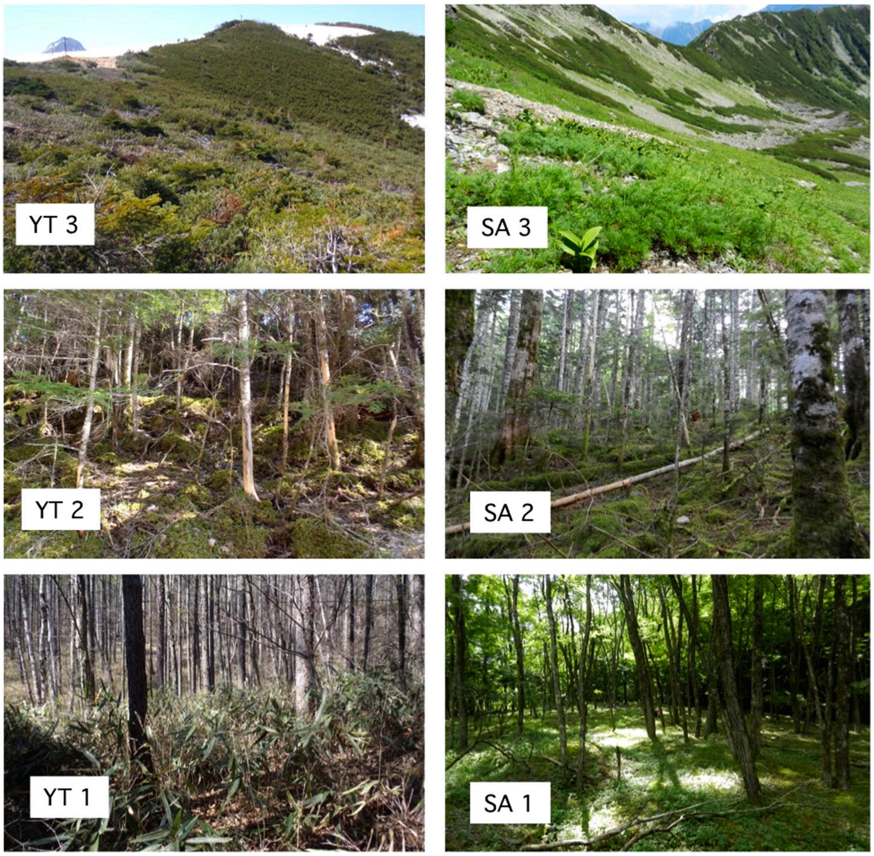

Figure 2. Views of the sampling sites of deer feces at the montane zone (YT 1, SA 1), the sub-alpine zone (YT 2, SA 2) and the alpine zone (YT 3, SA 3) of Mt Yatsugatake (YT 1–YT 3) and the Japanese South Alps (SA 1–SA 3). YT 1: *Sasa borealis*, a dwarf bamboo, was abundant, YT 2: undergrowth was poor, YT 3: Siberian dwarf pine shrubs were dominant, SA 1: forbs and browses grew, SA 2: understory was poor, SA 3: Siberian dwarf pine shrubs and alpine meadow grew.

pellets (n = 10) were dried at 65°C for 24 h and milled. They were analyzed using the Kjaldahl method (Kjeltec 2100 distillation unit). The water content was determined using the atmospheric pressure drying method (135°C for 2 h).

Statistical analyses

Proportions of the major foods in sika deer feces for each season was compared by the Mann–Whitney U-tests when two sites were available and by the Kruskal–Wallis test, followed by the Steel–Dwass post hoc test when three sites were available (Esumi Mac Statistic Analysis, Ver. 3.0, 2018). They were also compared among vegetational zones by the Kruskal–Wallis test with the Steel–Dwass post hoc test. Crude protein content was compared between two study sites by the Mann–Whitney test, and among seasons by the Kruskal–Wallis test with the Steel–Dwass post hoc test. The composition similarity of the deer fecal samples in each vegetational zone was compared between YT and SA by Whittaker's percentage similarity (PS, Whittaker 1952). PS between 10 samples at YT and 10 samples at SA were calculated and 100 PSs were obtained at each vegetational zone. PSs were compared among the three vegetational zones by the Kruskal–Wallis test with the Steel–Dwass post hoc test. Statistical standard (α) was set at 0.05.

Results

Differences in the fecal compositions by vegetational zones

The mean proportions of the major foods are shown in Fig. 3 (see Supplementary material Appendix 1 Table A1 for other foods). In August, the mean proportion of dwarf bamboo in YT 1 samples was 55.4%, which was significantly greater than in YT 2 samples (0.1%; Kruskal–Wallis test, $\chi^2 = 23.079$, $p = 0.000$; Steel–Dwass test, $t_2 = 3.963$, $p = 0.000$) and YT 3 samples (0.2%; $t_2 = 3.862$, $p = 0.000$; Fig. 3). There were more grasses in samples obtained at higher elevation. The proportion

Table 1. Sampling sites of sika deer feces in Mt Yatsugatake (YT 1–3) and the Japanese South Alps (SA 1–3).

Plot	Location	Elevation (m)	Plot	Location	Elevation (m)
YT 1	Minoto	1760	SA 1	Todai River	1000
YT 2	Mt Akadake	2300	SA 2	Kitazawa Pass	2030
YT 2	Mt Ioudake	2760	SA 3	Mt Senjougadake	3030

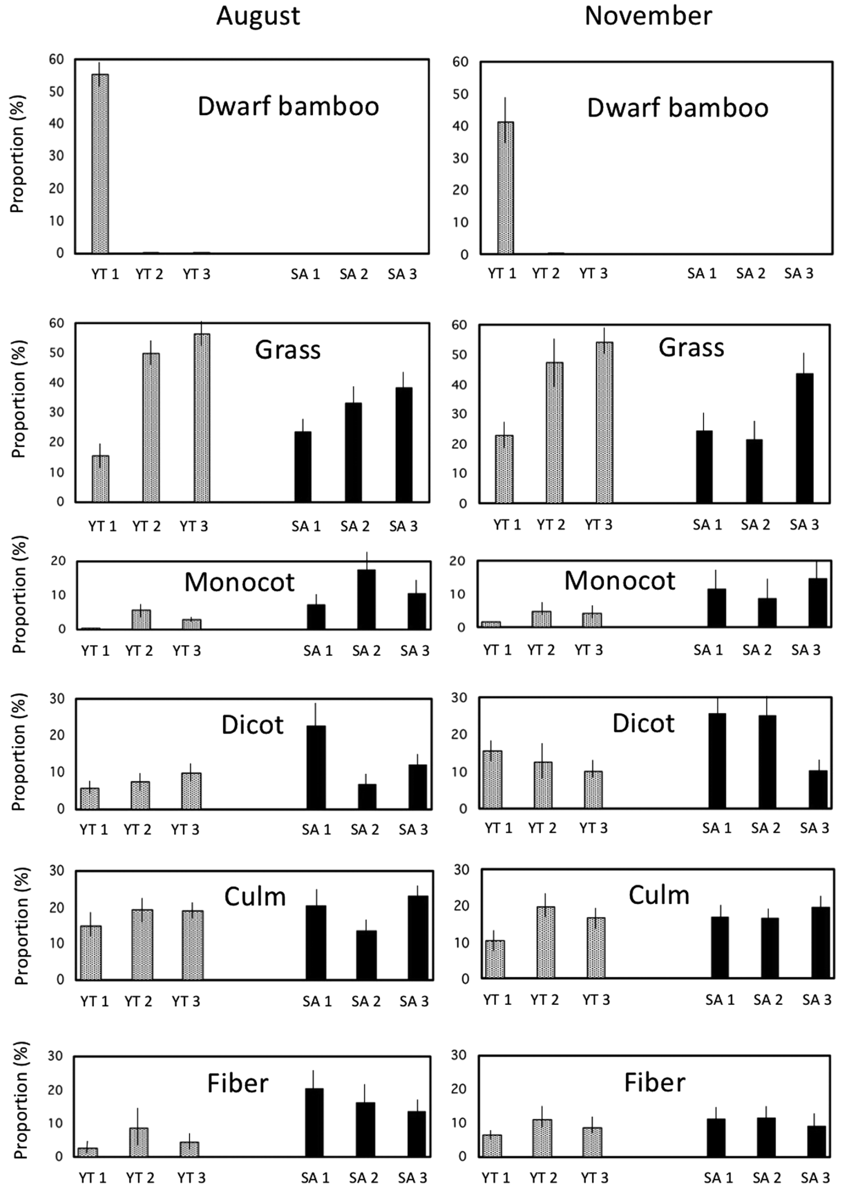

Figure 3. Proportions of the major foods in sika deer feces obtained from the montane (YT 1, SA 1), the middle subalpine (YT 2, SA 2) and the alpine zones (YT 3, SA 3) in Mt Yatsugatake (YT 1–3) and the Japanese South Alps (SA 1–3). Error bars indicate SD.

of grasses in YT 2 samples (49.5%) was higher than that in YT 1 samples (15.4%, Kruskal–Wallis test, $\chi^2 = 21.263$, $p = 0.000$; Steel–Dwass test, $t_2 = -3.780$, $p = 0.000$), but the proportions in YT 2 and YT 3 samples (56.4%) were not significantly different ($\chi^2 = -2.041$, $p = 0.103$). The proportions of grasses in SA 1 (23.5%) and SA 2 samples (33.2%, Kruskal–Wallis test, $\chi^2 = 11.404$, $p = 0.003$; Steel–Dwass test, $t_2 = -2.080$, $p = 0.094$), and those in SA 2 and SA 3 samples (38.3%, $t_2 = -0.984$, $p = 0.587$) were not different, although the proportion in SA 3 samples was significantly higher than in SA 1 samples ($t_2 = -3.413$, $p = 0.002$). There was a small proportion of monocots in samples from all zones, and the values were not significantly different between the zones, except between YT 1 (0.4%) and YT 2 (5.6%, Kruskal–Wallis test, $\chi^2 = 54.529$, $p = 0.001$; Steel–Dwass test, $t_2 = -3.732$, $p = 0.001$). The proportion of dicots in the samples obtained at high elevation seemed to be greater than those at low elevation in YT (Fig. 3), but the difference was not significant (YT 1–YT 2: Kruskal–Wallis test, $\chi^2 = 3.888$, $p = 0.143$; Steel–Dwass test, $t_2 = -1.022$, $p = 0.563$, YT 1–YT 3: $t_2 = -1.967$, $p = 0.121$, YT 2–YT 3: $t_2 = 0.910$, $p = 0.634$). The proportion of dicots in SA 1 samples (22.8%) was greater than that in SA 2 samples (6.8%, Kruskal–Wallis test, $\chi^2 = 14.400$, $p = 0.000$; Steel–Dwass test, $t_2 = 3.554$, $p = 0.001$); the proportion of dicots in SA 3 samples (12.3%) was significantly greater than that in SA 2 samples (6.8%, $t_2 = -2.385$, $p = 0.045$). Regarding culms, the proportion tended to be greater at higher elevations zones (Fig. 3), but significant difference was found only between YT 1 and YT 3 (Kruskal–Wallis test, $\chi^2 = 6.636$, $p = 0.036$; Steel–Dwass test, $t_2 = -2.575$, $p = 0.027$) and others were not significantly different (YT 1–YT 2: $t_2 = -1.853$, $p = 0.153$, YT 2–YT 3: $t_2 = 0.379$, $p = 0.924$). There was a larger proportion of fiber in YT 2 samples (8.5%) than YT 1 samples (2.5%, Kruskal–Wallis test, $\chi^2 = 8.651$, $p = 0.013$;

Steel–Dwass test, $t_2 = -2.847$, $p = 0.012$), but there was no difference between any other pair of sites. There was relatively more fiber in SA samples, but the values declined with elevation although difference was not significant among the sites (Kruskal–Wallis test, $\chi^2 = 4.555$, $p = 0.103$; SA 1–SA 2: Steel–Dwass test, $t_2 = -2.847$, $p = 0.012$; SA 1–SA 3: $t_2 = -1.444$, $p = 0.318$, SA 2–SA 3: $t_2 = -1.627$, $p = 0.234$, Fig. 3). In summary, dwarf bamboo was abundant in YT 1 samples and grasses were abundant in samples obtained at higher elevation in August.

A similar pattern was also observed in November (Fig. 3). There was a higher proportion of dwarf bamboo (41.2%) in YT 1 than YT 2 (0.2%, Mann–Whitney test, $U = 0$, $p = 0.000$). Samples at YT 3 did not contain dwarf bamboo. There were relatively more grasses in samples obtained at higher zones. The proportion of grasses in YT 2 samples (47.3%) was significantly higher than that in YT 1 samples (22.7%, Kruskal–Wallis test, $\chi^2 = 18.324$, $p = 0.000$; Steel–Dwass test, $t_2 = -3.275$, $p = 0.003$), but there was no significant difference between YT 2 and YT 3 samples (54.1%; $t_2 = -1.471$, $p = 0.305$). The proportion of grasses was not significantly different between SA 1 (12.3%) and SA 2 samples (10.6%, $t_2 = 0.718$, $p = 0.753$), but SA 3 samples had a higher proportion of grasses (23.7%) than SA 1 samples ($t_2 = -3.026$, $p = 0.007$). The proportion of monocots was greater in YT 3 samples than YT 1 samples (Kruskal–Wallis test, $\chi^2 = 5.647$, $p = 0.059$; Steel–Dwass test, $t_2 = -2.402$, $p = 0.043$) but there were not significant differences between YT 1 and YT 2 ($t_2 = -1.601$, $p = 0.245$) and YT 2 and YT 3 ($t_2 = -0.164$, $p = 0.985$). There was no significant difference among SA samples: SA 1–SA 2 (Kruskal–Wallis test, $\chi^2 = 3.050$, $p = 0.218$; Steel–Dwass test, $t_2 = 1.399$, $p = 0.341$), SA 1–SA 3 ($t_2 = -0.151$, $p = 0.987$) and SA 2–SA 3 ($t_2 = -1.589$, $p = 0.251$). Dicot content decreased in samples obtained at higher elevation and dicots were significantly more abundant in YT 1 (15.6%) than YT 3 samples (10.1%, Kruskal–Wallis test, $\chi^2 = 3.378$, $p = 0.025$; Steel–Dwass test, $t_2 = -2.574$, $p = 0.027$). There were more dicots in SA 2 samples (25.0%) than SA 3 samples (10.4%, $t_2 = 2.837$, $p = 0.013$). The proportion of culms seemed to increase with elevation (Fig. 3), but only the difference between YT 2 (19.6%) and YT 1 samples was significant (10.4%, $t_2 = -3.105$, $p = 0.005$). The proportion of culms was not different between SA 1 (25.6%) and SA 2 samples (25.0%, Kruskal–Wallis test, $\chi^2 = 1.235$, $p = 0.539$; Steel–Dwass test, $t_2 = 0.416$, $p = 0.909$), but SA 2 samples had significantly more culms than SA 3 samples (10.0%, $t_2 = 2.837$, $p = 0.013$). Fiber content was higher in YT 2 (11.0%) than YT 1 samples (6.4%, Kruskal–Wallis test, $\chi^2 = 9.524$, $p = 0.009$; Steel–Dwass test, $t_2 = -2.901$, $p = 0.010$), but there was no clear pattern by elevation. There was significantly less fiber in SA 3 samples (9.1%) than SA 1 samples (11.9%, Kruskal–Wallis test, $\chi^2 = 4.751$, $p = 0.093$; Steel–Dwass test, $t_2 = 2.431$, $p = 0.040$).

Seasonal comparisons

Fecal composition in three vegetational zones was compared between August and November at YT and SA (Supplementary material Appendix 1 Table A1). In YT 1 samples collected from August to November, there was a decrease in dwarf bamboo (Kruskal–Wallis test, $\chi^2 = 7.961$, $p = 0.019$; Steel–Dwass test, $t_2 = 2.721$, $p = 0.016$), but increases were seen in monocots (Kruskal–Wallis test, $\chi^2 = 9.441$, $p = 0.009$; Steel–Dwass test, $t_2 = -2.509$, $p = 0.032$), dicots (Kruskal–Wallis test, $\chi^2 = 15.522$, $p = 0.000$; Steel–Dwass test, $t_2 = -3.707$, $p = 0.001$) and fiber contents (Kruskal–Wallis test, $\chi^2 = 14.307$, $p = 0.001$; Steel–Dwass test, $t_2 = -2.620$, $p = 0.024$). No differences were found in YT 2 samples by month in most of the food plants: dwarf bamboo (Mann–Whitney test, $U = 31.5$, $p = 0.154$), grasses ($U = 41.5$, $p = 0.775$), monocots ($U = 35.0$, $p = 0.414$), dicots ($U = 23.5$, $p = 0.079$), culms ($U = 41.0$, $p = 0.744$) and fiber ($U = 26.5$, $p = 0.130$). Only fiber content increased from August to November in YT 3 samples ($U = 11.0$, $p = 0.003$).

At SA 1, only fiber content decreased from August to November (Kruskal–Wallis test, $\chi^2 = 13.553$, $p = 0.001$; Steel–Dwass test, $t_2 = 2.839$, $p = 0.013$) and increased from November to March ($t_2 = -3.027$, $p = 0.007$). In SA 2 samples, grasses (Mann–Whitney test, $U = 1.965$, $p = 0.049$) and monocots ($U = 2.116$, $p = 0.034$) decreased while dicots ($U = 3.479$, $p = 0.001$) and culms ($U = 3.712$, $p < 0.001$) increased. In SA 3 samples, only fiber decreased from August to November ($U = 2.728$, $p = 0.006$).

The above changes were not consistent among sites; for example, fiber increased in samples obtained from two YT sites from August to November, but decreased in those collected from two SA sites. Dicots increased in YT 1 and SA 2 samples from August to November, but did not change at other sites.

Percentage similarities

The PS values between YT and SA increased with elevation in both August and November (Fig. 4). The PS values were significantly different between the lower elevation montane zone (YT 1, SA 1) and the subalpine zones (YT 2, SA 2) (August: Kruskal–Wallis test, $\chi^2 = 210.134$, $p = 0.000$;

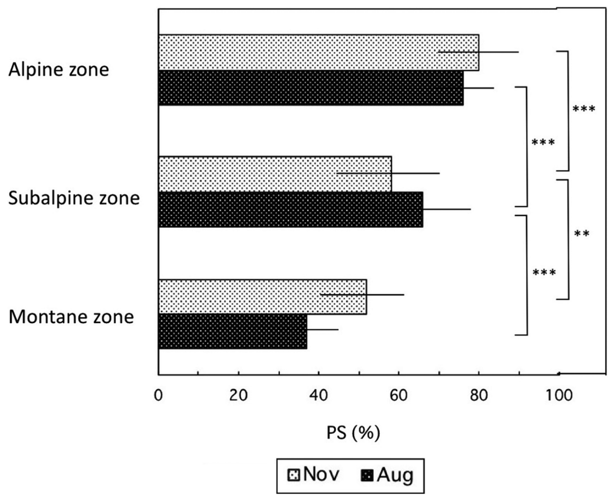

Figure 4. Percent similarities (PS) of sika deer fecal sample compositions between Mt Yatsugatake (YT) and the Japanese South Alps (SA), collected from different vegetational zones in August (light) and November (dark) 2011. Error bars indicate SD. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

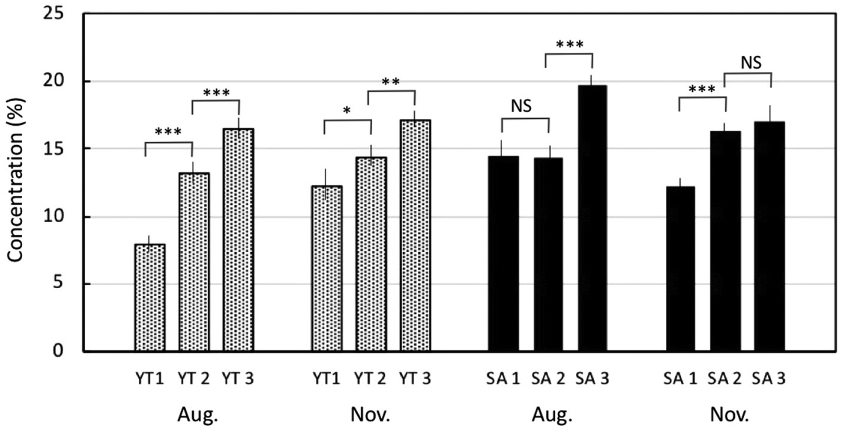

Figure 5. Crude protein content in sika deer feces collected from Mt Yatsugatake (YT 1–3) and the Japanese South Alps (SA 1–3) in August and November 2011. Error bars indicate SD. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS: not significant.

Steel–Dwass test, $t_2 = -11.895$, $p = 0.000$; November: Kruskal–Wallis test, $\chi^2 = 156.252$, $p = 0.000$; Steel–Dwass test, $t_2 = -3.184$, $p = 0.004$) and the subalpine and the higher elevation alpine zones (YT 3, SA 3) (August: Steel–Dwass test, $t_2 = -5.837$, $p = 0.000$, November: Steel–Dwass test, $t_2 = -10.244$, $p = 0.000$).

Fecal crude protein

The crude protein contents of deer feces obtained from different vegetational zones and seasons are shown in Fig. 5 (Supplementary material Appendix 1 Table A2).

1) Comparisons by different vegetational zones

For the YT samples obtained in August, the crude protein content increased with elevation (YT 1–YT 2: Kruskal–Wallis test, $\chi^2 = 42.226$, $p = 0.000$; Steel–Dwass test, $t_2 = -5.030$, $p = 0.000$; YT 2–YT 3: $t_2 = -5.092$, $p = 0.000$; Fig. 5); the pattern was similar in November (YT 1–YT 2: Kruskal–Wallis test, $\chi^2 = 31.699$, $p = 0.000$; Steel–Dwass test, $t_2 = -2.629$, $p = 0.023$; YT 2–YT 3: $t_2 = 4.060$, $p = 0.000$). For the SA samples obtained in August, no significant difference was found between SA 1 and SA 2 samples (Kruskal–Wallis test, $\chi^2 = 29.375$, $p = 0.000$; Steel–Dwass test, $t_2 = 0.292$, $p = 0.954$), but SA 3 samples had significantly higher crude protein than SA 2 samples ($t_2 = 6.480$, $p = 0.000$). In November, SA 2 samples had more crude protein than SA 1 samples (Kruskal–Wallis test, $\chi^2 = 32.559$, $p = 0.000$; Steel–Dwass test, $t_2 = -5.410$, $p = 0.000$), but no difference was found between SA 2 and SA 3 samples ($t_2 = -2.003$, $p = 0.112$).

2) Seasonal comparison

The fecal protein content at YT 1 was significantly higher in November than in August (Mann–Whitney test, $U = 21.0$, $p = 0.000$; Supplementary material Appendix 1 Table A2), but no seasonal difference was found in YT 2 samples ($U = 94.0$, $p = 0.200$) or YT 3 samples ($U = 106.0$, $p = 0.075$). The fecal protein content was higher in SA 1 samples ($U = 82.5$, $p = 0.004$) and SA 3 samples ($U = 66.0$, $p = 0.001$) collected in August than in November, but was higher in November than August for the SA 2 samples ($U = 90.0$, $p = 0.003$). Thus, there was no consistent seasonal change in fecal crude protein.

Discussion

Although differences in sika deer diet by vegetational zones have been studied previously (Takatsuki 1983, 1990b, 2009a), the alpine zone in central Japan has been inhabited by sika deer only for the last two decades and had not been studied until now. The deer cause vegetational changes and land degradation (Chubu Forest Management Office 2007, 2008, 2010, Nagaike 2012, Masuzawa 2015). This study is the first to quantify and compare the diets of sika deer in lower montane, subalpine and alpine zones of YT and the SA.

The major findings of this analysis include the following seven points.

1) Dwarf bamboos were predominant in the feces at YT 1. This is simply because dwarf bamboos were abundant only at YT 1.
2) Deciduous trees and shrubs were abundant at SA 1, which was well reflected in the fecal compositions (dicots: 22.8% in August, 25.6% in November), suggesting that dicots were an important food resource regardless of season.
3) Understories were dominated by conifers like *Tsuga* and *Abies* at YT2 and SA 2. The proportions of coniferous leaves in the feces were more at these subalpine sites than at other vegetational zones. However, the proportions in the feces were small (in August, 4.1% at YT 2, 2.7% at SA 2; in November, 2.5% at YT 2, 1.8% at SA 2), suggesting that conifers were not an important food source regardless of their abundance.
4) Our qualitative observations of habitats indicated that grasses were abundant in the alpine zone (Fig. 2), which was well reflected in the dominance of grasses in the feces (in August, 56.4% at YT 3, 38.3% at SA 3; in November, 54.1% at YT 3, 43.5% at SA 3). Grasses were also relatively abundant in the feces at the subalpine zones (in August, 49.9% at YT 2, 33.3% at SA 2; in November, 47.3% at YT 2, 21.5% at SA 2). However, observations of the subalpine habitat indicated that grasses were not abundant in these habitats (Fig. 2). Additional studies are needed to quantitatively compare the proportion of grasses in habitats, foraging patches and feces to determine if deer are selective for grasses.

5) Fiber was higher in the feces at SA 1 (20.5% in August, 11.5% in November) than at YT 1 (2.5% in August, 6.4% in November). Since fiber in the feces indicates less digestible twigs of woody plants and stems of forbs, it is difficult to interpret the fecal compositions by food availability. Less proportion of fiber at YT 1 may reflect the high abundance of dwarf bamboos at this site which is missing at SA 1 or relatively less woody plants there.
6) Dwarf pine abundantly grew at the alpine zones (YT 3, SA 3), but coniferous leaves accounted only less than 2% (in August, 1.4% at SA 3, 0.4% at SA 3; in November, 1/8% at YT 3, 0.3% at SA 3) in the deer feces. Again, additional studies are needed to quantitatively compare the proportion of pine in habitats, foraging patches and feces to determine if deer avoid this conifer.
7) Crude protein contents were higher at higher vegetational zones (Fig. 5). It may explain the reason of the recent invasion of the sika deer to the alpine zone.

Radiotelemetry studies on deer movements in central Japan showed that some deer that wintered in the lower areas ascended mountains in early summer, and stayed at the subalpine and alpine zones (Izumiyama and Mochizuki 2008, Izumiyama et al. 2009, Takii et al. 2012). Because sika deer are forest dwellers (Geist 1998, Takatsuki 2006), the alpine zone does not seem to be a suitable habitat for them because of the steep topography and lack of trees. Since only Siberian dwarf pine *Pinus pumila* shrubs and alpine meadows dominated by *Calamagrostis hakonensis*, *Veratrum album* and *Potentilla matsumurae* grew in the alpine zones (Chubu Forest Management Office 2010), the landscape is open, which is less preferred by sika deer (Takatsuki 1989b). Furthermore, alpine weather is unstable and may become cold even in summer. Despite these negative environmental factors, the alpine zone seems to provide high-quality forage. Since ruminants often face protein deficiency (Robbins 1992), high-protein plants are nutritionally valuable and the alpine zone is likely advantageous for sika deer in terms of forage quality. In fact, it is generally known that alpine plants are relatively high in nitrogen (Körner 1989). Some studies focusing on the foods of alpine ungulates provide evidence for the protein benefits of alpine vegetation. For example, wapiti *C. elaphus canadensis* in Alberta, Canada, migrated to the alpine zone to forage on high-protein plants (Morgantini and Hudson 1989, Hebblewhite et al. 2008). A study on bighorn sheep *Ovis canadensis* in southeastern Canadian Cordillera showed that plants at higher zones were more digestible and contained more protein, phosphorous and cellulose than plants at lower elevations (Johnston et al. 1968). Our results seem to support these former studies.

The recent invasion of sika deer into the alpine zone of central Japan reflects the population increase of the deer in the last three decades (Nakajima 2007). Ohashi et al. (2014) analyzed the factors associated with this phenomenon and showed that the range expansion occurred in areas with less snow. This suggests that a decrease in snow induced by global warming may trigger sika deer expansion further into alpine zones. Another likely factor is the decline in hunting pressure, which has decreased over the last three decades and may minimize the avoidance of open alpine zones by sika deer (Takatsuki 1989a). In 2015, there were 65% fewer hunters than in 1975 (<www.env.go.jp/nature/choju/docs/docs4/menkyo.pdf>). Additionally, deciduous forests were logged and coniferous trees, such as *Cryptomeria japonica* and *Chamaecyparis obtusa*, were intensively planted during the 1960s and the 1970s (Agetsuma 2007). These coniferous trees were densely planted, and prevented understory growth (Takatsuki 1990a), which resulted in a low carrying capacity of the deer. It is likely that the sika deer population expanded their range into higher areas, starting in the montane zone, followed by subalpine coniferous forests, and finally the alpine zone. Their effects on the alpine plants are large: many alpine forbs have shown a decline, while unpalatable forbs, such as *Ligularia dentata*, *Senecio cannabifolius* and *Artemisia sinanensis* thrive (Takatsuki 1989b, Watanabe et al. 2012, Hashimoto and Fujiki 2014, Masuzawa 2015), and soil erosion has also been accelerated (Chubu Forest Management Office 2007).

This is the first study to indicate that grasses are an important constituent of the diets of alpine sika deer in Japan. Since little is known regarding the effects of deer grazing in the alpine zone of central Japan (but see Nagaike 2012, Watanabe et al. 2012), the results of this study are important for future alpine deer management. This study has demonstrated the value of fecal analysis which can be compared to plant abundance within habitat to test for dietary preferences in the future.

Acknowledgements – Prof. T. Iriki at Azabu University advised the analysis of crude protein contents. A. Ohtsu and S. Yamamoto helped the analysis. Members of Bernina Alpine Club supported techniques of mountaineering.
Funding – This study was partly supported by Natural Parks Foundation (Volunteer Fund for Nature Conservation 2011).

References

Agetsuma, N. 2007. Ecological function losses caused by monotonous land use induce crop raiding by wildlife on the island of Yakushima, southern Japan. – Ecol. Res. 22: 390–402.

Akashi, N. and Terazawa, K. 2005. Bark stripping damage to conifer plantations in relation to the abundance of sika deer in Hokkaido, Japan. – For. Ecol. Manage. 208: 77–83.

Chamrad, A. D. and Box, W. W. 1964. A point frame for sampling rumen contents. – J. Wildl. Manage. 28: 473–477.

Chubu Forest Management Office. 2007. Report of deer damage in the conservation forest in Japanese South Alps. – Chubu Forest Management Office, in Japanese.

Chubu Forest Management Office. 2008. Report of deer damage in the conservation forest in Japanese South Alps. – Chubu Forest Management Office, in Japanese.

Chubu Forest Management Office. 2010. Report of deer damage at the alpine zone of Mt Yatsugatake. – Chubu Forest Management Office, in Japanese.

Geist, V. 1998. Deer of the world – their evolution, behavior and ecology. – Stackpole Books.

Hebblewhite, M. et al. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. – Ecol. Monogr. 78: 141–166.

Hashimoto, Y. and Fujiki, D. 2014. List of food plants and unpalatable plants of sika deer (*Cervus nippon*) in Japan. – Hum. Nat. 25: 133–160, in Japansese with English abstract.

Igota, H. et al. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. – Ecol. Res. 19 : 169–178.

Iida, T. et al. 2016. Effects of an increase in population of sika deer on beetle communities in deciduous forests. – Zookeys 625: 67–85.

Izumiyama, S. et al. 2008. Seasonal range use of sika deer which inhabits the sub-alpine zone in the southern Japan Alps. – Bull. Shinshu Univ. AFC 6: 25–32, in Japanese with English abstract.

Izumiyama, S. et al. 2009. GPS tracking of sika deer which inhabits the sub-alpine zone in the southern Japan Alps. – Bull. Shinshu Univ. AFC 7: 63–71, in Japanese with English abstract.

Johnston, A. et al. 1968. Chemical composition and in vitro digestibility of alpine tundra plants. – J. Wildl. Manage. 32: 773–777.

Körner, C. 1989. The nutritional status of plants from high altitudes. – Oecologia 81: 379–391.

Masuzawa, T. 2015. The alpine vegetation of Japanese South Alps and sika deer. – In: Maesako, Y. and Takatsuki, S. (eds), Threats of sika deer and the future of Japanese forests – effectiveness and limits of deer-proof fences for vegetation conservation. Bun-ichi Shuppan Co., Tokyo, pp. 173–184, in Japanese.

Morgantini, L. E. and Hudson, R. J. 1989. Nutritional significance of wapiti (*Cervus elaphus*) migrations to alpine ranges in western Alberta, Canada. – Arct. Alp. Res. 21: 288–295.

Nagaike, T. 2012. Effects of browsing by sika deer (*Cervus nippon*) on subalpine vegetation at Mt Kita, central Japan. – Ecol. Res. 27: 467–473.

Nagano Prefecture. 2016. Management plan for sika deer of Nagano Prefecture – Fourth period. – Nagano Prefecture, in Japanese.

Nakajima, N. 2007. Changes in distribution of sika deer in Japan. – In: Morimoto Y. and Yasuda, Y. (eds), Rebellion of wildlife and collapse of forest. Tokyo Sinrinbunka-kyokai, pp. 57–68.,in Japanese.

Ohashi, H. et al. 2007. Long-term changes in the species composition of plant communities caused by the population growth of sika deer (*Cervus nippon*) in Okutama, Tokyo. – Veg. Sci. 24: 123–151, in Japanese with English abstract.

Ohashi, H. et al. 2014. The impact of sika deer on vegetation in Japan: setting management priorities on a national scale. – Environ. Manage. 54: 631–640.

Okuda, K. et al. 2012. Effects of vegetation modification due to high deer density on breeding bird communities in Oku-Nikko – Japan. J. Jpn For. Soc. 94: 236–242.

Otsu, C. et al. 2011. Impacts of the sika deer on montane and subalpine grasslands in Chichibu-Tama-Kai National Park and surrounds, central Japan. – Veg. Sci. 28: 1–17, in Japanese with English abstract.

Robbins, C. T. 1992. Wildlife feeding and nutrition, 2nd edn. – Academic Press.

Sakuragi, M. et al. 2004. Female sika deer fidelity to migration route and seasonal ranges in eastern Hokkaido, Japan. – Mamm. Study 29: 113–118.

Seki, Y. and Koganezawa, M. 2012. Does sika deer overabundance exert cascading effects on the raccoon dog population? – J. For. Res. 18: 121–127.

Stewart, D. R. M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. – J. Appl. Ecol. 4: 83–111.

Takatsuki, S. 1978. Precision of fecal analysis: a feeding experiment with penned sika deer. – J. Mamm. Soc. Jpn 7: 167–180.

Takatsuki, S. 1983. The importance of *Sasa nipponica* as a forage for sika deer (*Cervus nippon*) in Omote-Nikko. – Jpn J. Ecol. 33: 17–25.

Takatsuki, S. 1989a. Edge effects created by clear-cutting on habitat use by sika deer on Mt Goyo, northern Honshu, Japan. – Ecol. Res. 4: 287–295.

Takatsuki, S. 1989b. Effects of deer on plants and plant communities. – Jpn J. Ecol. 39: 67–80.

Takatsuki, S. 1990a. Changes in forage biomass following logging in a sika deer habitat near Mt Goyo. – Ecol. Rev. 22: 1–8.

Takatsuki, S. 1990b. Summer dietary compositions of sika deer on Yakushima Island, southern Japan. – Ecol. Res. 5: 253–260.

Takatsuki, S. 2006. Ecological history of sika deer. – Tokyo Univ. Press, in Japanese.

Takatsuki, S. 2009a. Effects of sika deer on vegetation in Japan: a review. – Biol. Conserv. 142: 1922–1929.

Takatsuki, S. 2009b. North–south variations in sika deer ecology as a forest-dwelling cervid. – In: McCullough, D. et al. (eds), Sika deer: biology and management of native and introduced populations. Springer, Elsevier, Tokyo, pp. 217–230.

Takatsuki, S. et al. 2000. Seasonal up–down movements of sika deer at Mt Goyo, northern Japan. – Mamm. Study 25: 107–114.

Takii, A. et al. 2012. Seasonal migration of sika deer in the Oku-Chichibu Mountains, central Japan. – Mamm. Study 37: 127–137.

Tamura, A. 2013. Effects of time lag in establishment of deer-proof fences on recovery of floor vegetation and regeneration of tall trees in a beech forest diminished by sika deer browsing in the Tanzawa Mountains of central Japan. – J. Jpn For. Soc. 95: 8–14, in Japanese with English abstract.

Watanabe, O. et al. 2012. Effect of sika deer fencing on the recovery of alpine vegetation on the Mt Senjo in central Japan. – J. Fac. Agric. Shinshu Univ. 48: 17–27, in Japanese with English abstract.

Watanabe, T. and Takatsuki, S. 1993. Comparison of nitrogen and fiber concentrations in rumen and fecal contents of sika deer. – J. Mammal. Soc. Jpn 18: 43–48.

Whittaker, R. H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. – Ecol. Monogr. 22: 1–44.

Yamada, H. and Takatsuki, S. 2015. Effects of deer grazing on vegetation and ground-dwelling insects in a larch forest in Okutama, western Tokyo. – Int. J. For. Res. 2015: 1–9.

Yamanashi Prefecture 2017. Management plan for sika deer of Yamanashi Prefecture – Second period. – Yamanashi Prefecture, in Japanese.

Supplementary material (available online as Appendix wlb-00710 at <www.wildlifebiology.org/appendix/wlb-00710>). Appendix 1.