Why do sika deer, *Cervus nippon*, debark trees in summer on Mt. Ohdaigahara, central Japan?

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Abstract. Bark stripping by sika deer, *Cervus nippon*, causes severe damage to forests. The seasonality of bark stripping by deer and tree selection were examined on Mt. Ohdaigahara in central Japan. The chemical content and physical properties of the bark were analyzed. About 60% of all tree species suffer various degrees of seasonal bark stripping. Bark stripping is most intensive during summer when the deer's main forage, *Sasa nipponica*, is abundant, suggesting that bark stripping is not due to food shortages. The bark physical properties seem to affect barking selection among three coniferous species, but not its seasonality. The nutritive value of bark is lower than that of *S. nipponica*, which has high crude protein and hemicellulose contents in summer but an inadequate mineral balance in summer, suggesting that sika deer eat the bark either to balance the digestible nutrients of summer forage and/or to attain a proper mineral balance in summer.

Key words: bark chemical content, bark physical property, bark selection, bark stripping, *Cervus nippon*.

Cervids have a profound impact on forest ecosystems (Anderson and Loucks 1979; Takatsuki and Gorai 1994; Akashi and Nakashizuka 1999; Fuller and Gill 2001; Virtanen et al. 2002) by browsing, bark stripping and fraying (Gill 1992). Above all, the impact of bark stripping causes the most severe problems, resulting in die-back of overstory trees and forest decline. Thus, deer debarking has serious effects on plant communities (Miquelle and Van Ballenberghe 1989; Akashi and Nakashizuka 1999). Bark stripping by cervids occurs worldwide: red deer, *Cervus elaphus* L., in Europe (McIntyre 1972; Welch et al. 1987; Motta 1996) moose, *Alces alces* L., in North America and Scandinavia (Miquelle and Van Ballenberghe 1989; Faber 1996; Randveer and Heikkilä 1996), sambar, *Cervus unicolor* (Kerr), in India and New Zealand (Khan et al. 1994; Stafford 1997) and other cervids (Gill 1992; Parks et al. 1998). Bark stripping by sika deer, *Cervus nippon* Temminck, occurs in both primeval forests and managed plantations in Japan (Kaji et al. 1984; Oi and Itoya 1997; Yokoyama et al. 2001; Ueda et al. 2002; Ando et al.

2003; Nagaike and Hayashi 2003).

Sika deer in Japan have bark-stripping preferences (Sekine and Sato 1992; Kanzaki et al. 1998; Sakabe et al. 1998; Yokoyama et al. 2001; Ando et al. 2003). Miquelle and Van Ballenberghe (1989) also demonstrated that moose strip the bark of aspen and bebb willow, but not white spruce. Although seasonal observation of bark-stripping preference for many tree species is required to clarify why deer debark trees, there are still no detailed observations.

The seasonal change in bark stripping in coniferous plantations showed that bark stripping is frequent in winter and spring (Welch et al. 1987; Faber 1996; Oi and Itoya 1997; Ueda et al. 2002). In Europe and North America, McIntyre (1972), Welch et al. (1987), Miquelle and Van Ballenberghe (1989), Gill (1992) and Motta (1996) presumed that deer eat bark due to food shortages in winter. Khan et al. (1994) also explained bark stripping by sambar resulting from food shortages caused by drought. In northern Japan, Kaji et al. (1984), Oi and Itoya (1997) and Ueda et al. (2002) mentioned that bark

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stripping by sika deer coincided with food shortages in winter and early spring.

However, in the primeval forest on Mt. Ohdaigahara, Yokoyama et al. (1996) used fecal analysis to show that deer ate bark of coniferous trees throughout the year and that bark stripping may occur most frequently in summer. In addition, Yokoyama and Shibata (1998) showed that the biomass and crude protein content of the dwarf bamboo, *Sasa nipponica* (Makino) Makino et Shibata – the main forage of sika deer in this area – is highest in summer, suggesting that sika deer do not eat bark due to food shortages. The nutrients in bark (starch, water, sugar and other components) are not convincing evidence explaining why deer eat bark (Gill 1992).

Faber (1996) supposed the reason for bark stripping by moose in April and May was to ingest roughage for proper rumen function and/or to feed on a palatable food containing high starch and total carbohydrates. Oi and Itoya (1997) demonstrated that the bark of *Cryptomeria japonica* D. Don in plantations is easy to peel off in early spring when bark stripping occurs frequently, suggesting that the physical properties of bark affect the seasonal change in bark stripping and also affect the bark-stripping preference.

In this paper, we investigate (1) bark stripping seasonal occurrence and preference, (2) seasonal amount of stripped bark, (3) seasonal change in chemical content of bark compared to leaves of dwarf bamboo, the main forage of sika deer, and (4) seasonal change in physical properties of the bark of frequently stripped tree species. We clarify which tree species sika deer selectively debark, and when and why sika deer strip bark on Mt. Ohdaigahara.

Materials and methods

Study site

Mt. Ohdaigahara is located on the Kii Peninsula of central Japan (Fig. 1). Elevations vary from 1400 m in the west to 1600 m in the east with gentle slopes. Cool temperatures and heavy rainfall characterize the climate. The mean annual temperature and mean annual precipitation are 5.7°C and ≥ 4000 mm, respectively. The vegetation of the primeval forest on Mt. Ohdaigahara can be divided into two major types. The eastern area is covered with coniferous forest, dominated by *Picea jezoensis* Carr. var. *hondoensis* Rehd. and *Abies homolepis* Sieb. et Zucc. The western area is mixed forest,

Fig. 1. Location of Mt. Ohdaigahara, central Japan. •: Transect.

dominated by *Fagus crenata* Blume and *A. homolepis*. The dwarf bamboo, *S. nipponica*, covers most of the forest floor in the eastern area. The average density of sika deer on Mt. Ohdaigahara in spring 1997 was ca. 28 deer/km² (Maeji et al. 1999).

Field measurements

To determine the area of stripped bark, we established six belt transects (8 m × 50 m) on Mt. Ohdaigahara in July 1999 (Fig. 1). In each transect, we measured the diameter at breast height (dbh) of all woody plants (height ≥ 1.6 m). We measured the available bark area on the tree trunk (up to 1.6 m height) and butt swelling for deer by the method in Ando et al. (2003). When we found a stripping wound on a tree trunk, we marked the wound edges with tape to allow identification of new barking. On Mt. Ohdaigahara, there are two types of bark-stripping wounds caused by deer: feeding and fraying, which are classified easily by wound shape. In this study, only feeding wounds were checked. To clarify the seasonal change in bark stripping, we checked for new bark stripping on all trees every 2 months except in winter. We divided the seasons into spring (mid-May to mid-July), summer (mid-July to mid-September), fall (mid-September to mid-November), and winter (mid-November to mid-May).

To indicate deer preference for tree species, Ivlev's electivity index (E) was calculated as follows (Ivlev 1965):

$$E = (r_i - P_i) / (r_i + P_i) \quad (-1 \leq E \leq 1)$$

where, r_i is the ratio of damaged bark area of each species to total damaged bark area, and P_i is the ratio of available bark area of each species to total available bark area. $E = 0$ when deer bark randomly, > 0 when deer bark preferably, and < 0 when deer bark aversely.

Chemical analysis

To compare the chemical contents of bark stripped frequently by deer (Ando et al. 2003) and the leaves of dwarf bamboo, we collected the bark of *P. jezoensis* var. *hondoensis*, *A. homolepis* and *Clethra barbinervis* Sieb. et Zucc. and the leaves of two dwarf bamboos, *S. nipponica* and *Sasamorpha borealis* (Hack.) Nakai once every 2 months from September 1998 to July 2000. We selected five individuals of each tree species near the transects and collected bark (ca. 10 cm × 10 cm) including outer and inner bark and cambium from the trunk at breast

height using a chisel. Bamboo leaves (ca. 100 g, fresh weight) were clipped from plants near each transect. All samples were dried (60°C, 48 hours), milled, stored in a refrigerator, and then analyzed for crude protein, fibers (hemicellulose, cellulose and lignin) and minerals (Ca, Mg, Na, and K). We calculated the equivalent ratio of $K/(Ca + Mg)$ as an indicator of the mineral balance of the forage.

Crude protein is a typical indicator of the nutritional value of diet, and fiber is also an important indicator for evaluating feedstuffs of ruminant livestock. Four minerals are essential for bone formation (Ca and Mg), enzyme activation (Ca, Mg and K), lactation (Ca), nerve and muscle function (Ca, Mg and K), and regulation of body fluid volume and osmolarity (Na and K) (Robbins 1993; Okumura and Tanaka 1995).

Nitrogen content was analyzed by the Kjeldahl technique and converted to crude protein content by multiplying the nitrogen content by 6.25. Fiber was measured according to Van Soest and Wine (1967). Mineral content was determined by atomic absorption with atomic absorption spectrophotometer (AA-6200, Shimadzu, Kyoto, Japan).

Determination of physical properties

To clarify the physical properties of the bark of three coniferous species: *P. jezoensis* var. *hondoensis*, *A. homolepis* and *Chamaecyparis obtusa* (Sieb. et Zucc.) Endl., we examined the bark hardness and thickness once every month from April to November 2002. Three to five trees were sampled. The results were combined into the following periods: early spring (April and May), spring (June and July), summer (August and September), and fall (October and November). We could not examine any tests in winter (December to March) because of deep snow in this area.

We examined the bark hardness by two methods. A 2 cm × 10 cm incision with uncut top edge was made in the bark of a live tree. The bottom cut end was attached to a spring balance and the maximum tension needed to tear the bark away from the tree (bark unrendability) was measured. In another method, a 5 cm × 5 cm piece of bark including outer and inner bark was collected and its hardness (bark hardness) was measured with a soil sclerometer (Push Cone, Daiki Rika Kogyo, Tokyo, Japan). We also measured the thickness of outer, inner and total bark with a digital caliper.

Statistical analyses

The data of the stripped bark area of total (all trees), coniferous, broadleaf and each tree species in three years were pooled in four seasons and the difference among the seasons was analyzed using a one-way ANOVA and Tukey's H.S.D. test ($P < 0.05$). Differences among the chemical contents of the leaves and barks were also analyzed using a two-way ANOVA ($P < 0.05$). When the interaction between seasons and species was detected in a two-way ANOVA, a one-way ANOVA with a Bonferroni correction and Tukey's H.S.D. test ($P < 0.006$) in each chemical content was adopted for detecting the difference of species in each season. Differences among the physical properties of three coniferous species were analyzed using a two-way ANOVA and Scheffe's test ($P < 0.05$). When a two-way ANOVA showed the interaction between seasons and species, the differences among the species in each property were analyzed using

a one-way ANOVA with a Bonferroni correction and Scheffe's test ($P < 0.013$) in each season. SPSS 7.5J for Windows (SPSS Inc., Chicago, U.S.A.) was used for all tests.

Results

Occurrence of bark stripping

The results of the field measurements between July 1999 and July 2002 for the six transects on Mt. Ohdaigahara are shown in Table 1. Twenty five species (4 coniferous, 21 broadleaf) were observed in the six transects. Fifteen species (4 coniferous, 11 broadleaf) were barked on the trunk. The percentage of barked coniferous trees (69.0%) was higher than that of barked broadleaf trees (19.0%).

Both the total available bark area and the stripped bark area of the coniferous trees were larger than those of

Table 1. Total stripped area and electivity indices (E) in each species between July 1999 and July 2002 on six transects on Mt. Ohdaigahara. The real number observed at six transects (2,400 m²) was showed on the table.

Species	Number of trees	Number of barked trees	Basal area (m ²)	Mean dbh (cm $\pm$ SD)	Available bark area (m ²)	Stripped bark area (m ²)	E
Coniferous							
<i>Abies homolepis</i>	91	67 (73.6%)	3.22	20.1 $\pm$ 6.9	103.83	6.102	0.22
<i>Picea jezoensis</i> var. <i>hondoensis</i>	19	18 (94.7%)	1.24	27.8 $\pm$ 7.6	37.27	1.503	0.03
<i>Chamaecyparis obtusa</i>	29	12 (41.4%)	1.15	18.4 $\pm$ 13.0	33.50	0.808	-0.22
<i>Taxus cuspidata</i>	3	—	—	—	—	—	—
Broadleaf							
<i>Clethra barbinervis</i>	16	12 (75.0%)	0.07	6.7 $\pm$ 3.9	5.69	2.047	0.81
<i>Ilex geniculata</i>	5	3 (60.0%)	0.01	4.2 $\pm$ 0.8	1.04	0.068	0.27
<i>Sorbus commixta</i>	4	1 (25.0%)	0.06	13.3 $\pm$ 5.5	3.42	0.156	0.09
<i>Pourthiaea villosa</i> var. <i>laevis</i>	35	6 (17.1%)	0.07	4.4 $\pm$ 2.2	7.72	0.241	-0.10
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>	12	7 (58.3%)	0.18	12.8 $\pm$ 5.8	8.05	0.232	-0.14
<i>Viburnum wrightii</i>	4	1 (25.0%)	0.01	4.0 $\pm$ 3.6	0.75	0.014	-0.35
<i>Symplocos coreana</i>	31	3 (9.7%)	0.07	5.0 $\pm$ 2.2	7.89	0.064	-0.65
<i>Hamamelis japonica</i>	6	1 (16.7%)	0.07	12.1 $\pm$ 3.1	3.04	0.016	-0.76
<i>Acer shirasawanum</i>	38	2 (5.3%)	0.71	12.9 $\pm$ 8.6	27.50	0.018	-0.97
<i>Fagus crenata</i>	33	0 (0.0%)	1.88	20.6 $\pm$ 17.6	42.61	0	-1
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	5	0 (0.0%)	0.19	17.2 $\pm$ 14.8	6.78	0	-1
<i>Acer sieboldianum</i>	1	0 (0.0%)	—	—	—	—	—
<i>Berberis tschonoskii</i>	1	0 (0.0%)	—	—	—	—	—
<i>Betula grossa</i>	3	2 (66.7%)	—	—	—	—	—
<i>Eleutherococcus sciadophylloides</i>	3	0 (0.0%)	—	—	—	—	—
<i>Kalopanax pictus</i>	2	0 (0.0%)	—	—	—	—	—
<i>Phellodendron amurense</i>	1	1 (100%)	—	—	—	—	—
<i>Stewartia monadelpha</i>	1	0 (0.0%)	—	—	—	—	—
<i>Tilia japonica</i>	2	0 (0.0%)	—	—	—	—	—
<i>Viburnum dilatatum</i>	1	0 (0.0%)	—	—	—	—	—
<i>Viburnum furcatum</i>	1	0 (0.0%)	—	—	—	—	—
Subtotal							
Coniferous	142	98 (69.0%)	5.67	14.1 $\pm$ 12.6	176.15	8.423	0.12
Broadleaf	205	39 (19.0%)	3.57	14.7 $\pm$ 11.1	124.73	2.996	-0.22
Total	347	137 (39.5%)	9.24	15.7 $\pm$ 9.5	300.89	11.419	—

—: not calculated ($n \leq 3$).

broadleaf trees. *A. homolepis* had the largest available bark area and the largest stripped bark area of all tree species (Table 1). *P. jezoensis* var. *hondoensis* and *C. obtusa* showed relatively large available bark area and relatively large stripped bark area (Table 1). *Acer shirasawanum* Koidz. had a relatively large available bark area and a small stripped bark area. Although *F. crenata* had a relatively large available bark area, no barking was found during the study period. *C. barbinervis*, *Fraxinus lanuginosa* f. *serrata* (Nakai) Hara and *Pourthiaea villosa* (Thunb.) Dence. var. *laevis* (Thunb.) Stapf. showed relatively large stripped bark areas. Ten broadleaf species including *F. crenata* did not suffer any bark stripping during this study period.

Seasonal bark stripping

The seasonal change in the stripped bark area from

Fig. 2. The mean bark stripped area between July 1999 and July 2002, along six transects on Mt. Ohdaigahara, central Japan. Vertical bars show SD. Each season means from mid-May to mid-July (spring), mid-July to mid-September (summer), mid-September to mid-November (fall), and mid-November to mid-May (winter). Means followed by the different letters are significantly different (Tukey's H.S.D. test, $P < 0.05$).

July 1999 to July 2002 is shown in Fig. 2. The stripped bark area of total (all trees) in summer was significantly higher than that of other seasons (one-way ANOVA, $F = 11.679$, $P = 0.003$). The stripped bark area of coniferous trees in summer was also significantly higher than that of spring (one-way ANOVA, $F = 5.557$, $P = 0.023$). That of broadleaf trees showed a relatively indistinct peak in summer (one-way ANOVA, $F = 3.818$, $P > 0.05$).

The seasonal change in the stripped bark area of the six tree species that were largely stripped is shown in Fig. 3. The stripped bark area of *P. jezoensis* var. *hondoensis* had a clear peak in summer (one-way ANOVA, $F = 24.758$, $P < 0.001$). Although the seasonal change in the stripped bark area of coniferous trees peaked in summer (Fig. 2), *A. homolepis* and *C. obtusa* did not show a clear peak in summer (one-way ANOVA, $F = 1.299$, $P > 0.05$) (Fig. 3). New bark-stripping wounds were observed on *A. homolepis* in every season. The stripped bark area of *C. barbinervis* was relatively large in spring and summer (one-way ANOVA, $F = 2.644$, $P > 0.05$). *F. lanuginosa* f. *serrata* (one-way ANOVA, $F = 2.073$, $P > 0.05$) and *P. villosa* var. *laevis* (one-way ANOVA, $F = 1.082$, $P > 0.05$) did not show a clear seasonal change.

Bark selection

The number of barked tree species in spring was smaller than in other seasons (Table 2). The electivity index for all coniferous trees ($E = 0.12$) was higher than that for broadleaf trees ($E = -0.22$) (Table 1). The indices for coniferous species were relatively large, but those for broadleaf species varied with species. *C. barbinervis* had the largest electivity index ($E = 0.81$) followed by *Ilex geniculata* Maxim. (0.27) and *A. homolepis* (0.22) (Table 1). The electivity index for each tree species in each season is summarized in Table 2. The electivity indices for *A. homolepis* were relatively high in fall and winter. *P. jezoensis* var. *hondoensis* showed the highest electivity indices in summer. The electivity indices for *C. barbinervis* were very high in spring, summer and fall (Table 2).

Chemical contents

Figure 4 shows the seasonal change of the chemical contents of leaves and barks. There were significant differences among samples, seasons and their interactions in each chemical content (two-way ANOVA, Table 3). The crude protein and hemicellulose contents of the leaves of *S. nipponica* in each season were significantly

Fig. 3. The mean bark stripped area in six tree species stripped frequently in this study. Vertical bars show SD. Each season means from mid-May to mid-July (spring), mid-July to mid-September (summer), mid-September to mid-November (fall), and mid-November to mid-May (winter). Means followed by the different letters are significantly different (Tukey's H.S.D. test, $P < 0.05$).

Table 2. Electivity indices (E) in each tree species ($n \geq 4$) in four seasons on Mt. Ohdaigahara. The indices of three years were calculated with the data of stripped area which pooled in each season. Spring: mid-May to mid-July, Summer: mid-July to mid-September, Fall: mid-September to mid-November, Winter: mid-November to mid-May.

Species	Spring	Summer	Fall	Winter
Coniferous				
<i>Abies homolepis</i>	-0.74	0.10	0.29	0.40
<i>Picea jezoensis</i> var. <i>hondoensis</i>	-0.02	0.31	-0.13	-0.80
<i>Chamaecyparis obtusa</i>	-0.01	-0.12	-0.61	-0.35
Coniferous total	-0.35	0.12	0.13	0.20
Broadleaf				
<i>Clethra barbinervis</i>	0.94	0.81	0.81	0.24
<i>Fraxinus lanuginosa</i> f. <i>serrata</i>	-0.15	0.10	0.03	-1
<i>Ilex geniculata</i>	-1	0.57	-0.07	-1
<i>Hamamelis japonica</i>	-1	-0.79	-0.24	-1
<i>Pourthiaea villosa</i> var. <i>laevis</i>	0.44	-0.95	-0.80	0.25
<i>Acer shirasawanum</i>	-1	-1	-0.93	-0.92
<i>Fagus crenata</i>	-1	-1	-1	-1
<i>Symplocos coreana</i>	-1	-1	-0.48	-0.32
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	-1	-1	-1	-1
<i>Sorbus commixta</i>	-1	-0.90	-0.21	0.55
<i>Viburnum wrightii</i>	-1	0.05	-1	-1
Broadleaf total	0.27	-0.23	-0.27	-0.52

Fig. 4. Seasonal changes in each chemical content between September 1998 and July 2000. Error bars show SD. *: Hemicellulose was not detected in the bark of *P. jezoensis* var. *hondoensis*.

higher than those of bark (one-way ANOVA, Table 4). Although significant differences are detected in cellulose and Na by one-way ANOVA in each season (Table 4), the results of Tukey's H.S.D. test among samples in each season showed no clear trends between the bamboo leaves and tree bark. Lignin, which is an indigestible component, content of the tree bark was significantly higher than the contents of the bamboo leaves throughout the year (one-way ANOVA, Table 4). Except September 1998 and March 1999, Ca content of the tree bark was significantly higher than the contents of the leaves of *S. nipponica* throughout the year (one-way ANOVA, Table 4). The Mg content in the bark of *C. barbinervis* and the leaves of *S. nipponica* was significantly higher than the bark of *P. jezoensis* var. *hondoensis* and *A. homolepis* except May 1999. $K/(Ca + Mg)$ of the tree bark was significantly lower than that of the leaves of *S. nipponica* except March 1999 (one-way ANOVA, Table 4).

The crude protein, hemicellulose and K contents of

Table 3. The results of two-way ANOVA detecting the difference among bamboo leaves and tree barks in each chemical content.

Chemical content	Source of variation	<i>F</i>	<i>P</i>
Crude protein	Species	1686.323	<0.001
	Season	8.241	<0.001
	Species × Season	6.585	<0.001
Hemicellulose	Species	3469.414	<0.001
	Season	26.667	<0.001
	Species × Season	17.940	<0.001
Cellulose	Species	161.852	<0.001
	Season	13.200	<0.001
	Species × Season	3.850	<0.001
Lignin	Species	1019.248	<0.001
	Season	19.588	<0.001
	Species × Season	4.776	<0.001
Ca	Species	154.958	<0.001
	Season	12.423	<0.001
	Species × Season	2.911	<0.001
Mg	Species	275.733	<0.001
	Season	15.080	<0.001
	Species × Season	1.616	<0.001
Na	Species	17.835	<0.001
	Season	26.889	<0.001
	Species × Season	4.697	<0.001
K	Species	207.212	<0.001
	Season	7.170	<0.001
	Species × Season	3.936	<0.001
$K/(Ca + Mg)$	Species	333.475	<0.001
	Season	7.216	<0.001
	Species × Season	2.959	<0.001

S. nipponica had peaks in summer. The equivalent ratio of $K/(Ca + Mg)$ of *S. nipponica* overreached above 2.2 in May and July 1999 and July 2000, and peaked in July 1999.

Bark physical properties

Figure 5 shows the seasonal change of the physical properties of three coniferous species. There were significant differences among samples and sample-season interactions in bark unrendability (two-way ANOVA, species: $F = 26.093$, $P < 0.001$, season: $F = 2.667$, $P = 0.054$, interaction: $F = 3.280$, $P = 0.007$), which of *C. obtusa* was significantly higher than that of *P. jezoensis* var. *hondoensis* and *A. homolepis* in spring and fall (one-way ANOVA, Table 5). The bark of *A. homolepis* was significantly harder both in inner bark (two-way ANOVA, species: $F = 69.717$, $P < 0.001$, season: $F = 0.496$, $P = 0.612$, interaction: $F = 1.224$, $P = 0.312$) and in outer bark (two-way ANOVA, species: $F = 16.054$, $P < 0.001$, season: $F = 3.062$, $P = 0.055$, interaction: $F =$

Table 4. The results of one-way ANOVA detecting the difference among each chemical content of bamboo leaves and tree barks in each month.

Chemical content		Sep., 98	Nov., 98	Mar., 99	May, 99	Jul., 99	Sep., 99	Nov., 99	May, 00	Jul., 00
Crude protein	<i>F</i>	153.721	103.462	211.876	167.031	278.584	163.486	262.580	215.782	264.555
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Hemicellulose	<i>F</i>	281.956	254.692	311.638	1075.034	272.359	620.148	1021.573	489.150	380.287
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Cellulose	<i>F</i>	11.764	10.887	59.257	11.368	34.265	36.089	28.458	21.877	24.724
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Lignin	<i>F</i>	195.956	223.299	151.437	114.499	88.770	161.848	117.377	95.323	57.995
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Ca	<i>F</i>	6.646	35.260	6.688	16.327	35.741	29.639	20.374	38.477	21.528
	<i>P</i>	0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Mg	<i>F</i>	35.984	30.700	32.571	27.544	43.253	22.264	33.665	43.193	39.150
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Na	<i>F</i>	8.944	36.970	4.117	7.531	6.694	6.228	4.849	1.969	6.101
	<i>P</i>	<0.001	<0.001	0.014	0.001	0.001	0.002	0.007	0.138	0.002
K	<i>F</i>	42.179	12.645	28.137	27.141	31.034	73.322	50.150	26.643	21.163
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
K/(Ca + Mg)	<i>F</i>	35.188	26.218	30.869	36.305	86.305	79.627	32.906	56.013	39.843
	<i>P</i>	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table 5. The results of one-way ANOVA detecting the difference among each bark physical property of three coniferous species in each season.

Physical property		Early spring	Spring	Summer	Fall
Unrendability	<i>F</i>	4.598	17.962	0.191	18.621
	<i>P</i>	0.022	<0.001	0.828	<0.001
Thickness (total bark)	<i>F</i>	5.409	10.831	3.471	0.759
	<i>P</i>	0.021	<0.001	0.058	0.485
Thickness (inner bark)	<i>F</i>	17.515	26.124	32.538	9.900
	<i>P</i>	<0.001	<0.001	<0.001	0.002

0.239, $P = 0.915$) throughout seasons. The thickness of the outer bark of the three species was not significantly different (two-way ANOVA, species: $F = 1.397$, $P = 0.255$, season: $F = 4.136$, $P = 0.010$, interaction: $F = 2.992$, $P = 0.012$). The thickness of the total bark did not show the clear trends in each season. Although significant differences are detected in thickness of the total bark by two-way ANOVA (species: $F = 12.876$, $P < 0.001$, season: $F = 3.907$, $P = 0.013$, interaction: $F = 3.156$, $P = 0.009$), one-way ANOVA and Scheffe's test among samples in each season showed no clear trends among

Fig. 5. Seasonal changes in bark physical properties of three coniferous species, *Picea jezoensis* var. *hondoensis*, *Abies homolepis* and *Chamaecyparis obtusa*. Error bars show SD.

three species (Table 5). The significant difference among samples and sample-season interactions were detected in thickness of the inner bark (two-way ANOVA, samples: $F = 69.400$, $P < 0.001$, season: $F = 2.485$, $P = 0.069$, interaction: $F = 2.364$, $P = 0.040$), which of *C. obtusa* was significantly thinner than those of *P. jezoensis* var. *hondoensis* and *A. homolepis*, from early spring to summer (one-way ANOVA, Table 5). Hardness of the outer bark of the three species decreased as the year progressed; it was harder in spring and relatively softer in fall. Other properties did not show clear seasonal changes.

Discussion

Occurrence of bark stripping

Fifteen of the 25 tree species in the transects were barked by sika deer from July 1999 to July 2002. This was more than observed by Ando et al. (2003) and may be due to restricting the latter observation period for new barking to only 2 months in summer.

In this study, sika deer selected trees for bark stripping. In primeval forest, bark stripping by deer may change the forest composition (Miquelle and Van Ballenberghe 1989; Khan et al. 1994; Ando et al. 2003) because deer strip bark selectively and the tolerance of each species to bark stripping is different. Species that are debarked selectively and/or are not tolerant will decline and *vice versa*. Therefore, knowledge of bark-stripping preference can help in forecasting and conserving the future forest community.

Heavy bark stripping on coniferous trees is well known on Mt. Ohdaigahara (Yokoyama et al. 2001), and coniferous bark was consumed in large quantities in this study. Ivlev's electivity indices show that the most preferred species is *C. barbinervis* followed by *I. geniculata*. The coniferous species were stripped relatively lightly in comparison to some broadleaf species. In Nikko, deer prefer *A. homolepis* and *Quercus mongolica* Fisch. var. *grosseserrata* Rehd. et Wils. to *C. barbinervis* (Kanzaki et al. 1998). Sakabe et al. (1998) also showed that in Hokkaido, sika deer prefer some broadleaf species, *Ulmus laciniata* (Trautv.) Mayr and *Ulmus davidiana* Planch. var. *japonica* (Rehder) Nakai, and the preference for coniferous species is relatively low. Although Norway spruce, lodgepole pine and ash are stripped frequently by red deer in Europe, bark-stripping preference differs in each area (Gill 1992).

On Mt. Ohdaigahara, our results that bark stripping

peaked in summer follow the observation that the percentage of bark and twigs in the feces of sika deer tended to increase in summer (Yokoyama et al. 1996). One reason for intensive bark stripping in summer might be deer density because Ueckermann (1983), Kaji et al. (1984), Sekine and Sato (1992) and Gill (1992) found positive correlations between bark stripping and deer density. However, Maeji et al. (1999) showed that the deer densities estimated by the block count method in spring in 1997 and fall in 1996 on Mt. Ohdaigahara were 28.0 deer/km² and 30.9 deer/km², respectively, and densities in summer in 1996 and 1997 were 17.5 deer/km² and 22.8 deer/km², respectively. This might suggest that the deer density in summer on Mt. Ohdaigahara was not conspicuously higher than in spring and fall. Then, bark consumption by a deer might peak in summer on Mt. Ohdaigahara.

Bark stripping of sitka spruce, *Picea sitchensis* (Bong.) Carr. by red deer in western Scotland was more frequent in winter (Welch et al. 1987) and bark stripping of *Pinus sylvestris* L. by moose in south-central Sweden was more frequent in April and May (Faber 1996). The percentage of bark and twigs in the rumen contents or feces of sika deer in southernmost Honshu did not show any seasonal change (Jayasekara and Takatsuki 2000; Ikeda 2002). Deer in northern Japan strip bark intensively in winter, due to food shortages (Kaji et al. 1984; Ueda et al. 2002). However, this cannot explain why deer debark in summer on Mt. Ohdaigahara when the primary forage of sika deer, *S. nipponica*, has peak nutritional and quantitative values (Yokoyama and Shibata 1998).

Why do deer eat bark in summer?

This study showed that the bark of *A. homolepis* is relatively easy to be rent while being the hardest bark of the three coniferous species. It was also the bark most preferred by sika deer. The bark of *C. obtusa* was most difficult to be rent and most supple but sika deer showed no clear preference for it. Thus, among coniferous trees, sika deer on Mt. Ohdaigahara might prefer the bark which is harder and easier to be rent. Oi and Itoya (1997) reported that sika deer in Iwate Prefecture (northern Japan) strip the bark of *C. japonica* in spring when the bark is softest and easy to be rent. However, the physical properties of bark measured in this study showed no seasonal change and were not synchronized with bark stripping occurrence. These results suggest that the seasonal change in the occurrence of bark strip-

ping on Mt. Ohdaigahara is not affected much by the bark physical properties but more by other factors, such as seasonal changes in the chemical content of the main forage and/or bark.

The seasonal changes in crude protein, hemicellulose and K in *S. nipponica* peaked in summer, corresponding with the change in the occurrence of bark stripping. Crude protein and hemicellulose are common indices for evaluating forage quality in ruminants, and lignin is known as indigestible component (Itabashi 1998). The chemical analyses showed that bark is less nutritional because it contains relatively lower crude protein and higher fiber than the main forage (Faber 1996; Yokoyama and Shibata 1998; Ando et al. 2003). Faber (1996) suggests that moose eat pine bark as roughage for proper rumen function. It is known that feeding high quality forage, like grain, to ruminants causes excess drop in pH in rumen fluid and prevents proper rumen function. A sudden switch in feed from roughage to concentrate sometimes causes lactic acidosis (Hoshino 1985). Previous studies (Yokoyama and Shibata 1998) and this study show that the nutritional value (crude protein and hemicellulose) of *S. nipponica* surges in summer. We supposed that the bark intake in summer prevents bloat or lactic acidosis from upsetting rumen function.

It is known that excessive K intake causes relative deficiency of another minerals (Robbins 1993). Kemp and t'Hart (1957) reported that a high value of K/(Ca + Mg) exceeding 2.2 tends to cause grass tetany. The K/(Ca + Mg) value of *S. nipponica* samples exceeded 2.2 in May and July 1999 and July 2000, and peaked July 1999 (Fig. 4), because of the increasing of K in summer. Conversely, the values for the bark of three tree species were always below 2.2. These results suggest that the mineral balance of *S. nipponica* is inadequate in July. We conceived that sika deer on Mt. Ohdaigahara feed on bark containing relatively large amounts of Ca to offset the poor mineral balance of *S. nipponica*. In addition, summer is the season for antler growth in male deer and for lactating in female deer, both of which require high Ca intake. To clarify the impact of Ca and Mg in bark, we need to assay the percentage of Ca and Mg derived from bark in the total Ca and Mg intake.

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