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Title: **Food habits of Japanese deer in an evergreen forest: Litter-feeding deer**

Short title: Forest litter-feeding Japanese deer

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Abstract

We observed the feeding behaviors of wild Japanese sika deer (*Cervus nippon yakushimae*) in a warm temperate broad-leaved evergreen forest of the island of Yakushima using the focal animal sampling method from April 2002 to June 2006. Sika deer fed on species of at least 73 woody plants, 13 vines, 8 herbaceous plants, 8 ferns, 1 moss, and 3 fungi. We investigated time spent feeding on each food category in each season (spring: April–June; summer: July–September; autumn: October–December; winter: January–March). During each season, 45.6–59.8% of the deer diet consisted of fallen woody leaves. Half of the fallen leaves were those tinged with red and yellow colors. Fallen reproductive parts of plants constituted 8.7–23.7% of the seasonal deer diet. In contrast, living woody parts of plants and herbaceous plants, including ferns and moss, constituted 4.4–22.5% and 0.8–9.2% of the seasonal diet, respectively. Deer also fed on animal matters as minor food items, such as the feces of monkeys and raccoon dogs, bones of deer and monkeys, and bird carcasses. Animal matters constituted 0.3–1.6% of the seasonal diet. Sympatric monkeys supplied food to deer as a result of their daily activities. Monkey-supplied foods

comprised 1.7–10.9% of the seasonal diet of sika deer. Monkeys tended to supply many fruits and seeds. Overall, 75.0% of the annual deer diet consisted of forest litter, even though deer had access to abundant living edible leaves in the study area. Therefore, sika deer in this forest ecosystem function ecologically as decomposers rather than primary consumers.

Key words: Japanese sika deer *Cervus nippon yakushimae*, decomposer, warm temperate forest, litter fall, monkey

Introduction

Ungulates are distributed from tropical to arctic zones and from humid to arid regions, exhibiting a wide range of morphology, physiology, social systems, and ecology, including food habits (e.g., Macdonald 1984). They play important roles in various ecosystems as environmental engineers or keystone species (Cote et al. 2004). To date, a tremendous body of knowledge regarding ungulate food habits has accumulated from cooler temperate zones to sub-arid regions, and relatively open habitats (e.g., Clutton-Brock et al. 1982; Gagnon and Chew 2000; Gebert and Verheyden-Tixier 2001). In contrast, information from warmer regions of heavily forested areas has been quite limited. To adequately understand the general features of ungulate feeding ecology, the food habits of forest ungulates in warmer regions must be examined. Several quantitative studies have documented the food habits of ungulates in warm temperate and tropical forests (e.g., *Mazama spp.*: Gayot et al. 2004; *Cervus timorensis*: De Garine-Wichatitsky et al. 2005; *Odocoileus virginianus*: Arceo et al. 2005; *Hyemoschus aquaticus* and

Cerphalophus spp.: Dubost 1984). These ungulate species exhibit a variety of food habits and range from frugivores to grazers.

Japanese sika deer (*Cervus nippon*) are distributed widely from tropical to subarctic regions (Macdonald 1984). Seven subspecies of deer inhabit the Japanese Archipelago (Macdonald 1984), and they exhibit a gradient in body size from south to north (Whitehead 1993). Among these, the largest subspecies, *C. n. yesoensis*, inhabits boreal forests in the northern regions of Japan. In contrast, the smallest subspecies, *C. n. yakushimae*, lives in evergreen broad-leaved forests in marginal areas of the warm temperate and subtropical zone. The body weights of adult individuals vary by several times between these two subspecies (Agetsuma et al. 2003). Ecological studies of Japanese sika deer have primarily occurred in cool temperate zones, although several fecal analyses have been conducted in warm temperate zones. Campos-Arceiz and Takatsuki (2005) examined the food habits of sika deer along a latitudinal gradient from warm to cool temperate zones. They demonstrated a strong dependence on graminoids in northern deer populations (70–90% of diet) but less so in southern populations. However, some habitats of the study populations included artificially disturbed areas, such as pastures, logged and plantation forests. In such areas, more graminoid plants may exist than in the original habitats, and deer would likely become grazers. One goal of this study was to examine the seasonal diet composition and food habits of the smallest subspecies of Japanese sika deer (*C. n. yakushimae*) in a relatively undisturbed warm temperate evergreen forest.

Research on the diet composition of ungulate species has primarily been conducted using observations of traces of feeding and analyses of fecal and stomach samples (e.g., Arceo et al. 2005; Campos-Arceiz and Takatsuki 2005; De Garine-Wichatitsky et al. 2005; Dubost 1984; Gayot et al. 2004). However, these

methods may be insufficient to examine the feeding ecology and ecological functions of deer in ecosystems. For example, fecal and stomach analyses may not adequately detect soft tissues of plants. In addition, the discrimination of living from fallen leaves would be difficult using these methods, although this distinction is crucial to evaluating the functions of ungulates within ecosystems. Living plant feeders are defined as primary consumers, whereas forest litter feeders are considered decomposers. To appropriately characterize the functions of ungulates in ecosystems, and consider deer management plans, direct observations of deer feeding behaviors are necessary. Therefore, another goal of this study was to determine a facet of ecological function of *C. n. yakushimae* in a forest ecosystem through behavioral observations.

Materials and methods

Study area and deer population

Cervus nippon yakushimae is one of the smallest subspecies of Japanese sika deer (Whitehead 1993). The body weights of bucks (≥ 4 -years-old) range from 24–37 kg ($n = 8$), and those of does (≥ 3 -years-old) range from 19–25 kg ($n = 10$; Agetsuma, unpubl. data). This subspecies inhabits nearly the entirety of island of Yakushima (503 km²: 30°N, 130°E). Yakushima is a mountainous island whose highest peak reaches 1836 m above sea level. Altitudinal vegetational changes occur from peak to coast, ranging from grasslands of dwarf bamboo (*Pseudosasa owatarii*), shrubby areas of rhododendrons (*Rhododendron yakusimanum*), conifer forests of cedar (*Cryptomeria japonica*), fir (*Abies firma*) and hemlock (*Tsuga sieboldii*), and deciduous forests to evergreen broad-leaved forests. An analysis of deer feces on Yakushima

in the summer suggested that deer depend on broad leaves in most parts of the island, although in conifer forests and dwarf bamboo grasslands, they largely depend on graminoids (Takatsuki 1990).

We established our study area (ca. 15 km²) in a warm temperate evergreen broad-leaved forest on the west coast of Yakushima (0–250 m above sea level). Most parts of the area were designated as National Park and World Natural Heritage. The annual mean temperature is approximately 21°C, which corresponds to the transition between subtropical and warm temperate zones (Tagawa 1994). Annual precipitation is approximately 2600 mm (Tagawa 1980). A road runs through the study area from south to north. The vegetation of the study area mainly consists of ~40-year-old secondary forest as well as some primary forest, dominated by species of Fagaceae, Myrsinaceae, and Lauraceae (Agetsuma 1995). Subtropical plants, such as *Ficus superba*, *F. microcarpa*, and *Cyathea boninsimensis* are also present. The plant species diversity of the forest is very high (Tagawa 1980). On the other hand, forest floor vegetation does not develop in the study area, maybe because of shading by evergreen trees. Several fern species are rather dominant on forest floor. The area also includes small isolated plantations of *Cryptomeria japonica*, as well as small grasslands along roadsides, the seashore, and on mudslides. Orange orchards border the northern end of the study area.

The density of deer in the area is very high (>80 head km⁻²; Agetsuma et al. 2003). Tsujino et al. (2004) reported that deer densities have been increasing since 1988; however, the population density may be higher in the 1960s (Agetsuma 2007). No natural predators originally inhabited Yakushima (Environment Agency 1984), and any hunting and control of wildlife is prohibited in most parts of the study area. Deer in the study area were not easily frightened, and some appeared well habituated to researchers. Japanese monkeys (*Macaca fuscata yakui*) are also very dense in the study area (ca. 60–70 head km⁻²; Agetsuma and

Sugiura, 2007).

Behavioral Observations

Observations of deer behaviors were intermittently conducted from April 2002 to June 2006. We chose 15 identified deer which were wild but well-habituated to researchers (5 bucks: 3- to more than 5-years-old; 6 does: 2- to more than 5-years-old; 4 juveniles: 0 to 1-year-old during the observation period) for observation using the focal-animal sampling method (Altmann 1974). We followed the focal animals and recorded their behaviors at a distance of 1.5-10 m every 2 minutes on each observation day as long as possible. Behaviors were classified into moving, standing, lying down, searching for food, feeding, and others. We recorded the parts of food eaten and the species identity of food, when possible. Food parts were categorized into living woody parts (leaves, bark, branches, and roots), fallen woody parts (leaves, branches, and reproductive parts, such as unripe and ripe fruit, seeds, and flowers), decaying logs, living and dried herbaceous plants (monocots and dicots), ferns, mosses, fungi, animal matters, water, and licked materials. We further categorized the condition of fallen woody leaves as fresh green leaves, red- and yellow-tinged leaves, or dried brown leaves. For cases when deer fed on 2 or more plant parts simultaneously, such as clusters of fallen fruits and leaves, we counted them as independent feeding records. In the study area, monkeys sometimes supply food to deer as a result of their daily activities (Majolo and Ventura 2004). Thus, we also recorded whether the food was supplied by monkey activity. Observations of food supplied by monkeys involved the following: food dropped from trees by monkeys; food that become available to deer because monkeys bent branches with food attached; fallen food with traces of feeding by monkeys; and

monkey feces. We were unable to confirm all cases of food being dropped by monkeys prior to the arrival of the focal deer; thus, the extent of food supplied by monkeys in the diet of deer was likely underestimated.

All feeding records were pooled into four seasons (spring: April–June; summer: July–September; autumn: October–December; winter: January–March). The contribution of food items to the overall diet was evaluated by time spent feeding on the food items, which reflects amount of efforts by animals to obtain the food items (e.g. Agetsuma 1995; Sharma et al. 1998). In this study, percentage of time spent feeding on each food item was expressed as the proportion of the number of feeding records of each food category to the total number of feeding records in each season. Differences in diet composition were tested using χ^2 tests. The annual diet composition was obtained by averaging the four seasonal diet compositions.

Living food tree availability

To investigate the forest structure and vertical distribution of potential living food resources for deer, we conducted a vegetational survey over 30 ha at the center of the study area. We established 8 belt transects of 5×50 m and 1 belt transect of 5×25 m (a total of 2,125 m²) on various topographies. From September to October 2003, we identified and measured the height (H) and lowest branch height (LBH) for all sapling of ≥ 40 cm in height and of < 15.5 cm in girth at breast height. We also checked for traces of deer feeding on the saplings. Adult deer in the study area can reach 120 cm in height without standing on their hind legs. Thus, the living parts of plants ≤ 120 cm in height were considered available resources for deer.

Results

Diet composition

We obtained a total of 6,405 feeding records during the study period (spring, $n = 2,657$; summer, $n = 1,397$; autumn, $n = 1,220$; winter, $n = 1,131$). Among these, 96.5% of the records could be categorized into a food item category, and 57.6% could be identified to the species level. Most records that could not be identified to species were those of fallen leaves. Focal deer fed on species of at least 73 woody plants, 13 vines, 8 herbaceous plants, 8 ferns, 1 moss, and 3 fungi (Appendix).

<Table 1 about here>

For each season, 45.6–59.8% of the diet consisted of fallen woody leaves (53.5% of the annual diet; Table 1). Deer consumed more leaves tinged with red and yellow (47.0% of fallen leaves in the annual diet) than fresh green leaves (35.3%; χ^2 test: $\chi^2 = 203.6$, $df = 6$, $p < 0.001$; Table 2). Evergreen broad-leaved forests in the study area provided the tinged leaves throughout the year. Therefore, tinged leaves comprised one of the major food resources for deer in all seasons. Deer appeared to exhibit species selectivity for fallen leaves. The main species of fallen leaves consumed by deer were *Elaeocarpus sylvestris*, *Rhus succedanea*, *Daphniphyllum teijsmannii*, *Ficus erecta*, *Neolitsea sericea*, and *Schefflera octophylla*. When deer fed on fallen leaves, including tinged leaves of these species, they tended to sequentially pick leaves of the same species from the forest litter-fall, even if other fresh fallen green leaves and living leaves were available during the course of foraging. Deer also fed on fallen branches (1.1% of annual diet) as well as tinged and dried herbaceous plant leaves (0.8%; Table 1).

<Table 2 about here>

Fallen reproductive parts of plants (ripe and unripe fruit, seeds, and flowers) were the second most

consumed parts, comprising 8.7–23.7% of the seasonal diet (18.0% of the annual diet; Table 1). Deer fed on fallen flowers of *Idesia polycarpa*, *Camellia japonica*, and *Styrax japonica*, seeds of *R. succedanea* and *Zanthoxylum ailanthoides*, and fruits of *Myrica rubra* and three *Ficus* species. In addition, deer fed on fallen acorns of *Lithocarpus edulis* and *Quercus salicina*. Deer also exhibited some species selectivity toward certain reproductive parts. On one observation day, the focal buck only picked up fruits of *F. pumila* and completely ignored fruits of *F. superba*, both of which had fallen in the same place.

For living-plant feeding, woody leaves comprised 3.9–20.5% of the seasonal diet (11.3% of the annual diet), other woody parts (bark, branches, and roots) comprised 0.3–4.6% (1.9%), herbaceous plants were 0.0–5.0% (1.8%), and ferns and mosses comprised 0.8–4.9% (3.6%; Table 1). Among the herbaceous plants, graminoids contributed only 0.0–2.3% (0.7%) of the seasonal diet. Herbaceous plants tended to be eaten along roadsides and near the seashore in the northern and southern parts of the study area.

Minor food items included fungi (1.7% of the annual diet); decaying logs (0.7%); licking soil, litter and plant surfaces (0.6%); and water (0.5%; Table 1). We were unable to identify most of the matter licked by deer. During observation, one focal doe licked soil with traces of animal urine. Deer also fed on animal matters such as feces of monkeys and raccoon dogs (*Nyctereutes procyonoides*) (0.2%), bones of deer and monkeys (0.7%), and a small bird carcass and a feather (0.1%).

The three main food categories (fallen woody leaves, reproductive parts, and living woody leaves) exhibited significant seasonal variation ($\chi^2 = 421.2$, $df = 9$, $p < 0.001$). Feeding on fallen leaves was lower in the winter, whereas feeding on reproductive parts was lower in the summer. In contrast, living woody leaf consumption increased in summer and winter.

Table 1 also presents the contributions of forest litter (i.e., fallen leaves, branches, reproductive parts, etc.) and living plant parts (woody leaves, bark, roots, herbaceous plants, etc.) to the deer diet. Forest litter comprised more than 60.0% of the deer diet during each season and 75.0% of the annual diet. In contrast, living plants comprised, at most, 27.5% of the seasonal diet and 18.7% of the annual diet.

<Table 3 about here>

Monkey-supplied food comprised 1.7–10.9% of the seasonal deer diet (7.0% of the annual diet; Table 3). The contribution of monkey-supplied food varied seasonally ($\chi^2 = 158.6$, $df = 3$, $p < 0.001$), and the amount of reproductive parts in monkey-supplied food (Table 3) differed from that in the entire seasonal diet in summer, autumn, and winter (Table 1; spring, $\chi^2 = 3.1$, ns; for other seasons, $\chi^2 > 30.9$, $df = 1$, $p < 0.001$). The percentage of reproductive parts tended to be higher in monkey-supplied food than in the seasonal diets. Moreover, for fallen leaves, the percentage of green leaves supplied by monkeys was higher (Table 3) than those in the seasonal diets (Table 2; for all seasons, $\chi^2 > 212.7$, $df = 1$, $p < 0.001$).

Living food tree availability

We found 31 woody species in the belt transects, among which 14 species exhibited traces of feeding by deer. However, for the remaining 17 species with no traces of feeding, the living parts of 12 were fed upon by focal deer during behavioral observations. Thus, at least 26 species of saplings serve as potential food items for deer. Figure 1 presents the sapling density recorded of each height size class ($n = 1,125$) and each LBH class ($n = 1,127$) in the belt transects. Smaller saplings were much more abundant relative to larger saplings, showing a typical reverse J-shaped vegetation structure. About 83.4 % of saplings ≤ 120 cm in

height (H) were of species with traces of feeding (the 14 species), and 94.1 % were of edible species (the 26 species; Fig. 1). In addition, 84.2 % of saplings having branches ≤ 120 cm in height (LBH) were of species with traces of feeding, and about 95.2 % were of edible species. The percentage of edible species varied across H classes ($\chi^2 = 11.5$, $df = 3$, $p < 0.01$) but not across LBH classes ($\chi^2 = 4.2$, $df = 2$, ns).

<Figure 1 about here>

Discussion

Japanese sika deer (*C. n. yakushimae*) in a warm temperate evergreen forest depended mainly on forest litter fall, especially fallen leaves, across seasons (Table 1). Litter is typically considered an alternative food item for deer under conditions of either food depletion in the winter (Ditchkoff and Servello 1998) or high deer feeding pressure (Takahashi and Kaji 2001) in cool temperate zones. Then, litter fall has been evaluated as unimportant foods for Japanese sika deer in warmer areas (Jayasekara and Takatsuki 2000). In contrast, in our study area, even though the density of deer was quite high (>80 individuals km^{-2} ; Agetsuma et al. 2003), living plant resources remained available to deer (Fig. 1). However, deer preferred to feed on fallen leaves than on living plants. When deer sequentially foraged, they tended to select fallen leaves of the same species, even if other potential living foods were nearby. Moreover, when deer encountered both green and yellow/red fallen leaves, they occasionally fed on only yellow/red fallen leaves.

Our direct observations of deer feeding behavior revealed detailed food habits of Japanese sika deer in a warm temperate forest as well as the ecological function of deer in the study area. The majority (75%) of the diet of deer consisted of forest litter, whereas less than 20% was comprised of living plants (Table 1). These

results indicate that deer in this area primarily acted as decomposers rather than primary consumers.

Approximately 1% of the deer diet was composed of animal matters. The feces of monkeys and raccoon dogs may contain gut cells of these animals as well as undigested leaves, fruits, and seeds. Male red deer (*C. elaphus*) sometimes feed on antlers, bones, and living and dead vertebrates. Such behaviors may indicate that male deer tend to feed on animal matter to ingest minerals for making antlers (Whitehead 1993). However, in our observations, all cases of deer feeding on bones, carcass of a small bird, and a bird feather were found in female individuals. Thus, animal matter feeding is not restricted to male deer.

Based on the feeding categories of Gagnon and Chew (2000), species whose diets are composed of more than 70% woody and dicot plants are considered browsers. Therefore, deer in the study area can be classified as browsers. However, Takatsuki (1990) reported that deer feces from the grassland zone of Yakushima consisted primarily of graminoids (dwarf bamboo) in the summer. In addition, the largest subspecies, *C. n. yezoensis*, exhibited broad variation in their dependency on graminoids between locations (70–90%: Campos-Arceiz and Takatsuki 2005; around 20%: Yokoyama et al. 2000). Therefore, deer can easily switch their food habits from browsing to grazing based on the surrounding food environment, even in the same subspecies.

We employed percentage of time spent feeding on each food item to evaluate significance of the food item in diet (e.g. Agetsuma 1995; Sharma et al. 1998). This method may not represent exact percentages of total dry weight of each food items ingested. Combining data of bite rate and bite unit weight with the feeding time of each food item will make much precise estimation of their diet. However, even if such corrections of the diet composition would be conducted, our conclusion that deer in the study area mainly

depended on forest litter and showed browser feeding habit may be unchanged.

The modification and destruction of vegetation by deer occurs worldwide (e.g., Fuller and Gill 2001; Husheer et al. 2003; Cote et al. 2004). Kaji et al. (1991) reported that extensive structural changes caused by Japanese sika deer in forests could happen within only four years after deer density reached up to 30 individuals / km². However, these studies have primarily occurred in cool temperate zones. In our study area, by contrast, the sapling size class structure exhibited a typical reverse J-shape, and most small saplings were edible for deer (Fig. 1) even under very high deer densities (Agetsuma et al. 2003). In addition, the percentage of edible plants within the LBH classes did not differ across height layers. These results mean that a browse line caused by very high feeding pressure of ungulates (Vila et al. 2003) was not apparent in the study period. Although Tsujino and Yumoto (2004) reported impacts of deer on seedlings in the study area, Koda et al. (2008) did not detect actual decreases in the sapling densities of deer-preferred species from 1992 to 2005. The future effects of deer on vegetation are unknown, their influence in the study area appear quite limited relative to those reported in areas with high deer densities (e.g., Fuller and Gill 2001; Kaji et al. 1991; Vila et al. 2003).

One potential reason for the minimal impact of deer is that the main ecological function of deer in the study forest was as decomposers rather than primary consumers. Living parts of plants comprised less than 20% of the annual diet of deer in this study (Table 1); thus, feeding pressure on saplings would likely be relaxed. Monkeys may also facilitate deer feeding on litter fall. Monkey activities provided 7% of the deer diet (Table 3). Among the monkey-supplied foods, the proportion of reproductive plant parts was higher than in the whole diet. In general, fruits have higher energy content than do other food parts (Milton 1993).

Deer appeared to prefer green fallen leaves supplied by monkeys (Table 3), although in other situations, they tended to feed on tinged leaves (Table 2). Generally, leaves in higher layers of the crowns contain more energy and protein although they are rich in secondary compounds (Ellsworth and Reich 1993; Fortin and Mauffette 2002; Nakamura et al. 2008). Without monkeys in the forest, deer might feed on much living plants.

As a whole, we indicated that the deer preferred fallen leaves (Table 1), especially tinged leaves (Table 2), to the available intact leaves (Fig. 1). There are several possible causes for it. Fallen leaves might contain less secondary compounds because rain might elute soluble secondary compounds such as tannin. In addition, deer could obtain more amount of food in dry weight at a time from fallen leaves which have lower water content. However, these causes remain to be investigated by further researches.

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Table 1. Dietary composition of wild Japanese sika deer in a warm temperate broad-leaved forest (%).

	fallen woody ^a			decaying	dead	animal	living woody ^b		living ^b				licked		forest	living
	leaf	branch	fruit/seed	log ^a	herb ^{ac}	matter ^{ad}	leaf	other ^e	herb	fern ^f	fungus	water	material ^g	UI ^h	litter	plant
spring	56.8	0.3	21.8	0.2	0.3	0.5	7.5	0.3	2.0	4.9	1.7	0.1	0.8	3.0	79.9	14.6
summer	52.0	0.6	8.7	0.7	0.9	0.3	13.5	4.6	5.0	4.2	4.3	0.6	0.5	4.0	63.3	27.3
autumn	59.8	2.5	23.7	0.5	1.4	1.6	3.9	0.6	0.0	0.8	0.0	0.7	0.6	4.0	89.5	5.2
winter	45.6	1.1	17.7	1.3	0.4	1.3	20.5	2.0	0.4	4.6	0.8	0.6	0.4	3.2	67.5	27.5
annual	53.5	1.1	18.0	0.7	0.8	0.9	11.3	1.9	1.8	3.6	1.7	0.5	0.6	3.5	75.0	18.7

^a forest litter, ^b living plant, ^c tinged and dried herbaceous plant and fern, ^d animal feces, bone and carcass of bird, ^e branch, bark and root, ^f fern and moss, ^g plant, litter and soil, ^h unidentified item.

Table 2. Composition of colors of fallen leaf fed by deer (%).

season	green	red & yellow	brown	unidentified
spring	35.5	58.6	5.8	3.8
summer	31.4	49.6	19.0	4.5
autumn	28.0	50.8	21.1	2.8
winter	46.3	29.1	24.6	3.4
annual	35.3	47.0	17.7	3.6

Table 3. Dietary composition of monkey-supplied foods (%).

contribution to whole diet								
	fallen woody leaf			fallen	fallen	living	feces	total
	green	red & yellow	brown	branch	fruit/seed	woody leaf ^a		
spring	1.1	0.0	0.0	0.0	0.6	0.0	0.0	1.7
summer	1.3	0.5	0.0	0.3	4.2	0.2	0.3	6.8
autumn	2.8	0.4	0.0	1.0	6.7	0.0	0.0	10.9
winter	3.9	0.1	0.0	0.2	4.5	0.0	0.1	8.8
annual	2.3	0.2	0.0	0.4	4.0	0.0	0.1	7.0
composition within monkey-supplied foods								
	fallen woody leaf			fallen	fallen	living	feces	total
	green	red & yellow	brown	branch	fruit/seed	woody leaf ^a		
spring	65.2	0.0	0.0	0.0	32.6	0.0	2.2	100.0
summer	18.9	7.4	0.0	4.2	62.1	3.2	4.2	100.0
autumn	25.6	3.8	0.0	9.0	61.7	0.0	0.0	100.0
winter	44.4	1.0	0.0	2.0	51.5	0.0	1.0	100.0
annual	38.5	3.0	0.0	3.8	52.0	0.8	1.8	100.0

^a deer fed on leaves from branches bended by monkeys.

Appendix Identified food species and part of Japanese sika deer in a warm temperate broad leaved forest

species	life form	fallen leaf*1	branch	flower	fruit/seed	living leaf	others*2	animal matter
<i>Ardisia sieboldii</i>	E	○	○		○	○	○	
<i>Camellia japonica</i>	E	○		○	○	○		
<i>Camellia sasanqua</i>	E	○		○		○		
<i>Castanopsis sieboldii</i>	E	○						
<i>Cinnamomum camphora</i>	E	○			○			
<i>Cinnamomum daphnoides</i>	E					○		
<i>Cleyera japonica</i>	E	○				○		
<i>Crateva religiosa</i>	E	○					○	
<i>Damnacanthus indicus</i>	E					○		
<i>Daphniphyllum teijsmannii</i>	E	○	○	○	○			
<i>Dendropanax trifidus</i>	E	○						
<i>Diospyros morrisiana</i>	E	○						
<i>Distylium racemosum</i>	E					○		
<i>Elaeagnus macrophylla</i>	E					○		
<i>Elaeocarpus japonicus</i>	E	○		○			○	
<i>Elaeocarpus sylvestris</i>	E	○						
<i>Eurya emarginata</i>	E					○		
<i>Eurya japonica</i>	E	○				○		
<i>Ilex goshiensis</i>	E					○	○	
<i>Ilex rotunda</i>	E	○						
<i>Lithocarpus edulis</i>	E	○	○	○	○	○		
<i>Litsea acuminata</i>	E	○				○		
<i>Machilus thunbergii</i>	E	○	○	○	○	○		
<i>Maesa tenera</i>	E	○			○*6	○		
<i>Michelia compressa</i>	E	○			○			
<i>Myrica rubra</i>	E				○	○		
<i>Myrsine seguinii</i>	E	○				○		
<i>Neolitsea aciculata</i>	E	○	○			○		
<i>Neolitsea sericea</i>	E	○	○	○	○		○	
<i>Oreocnide pedunculata</i>	E	○	○		○			
<i>Pittosporum tobira</i>	E			○				
<i>Psychotria rubra</i>	E	○				○		
<i>Quercus phillyraeoides</i>	E	○				○		
<i>Quercus salicina</i>	E	○	○		○	○		
<i>Rhaphiolepis indica</i>	E	○			○	○		
<i>Rubus sieboldii</i>	E					○		
<i>Schefflera octophylla</i>	E	○			○			
<i>Symplocos glauca</i>	E	○						
<i>Symplocos lucida</i>	E	○				○		
<i>Symplocos prunifolia</i>	E			○				
<i>Syzygium buxifolium</i>	E					○		
<i>Ternstroemia gymnanthera</i>	E	○			○			
<i>Trema orientalis</i>	E	○	○					
<i>Vaccinium bracteatum</i>	E	○						
<i>Aucuba japonica</i>	E*3	○						
<i>Citrus sp.</i>	E*4				○			
<i>Cryptomeria japonica</i>	E C*4	○						
<i>Anodendron affine</i>	E V			○	○	○		
<i>Ficus pumila</i>	E V				○	○		
<i>Ficus thunbergii</i>	E V					○		
<i>Hoya carnosa</i>	E V					○		
<i>Psychotria serpens</i>	E V	○				○		
<i>Lonicera affinis</i>	E V	○				○		
<i>Morinda umbellata</i>	E V	○						
<i>Stephania japonica</i>	E V					○		
unidentified sp.	E V	○						
<i>Acer morifolium</i>	D	○						
<i>Buddleja curviflora</i>	D					○		
<i>Callicarpa japonica</i>	D	○						
<i>Diospyros japonica</i>	D	○						
<i>Euodia meliifolia</i>	D			○			○	
<i>Euscaphis japonica</i>	D	○		○	○			
<i>Ficus erecta</i>	D	○	○		○	○	○	
<i>Ficus superba</i>	D	○			○		○	

Appendix continued

species	life form	fallen leaf*1	branch	flower	fruit/seed	living leaf	others*2	animal matter
<i>Firmiana simplex</i>	D	○				○		
<i>Glochidion obovatum</i>	D					○		
<i>Hibiscus makinoi</i>	D	○				○		
<i>Hydrangea grosseserrata</i>	D					○		
<i>Idesia polycarpa</i>	D	○		○	○			
<i>Lagerstroemia subcostata</i>	D					○		
<i>Mallotus japonicus</i>	D	○		○	○			
<i>Melia azedarach</i>	D	○		○	○			
<i>Morus australis</i>	D	○						
<i>Premna microphylla</i>	D	○						
<i>Rhododendron tashiroi</i>	D	○				○		
<i>Rhus succedanea</i>	D	○	○	○	○			
<i>Rubus croceacanthus</i>	D					○		
<i>Rubus grayanus</i>	D					○		
<i>Styrax japonica</i>	D	○		○	○		○	
<i>Swida macrophylla</i>	D	○	○		○	○		
<i>Vernicia cordata</i>	D	○						
<i>Zanthoxylum ailanthoides</i>	D	○			○		○	
<i>Actinidia rufa</i>	D V				○			
<i>Parthenocissus tricuspidata</i>	D V	○				○		
<i>Vitis coignetiae</i>	D V	○						
<i>Boehmeria holosericea</i>	dicot					○		
<i>Chamaesyce prostrata</i>	dicot					○		
<i>Farfugium japonicum</i>	dicot					○		
<i>Gnaphalium japonicum</i>	dicot					○		
<i>Oxalis sp.</i>	dicot					○		
<i>Ampelopsis brevipedunculata</i>	dicot V	○						
<i>Alocasia odora</i>	monocot	○						
<i>Arisaema serratum</i>	monocot					○		
<i>Miscanthus sinensis</i>	monocot*5					○		
<i>Arachniodes aristata</i>	fern					○		
<i>Arachniodes sporadosora</i>	fern					○		
<i>Dicranopteris linearis</i>	fern	○				○		
<i>Gleichenia japonica</i>	fern					○		
<i>Lemmaphyllum microphyllum</i>	fern					○		
<i>Nephrolepis cordifolia</i>	fern	○				○		
<i>Pteridium aquilinum</i>	fern					○		
<i>Pteris wallichiana</i>	fern	○				○		
<i>Conocephalum conicum</i>	moss					○		
<i>Auricularia polytricha</i>	fungus				○			
<i>Hohenbuehelia reniformis</i>	fungus				○			
<i>Tremella fuciformis</i>	fungus				○			
<i>Cervus nippon yakushimae</i>	animal							bone
<i>Macaca fuscata yakui</i>	animal							feces, bone
<i>Nyctereutes procyonoides</i>	animal							feces

life form, E: evergreen broad leaved tree, V: vine, EC: evergreen conifer tree, D: deciduous tree.

*1: fallen leaf including tinged and dried herbaceous leaf. *2: bark, branch and root.

3: one branch brought from other place by human, 4: planted and abandoned tree, *5: graminoid plant.

*6: fruit attached living branch.

Fig. 1

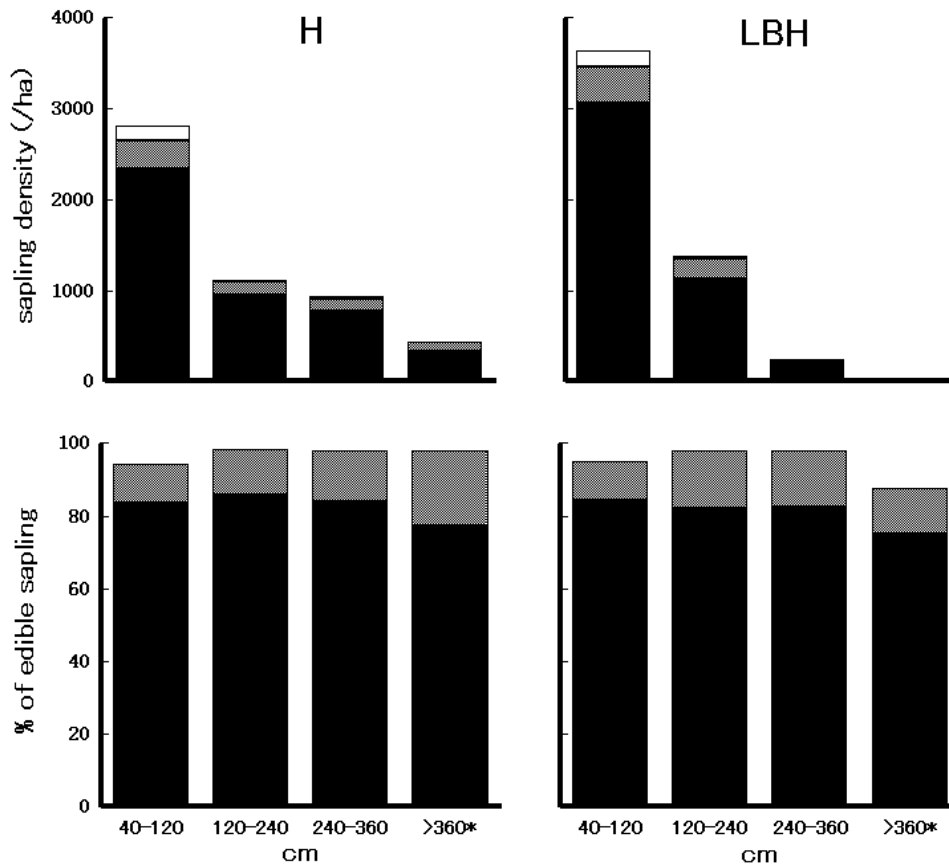


Figure 1. Sapling densities of each layer (i.e., class) of sapling height (H) and lowest branch height (LBH).

Solid bars indicate saplings of species with traces of feeding by deer (14 species), shaded bars indicate saplings of other edible species (12 species), and open bars indicate saplings of species that could not be confirmed as edible during the observation period. Layers “>360*” indicate saplings and branches that are greater than 360 cm in height but less than 15.5 cm in girth at breast height.