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Food and habitat selection of *Lepus brachyurus lyoni* Kishida, a near-threatened species on Sado Island, Japan

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Abstract. We determined the environmental requirements for *Lepus brachyurus lyoni* on Sado Island, Japan, during the winter when food resources are low. Hare track survey sites were classified by vegetation type. The movement distances of hares, which indicated habitat preference, were evaluated as the relative length of tracks in a 1-ha area. In addition, we examined browse marks on plants and the protein content of plants to determine the preferred plant species. Movement distances of hares decreased significantly with increasing tree stand height, mean tree diameter, basal area of the tree stand, and forest canopy closure, but increased with branch-and-stem density. The percentage of browse marks on the branches of tree/shrub species decreased significantly with increasing branch-and-stem diameter. The rate of feeding increased significantly with increased protein content in the branches. These findings suggest that hares prefer shrub stands with high branch-and-stem density to mature forests, which have lower branch-and-stem densities. Hares also prefer branches and stems containing large amounts of protein. Young stands offering many shrub species as food resources and shelter constitute preferable environments for hares.

Key words: crude protein, food preferences, habitat, *Lepus brachyurus lyoni*, track survey.

Lepus brachyurus lyoni Kishida, a subspecies of the Japanese hare (*Lepus brachyurus* Temminck), is only distributed on Sado Island, Japan, and is characterized by shorter hind legs compared to other subspecies of the Japanese hare (Kishida 1937). After World War II, from 1945 to 1955, Japanese cedar (*Cryptomeria japonica*) and Japanese red pine (*Pinus densiflora*) were planted throughout Sado Island for timber production, and these plantations provided good food resources for hare populations. Because hares consumed not only shrub species growing in the plantations but also saplings, they were considered a pest animal; control efforts were undertaken, including the introduction of predators, such as Japanese martens (*Martes melampus melampus*) and Japanese foxes (*Vulpes vulpes japonica*) (Sato 1998). Many studies have examined methods for controlling *L. brachyurus lyoni* populations, which had increased due to the increased food resources available in plantations (e.g., Toyoshima and Takata 1955; Toyoshima et al. 1969, 1970; Saito et al. 1978; Toyoshima 1978; Sato 1998). As a result of the successful control measures and changes in habitat condition, populations of this subspecies have been decreasing rapidly in recent years, and *L. brachyurus lyoni* has been designated a "near-threatened species" in both Niigata Prefecture and Japan as a whole (Niigata Prefecture 2001; Ministry of the Environment of Japan 2007).

Hares are the primary prey of higher predators, such as the Golden Eagle (Shimano et al. 2001, 2006; Ishima et al. 2007; Yamaguchi et al. 2008), Japanese martens, and Japanese foxes (Suzuki et al. 1976; Kondo 1980; Sato 1998), and are therefore a key component of ecosystems in Japan.

Japanese hares generally consume trees in winter and herbs in summer (Otsu 1969), and they tend to inhabit shrubby sites (Shimano et al. 2003, 2006). However, studies on *L. brachyurus lyoni* are rare, with the exception of estimations of hare populations and the extent of forest damage (Toyoshima and Takata 1955; Toyoshima et al. 1969, 1970; Saito et al. 1978; Toyoshima 1978). To conserve this hare species, its preferred habitat and food resources must be thoroughly documented. Thus, to improve the ecosystem management of *L. brachyurus lyoni*, we determined the environmental requirements of

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this subspecies during the winter season, when food resources are limited.

Study area and methods

Study area

The study areas were located on Sado Island, Niigata Prefecture, Japan. Sado Island has northern and southern mountain ranges, with a plain dividing the two; the island's highest peak is Kinpokusan (1,173 m above sea level). We conducted both track and browse surveys within the Osado and Kosado mountain ranges. The study sites for both surveys ranged from 100 to 520 m in altitude in the Osado Mountains and were located between 110 and 250 m in the Kosado Mountains (Fig. 1A, B).

In Aikawa, the average annual temperature is 13.6°C and the maximum monthly mean temperature is 29.0°C in August; the minimum temperature is 0.3°C in January and the annual precipitation is 1514.1 mm (Japan Meteorological Agency 2002, Fig. 1). Kira's warmth index (Kira 1948) is 106.5°C･month, which is typical of a warm-temperate zone. According to Miyawaki (1993), the warmth index of the Osado Mountains, the northern mountain range, ranges from 65 to 85°C･month, which is typical of a cool-temperate zone, whereas the warmth index of the Kosado Mountains in the south ranges from 85 to 100°C･month, which is typical of a warm-temperate zone.

Track survey

We evaluated the site preferences of hares by comparing the length of hare tracks (trails) among all vegetation types with snow cover. Some studies have examined hare habitat selection with tracks on snow cover like INTGEP (Hayashi et al. 1973; Toyoshima 1978; Yoshida and Matsueda 1984; Japanese Wildlife Research Society 1997; Yatake et al. 2003). In this study, we used hare tracks within a unit area as an indicator of hare site preference.

We walked forestry roads in the winter and found hare tracks on snow cover in the forests (Fig. 1A). We measured the lengths of hare tracks when they were found. When measuring track lengths, we noted the vegetation type (e.g., *C. japonica* forest, *Quercus serrata* forest, *P. densiflora* forest, *Weigela hortensis* scrub) and marked the forest stand so that we could return to the site during the summer survey to better understand the forest structure and the branch-and-stem density. Open sites, such as rice fields, where hare tracks were easily covered by snow, were not surveyed because hare track length in such sites will not necessary indicate hare habitat preference.

Some hare tracks moved linearly, but other tracks meandered as the individual fed on the branches of shrubs. Hare tracks that approximately followed a straight line were considered indicative of poor-quality sites (Fig. 2B), whereas randomly moving tracks accompanied by evidence of foraging indicated high-quality

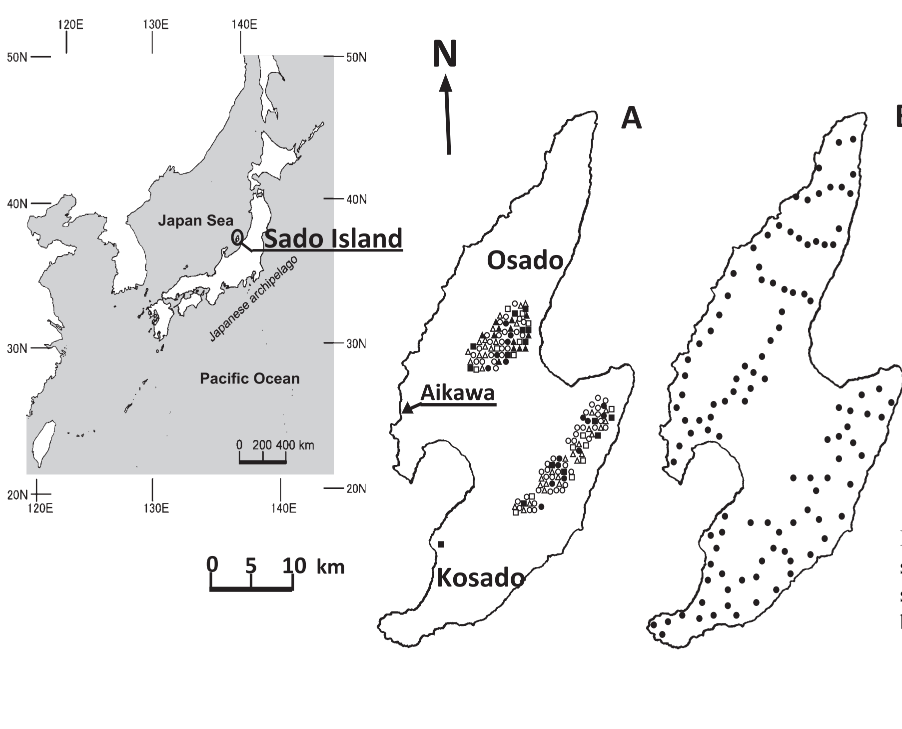

Fig. 1. Locations of the study sites. A: Study sites for the hare track surveys. Symbols are the same as in Table 1. B: Study sites for the browse mark surveys.

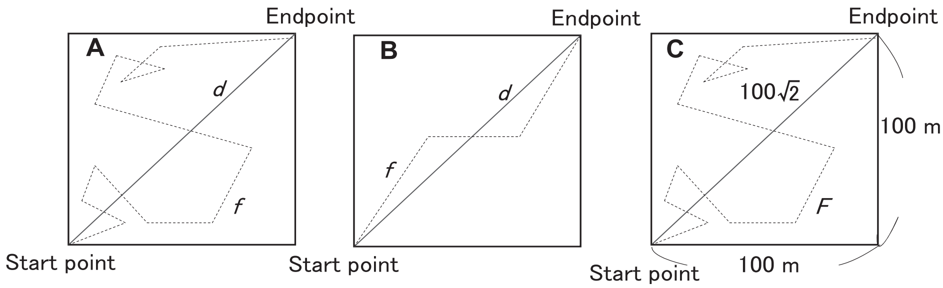

Fig. 2. Determination of the movement distance of hares (an index of habitat preference) in the hare track survey. Plots of hare tracks with enclosing squares. Hare tracks have distinguishable starting and ending points within plant communities. After we measured the actual length of a hare track (f), we measured the distance between the start and endpoints to determine the area of the plot. We calculated the area of a square encompassing the start and endpoints in which the two points defined the diagonal (d) of the square. If a hare moves randomly under high-quality conditions, the length of the track within the square will be long (A). If a hare moves straight through areas of poor condition, the length of the track is short and nearly equal to the length of the diagonal of the square (B). Here, F is a converted movement distance per hectare.

sites (Fig. 2A). Therefore, the length of a track within a square (see below) provides a good indicator of hare site preference (Shimano and Shimizu 2009).

Hare tracks have distinguishable starting and ending points within plant communities because snow debris falling from tree branches hides hare tracks. Tracks left on the snow cover sometimes disappear after a snowfall in open sites (e.g., canopy gaps). In some cases, hare tracks continue between different vegetation types, but when the vegetation type changed, the tracks were considered to have reached an endpoint.

After we measured the actual length of a hare track, we also measured the distance between the start and endpoints to determine the area of the plot. We also calculated the area of a square encompassing the start and endpoints, with the two endpoints located along the diagonal. This is an important point when using a square to encompass the start and endpoints as the two ends of the diagonal because if plot size is established freely, the track length per area should also change freely, even if the actual track length remains the same (Shimano and Shimizu 2009). Distances were measured using a laser distance meter (LASER600; Nikon, Tokyo, Japan).

Among the 151 sites in this study, the actual sizes of the squares calculated using the lengths of the diagonals between the start and endpoints ranged from 35 to 7880 m^2. The measured movement distances (track length) were converted to relative lengths within 1-ha areas (movement distance) as follows (Shimano and Shimizu 2009):

$$F = 100\sqrt{2}\, f d^{-1},$$

where d is the diagonal length between the starting point and the endpoint in an actual plot, f is the track length in the plot, F is the converted movement distance per hectare (Fig. 2), and $100\sqrt{2}$ is the diagonal length of a 1-ha square. The formula follows from $d{:}f = 100\sqrt{2}:F$. We defined the track length as the actual length of the hare tracks in each plot and the movement distance as the converted length per hectare. Tracks were found in all vegetation types.

From 28 December 2005 to 2 January 2006, 8 February to 9 March 2006, 1 January to 5 January 2008, and 2 February to 5 February 2008, we examined hare tracks in the Osado and Kosado Mountains to assess vegetation use by hares during winter.

Forest structure survey

In the summer, we surveyed tree height, diameter at breast height (DBH) for trees, and the density of all trees at the 151 sites where hare tracks were found during the previous winter. An area surrounding the hare tracks was established for the tree measurements. In 99 of the 151 stands, the size of the forest structure survey area was 10 × 10 m. When the area of a plant community was smaller than 10 × 10 m, the survey area depended on the community area. Within the forest survey, 45 sites were smaller than 10 × 10 m, with areas ranging from 9 to 64 m^2. In seven mature forest stands, we set the area as 15 × 15 m because the track-survey sites were larger than those in other stands. Tree diameter was measured at 1.3 m above the ground. The basal area (BA) of trees in each site was also calculated from the DBH data.

Branch-and-stem density survey

To characterize the abundance of food available to hares in winter in the area where we conducted the hare

Table 1. Vegetation types at hare track surveys

Vegetation types	Symbols in Fig. 1A	Height of tree (m) Mean ± *SD*	DBH (cm) Mean ± *SD*	BA (m^2/ha) Mean ± *SD*	Tree density (no./ha) Mean ± *SD*	Branch-and-stem density (no./ha) Mean ± *SD* at 1.5 m above ground	The number of study sites
Japanese cedar	○	8.4 ± 5.0	11.4 ± 6.3	47.2 ± 37.2	303.9 ± 202.2	111.6 ± 192.8	56
Quercus spp.	△	5.4 ± 2.7	6.7 ± 2.4	41.8 ± 29.8	492.1 ± 275.0	239.1 ± 183.1	36
Japanese pine	□	4.3 ± 3.8	5.4 ± 3.2	25.7 ± 21.4	650.0 ± 448.4	563.9 ± 429.7	15
Weigela hortensis	●	2.6 ± 1.7	3.5 ± 1.8	18.6 ± 16.0	670.8 ± 405.7	581.6 ± 324.6	16
Planted beech	▲	1.1 ± 1.0	2.9 ± 4.2	6.1 ± 10.1	473.0 ± 366.8	1330.0 ± 1630.7	13
mixed	■	2.9 ± 1.9	4.4 ± 2.5	32.9 ± 18.5	1070.1 ± 515.9	559.7 ± 491.9	15

DBH: tree diameter at breast height.
BA: basal area of trees in a study area.

track survey, we surveyed branch-and-stem density in the summer 2006 and 2008; measurements were made at a height of 1.5 m above ground because hares could reach branches ≤0.5 m above the snow. Mean snow depth is approximately 1 m. We hypothesized that branch-and-stem density, rather than the density of individual shrubs, would most strongly affect food resource use. Shimano et al. (2006) reported that the density of hare fecal pellets tended to be higher in sites with more shrubby vegetation. They noted that high pellet density implied preferred habitat for hares. Sites with high branch-and-stem densities would also provide shelter against predators and inclement weather (Litvaitis et al. 1985; Koehler 1990). The branch-and-stem density survey was most frequently conducted in areas of 100 m^2 (ranging from 9 to 225 m^2). The vegetation types found in each hare track survey site are listed in Table 1.

Forest canopy closure rate

In winter 2006, we estimated the forest canopy closure rates at 90 study sites. We estimated forest canopy closure from hemispherical photographs taken with a fisheye lens (COOLPIX 5400; Nikon; Fisheye Lens Converter FC-E9 0.2X; Nikon). Because canopy closure affects the growth of forest floor plants, which can serve as food resources for hares, we analyzed the relationship between closure and hare movement distances. Photographs were taken with the camera located 1.5 m above the ground, which was the mean shrub height, at the center of each site. We scanned the photographs into a personal computer and calculated canopy closure using the software "Lia 32" provided by Dr. K. Yamamoto, Nagoya University, Japan.

Browse mark and branch-and-stem diameter surveys

We investigated browse marks from 3 to 6 March and from 26 August to 9 September 2006 to determine which vegetative species were consumed by hares (Fig. 1B). We surveyed a total of 110 shrub stands (two shrub stands per 1 km) along 14 forestry roads that covered almost all forested areas on Sado Island. Japanese hares mainly feed on herbs in summer, whereas they feed on trees in winter because herbs are covered by snow. Therefore, we examined branch and stem diameters and the heights of browse marks on the branches and stems in each area (ranging from 4 to 25 m^2). We counted the number of branches and browse marks at and above 1.0 m to account for snow accumulation. The browse mark percentage for a species was calculated as (the number of browse marks/the number of branches and stems) × 100 (%) (Table 2). The number of browse marks and the number of browsed branches and stems were the same, because the tips of branches and stems were browsed. The distribution of browse marks represented the distribution of foraging hares in winter. To determine the distribution area in winter, we recorded the survey points using a GPS receiver (map21EX; EMPEX, Tokyo, Japan).

Crude protein content of branches with browse marks

We measured the protein contents of branches and stems to evaluate the food quality for hares and to determine why hares preferred certain species. We estimated crude protein in trees based on the total nitrogen content of the branches.

We measured crude protein contents in 16 shrub species of 30 species; results are shown in Table 2. In the browse marks survey (the percentages of browse

Table 2. Browsed plant species (and two plantation species) and the percentage of browse marks, protein contents of branches, mean branch-and-stem diameters, and the numbers of branches and stems

Species code	Plant species	The percentage of browse marks (%) ± *SD*	Crude protein content of branches (mg/g) ± *SD*	Mean branch-and-stem diameter (cm) ± *SD* higher than 1.0 m above ground	The number of branches and stems (no./883 m^2)
1	*Helwingia japonica*	44.3 ± 37.8	37.8 ± 10.8	0.9 ± 0.2	65 (0.8)
2	*Actinidia polygama*	42.0 ± 36.6	57.2 ± 21.1	0.6 ± 0.3	80 (1.0)
3	*Staphylea bumalda*	35.7 ± 29.2	34.1 ± 4.3	0.6 ± 0.3	367 (4.7)
4	*Rubus palmatus* var.*coptophyllus*	31.8 ± 34.0	66.7 ± 21.4	0.6 ± 0.4	592 (7.6)
5	*Callicarpa japonica*	27.3 ± 28.7	27.7 ± 6.5	0.5 ± 0.4	331 (4.1)
6	*Prunus verecunda*	26.5 ± 26.1		1.0 ± 0.3	64 (0.8)
7	*Weigela hortensis*	26.4 ± 23.0	46.2 ± 13.1	1.1 ± 1.0	2115 (27.1)
8	*Clethra barvinervis*	26.2 ± 26.6	27.4 ± 9.9	0.9 ± 1.1	651 (8.3)
9	*Salix bakko*	25.7 ± 21.4		0.8 ± 0.3	303 (3.9)
10	*Mallotus japonicus*	25.6 ± 37.7	58.7 ± 18.9	1.1 ± 0.8	141 (1.8)
11	*Amorpha fruticosa*	25.0 ± 24.1		0.7 ± 0.3	307 (3.9)
12	*Stachyurus praecox*	24.8 ± 25.6	38.8 ± 10.8	0.8 ± 0.4	501 (6.4)
13	*Hydrangea serrata*	18.4 ± 22.5		0.9 ± 0.2	47 (0.6)
14	*Viburnum dilatatum*	17.9 ± 21.1		0.8 ± 0.8	265 (3.4)
15	*Acer japonicum*	17.5 ± 21.7		0.6 ± 0.4	83 (1.1)
16	*Lespedeza cyrtobotrya*	17.2 ± 27.7	23.6 ± 10.7	0.5 ± 0.3	167 (2.1)
17	*Lindera umbellata* var.*membranacea*	15.5 ± 32.7	36.5 ± 16.7	0.8 ± 0.8	365 (4.7)
18	*Acer palmatum* var. *matsumurae*	15.4 ± 20.5		0.2 ± 0.1	37 (0.5)
19	*Rubus crataegifolius*	14.8 ± 25.8		0.6 ± 0.3	99 (1.3)
20	*Corylus sieboldiana*	13.9 ± 26.7		0.6 ± 0.6	123 (1.6)
21	*Acer rufinerve*	12.5 ± 19.1		1.0 ± 1.2	339 (4.3)
22	*Quercus serrata*	11.0 ± 17.5	20.7 ± 6.6	0.8 ± 0.7	257 (3.3)
23	*Acer mono* var. *mayril*	8.3 ± 18.0		1.9 ± 1.7	60 (0.8)
24	*Castanea crenata*	7.3 ± 15.2	13.3 ± 7.9	2.2 ± 3.2	93 (1.2)
25	*Rhus trichocarpa*	4.6 ± 13.8		1.2 ± 1.2	34 (0.4)
26	*Fraxinus sieboldiana*	2.7 ± 7.8		0.7 ± 0.4	53 (0.7)
27	*Aucuba japonica* var. *borealis*	1.2 ± 5.3	19.7 ± 12.1	0.8 ± 0.4	138 (1.8)
28	*Swida controversa*	0.8 ± 2.2		1.9 ± 1.6	45 (0.6)
29	*Pinus densiflora*	0	5.7 ± 2.6*	6.8 ± 7.9*	74 (0.9)
30	*Cryptomeria japonica*	0	7.0 ± 4.3*	7.4 ± 4.0*	6 (0.1)
	total				7802 (100.0)

* The branch diameters of *Pinus densiflora* (29) and *Cryptomeria japonica* (30) at a height of 1.0 m above ground were large; therefore, crude protein content measurements included samples that were of similar size to other tree samples: branch diameters were almost 0.5 cm, branches were located 1.5 m above ground, and all sampled branches had grown during the year of sampling. The percentage of browse marks is an indicator of food resource use ([the number of browse marks/the number of branches and stems] × 100 [%]). Crude protein content is an indicator of food quality. The numbers of branches and stems were surveyed during the branch-and-stem density survey within a total area of 883 m^2. The numbers in parentheses are the percentages.

marks (%) in Table 2), some species were found to be eaten more frequently than others. Thus, we selected nine species (species codes 1–5, 7, 8, 10, 12) that were eaten frequently, three species (16, 17, 22) that were eaten with moderate frequency, and two species (24, 27) that were not eaten frequently for measuring crude protein content (Table 2). Two other species, *P. densiflora* (29) and *C. japonica* (30), were also selected because they are well-known food species of hares (Inukai 1953; Toyoshima and Takata 1955; Otsu 1969; Toyoshima et al. 1970; Takata et al. 1973; Toyoshima 1978; Hiraoka et al. 1979), although browse marks have not recently been observed on these species on Sado Island. In the browse mark survey, we recorded both the branch and stem number and the diameter of branches and stems of the trees higher than 1.0 m (Table 2), but we collected only the branch and stem density for the forest structure survey at heights of 1.5 m above ground (Table 1). Thus, the branch and stem diameters in Table 2 and branch and stem densities in Table 1 were based on the different sources. All of the branches sampled for crude protein content grew in the sampling year. Here, we used only branch and stem parts without leaves to represent food materials eaten by hares in the winter, although *P. densiflora*, *C. japonica* and *Aucuba japonica* var. *borealis* have evergreen leaves. In the browse mark survey, although the mean branch and stem diameters of *P. densiflora* (29) and *C. japonica* (30) were larger than those of the other species (Table 2), we collected branch samples of almost 0.5 cm diameter because we used only the current year's branches for the crude protein content analysis. Sampling was conducted during the snow-cover season on 26 November 2006.

Twenty samples were collected for each of the 16 shrub species, for a total of 320 samples. Samples were oven-dried at 60°C for 24 h. Dry samples of 0.5–1.0 mg were wrapped in tin foil and weighed. Subsequently, samples were ground into a powder using a metal file, and total nitrogen content was measured using an Elementar Analysensysteme EA1112 (Thermo Finnigan, San Jose, CA, USA). Crude protein content (dry weight) was calculated from the total nitrogen content of samples as follows: total nitrogen (mg/g) × 6.25 = protein quantity of the branch (mg/g), where 6.25 is the nitrogen-protein conversion factor (Yoshikawa and Ashida 1998).

Results

Track surveys and forest canopy closure rates

Mean tree heights at the study sites ranged from 1.1 to 8.4 m (Table 1). Movement distances of hares decreased as the mean stand height increased ($r = -0.19$, $P < 0.05$; Fig. 3A). Mean tree diameters ranged from 2.9 to 11.4 cm. Movement distances of hares decreased as the tree diameter (DBH) increased ($r = -0.18$, $P < 0.05$; Fig. 3B). Movement distances of hares decreased as the BA increased, where BA implies the development of the tree stand ($r = -0.18$, $P < 0.05$; Fig. 3C). However, movement distances of hares increased as the branch-and-stem density at 1.5 m above the ground increased ($r = 0.20$, $P < 0.05$; Fig. 4A).

Hare movement distance significantly decreased as the forest canopy closure rate increased ($r = -0.28$, $P < 0.01$; Fig. 4B).

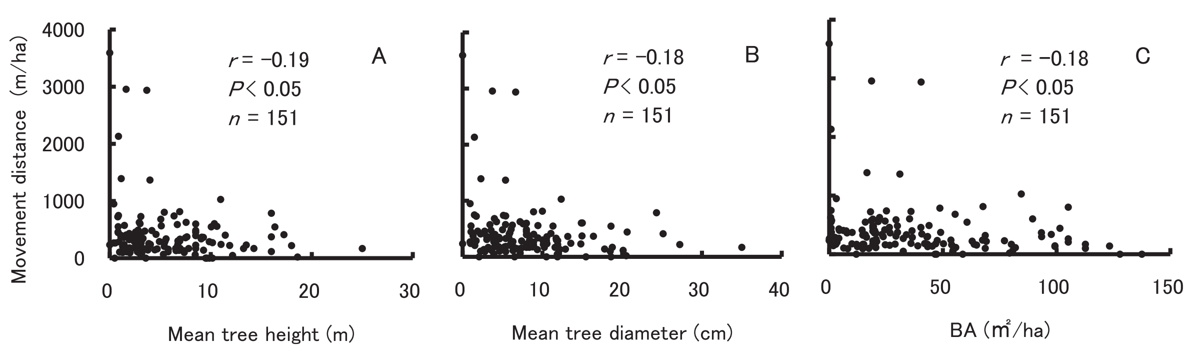

Fig. 3. The relationship between several aspects of forest structure and movement distance (i.e., habitat usage index of hares). A: Relationship between the mean tree height and movement distance. B: Relationship between the mean tree diameter and movement distance. C: Relationship between the basal area (BA) and movement distance.

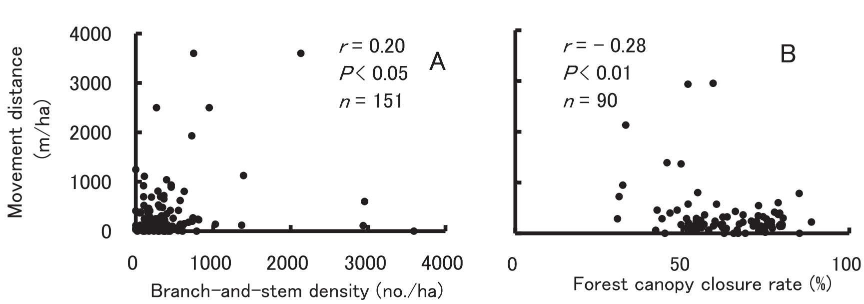

Fig. 4. The relationships between branch-and-stem density (food resource index), canopy closure (%), and movement distance (habitat usage index of hares). A: Relationship between the density of branches and stems at 1.5 m height and movement distance. B: Relationship between the forest canopy closure rate and movement distance.

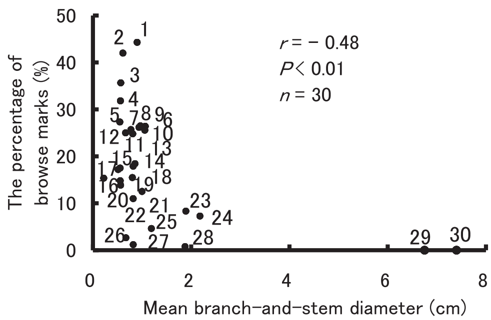

Fig. 5. Relationship between the mean branch-and-stem diameter and the percentage of browse marks (an index of food preference) for all plant species. Species codes are as in Table 2.

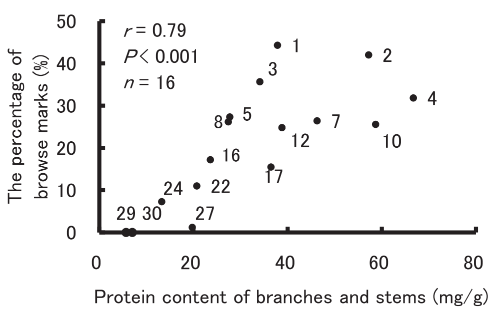

Fig. 6. Relationship between the protein content of branches and stems (an index of nutrient content) and the percentage of browse marks (an index of food preference). Species codes are as in Table 2.

Browse mark survey

The percentage of browse marks on the branches and stems of each species decreased significantly with increasing branch and stem diameter, and hares consumed thin branches that ranged from 0.5 to 1.0 cm in diameter ($r = -0.48$, $P < 0.01$; Fig. 5). *P. densiflora* (29) and *C. japonica* (30), which had mean branch-and-stem diameters of 6.8 and 7.4 cm, respectively, showed no evidence of browsing. When we removed these two species from the calculation, the relationship between branch and stem diameter and the browse mark percentage remained significant ($r = -0.40$, $P < 0.05$). We found browse marks on vegetation at 81 of the 110 study points.

Browse marks were frequently found on the branches of *Helwingia japonica* (1), *Actinidia polygama* (2), *Staphylea bumalda* (3), and *Rubus palmatus* (4). All of the species that were heavily browsed had thin branches (Table 2, Fig. 5).

Browse marks and branch protein content

The percentage of browse marks increased significantly with increased branch protein content ($r = 0.79$, $P < 0.001$; Fig. 6). *Rubus palmatus* var. *coptophyllus* (4), *Mallotus japonicas* (10), and *A. polygama* (2) contained large amounts of crude protein, whereas *C. japonica* (30) and *P. densiflora* (29) had lower levels of crude protein content compared to the other trees (Table 2, Fig. 6).

Discussion

Favorable sites for hares

Hare movement distances decreased significantly with increasing stand height, tree DBH, and stand BA values (Fig. 3). Moreover, hare movement distances significantly increased when the density of branches and stems was high (Fig. 4A), although the correlation coefficients were not high. These findings suggest that hares prefer areas with high branch-and-stem densities over mature forests, which have lower branch-and-stem densities. Therefore, suitable sites for this species include young stands containing small-diameter trees. As mentioned above, the preferred food plants in shrub stands included *H. japonica* (1), *A. polygama* (2), *S. bumalda* (3), and *R. palmatus* var. *coptophyllus* (4) (Table 2).

Additionally, movement distances were significantly higher when the forest canopy closure rate was low (Fig. 4B), suggesting that hares preferred areas with low forest canopy closure and a dense understory. Shrubs may serve food resources more frequently when light penetration to the forest floor is higher. Therefore, maintaining light penetration to the forest floor will provide more food and shelter for hares. Such management of young forests is necessary to conserve this subspecies of the Japanese hare.

Shimano et al. (2006) indicated that a different subspecies of the Japanese hare, *L. brachyurus angustidens*, prefers shrub stands with low values for canopy tree density, DBH, BA, stand height, and canopy closure in Japanese cedar plantations. Torii (1990) noted that hare movement distances at night were affected by food abundance. Snowshoe hares (*L. americanus*) in North America prefer sites with dense ground cover, such as open forests or deforested scrublands, as well as grasslands (Wolff 1980). Besides the consideration of food resources, many studies have documented the importance of understory density for shelter (Litvaitis et al. 1985; Koehler 1990; Shimano et al. 2001, 2006), which is consistent with our results. We conclude that hares prefer sites with a dense understory and low canopy closure; this is consistent with our current results and past studies, although our results showed low correlation coefficients.

Favorable foods

Slender branches tended to be eaten more frequently (Table 2, Fig. 5). Our results indicated that hares primarily browsed upon *H. japonica*, *A. polygama*, and *S. bumalda*. Otsu (1969) reported that Japanese hares preferred leaves, buds, shoots, and tree bark in winter. He also indicated that hares did not consume thick branches and concluded that hares preferred *C. japonica* (an evergreen tree), *Acer* spp., *Acanthopanax sciadophylloides*, *Paulownia tomentosa*, *Aralia elata*, papilionaceous species, and fruit trees (Otsu 1969). The hare subspecies *L. brachyurus brachyurus* prefers *C. japonica* (Horino and Kuwahata 1984), and *L. timidus ainu* prefers *P. densiflora* because it is an evergreen species (Inukai 1953). Our results were similar to those of past studies in that *L. timidus* preferred the buds and shoots of trees and did not eat branches >1.0 cm in diameter (Aanio 1983) and *L. brachyurus* preferred the twigs and stems less than 3 mm in diameter (Yamada 1991). These findings indicated that mature stems of *C. japonica* and *P. densiflora* were not consumed by hares (Table 2). Moreover, *C. japonica* and *P. densiflora* had lower crude protein levels compared to other tree species (Table 2).

Hares appear to prefer branches and stems containing large amounts of protein (Table 2, Fig. 6). Protein is the main constituent of organisms and is thus one of the most important nutrients (Protein Research Foundation 2000). Therefore, hares may prefer habitats containing shrubs with high protein content branches. Japanese hares frequently consume the younger bark of *P. tomentosa* because it contains large amounts of protein (Otsu 1974). These results indicate that hares likely require substantial protein in the winter and therefore prefer foods with high protein content.

Although Yamada and Kawamoto (1991) noted that Japanese hares do not necessarily need a large amount of protein, Otsu (1974) reported that hares preferentially consume protein within the bark of *P. tomentosa*, which is consistent with our findings.

Consequently, well eaten specimens of *H. japonica*, *A. polygama*, *S. bumalda*, and *R. palmatus* var. *coptophyllus* had small-diameter branches and stems (<1 cm), and high crude protein levels. In contrast, *C. japonica* and *P. densiflora* had thick branches and stems with low protein levels; thus, on Sado Island, browse marks were not observed on these species, despite previous reports that hares feed upon them (Inukai 1953; Toyoshima and Takata 1955; Otsu 1969; Toyoshima et al. 1970; Takata et al. 1973; Toyoshima 1978; Hiraoka et al. 1979).

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