Seasonal habitat selection of an expanding sika deer Cervus nippon population in eastern Hokkaido, Japan

Authors: Sakuragi, Mayumi, Igota, Hiromasa, Uno, Hiroyuki, Kaji, Koichi, Kaneko, Masami, et al.

Source: Wildlife Biology, 9(2) : 141-153

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.036

Seasonal habitat selection of an expanding sika deer *Cervus nippon* population in eastern Hokkaido, Japan

Mayumi Sakuragi, Hiromasa Igota, Hiroyuki Uno, Koichi Kaji, Masami Kaneko, Rika Akamatsu & Koji Maekawa

Sakuragi, M., Igota, H., Uno, H., Kaji, K., Kaneko, M., Akamatsu, R. & Maekawa, K. 2003: Seasonal habitat selection of an expanding sika deer *Cervus nippon* population in eastern Hokkaido, Japan. - Wildl. Biol. 9: 141-153.

Sika deer *Cervus nippon* in Hokkaido, Japan, have recovered from a population bottleneck about 120 years ago and their distribution has expanded rapidly in the last three decades. We tracked 53 radio-collared female sika deer, and obtained 4,430 locations during the 25-month study period from April 1997 to April 1999. We examined the seasonal distribution of female sika deer in relation to spatial landscape features (snow depth, vegetation, bamboo grass and roads) with a logistic regression model using a geographic information system database. We presented a population-landscape scale evaluation of sika deer habitat for summer and winter within the telemetry study area (TSA) using resource selection functions. We then extrapolated the model to the rest of eastern Hokkaido to discuss the seasonal migration for an expanding population. Most radio-collared sika deer (71%) moved between high-elevation summer and low-elevation winter ranges, whereas some (29%) moved between low-elevation summer and similar or high-elevation winter ranges. During winter, sika deer selected middle elevation habitats (200-400 m a.s.l.) with both a relatively low snow depth and the presence of coniferous and mixed forests. On the other hand, sika deer were widely distributed regardless of elevation during summer, although they were further from roads and less often in agricultural lands. Within the TSA, the suitable habitat was very limited during winter compared with during summer. Although migration from summer to winter ranges may depend on the abundance and distribution of suitable winter habitat at a landscape scale, migration from winter to summer ranges could not be explained from this study. Our approach is useful for understanding the relationships among seasonal habitat selection, seasonal migration and the expansion of the population.

Key words: Cervus nippon, geographic information system, habitat selection, logistic regression, radio-telemetry, resource selection function, sika deer

Mayumi Sakuragi, Hiromasa Igota & Koji Maekawa, Laboratory of Boreal Forest Conservation, Field Science Center for Northern Biosphere, Hokkaido University, N.9W.9 Kita-Ku, Sapporo 060-0809, Japan - e-mail addresses: sakuram@cocoa.ocn.ne.jp (Mayumi Sakuragi); igota@cocoa.ocn.ne.jp (Hiromasa Igota); mkoji@ffc.hokudai.as.jp (Koji Maekawa)
Hiroyuki Uno, Eastern Hokkaido Wildlife Research Station, Hokkaido Institute of Environmental Sciences, 2-2-54 Urami, Kushiro 085-0835, Japan - e-mail: uno@hokkaido-ies.go.jp
Koichi Kaji & Masami Kaneko, Hokkaido Institute of Environmental Sciences, N.19W.12 Kita-Ku, Sapporo 060-0819, Japan - e-mail addresses: kaji@hokkaido ies.go.jp (Koichi Kaji); kaneko@rakuno.ac.jp (Masami Kaneko)*
Rika Akamatsu, EnVision, 5-2-201, N.9W.4 Kita-Ku, Sapporo 060-0809, Japan - e-mail: moe-ri@ivory.plala.or.jp

*Present address: Department of Regional Environment Studies, Faculty of Environment systems, Rakuno Gakuen University, 582, Midori-Machi, Bunkyodai, Ebetsu 069-8501, Japan

Corresponding author: Koichi Kaji

Received 12 August 2002, accepted 22 November 2002

Associate Editor: Jan Lindström

Effective management of wildlife populations largely depends upon understanding and predicting their habitat needs (Clark, Dunn & Smith 1993). Conservation biologists and resource managers face complex challenges in managing large animals, especially migratory mammals, because they often move or migrate long distances crossing both good and poor habitat. Management across disjunctive areas of suitable habitat is necessary (Mlandenoff, Sickley & Wydeven 1999). Therefore, management can benefit from large-scale evaluation and mapping of seasonally favourable habitat distribution of these species on a landscape scale (Mlandenoff et al. 1999). From a viewpoint of wildlife management or conservation, some studies have presented the prediction of potential or favourable habitat of a target species (Mlandenoff, Sickley, Haight & Wydeven 1995, Kaji, Miyaki, Saitoh, Ono & Kaneko 2000), or the relationship between the distribution of a species and human activities (Pereira & Itami 1991, Mace & Waller 1996, Mace, Waller, Manley, Lyon & Zuuring 1996, Mace, Waller, Manley, Ake & Wittinger 1999).

Many populations of large herbivores such as wildebeest *Connochaetes taurinus*, zebra *Equus burchelli* and Thompson's gazelle *Gazella thompsoni* in Africa (Maddock 1979), and mule deer *Odocoileus hemionus hemionus* (Garrott, White, Bartmann, Carpenter & Alldredge 1987), moose *Alces alces* (Edwards & Ritchey 1956), black-tailed deer *O. hemionus* (Loft, Menke & Burton 1984), and white-tailed deer *O. virginianus* (Larson, Rongstad & Terbilcox 1978) in North America migrate between seasonal ranges. Migration of these animals has probably evolved to take advantage of spatial and temporal variations in the environment (French, Reed, Calambokidis & Cubbage 1989). Fryxell & Sinclair (1988) demonstrated that seasonal migration has important implications for the structure and dynamics of large herbivore communities.

Northern ungulates migrate between their summer and winter ranges, and a great deal of data on seasonal movement and factors affecting seasonal habitat selection of ungulate species in temperate ecosystems have been reported (Loft et al. 1984, Schoen & Kirchhoff 1985, Kufeld, Bowden & Schrupp 1989, Van Deelen, Champa, Hamady & Haufler 1998). Snow depth (Klein & Olson 1960, Garrott et al. 1987), vegetation cover (Bloom 1978, Wallmo & Schoen 1980, Kufeld, Bowden & Schrupp 1988), forage (Hobbs & Spowart 1984, Garrott et al. 1987, Kufeld et al. 1989), and road systems (Rost & Bailey 1979) have been demonstrated as factors affecting winter habitat selection. On the other hand, habitat quality (Loft et al. 1984, Bowyer 1986, Kufeld et al. 1989, Nicholson, Bowyer & Kie 1997), forage (Garrott et al. 1987), vegetation cover (Loft et al. 1984), human disturbance (Nicholson et al. 1997) and predation (Riley & Dood 1984, Festa-Bianchet 1988) have been implicated as factors affecting summer habitat selection. Previous studies suggested that snow depth and bamboo grass *Sasa* spp. variety (Kaji et al. 2000) and vegetation cover (Hokkaido Institute of Environmental Sciences 1994) were important variables limiting sika deer *Cervus nippon* distribution in Hokkaido, Japan. The importance of bamboo grass as winter forage has been recognised for sika deer in Japan (Takatsuki 1986, 1993, Yokoyama, Kaji & Suzuki 2000). Most of these studies do not consider the population status or historical background of the population dynamics (but see Mlandenoff et al. 1999, Kaji et al. 2000). Therefore, studies of the relationship between seasonal habitat selection and seasonal migration in relation to expansion of population size and distribution are needed.

Sika deer historically occurred throughout Hokkaido, the northernmost island in Japan, and they migrated seasonally between the west, where snows are heavy, and east, where wintering grounds are more open (Inukai 1952). Sika deer on Hokkaido have a reduced level of genetic variation because of a population bottleneck (Nagata, Masuda, Kaji, Kaneko & Yoshida 1998) about 120 years ago, caused by overharvest and heavy snowfall (Inukai 1952). Through the genetic differences among the populations, Nagata et al. (1998) described three subpopulations (Daisetsu, Akan and Hidaka) consisting of individuals from the main three coniferous forests in Hokkaido (Fig. 1).

Under government protection, the number of sika

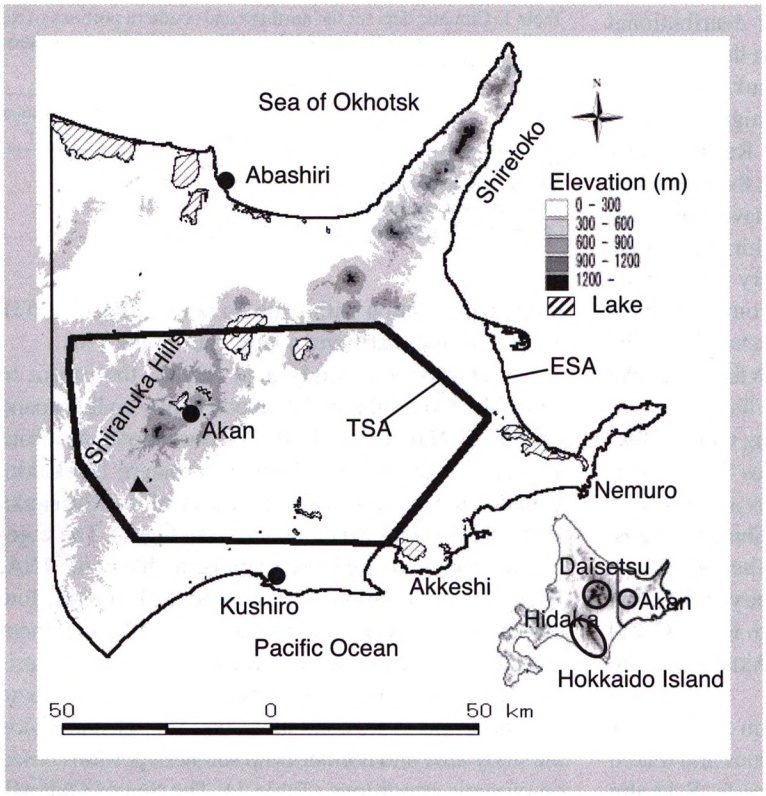

Figure 1. Location of the telemetry study area (TSA) in eastern Hokkaido, Japan, where seasonal resource selection function models were developed. All radio-collared deer were captured on the Shiranuka Hills (▲). On the inserted map of Hokkaido three genetically differential populations of sika deer are indicated (Nagata et al. 1998).

deer gradually recovered during the last three decades (Kaji et al. 2000). Elimination of wolves *Canis lupus*, replacement of native mixed hardwood forests with conifer plantations, and increased pasture acreage likely contributed to the expansion in deer distribution (Kaji et al. 2000). By the mid-1970s, sika deer occupied most available habitat in the eastern half of the island (Kaji et al. 2000). Damage to agriculture and forestry by sika deer remained at low levels from the mid-1950s through the mid-1970s, but increased dramatically to nearly USD 15 million in 1990 and to over USD 30 million in 1996 (Kaji et al. 2000). As the range of sika deer expanded, agricultural and forest damage increased, resulting in relaxed hunting regulations. Total harvest fluctuated between 2,000 and 3,000 animals during 1970-1989 and increased to 16,134 animals in 1990 and 46,634 animals in 1996 as more areas were opened for hunting and antlerless harvest was allowed (Kaji et al. 2000). The population of sika deer reached a peak about 1996 and tended to decrease gradually due to heavier hunting (Hokkaido Government 1998).

The deer population recovery and expansion in eastern Hokkaido may have originated from the Akan subpopulation (Nagata et al. 1998). Eastern Hokkaido is a largely continuous suitable habitat for sika deer (Hokkaido Institute of Environmental Sciences 1994, Kaneko, Kaji & Ono 1998, Kaji et al. 2000). Based on the background of the sika deer population in eastern Hokkaido, we predict that seasonal habitat selection in the expansion of the population is closely related to present patterns of seasonal migration in eastern Hokkaido. However, the relationship between seasonal habitat selection and seasonal migration remains poorly understood.

Bowyer (1986), Scarbrough & Krausman (1988) and Bowyer, Kie & Ballenberghe (1996) have reported sexual differences in the use of forages, habitats and space by deer. As female deer may be able to increase their reproductive success by producing more and healthier young, habitat selection will probably be more important for females than for males. Therefore, a possible relationship between migration and habitat selection may be clearer for females than for males, which is why we focused our study on females. In this paper, we examine the seasonal distribution of radio-collared female sika deer in relation to spatial landscape features using a logistic regression model based on a geographic information system (GIS) database, and examine the factors affecting seasonal habitat selection of an expanding population. We then present a population-landscape scale evaluation of sika deer habitat for summer and winter using resource selection functions (RSF; Manly, McDonald & Thomas1993), and demonstrate how seasonal migration is related to distribution of suitable habitat on a landscape scale. Further, we extrapolate the RSF model to the remainder of eastern Hokkaido to discuss the seasonal migration in relation to the expansion of the population.

Material and methods

We conducted the telemetry study in 7,466 km^2 of eastern Hokkaido (see Fig. 1). The Shiranuka Hills is one of the largest and most important wintering areas for sika

deer, which have been expanding their distributional range in eastern Hokkaido during the last three decades (Kaneko et al. 1998). Within the Shiranuka Hills wintering population, both resident and migratory individuals occur (H. Igota, unpubl. data). Resident deer remain in the Shiranuka Hills throughout the year while migratory deer migrate seasonally and have their summer ranges to the north and east of the Shiranuka Hills. The telemetry study area (TSA) boundary was defined by the minimum convex polygon encompassing all seasonal movements of the radio-collared deer. The Shoro River and several roads run through the Shiranuka Hills from north to south. Many hunters have access to this area using the roads to hunt deer during winter (Hokkaido Institute of Environmental Sciences 1995). Plantations of Sakhalin fir *Abies sachalinensis* and Sakhalin spruce *Picea glehnii* occur in parts of the Shiranuka Hills. The climate of the study area is cool and humid with an average temperature of -10.4°C in February and 17.4°C in August, the mean annual temperature is 3.6°C and annual precipitation is 1,200 mm at Akan (Igarashi 1986).

The high elevation regions (300-800 m a.s.l.) of the TSA are primarily composed of coniferous and mixed forests. Conifers, Yezo-spruce *P. jezoensis*, Sakhalin fir and Sakhalin spruce, are dominant and mixed with Japanese linden *Tilia japonica* and Japanese oak *Quercus crispula* in mountainous areas over 400 m. Alpine species such as Erman's birch *Betula ermanii* and Japanese stone pine *Pinus pumila* dominate above 800 m. Most natural forests are classified as 'pan mixed forest' with conifers and broad-leaved trees typical of the transition between temperate and subarctic zones (Tatewaki 1958). The low elevation regions (below 300 m) are dominated by urban development and agriculture, but deciduous forests and plantations of Japanese larch *Larix leptolepis* persist in this area. Deciduous broad-leaved forest is comprised of Japanese oak, Japanese white birch *B. platyphylla*, painted maple *Acer mono*, Japanese linden, Japanese elm *Ulmus davidiana*, Japanese ash *Fraxinus mandshurica*, Amur cork tree *Phellodendron amurense*, caster aralia *Kalopanax pictus*, and willow *Salix* spp. (Igarashi 1986). Dominant undergrowth is bamboo grass *Sasa* spp., which covers 90% of the Hokkaido forests (Toyooka, Sato & Isizuka 1983). There are four species of bamboo grasses. The largest, *S. kurilensis* (Sk), is found primarily in the west where snowfall is heavy. *S. senanensis* (Ss) is a medium-sized bamboo grass which is found in broad-leaved and mixed forests with intermediate snow accumulation. *S. nipponica* (Sn), the smallest bamboo grass, is found in the southeastern region with little snowfall. *S. borealis* (Sb) has a very limited distribution within the Sn range (Matsui 1963). Sn and Ss dominate over a large part of the TSA.

Table 1. Climatic data for the northern and southern portions of the study area in eastern Hokkaido, Japan (Japan Weather Association Hokkaido Regional Head Office 1991).

	Northern Portion (Abashiri)	Southern Portion (Kushiro)
Mean annual temperature (°C)	6.0	5.7
Annual precipitation (mm)	815	1043
Maximum snow depth (cm)	59	40
Duration of >50-cm snow depth (days)	15	3

The extrapolated study area (ESA), the extent to which the Akan subpopulation potentially could expand its range (Nagata et al. 1998), encompassed about 15,847 km^2 of sika deer habitat in eastern Hokkaido, bounded to the west by the boundary of the Shiranuka Hills and the Daisetsu mountains (see Fig. 1). The vegetation structure of the ESA is similar to that of the TSA. High elevation regions are covered with forests, low elevation regions are dominated by urban development and agriculture, and the undergrowth is composed primarily of Sn and Ss. The Shiretoko Hills and Akan mountain ranges are continuous (see Fig. 1), and divide the study area into northern and southern portions based on climatic conditions (Table 1). The Sea of Okhotsk affects the climatic characters of the northern, and the Pacific Ocean the southern portions of the mountains, respectively (Japan Weather Association Hokkaido Regional Head Office 1991).

A total of 53 female sika deer were captured within the Shiranuka Hills with anesthetic guns in April 1997 (19 individuals), March 1998 (31 individuals), and March 1999 (three individuals). Captured deer (37 adults, six yearlings, 10 fawns) were fitted with VHF radio collars (144 MHz, ATS, Isanti, Minesota, USA or Lotek Engineering, Inc., Newmarket, Ontario, Canada) with an expected battery life of three years, and ear tags for visual identification. From April 1997 to April 1999, deer were located by triangulation procedures (White & Garrott 1990) during daylight hours from the ground with radio-equipped trucks and on foot every two or three days. Triangulation bearings were taken with a 107-cm, 3-element Yagi antennae and receivers (FT-290mk II, YAESU MUSEN, Tokyo, Japan). Locations were recorded on 1:25,000 scale topographic maps. We also recorded the location of each marked individual that was visually observed.

To account for inherent errors in triangulated deer locations, we estimated the circular error associated with telemetry by calculating the 99% confidence limits (Murakami & Mano 1998) for the average distance of our estimates from actual locations of radio-collars placed at

60 locations. The average error in locations was 145 m ± 149 (SD) and the upper 99% confidence limits was 196 m. We considered all habitats that occurred within a 196-m circle as an estimate of the habitat at that location. Moreover, radio-telemetry location from the ground has limitations regarding the area that we could search by roads. All telemetry locations (N = 4,837) from 1997 to 1999 were distributed within 5 km from road networks (99.7% of TSA), and 80% of those were within 1 km of road networks (68.9% of TSA).

Deer locations were grouped into seasons based on the movement behaviour of sika deer. We defined the seasonal ranges of migratory deer during the period when movements stabilised over time (i.e. localised movements within areas over extended periods that were separated from another area of localised movement in time). Winter was defined as November to April for resident deer, and the period when migratory deer stabilised in their winter ranges. Summer was defined as May to October for resident deer, and the period when migratory deer stabilised in their summer ranges. Spring and fall were defined as the periods when locations fell sequentially between the summer and winter ranges for migratory deer, and data for these periods were not needed in determining habitats for summer and winter ranges in this study.

To define habitat characteristics, we developed a 1-km block database map containing habitat variables with a GIS. We used the GIS software ArcView 3.1 (Environmental Systems Research Institute, Inc., Redlands, California, USA). The TSA consisted of 7,466 blocks, and the ESA consisted of 16,582 blocks excluding 120 blocks that fell within lakes. We used the snow depth and elevation data of national land numerical information (National Land Agency 1992). Although the snow depth was the mean during winter for the 30-year period (1955-1984) and was not real time data during our study period, it represented the geographical distribution of relative snow depth throughout Hokkaido. We used the digital road map (Pasco digital map, Tokyo, Japan), and distance to road of a block was defined as the distance from the center of the block to the nearest road. We generated a 30-m grid vegetation database from Natural Environment Information GIS (Environment Agency 1997). Vegetation types were classified into six types (coniferous forest, mixed forest, deciduous forest, agricultural land, Japanese larch forest and alpine vegetation) and were defined as the area percentage of each vegetation type within the block. We used a 1:200,000 distribution map of bamboo grass species in Hokkaido (Toyooka, Sato & Isizuka 1984). Bamboo grass forage value was ranked in the order Sn > Ss > Sb > Sk by Kaji et al. (2000) based on availability (Hokkaido Government 1987, Takatsuki 1992a), grazing tolerance (Matsui 1963, Agata, Kubota & Kamata 1979) and nutritional value (Ohara 1948, Kawai, Juni, Yasue, Ogawa, Hata, Kondo, Okubo & Asahida 1995, Yamane & Furubayashi 1997). We assigned the blocks the relative forage value of each species according to Kaji et al. (2000). Bamboo grass forage value (scores in parentheses) were none (0), Sk (1), Sk+Ss (2), Sb or Sn + Sb or Ss + Sb (3), Ss (4), Ss + Sn (5), Sn (6) (see Kaji et al. 2000).

Sika deer telemetry coordinates from 1997 to 1999 were pooled to assess habitat selection at a population-landscape scale (Johnson 1980). Telemetry sample sizes were 2,384 locations for summer and 2,046 locations for winter. The blocks containing the 196-m circle of the telemetry locations were defined as used blocks, and we compared habitat variables of used blocks between summer and winter using a Mann-Whitney's U test to examine for seasonal differences in habitat use. In order to examine habitat selection, we compared habitat variables of used blocks with available blocks by maximum-likelihood logistic regression (Manly et al. 1993). A total of 1,999 random blocks were selected within the TSA to evaluate availability using the ArcView extension MOVEMENT (Hooge & Eichenlaub 1998). The proportions of random coordinates selected within 1 km and within 1-5 km of roads were chosen to be comparable to the proportions in the telemetry dataset (80 and 20%, respectively). All values were categorised for logistic regression analysis (Table 2).

Table 2. Categorisation of habitat variables for logistic regression analysis.

Habitat variable	Category		
	Range	Increment	Endpoints
Snow depth	1 - 9	25 cm	< 24 cm, > 200 cm
Elevation	1 - 5	300 m	< 299 m, > 1200 m
Coniferous forest	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Mixed forest	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Deciduous forest	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Agricultural land	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Japanese larch forest	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Alpine vegetation	0 - 5	20 %	0 for 0 %, < 19 %, > 80 %
Bamboo grass variety	0 - 6	-	-
Distance to road	1 - 11	500 m	< 499 m, > 5000 m

Snow depth was used only for winter analysis. Elevation was excluded from logistic regression analysis because it should correlate with snow depth or vegetation, and habitat selection of sika deer should be affected by snow depth, vegetation, or roads, not directly by elevation. We examined multi-collinearity among independent variables by a Variance Inflation factor (VIF). There was no significant multi-collinearity (all VIF < 3) according to Hayakawa (1986; if VIF > 10, there is a significant multi-collinearity). For each season, the model was developed using signif-icant ($P < 0.05$) variables by a backward stepwise elimination with the likelihood-ratio criterion. The model was ascertained by comparing the model containing all variables to the 'no selection model' (Hosmer & Le-meshow 1989). The logistic regression coefficients represented the contribution of each variable to explain resource selection relative to random availability. The association and power of each variable was ascertained by each coefficient's sign (negative or positive) and strength (-2 log likelihood-ratio: -2LLR).

For each season, we calculated RSF using the equation from Manly et al. (1993):

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_p x_p),$$

where $w(x)$ is the RSF, x_i is habitat variables from 1 to p, β_i is coefficient estimates for each habitat variables x_i, and $\beta_1 x_1 + \ldots + \beta_p x_p$ represents the available resource units. The RSF values represented the relative probability of use of each unique variable combination by sika deer. The RSF values were scaled as probability by dividing each RSF value by the largest RSF value for each season. Calculations were made with the GIS to produce a map containing RSF values within each 1-km block within the TSA, and then throughout the ESA. The extrapolation of TSA coefficients to the ESA assumed that

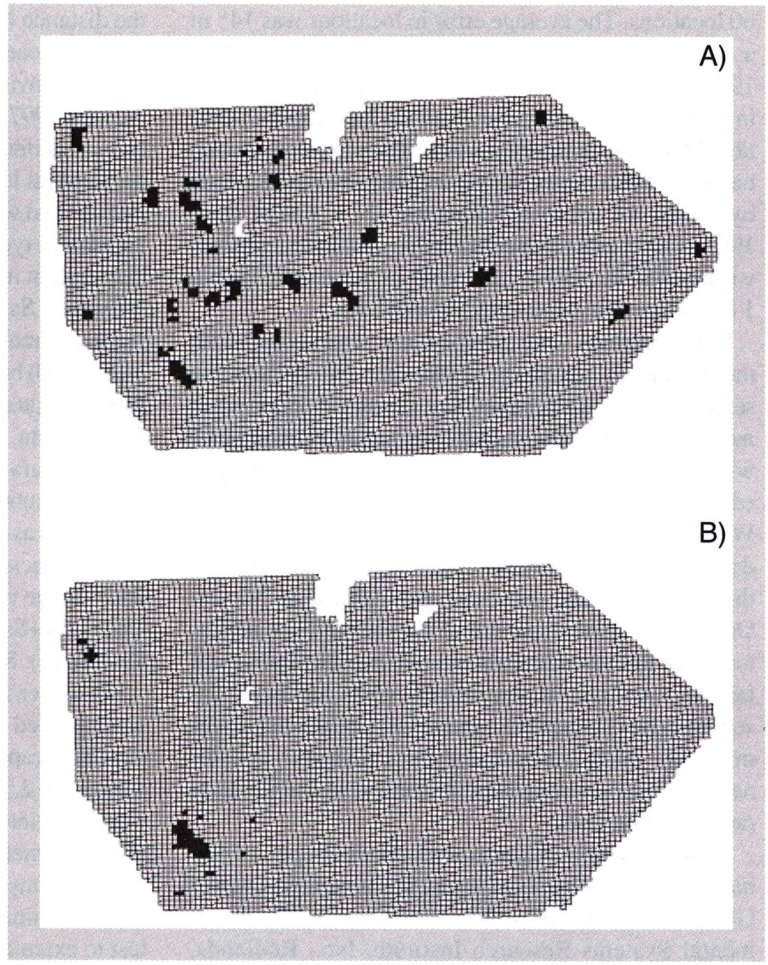

Figure 2. The telemetry study area showing the 1-km blocks (■) used during summer (A) and winter (B).

Table 3. Data on summer and winter habitat variables for radio-collared female sika deer in eastern Hokkaido, Japan, during 1997-1999.

	Summer		Winter		Mann Whitney's U test		
Variable	X	SD	X	SD	U	Z	P
Snow depth (cm)	88.0	28.1	59.4	8.3	2100.0	-7.761	<0.001
Elevation (m)	371.2	203.5	303.3	72.1	5175.0	-2.312	0.021
Coniferous forest (%)	34.5	33.5	27.5	21.5	6185.5	-0.524	0.600
Mixed forest (%)	24.5	31.0	32.9	26.5	4807.5	-3.046	0.002
Deciduous forest (%)	16.2	25.3	22.2	26.8	5258.5	-2.252	0.024
Agricultural land (%)	7.4	16.9	2.9	11.4	5753.0	-1.666	0.096
Japanese larch forest (%)	8.8	18.5	6.5	17.9	6036.5	-0.934	0.350
Alpine vegetation (%)	0.7	3.7	0.3	1.8	6290.5	-0.808	0.419
Bamboo grass variety	2.6	2.4	2.4	3.0	6478.5	-0.003	0.998
Distance to road (m)	1256.4	1045.7	606.5	469.9	4222.0	-4.001	<0.001

Table 4. Logistic regression coefficients for the final model for summer and winter with only significant variables (P < 0.05) entered.

	Summer				Winter			
Variable	ß	SE	-2LLR	P	ß	SE	-2LLR	P
Snow depth					-1.530	0.237	57.082	<0.001
Coniferous forest	0.318	0.052	39.291	<0.001	0.504	0.111	20.212	<0.001
Mixed forest	0.196	0.051	14.957	<0.001	0.418	0.092	20.508	<0.001
Deciduous forest								
Agricultural land	-0.216	0.075	8.906	0.004	-0.887	0.246	20.837	<0.001
Japanese larch forest	0.170	0.073	5.156	0.020				
Alpine vegetation	-0.503	0.231	6.381	0.029				
Bamboo grass variety								
Distance to road	0.154	0.038	16.227	<0.001	-0.369	0.130	10.498	0.004
Constant	-3.062	0.234		<0.001	-0.234	0.529		0.658

the same factors controlling RSF levels in the TSA applied as well to the ESA. We considered the area of less than 1% RSF as the boundary of suitable and unsuitable habitat for sika deer in the TSA, because 1% RSF has an extremely low probability of use. We used the computer software SPSS (SPSS Inc. Chicago, Illinois, USA) for data analyses.

Results

The summer and winter telemetry locations were contained in 240 and 54 blocks, respectively (Fig. 2). A comparison of habitat variables indicated no significant difference in coniferous forest, agricultural land, Japanese larch forest, alpine vegetation and bamboo grass variety used by sika deer between summer and winter (Table 3). Snow depth of blocks used during summer were significantly greater than those used during winter. Elevation of blocks used during summer was more variable than the elevation of blocks used during winter, and the elevation range during summer (10-977 m) included the elevation range during winter (129-486 m). Most radiocollared sika deer (71%) moved between high elevation summer and low elevation winter ranges, whereas some (29%) moved between low elevation summer and similar or high elevation winter ranges. Coniferous and mixed forests together comprised the majority (about 60%) of all vegetation types used during both summer and winter. Use of mixed and deciduous forests was significantly greater during winter than during summer. Agricultural land comprised a small proportion of used blocks, but was somewhat larger during summer than during winter. Alpine vegetation was a minor component of blocks used by deer in either season. Distance to roads was significantly greater for blocks used during summer than during winter.

The logistic regression model was significantly different from the 'no selection model' for summer (-2LL = 1335.252, $\chi^2 = 189.961$, df = 6, P < 0.001, $r^2 = 0.165$), and winter (-2LL = 367.283, $\chi^2 = 132.196$, df = 5, P < 0.001, $r^2 = 0.289$). Variables, eliminated by backward stepwise regression from the final model, were Japanese larch forest and alpine vegetation for winter, and deciduous forest and bamboo grass variety for both seasons (Table 4). During summer, females were more often in

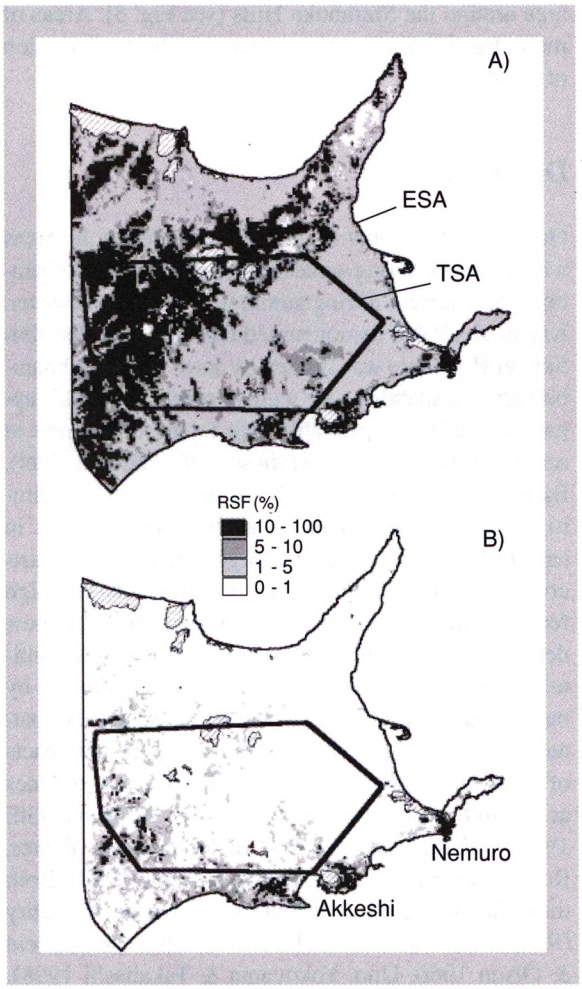

Figure 3. Resource selection probability functions (RSF) during summer (A) and winter (B) for the telemetry study area (TSA) and the extrapolated study area (ESA). Each 1-km block represents the relative probability of use by female sika deer. White areas represent RSF values of less than 1%.

coniferous, mixed or Japanese larch forests and less often in agricultural land or alpine vegetation, and further from roads. During winter, females were more often in coniferous or mixed forests and less often in agricultural land or areas with deep snow, and closer to roads.

Within the TSA, the area of less than 1% RSF was extremely small during summer (0.4% of TSA), but relatively large during winter (80.0% of TSA). During winter, the remaining 20% area of greater than 1% RSF appeared around the Shiranuka Hills (Fig. 3). For the ESA, the area of less than 1% RSF was 1.2% and 81.9% for summer and winter, respectively. Although almost all of the ESA was over 1% RSF during summer, mountainous area with coniferous or mixed forest and without roads tended to have a higher RSF value. During winter, the area of more than 1% RSF appeared around the Akkeshi and Nemuro area in addition to the area around the Shiranuka Hills (see Fig. 3). Areas of more than 1% RSF rarely appeared in the north portion of the ESA.

Discussion

Our study shows that female sika deer select the areas with less snow during winter, but are not attracted to bamboo grass variety during summer or winter. However, Kaji et al. (2000) demonstrated that sika deer distribution on Hokkaido was limited by snow depth and bamboo grass availability with a great forage value. This apparent conflict is probably due to the difference of scale on habitat selection (Johnson 1980, Powell 1994). Bamboo grass variety may be an important factor limiting sika deer distribution on Hokkaido, but not in eastern Hokkaido, because a large part of TSA of eastern Hokkaido is dominated by the species with a high forage value (Sn and Ss). We demonstrate that snow depth is the predominant factor affecting winter habitat selection of sika deer within the area dominated by bamboo grass variety with a high forage value. This pattern is consistent with the current knowledge of impacts of snow on ungulate behaviour. Deep snow reduces access to forage for ungulates (Gilbert, Wallmo & Gill 1970) and increases the cost of locomotion (Parker, Robbins & Hanley 1984, Fancy & White 1987). Both these factors could contribute to increased mortality (Robinette, Julander, Gashwiler & Smith 1952, Klein & Olson 1960, Uno, Yokoyama & Takahashi 1998), and/or could affect subsequent maternal care of young (Langenau & Lerg 1976, White & Luick 1984).

Garrott et al. (1987) suggested that migration is obligatory for mule deer occupying high elevation mountainous areas during summer, as snow accumulation precludes use of these areas during winter. Similarly, many studies have reported the movement between high elevation summer and low elevation winter ranges with less snow (Schoen & Kirchhoff 1985, Albon & Langvatn 1992). Previous studies on sika deer in the central and northern parts of the island of Honshu in Japan also reported this type of movement (Maruyama 1981, Ito & Takatsuki 1987). Nevertheless, some radio-collared sika deer inhabiting eastern flatlands moved between low elevation summer and similar or high elevation winter ranges in our study. This pattern of movement has not been reported before in sika deer or other ungulates. It demonstrates the importance of habitat variables in selecting winter ranges, within the constraints imposed by climatic variables such as snow depth.

During winter, the habitat selection of sika deer was positively associated with coniferous and mixed forests. These are likely important winter habitats for sika deer to access food resources in Hokkaido (Hokkaido Institute of Environmental Sciences 1994, Kaji 1995). There are many studies indicating the importance of mature coniferous forest to deer during winter. Old-growth forest has been shown to provide protection from deep snow, access to nutritional forage, and essential winter habitat for Sitka black-tailed deer *O. hemionous sitkensis* on Admiralty Island, southeast Alaska (Bloom 1978, Wallmo & Schoen 1980). Vegetation cover may provide rest sites, protection and/or refuge from severe climatic conditions, predators and human activities (Hamilton, Drysdale & Euler 1980, Takatsuki 1989, 1992b). Only coniferous and mixed forests provide cover during winter in this area. We suggest that higher elevation habitats (over 400 m) are not suitable for deer during winter because of deep snow, and eastern lower elevation habitats (below 200 m) are not suitable for deer because of the lack of coniferous and mixed forests. Therefore, during winter, sika deer selected middle elevation habitats (200-400 m) with both a relatively low snow depth and the presence of coniferous and mixed forests. It is therefore likely that our data confirm the importance of vegetation cover for northern ungulates. During summer, sika deer were widely distributed regardless of elevation within the TSA, although highest elevation habitats (over 1,000 m) dominated by alpine vegetation were not selected and had less than 1% RSF value. This is probably because deciduous and Japanese larch forests in eastern low elevation regions, in addition to coniferous and mixed forests, also play a role in providing cover for deer during summer. Our data also likely support the importance of vegetation cover for deer during summer as well as during winter. Deer were less often in agri-

cultural lands during summer, and this is probably due to avoidance of hunters (Sakuragi, Igota, Uno, Kaji, Kaneko, Akamatsu & Maekawa 2002).

Considering the limitation of our radio-telemetry location from roads, we chose the random coordinates to evaluate availability within 1 km and within 1-5 km of roads with the proportions in the telemetry data set (80 and 20%, respectively). Thus the limitation of our radio-telemetry location from roads could be cleared by this treatment because habitat selection analysis showed that the deer were further from roads during summer and closer to roads during winter. During summer, deer may be able to select habitats further from roads to conceal from human disturbance because a wide area is available for deer. Female deer may especially avoid human disturbance during calving (Unsworth, Kuck, Garton & Butterfield 1998). During winter, however, sika deer may be forced to select habitats closer to roads because the selection is strongly affected by snow depth and the presence of coniferous and mixed forests. Studies of the responses of white-tailed deer to vehicles (Behrend & Lubeck 1968) and to snowmobiles (Dorrance, Savage & Huff 1975) suggested that hunted populations were less apt to habituate to these disturbances than were unhunted populations. If sika deer were free to select habitats, they might be distributed further away from roads even during winter, at least during the hunting season (November to January), because during this period many hunters use roads in this area to hunt sika deer (Hokkaido Institute of Environmental Sciences 1995). Rost & Bailey (1979) indicated that mule deer and elk *C. canadensis* avoided roads, and it might be primarily a characteristic of hunted populations. On the other hand, deer may use roads during winter after the hunting season because roads are easier to travel for animals (Mladenoff et al. 1999).

Within the TSA, the abundance and distribution of suitable habitat for deer changes considerably between summer and winter, with winter habitat of sika deer being very limited. The origin of migration patterns may be understood on the basis of the difference in abundance and distribution of suitable habitat between summer and winter. Deer may move from summer to winter ranges if they cannot overwinter on their summer ranges. This leads to the conclusion that seasonal migration could have developed as a way to avoid undesirable conditions at a particular time of year (Vaughan, Ryan & Czaplewski 2000). This provides an explanation why deer move from summer to winter ranges, but the question why deer move from winter to summer ranges remains undetermined. Resident deer can and do oversummer on winter ranges without migration. Current evidence suggests that migration is generally selected for as a means of enhancing access to high-quality food and/or reducing the risk of predation (Fryxell & Sinclair 1988). Selection should favour individuals that migrate, if by migrating, their reproductive success is enhanced (Baker 1978). Because of environmental fluctuation and individual differences in costs of migration, several strategies related to migration can occur in the same species or in the same population (Fretwell 1972). To answer the question, we should consider other habitat variables and/or some other factors in relation to migration events, such as survivorship and birth rate (Caughley 1977), quality and availability of forage (Taylor & Taylor 1977, Fryxell & Sinclair 1988) and selection of favourable environment for breeding and parenting (Bowyer, Kie & Ballenberghe 1998). Coefficient of determination of logistic regression models was higher for winter (0.289) than for summer (0.165), although the low coefficients of determination of logistic regression models for summer and winter suggested that the majority of the variance in the deer distribution might have been left unexplained. This implies that suitable winter habitats could be relatively well predicted from spatial landscape features at this scale (i.e. 1-km block), but suitable summer habitats are less predictable based on only these spatial landscape features.

The extrapolation of coefficients for the TSA to the ESA reveals that additional other winter habitats are suitable for deer in the southern portion of the ESA. Deer use these areas during winter (Kaji et al. 2000), indicating that the prediction of this model agrees with the actual sika deer distribution. However, our prediction of suitable winter habitats may be underestimated, especially in the northern portion of the ESA. A possible reason may be the climatic difference between the northern and southern portions: snowfall is heavier in the northern portion than in the southern portion.

The extrapolation study gives us some suggestions for winter and summer habitat selection in relation to the expansion of the population. Although some of the migratory radio-collared deer have their summer ranges closer to Akkeshi or Nemuro than to the Shiranuka Hills, all of them move to the Shiranuka Hills regardless of the presence of closer winter habitats. This phenomenon may reflect the expansion of the sika deer population in eastern Hokkaido, because the eastern Hokkaido deer population originated from the Akan population (Nagata et al. 1998). Other winter habitat areas such as Akkeshi and Nemuro may be newly selected winter habitats in recently reoccupied ranges.

Although a large part of the ESA is suitable for deer during summer, the extent of the summer range of the

radio-collared deer is limited and no deer had their summer range south and west of the Shiranuka Hills. A possible reason for this may be the presence of other sika deer populations or male sika deer in these areas. Summer habitat selection might be affected by various factors such as, for example, the connectivity of corridor habitat from the winter to the summer ranges and costs of migration. However, what drives sika deer movements from winter to summer habitats still needs to be investigated. In addition, fidelity to seasonal ranges and migration route or migration tradition may be an important factor affecting the present pattern of seasonal migration. Matrilineal family groups of female and fawn white-tailed deer migrate together (Nelson & Mech 1981) and show fidelity and often exclusive use of seasonal ranges (Tierson, Mattfeld, Sage & Behrend 1985, Aycrigg & Porter 1997). Migration tradition is maintained through social interactions (Van Deelen et al. 1998), and fawns and yearlings learn the migration traditions of their social groups and remain faithful to them throughout life (Nelson & Mech 1981, 1984, Nixon, Hansen, Brewer & Chelsivig 1991). These assumptions need to be examined in future studies of sika deer and other species.

Conclusions

Our study examined the summer and winter habitat selection of an expanding sika deer population at a landscape scale, and presents a landscape-scale evaluation of sika deer habitat for summer and winter in eastern Hokkaido, Japan. Movements of some individuals between low elevation summer and similar or high elevation winter ranges in our study were exceptions to the movement reported from previous studies (Maruyama 1981, Schoen & Kirchhoff 1985, Garrott et al. 1987, Ito & Takatsuki 1987, Albon & Langvatn 1992). Snow depth and coniferous and mixed forests affected the winter habitat selection of sika deer, and migration from summer to winter ranges was dependent on the abundance and distribution of suitable winter habitat on a landscape scale. However, we could not explain migration from winter to summer ranges from the population-landscape scale study above.

Our study supported the assumption that the eastern Hokkaido deer population might have originated from the Akan subpopulation. Although some authors have already demonstrated that a landscape-scale habitat evaluation of a target species is useful for management and conservation (Pereira & Itami 1991, Mace et al. 1996, Mlandenoff et al. 1999, Kaji et al. 2000), our study is the first in which this approach has been applied to an expanding population, and demonstrates the relationships among seasonal habitat selection, seasonal migration and the expansion of the population.

Acknowledgements - we thank D.R. McCullough for providing suggestions and advice and for critically reviewing this manuscript. We are very grateful to S. Hamasaki, M. Kishimoto, Y. Kamiyama, the staff of the Wildlife Management Office, EnVision, and the Hokkaido Government for capturing deer and supporting our work. We also thank T. Suzuki, Buheaosier, S. Shimada, S. Kameyama and K. Waseda for helping us with the data analysis, and Y. Furukawa, H. Takahashi, J. Tanaka and H. Hamamoto for assisting with collection of location data. We thank the Akan Town Office, Shiranuka Town Office, Teshikaga Town Office, and H. Sugawara for supporting our work. We acknowledge K. Tamada, T. Saitoh and the students of the Laboratory of Boreal Forest Conservation, Hokkaido University for stimulating discussions. This study is supported by the Hokkaido Government and by a Grant-in-Aid for Scientific Research (14000353 to MS and 14340240 to KM) from the Ministry of Education, Culture, Sports, Science and Technology, and the Agency of Japan Society for the Promotion of Science.

References

Agata, W., Kubota, F. & Kamata, E. 1979: Ecological characteristics and dry matter production of some native grasses in Japan. Effects of clipping on the dry matter production of Sasa nipponica. - Journal of Japanese Grass Science 25: 103-109. (In Japanese).

Albon, S.D. & Langvatn, R. 1992: Plant phenology and the benefits of migration in a temperate ungulate. - Oikos 65: 502-513.

Aycrigg, J.A. & Porter, W.F. 1997: Sociospatial dynamics of white-tailed deer in the central Adirondack mountains, New York. - Journal of Mammalogy 78: 468-482.

Baker, R.R. 1978: The evolutionary ecology of animal migration. - Holmes & Meier Publishers, Inc., New York, USA, 1012 pp.

Behrend, D.F. & Lubeck, R.A. 1968: Summer flight behavior of white-tailed deer in two Adirondack forests. - Journal of Wildlife Management 32: 615-618.

Bloom, A.M. 1978: Sitka black-tailed deer winter range in the Kadashan Bay area, southeast Alaska. - Journal of Wildlife Management 42: 108-112.

Bowyer, R.T. 1986: Habitat selection by southern mule deer. - California Fish and Game 72: 153-169.

Bowyer, R.T., Kie, J.G. & Ballenberghe, V.V. 1996: Sexual segregation in black-tailed deer: effects of scale. - Journal of Wildlife Management 70: 10-17.

Bowyer, R.T., Kie, J.G. & Ballenberghe, V.V. 1998: Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? - Journal of Mammalogy 79: 415-425.

Caughley, G. 1977: Analysis of vertebrate populations. - John Wiley and Sons, London, Great Britain, 234 pp.

Clark, J.D., Dunn, J.E. & Smith, K.G. 1993: A multivariate model of female black bear habitat use for a geographic information system. - Journal of Wildlife Management 57: 519-526.

Dorrance, M.F., Savage, P.J. & Huff, D.E. 1975: Effects of snowmobiles on white-tailed deer. - Journal of Wildlife Management 39: 563-569.

Edwards, R.Y. & Ritchey, R.W. 1956: The migrations of a moose herd. - Journal of Mammalogy 37: 486-494.

Environment Agency 1997: Natural Environment Information GIS. - Nature Conservation Bureau, Tokyo, Japan, CD-rom.

Fancy, S.G. & White, R.G. 1987: Energy expenditures for locomotion by barren-ground caribou. - Canadian Journal of Zoology 65: 122-128.

Festa-Bianchet, M. 1988: Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. - Oecologia 75: 580-586.

French, D.P., Reed, M., Calambokidis, J. & Cubbage, J.C. 1989: A simulation model of seasonal migration and daily movements of the northern fur seal. - Ecological Modelling 48: 193-219.

Fretwell, S.D. 1972: Populations in a seasonal environment. - Princeton University Press, Princeton, New Jersey, USA, 217 pp.

Fryxell, J.M. & Sinclair, A.R.E. 1988: Causes and consequences of migration by large herbivores. - Trends in Ecology & Evolution 3: 237-241.

Garrott, R.A., White, G.C., Bartmann, R.M., Carpenter, L.H. & Alldredge, A.W. 1987: Movements of female mule deer in northwest Colorado. - Journal of Wildlife Management 51: 634-643.

Gilbert, P.F., Wallmo, O.C. & Gill, R.B. 1970: Effect of snow depth on mule deer in Middle Park, Colorado. - Journal of Wildlife Management 34: 15-23.

Hamilton, G.D., Drysdale, P.D. & Euler, D.L. 1980: Moose winter browsing patterns on clear-cuttings in northern Ontario. - Canadian Journal of Zoology 58: 1412-1426.

Hayakawa, T. 1986: Basis of regression analysis. - Asakurashoten, Tokyo, Japan, 207 pp. (In Japanese).

Hobbs, N.T. & Spowart, R.A. 1984: Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. - Journal of Wildlife Management 48: 551-560.

Hokkaido Government 1987: Report on animal distributions - mammals. The second basic survey on natural environment conservation. - Hokkaido Nature Preservation Division, Sapporo, Japan, 115 pp. (In Japanese).

Hokkaido Government 1998: Management plan for sika deer population in eastern Hokkaido. - Nature Environment Division, Sappro, Japan, 16 pp. (In Japanese).

Hokkaido Institute of Environmental Sciences 1994: Result of a survey related to sika deer and brown bear sighting in Hokkaido. - Hokkaido Institute of Environmental Sciences, Sapporo, Japan, 63 pp. (In Japanese).

Hokkaido Institute of Environmental Sciences 1995: Result of a survey related to sika deer and brown bear inhabit in Hokkaido. - Hokkaido Institute of Environmental Sciences, Sapporo, Japan, 164 + 30 pp. (In Japanese).

Hooge, P.N. & Eichenlaub, W.M. 1998: Animal movement extension to arcview. Ver1.1. - Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Hosmer, D.W. & Lemeshow, S. 1989: Applied logistic regression. - John Wiley and Sons, New York, New York, USA, 373 pp.

Igarashi, T. 1986: Forest vegetation of the Akan National Park, Hokkaido, Japan. - Research Bulletins of the College Experiment Forests, Faculty of Agriculture, Hokkaido University 43: 335-494. (In Japanese).

Inukai, T. 1952: The sika deer on Hokkaido and its rise and decline. - Hoppo Bunka Kenkyu Hokoku (The Report of Northern Cultural Research of Hokkaido University) 7: 1-45. (In Japanese).

Ito, T. & Takatsuki, S. 1987: The distribution and seasonal movements of sika deer in the Mt. Goyo area, Iwate Prefecture. - Bulletin of Yamagata University 11: 411-430.

Japan Weather Association Hokkaido Regional Head Office 1991: Climate of Hokkaido. - Japan Weather Association Hokkaido Regional Head Office, Sapporo, Japan, CD-rom. (In Japanese).

Johnson, D.H. 1980: The comparison of usage and availability measurements for evaluation resource preference. - Ecology 61: 65-71.

Kaji, K. 1995: Deer irruptions - A case study in Hokkaido, Japan. - The Journal of the Mammalogical Society of Japan 35: 35-43. (In Japanese with an English summary).

Kaji, K., Miyaki, M., Saitoh, T., Ono, S. & Kaneko, M. 2000: Spatial distribution of an expanding sika deer population on Hokkaido Island, Japan. - Wildlife Society Bulletin 28: 699-707.

Kaneko, M., Kaji, K. & Ono, S. 1998: Analysis of habitat change and sika deer distribution on Hokkaido. - The Journal of the Mammalogical Society of Japan 38: 49-59. (In Japanese with an English summary).

Kawai, M., Juni, K., Yasue, T., Ogawa, K., Hata, H., Kondo, S., Okubo, M. & Asahida, Y. 1995: Intake, digestibility and nutritive value of Sasa nipponica in Hokkaido native horses. - Journal of Equine Science 6: 121-125.

Klein, D.R. & Olson, S.T. 1960: Natural mortality patterns of deer in Southeast Alaska. - Journal of Wildlife Management 24: 80-88.

Kufeld, R.C., Bowden, D.C. & Schrupp, D.L. 1988: Habitat selection and activity patterns of female mule deer in the Front Range, Colorado. - Journal of Range Management 41: 515-522.

Kufeld, R.C., Bowden, D.C. & Schrupp, D.L. 1989: Distribution and movements of female mule deer in the Rocky Mountain foothills. - Journal of Wildlife Management 53: 871-877.

Langenau, E.E., Jr. & Lerg, J.M. 1976: The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. - Applied Animal Ethology 2: 207-223.

Larson, T.J., Rongstad, O.J. & Terbilcox, F.W. 1978: Movement and habitat use of white-tailed deer in southcentral Wisconsin. - Journal of Wildlife Management 42: 113-117.

Loft, E.R., Menke, J.W. & Burton, T.S. 1984: Seasonal move-

ments and summer habitats of female black-tailed deer. - Journal of Wildlife Management 48: 1317-1325.

Mace, R.D. & Waller, J.S. 1996: Grizzly bear distribution and human conflicts in Jewel Basin Hiking Area, Swan Mountains, Montana. - Wildlife Society Bulletin 24: 461-467.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J. & Zuuring, H. 1996: Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. - Journal of Applied Ecology 33: 1395-1404.

Mace, R.D., Waller, J.S., Manley, T.L., Ake, K. & Wittinger, W.T. 1999: Landscape evaluation of grizzly bear habitat in western Montana. - Conservation Biology 13: 367-377.

Maddock, L. 1979: Dynamics of an Ecosystem. - In: Sinclair, A.R.E. & Norton-Griffiths, M. (Eds.); Serengeti. University of Chicago Press, Chicago, Illinois, USA, pp. 104-129.

Manly, B.F.J., McDonald, L.L. & Thomas, D.L. 1993: Resource selection by animals. Statistical design and analysis for field studies. - Chapman & Hall, London, Great Britain, 177 pp.

Maruyama, N. 1981: A study of the seasonal movements and aggregation patterns of sika deer. - Bulletin of Faculty of Agriculture, Tokyo University of Agriculture and Technology 23: 1-85. (In Japanese with an English summary).

Matsui, Z. 1963: On the ecological and sylvicultural treatments of Sasa-bamboo, and its industrial utilization in Hokkaido. - Annual Report of Hokkaido Forestry Experimental station, Sapporo, Japan, pp. 186-229. (In Japanese with an English summary).

Mladenoff, D.J., Sickley, T.A., Haight, R.G. & Wydeven, A.P. 1995: A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. - Conservation Biology 9: 279-294.

Mladenoff, D.J., Sickley, T.A. & Wydeven, A.P. 1999: Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. - Ecological Applications 9: 37-44.

Murakami, T. & Mano, T. 1998: Improvement of errors in radiotelemetry locations of brown bears, Ursus arctos, in Hokkaido, Japan. - Mammal Study 23: 41-48.

Nagata, J., Masuda, R., Kaji, K., Kaneko, M. & Yoshida, C. 1998: Genetic variation and population structure of the Japanese sika deer (Cervus nippon) in Hokkaido Island, based on mitochondrial D-loop sequence. - Molecular Ecology 7: 871-877.

National Land Agency 1992: National Land Information System. - National Land Information Office, Planning and Coordination bureau, Tokyo, Japan, CD-rom.

Nelson, M.E. & Mech, L.D. 1981: Deer social organization and wolf predation in northeastern Minnesota. - Wildlife Monographs 77: 1-53.

Nelson, M.E. & Mech, L.D. 1984: Home-range formation and dispersal of deer in northeastern Minnesota. - Journal of Mammalogy 65: 567-575.

Nicholson, M.C., Bowyer, R.T. & Kie, J.G. 1997: Habitat selection and survival of mule deer: tradeoffs associated with migration. - Journal of Mammalogy 78: 483-504.

Nixon, C.M., Hansen, L.P., Brewer, P.A. & Chelsivig, J.E. 1991: Ecology of white-tailed deer in an intensively farmed region of Illinois. - Wildlife Monographs 118: 1-77.

Ohara, H. 1948: Livestock dietetical researches of bamboo grass in Hokkaido. - Report of Hokkaido Agricultural Experimental station 42: 1-203. (In Japanese).

Parker, K.L., Robbins, C.T. & Hanley, T.A. 1984: Energy expenditures for locomotion by mule deer and elk. - Journal of Wildlife Management 48: 474-488.

Pereira, J.M. & Itami, R.M. 1991: GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. - Photogrammetric Engineering and Remote Sensing 57: 1475-1486.

Powell, R.A. 1994: Effects of scale on habitat selection and foraging behavior of fishers in winter. - Journal of Mammalogy 75: 349-356.

Riley, S.J. & Dood, A.R. 1984: Summer movements, home range, habitat use, and behavior of mule deer fawns. - Journal of Wildlife Management 48: 1302-1310.

Robinette, W.L., Julander, O.J., Gashwiler, S. & Smith, J.G. 1952: Winter mortality of mule deer in Utah in relation to range condition. - Journal of Wildlife Management 16: 289-299.

Rost, G.R. & Bailey, J.A. 1979: Distribution of mule deer and elk in relation to roads. - Journal of Wildlife Management 43: 634-641.

Sakuragi, M., Igota, H., Uno, H., Kaji, K., Kaneko, M., Akamatsu, R. & Maekawa, K. 2002: Comparison of diurnal and 24-hour sampling of habitat use by female sika deer. - Mammal Study 27: 1-5.

Scarbrough, D.L. & Krausman, P.R. 1988: Sexual segregation by desert mule deer. - The South-western Naturalist 33: 157-165.

Schoen, J.W. & Kirchhoff, M.D. 1985: Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, Southeast Alaska. - Journal of Wildlife Management 49: 96-103.

Takatsuki, S. 1986: Food habits of Sika deer on Mt. Goyo, Northern Honshu. - Ecological Research 1: 119-128.

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

Takatsuki, S. 1992a: Foot morphology and distribution of sika deer in relation to snow depth in Japan. - Ecological Research 7: 19-23.

Takatsuki, S. 1992b: A case study on the effects of a transmission-line corridor on Sika deer habitat use at the foothills of Mt Goyo, northern Honshu, Japan. - Ecological Research 7: 141-146.

Takatsuki, S. 1993: On the food habits of Chinese cervids: A consideration based on the food habits of sika deer of Japan. - In: Ohtaishi, N. & Sheng, I.H. (Eds.); Deer of China. Elsevier, Amsterdam, Holland, pp. 187-195.

Tatewaki, M. 1958: Forest ecology of the island of the North Pacific Ocean. - Journal of the Faculty of Agriculture of Hokkaido University 50: 371-472.

Taylor, L.R. & Taylor, R.A. 1977: Aggregation, migration, and population mechanics. - Nature 265: 415-421.

Tierson, W.C., Mattfeld, G.F., Sage, R.W., Jr. & Behrend, D.F. 1985: Seasonal movements and home ranges of white-tailed deer in the Adirondacks. - Journal of Wildlife Management 49: 760-769.

Toyooka, K., Sato, M. & Isizuka, S. 1983: The distribution map of Sasa group in Hokkaido. - Explanatory Note. Hokkaido Branch, Forestry and Forest Products Research Institute, Sapporo, Japan, 36 pp. (In Japanese).

Toyooka, K., Sato, M. & Isizuka, S. 1984: The distribution map of Sasa group in Hokkaido. - New Technical Report 10. Hokkaido Branch, Forestry and Forest Products Research Institute, Sapporo, Japan.

Uno, H., Yokoyama, M. & Takahashi, M. 1998: Winter mortality pattern of Sika deer (Cervus nippon yesoensis) in Akan National Park, Hokkaido. - The Journal of the Mammalogical Society of Japan 38: 233-246. (In Japanese with an English summary).

Unsworth, J.W., Kuck, L., Garton, E.O. & Butterfield, B.R. 1998: Elk habitat selection on the Clearwater National Forest. - Journal of Wildlife Management 62: 1255-1263.

Van Deelen, T.R., Champa, H., Hamady, M. & Haufler, J.B. 1998: Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. - Journal of Wildlife Management 62: 205-213.

Vaughan, T.A., Ryan, J.M. & Czaplewski, N.J. 2000: Mammalogy. - Saunders College Publishing, Orland, USA, 565 pp.

Wallmo, O.C. & Schoen, J.W. 1980: Response of deer to secondary forest succession in southeast Alaska. - Forest Science 26: 448-462.

White, G.C. & Garrott, R.A. 1990: Analysis of Wildlife Radio-tracking Data. - Academic Press, San Diego, USA, 383 pp.

White, R.G. & Luick, J.R. 1984: Plasticity and constraints in the lactational strategy of reindeer and caribou. - Symposia of the Zoological Society of London 51: 215-232.

Yamane, M. & Furubayashi, K. 1997: Evaluation of food condition in Sugi Hinoki Plantation. - In: Environment Department of Kanagawa Prefecture (Ed.); Report on the natural environmental study in Tanzawa-Ooyama. Kanagawa Prefecture, Japan, pp. 398-400. (In Japanese).

Yokoyama, M., Kaji, K. & Suzuki, M. 2000: Food habits of sika deer and nutritional value of sika deer diets in eastern Hokkaido, Japan. - Ecological Research 15: 345-355.