

Predicting the impact of landscape heterogeneity on
crop-raiding Japanese macaques using spatial and
temporal scale approach

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Chapter 1

General Introduction

Background and objective

Human–wildlife conflicts have reported from all over the world. There are two kinds of conflicts. One is a conflict "from humans to wildlife" such as the extinction or reduction of populations according to high hunting pressures or habitat destruction and fragmentation by human activity (e.g. Robinson et al. 1992; Steadman 1995). Another is a conflict "from wildlife to humans" such as the transfer of disease to livestock and people, preying upon livestock, and the crop damage (e.g. Tilson and Nyhus 1998; Bengis et al. 2002; Michalski et al. 2006). The aspect of the former conflict is "conservation of biodiversity", and the later is "Management against wildlife damage". In this research, conflict as “Management against wildlife damage” was treated. Such conflict present serious problems and have become an integral component of contemporary wildlife management (Conover, 2002; Storm et al., 2007). To develop an appropriate relationship between people and wildlife, it is important to have an understanding of wildlife behavior (e.g., habitat use, resource selection, and preference) and to develop appropriate technologies and management methods.

A basic question in animal ecology is to understand the factors and processes determining the species distribution/abundance, habitat use, resource selection, and preference in space and time (Brown et al. 1995, Greenwood et al. 1996). The environment is characterized as a system of covarying and interacting gradients that vary across space and through time due to local biotic interactions, abiotic processes,

conditions, and disturbance. The level of the organism and the scale of its direct interactions with the environment is the fundamental focus (Wiens et al., 1993). However, it is essential to extend understandings from fine scales in space and time by various spatial and temporal approaches (Shugart et al., 1988; Jeffers, 1988). Multi-scale gradient approach which includes space and time predict species responses as functions of continuously varying environmental gradients. Then, how an animal uses a habitat (e.g., for foraging, nesting, resting, moving) depends on the type of environment the animal is in (Johnson, 1980). Habitat selection is considered a multi-level hierarchical process where the patterns of selection are modulated by environmental factors such as the type of land-cover, configuration, and connection over specific spatial scales and time (Johnson, 1980; Orians and Wittenberger, 1991). It is an important function in animal ecology, and is frequently defined as behavioral adjustment to the heterogeneous distribution of landscape components (Johnson, 1980; Rosenweig, 1981; Boyce and McDonald, 1999). The goal of analysis in animal habitat study is to link patterns of habitat use with environmental drivers across space, through time, and across a range of spatial and temporal scales to account for the influences of spatial complexity and temporal dynamics in landscape structure (Cushman et al., 2010).

In Japan, the conflict caused by mid-sized mammals is significant. These mammals, which include wild boars (Honda, 2009), Sika deer (Kaji et al., 2000; Ueda et al., 2003), Asiatic black bears (Oka et al., 2004), and Japanese macaques (Mochizuki et al.,

2009), can damage crops and cause injuries to humans depending on the situation. Conflicts caused by these mammals have become serious, amounting to 13 billion yen (150 million US dollars) in Japan (Ministry of Agriculture, Forestry and Fisheries, 2009). Japanese macaques live the farthest north of any nonhuman primate species (range 30°21–41°08_N) and utilize various habitat types, such as cool-temperature deciduous forests, warm-temperature evergreen forests, and human settlements including farmlands (Suzuki, 1965; Wada and Tokida, 1981; Yamada and Muroyama, 2010). Due to these temperate habits, the Japanese macaque is known worldwide as the “snow monkey.” The behavior of macaques is quite varied and depends on the home range, human land use, and regional environment. Therefore, management of macaque habitat is necessary for the effective management of this species.

The objective of this study is to suggest the information for resolving human-wildlife conflicts caused by crop-raiding Japanese macaques following multi-scale gradient modeling approach including spatial and temporal variation of landscape structure. First, I clarify the relationship between habitat use by Japanese macaques and landscape structure within their home ranges. Second, as the evaluation of the temporal variation, I investigated seasonal home range behavior of crop-raiding Japanese macaques. Third, long term change in the potential distribution of the Japanese macaque was predicted using 1970's and 2000's satellite imagery. Fourth, I evaluate the spatial scale dependency on crop damage by Japanese macaques. Finally, I discuss risk management of

crop damage by the Japanese macaques along the spatial and temporal variation of landscape structure.

Chapter 2

The influence of forest boundary shape and environmental variables on farmland invasion by wild Japanese macaques

Introduction

Recently, crop damage caused by wildlife has become a serious problem in Japan (Miura 1999, 2008). To develop an appropriate relationship between people and wildlife, it is important to have an understanding of wildlife behavior and to develop appropriate technologies and management methods. Crop damage by Japanese macaques (*Macaca fuscata*) is remarkable, amounting to 40 million yen in Niigata Prefecture. This accounts for 47% of all wildlife damage costs in the prefecture. Solutions to such losses should be developed within the context of a harmonious relationship between humans and wildlife. Japanese macaques generally live in forests (Koganezawa 1991), and crop damage is elevated in farmland bordered by woodlands (Sprague 2007). Crop damage by macaques differs among troops and environments (Suzuki 2003). Therefore, development of appropriate management guidelines is dependent on an understanding of macaque behavior within a range of habitat types.

Driving macaques away from the farmland has been used as a technique to limit crop damage. However, the effect of this technique is not consistent with crop damage due to variations in macaque home ranges, land usage, and regional environments. Conover (2002) demonstrated the importance of manipulating habitat to reduce damage. However, before doing so, it is necessary to evaluate damage-related environmental factors (Honda et al. 2009). Existing reports give accounts of the relationship between habitat configuration and crop damage (Naughton-Traves et al. 1998, Hill 2000, Saj et al. 2001,

Iwasaki and Sprague 2005). However, the spatial patterns of habitats (e.g., size and shape) have been little studied. Selected landscape indices have been used to quantify habitat spatial patterns, and this procedure has been applied to wildlife conservation planning. A specific conservation plan is initiated by capturing habitat patterns as defined by landscape indices such as size, shape and configuration (McGatigal and McComb1995, Hansen et al. 2001, Gray et al. 2004). Therefore, it is also important to examine the relationships between habitat landscape indices and crop damage caused by wildlife.

The behavior of macaques is quite varied and depends on home range, human land use, and regional environment; the extent of crop damage is also varied. As a starting point, it is necessary to describe the behavior of wild macaque troops in a range of environments. Reports on macaque troop behavior are available, as they are measurements of the amount of damage they inflict on crops (Suzuki 2003, Enari et al. 2005, Yoshida et al. 2006). However, descriptions of ecological differences among troops are few. For managing crop damage, it is essential to focus on differences between troops.

I examined two macaque troops with adjacent home ranges. To evaluate differences in habitats, landscape indices (i.e., size, shape, and configuration) were calculated. I also examined differences in farmland invasion between the two troops. My primary objective was to determine the relationship between troop behaviors and landscape indices, with the ultimate aim of controlling crop damage through management of macaque habitat.

Materials and Methods

Study area

The study area was Shibata City, Niigata Prefecture ($37^{\circ} 57'N$, $139^{\circ} 19'E$, 532 km^2 , Fig. 1). The elevation ranged from -19 to 1496m above sea level, and forests cover 64% of ground area. Crops in this region have been damaged by macaques since 1983, and the area affected has expanded gradually. An investigation in Shibata City revealed 14–17 troops that included a total of up to 700–800 individuals. The intensity of crop damage is increasing, and the risk of life-threatening injuries through home invasion has become a concern. Annual crop damage costs approach 15 million yen on average, with yearly fluctuations. Hunting has been used as a remedial measure, which exterminated about 100 monkeys each year. However, hunters have now taken the lead in driving macaques away from farmland, usually from June to November, the period of the most intense crop damage.

Locations of the Japanese macaques

I studied the “Yonekura” and “Otsuki” troops using data acquired by hunters during 2004–2006 (Fig. 2). The information gathered includes location data obtained by radio telemetry, a method widely used for tracking wildlife. The location data are acquired by attaching the transmitter to wildlife, and the signal is received by a Yagi antenna and receiver. The antennae have strong directionality and are often used on animals whose

native habitat makes direct observation difficult (White and Garrot 1990). In total, location data were collected for 207 and 249 members of the Yonekura and Otsuki troops, respectively. I used LT-01 (CIRCUIT DESIGN, Inc.) transmitters and IC-R20 (ICOM, Inc.) receivers.

Calculation of Landscape Indices

The locations of the macaques were visualized using Geographical Information System (GIS) software (ArcGIS 9.2; Environmental Systems Research Institute, Inc.). The home range areas of the two troops were determined using the Minimum Convex Polygon method (MCP). MCP is a method for constructing a polygon that connects boundary location points defining home range areas (Ozaki and Kudo 2002, Saeki and Waseda 2006). Although home range size may be overestimated, MCP is a simple and easy method (Ozaki and Kudo 2002, Saeki and Wasrde 2006) that allowed us to compare the troops.

Land cover was classified using ERDAS IMAGINE 9.2 software (Leica Geosystems, Inc.) to plot landscape composition of the study area. The satellite images used (ALOS/AVNIR-2 image) were captured on 27 February in 2006, 27 May in 2006, and 12 August in 2007. The data were orthorectified with a digital elevation model. All satellite data were geo-coordinated to the Universal Transverse Mercator system. Shade caused by topographic relief can create serious obstacles to analysis of remote sensing

data. I used the Minneart topographic correction method to offset topographic effects (Murakami 2007). Moreover, to correct for the influence of atmosphere between seasons, I matched a digital number using a pseudo invariant target (Hall et al. 1991, Schroeder et al. 2006) between sets of satellite data (Awaya and Tanaka 1999). For accurate classification, I prepared multi-temporal normalized difference vegetation index (NDVI, Mynrei and Asrar 1994) composite images. I applied supervised classification to the composite images (Murakami et al. 2001). NDVI was calculated from the ALOS/AVNIR-2 data captured a three different times. It is defined as

$$NDVI = \frac{NIR - RED}{NIR + RED} \quad (1)$$

where RED and NIR are the visible red and near-infrared reflectance factors, respectively. I postulated that forest, urban land, and farmland could be classified accurately by stacking NDVI images from February, May, and August. The land-cover map was classified from NDVI composite images by supervised classification with maximum likelihood. Patches of land cover were classified into five categories (i.e., forest, farmland, urban, grass, and water) (Fig 2). The landscape map kappa coefficient (representing classification accuracy) was 0.82.

The home range plots of the two troops were overlain on the land-cover map (Fig. 2), and the patches including the home range were counted. To compare habitat differences between troops, I calculated the landscape index of each patch using FRAGSTATS 3.3 (McGarigal and Marks 1995). Indices calculated by this software are

classified according to five dimensions (i.e., size, shape, core area, diversity, and configuration). I selected habitat size, shape, and configuration based on previous studies (Hansen et al. 2001, Herzog et al. 2001, Gray et al. 2004) that quantified landscape structure in a variety of ecosystems and examined the relationship between landscape structure and landscape function. I applied five landscape metrics: Large Patch Index (LPI), Mean Patch Size (MPS), Landscape Shape Index (LSI), Area-Weighted Mean Shape Index (AWMSI) and Interspersion and Juxtaposition Index (IJI) (Table 1). For the analysis, I chose forest patches within macaque habitat, urban patches that are risk factors for macaques, and farmland patches that are food resources for macaques.

Relationship between Farmland Invasion and Environmental Factors

To determine environmental characteristics of farmland invasion, I compared points where farmland was invaded with points where farmland was not invaded. The macaque location data were overlain on the land-cover map. I defined the macaque locations on the farm land as “farmland invasion”. Some artifact is possible in these location points because radio telemetry data may produce sampling bias when the tracking duration is long (Palomars and Delibes 1992, Revilla et al. 2000). In my study, sampling bias was small because I used data from 3 years. Of the samples with farmland invasion, 22 were from the Yonekura troop and 46 were from the Otsuki troop. I applied a random-variate generation method in GIS to randomly generate the same number of points in the farm

land. This sample of points was classified as “no farmland invasion.” To improve the reliability of the data, the “no farmland invasion” points that exist within 200 m of the “farmland invasion” points were excluded, as 200 m is the average distance that a macaque moves in about an hour (Suzuki 2003). Total sample sizes for “farmland invasion” and “no farmland invasion” categories combined were 44 and 92 for the Yonekura and Otsuki troops, respectively (Fig. 3 and 4).

Each environmental factor (topography and human disturbance) was selected from previous research and calculations were made using GIS (Table 2). To control for confounding factors, topography and human disturbance factors were validated (Rothman 2002). Distance from forest boundary was selected as topographic factor. Naughton-Traves et al. (1998) and Saj et al. (2001) suggested that this factor is important with regard to the extent of crop damage by wildlife. Distance from water, which Wilson et al. (2005) reported as a risk factor, was added. Distances from urban lands and roads were selected as human disturbance factors because these variables are believed to be risk factors for macaques. Distance from farmland bounded by exclusion devices such as electric fences (hereafter, distance from fence) was selected for inclusion. I used the land-cover map to calculate the distance from forest boundary, water, and urban lands. To calculate the distance from roads (only roads > 5m wide were used), a 1:25,000 digital map spatial-data framework (Geographical Survey Institute) was used. The position of the fenced farmland was recorded using GPS (GPSMAP60Cx; Garmin, Inc.) in the field

survey.

Statistical Analysis: Generalized Linear Mixed Model

To examine the relationships between farmland invasion and each environmental factor, I used a generalized linear mixed model (GLMM: Faraway 2006, binomial error structure, logit link function) because this method controls for confounding factors (Rothman 2002) and allows for spatial autocorrelation between neighboring sub-compartments (Crawley 2005). The dependent variable was presence or absence of invasion, and five independent variables were considered as candidate environmental factors. The point numbers of the location data were applied as random effects. Unobservable effects thought to influence the model were treated as random effects (Crawley 2005). In this analysis, it becomes possible by applying point numbers as random effects to treat each location data as independent.

To calculate the importance of variables (IOV), the model-averaging method was employed. The model-averaging method was applied instead of model selection techniques because the former allows for unbiased and robust parameter estimation (Johnson and Omland 2004). IOV ranged from 0 to 1, and more important variables were given larger values. I tested for collinearity among variables using the variance inflation factor (VIF), where $VIF > 10$ denotes multi-collinearity (Robert and O'Brien 2007). Model accuracy was determined by comparing observed and predicted data. To calculate overall

accuracy, the cut-off point was set to 50%. The cut-off point of 50% was most often applied in model accuracy evaluation (Hosmer and Lemeshow 2000). Analyses were performed using R ver.2.8.1 (R development core team 2011).

Results

Differences between Macaque Habitats

Table 3 shows landscape indices for forest, urban land, and farmland for each troop. LPI and MPS (index of patch size) values were high in the Yonekura troop forest land, whereas urban land and farmland in the Otsuki troop habitat showed high values. These results indicated that the forest patch used by the Yonekura troop is rather more clumped than is that of the Otsuki troop. LSI and AWMSI (index of the patch shape) showed high values for forest, urban land, and farmland in the Otsuki troop habitat. These results indicated that the habitat of the Otsuki troop has a complex shape. IJI, the index of patch configuration, had low values in the Otsuki troop farmland. The value of IJI (index of patch configuration) was low in the farmland of the Otsuki troop. This result indicates that farmland in the Otsuki troop habitat had a connected structure.

Difference between Troops

The estimated relationships between the invasion of farmland and environmental factors are presented in Tables 4 and 5. In these models, distance from forest boundaries and roads affected both troops in the same manner. Distance from forest boundary was an important factor for macaque invasion of farmland. Moreover, distance from roads was a contributory risk factor for both troops, suggesting they invade farmland that is near the forest boundary and far from any roads. The effect of distance from a fence differed

between troops. For the Yonekura troop, the value was positive, indicating that the distance from fences influenced the risk of invasion. The value was negative for the Otsuki troop, indicating that the distance from fences did not influence the likelihood of invasion. The Otsuki troop invades fenced farmland, whereas the Yonekura troop tends to avoid fenced farmland. Other factors were of low importance (< 0.9) and therefore did not significantly affect farmland invasion. Maximum VIF of the integrated model was low. For the Yonekura and Otsuki troop models, VIF were 2.49 (< 10) and 3.45 (< 10), respectively, indicating no multi-collinearity. The model classifications were calculated comparing the predictive models and observed data (Table 6). The overall model accuracies were 84% and 85% for the Yonekura and Otsuki troops, respectively.

Discussion

From comparison of landscape index (Table 3), the habitat of the Yonekura troop is well forested, and the habitat shape is simple. The habitat of the Otsuki troop covered large tracts of urban land and farmland, the habitat shape was complex, and the farmland had a connected structure. By this difference, it is thought that the dependence to farmland changes in both troops. Since large tract of urban land and farmland exists compared with Yonekura troop in the habitat of Otsuki troop, the dependence to farmland may be high. Moreover, probably, it is related to ease of farmland invasion that the forest boundary shape is also complicated.

GLMM demonstrated that environmental factors affecting farmland invasion were distance from the forest boundary, distance from roads, and distance from fences (Table 4 and 5). The importance of forest boundary corroborates results of Naughton-Treves et al. (1998) and Saj et al. (2000). The distance from road was risk factor for both troops and it supports that wildlife does not use human activity area (Mochizuki et al. 2009, Yamada and Muroyama 2010). Although there was no effect of fences at Otsuki troop, it was effective in Yonekura troop. This indicates the effect of fences is case by case. Fences can be effective if they are properly maintained. About the effect of fences, the habituation to farmland may be related ineffective at Otsuki troop. Moreover, attractive food may exist in the farmland surrounded on the fence. The results of GLMM indicate the Yonekura troop appears to invade farmland near to the forest

boundary and far from roads and fences. The Otsuki troop appears invade farmland far from roads and near the forest boundary and fences. The classification accuracies of the models were high, indicating they are adequate for practical purposes.

The difference between troop behaviors likely relates to habitat differences, which are clearly shown in the landscape indices. In particular, the forest boundary shape and habitat configuration are important. Conover (2002) and Grey et al. (2004) suggested a relationship between behavior and the farmland/forest boundary. The Otsuki troop habitat encompassed large areas of farmland, which is easily invaded because of the complex shape of the forest boundary. Moreover, farmlands within the range of the Otsuki troop have a connected structure, allowing macaque easy access to resources across adjacent farms. Enari et al. (2005) suggested that a foraging strategy that combines farm products with natural food sources provides a steady food supply through the year. A troop that applies this strategy will undergo rapid population growth. Taming wild animals by feeding them also contributes to farmland invasion. One likely reason for the ineffectiveness of farm fencing in reducing Otsuki troop invasion is that high population growth (fuelled by farm food) forces the animals to forage outside their natural habitat. Even when troop home ranges are adjacent, I believe habitat differences can account for behavioral differences.

In conclusion, I propose management of the distance between forest boundary and farmland as a means of controlling damage. Clearly, farms close to forest are at high

risk from my models. Conover (2002) demonstrated that wildlife damage is controlled by managing the configuration of urban land, farmland, and forest on large scales. The insertion of buffer zone between farmland and forest can reduce damage (The Ministry of Agriculture, Forestry, and Fisheries 2007). It is possible to extend the distance between farmland and forest by intension of buffer zone. In addition, installation of the artificial thing (e.g., road, human settlement) is also important. It is reported that wild animals dislike the place with human activities (Mochizuki et al. 2009, Yamada and Muroyama 2010). In my models, the distance from road was risk factor for macaque troops. The result of the models also supports these reports. To reduce crop damage by Japanese macaques, the management of land use is required. Moreover, the spatial configuration of farmland and the shape of the forest boundary should be managed, as these both affect the invisibility of farmland. Since only two Japanese macaque troops are treating in this study, quantification is difficult, but the spatial configuration and patch shape is also important for the management of crop damage.

Finally, it will be necessary to increase the generalizability of my findings by studies that include more than two troops of macaques. In addition, the similar investigations that treat landscape index and environmental variables are required not only about Japanese macaques but also other wild animals (e.g., wild boar [*Sus Scrofa*], sika deer [*Cervus nippon*], Asiatic black bears [*Ursus thibetanus*]).

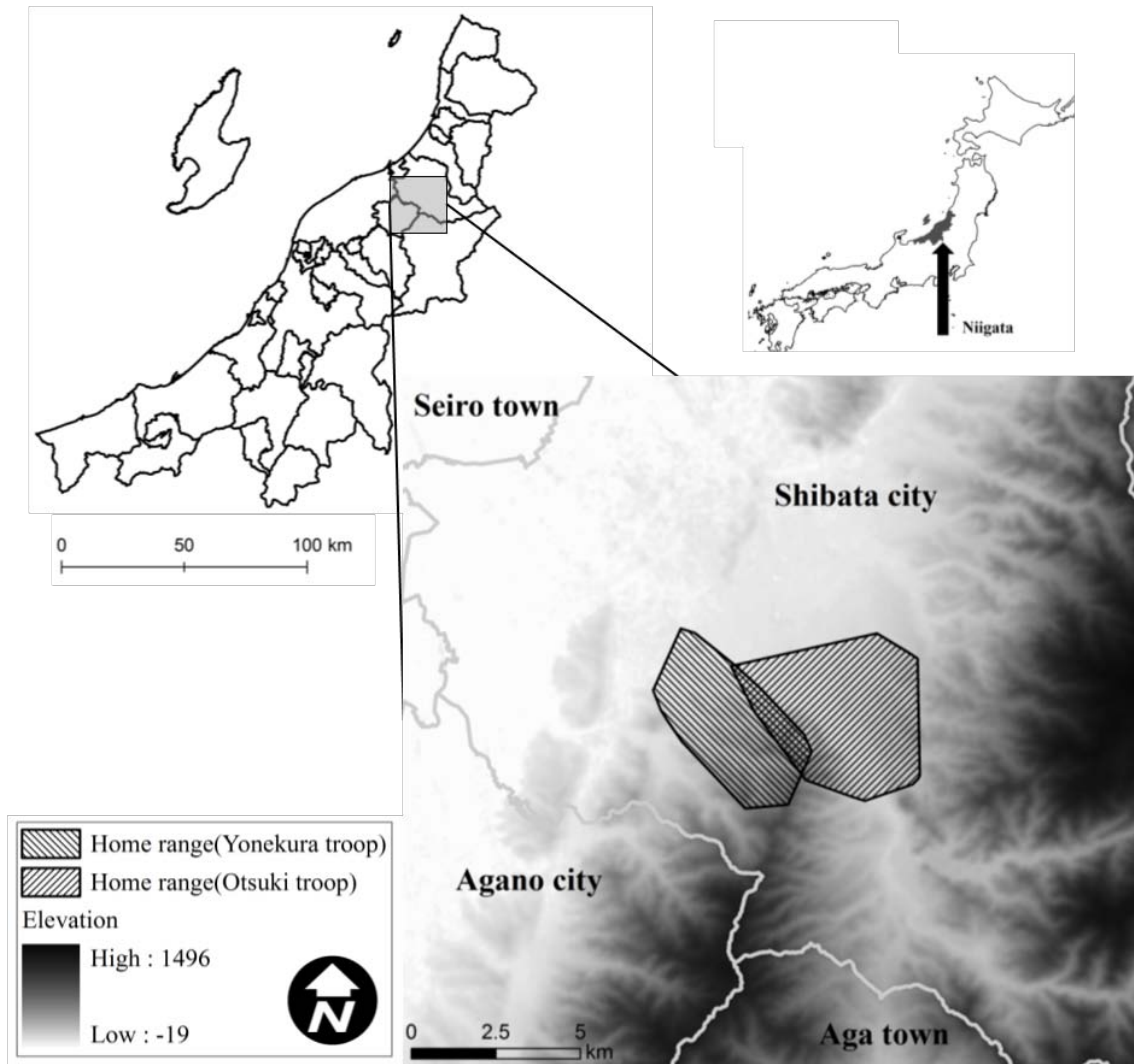


Figure 1. Location of study area and home range of macaque troops.

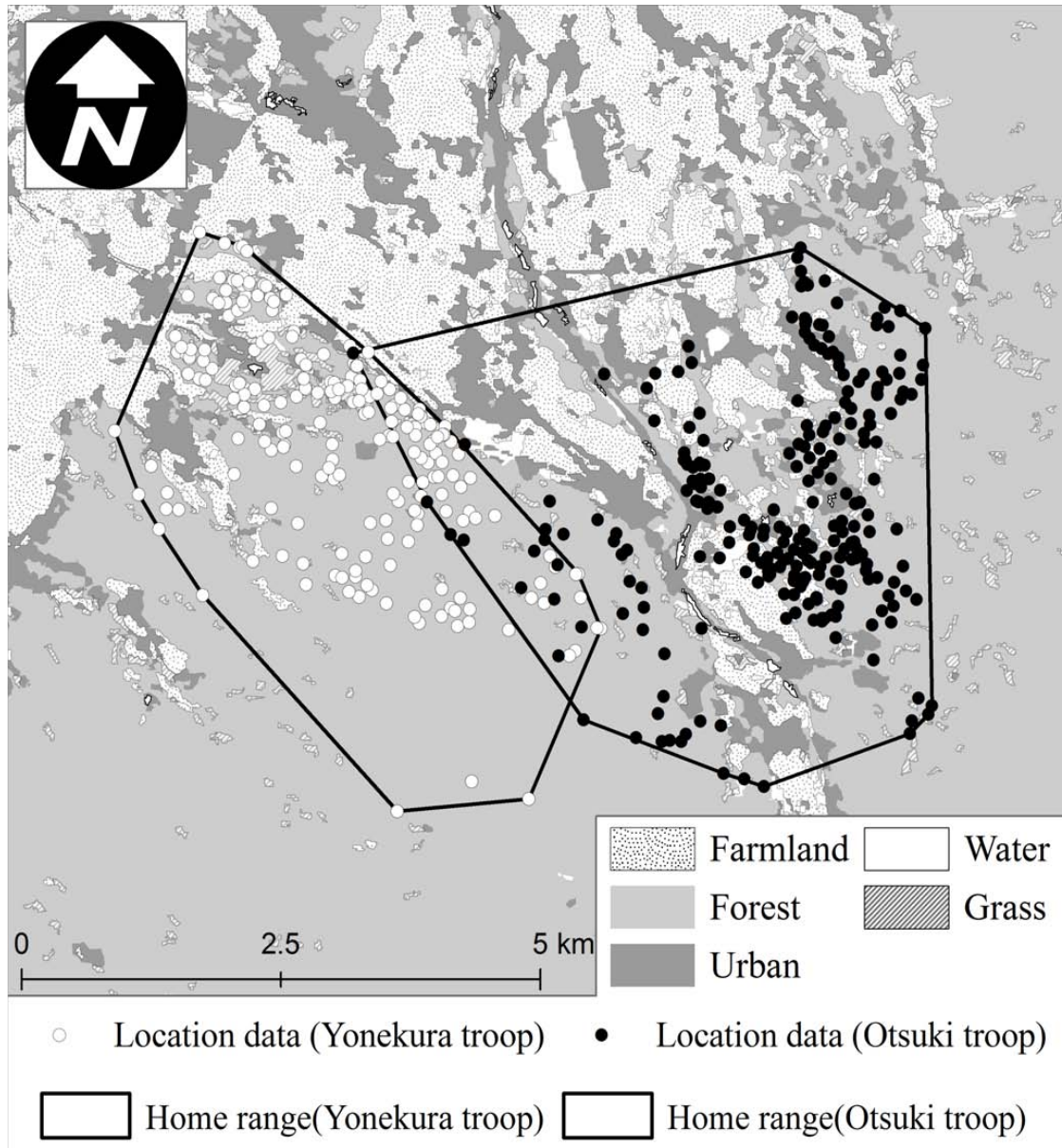


Figure 2. Land-cover map classified using ALOS/AVNIR-2 and home range area of Yonekura troop and Otsuki troop determined by using Minimum Convex Polygon method. Each patch was classified into five classes (Farmland, Forest, Urban, Water and Grassland).

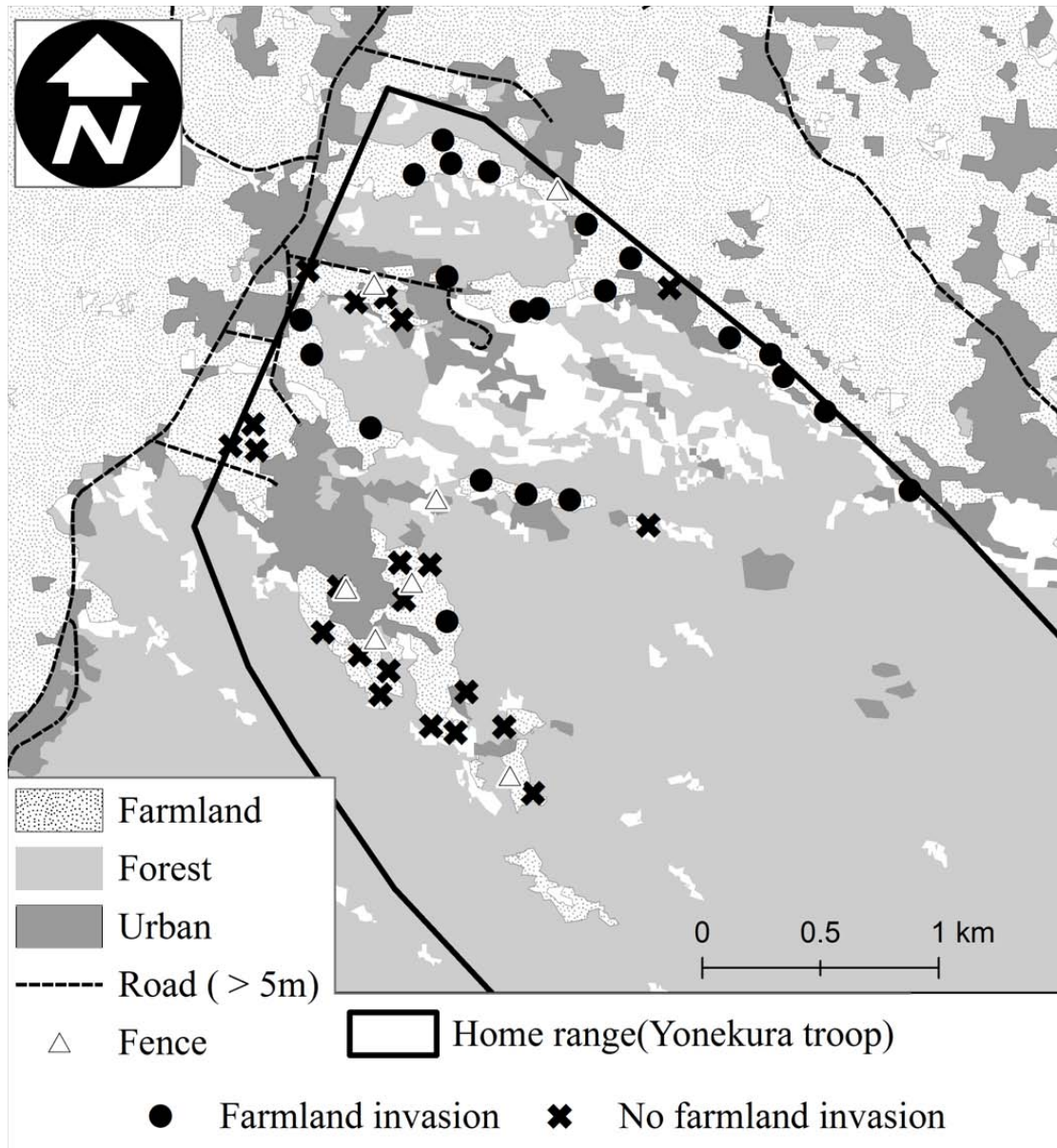


Figure 3. The invasion of farmland by Yonekura troop. Presence and absence data was applied.

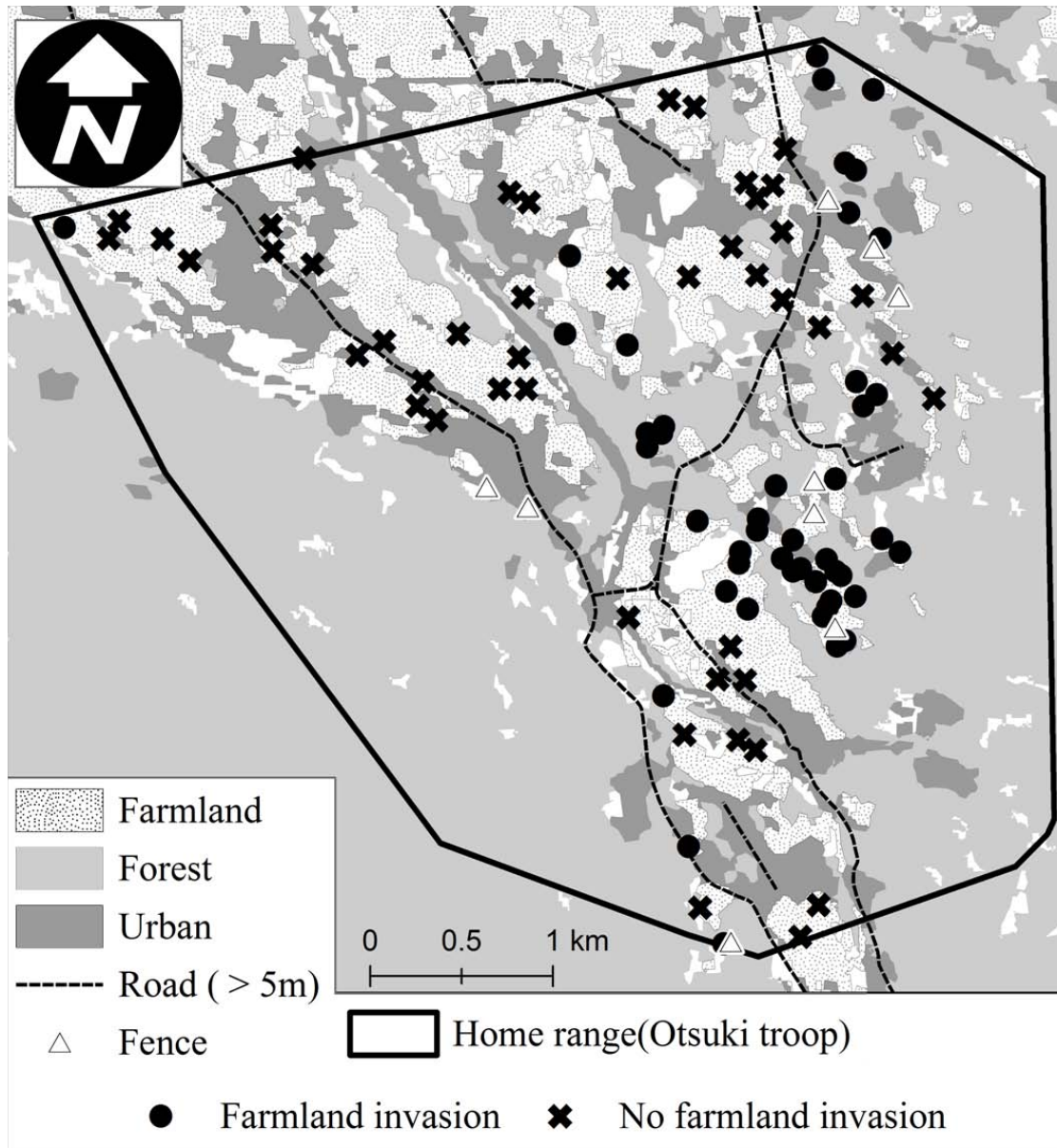


Figure 4. The invasion of farmland by Otsuki troop. Presence and absence data was applied.

Table 1. Indices used to evaluate the difference of habitats. Yonekura troop and Otsuki troop.

Acronym	Index name (unit)	Description
LPI	Largest patch index (%)	The largest patch index indicates the share of the landscape that is occupied by the largest patch of the landscape.
MPS	Mean patch size (ha)	Mean patch size is computed by dividing the total landscape (or land-use type) area by the number of patches.
LSI	Landscape shape index	In the landscape shape index, the sum of all patch perimeters is divided by a figure equivalent to the perimeter of a circle with the same area as the landscape area. LSI increases with increasing overall complexity of patch shapes.
AWMSI	Area-weighted mean shape index	Similar to mean shape index, mean patch shape complexity; equals 1 when all patches are circular and increases as patches become non circular, but patch shape index weighted by patch area
IJI	Interspersion and juxtaposition index (%)	The interspersion and juxtaposition index is calculated from the relationship between the length of each edge type and total edge of the landscape, divided by a term based on the number of land use types. IJI approaches 0 when adjacencies are unevenly distributed; IJI = 100 if all patch types are equally adjacent to all other patch types.

Table 2. List of environmental variables.

Dependent variables		Independent variables	
The invasion of farmland	Presence = 1	Distance from forest boundary	X_1
	Absence = 0	Distance from road	X_2
		Distance from water	X_3
		Distance from urban	X_4
		Distance from fence	X_5

Table 3. Comparison of landscape indices. (Yonekura troop and Otsuki troop).

	Forest		Urban		Farmland	
	Yonekura	Otsuki	Yonekura	Otsuki	Yonekura	Otsuki
LPI(%)	82.60	27.87	2.48	9.40	2.23	4.33
MPS (ha)	74.33	30.07	2.05	4.73	5.95	9.05
LSI	5.54	11.20	9.00	15.91	7.59	13.86
AWMSI	4.29	6.08	3.08	6.12	2.88	3.98
IJI(%)	74.93	74.78	55.90	52.22	61.89	43.26

Table 4. Model of the invasion to farmland by Yonekura troop. Environmental factors affecting invasion of farmland were analyzed.

	Model averaged estimate	Standard error	IOV	<i>p</i> -value	VIF
Intercept	1.442	1.769	-	0.415	-
X_1	-0.019	0.008	0.940	0.012	1.830
X_2	0.002	0.001	0.860	0.045	1.390
X_3	-0.001	0.001	0.430	0.494	1.810
X_4	0.004	0.006	0.490	0.450	1.820
X_5	0.003	0.002	0.900	0.020	2.010

Table 5. Model of the invasion to farmland by Otsuki troop. Environmental factors affecting invasion of farmland were analyzed.

	Model averaged estimate	Standard error	IOV	<i>p</i> -value	VIF
Intercept	1.031	1.042	-	0.322	-
X_1	-0.018	0.009	1.000	0.004	1.230
X_2	0.004	0.002	0.840	0.043	1.410
X_3	0.000	0.001	0.230	0.832	1.420
X_4	0.007	0.006	0.540	0.254	1.380
X_5	-0.002	0.001	0.860	0.042	1.380

Table 6. Classification accuracy of prediction models.

		Yonekuta troop			Otsuki troop				
		Observed			Observed				
		Invade presence	Invade absence	Total			Invade presence	Invade absence	Total
Predicted	Invade presence	19	3	22	Predicted	Invade presence	40	6	46
	Invade absence	4	18	22		Invade absence	8	38	46
	Total	23	21	44		Total	48	44	92

In Yonekura troop, sensitivity = 82.6% (19/23); specificity = 85.7% (18/21); overall accuracy = 84.1% (37/44). In Otsuki troop, sensitivity = 83.3% (40/48); specificity = 86.3% (38/44); overall accuracy = 84.7% (78/92).

Chapter 3

Predicting dynamic home range sizes of Japanese macaques using a vegetation index derived from remotely sensed data

Introduction

Many animals have adapted to seasonal variation in food sources such as grain or other vegetation in their environment (Wiegand et al., 2008). Seasonal changes within an animal's habitat may affect its feeding, migration, and other behaviors (Hellgren, 1998; Hurlbert & Haskell, 2002). In particular, seasonal patterns of resource availability may influence habitat selection and use (Wiegand et al., 2008; Loveridge et al., 2009). The size of an animal's home range can be mediated by resource availability. High resource levels may result in smaller home range areas (Mills & Knowlton, 1991). However, when resources are patchy, larger areas may be needed to encompass the spatial and seasonal variability of resources (MacDonald & Carr, 1989). Understanding home range behavior and seasonal changes in resources is important for wildlife management and conservation.

The relationship between home range behavior and resource availability has been studied in relation to topography, landscape structure, and vegetation type (e.g., McLoughlin & Ferguson, 2000; Neilsen et al., 2003; Said & Servanty, 2005). However, these studies did not examine the effects of seasonal variation in the environment or home range behavior, which were suggested to be important by other authors (MacDonald & Carr, 1989; Wiegand et al., 2008; Loveridge et al., 2009). Remotely sensed data, including aerial photographs and satellite imagery, can be effective tools for investigating seasonal changes. Satellite-based spectral indices, such as the normalized difference vegetation index (NDVI; Asrar, 1989), are useful tools for predicting animal habitats in relation to

resource availability. NDVI can be used as a surrogate for vegetation structure or overall annual productivity and biomass (Mace et al., 1996; Osborne, Alonso & Bryant, 2001; Zinner, Pelaez & Torkler, 2002). For example, NDVI is often assumed to correlate with seasonal resource availability (Nilsen, Herfindal & Linnell, 2005; Wittemyer, Rasmussen & Douglas-Hamilton, 2007). The seasonal pattern of NDVI may thus be useful for predicting the relationship between home range size and seasonal resource availability.

Crop damage by medium-sized mammals is a serious problem in wildlife management in Japan (Ohdachi et al., 2009). Mammals such as the Asiatic-black bear (*Ursus thibetanus*), wild boar (*Sus scrofa*), and Japanese macaque (*Macaca fuscata*) have adapted to low resource availability during summer and winter (Nakagawa, 1989; Nakagawa, 1997; Tsuji et al., 2006). Seasonal changes in grains and other vegetation help regulate population dynamics in natural habitats, but these regulatory mechanisms may be altered in human-dominated environments. For example, crop-raiding by Japanese macaques has increased since the late 1970s and may have affected population dynamics.

Japanese macaques are endemic to Japan and are the northernmost non-human primate species (range 30°21'N–41°08'N, Wada & Tokida, 1981). They have a high ability to adapt to varying environmental conditions and are found in several regions of Japan. Macaque behavior varies depending on the home range size, human land use, and regional environment. The extent of crop damage caused by macaques also varies. Previous studies have described macaque troop behavior as well as crop damage (Enari,

Matsuno & Maruyama, 2005; Yamada & Muroyama, 2010; Mochizuki & Murakami, 2011). The behavior of crop-dependent Japanese macaques may differ from that of populations that feed on natural vegetation. Basic ecological information on the behavior of crop-dependent Japanese macaques is necessary for risk management for crop protection as well as for appropriate wildlife management and conservation. Although a number of studies have described relationships between vegetation quality and Japanese macaques (e.g., Tsuji et al., 2008; Tsuji, Sato & Sato, 2011), these studies did not consider the effect of crop plants on behavior. Seasonal variation in vegetation quality is particularly important for understanding the behavior of crop-dependent Japanese macaques and the resultant crop damage.

Spatial scale is particularly important when using satellite-based ecological indices in wildlife research (Cushman, 2010). Previous wildlife studies using satellite-based ecological indices such as NDVI focused on broad scales at the country or continent level (Mueller et al., 2008; Wittemyer et al., 2007; Loveridge et al., 2009; Young & van Aarde, 2010). Furthermore, those studies used imagery from the National Oceanic and Atmospheric Administration's Advanced Very High-Resolution Radiometer (AVHRR) or Terra Moderate-Resolution Imaging Spectroradiometer (MODIS). Although these satellite sensors have high observation frequency, allowing for examination of temporal changes in vegetation, they have low spatial resolution. In research on human-wildlife conflicts, a more local spatial scale is necessary (Conover, 2002). Thus, satellite imagery

with higher spatial resolution is necessary. However, high-resolution satellite imagery has less frequent observations. In this study, I used imagery obtained by the Advanced Visible and Near Infrared Radiometer type 2 (AVNIR-2) on-board the Advanced Land-Observing Satellite (ALOS). These data have 10-m spatial resolution. I used three seasonal data sets (late spring, summer, and early winter) observed by ALOS/AVNIR-2 as fixed factors for home range behavior analysis.

The natural resources of Japanese macaques (i.e., fruits and nuts) increase during spring and autumn, and decrease in summer and winter (Tsuji et al., 2011). I investigated multiple troops of crop-raiding Japanese macaques from early summer to early winter. I predicted changes in home range size by changes in NDVI using remote sensing. By evaluating home range behavior in the transitions to periods of reduced natural resources, I aimed to clarify the relationship between home range size and seasonal variation in vegetation quality of crop-dependent Japanese macaques.

Methods and Materials

Study area

The study was conducted in Shibata city, Niigata Prefecture, Japan (37° 57'N, 139° 19'E, 532 km², Fig. 1). Shibata city had a population of 102,188 with a density of 190 people/km² in 2009. The mean annual temperature is 12.5°C, mean annual precipitation is 1109 mm, and maximum snow depth is 400 mm (snowfall typically occurs between December and March). Elevation ranges from -19 to 1496 m above sea level, and forests cover 64% of the area. The forests are primarily secondary forests dominated by oak (*Quercus cripula*) and conifer plantations of Japanese cedar (*Cryptomeria japonica*), Japanese red pine (*Pinus densiflora Sieb*), and hinoki cypress (*Chamaecyparis obtusa*). Forestry is declining in the region and many plantations have been abandoned.

Crops in this region have been damaged by macaques since the late 1970s, and the area affected has gradually expanded. A survey of Japanese macaques in Shibata city revealed 14–17 troops that included a total of up to 700–800 individuals. The intensity of crop damage has increased, and the risk of human injuries caused by raiding macaques has become a concern. Annual losses due to crop damage vary widely but average 15 million yen (about US\$170,000). The main crops damaged are paddy rice, soybeans, potatoes, and corn. Damage to paddy rice is the most severe, and crop damage often occurs in August when natural food resources are scarce. Hunting has been used as a remedial measure and has eliminated about 100 monkeys each year. Hunters have recently taken the lead in

driving macaques away from farmland, usually from May to November, when the most intense crop damage occurs.

Radio-tracking of Japanese macaques

I used VHF-radio tracking to monitor crop-damaging Japanese macaques and investigate their behavior, home range, and migration in the study area. This method has been widely used for tracking wildlife. In my study, I attached a transmitter to an animal and the signal was received by a Yagi antenna and receiver. These antennae have strong directionality and are often used on animals whose native habitat makes direct observation difficult (White & Garrot, 1990). Monitoring was performed from May to November when the majority of crop damage occurs and was begun in 2004 in Shibata city. The estimated tracking error was approximately 100 m. The location of Japanese macaques was determined from one point an hour using triangulation. I was able to determine habitat use in addition to location because the data were acquired continuously throughout a day.

Twelve troops were selected for radio-tracking. Of these, I focused on the Ishikawa (IK), Sanko (SK), Kawahigashi (KH), Otsuki (OT), and Yonekura (YK) troops (Fig. 1). These troops have been continuously monitored for four years. For this study, I used the location data from 2005 to 2008. These troops were selected because they have not divided during the four years of monitoring, allowing us to clearly investigate the troops over time. Each of these troops contained over 30 individuals and has caused

serious crop damage in Shibata city.

Home range sizes of the target troops were estimated using the fixed kernel method of the Home Range Tool (Rodgers et al., 2007), an extension of ArcGIS 9.3 (ESRI Inc.). Several methods have been used to estimate home range sizes of wildlife, including minimum convex polygon (Mohr, 1947), grid cell count (Siniff & Tester, 1965), harmonic mean (Dixon & Chapman, 1980), and fixed and adaptive kernel methods (Worton, 1989). Among the various home range estimators, adaptive and fixed kernel methods were found to have highest estimation ability (Kernohan, Gitzen & Millspaugh, 2001). Kernel home range methods offer several advantages over previous estimators. Kernel estimators are free of distributional assumptions and perform well in simulations, even when multiple bivariate normal distributions are combined to produce complex multimodal home ranges (Worton, 1995; Seaman et al., 1999). In this study, I estimated home ranges of each troop during three periods: late spring, summer, and early winter from 2005 to 2008 (Table 1). These periods coincided with the acquisition time of ALOS/AVNIR-2 satellite imagery. The smoothing parameter, which is a critical component in kernel density, was defined using least-squares cross-validation (LSCV).

Remotely sensed data collection and processing

Temporal ALOS/AVNIR-2 data were used to evaluate vegetation quality for Japanese macaques in three time periods, representing late spring (image captured on 27 May 2006

at solar elevation 70°, solar azimuth 146°), summer (12 August 2007 at solar elevation 59°, solar azimuth 139°), and early winter (9 November 2006 at solar elevation 33°, solar azimuth 159°). The data were ortho-rectified with a 10-m digital elevation model obtained from the Japanese Geospatial Survey. All satellite data were geo-coordinated to zone 54 of the Universal Transverse Mercator projection system within one pixel root mean-square error (RMSE). Shade caused by topographic relief can be problematic in the analysis of remotely sensed data. The Minnaert topographic correction method was applied to offset topographic effects (Meyer et al., 1993). To evaluate the vegetation quality of Japanese macaques, NDVI was calculated from the ALOS AVNIR-2 data as

$$NDVI = \frac{NIR - RED}{NIR + RED} \quad (1)$$

where RED and NIR are the visible red and near-infrared reflectance factors, respectively. NDVI was calculated for May, August, and November, and used as the index of vegetation quality for Japanese macaques. NDVI has been previously used as an index of food availability and vegetation cover (Murwia & Skidmore, 2005; Mueller et al., 2008; Young, Ferreira & van Aarde, 2009). I divided the study site into 10-m pixel grid cells (i.e., the resolution of ALOS/AVNIR-2 imagery). NDVI was calculated as the sum of mean values within the home range of each troop and ranges from -1 to 1. Negative values indicate an urban area or bare land and positive values indicate vegetation. ERDAS IMAGINE 9.3 (Leica Geosystems, Inc.) and ArcGIS 9.3 (ESRI, Inc.) were used to correct and process the data.

Relationship between habitat quality and home range size of Japanese macaques

I compared differences by season in NDVI and home range size using multiple comparisons with Tukey's contrasts in the "multcomp" package (Hothorn, Bretz & Westfall, 2008) of R ver. 2.13.0 (R Development Core Team, 2011). I used a gamma error distribution for home range size and Gaussian error for NDVI, with the 95% confidence interval to test for significance.

I compared vegetation during the transitions to summer (May to August) and winter (August to November) in two separate models. Pooled home range size was used as the dependent variable and six variables of change in NDVI were used as explanatory variables: SIZE_VI_INC, SIZE_VI_DEC, NUM_VI_INC, NUM_VI_DEC, AMT_VI_INC, and AMT_VI_DEC (see Table 2 for descriptions of these variables). I calculated patch size, number of patches, and change in patches within the home range of Japanese macaques in each transition period (Fig. 2). Patches were defined by the following processes. I used change detection to calculate the change in NDVI between satellite data obtained in different periods. Atmospheric differences might result in false detection of vegetation change (Yang & Lo, 2000). Thus, I used principal component analysis to correct for the influence of the atmosphere (Fig. 3; Awaya & Tanaka, 2003; Rogan et al., 2003; Mochizuki & Murakami, 2011). In principal component analysis of NDVI composite imagery, the first principal component is analogous to regression

analysis (digital number matching; Awaya & Tanaka, 1999) and represents a luminosity compensation technique. The second principal component represents the change between the two time periods. These analyses were calculated using linear mixed-effects models with Markov chain Monte Carlo (MCMC) simulation in the “lmer” and “mcmcsmpl” methods of the “lme4” package in R (Bates, 2005).

The order of the data processing was as follows. First, a composite image of NDVI was created from the two time periods of the transition. Next, principal component analysis was applied to this composite image, and principal component imagery was created. Finally, pixels in which change was detected for the second principal component were determined using supervised classification with maximum likelihood, and the threshold value of the change detection was determined. The second principal component imagery was classified into the three classes: areas with increased NDVI, areas with decreased NDVI, and unchanged areas. I defined these areas as patches with NDVI change. Finally, a 5×5 majority filter was applied to remove small pixels.

In the linear mixed-effects model, I used a Gaussian error distribution. Troops and years were treated as random effects and troops were nested within years. MCMC was used to estimate parameters. I performed one chain of 10,000 steps in the MCMC simulations. If the 95% confidence interval of an explanatory variable did not include 0, I considered the variable to be significant. ERDAS IMAGINE 9.3 (Leica Geosystems Inc.) was used for change detection, and R (Develop Core Team, 2011) was used for linear

mixed-effects model and MCMC sampling.

Results

The home range sizes of each troop, which were estimated by a kernel method with LSCV, changed in each period. The average home range size of all troops in all years was 3.34 ± 1.81 (SD) km² in late spring, 1.94 ± 1.29 (SD) in summer, and 3.74 ± 2.21 (SD) in winter. Home range size in summer season was the smallest in other seasons and the variation was also the minimum. Average home range size decreased from late spring to summer and expanded from summer to early winter (Fig. 4). Home range sizes were significantly smaller in summer than in spring or winter from the result of the 95% interval credit using multiple comparison (Fig. 5 (a)). In the vegetation quality, mean NDVI values were 0.24 ± 0.26 (SD) in late spring, 0.38 ± 0.22 (SD) in summer, and 0.23 ± 0.16 in early winter. NDVI in summer season was the highest value in other seasons. In the analysis of seasonal change in vegetation quality, NDVI increased from late spring to summer, and decreased from summer to early winter in contrast with change of home range size (Fig. 6). NDVI value differed significantly between summer and other two months from the result of the multiple comparison (Fig. 5 (b)).

The changes in NDVI during the two transitions represent seasonal variation in vegetation quality (Fig. 2). These changes represent seasonal variation of vegetation quality. The result of linear-mixed models was shown in Table 3. I evaluated the home range behavior from late spring to summer and from summer to early winter. During the spring to summer transition, home range behavior was positively correlated with

NUM_VI_INC and negatively correlated with NUM_VI_DEC. Other variables were not significant from the 95% interval credit. NUM_VI_INC was more important than NUM_VI_DEC. In the transition from summer to early winter, home range size was positively correlated with SIZE_VI_INC and NUM_VI_INC, and negatively correlated with SIZE_VI_DEC. Other variables were not significant from 95% interval credit. SIZE_VI_INC was most important variable, followed by SIZE_VI_DEC. The important factor for home range behavior was changed from the number of patches to the patch size by the change of temporal scale.

Discussion

Vegetation, as represented by NDVI, increased in summer within the habitat of Japanese macaques. The home range size of Japanese macaques also significantly decreased in summer compared to spring and winter, suggesting that vegetation is responsible for the change in home range size. The NDVI values within forest regions would not differ from June to August in the temperate study area (Delbart et al., 2005; Fisher, Mustard & Vadeboncoeur, 2006). Therefore, the change in the farmland NDVI value likely affected the behavior of Japanese macaques. Agriculture is the primary industry in the study area, and the increase in NDVI likely reflects the growth of paddy rice and other crops. Japanese macaques primarily damage paddy rice, soybean, potato, and corn, which grow during the summer season.

In general, animals' home ranges depend on the availability, dispersion, and predictability of resources (Macdonald & Carr, 1989). When resource availability is low, larger areas may be needed to encompass the spatial and temporal variability of these resources (Macdonald & Carr, 1989; Loveridge et al., 2009). Food resources within natural habitats of Japanese macaques, such as mountain forests, are scarce during summer and winter, and Japanese macaques often expand their home ranges during these seasons to search for food (Nakagawa, 1989; Nakagawa, 1997; Tsuji et al., 2006). However, the target troops in this study contracted, rather than expanded, their home range size in summer. This result suggests that the target troops depend on crops rather

than native vegetation during the summer. Agricultural crops are not grown in mountainous forest areas; therefore, the target troops did not need to search these areas for food. Home ranges of Japanese macaques expanded in early winter, coinciding with the end of the agricultural growing period.

The linear models comparing home range behavior of crop-dependent Japanese macaques and change in vegetation quality suggested that change in NDVI at the patch level contributed to the expansion of home ranges. The number of patches was the only variable significant for home range size during the transition from late spring to summer. Patch size and the amount of change in NDVI were not significant for the spring to summer transition. During the transition from summer to early winter, patch size and increase in the number of patches were significant, but the overall amount of vegetation change was not significant. Winter is the season of least vegetation. High nutritive foods such as agricultural crops decrease, as do grasslands, resulting in chronic food shortage. Therefore, Japanese macaques depend on not only the number of vegetation patches but also the patch size. In periods of low food availability, Japanese macaques prefer large food patches with high quality (Nakagawa, 1989). This tendency was seen in my results for winter. The important factor for home range behavior was changed from the number of patches to the patch size by the change of temporal scale. The importance of patch size and/or the number of patches has been reported for many years (Simberloff & Abele, 1976; Soule & Simberloff, 1986). My findings suggest that the required patch

compositions for Japanese macaques are changed by seasonal variability.

The amount of change in NDVI was not significant for either temporal transition. The main land-cover types within the macaques' home range were forest and farmland. Most change during the times I examined was on farmland. Food shortages occur twice per year (in summer and winter) for wild Japanese macaques that depend solely on natural food resources in forests and these shortages help regulate the population size of Japanese macaques (Izawa, 1988; Hanya et al., 2004). However, troops that depend on crops, which have high nutrients, avoid summer food shortages (Enari et al., 2005). This allows population sizes of Japanese macaques to increase, which in turn leads to increased crop damage, particularly when macaques raid several types of crops. My study did not consider landscape heterogeneity such as habitat connectivity or fragmentation. These factors should be examined in future studies. However, by evaluating the relationship between home range behavior and change in vegetation quality using only NDVI, I detected changes in home range behavior of crop-dependent Japanese macaques between seasons. My results suggest that the behavior of crop-raiding Japanese macaques differs from their behavior in a natural condition. The ecology of Japanese macaques under natural conditions has been studied for many years (Yamagiwa, 2010), but there is little information on the ecology of crop-dependent macaques. Such information is increasingly important for management of human-wildlife conflicts and primate conservation. My finding that the home range size of Japanese macaques decreases in the summer should

help inform management objectives.

However, neither land use nor vegetation type can be represented completely by NDVI (Ito et al., 2006); planting status is also not included. NDVI provides information only on the existence and amount of vegetation. To more precisely determine the quality of wildlife habitat, it is necessary to use other geo-informatics (e.g., vegetation and land-use maps). However, NDVI can be calculated using only satellite data and provides a suitable index of wildlife habitat in cases when land-use or vegetation-type data are not available (Stickler & Southworth, 2008). NDVI provides information that cannot be explained by only the land-cover condition, distribution of vegetation, or landscape structure. It is also possible to detect habitat use, selection, preference, and abundance from NDVI for every season, allowing comparisons of seasonal changes in food resources in relation to animal migrations (Musiega & Kazadi, 2004; Mueller et al., 2008; Wittemyer et al., 2007; Loveridge et al., 2009; Young et al., 2009). Evaluating the effectiveness and limitations of NDVI as an indicator of wildlife habitat is important. I propose that NDVI is an effective indicator for evaluating wildlife behavior in response to vegetation quality, particularly for management of human-wildlife conflicts.

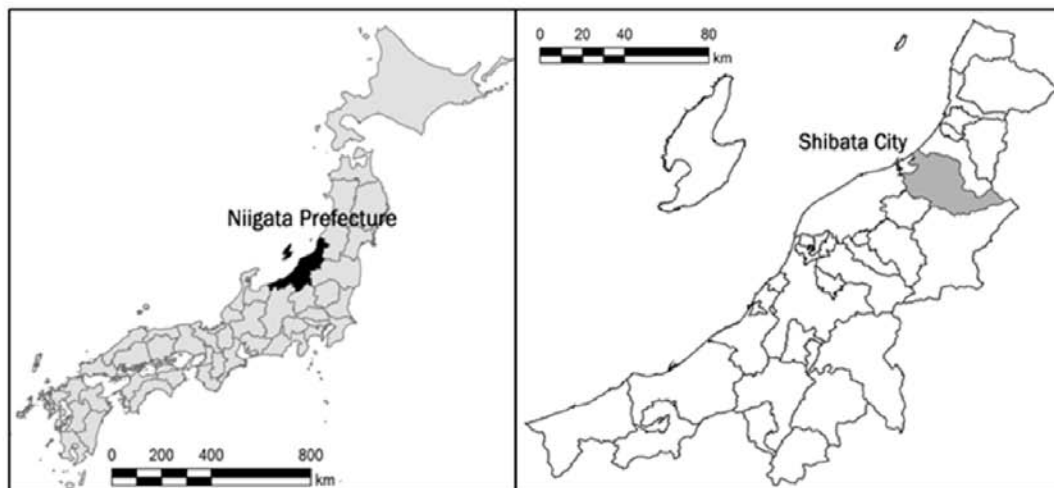
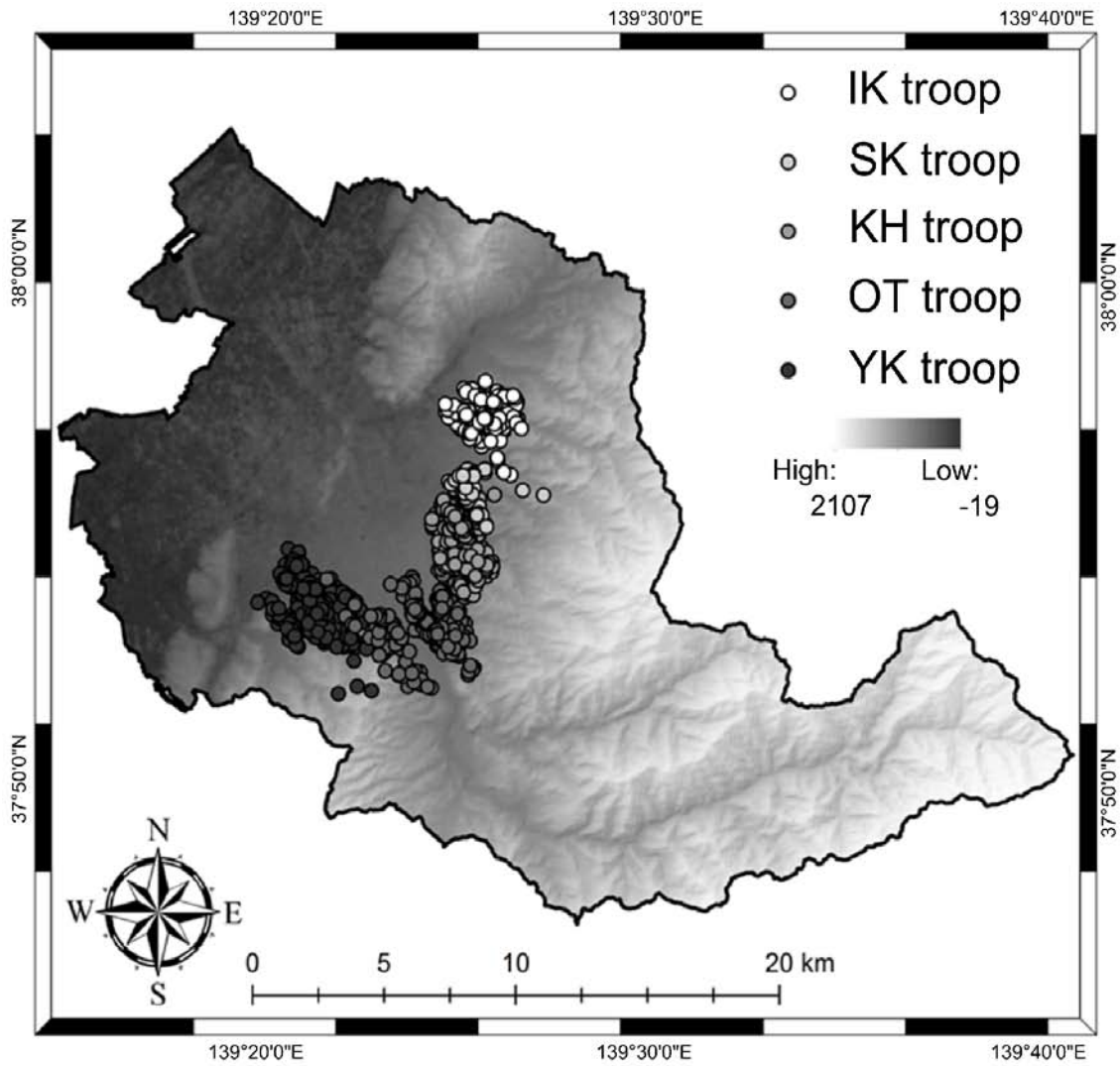


Figure 1. Study area and the location of Japanese macaques collected by VHF-radio telemetry.

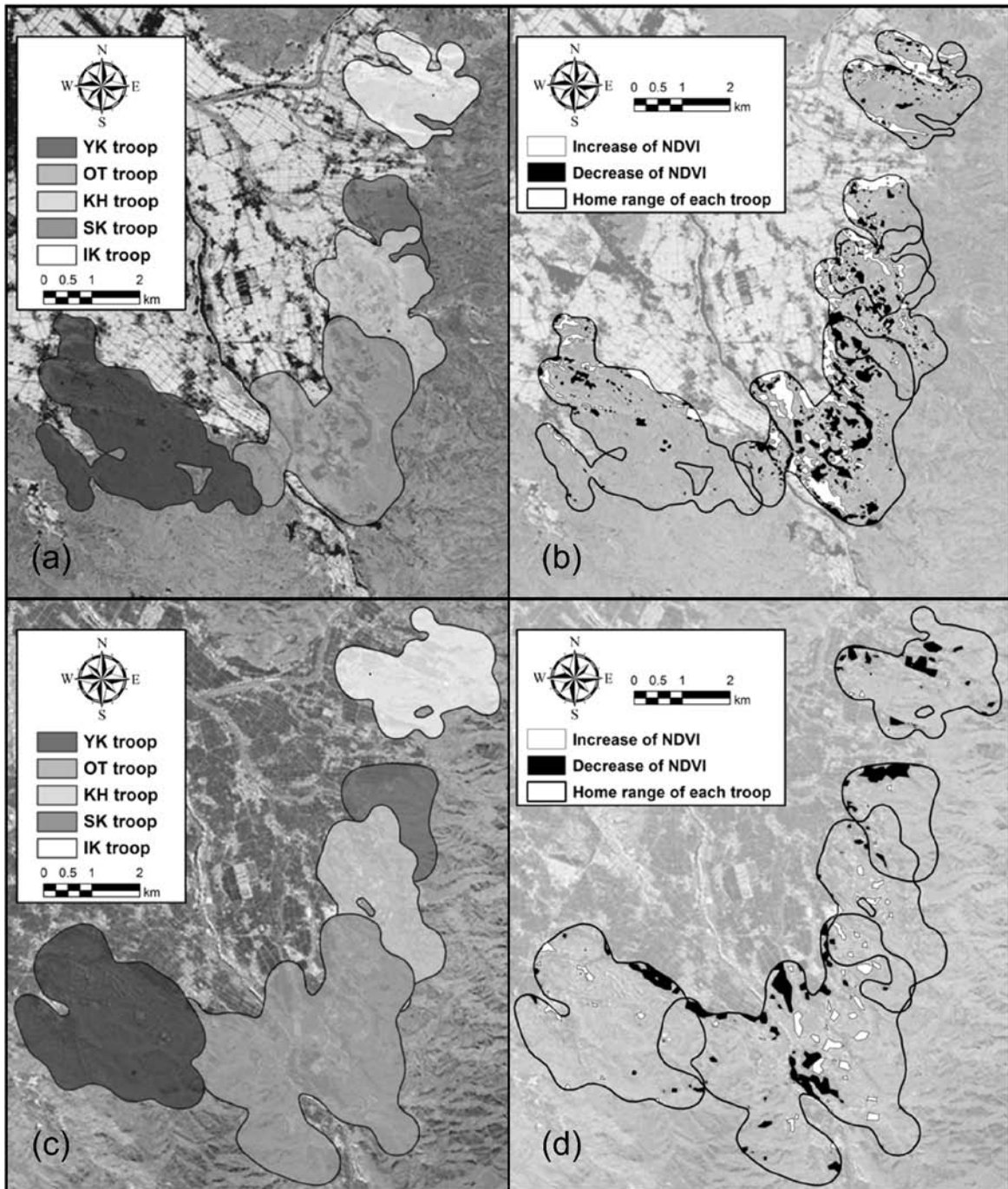


Figure 2. The relationships between the home range sizes and the change in NDVI. (a) and (b) Home range of target troops using kernel density method and change in NDVI imagery using principal component analysis. (c) and (d) Distribution of patch which defined using maximum likelihood method as threshold value within macaque troops. (a) and (c) The transitions to summer. (b) and (d) The transitions to early winter.

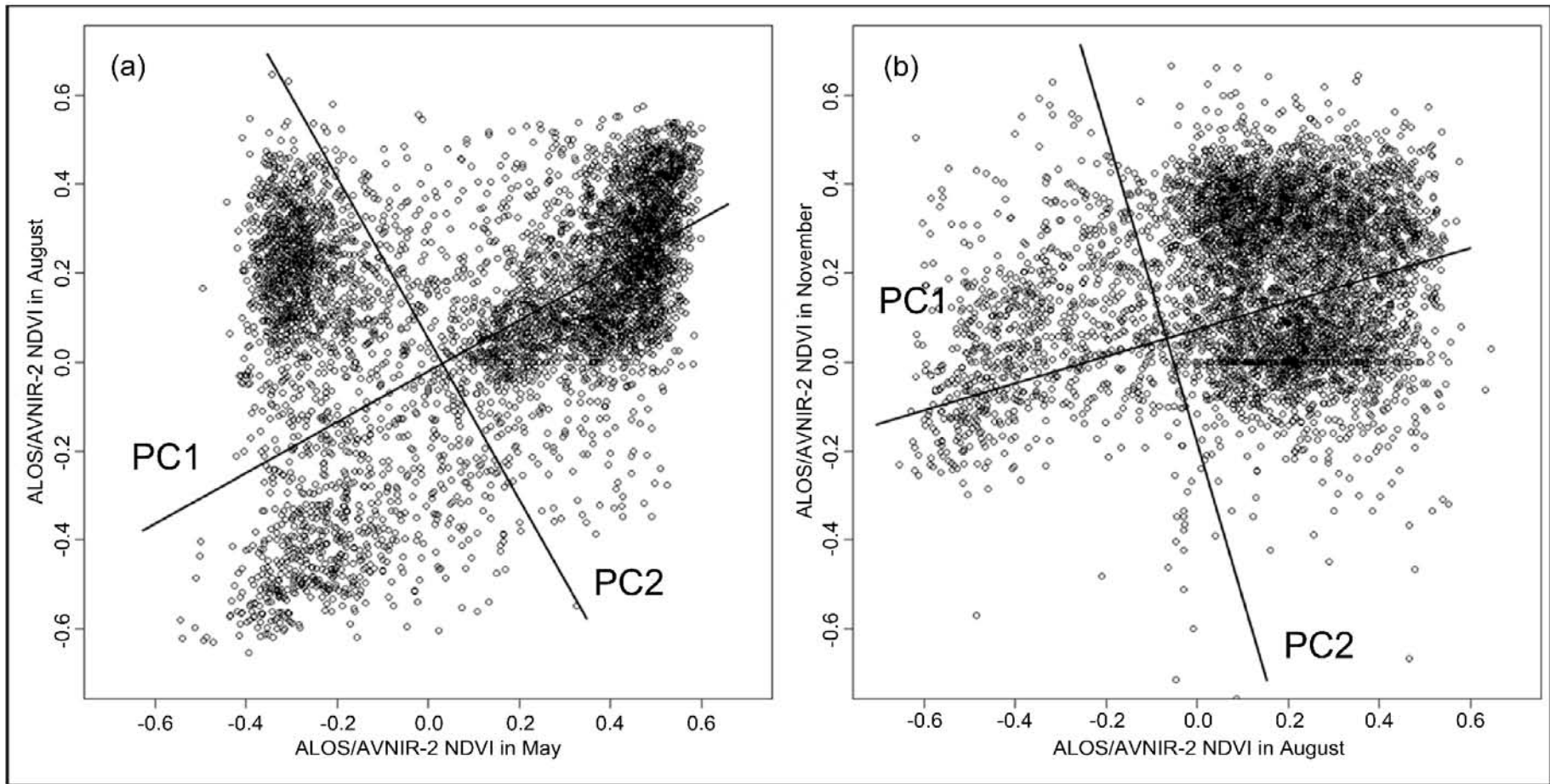


Figure 3. Change detection using principal component analysis for NDVI composite imagery. (a) Change detection from May to August. (b)

Change detection from August to November.

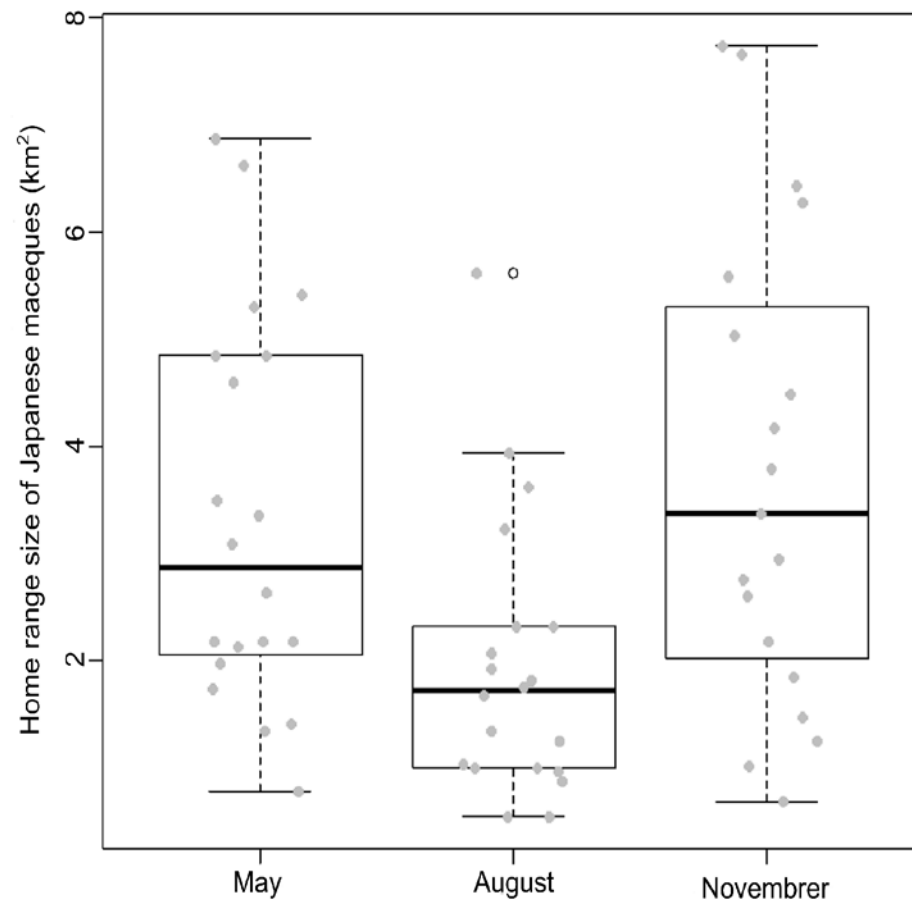


Figure 4. Seasonal changes in home range size of Japanese macaque troops with each troop and each observed year. The original data were jittered within each boxplot.

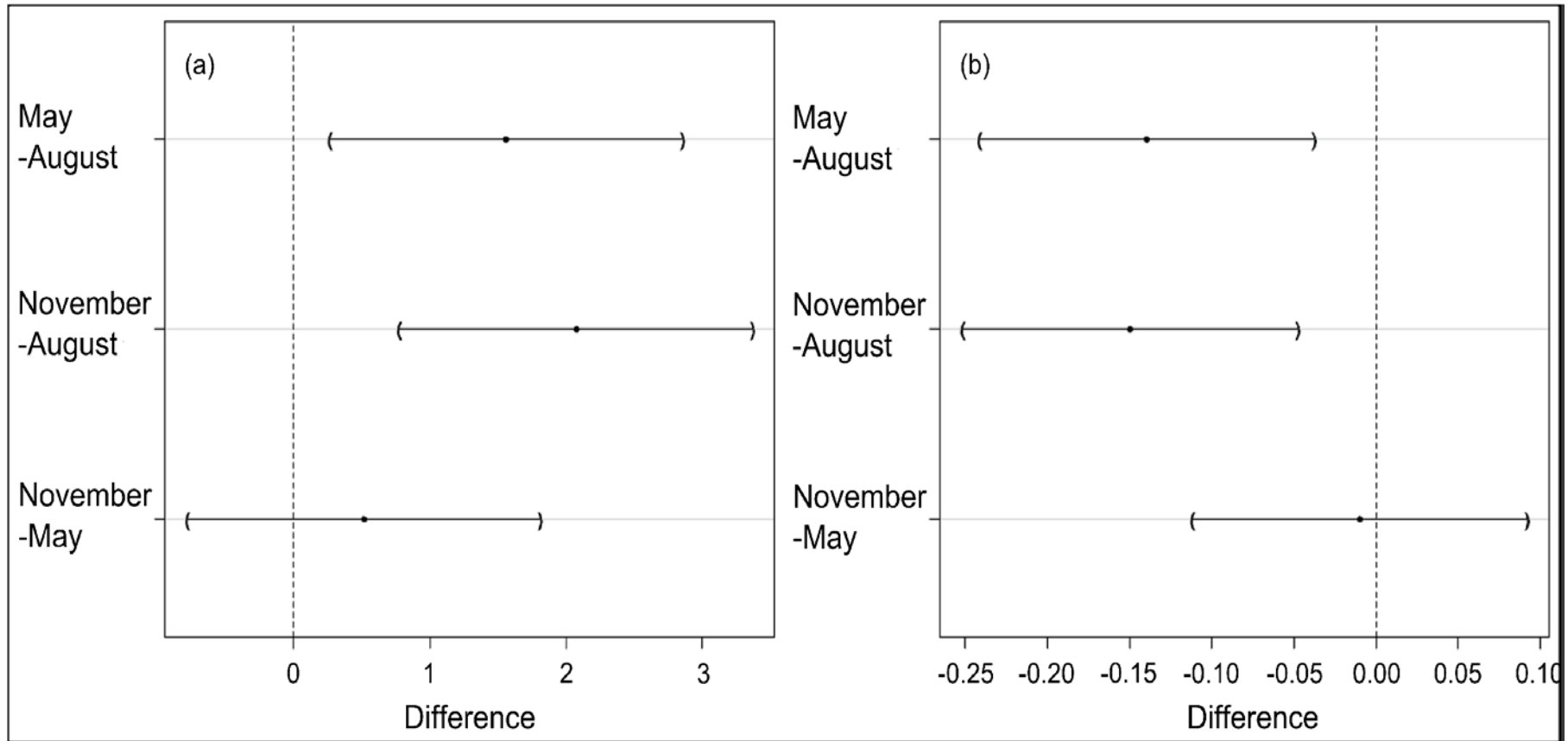


Figure 5. Results of multiple comparison with Tukey contrasts. If the 95% confidence interval did not include 0, I considered the difference between each season to be significant. (a) The 95% confidence interval of home range size. (b) The 95% confidence interval of NDVI.

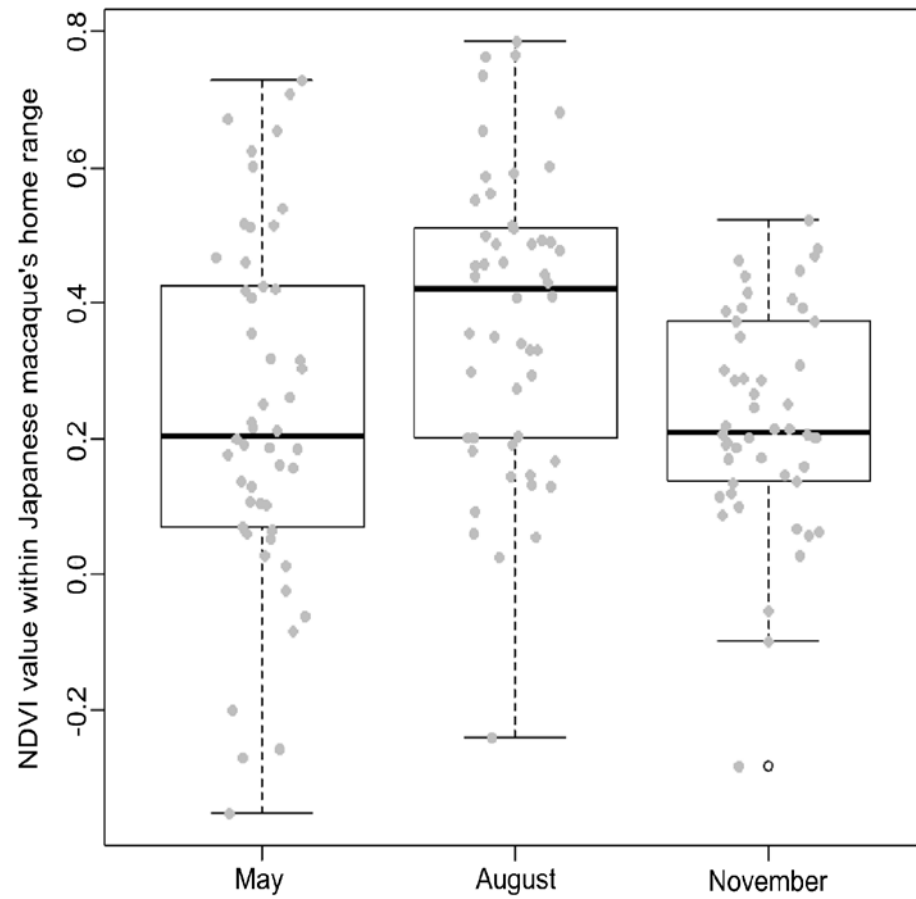


Figure 6. Seasonal changes in NDVI with the location of Japanese macaques. The original data were jittered within each boxplot.

Table 1. Dates of Japanese macaque survey and matching period for NDVI.

Term	Definition	Macaque survey (2005-2008)		NDVI of ALOS/AVNIR-2
		Start	End	
May	Late spring	11-May	20-Jun	27-May, 2006
August	Summer	1-Aug	30-Aug	12-August, 2007
November	Early winter	20-Oct	15-Nov	9-November, 2006

Table 2. List of explanatory variables for modeling to evaluate the relationships between home range behavior and seasonal change in NDVI.

For patch based variables, mean and SD are shown for each variables.

Variables	Description		Change from May to Aug	Change from Aug to Nov
SIZE_VI_INC	Patch size with NDVI increases	Mean	0.48	0.17
		SD	0.53	0.22
SIZE_VI_DEC	Patch size with NDVI decreases	Mean	0.48	0.31
		SD	0.54	0.51
NUM_VI_INC	Number of patches with NDVI increases	Mean	65.45	19.89
		SD	47.63	21.81
NUM_VI_DEC	Number of patches with NDVI decreases	Mean	93.25	20.74
		SD	60.63	21.38
AMT_VI_INC	Increment of NDVI within home range	Mean	0.61	0.14
		SD	0.04	0.08
AMT_VI_DEC	Decrement of NDVI within home range	Mean	0.23	0.35
		SD	0.03	0.16

Table 3. Posterior distribution of coefficients of two models (the transition period from late spring to summer, the transition period from summer to early winter).

Variables	Model of change			Model of change		
	in May to August			in August to November		
	Mean	2.5%	97.50%	Mean	2.5%	97.50%
Intercept	2.108	-4.110	8.228	-0.865	0.876	2.667
SIZE_VI_INC	-0.866	-2.360	0.632	30.364*	12.022	49.393
SIZE_VI_DEC	0.603	-0.856	2.019	-5.859 *	-9.511	-2.167
NUM_VI_INC	0.013*	0.000	0.027	0.181*	0.041	0.243
NUM_VI_DEC	-0.006*	-0.013	-0.001	-0.007	-0.064	0.134
AMT_VI_INC	-4.532	-14.240	5.549	-3.014	-19.583	13.278
AMT_VI_DEC	0.491	-6.739	7.602	-0.138	-4.666	4.443

Asterisks indicates that 95% credible interval of a parameter did not overlap 0.

Chapter 4

Change in habitat selection by Japanese macaques and habitat fragmentation analysis using temporal remotely sensed data

Introduction

Human–wildlife conflicts can result in crop and forestry damage and loss of life. Such conflicts present serious problems worldwide and have become an integral component of contemporary wildlife management (Conover, 2002; Storm et al., 2007). Wildlife has adapted to changes in forest dynamics over long periods (Bengtsson et al., 2000), and changes in forest management may affect animal behavior (Johnson et al., 1992; Mannan et al., 1994; Nielsen et al., 2008; Cushman et al., 2010). Thus, it is important to evaluate the relationship between change in forest configuration and human–wildlife conflicts. To plan wildlife management, I must first understand the details of resource selection by wildlife, considering landscape structure (Johnson, 1980; Jones, 2001; Conover, 2002; Manly et al., 2002; Braun, 2005).

In Japan, the conflict caused by mid-sized mammals is significant. These mammals, which include wild boars (Honda, 2009), Sika deer (Kaji et al., 2000; Ueda et al., 2003), Asiatic black bears (Oka et al., 2007), and Japanese macaques (Mochizuki et al., 2009), can damage crops and cause injuries to humans depending on the situation. Conflicts caused by these mammals have become serious, amounting to 13 billion yen (150 million US dollars) in Japan (Ministry of Agriculture, Forestry and Fisheries, 2009). Japanese macaques live the farthest north of any nonhuman primate species (range 30°21–41°08'N) and utilize various habitat types, such as cool-temperature deciduous forests, warm-temperature evergreen forests, and human settlements including farmlands

(Suzuki, 1965; Wada and Tokida, 1981; Yamada and Muroyama, 2010). Due to these temperate habits, the Japanese macaque is known worldwide as the “snow monkey.” The behavior of macaques is quite varied and depends on the home range, human land use, and regional environment. Therefore, management of macaque habitat is necessary for the effective management of this species.

An important underlying notion in wildlife habitat analysis is that the spatial configuration of landscape patches influences ecological characteristics (Hansen et al., 2001). Landscape configuration is the physical distribution and spatial character of patches within a landscape mosaic (Forman and Godron, 1986; McGarigal & Marks, 1995). Thus, it is necessary to quantify land-cover type and the landscape mosaic. To this end, earth observation data such as satellite imagery and aerial photography are suitable for detecting landscape structure. Remotely sensed data can represent surface conditions over long periods, allowing for evaluations of land-cover changes such as forest fragmentation within wildlife habitats (Linke et al., 2009; Coops et al., 2010).

Predictive habitat models that can account for environmental factors related to human–wildlife conflict are effective for wildlife management (Manly et al., 2002; Austin, 2007; Hegel et al., 2010). Models can help assess the impact of changing land use and identify potential conflicts with human activities (Johnson et al., 2004; Klar et al., 2008). Furthermore, changes in habitat selection from the past to the present can be predicted by extrapolating the model to past conditions. The information used to evaluate such change

can be very useful when considering the scale of human–wildlife conflicts (Warren et al., 2001; Onyeahialam et al., 2005; McDermid et al., 2010).

The influence of habitat changes caused by deforestation and disturbance can also be evaluated by combining habitat models and remotely sensed data (Saunders et al., 1991; Forman, 1995; Hansen et al., 2001). I used temporal remotely sensed data to detect changes in landscape configuration. The impacts of forest fragmentation on spatial habitat selection by wildlife were also evaluated. In this study, I focused on the 1970s, when little damage was caused by Japanese macaques, and the 2000s, when the damage became remarkable. Using Landsat multispectral scanner data (MSS data) in 1978 and ALOS/AVNIR-2 data (AVNIR-2 data) in 2007, a habitat-selection map for Japanese macaques was created in two stages, aimed at evaluating the change over a 29-year period. Over long periods, landscape structure was changed because of human disturbances or vegetational transitions. By such change, the distribution of Japanese macaques could have expanded, resulting in increased conflicts. The objective of this study was to determine changes in habitat selection in response to forest fragmentation by combining Geographic Information System (GIS), satellite remote sensing, and habitat-model data. In particular, change in habitat selection was predicted from the change in forest configuration, and the process that resulted in the current conflict situation was considered.

Materials

Taxonomy

I used the Integrated Taxonomic Information System (www.itis.org and taxonomic serial numbers: TSN) to define animal and plant species. The TSN of the Japanese macaque is 555659.

Study area

The study area was Shibata city, Niigata Prefecture, Japan (37° 57'N, 139° 19'E, 532 km², Fig. 1). Population density was about 190 inhabitants per km² in 2009. The elevation ranges from -19 to 1496 m above sea level. The forest cover of the study area was 64% and was composed mostly of secondary forest dominated by oak (*Quercus* L., TSN: 19276) and conifer plantations of Japanese cedar (*Cryptomeria japonica*, TSN: 501832) and Japanese red pine (*Pinus* L., TSN: 18035). The mean annual temperature is 12.5°C, the mean annual precipitation is 1109 mm, and the maximum snow depth is 950 mm (snowfall typically occurs during December–March).

Crops in this region have been damaged by macaques since the late 1970s (Agetsuma, 2007), and the area affected has expanded gradually. An investigation in Shibata City revealed 14–17 troops that included a total of up to 700–800 individual macaques. The intensity of crop damage is increasing, and the risk of life-threatening injuries through home invasion has become a concern. Annual crop damage costs

approach 15 million yen on average, with yearly fluctuations (Mochizuki et al., 2009). The main crops damaged are paddy rice (*Oryza sativa*, TSN: 41976), soybean (*Glycine max*, TSN: 26716), potato (*Solanum tuberosum* L., TSN: 505272), and corn (*Zea mays* L., TSN: 42269).

Location data of Japanese macaques

Twelve troops of Japanese macaques were studied using data acquired from June to November during 2005–2007 by hunters. The information gathered included location data obtained by VHF-radio-tracking, a method widely used for tracking wildlife. The location data were acquired by Yagi antennae and receivers, which received signals from transmitters attached to wildlife. The antennae have strong directionality and are often used with animals whose native habitat makes direct observation difficult (White and Garrot, 1990). Two location points per day for each of the 12 troops were acquired with 1,989 total points collected. The estimated radio-tracking error was 100 m. I used LT-01 (Circuit Design, Inc.) transmitters and IC-R20 (Icom, Inc.) receivers.

Digital data collection and processing

Two scenes of remotely sensed imagery (MSS and AVNIR-2) were acquired to provide both a past and a more recent land-cover map of the study area. A Landsat MSS image acquired on July 29, 1978, with a solar elevation of 57.71° and azimuth of 115.44° was

used to represent the study area with little crop damage by macaques in the late 1970s. An ALOS/AVNIR-2 image with a solar elevation of 59.00° and azimuth of 130.00° was acquired on August 12, 2007, to represent a more recent landscape composition that had experienced remarkable crop damage by macaques.

The 2007 AVNIR-2 image was geo-referenced using ERDAS IMAGINE 9.3 (ERDAS, Inc.) to the Universal Transverse Mercator (UTM) system with a root mean square error (RMSE) of 0.86 pixels. An image-to-image correction was applied to the 1978 MSS imagery with a RMSE of 0.73 pixels. The MSS imagery was re-sampled to match the 10-m pixel resolution of the AVNIR-2 scene. Shade caused by topographic relief can create serious obstacles to analysis of remote sensing data. A Minnaert topographic correction method was applied to offset topographic effects (Meyer et al., 1993). I used the digital number (hereafter DN) in an observation wavelength band and the normalized difference vegetation index (NDVI; Asrar, 1989), which shows vegetation quantity, to classify the land-cover of the study area. NDVI is defined as

$$NDVI = \frac{NIR - RED}{NIR + RED} \quad (1)$$

where *RED* and *NIR* are the digital numbers of the visible red and near-infrared bands, respectively.

Methods

Land-cover classification for 2007

Land-cover for 2007 was classified by object-oriented classification using AVNIR-2 data.

I used the commercial software eCognition ver. 4 (Definiens Imaging, Inc.) to conduct object-oriented multi-scale image analysis (Baatz and Schaepe, 2000). Segmentation represents the first step of any object-oriented classification. Through this segmentation technique, individual pixels are perceived as the initial regions. A region-growing procedure for segmentation was used for land-cover classification. In eCognition, the segmentation is a bottom-up region-merging technique, where the smallest object contains one pixel. In this process, adjacent pixels in image objects are totaled by considering spectral and shape features. This process stops when the smallest growth exceeds the threshold defined by the scale parameter (Benz et al., 2004). Segmentation with different scale parameters can be done to form a hierarchical network of image objects. In addition, the relationships of image objects defined at different scales can be used for classification (Conchedda et al., 2008; Mallinis et al., 2008). The segmentation analysis at fine and coarse scales is important in object-oriented image classification because extracted boundaries of the dominant objects occur at corresponding scales (Hall et al., 2004).

First, AVNIR-2 data were segmented into a homogeneous object. In the segmentation process, the object-amount feature and the object-form and -size features were used. The parameters were scale: 10, shape: 0.3, and compactness: 0.4. Next,

land-cover classification was implemented based on the image objects. In this study, in order to detect the environmental factors related to habitat selection, the land-cover classification was taken as the information about vegetation and human impact. I defined seven classes: broad-leaved, conifer, grassland, farmland, urban land, bare land, and water area. A classification and regression tree system (CART: Breiman et al., 1984) model was applied for land-cover classification using image object features that were the mean and standard deviance of the DN and NDVI (Fig. 2). The CART computations were conducted in R-2.8.1 (R Development Core Team, 2008). This method is a classification tree technique based on binary recursive splitting, which divides the data into homogeneous groups. For each split, the best predictor variables for assigning the observations to one of the child nodes can be determined using the Gini index (Breiman et al., 1984). The classification training data were extracted from the area in which land covering could be clearly checked using an aerial photograph from 2006 and field verification as reference data.

The accuracy of the land-cover map was assessed using an aerial photograph. I applied the Kappa coefficient and standard error for the accuracy assessment (Stehman and Czaplewski, 2003; Nusser and Klaas, 2003). The error matrix, Kappa coefficient, and standard error were computed using R-2.8.1 (R Development Core Team, 2008; Rossiter 2004). The overall accuracy was 91.8%, and the Kappa coefficient was 0.89 (Table 1). The standard error of each class was low. However, the reliability of the classification of

grassland and bare land was low, based on standard error. A total of 555 points were checked to calculate the accuracy of each class. Mallinis et al. (2008) reported that high-precision classification could be attained by combining object-oriented image classification and the CART method. My results confirm the same findings for land-cover mapping.

Land-cover classification for 1978

A 1978 land-cover map was derived for the change detection analysis. A simple comparison of past and present contains errors because of the differences between AVNIR-2 and MSS imagery in original spatial resolution. Specifically, the 80-m pixel size of the MSS sensor limited the delineation of small or narrow landscape patches, such as avalanche patches and riparian areas (Hansen et al., 2001). Therefore, to minimize the errors caused by differences in spatial resolution, only the changes from 1978 to 2007 were classified. Furthermore, the technique of overlaying the change areas onto the 2007 land-cover map was applied.

First, the NDVI composite image was prepared by stacking AVNIR-2 and MSS imagery. Using NDVI, the changes from vegetation areas to urban or bare land areas were represented. Due to the difference in intensity, when the change detection is performed, the part that did not originally change may be expressed as change (Yang and Lo, 2000). Therefore, it is necessary to correct the intensity. In this study, the correction of intensity

and change detection were extracted by applying principal component analysis (Awaya and Tanaka, 2003). In principal component analysis, the first principal component can be expected to show almost the same effect as the regression analysis (DN matching; Awaya and Tanaka, 1999), which is a radiometric correction technique like the pseudo-invariant target method (Hall et al., 1991). In addition, the second principal component is expressed as the change detection from a past to a more recent view (Fig. 3).

The threshold value was determined with the nearest-neighbor method for the second principal component imagery and was classified into the three classes: “NDVI plus,” “NDVI minus,” and “no change.” Then, only the changed area was masked to the MSS imagery, and the object-oriented image classification was applied for the masked area. In the segmentation of the MSS imagery, the parameters were scale: 4, shape: 0.3, and compactness: 0.4. The nearest-neighbor method was applied for land-cover classification, which considered seven classes, broad-leaved, conifer, grassland, farmland, urban land, bare land, and water areas, as the classification of the 2007 land-cover map. The image data were considered alongside the land-cover map, which showed little crop damage caused by Japanese macaques. The classification training data were extracted from the area for which land cover could be clearly checked using aerial photographs from 1975 as reference data.

The accuracy was assessed using an aerial photograph. The error matrix, Kappa coefficient, and standard error were computed from the classification results. The overall

accuracy was 88.7%, and the Kappa coefficient was 0.84 (Table 2). For the 2007 classification, the standard error of each class was low. However, the reliability of the classification of grass land, bare land, and water areas was low based on standard error. A total of 550 points were checked to calculate the accuracy of each class. The error produced from the resolution differences between satellite imagery could be reduced by applying change detection using principal component analysis and object-oriented image classification. This method was effective because land-cover changes occurred not in a pixel unit but in a fixed domain.

Comparison of spatial patterns in 1978 and 2007 land cover

The land-cover maps of 1978 and 2007 were compared to detect changes during the 29-year period. In the simple comparison of landscape composition in 1978 and 2007, a range was included in which Japanese macaques were not present. Therefore, the area within the forest and the landscape structure less than 300 m from the forest boundary, which is the main habitat for the macaques, was extracted, and the change in forest configuration from 1978 to 2007 was evaluated. Quantification and comparison of the spatial pattern of forest patches between time periods was conducted using landscape indices selected after considering recent forest fragmentation studies (Linke et al., 2009; Coops et al., 2010). I used FRAGSTATS 3.3 build 5 (McGarigal et al., 2002). I applied six landscape indices that represented the patch fragmentation: number of patches, edge

density, mean patch size, area-weighted mean patch size, mean shape index, and area-weighted mean shape index (McGarigal and Marks, 1995). Leitão et al., (2006) and Linke et al. (2009) suggested that patch-based metrics could have large bias and that area-weighted metrics may constrain the aspects of landscape structure that can be measured. In this study, I used patch-based metrics and area-weighted metrics to restrict the bias of each metric.

Statistical analysis

I analyzed habitat selection within home ranges of Japanese macaques. A use-availability approach was designed, which had the advantage of not assuming that some areas were never used by troops of Japanese macaques, in contrast to presence–absence models (Guisan and Zimmermann, 2000; Manly et al., 2002; Boyce et al., 2002; Martinez et al., 2003; Pearce and Boyce, 2006; Klar et al., 2008). In this study, my model design was categorized as sampling protocol A and sampling design I following Manly et al. (2002).

The location data comprised a total of 1,989 data points and were treated as habitat-use points by macaques. As a sample of availability, the same number of habitat use points was distributed within the home range, defined by the 100% minimum convex polygon (MCP) method. These random location data were treated as habitat availability points ($n = 1,989$). The use-availability data were divided into model training and verification data. Huberty's rule was used to determine the training data and verification

data (Huberty, 1994). On the basis of this rule, a verification ratio of 20% was determined (Boyce et al., 2002).

I considered habitat selection on the scale of each troop using environment variables. Johnson (1980) defined selection as “the process in which an animal actually chooses a resource or habitat.” Attempts to quantify selection as a function of environmental variables have led to the development of resource selection functions (Boyce and McDonald, 1999; Manly et al., 2002; Aarts et al., 2008). Habitat selection analysis was based on information–theoretic methods that included a priori specification and mathematical formulation of different hypotheses and their final confrontation rewarding for parsimony (Johnson and Omland, 2004). Environmental variables related to the habitat selection of Japanese macaques were selected using a deductive approach and expert knowledge (Table 3). I selected elevation (m), maximum snow depth (m), mean temperature in winter (°C), and distance to river (m) as topographical and meteorological factors (Honda, 2009). The ratio of broad-leaved deciduous forest, ratio of coniferous forest, ratio of grassland, distance to grass land (m), and amount of edge between broad-leaved deciduous forests and farmland (m) were selected as vegetation factors (Naughton-Treves et al., 1998; Agetsuma, 2007). As human-impact factors, the ratio of farmland, the ratio of urban land, distance to farmland, distance to urban land, and distance to road (m) were selected (Yamada and Muroyama, 2010; Honda, 2009). A 10-m-grid digital elevation model (DEM), a 1:25,000 digital map (Geographical Survey

Institute, 2002), a climatic data map (Meteorological Agency, 2000), and a land-cover map generated from remotely sensed data were employed for these variables. The ratios were calculated from a land-cover map within a 1000-m buffer of each point. The mean distance that Japanese macaques move in one day is 1000 m. The distance was calculated as the shortest distance between points and the environmental factors using ArcGIS 9.3 (ESRI, Inc.). Hawth's Analysis Tools (Beyer 2004) were used for the generation of random points.

I used the Random Forests method (Breiman et al., 2001), implemented in R (Liaw and Wiener, 2002), to examine the relationship between use-availability by macaques and each environmental variable. This approach combines many different trees based on bootstrap samples of the training data set. In a typical bootstrap sample, approximately 63% of the original observations occur at least once. Observations in the original data set that do not occur in a bootstrap sample are called out-of-bag observations. Random selection of variables is considered for the choice of splits in each node. This random selection diminishes correlation among the trees in the ensemble and keeps the bias low. Breiman (2001) proposed that the Random Forest approach rarely over-fits, and that this method provides efficient predictions with large numbers of independent variables. The out-of-bag observations were used to determine variable importance and an unbiased estimate of generalization error. I built 500 trees by default. The number of variables to randomly select was chosen to minimize the final regression error. In this

study, partial dependence plots (Hastie et al., 2001) were used to graphically characterize relationships between each predictor variable and predicted probabilities of species occurrence obtained from the Random Forest analysis.

I assessed predictive accuracy using the Receiver Operating Characteristic (ROC) Area Under the Curve (AUC), with AUC values of 0.9 and above representing high model accuracy, 0.7–0.9 indicating good model accuracy, and <0.7 showing low model accuracy (Swets, 1998). The cut-off probability for use-availability of Japanese macaques used the minimum absolute difference between sensitivity and specificity values (Liu et al., 2005). For the ROC curve, the ROCR library available in R was employed (Sing et al., 2005).

Extrapolation to the macro-scale of the model

To identify the occurrence which is the result of habitat selection of Japanese macaques, the optimal model was extrapolated to the land-cover map created from the 2007 AVNIR-2 imagery and the 1978 MSS imagery. I generated points at 50-m intervals within the study area and calculated the environmental factors at these points. The map of predicted occurrences, which is the habitat selection response for 2007 and 1978 consisting of 50 × 50-m grids, was created using the Random Forest results. Hawth's Analysis Tools (Beyer, 2004) were used for generating the 50-m individual points.

Results

Land-cover change in the study area

In the simple comparison of landscape composition in 1978 and 2007, a range was included in which Japanese macaques were not present. Therefore, the change in habitat configuration from 1978 to 2007 was evaluated using fragmentation analysis by comparing landscape indices (Table 4). The number of patches within macaque habitat decreased. The mean patch size and mean shape index increased over the 29-year study period. Edge density increased in forest and decreased in grassland, farmland, and urban areas. Area-weighted mean patch size increased in forest and grassland but decreased in farmland and urban areas. The area-weighted mean shape index decreased only in urban areas. Broad-leaved deciduous and coniferous forests showed similar tendencies toward forest fragmentation. However, the ratio of change in forest fragmentation differed.

Model selection and evaluation

The importance of predictor variables evaluated by the Random Forest model with out-of-bag samples is shown in Fig. 4. The measure of variable importance computes the total decrease in node impurities (Gini index) for each variable given by the splitting of the variable. Highly ranked variables were the ratio of coniferous forest, ratio of farmland, distance to farmland, and maximum snow depth. I checked the response curves between predicted values and highly ranked important variables using a partial dependence plot

(Fig. 5). When the ratio of coniferous forest showed a small area of coniferous forest, high predicted values were acquired. This tendency of partial dependence plot was also similar for the ratio of farmland and distance to farmland. The rate of farmland had the optimal range of 5% – 20%. The distance to farmland had the optimal range of 200m – 300m. For maximum snow depth, when snow coverage was increased, high predicted values were shown. The AUC was 0.96 for the Random Forest model, indicating that the habitat selection of Japanese macaques was predicted by the model with high precision.

Change in habitat selection of Japanese macaques

Potential maps of the occurrence, which is the result of habitat selection for 1978 and 2007 are shown in Fig. 6 (a), (b). To evaluate changes in the main habitats of Japanese macaques, these maps depicted only the forest region and areas less than 300 m from the forest boundary. From 1978 to 2007, habitat selection within the macaque habitat changed substantially (Fig. 6 (c)). The relation of the class probability of binary classification in 1978 and in 2007 is plotted in Fig. 6 (d). These figures show that the relative occurrence of Japanese macaques changed considerably from 1978 to 2007 as a result of changes in habitat selection. These changes are the result of changes in topography, meteorology, vegetation, and human impact within their habitat.

Discussion

Land-cover change analysis in 1978 and 2007

The fragmentation analysis showed decline in the coniferous forests in the study area. Results of the fragmentation analysis of the forest region indicated a similar tendency towards change in broad-leaved deciduous forests and coniferous forests. However, the amount of change was different. In particular, the ratios of change in edge density and area-weighted mean patch size were two times different between broad-leaved deciduous forests and coniferous forests. These results suggest that coniferous forest patches not only became smaller, but also became more similar in size during the 29-year period (Hansen et al., 2001; Linke et al., 2009). The reduction in the number of patches indicates that coniferous forest changed in relation to other landscape structures (e.g., broad-leaved deciduous forests). The analyses of areas in which past forestry activities have now been abandoned suggest that artificial plantations consisting of coniferous forest have changed to broad-leaved deciduous forest and/or broad-leaved and coniferous mixed forest. Therefore, the mean patch size of broad-leaved deciduous forest increased greatly. In grassland and farmland, as edge density decreased and mean-patch size increased, patches became larger and more connected. Conversely, large-scale patches disappeared from grassland as area-weighted mean patch size decreased. Similarly, with change in land use by agricultural development, area-weighted mean patch sizes increased in farmland (McGarigal and Marks, 1995). These results indicate that food resources for Japanese

macaques increased from 1978 to 2007. For urban areas, all landscape metrics except for the number of patches increased from 1978 to 2007, indicating that the population increased, as did the number of residences and city areas.

Model approach and habitat selection

Of the topographical and meteorological factors, maximum snow depth contributed to habitat selection because of the aforementioned adaptive ability of Japanese macaques. Japanese macaques can inhabit the highest latitudes among primates except for humans (Suzuki, 1965; Wada and Tokida, 1981). They can adapt to cold, snow coverage, and other conditions that are risky for other animals. My model represents features of the “snow monkey.” My model also shows that Japanese macaques prefer areas near farmland. This conclusion is supported by previous research (e.g., Naughton-Treves et al., 1998; Saj et al., 2001), which has shown similar results, further indicating that my results are reliable. Japanese macaques depend on crops as food resources (e.g., paddy rice, soybean, potato, and corn). However, when examining the ratio of farmland, it was not apparent that macaques selected areas with large amounts of farmland for food resources. Japanese macaques may choose a risky habitat to eat crops that are attractive food resources. On the other hand, coniferous forests are a risk factor for macaques. The Random Forest model indicated that the ratio of coniferous forests was the most important variable for habitat selection. Macaques may not use coniferous forests because of a lack of food resources

(Imaki et al., 2006). The results of my habitat-selection model, as well as from previous research, also suggest that Japanese macaques do not select large-scale coniferous forest patches.

Change in land-cover and habitat selection from 1978 to 2007

Over 29 years, coniferous forest and farmland have changed greatly in the Japanese macaque habitat (Table 4). My Random Forest modeling results indicated that coniferous forest was a risk factor, while farmland was an important food resource for macaques. The results suggest that forest influence and food resource configuration changes have direct effects on macaque habitat selection. Clear changes can be seen when comparing maps of relative occurrences of Japanese macaques in 1978 and 2007 (Fig. 6). The area in which the predicted value increased from 1978 to 2007 was related to the reduction in coniferous forest. The home range of Japanese macaques is thought to have increased with the decline in coniferous forest over the 29-year period. The relationship between the coniferous forest and the behavior of Japanese macaques has been previously studied (Izawa et al., 1985; Takizawa et al., 1999). These reports suggested that Japanese macaques inhabited the edge between forest and farmland due to the destruction of habitat that accompanied the expansion of coniferous forests. Crop damage by macaques increased in the late 1970s along with afforestation with artificial plantations of coniferous forest (Agetsuma, 2007). On the other hand, I suggest that the expansion of crop damage

in the 2007 resulted from a decline in coniferous forest. Forestry activities are rarely performed in the study area at present. The afforestation area that consists of a coniferous forest had not been managed. Therefore, the broad-leaved deciduous forest is mixed in the coniferous forest. This transition from coniferous forest to broad-leaved deciduous forest suggests that the cultivated species of broad-leaved deciduous forest spread from farmland areas and continues to grow (Kobayashi and Koike, 2010). This also suggests a decline in coniferous forest as a risk factor along the forest edge. Furthermore, the home range of macaques was expanded as a result of the reduction in the coniferous forest as a risk factor. Therefore, macaque troops were divided, and it is possible that they have become distributed over a wider area. This suggestion can also be inferred from the dotted area marking where predicted values increased in the habitat. The number of troops identified in the study area was 14–17 (troops for radio tracking = 12), and troop densities were estimated to be 0.04 to 0.05 troop/km². Compared with other areas, these numbers represent many troops and a high troop density (e.g., Shirakami region, Aomori Prefecture, eight troops with 0.03 troop/km²; Enari et al., 2006). This supports the idea that the macaque troops were divided and distributed in the study area. Moreover, macaques have also been influenced by the increase in farmland. From 1978 to 2007, the agricultural form changed greatly and, as a result, farmland became a large-scale food resource for Japanese macaques. The change in nutritional state resulting from consumption of agricultural products would also influence the expansion in macaque distribution. My results suggest

that the distribution of Japanese macaques has expanded due to changes of the spatial configuration of forests and food resources from 1978 to 2007. At the same time, human–wildlife conflicts have occurred due to the changes in Japanese macaque habitat.

In conclusion, my study demonstrates that changes in landscape configuration in Japanese macaque habitats are important for their distribution and resource selection. I strongly emphasize the necessity for forest management to reduce crop raiding. Forest management which harvests continuously without management abandonment is recommended. With suitable forest management, artificial plantations of coniferous forest can serve as a barrier to destructive behavior by Japanese macaques, according to the habitat model.

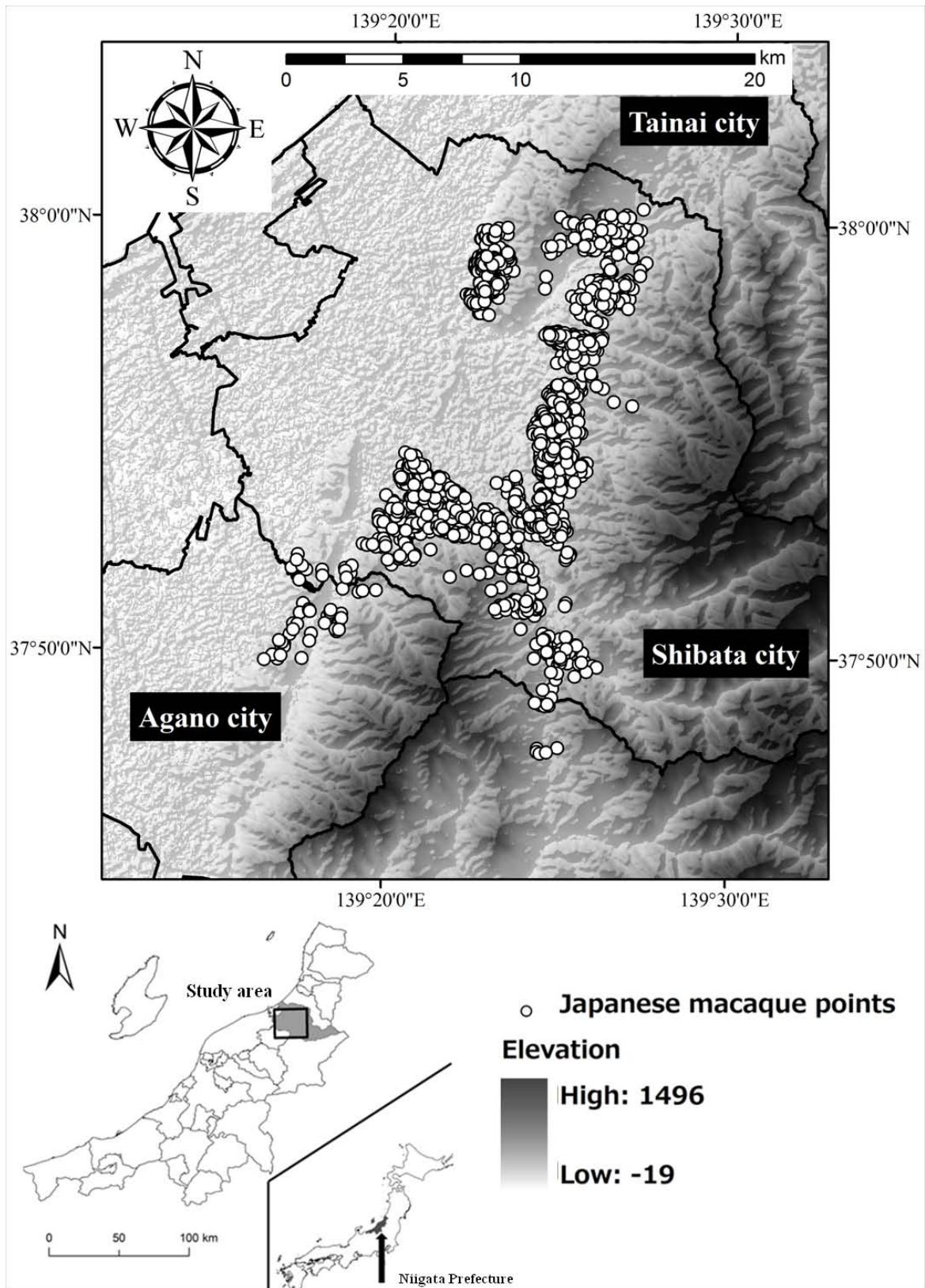


Figure 1. The study area and the location data of Japanese macaques using VHF- radio-tracking.

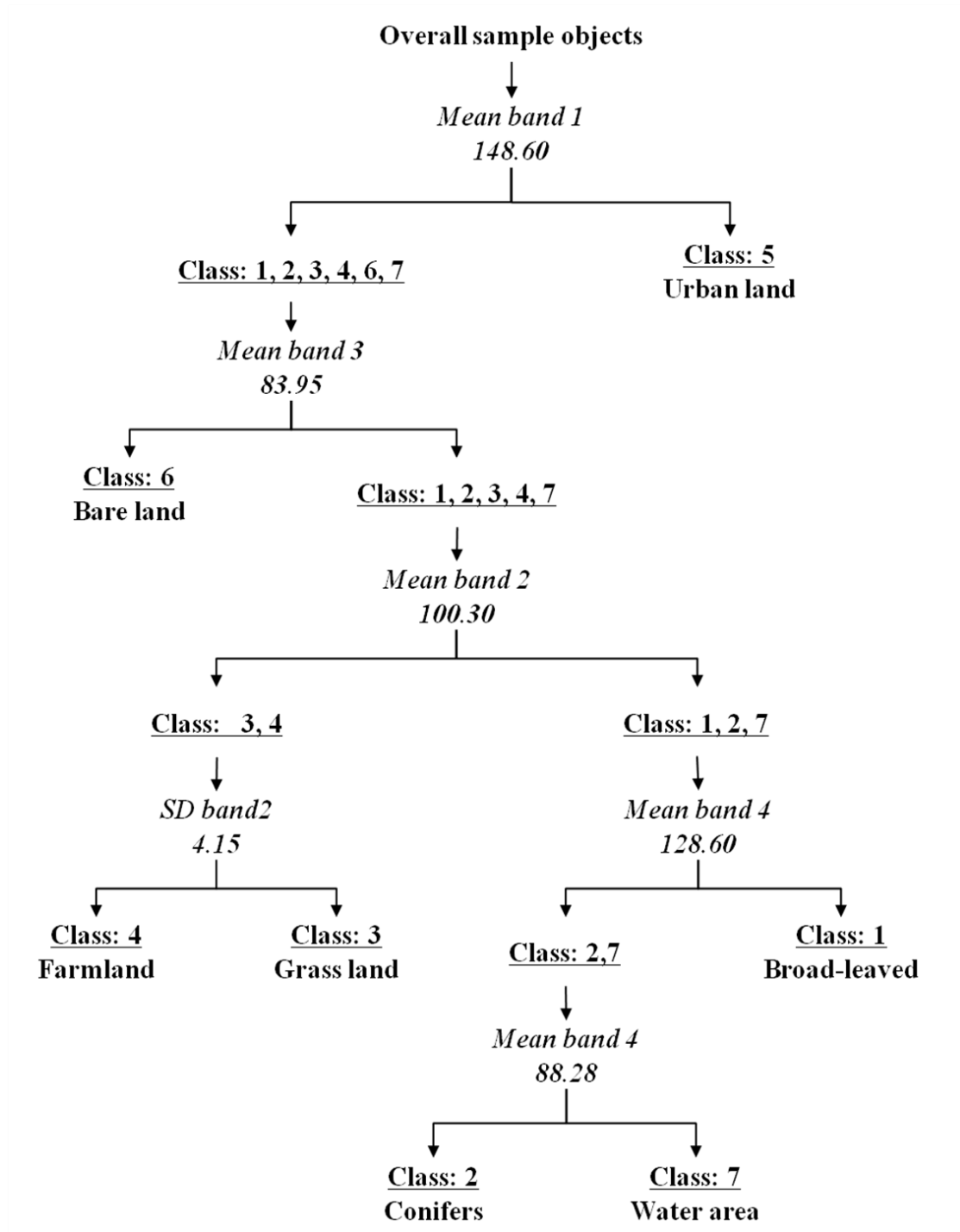


Figure 2. Optimal classification tree for the discrimination of the classification applied for AVNIR-2, 2007 data using CART. Mean band 1 to 4: The mean value of digital number in each image object. SD band 1 to 4: The standard deviation of digital number in each image object.

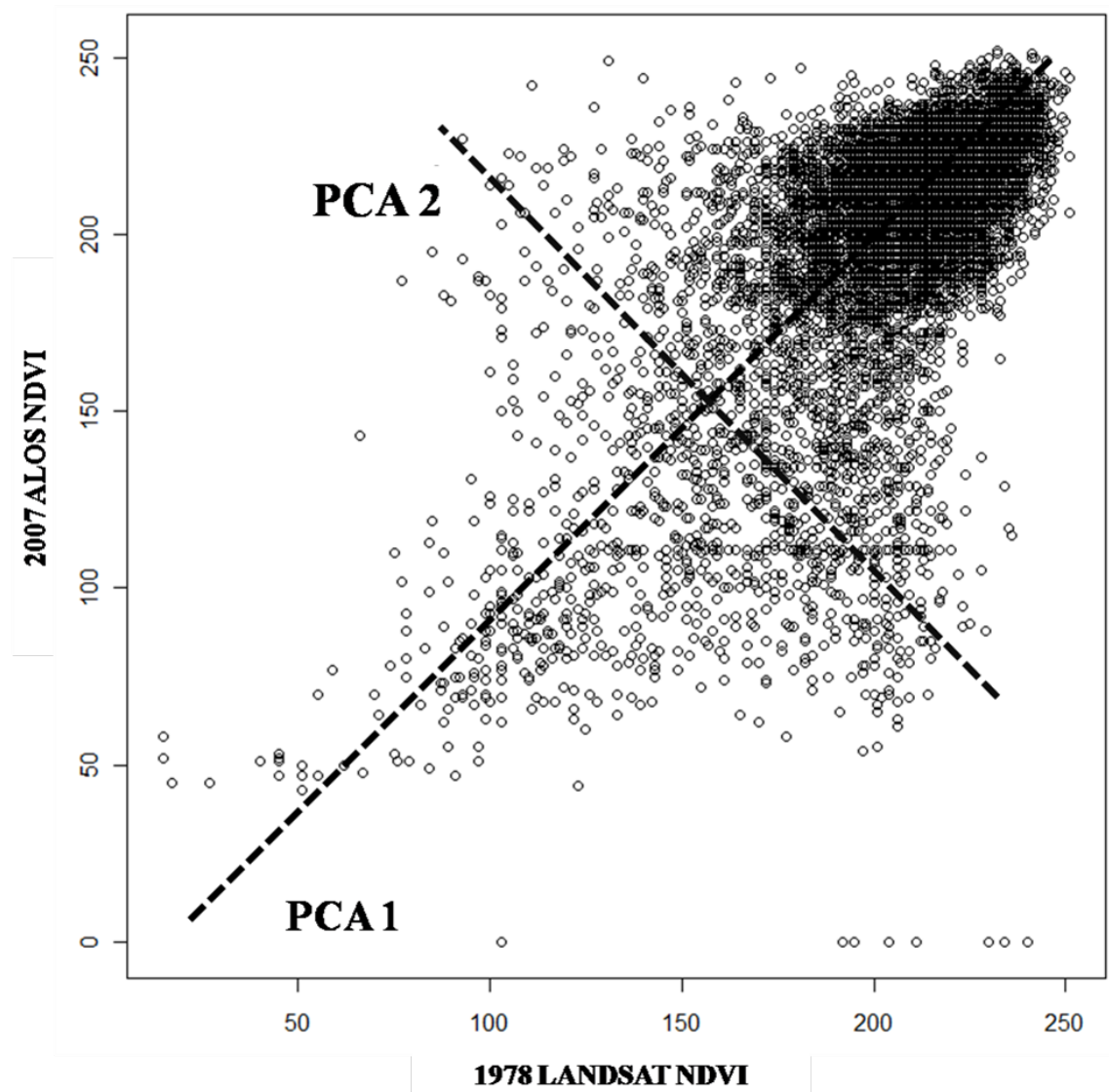


Figure 3. Principal Component Analysis applied for NDVI composite image. The first principal component (PCA1) means the correction of intensity and the second principal component (PCA2) means change detection of two periods in 1978 and 2007.

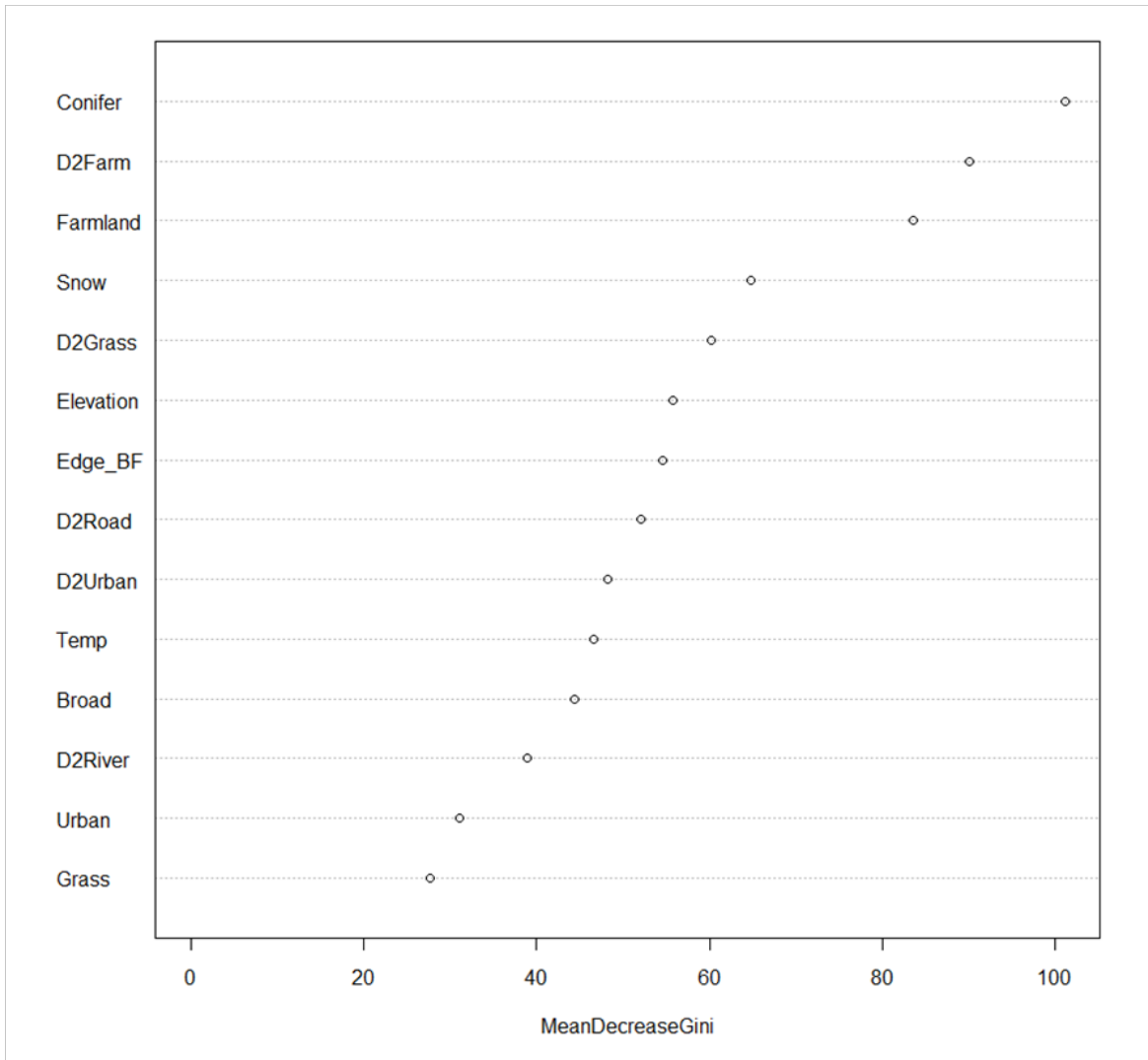


Figure 4. Variable importance plot for predictor variables from Random Forest classifications used for predicting the occurrence of Japanese macaques.

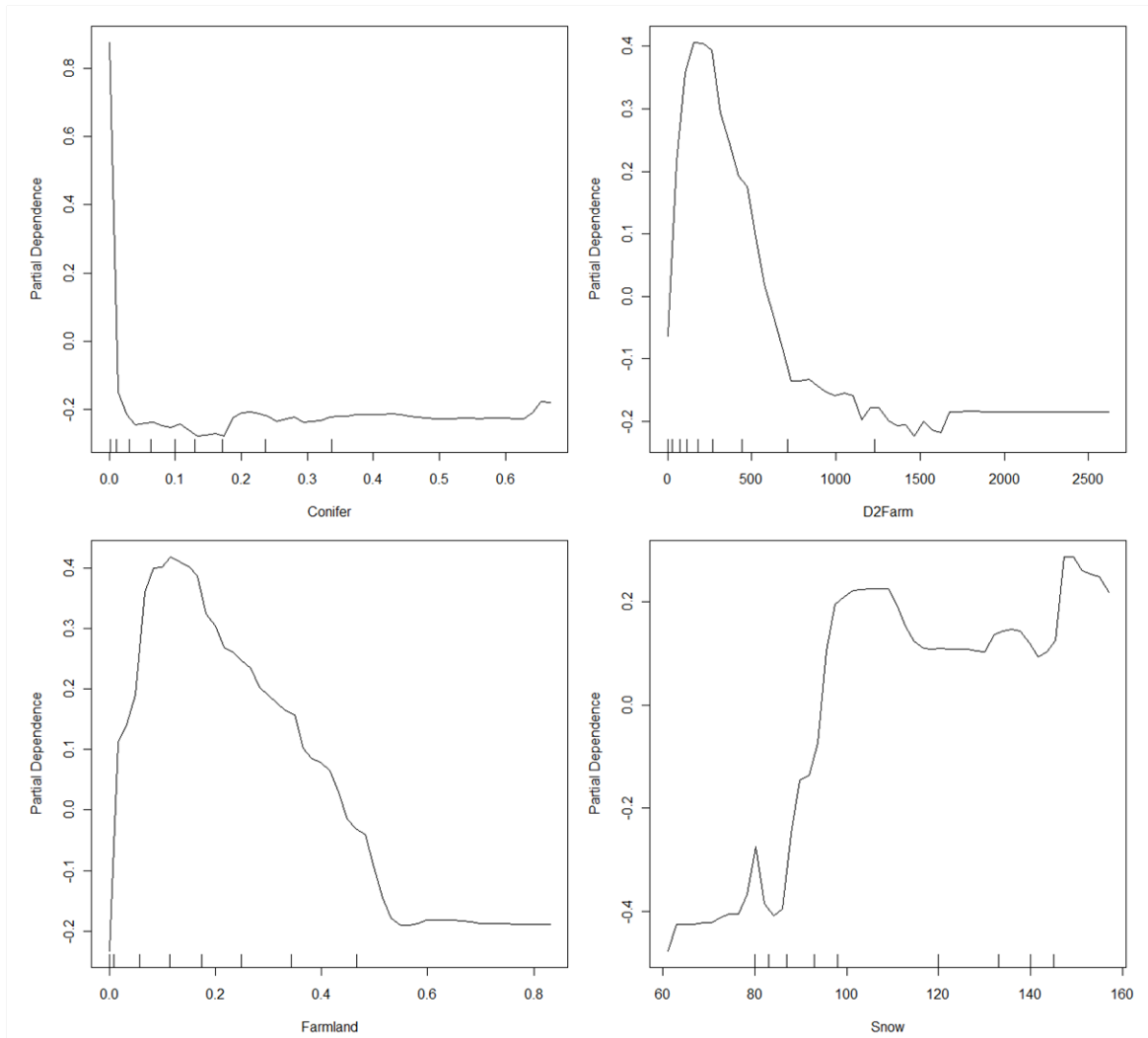


Figure 5. Partial dependence plots for high ranked predictor variables for Random Forest predictions of the occurrence of Japanese macaques. Partial dependence is the dependence of the probability of occurrence on one predictor variable after averaging out the effects of the other predictor variables in the model.

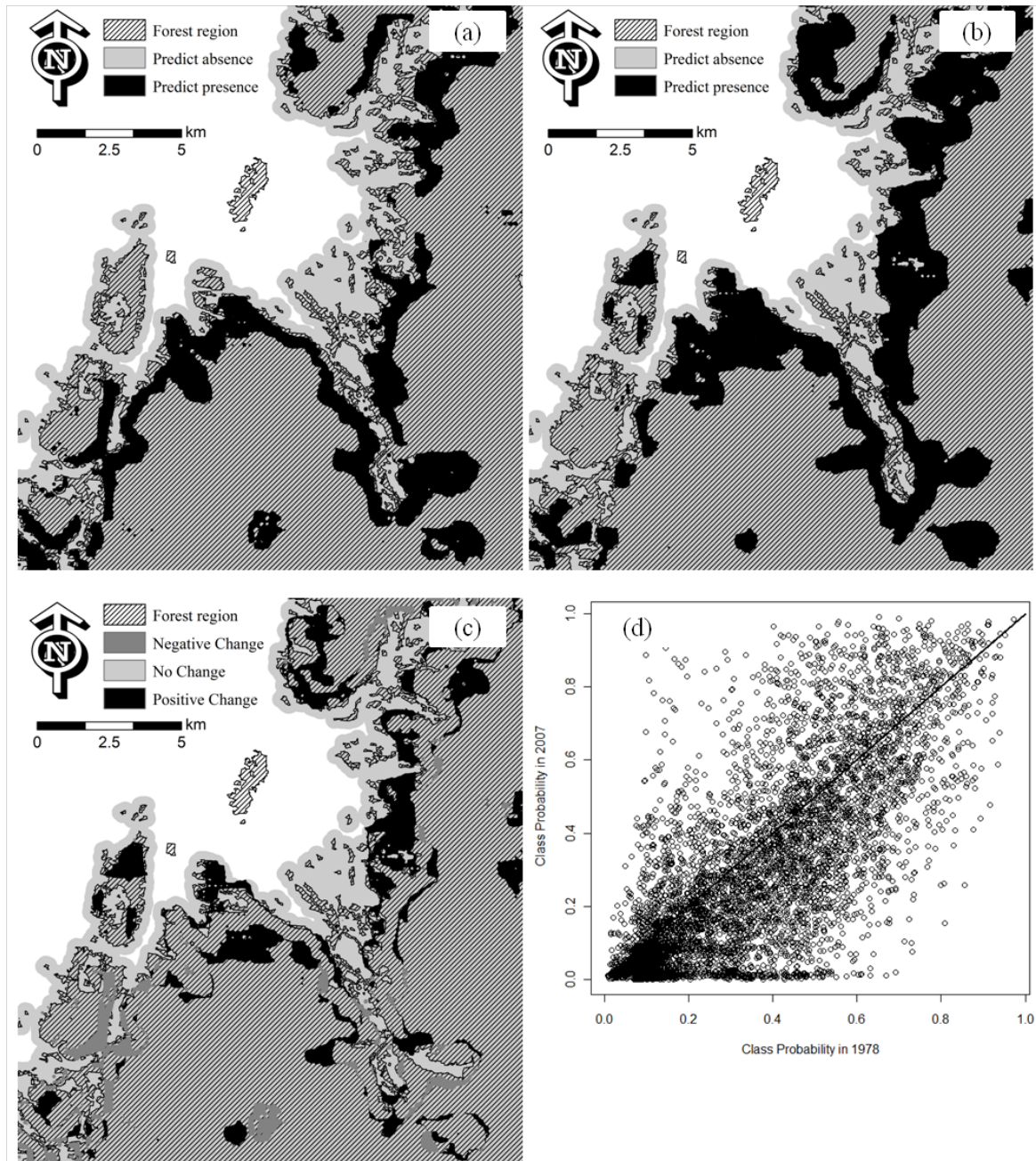


Figure 6. Evolution of the occurrence which is the result of habitat selection. The result of extrapolation in 1978 (a), and 2007 (b). Change in habitat selection of Japanese macaques from 1978 to 2007 (c). The plots of the class probability in 1978 and in 2007 (d).

Table 1. The classification accuracy and error matrix of the 2007 land-cover map.

	Broad	Conifer	Grass	Farm	Urban	Bare	Water	Row Total	Column Total	Producer's (%)	Standard error	User's (%)	Standard error
Broad	186	4	1	3	-	-	-	194	200	89.2	0.002	93.5	0.002
Conifer	6	54	1	1	-	-	-	62	60	88.7	0.006	85.5	0.005
Grass	5	2	16	8	-	-	-	31	20	78.8	0.020	49.8	0.017
Farm	3	-	2	188	-	-	-	193	200	90.8	0.001	95.9	0.002
Urban	-	-	-	-	36	5	-	41	40	89.2	0.009	86.8	0.008
Bare	-	-	-	-	4	15	-	19	20	74.1	0.022	78.2	0.023
Water	-	-	-	-	-	-	15	15	15	100	0.000	100	0.000

Overall accuracy=0.92, Kappa=0.88, 95 % confidence limits for kappa: 0.8569 ... 0.9202

Table 2. The classification accuracy and error matrix of the 1978 land-cover map.

	Broad	Conifer	Grass	Farm	Urban	Bare	Water	Row Total	Column Total	Producer's (%)	Standard error	User's (%)	Standard error
Broad	184	5	-	8	-	-	-	197	200	87.5	0.002	89.6	0.002
Conifer	9	62	3	5	-	-	-	79	70	86.7	0.006	75.3	0.005
Grass	3	3	14	8	-	1	-	29	20	68.3	0.021	46.3	0.020
Farm	4	-	2	176	-	2	1	185	200	81.9	0.002	92.4	0.002
Urban	-	-	-	2	28	2	-	32	30	92.9	0.011	86.8	0.009
Bare	-	-	1	1	2	10	-	14	15	65.8	0.032	70.6	0.033
Water	-	-	-	-	-	-	14	14	15	93.2	0.000	100	0.018

Overall accuracy=0.88, Kappa=0.84, 95 % confidence limits for kappa: 0.8071 ... 0.8809

Table 3. List of environmental variables and ranges of variable value considered in the analysis of habitat selection by Japanese macaques.

Variable	Description	Range	Mean \pm S.D	Mean \pm S.D
			Presence	Absence
<i>Topography and Meteorology</i>				
Elevation	Elevation (m)	8.5–366.1	82.1 \pm 39.1	105.1 \pm 62.1
Snow	Maximum snow depth (m)	0.6–2.1	1.4 \pm 0.4	1.3 \pm 0.4
Temp	Mean temperature in winter season ($^{\circ}$ C)	-2.2 – -10.5	-3.8 \pm 1.7	-4.1 \pm 1.9
D2River	Distance to river (m)	0.0 – 1346.2	362.9 \pm 215.9	361.6 \pm 243.8
<i>Vegetation</i>				
Broad	Ratio of broad-leaved in 1000m buffer of each point	0.0–100.0	58.1 \pm 20.7	60.6 \pm 26.9
Conifer	Ratio of conifers in 1000m buffer of each point	0.1–99.2	11.8 \pm 20.0	15.9 \pm 27.0
Grass	Ratio of grass land in 1000m buffer of each point	0.1–99.5	3.8 \pm 10.1	3.7 \pm 11.0

Table 3. Continued.

Variable	Description	Range	Mean \pm S.D	
			Presence	Absence
D2Grass	Distance to grass land (m)	0.0–2366.8	335.3 \pm 262.7	693.8 \pm 591.6
Edge_BF	Amount of edge between broad-leaved and farmland (m)	0.0–5528.7	1455.9 \pm 1079.7	925.6 \pm 1200.3
<i>Human-impact</i>				
Farm	Ratio of farmland in 1000m buffer of each point	0.0–93.5	10.5 \pm 10.3	10.5 \pm 21.8
Urban	Ratio of urban land in 1000m buffer of each point	0.0–82.5	9.0 \pm 4.0	8.0 \pm 5.0
D2Farm	Distance to farmland (m)	0.0–2620.1	216.5 \pm 238.4	606.2 \pm 665.5
D2Urban	Distance to urban land	0.0–3041.1	490.8 \pm 357.6	829.3 \pm 683.9
D2Road	Distance to road (>5m)	0.3–3808.2	581.1 \pm 428.1	760.6 \pm 0.88

Table 4. Change of land-cover in the Japanese macaque's habitat using fragmentation metrics.

	Broad leaved	Conifers	Grass	Farmland	Urban
<i>Number of patches</i>					
1978	331	444	428	333	283
2007	147	340	276	233	253
Change	-184	-104	-152	-100	-30
Ratio of change	-55.59	-23.42	-35.51	-30.03	-10.6
<i>Edge density</i>					
1978	37.67	21.62	12.27	22.46	3.66
2007	42.82	27.78	9.74	21.69	5.19
Change	5.15	6.16	-2.53	-0.77	1.53
Ratio of change	13.67	28.49	-20.62	-3.43	41.8
<i>Mean patch size</i>					
1978	49.84	6.98	2.22	11.14	0.72
2007	112.29	8.23	2.55	16.01	1.59
Change	62.45	1.25	0.33	4.87	0.87
Ratio of change	125.3	17.91	14.86	43.72	120.83

Table 4. Continued.

	Broad leaved	Conifers	Grass	Farmland	Urban
<i>Area-weighted mean patch size</i>					
1978	14273.6	90.89	21.78	465.07	5.99
2007	12258.2	44.76	17.26	666.88	7.56
Change	-2015.3	-46.13	-4.52	201.81	1.57
Ratio of change	-14.12	-50.75	-20.75	43.39	26.21
<i>Mean shape index</i>					
1978	1.46	1.36	1.45	1.58	1.28
2007	1.88	1.78	1.68	1.74	1.39
Change	0.42	0.42	0.23	0.16	0.11
Ratio of change	28.77	30.88	15.86	10.13	8.59
<i>Area-weighted mean shape index</i>					
1978	13.11	2.47	1.98	7.05	1.75
2007	14.94	2.82	2.27	7.94	1.73
Change	1.83	0.35	0.29	0.89	-0.02
Ratio of change	13.96	14.17	14.65	12.62	-1.14

Chapter 5

Scale dependency and functional responses
in resource selection by crop-raiding
Japanese macaques

Introduction

How an animal uses a habitat (e.g., for foraging, nesting, resting, moving) depends on the type of environment the animal is in (Johnson, 1980). Habitat selection is considered a multi-level hierarchical process where the patterns of selection are modulated by environmental factors such as the type of land-cover, configuration, and connection over specific spatial scales (Johnson, 1980; Orians and Wittenberger, 1991). It is an important function in animal ecology, and is frequently defined as behavioral adjustment to the heterogeneous distribution of landscape components (Johnson, 1980; Rosenweig, 1981; Boyce and McDonald, 1999). In habitat selection, four hierarchical orders based on different spatial scales of use are important: the geographic range of an animal species, the selection of a home range, the selection of resources within the home range, and the selection of food within a foraging patch (Johnson, 1980). The first two are usually based on broad features of the environment, and habitat use within a home range is decided by the resources that are most important at smaller spatial scales, such as food availability (Rettie and Messier, 2000). Hence, the scale of a home range is largely determined by foraging behavior (Morris, 1987). To manage wildlife ecosystems appropriately, it is important to understand the preferred foraging habitat of a species.

Resource selection functions (RSFs) can be applied to evaluate the influence of scale and heterogeneity on habitat selection. RSFs are defined as functions that are proportional to the probability of an animal using a given resource (Manly et al., 2002).

RSFs can be estimated by comparing the use of a resource in a landscape structure to the overall resource availability (Boyce et al., 2003). Furthermore, the link between an animal's behavioral mechanisms and environmental factors can be evaluated from functional responses (Mauritzen et al., 2003; Gillies et al., 2006; Godvik et al., 2009). Landscape structure generally refers to the scale effect, defined in terms of grain and extent (Turner et al., 2001). Grain is the minimum resolution of the data, defined as the cell size of landscape distribution. Extent is the domain of the data, defined as the size of the area used by an animal, the overall study area, or a particular landscape type. In wildlife studies, grain and extent may be defined as the finest spatial scale of habitat heterogeneity to which an organism responds (Kotliar and Wiens, 1990; Thompson and McGarigal, 2002). Therefore, hierarchal habitat selection is thought to be a solution to cope with spatial heterogeneity in resource availability (Levins, 1968). The hierarchical process of habitat selection suggests that different environmental factors determine habitat selection at different spatial scales (Kie et al., 2002). Even within a home range, the ecological relevance of environmental factors such as the type of land-cover, configuration, and connection has heterogeneity. Animals may use different areas within their home ranges for different behaviors due to the spatial distribution of different resources (Marzluff et al., 2001; Indermaur et al., 2009). To ensure suitable wildlife management or conservation strategies at the home range level, an understanding of hierarchical habitat selection within that range is necessary.

Risk management for human–wildlife conflicts is an urgent issue worldwide (Conover, 2002). In Japan, crop damage caused by Japanese macaques is significant, and they forage on several crops including rice, corn, and soybean (Mochizuki and Murakami, 2011a). Conflicts caused by Japanese macaques have become serious, amounting to 1 500 million yen (15 million US dollars) (Ministry of Agriculture, Forestry and Fisheries, 2009). Japanese macaques live the farthest north of any nonhuman primate species (range 30°21'–41°08'N) and utilize various habitat types, such as cool-temperature deciduous forests, warm-temperature evergreen forests, and human settlements, including farmland (Suzuki, 1965; Wada and Tokida, 1981; Yamada and Muroyama, 2010). It is known worldwide as the snow monkey. The behavior of macaques is quite varied and depends on the regional environment. Therefore, understanding and managing the ecology of Japanese macaques for every region is important. Crop raiding is one aspect of habitat usage, and is the result of resource selection. Therefore, it is important to consider the hierarchical process of resource selection over multi-spatial scales when preparing suitable management plans. Effective management, based on resource selection by crop-raiding Japanese macaques, is necessary for the successful risk management of human–wildlife conflicts in this region.

I investigated the effects of scale on RSFs by crop-raiding Japanese macaques. Changes in the spatial extent of the home ranges of 13 macaque troops were evaluated after estimating home ranges based on radio tracking data collected during 2008–2009.

Then I compared the proportional use of crops with the proportional availability of crops, within each troop's home range to determine the relative foraging selection of the macaques. Buffers around the crop damaged/non-damaged locations were used to determine the proportional use/availability of resources. Six buffer sizes (100, 500, 1000, 1500, 2000, and 2500 m) were applied, and I made comparisons using RSFs across all six spatial extents. When evaluating scale dependency, I compared a typical risk map of crop damage to a multi-scale gradient map of the risk probability of crop damage. Based on my results, I propose that a suitable strategy for wildlife management within existing landscape ecology conditions can be determined using a multi-scale gradient map.

Materials and Methods

Study area

The study area was Shibata City, Niigata Prefecture, Japan (37°57'N, 139°19'E, 532 km², Fig. 1). The population density was about 190 inhabitants per km² in 2009. The elevation ranged from -19 to 1496 m above sea level. The forest cover of the study area was 64% and was composed mostly of secondary forest dominated by oak (*Quercus* L.) and conifer plantations of Japanese cedar (*Cryptomeria japonica*) and Japanese red pine (*Pinus* L.). The mean annual temperature in the region is 12.5°C, the mean annual precipitation is 1109 mm, and the maximum snow depth is 950 mm (snowfall typically occurs during December–March).

Crops in this region have been damaged by macaques since the late 1970s (Agetsuma, 2007), and the area affected has gradually expanded. An investigation in Shibata City revealed the presence of 14–17 troops that included a total of up to 700–800 individual Japanese macaques. Troops have been radio-tracked since 2004 by the hunters association in Shibata City. As of 2012, 13 troops of crop-raiding Japanese macaques have been monitored. The monitoring is performed from May to November when crop damage by Japanese macaques is most serious. The intensity of crop damage is increasing, and the risk of life-threatening injuries through home invasion has become a concern. Annual crop damage fluctuates but costs approach 15 million yen on average in Shibata city, Niigata Prefecture (Mochizuki and Murakami, 2011a). The main crops

raided by Japanese macaques are rice (*Oryza sativa*), soybean (*Glycine max*), potato (*Solanum tuberosum* L.), and corn (*Zea mays* L.).

Data collection: Crop damage and the home range of Japanese macaques

I tracked Japanese macaques from May to November, which is the season of maximum crop damage, in 2008 and 2009. Thirteen troops of crop-raiding Japanese macaques were studied. The information gathered included location data obtained by VHF radio-tracking, a method widely used for tracking wildlife. The location data were acquired by six-element Yagi antennae and receivers, which received signals from transmitters attached to individual macaques. The antennae have strong directionality and are often used with animals whose native habitat makes direct observation difficult (White and Garrott, 1990). Two location points per day for each of the 13 troops were acquired. The estimated radio-tracking error was 100 m. I used LT-01 (Circuit Design, Inc.) transmitters and IC-R20 (Icom, Inc.) receivers.

Using the location data of the Japanese macaques, home range sizes were estimated using the 100% minimum convex polygon method (100% MCP: Mohr, 1947) with a geospatial modeling environment (GME: Beyer, 2011) in ArcGIS 10 (ESRI Inc.). There are many methods for estimating home ranges, including MCP (Mohr, 1947), grid cell count (Siniff and Tester, 1965), fixed and adaptive kernels (Worton, 1995), and

others. I used MCP because it can produce more accurate estimations than the kernel method when there are fewer than 200 location points (Boyle et al., 2009). The estimated home ranges are presented in Table 1.

I surveyed the damage to crops by Japanese macaques during harvest season (from July to September in 2008, 2009, and 2010) at the home range scale. If I had targeted all of the cropland in Shibata City, by including areas where the radio-tracked Japanese macaques were not present, despite the presence of suitable habitat, I would not have been able to appropriately evaluate the factors most associated with crop damage. In the field surveys of 2008 and 2009, the cropland raided by Japanese macaques was recorded for all locations in Shibata City. There were a total of 312 crop damage events that occurred within home ranges (Fig. 1). To detect the undamaged area, I used pseudo absence points, which were generated randomly within each home range. These random location data points were treated as sampling sites for undamaged cropland ($n = 312$). The absence of any crop damage in these pseudo absence points was verified by a field survey in 2010. I confirmed that the crop-raiding Japanese macaques did not raid the pseudo absence points. The data for the sites of occurrence and absence of crop damage (total number = 624) were applied to model training data. As model verification data, a total of 200 data points from damaged and undamaged crops were acquired in a field survey during 2010. In this survey, I recorded each location using a handheld GPS unit (Garmin GPSMAP 60Cx, Garmin Inc.).

Geo-information: Land cover, Topography, and Countermeasures

A digital land cover map was used to determine the environmental variables associated with crop damage. This map was created from satellite data captured on 12 August 2007 (ALOS/AVNIR-2 with 10 m grid spatial resolution). For land cover classification, the object-oriented image classification and the classification and regression tree method were combined (see details: Mochizuki and Murakami, 2011a). This map consisted of seven classes: broad-leaved deciduous forest, coniferous forest, grassland, cropland, urban area, bare land, and water area. The accuracy of the land-cover map was assessed using an aerial photograph captured in 2006. The overall accuracy was 91.8%, and the Kappa coefficient was 0.89. Because the land cover map was of high-precision, it was suitable for the statistical analysis of RSFs.

Streams were detected from the digital elevation model (DEM: 10 m grid spatial resolution), which can be used to identify streams at a regional scale of 1:25,000 with the hydrology tool in the spatial analyst extension of ArcGIS 10. In this study, the water area on the land cover map and the streams identified from the DEM were combined and defined as river area within each home range. The road network was identified from a 1:25 000 digital map, which provided a spatial data framework (Geographical Survey Institute). Only roads more than 5 m wide were recorded because smaller roads are not considered to hinder the movement of Japanese macaques (Mochizuki and Murakami, 2011b).

I also surveyed fences and alarms, which are used as countermeasures for crop damage. For fencing, I recorded corrugated iron, net, fishnet, and wire mesh fences. Although electric fences have an effect on damage control, no croplands were protected by an electric fence in the study area. Alarm equipment is often used for damage control by sounding an alarm when Japanese macaques approach cropland. I recorded the spatial configuration of these two types of countermeasures (fencing and alarms) within each home range.

Environmental variables across multiple spatial extents

To evaluate the scale dependency of RSFs for Japanese macaques, a multiple scale analysis was employed. I focused on the changes in spatial extent of the macaques' home ranges. Multiple buffers were generated from the occurrence and absence of crop damage data, and the environmental variables were measured. Each buffer was generated from the center of the occurrence and absence of crop damage data points (The diagram of each spatial extent for the buffer analysis: Appendix A, Fig. A.1). Environmental variables related to the occurrence of crop damage were selected using a deductive approach and expert knowledge (e.g., Naughton-Treves et al., 1998; Agetsuma, 2007; Honda, 2009; Yamada and Muroyama, 2010; Mochizuki and Murakami, 2011a). To explain the RSFs, 16 environmental variables associated with crop damage were applied (full list of variables in Appendix A, Table A.1): the ratio of broad-leaved deciduous

forests (BROAD), the ratio of coniferous forests (CONIFER), the ratio of grassland (GRASS), the ratio of urban area (URBAN), the shape index of forest edge (SHAPE), the minimum distance to forest edge (D2FOREST), the minimum distance to broad-leaved deciduous forests (D2BROAD), the minimum distance to coniferous forests (D2CONIFER), the minimum distance to grassland (D2GRASS), the minimum distance to urban area (D2URBAN), the minimum distance to water areas including streams (D2WATER), the minimum distance to roads more than 5 m wide (D2ROAD), the minimum distance to fences (D2CM1), the minimum distance to alarms (D2CM2), the number of fences (CM1), and the number of alarms (CM2). The ratios were calculated from a land-cover map within multiple buffers of each point. Because I did not use the ratio of bare land and water area as an environmental variable, the summary of the ratio of land cover adopted was less than 100%. The shape of the forest edge was calculated from forest coverage using FRAGSTATS ver. 3.3, which is standalone software for measuring landscape patterns (McGarigal et al., 2002). The distances were calculated as the shortest distance between each point and the geo-information using GIS software.

RSFs with Random Forests algorithm

I analyzed the habitat selection of crop-dependent Japanese macaques within six home range scales. A use-availability approach was used instead of presence-absence models (Guisan and Zimmermann, 2000; Manly et al., 2002; Boyce et al., 2002; Pearce and

Boyce, 2006), to allow for the possibility that some areas were never used by troops of Japanese macaques. My model design was categorized as sampling protocol B and sampling design I, following Manly et al. (2002). The occurrence and absence of crop damage data were used as the independent variables, and the 16 environmental variables were used as the explanatory variables in the RSFs. I assumed that the occurrence and absence of crop damage data were spatially independent because the values of Moran's I for the distribution of crop damage were low ($I > |0.2|$). I assumed that there were no spatial autocorrelations between each cell as in previous studies (e.g., van Langevelde and Wynhoff, 2009). There were no significant correlations among environmental variables ($r < 0.6$).

Random Forests (RF) classification (Breiman, 2001), implemented in R (Liaw and Wiener, 2002), was applied to examine the relationship between use-availability by Japanese macaques and each environmental variable. This approach combines many different trees based on bootstrap samples of the training data set. In training, the RF classification algorithm creates multiple trees, each trained on a bootstrapped sample of the training data. In a typical bootstrap sample, approximately 63% of the original observations occur at least once. Observations in the original data set that do not occur in a bootstrap sample are called out-of-bag observations. Random selection of variables is considered for the choice of splits in each node. Then it searches only across a randomly selected subset of input variables to determine a split. This random selection diminishes

correlation among the trees in the ensemble and keeps the bias low. Breiman (2001) proposed that the RF approach rarely over-fits, and provides efficient predictions with large numbers of independent variables. The out-of-bag observations were used to determine variable importance and an unbiased estimate of generalization error. I built 500 trees by default. The number of randomly selected variables was chosen to minimize the final regression error. I performed RF classification at every spatial extent (100, 500, 1000, 1500, 2000, and 2500 m) and evaluated the variables importance and functional response curve. In this study, variable importance plot (Breiman, 2001) was used to show which variables are important. Furthermore, partial dependence plots (Hastie et al., 2001) were used to graphically characterize relationships between each predictor variable and the predicted probabilities of the occurrence of crop damage obtained from the RF analysis as a functional response by Japanese macaques.

I assessed predictive accuracy using the receiver operating characteristic (ROC) area under the curve (AUC), with AUC values of 0.9 and above indicating high model accuracy, 0.7–0.9 indicating good model accuracy, and <0.7 indicating low model accuracy (Swets, 1988). I calculated mean bootstrap AUC scores and 95% bootstrap (B = 10 000) confidence intervals using the verification data (n=200) recorded in the 2010 field survey. The cut-off probability for the occurrence and absence of crop damage by Japanese macaques was based on the minimum absolute difference between sensitivity and specificity values (Liu et al., 2005). For the ROC curve, the ROCR library available

in R was employed (Sing et al., 2005). All statistical analyses were conducted using the statistics package R version 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria).

Risk map with multi-scale gradient

To identify the risk of crop damage resulting from habitat selection of Japanese macaques, the models using each home range scale were extrapolated to every division of cropland in Shibata City. I generated points at the center of all cropland within the study area, and calculated the environmental factors at these points. Evaluating one against the other in terms of the amounts and patterns of quality habitat would yield drastically different results (Cushman et al., 2010). Hence, I compared a typical categorical representation of crop damage to a multi-scale gradient representation to evaluate the scale dependency on a predictive risk map of crop damage by Japanese macaques. A binary map that predicted the occurrence/absence of crop damage at the optimal spatial extent of each home range was used as the typical categorical representation. For multi-scale gradient representation, I added the prediction probability of all spatial extents to a binary map with the optimal spatial extent.

Results

Suitable spatial extent and environmental variables for crop damage prediction

The optimum spatial extent for predicting crop damage was the 1000 m buffer size, which produced the highest AUC values ($AUC > 0.85$, Fig. 2). The 100 and 500 m buffer sizes were unsuitable ($AUC < 0.8$). The other spatial extents tested (1500, 2000, 2500 m buffer size) had comparatively higher AUC values ($AUC > 0.8$). The importance of the environmental variables differed according to the spatial extent. For example, SHAPE was more important at smaller spatial extents (100 and 500 m) than at larger ones, whereas D2URBAN was more important at the largest spatial extents. At the optimal 1000 m buffer size, the important environmental variables included BROAD, CONIFER, GRASS, D2URBAN, and others shown in Fig. 3. In general, environmental variables related to landscape structure, including the influence of human disturbance on forest configuration, became increasingly important with an increase in spatial extent. Interestingly, countermeasures such as fences and alarms did not contribute to the habitat selection of the crop-raiding Japanese macaques, suggesting that these countermeasures are not very effective.

I also evaluated the functional responses between the occurrence of crop damage and environmental variables associated with the crop-raiding Japanese macaques. The top five environmental variables were detected from the model predictions for each

spatial extent (Fig. 4). At the 100 m buffer size, the BROAD variable was positively correlated with the prediction of crop damage. The prediction probabilities of D2FOREST and D2BROAD were high at 60 to 100 m. The response of the SHAPE variable at 100 m buffer indicated a high probability of crop damage at middle spatial extents. At 500 m, BROAD and SHAPE had the same tendencies as they did at 100 m, whereas CONIFER had a positive correlation and URBAN had a negative correlation. At 1000 m, BROAD and CONIFER both had a positive correlation, GRASS had a negative correlation, and the damage probability of D2URBAN increased with distance from urban areas. In general, the damage probability was lower when there was a low ratio of grassland. The functional responses at 1500 m showed the same tendencies as those at 1000 m. At 2000 m, CONIFER, D2CONIFER, and BROAD had positive correlations, whereas D2URBAN had a negative correlation. The functional responses at 2500 m showed the same tendencies for CONIFER, D2CONIFER, and D2URBAN as those at 2000 m buffer, whereas D2FOREST had a positive correlation. At both 2000 and 2500 m, the damage probabilities of D2CONIFER and D2FOREST were higher in regions closer to forest.

Binary and multi-scale gradient map of crop damage prediction

Risk maps of crop damage by the Japanese macaques extrapolated using the models of RF classification were shown in Fig. 5. The binary map was created using the

optimal spatial extent (1000 m buffer size), and predicted 60.5% undamaged area and 39.5% damaged area. Then a multi-scale gradient map was created using all spatial extents and reflecting the degree of scale dependency of the crop-raiding Japanese macaques. The area where the influence of spatial extent was determined to be small was limited in the study area as a whole, indicating that prediction of crop raiding is substantially affected by spatial scale dependency. The only area that was not influenced by scale was a complex forest located far from the urban area.

Discussion

Scale dependency and functional response of the Japanese macaques

The accuracies of predicted crop damage using the RF classification differed by spatial extent, where larger extents were generally more accurate (Fig. 2). The optimum spatial extent was 1000 m buffer size. Larger spatial extents also had high prediction accuracies, whereas the 100 and 500 m scales did not. These results suggest that middle or large spatial extents may be important in the habitat selection of Japanese macaques. Some studies have suggested a relationship between an animal's resource selection and its home range size (Hansen et al., 2009; Gehrt et al., 2009; Herfindal et al., 2009), and that resource selection is influenced by landscape heterogeneity such as vegetation cover, forest configuration, and prey abundance at a defined spatial scale (Johnson, 1980). Heterogeneity of resources is fundamental to variation in resource selection amongst different spatial scales. At the extreme, selection cannot occur in a homogeneous landscape (Boyce et al., 2003). Therefore, at small spatial extents, such as the 100 or 500 m buffer sizes, where it is difficult to detect landscape heterogeneity, defining the spatial extent of the home range level (which consists of various landscape structures) is necessary. My results also demonstrate the importance of linking resource selection to the home range size. To evaluate the RSFs of the Japanese macaques, the landscape heterogeneity within the spatial extent of the 1000 m buffer size has to be taken into

consideration.

The environmental factors that are generally associated with habitat selection by Japanese macaques are those associated with broad-leaved deciduous forests and coniferous forests (Imaki et al., 2006; Yamada and Muroyama, 2010). Human populations (i.e., the factor of human disturbance) are usually avoided by the macaques (Mochizuki and Murakami, 2011b). My results for the RSFs also suggest that forest configuration and distance to human disturbance are limiting factors for resource selection by Japanese macaques. One of the advantages of using RSFs is that they can be constructed using environmental variables over a variety of scales, and availabilities can be evaluated at multiple spatial scales (Boyce et al., 2003). I observed that the ratio of the broad-leaved deciduous forests and the coniferous forests, and the distance to urban areas in the buffer were the important variables in my models for almost all spatial extents studied. However, the importance of environmental variables depended on the spatial extent analyzed. For example, at small spatial extents, the shape of the forest edge contributed to damage prediction as much as did forest configuration. Because at smaller spatial extents, the landscape structure is more homogeneous (Boyce et al., 2003), variables such as fragmented forest edges become important. In the complicated edge environment, Japanese macaques may easily access cropland. At intermediate spatial extents, the ratio of grassland was related to crop damage by Japanese macaques. Grassland mainly exists between forest regions and croplands and functions as a buffer

zone for crop-raiding Japanese macaques. Local governments are promoting the maintenance of such buffer zones as a countermeasure against raiding macaques. My results support the potential effectiveness of such an initiative. At larger spatial extents, the influence of human disturbance was greater. Usually, human disturbance is a limiting factor on the behavior of wildlife (Gehrt et al., 2009; Godvik et al., 2009). However, in the present study, the distance to an urban area, rather than the ratio of an urban area, functioned as the limiting factor on the RSFs of the macaques. Rather than the rate of human disturbance occupied to the habitat of Japanese macaques, the distance to human disturbance may directly influence the resource selection. My results also indicated that countermeasures such as fences and alarms are ineffective in the study area. To reduce crop damage by the macaques in this area, it may be necessary to reevaluate and revise the use of these countermeasures.

I also evaluated the functional responses associated with crop damage in terms of environmental factors. The trends in responses of the environmental factors were not differed among the gradation of spatial extents. It means the functional responses in RSFs by crop-raiding Japanese macaques were not influenced, although the scale differences with the spatial extents were influenced to the importance of environmental variables in RSFs. Using the functional responses associated with each environmental variable, critical threshold can be defined for the occurrence of crop damage. The probability of crop damage was high when the area ratio of broad-leaved deciduous

forest was more than 60% and that of coniferous forest was more than 10% in all model predictions. This indicates that broad-leaved deciduous forests are the main habitats of Japanese macaques. Japanese macaques may not prefer coniferous forests because of a lack of food resources (Imaki et al., 2006; Mochizuki and Murakami, 2011a). Therefore, the threshold for damage occurrence associated with coniferous forest might be low. However, coniferous forests in the study area function as corridors, which connect main habitats and foraging sites, including croplands. The landscape structures of corridors are important factors for resource selection by wildlife. In the present study, crop damage also occurred when the distance to the urban area was more than 500 m in all models. Other thresholds for crop damage in the functional responses were constant regardless of spatial scale. Clarifying the critical thresholds for every environmental factor could aid landscape management for crop protection.

Binary and multi-scale gradient maps for crop damage prediction

Comparing binary and multi-scale gradient maps can be useful for wildlife management (Cushman et al 2010). In the present study, the binary map represents the predictive occurrence of crop damage using the optimal home range spatial extent of 1000 m buffer size for accurate prediction of crop raiding. The multi-scale gradient map represents the average value of the predicted probability of crop damage over all spatial extents (100, 500, 1000, 1500, 2000, and 2500 m buffer sizes; Fig. 5). Comparing the two maps

reveals that the binary map systematically overestimated the probability of crop damage and underestimated the lack of damage, which is a general property of the representation of the prediction (Cushman et al., 2010). It has important implications for assessing effects over multiple spatial scales.

In conclusion, the results of the present study suggest that scale dependency is important in the RSFs of wildlife, such as Japanese macaques. Therefore, in wildlife management, it is necessary to detect differences in resource selection among different spatial scales, and manage habitats at these scales, which will lead to more effective countermeasures for crop protection. In particular, my results show that, at small spatial extents including the individual scale, edge environments are very important. At intermediate spatial extents including the home range scale, grasslands that serve as buffer zones are important. At large spatial extents including the population scale, the planning of land use modification is necessary for appropriate wildlife management.

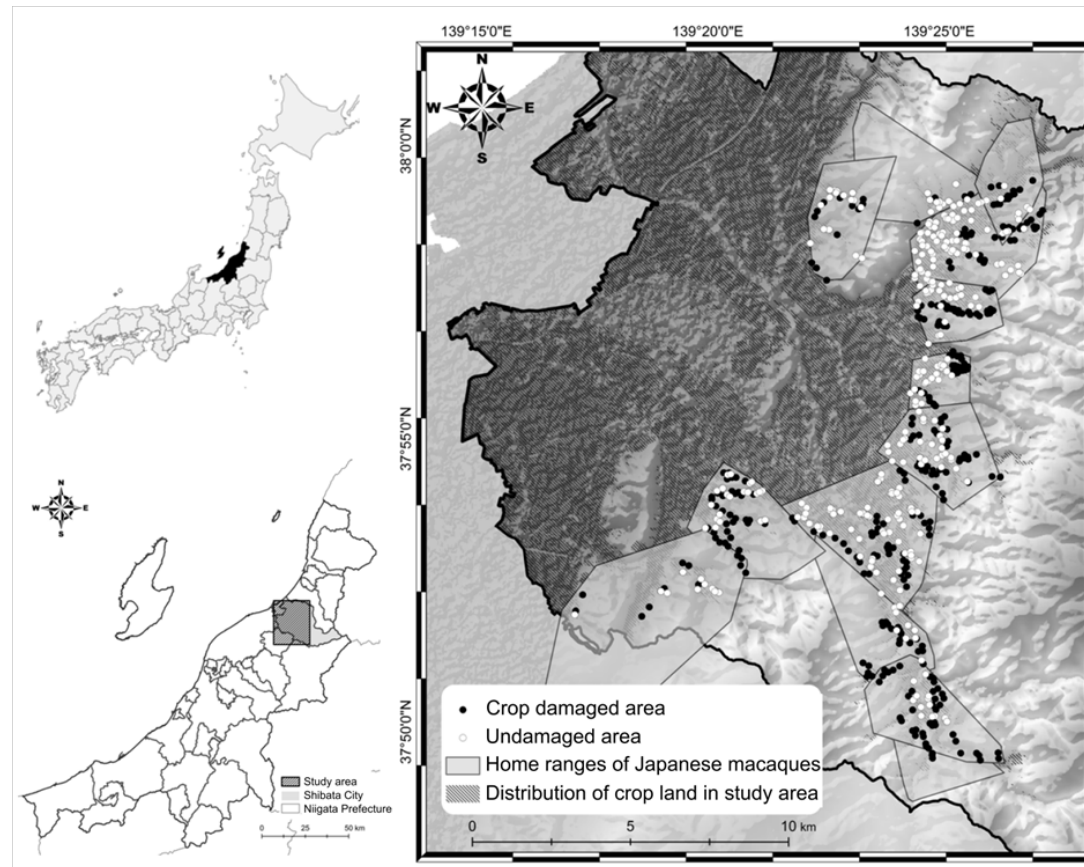


Figure 1. Location of the study area: Shibata city, Niigata Prefecture, Japan. Black dots indicate the crop damaged areas from 2008 to 2009. White dots indicate the undamaged crop land in 2010. Home ranges of each Japanese macaque's troop were represented by the minimum convex polygon using the radio tracking data from 2008 to 2009.

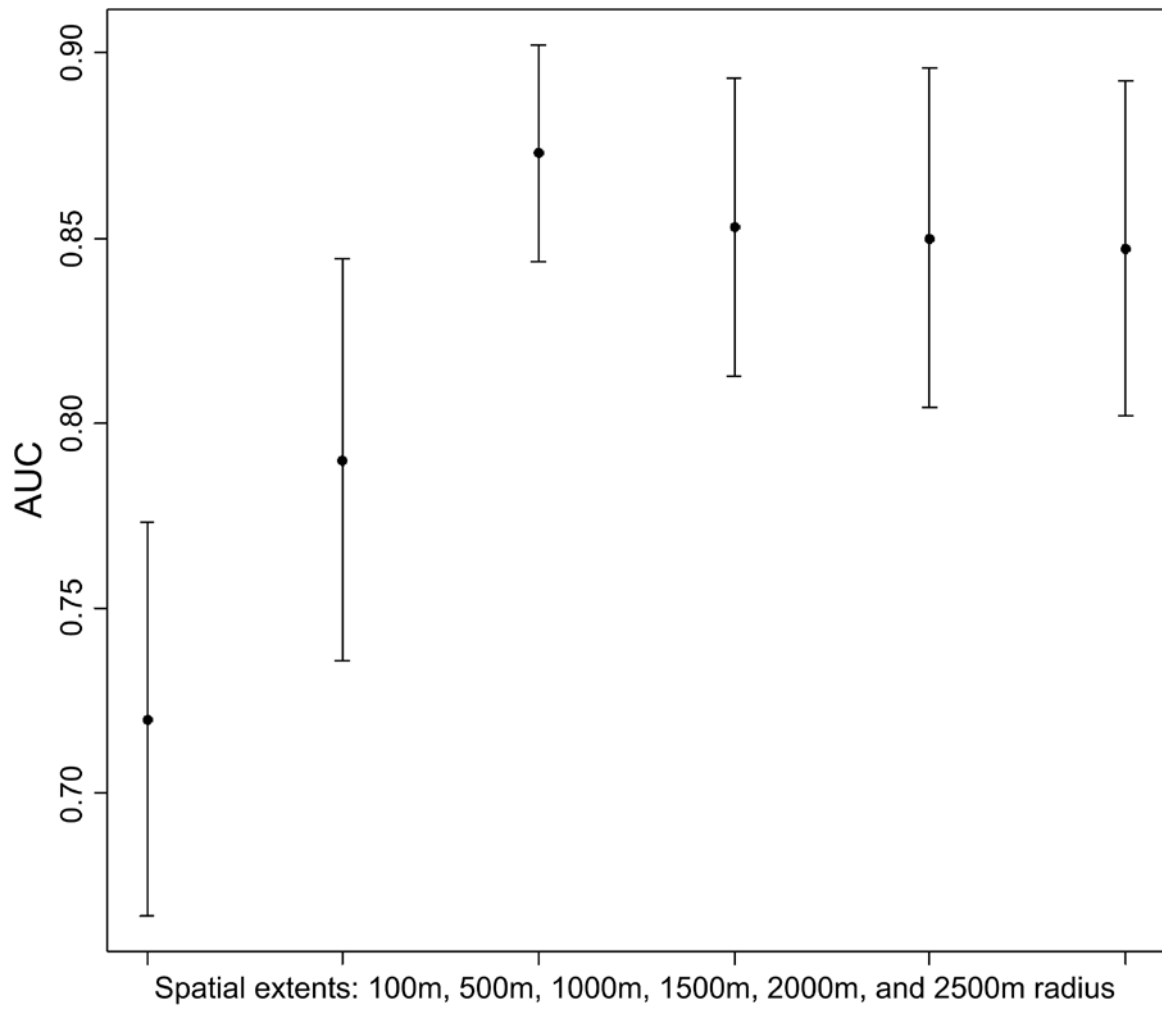


Figure 2. Area under the curve (AUC) and 95% confidence interval for each spatial extent model of the predicting crop damage by the Japanese macaques at the within-home range scale.

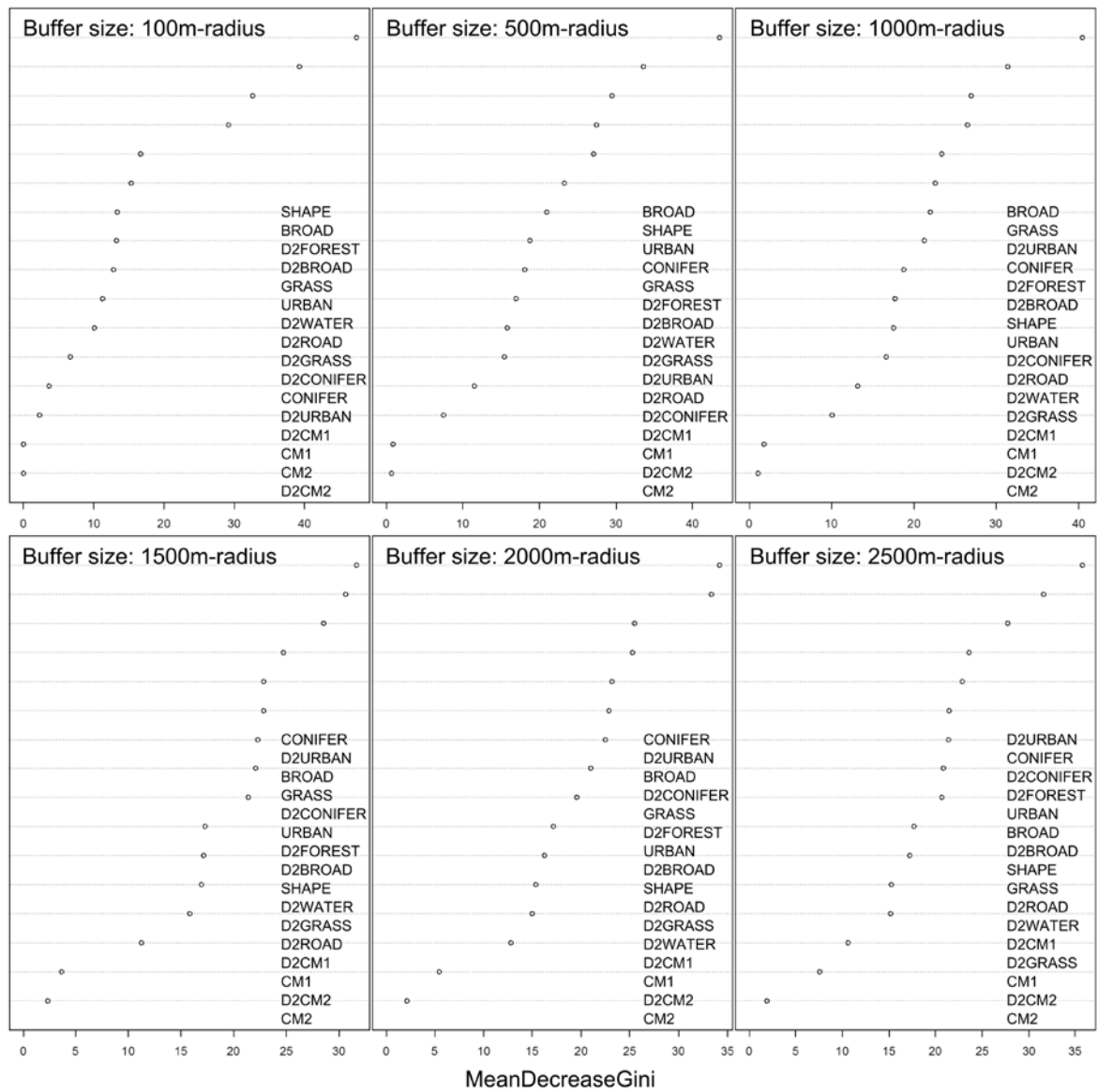


Figure 3. Variable importance plot in each spatial extent for predictor variables from Random Forest classifications used for predicting the occurrence of crop damage by Japanese macaques.

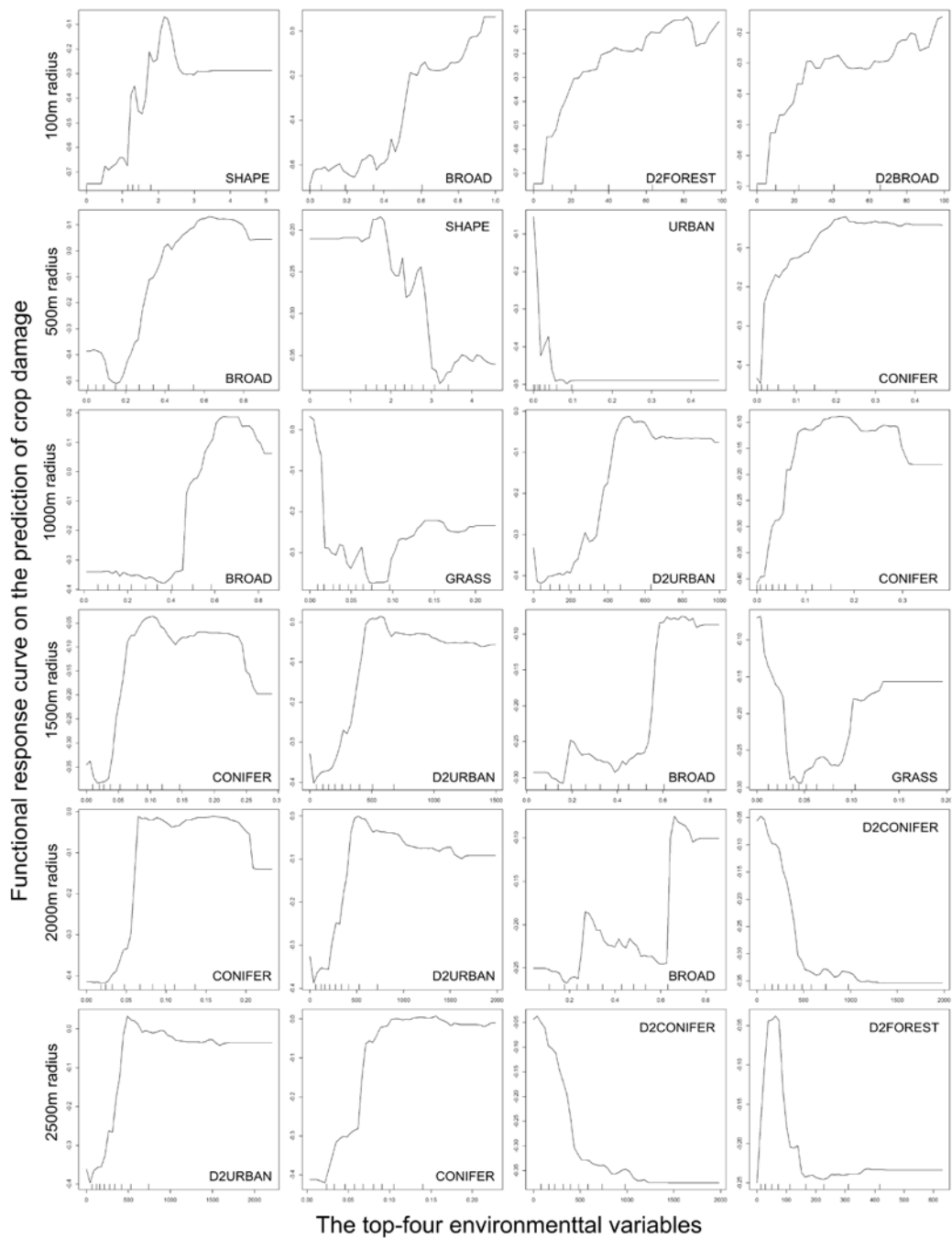
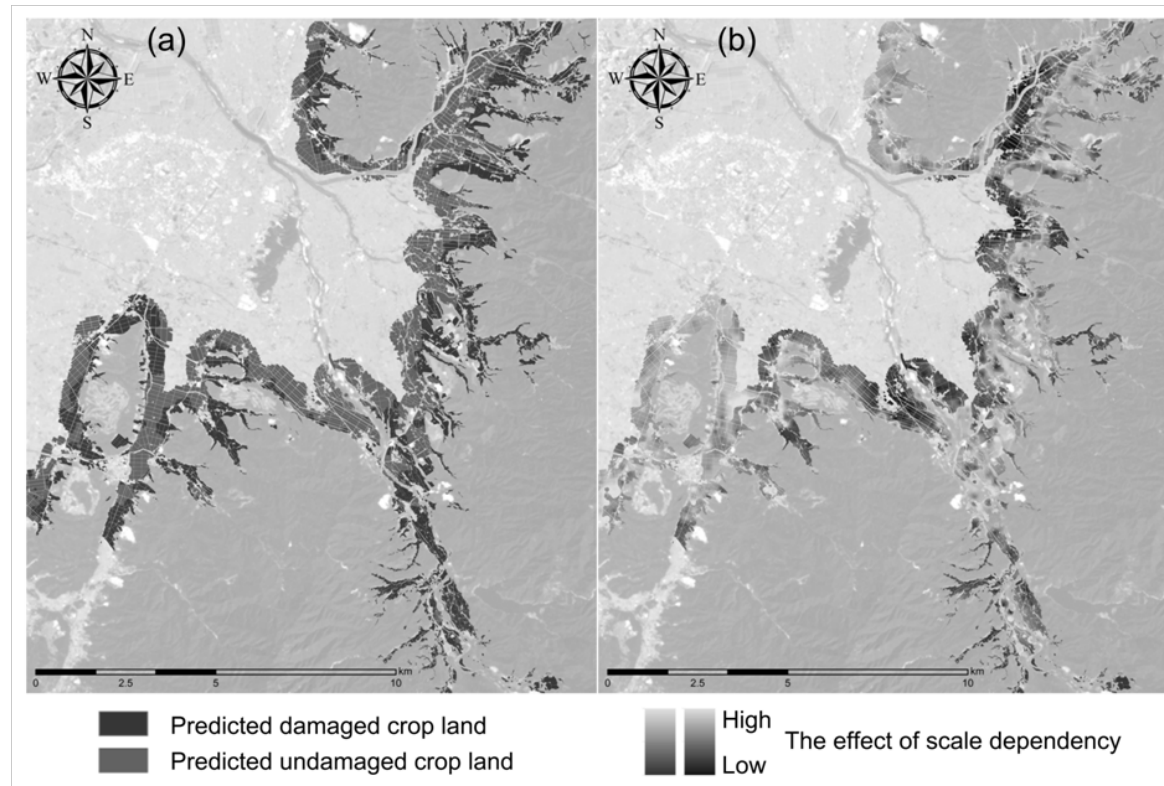


Figure 4. Functional responses by the crop-raiding Japanese macaques in each spatial extent using the partial dependence plots for high ranked predictor variables for Random Forest predictions. Partial dependence is the dependence of the probability of occurrence on one predictor variable after averaging out the effects of the other predictor variables in the model.



1

2 Figure 5. Evaluation of the crop damage which is the result of resource selection functions by the Japanese macaques. (a) Binary
 3 representation of the crop damaged (black) and undamaged (gray) from the random forest classification with the optimal spatial extent
 4 (1000m-radius buffer size). (b) Gradient representation of the risk prediction in crop damage, including the probability of multiple spatial
 5 extents.

Table 1. Numbers of the radio tracked locations and home range sizes for each Japanese macaque's troop.

Troop ID	Number of locations	Home range size (km ²)
AK	118	25.34
AS	118	5.55
IK	126	3.80
KH	112	4.97
MD	182	6.36
NT	82	6.54
OT	168	12.67
SK	180	3.26
TD	128	8.08
YK	168	7.65
YU	172	8.07
YY	78	8.93
ZN	172	10.12

APPENDIX A

Figure A.1. The diagram of each spatial extent for the buffer analysis. As the independent variables, the environmental variables such as landscape structure, landscape configuration, and countermeasures are calculated within buffers.

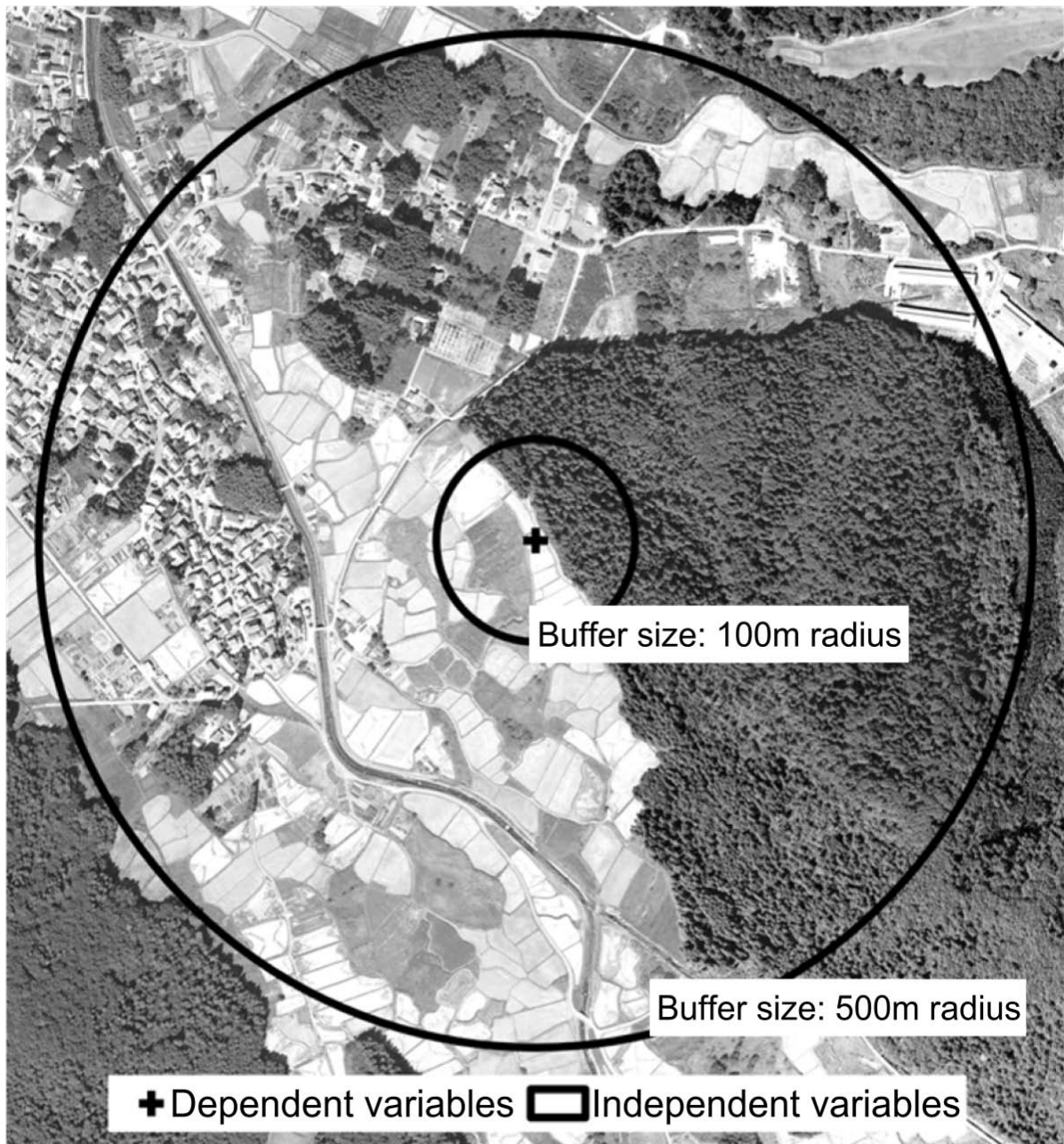


Table A.1. List of environmental variables and ranges of variable value considered in the analysis of resource selection functions by the crop raiding Japanese macaques.

Variable	Description	Mean \pm S.D (occurrence)	Mean \pm S.D (absence)	Range
BROAD	Ratio of broad-leaved deciduous forests within each spatial extent	0.44 \pm 0.20	0.36 \pm 0.19	0.00 - 0.99
CONIFER	Ratio of coniferous forests within each spatial extent	0.08 \pm 0.07	0.05 \pm 0.06	0.00 - 0.55
SHAPE	Shape index of forest edge	3.63 \pm 1.70	3.90 \pm 1.90	0.00 - 8.77
GRASS	Ratio of grass land within each spatial extent	0.03 \pm 0.04	0.04 \pm 0.04	0.00 - 0.42
URBAN	Ratio of urban area within each spatial extent	0.01 \pm 0.02	0.02 \pm 0.03	0.00 - 0.42
D2FOERST	Minimum distance to forest regions from sample points	59.77 \pm 49.32	81.55 \pm 101.75	0.00 - 787.46
D2BROAD	Minimum distance to broad-leaved forests from sample points	63.64 \pm 52.35	85.02 \pm 102.34	0.00 - 787.46
D2CONIFER	Minimum distance to coniferous forests from sample points	199.93 \pm 208.40	298.84 \pm 324.19	0.00 - 1830.03

Table A.1. Continued.

Variable	Description	Mean \pm S.D	Mean \pm S.D	Range
		(occurrence)	(absence)	
D2GRASS	Minimum distance to grass land from sample points	198.39 \pm 206.06	177.73 \pm 155.42	0.00 - 1574.33
D2URBAN	Minimum distance to urban area from sample points	340.55 \pm 349.97	237.85 \pm 264.45	0.00 - 2032.73
D2WATER	Minimum distance to water regions and streams from sample points	195.30 \pm 190.56	241.80 \pm 225.89	0.00 - 1156.03
D2ROAD	Minimum distance to roads more than 5m wide from sample points	299.95 \pm 353.68	248.93 \pm 264.45	0.00 - 2056.79
CM1	Countermeasure: The number of fences	4.40 \pm 4.70	4.36 \pm 4.68	0 - 20
CM2	Countermeasure: The number of alarms	0.20 \pm 0.55	0.26 \pm 0.60	0 - 2
D2CM1	Minimum distance to fences from sample points	358.02 \pm 402.92	386.69 \pm 423.72	0.00 - 2424.23
D2CM2	Minimum distance to alarms from sample points	179.29 \pm 501.67	152.38 \pm 454.45	0.00 - 2492.01

Chapter 6

General Discussion

Risk management of crop damage by the Japanese macaques

In the Chapter 2, I clarified the relationship between the crop-raiding Japanese macaques and the effect on landscape structure. Existing reports give accounts of the relationship between habitat configuration and crop damage by other primate species (Naughton-Traves et al. 1998, Hill 2000, Saj et al. 2001). Responses of the environmental variables such as the distance from forest boundary and roads to crop damage were same in each macaque's troop. Fundamentally, there is no difference in the environment which the Japanese macaques prefer. However, response of the countermeasure (in this study: fence) was different in each troop. I suggested this difference may be caused in the heterogeneity of landscape structure in their home ranges. According to the results in Chapter 2, I proposed the importance of habitat management in each macaque's troop for crop protection.

Then, is habitat management effective in the measure against crop damage by Japanese macaques through one year? Seasonal changes within an animal's habitat may affect its feeding, migration, and other behaviors (Hellgren, 1998; Hurlbert & Haskell, 2002). In particular, seasonal patterns of resource availability may influence habitat selection and use (Wiegand et al., 2008; Loveridge et al., 2009). I paid my attention to the seasonal variation as the effect of temporal scale to habitat use in Chapter 3. The home range size of crop-raiding Japanese macaques was changed through season. Home

range was expanded in summer from late spring and it became small from summer in early winter. In the natural troop of the Japanese macaques which is not depended on crops, since home range is expanded in food scare season such as summer and winter, I guessed this phenomenon is the special characteristic of the crop-raiding Japanese macaques. The seasonal variation of home range size was related to the growth of crops. The number of the foraging patches had contributed to home range size in summer, and the size of the foraging patches had contributed in winter. According to these results, I propose that the crop-raiding Japanese macaques have a different foraging strategy from the natural troops of Japanese macaques. Therefore, I have to implement the measure of crop protection in consideration of a seasonal variation in habitat use by Japanese macaques.

Habitat selection by wildlife are influenced not only the seasonal changes but also long-term changes (Warren et al., 2001; Onyehialam et al., 2005; McDermid et al., 2010). In Chapter 4, I forecasted the change in habitat selection by crop-raiding Japanese macaques along the habitat fragmentation from 1978 to 2007. As the results, habitat selection by Japanese macaques relates the percentage of the coniferous forest within their habitat. Moreover, the potential habitat for the Japanese macaques was expanded from 1978 to 2007. Crop damage by macaques increased in the late 1970s along with afforestation with artificial plantations of coniferous forest (Agetsuma, 2007). On the other hand, I suggest that the expansion of crop damage in the 2007 resulted from a

decline in coniferous forest. Forestry activities are rarely performed in the study area at present. The afforestation area that consists of a coniferous forest had not been managed. Therefore, the broad-leaved deciduous forest is mixed in the coniferous forest. This transition from coniferous forest to broad-leaved deciduous forest suggests that the cultivated species of broad-leaved deciduous forest spread from farmland areas and continues to grow (Kobayashi and Koike, 2010). This also suggests a decline in coniferous forest as a risk factor along the forest edge. Furthermore, the home range of macaques was expanded as a result of the reduction in the coniferous forest as a risk factor. My study demonstrates that changes in landscape configuration in Japanese macaque habitats are important for their distribution and resource selection. I strongly emphasize the necessity for forest management to reduce crop raiding. Sustainable forest management is recommended. With suitable forest management, artificial plantations of coniferous forest can serve as a barrier to destructive behavior by Japanese macaques, according to the habitat model.

Then, I considered a hypothesis that there is a spatial scale dependency in crop damage by Japanese macaques. Landscape structure generally refers to the scale effect, defined in terms of grain and extent (Turner et al., 2001). Grain is the minimum resolution of the data, defined as the cell size of landscape distribution. Extent is the domain of the data, defined as the size of the area used by an animal, the overall study area, or a particular landscape type. In wildlife studies, grain and extent may be defined

as the finest spatial scale of habitat heterogeneity to which an organism responds (Kotliar and Wiens, 1990; Thompson and McGarigal, 2002). Therefore, hierarchal habitat selection is thought to be a solution to cope with spatial heterogeneity in resource availability (Levins, 1968). I clarified the spatial scale dependency applying multiple buffer analysis. The optimal spatial scales explaining crop damage by Japanese macaques were more than 1000 m radius buffer size. The environmental variables less than 1000 m radius buffer size were difficult to explain the prediction of crop damage. Therefore, it is necessary to perfume the risk management of crop damage in the comparatively broad range such as the home range of Japanese macaque's troop. In wildlife management, it is necessary to detect differences in habitat selection among different spatial scales, and manage habitats at these scales, which will lead to more effective countermeasures for crop protection.

In these studies, there was a strong relation between the change of the habitat which is caused by the spatial and temporal gradients and the behavior of the Japanese macaques (in Chapters 3, 4, and 5). Moreover, my research showed a possibility that this relation was different for every macaque's troop (in Chapter 2). These results suggest that risk management in each troop is important for crop protection. For the appropriate management of crop-raiding Japanese macaques, the monitoring of each troop is a first step. I can also identify high-risk cropland from environmental factors (e.g. distance from forest edge). In such places, it would be possible to reduce crop damage by appropriate

countermeasures such as electric fence. I also suggest that re-design of land use will be needed to control future damage (Eguchi 2008). Changing the management method for every season (e.g. introducing the fences in each agricultural field in food scare season) will also be effective. For establishing a comfortable relationship between wildlife and humans, it is necessary to understand a boundary between wildlife habitats and human activities. Then, landscape management under the spatial and temporal variation will assume an important role for risk management.

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Summary

In this paper, I focused human–wildlife conflict caused by crop-raiding Japanese macaques. To develop an appropriate relationship between people and Japanese macaques, it is important to have an understanding of the Japanese macaque’s behavior. The objective of this study is to suggest the information for resolving human-wildlife conflicts caused by crop-raiding Japanese macaques following multi-scale gradient modeling approach including spatial and temporal variation of landscape structure.

In the Chapter 2, I calculated landscape indices of their habitats and measured differences in frequency of farmland invasion between the Japanese macaque’s troops. The objective of this chapter was to determine the relationship between troop invasion frequency and landscape indices. Location data of the “YK” and “OT” troops were collected by radio telemetry from 2004 to 2006. A land-cover map was acquired from remotely sensed imagery. To discern differences between troop habitats, the landscape index of each patch was calculated. Size, shape, and configuration of habitat were selected from deductive approach. A generalized linear mixed model was applied to identify environmental factors contributing to farmland invasion by the troops. The home range area of the OT troop was larger than that of the YK troop, and within the ranges, the ratio of farmland to home range and the ratio of urban land to home range was higher for the OT troop. For each landscape index, a difference was found between the habitats of the two troops. In models of the two troops, distance between farmland and forest boundary and distance from a road were important factors. Moreover, the frequency of

farmland invasion differed in distances from enclosure fences. Differences in farmland invasion between troops were attributable to differences in habitat landscape indices. The shape of the OT troop habitat was relatively complex, increasing opportunities for macaques to come in contact with farmland.

Using a satellite-based vegetation index, I evaluated the changes in home range sizes of Japanese macaques during the seasonal transitions to summer and winter for four years in the Chapter 3. The objective of this chapter was to clarify the relationship between change in the home range size of Japanese macaque troops and seasonal variation in NDVI. From late spring to summer, home range size decreased and the vegetation index increased. From summer to early winter, home range size increased and the vegetation index decreased. I predicted the changes in home range size by NDVI increases and decreases. The results of patch-based analyses using linear-mixed models showed that the number of habitat patches was most important for predicting home range behavior during the transition to summer, whereas patch size was most important during the transition to winter. Summers are a period of food shortage for Japanese macaques in their natural forest habitat, but many troops have adapted to feed on agricultural crops during the summer. Therefore, the number of patches is an important factor determining home range behavior. Japanese macaques prefer large resource patches during periods of low resource availability. The results show ecological differences between crop-dependent and natural troops of Japanese macaques.

The aim of the Chapter 4 was to evaluate changes in macaque habitat selection during a 29-year period. I focused on the 1970s, when little crop damage was caused by Japanese macaques, and the 2000s, when the damage became remarkable. Landsat/MSS from 1978 and ALOS/AVNIR-2 from 2007 were employed for land-cover mapping. I applied a Random Forest model for machine learning and data mining to predict the habitat selection of macaques. Several important environmental factors were identified for macaque habitat selection: the ratio of coniferous forest to farmland, distance to farmland, and maximum snow depth. The Random Forest model was extrapolated to the 1978 land-cover map. Over the 29-year period, coniferous forest changed to broad-leaved forest and/or mixed forest within the macaque habitat area. Coniferous forests were not selected as food resources by Japanese macaques. I indicated that habitat selection by Japanese macaques changed over the study period. The results show that the home range of macaques expanded, and macaques may now be distributed over a wider area as a result of changes in landscape configuration.

Resource selection functions can be influenced by the heterogeneity of landscape structures, and landscape heterogeneity occurs over multiple spatial scales. In the Chapter 5, I investigated the scale dependency and functional responses of Japanese macaques using multiple scale analysis. The occurrence of crop damage was predicted at the within-home range scale using environmental variables linked with resource selection. Sixteen environmental variables were defined including aspects of the type of landscape

configuration, human disturbance, topography, and countermeasures that have been employed. The Random Forests algorithm was used to predict the crop damage. The most suitable spatial extent for crop damage prediction was the buffer with a 1000 m radius. The importance of variables was differed among spatial extents. However, the functional responses for each environmental variable were not influenced by the differences in spatial extent. These results suggest that the limiting factors for crop damage depended on spatial extent with the functional responses in resource selection remaining constant across spatial extents. These results may aid wildlife management planning, for which it is necessary to detect differences in resource selection across different spatial scales.

In these studies, there was a strong relation between the change of the habitat which is caused by the spatial and temporal gradients and the behavior of the Japanese macaques (in Chapters 3, 4, and 5). Moreover, my research showed a possibility that this relation was different for every macaque's troop (in Chapter 2). These results suggest that risk management in each troop is important for crop protection. For the appropriate management of crop-raiding Japanese macaques, the monitoring of each troop is a first step. For establishing a satisfactory relationship between wildlife and humans, it is necessary to understand a boundary between wildlife habitats and human activities. Then, landscape management under the spatial and temporal variation will perform an important role for risk management.