Development of the new protocol for habitat modeling of urban red fox to improve *Echinococcus multilocularis* control strategy

エキノコックス症対策のための 都市型アカギツネ生息地モデリング法の開発

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ABBREVIATIONS

AIC	Akaike's information criterion
AUC	area under the curve
HAE	human alveolar echinococcosis
ROC	receiver operating characteristic
UPA	urbanization promoting area

ABBREVIATIONS OF VARIABLES

L-blank	linear distance to bland space
L-farm	linear distance to farmland
L-green	linear distance to green covered area
L-nroad	linear distance to narrow road
L-ocpbl	linear distance to occupied building
L-river	linear distance to riverbed
L-vctbl	linear distance to vacant building
L-water	linear distance to water place
L-wroad	linear distance to wide road
BLANK	percentage of blank space
FARM	percentage of farmland
GREEN	percentage of green covered area
NROAD	percentage of narrow road
OCPBL	percentage of occupied building
RIVER	percentage of riverbed
VCTBL	percentage of vacant building
WATER	percentage of water place
WROAD	percentage of wide road

INTRODUCTION

The establishment of effective strategies for zoonoses control is needed urgently in order to minimize infection risks to humans, because wildlife and human habitats are becoming rapidly overlapped (Kubo and Shoji, 2014) as changes occur in the global environment.

Echinococcus multilocularis Leuckart, 1863 is a parasite perpetuated in a sylvatic cycle mainly between wild carnivores (definitive hosts) and rodents (intermediate hosts). Infection of humans occurs by the accidental ingestion of the parasites eggs, which are provided from the feces of the definitive hosts. This ingestion will cause the human alveolar echinococcosis (HAE), which constitutes a serious zoonosis (Figure 1). The number of cases of HAE has been increasing in recent years in central Europe, parts of North America, and parts of Asia including Japan (Eckert and Deplazes, 2004; Eckert et al., 2001).

In Japan, HAE is endemic in Hokkaido, the northernmost prefecture. Here, the red fox, *Vulpes vulpes* Linnaeus, 1758, is the main definitive host (Oku and Kamiya, 2003) and acts as a vector of *E. multilocularis* toward humans.

The red fox is a common wildlife in Hokkaido, and it is known to have a high capacity for adaptation to artificial environments. In fact, their habitat has expanded into urban areas of many cities worldwide in recent decades (Deplazes et al., 2002; Harris, 1981; Hegglin et al., 2003; Janko et

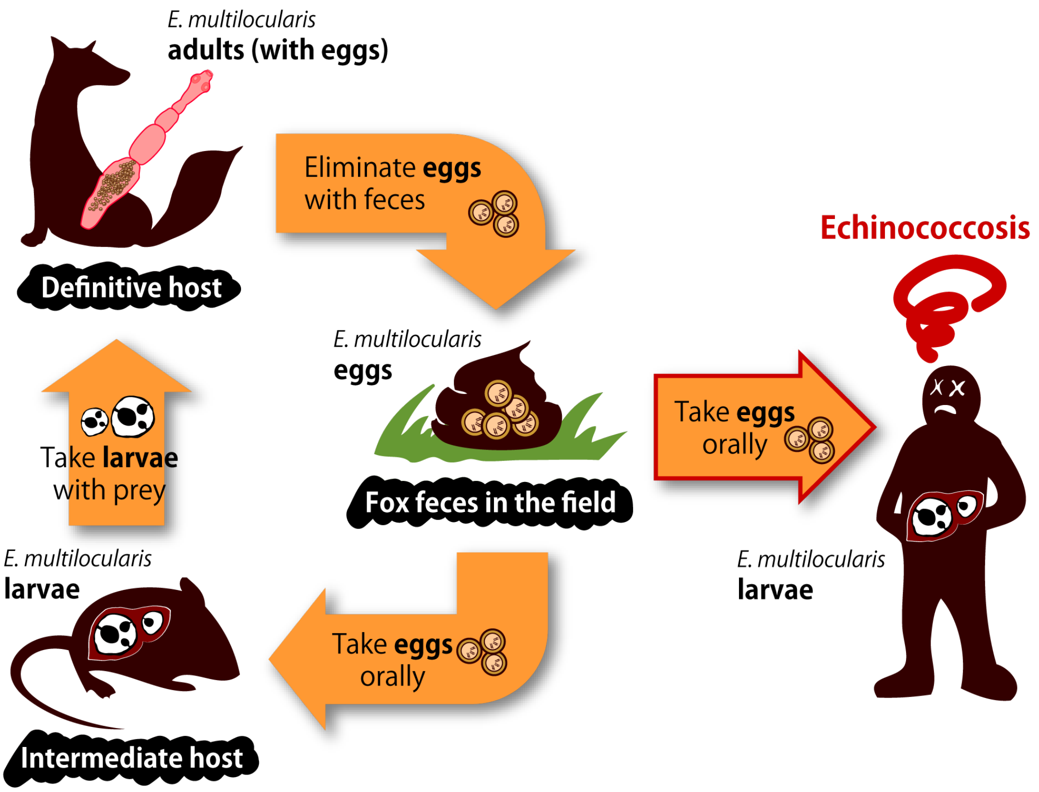


Figure 1. Lifecycle and transmission route of *Echinococcus multilocularis*.

al., 2011). This urbanization of red foxes has been reported in Hokkaido as well (Oku et al., 2005; Takahashi et al., 2003; Tsukada et al., 2000; Uraguchi et al., 2009). Moreover, *E. multilocularis* is prevalent among the urban fox population there (Oku et al., 2005; Tsukada et al., 2000). The urbanization of infected red foxes leads to contamination of these areas with eggs of *E. multilocularis* and raises the exposure risk of residents to the pathogenic eggs.

In order to cut the transmission route of *E. multilocularis* from red foxes to human, fox culling in the wide target areas had been taken place in many countries for long time; however, few cases have been succeeded. A report from France revealed that the culling of transmitter animals in target area does not prevent the area contamination (Tuyttens et al., 2000). The reason for this failure is that the population of the red fox in the target area will be replaced immediately by immigrants from surrounding population, which may be infected (Deplazes et al., 2002) (Figure 2-A). Hence, the fox removing is unsuited as the control strategy. Additionally, extermination of the animals on the top of regional ecosystem inflicts immeasurable damage on the balance of the ecosystem. Deworming of foxes by baiting with anthelmintic praziquantel is an alternative method that is noninvasive and systematic control based on favorable strategy required from both standpoints of biodiversity conservation and performance advance of zoonosis control.

Previous studies have demonstrated that anthelmintic baiting

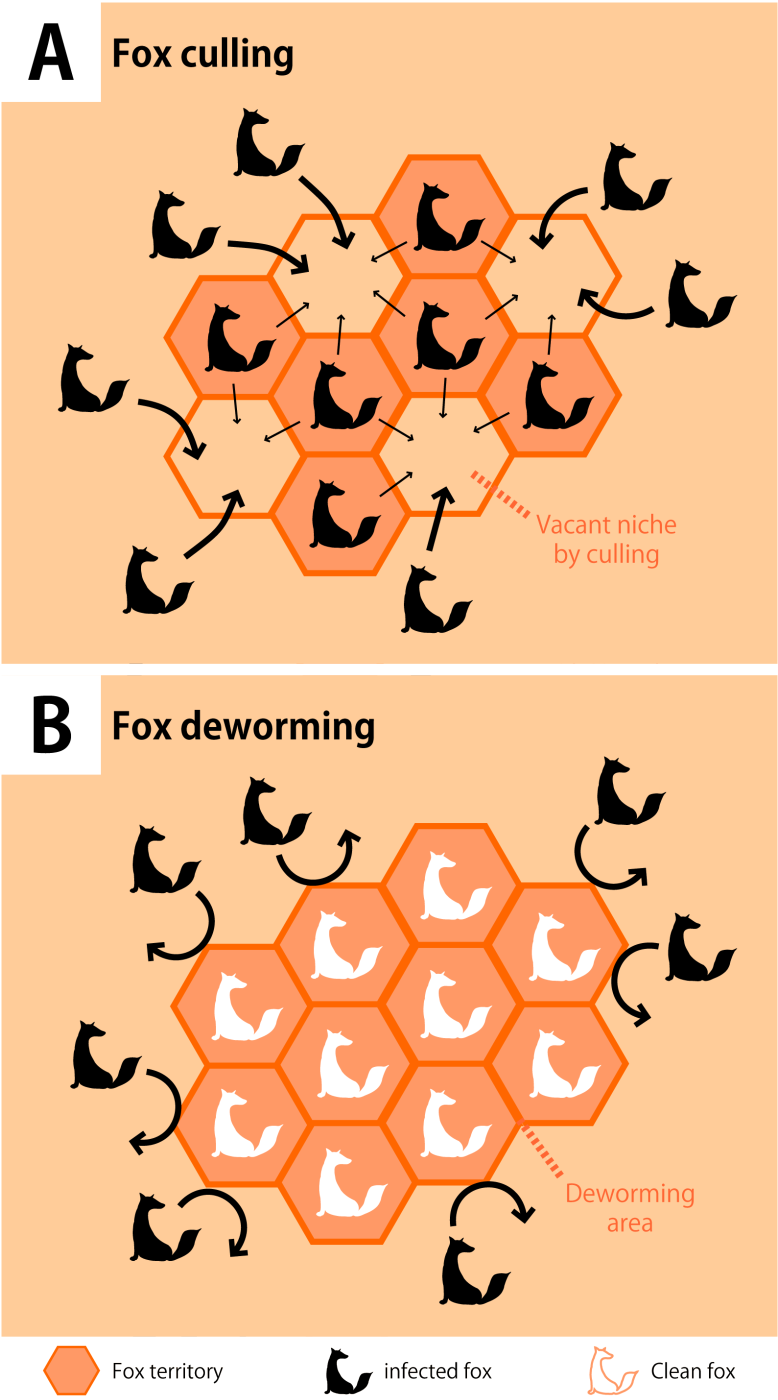


Figure 2. Effect of immigration of red fox population depending on the two methods of echinococcosis control strategies.
Box A shows the effect of fox culling. Infected foxes will be immigrated to vacant niches.
Box B shows the effect of fox deworming. Clean foxes protect the area against infected fox's immigration from outside the deworming area.

successfully reduced *E. multilocularis* prevalence in the red fox population in several countries (Hegglin and Deplazes, 2008; Hegglin et al., 2003; Inoue et al., 2007; Janko and König, 2011; König et al., 2008; Kamiya et al., 2006; Rausch et al., 1990; Romig et al., 2007; Schelling et al., 1997; Tackmann et al., 2001; Takahashi et al., 2013; Takahashi et al., 2002; Tsukada et al., 2002). The advantage of this method is to cause the target area be occupied by an uninfected fox population instead of making vacant niche by random culling (Figure 2). Once the target area is occupied, the area will be protected as the territories of fox families, making it hard for the population in this area to be replaced by other, potentially infected, individuals from outside. The prevalence could decrease if the foxes are kept as a "clean population". This is the reason why deworming by anthelmintic baiting is the most effective and realistic method for *E. multilocularis* control so far.

Although effective, anthelmintic baiting requires continuous effort to keep the fox population in the target area clean. Fox territories are maintained by females and inherited from mother to daughter; meanwhile, males are always provided from outside of the mother's family in mating season. Even if family members are kept clean, the risk of re-infection increases again during the annual immigration. Achieving the maximum effect at the minimum cost is fundamental for sustainable bating, hence identifying the most suitable locations for delivering baits is necessary (Eisen and Eisen, 2008; Eisinger and Thulke, 2008; Selhorst et al., 2001;

Thulke et al., 2004).

Current strategies of delivering baits are roughly classified into two types. Although both strategies have been produced results, those are not the most suitable methods for Hokkaido fox population. One method is random delivering in entire surface of the large area by aircraft, which is used in southwestern Germany (Romig et al., 2007). It is suitable for the areas with high fox densities like cities in Europe (e.g. 0.188-2.035 fox families/km^2 in U. K. (Harris and Rayner, 1986), 1.4-3 foxes/km^2 in southwestern Germany (Romig et al., 2007), and 11 adult foxes/km^2 in Zurich, Switzerland (Gloor, 2002)); however, it should be highly inefficient and unprofitable in the areas having low fox densities like cities in Hokkaido (e.g. 0.080 fox families/km^2 in Sapporo (Uraguchi et al., 2009)). The other baiting method is pinpoint delivering at places that are most likely to be frequented by foxes based on the witness information of individuals or dens (Hegglin et al., 2003; Inoue et al., 2007; Kamiya et al., 2006; Takahashi et al., 2013). This method has been applied in Hokkaido, and it still has room for improvement although its deworming effect has been guaranteed. In this method, delivering locations are determined on the basis of the current fox distribution. This basis is certainly reliable for the present, but this approach cannot adapt the prospective changes in fox distribution pattern. Specifying the potential sites for fox inhabiting would solve the problem fundamentally. Accordingly, clarifying the pattern of habitat use to standardize the target locations for delivering baits could improve the cost-benefit performance of anthelmintic baiting.

The target location for delivering baits should be related to the habitat use of red foxes (Janko et al., 2011; König et al., 2012; Takyu et al., 2013), especially around dens, which are the pivot of their habitation (Figure 3). A red fox family has their dens in several places and depends on the sites throughout the breeding season. During the breeding season, they are likely to intake baits around the dens constantly because they invariably come back to any one of their dens at least once a day. Hence, the requirements for fox denning are the key to determining the target location where baits should be delivered. Standardized denning requirements could be clarified by establishing a model that extracts key environmental factors.

A general modeling method exists for standardizing the habitat selection of arthropods (Ayala et al., 2009; Cecchi et al., 2008; Eisen and Eisen, 2008; Gibson et al., 2004; Menach et al., 2005; Ogden et al., 2008; Sutherst and Bourne, 2009); however, this method is not applicable to modeling the habitat use of urban foxes. This general modeling method is appropriate for risk prediction of vector-borne diseases mechanically transmitted by arthropods, which targets the macro-scale area. On the other hand, the fox model is intended for the risk prediction of echinococcosis, which is a parasitic zoonosis indirectly transmitted by a mid-sized, generalist species inhabiting urban landscapes. Three major problems must be solved to apply the existing method to habitat use

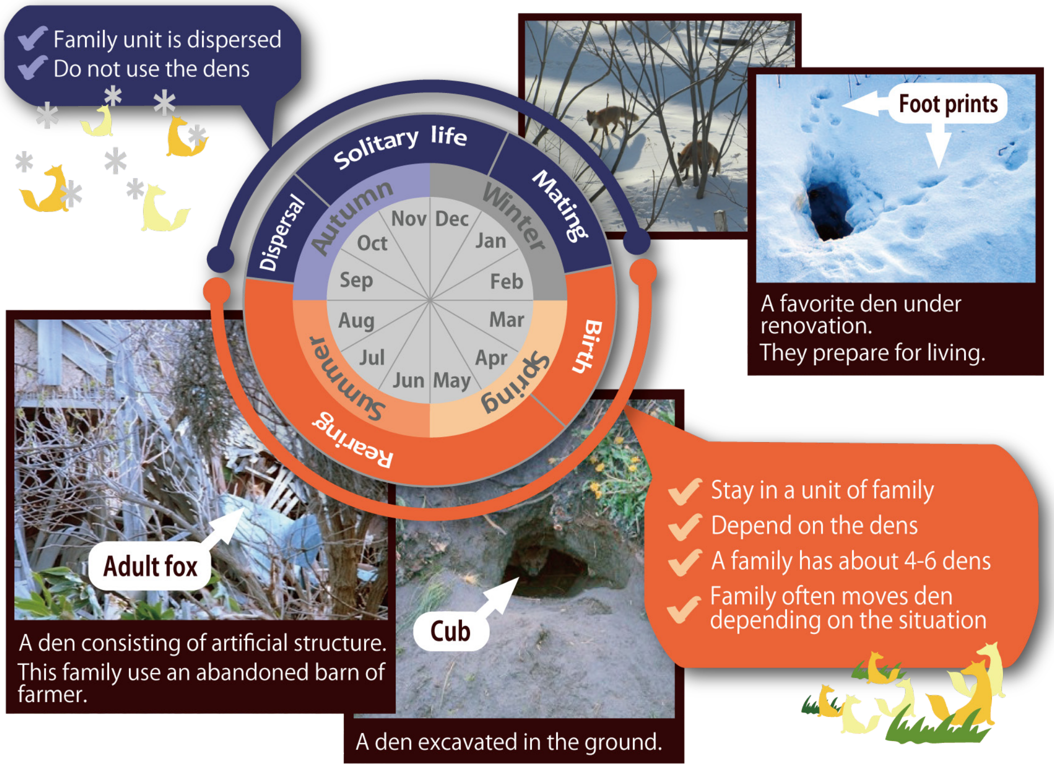


Figure 3. Annual behavior and usage of dens by *Vulpes vulpes* (red fox) in Hokkaido.

modeling for red foxes: 1) the general modeling approach uses the "abundance" of vector individuals as its modeling target (= objective variable); however, "presence or absence" is suitable for fox den modeling considering its low densities; 2) the general modeling approach uses land use or vegetation categories on existing thematic maps as predictor variables to extract the critical factors from them, but these variables should be based on habitat use of the target animals, urban red foxes; 3) the size of unit in the general modeling approach is based on the grid size (= resolution) of existing thematic maps; however, the range affecting their denning cannot be represented by the resolution of these maps.

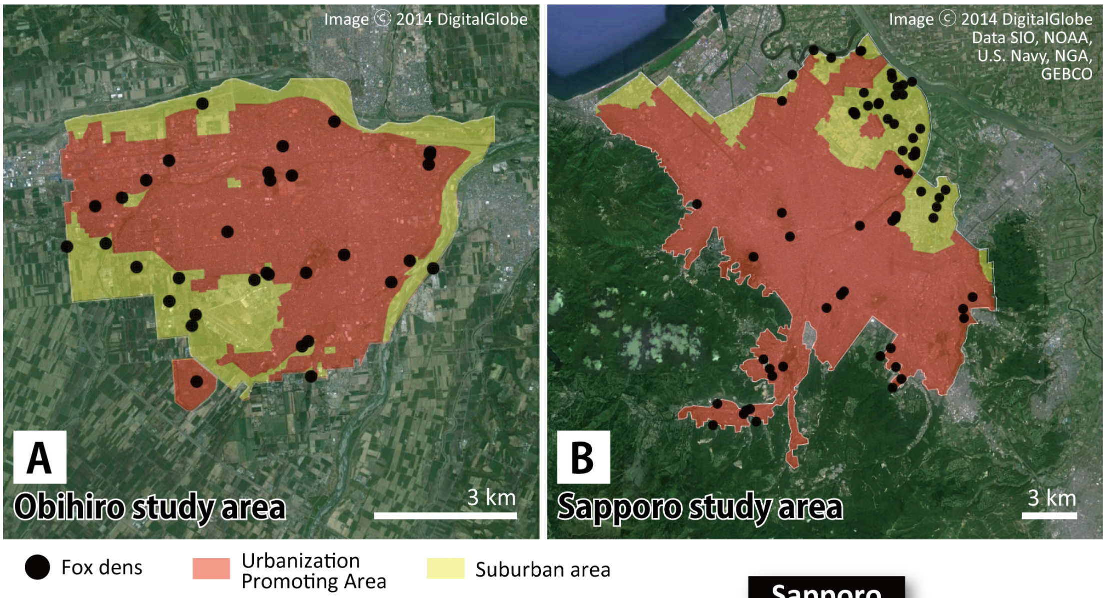
In the present study, I tried to establish a valid fox denning model by developing the new protocol of modeling method in order to specify the potential habitat of urban fox dens (Analysis 1). The established model identifies the suitable locations for delivering anthelmintic baits. The modeling protocol was designed to extract key environmental factors for denning, and not only that, to extract the key spatial scale which means the range they pay attention to (named "heeding range") when they select the den sites, simultaneously. This is the first approach to establish a comprehensive micro-habitat model for mid-sized and generalist mammals in consideration of specifying the requisite spatial scales for the target populations. The protocol for the modeling process is presented visually. In addition to the spatial modeling, two traditional univariate analyses were conducted to compare the results (= extracted factors) between the analyses by traditional methods and by modeling (Analysis 2). The extracted factors by the traditional analyses in the present urban study areas are also compared with the results from other places reported in previous studies to discuss the differences in fox denning requirements depending on habitat types. Control strategies for *E. multilocularis* are also discussed.

MATERIALS & METHODS

M1. Study areas

The study areas were urban regions of Obihiro and Sapporo cities in Hokkaido, the northernmost prefecture of Japan (N 41°21′-45°33′, E 139°20′-148°53′). Hokkaido belongs to the subarctic zone and shows a continental climate, and it usually snows from November to March although the annual amount of snowfall varies depending on the province. Obihiro City is a small city located in the eastern part of the island. Sapporo City is the prefectural capital and located in the western part of Hokkaido Island, and in which *E. multilocularis* has been fixed in red foxes. The densities of red foxes in urban areas of Hokkaido is relatively lower (e.g. 0.080 families /km^2 in Sapporo (Uraguchi et al., 2009)) than in other cities in Europe (e.g. 0.188-2.035 fox families /km^2 in U. K. (Harris and Rayner, 1986), 1.4-3 foxes /km^2 in southwestern Germany (Romig et al., 2007), and 11 adult foxes /km^2 in Zurich, Switzerland (Gloor, 2002)). Both of the study areas are composed almost entirely of artificial environments, including urban parks and farmland; however, these two study areas are different in the scale of each component, i.e. surface area, human population size, and human population density.

A map of the Obihiro study area is given in Figure 4-A. This study area (about 59.8 km^2) consists of whole of the Urbanization Promoting



	Study area	Urbanization Promoting Area	Suburban area	population density
Obihiro	59.8 km^2	41.9 km^2 (80%)	17.9 km^2 (20%)	4,400 /km^2
Sapporo	367.9 km^2	294.3 km^2 (70%)	73.6 km^2 (30%)	7,400 /km^2

Figure 4. Maps showing the landscape structures and fox dens distributions in the two study areas.
The proportion of the Urbanization Promoting Area and surrounding suburban area, and population densities are also shown.

Area (UPA; about 41.9 km^2) and its surrounding suburban area (about 17.9 km^2). The UPA is composed of a mosaic of dwellings, commercial areas, urban parks, urban green spaces, and riverbeds. The surrounding suburban area is composed of urban parks, an area of continuous farmlands, and riverbeds of two large rivers, plus some small rivers and streams. The human population of the study area is approximately 167,000, which amounts to 96% of the total population of whole city. The population density is about 4,400 people /km^2.

A map of the Sapporo study area is given in Figure 4-B. This study area (about 367.9 km^2) consists of whole of the UPA (about 249.3 km^2) and its surrounding suburban area (about 73.6 km^2). The UPA is composed of a mosaic of dwellings, commercial areas, urban parks, urban green spaces, and riverbeds. The surrounding suburban area is composed of large urban parks, urban farmland, and riverbeds of two big rivers, plus some small rivers and streams. The human population of the study area is approximately 1,855,000, which is around 99% of the total population of the whole city. The population density is about 7,400 people /km^2.

M2. Analysis policy

Modeling was conducted in urban areas of Obihiro and Sapporo cities in Hokkaido, Japan, in which red fox populations have been established. The modeling protocol is given below (see METHODS: M3. Analysis 1).

In addition to establishment of the new model above, denning factors extracted using other two traditional univariate analyses to compare the results between the methods. The factors extracted by the traditional approaches are also compared with the results from previous studies conducted in non-urban areas (Krim et al., 1990; Meia and Weber, 1992; Nakazono and Ono, 1987; Roman, 1984; Scott and Selko, 1939; Sheldon, 1950; Uraguchi and Takahashi, 1998; Zhou et al., 1995) to discuss the differences in fox denning requirements depending on habitat type. The protocols of the two traditional analyses are also given below (see METHODS: M4. Analysis 2).

M3. Analysis 1: Den site selection modeling

The modeling process was designed to extract the critical environmental requirements for den site selection by urban red foxes. The environmental requirements in this study is pronounced as the combination of the most affecting landscape factors on their den site selection (hereinafter referred to as "key factors") and the most affecting spatial scale ("key scale"). The "key scale" is not the same as the home range or territory but the "heeding range", in which they would be more nervous about disturbance and secure resources compared with outside the range within their home range. I aimed to extract the best combination of the "key factors" and the "key scale" through the modeling simultaneously, which is performed by all possible subsets models selection using logistic regression analysis and subsequent Akaike's information criterion (AIC) inspection. The protocol for the modeling process is given below and in Figure 5.

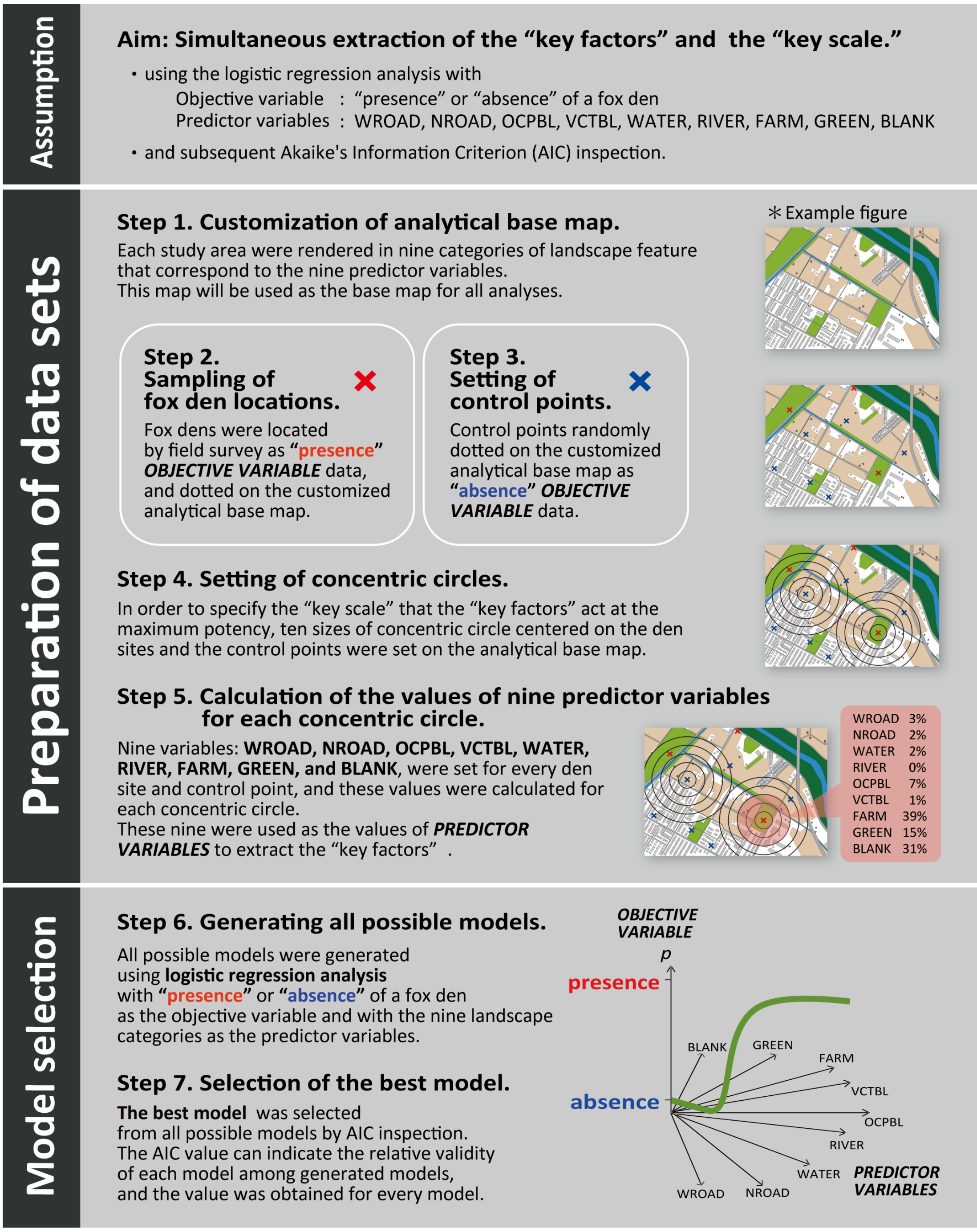


Figure 5. The protocol for the modeling process.
*See also the legend of Figure 6: box A.

M3-1. Assumptions of the modeling

The regression analysis consisted of the presence or absence of a fox den as the objective variable, and nine categories of landscape features as the predictor variables. The nine predictor variables were presented by percentages of area occupied by nine categories of landscape features: "wide road" (WROAD), "narrow road" (NROAD), "occupied building" (OCPBL), "vacant building" (VCTBL), "water place" (WATER), "riverbed" (RIVER), "farmland" (FARM), "green covered area" (GREEN), and "blank space" (BLANK). These were equipped for analyzing urban habitat use by red foxes based on previous studies on fox habitat selection (Krim et al., 1990; Meia and Weber, 1992; Nakazono and Ono, 1987; Roman, 1984; Scott and Selko, 1939; Sheldon, 1950; Uraguchi and Takahashi, 1998; Zhou et al., 1995). These variables were carefully chosen to reflect the sensitivity of foxes against artificial structures when they select the den sites.

Detailed definitions of landscape feature categories and those of corresponding variables and abbreviations are shown in Table 1.

M3-2. Modeling process

The detailed modeling process is described below. The process consists of the preparation of data sets (*Step 1-5*) and model selection (*Step 6-7*). A series of modeling processes was performed using statistical software R 3.0.3 (The R Project for Statistical Computing) (R Core Team,

Table 1. Definitions of the landscape feature categories and terms, and their corresponding variables and abbreviations.

Category of landscape feature	Definition of term	Abbreviation of modeling variable	Abbreviation of linear distance variable
Wide road*	Paved roads (≥ 5.5 m width) and railways.	WROAD	L-wroad
Narrow road*	Paved roads (< 5.5 m width) and unpaved roads.	NROAD	L-nroad
Water place*	Rivers, streams, and drains.	WATER	L-water
Riverbed*	Vegetated or dried areas along rivers.	RIVER	L-river
Occupied building**	Buildings that are always occupied by human activity, i.e. dwelling houses, outlets, and schoolhouses.	OCPBL	L-ocpbl
Vacant building**	Buildings that are not always occupied by human activity, i.e. barns, garden sheds, and garages.	VCTBL	L-vctbl
Farmland***	Meadowlands and croplands.	FARM	L-farm
Green covered area***	Green covered areas except for riverbeds and farmlands, i.e. urban parks and urban green spaces.	GREEN	L-green
Blank space***	Remaining areas that do not have any roads, rivers, water, buildings, or vegetation.	BLANK	L-blank

* Based on definition of numerical information maps.
** Based on definition of numerical information maps and house maps.
*** Extracted from aerial photographs.

2014) and the R packages of all.logistic (Aoki) and glm2 (Marschner, 2012).

Step 1. Customization of analytical base maps

A specialized analytical base map was prepared for each study area by customizing existing thematic maps to render the whole study area in nine categories of landscape features: “wide road”, “narrow road”, “occupied building”, “vacant building”, “water place”, “riverbed”, “farmland”, “green covered area”, and “blank space”.

The categories “occupied building” and “vacant building” were distinguished to investigate whether foxes were sensitive to the presence of humans or artificial structures. “Water place” and “riverbed” were distinguished for detailed investigation of the reason why foxes prefer den sites near a river. It was reported previously that red foxes prefer sites near a river; however, it has not yet been clarified whether they are attracted to rivers just as a source of water or whether they are attracted to other environmental factors associated with the river, such as a riverbed with a slope and dry sand that may enable them to dig easily, fewer invaders, many rodents as food, etc. (Takeuchi and Koganezawa, 1992; Uraguchi and Takahashi, 1998). The category “farmland” was distinguished from “green covered area” to determine if foxes are sensitive to disturbance by farmers or tractors.

The landscape data was referenced from several numerical information maps from the National Land Numerical Information download service (Geographical Survey Institute, Japan (Geographical Survey Institute)) and the Fundamental Geospatial Data 25000 Web Map Service (Geographical Survey Institute, Japan (Geographical Survey Institute)), Residential Maps (Hokkaido-Chizu Co., Ltd. (Hokkaido-Chizu Co., b) and ZENRIN Co., Ltd. (ZENRIN, 2003, 2006)), aerial photographs (PHOTEC Co., Ltd. (PHOTEC Co.) and Google Earth (Google)), and field inspection. The rendering process was performed using geographic information system software (free software: Quantum GIS 1.8.0, QGIS Development Team (QGIS Development Team)), a photo-retouching software (free software: Paint.NET 3.5.10 (Brewster and Jackson)), and image analysis software (free software: Image J, U. S. National Institutes of Health (Rasband)). The latter two were used to extract and ascertain borders of farmlands, green covered areas, and blank spaces from aerial photographs, because these landscape features were not distinguished fully in the numerical information maps.

These customized maps were used as the base maps for all analyses described below. Detailed definitions of the nine landscape feature categories are shown in Table 1. An example customized map is shown in Figure 6.

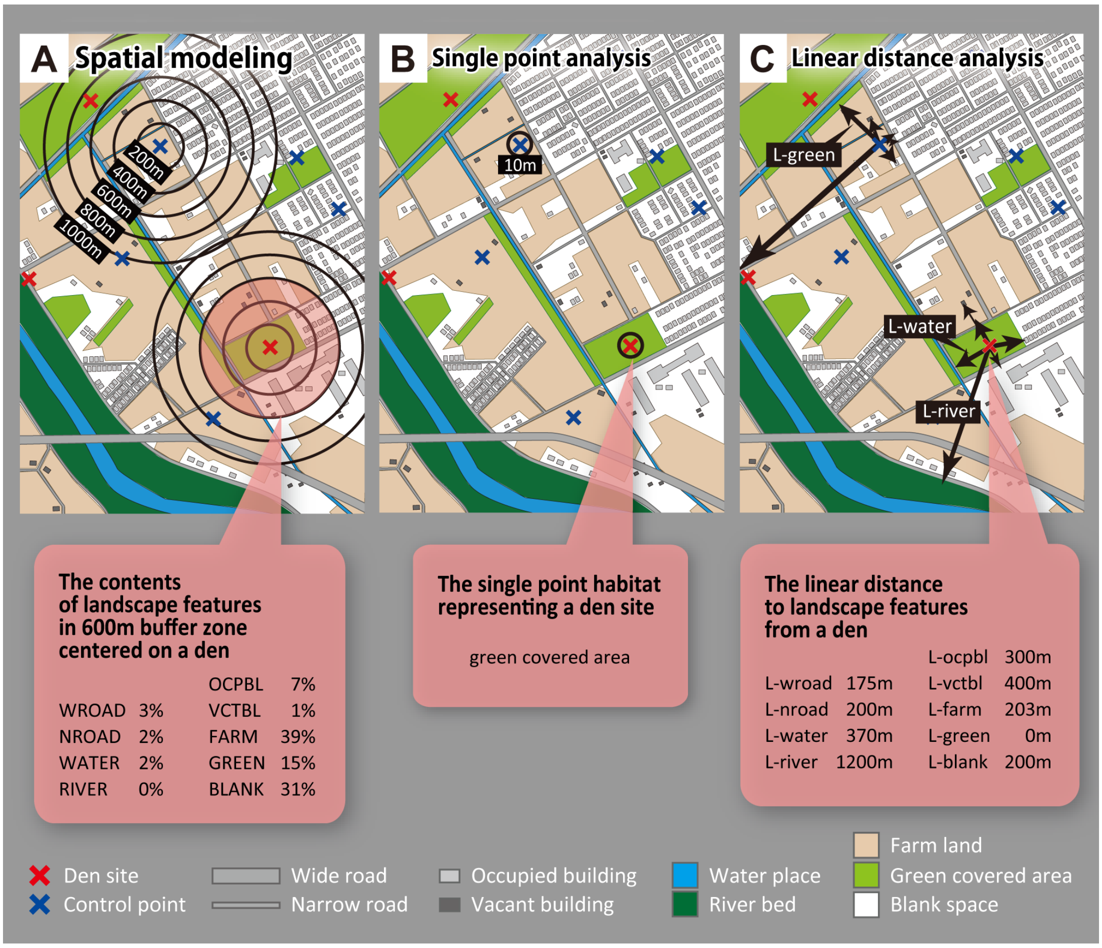


Figure 6. Example of customized analytical base map and calculation methods by use of three types of predictor variables.

Box A shows an example of the calculation of the values of nine variables for spatial modeling. Black open circles indicate ten sizes of concentric circles (100-1000 m in radius, at 100 m intervals) centered on a den site or a control point. In this figure, only circles of 200, 400, 600, 800, and 1000 m are shown. The pink circle indicates a 600 m concentric circle. Percentages of the area occupied with the nine landscape feature categories included in the circle centered on a den site were calculated as shown in the pink call-out.

Box B shows an example of habitat determination by single point analysis. Black open circles indicate a 10 m radius circle centered on a den point or a control point. Just one habitat of a den site included in the radius is determined as shown in the pink call-out.

Box C shows an example of measurements of the values of nine variables for linear distance analysis. Black arrows indicate the shortest distances to the nine landscape feature categories from a den site or a control point. The distances to the nearest nine landscape features from a den site were measured as shown in the pink call-out.

Step 2. Sampling of fox den locations

Fox dens were located as “presence” values of objective variable, and den locations were dotted on the customized analytical base map.

Dens were found by exploring all vegetated areas and unpaved ground along the riverbed from 2002 to 2004 in the Obihiro study area (Figure 4-A), on the basis of the results of questionnaire surveys conducted with staff of city cleaning departments, students of twelve public junior high schools, and farming families. Exploration was carried out from 2004 to 2007 in the Sapporo study area (Figure 4-B) with the support of hunters in addition to location data collected from farmers and previous reports (Oku et al., 2005; Tsukada et al., 2000). All tunnels with a diameter of circa 20 cm excavated by animals were regarded as red fox dens (Nakazono, 1970; Uraguchi and Takahashi, 1998). Another animal that may use such dens around the study areas is *Nyctereutes procyonoides* Gray, 1834 (Raccoon dog), but this is a nonnative species and has not taken root yet in the present study areas. The location data of all dens found through the field surveys were recorded using a GPS receiver (Garmin Ltd., GPS 12CX), and plotted on the customized analytical base map.

Step 3. Setting of control points

As against the points with dens present, control points were dotted randomly on the customized analytical base map as “absence” objective variable data.

In total, 120 points in the Obihiro and 730 points in the Sapporo study areas were generated randomly as points with dens absent on the customized analytical base map. The random points were eliminated and generated newly if they were located on roads, in occupied buildings, or in water. Points on farmland were accepted as control points in this study.

Step 4. Setting of concentric circles

In order to specify the "key scale", ten sizes of concentric circles were set.

An example of these concentric circles is shown in Figure 6-A. The circles were 100 m in radius centered on every den and control point on the analytical base map, and each circle was expanded to 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m from each point in a concentric pattern (200, 400, 600, 800, 1000 m circles are shown in Figure 6-A). The "key scale" was determined from these circles. The values of variables defined in *Step 5* were calculated for each circle around all den sites and control points.

Step 5. Calculation of the values of nine variables for each concentric circle

The values of nine variables within each concentric circle set in *Step 4* were calculated as predictor variables. This calculation was carried out for each size of concentric circle for every den site and control point (as in

Figure 6-A: pink balloon).

Step 6. Generating all possible models

All possible models (${}_9C_1$ + ${}_9C_2$ + ${}_9C_3$ +... + ${}_9C_9$ = 511 models) were generated using logistic regression analyses with “presence” or “absence” of a fox den as the objective variable (see *Steps 2 and 3*), and nine landscape variables: WROAD, NROAD, OCPBL, VCTBL, WATER, RIVER, FARM, GREEN, and BLANK as the predictor variables (see *Step 5*). This procedure was conducted for each of the concentric circles (see *Step 4*).

Step 7. Selection of the best model

Out of all models generated in *Step 6*, the most parsimonious model was selected using AIC inspection. The AIC can indicate the relative validity of each model among all the models generated. The lower the AIC value is, the higher the relative validity of the model will be. The rank of the models can be determined using the AIC value only among the values generated for the same objective variable from the same set of predictor variables. For example, the AIC values for the models of Obihiro and Sapporo study areas cannot be compared.

M3-3. Model validation

The best models established here were validated by the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. The AUC can be used to validate the model's accuracy, i.e. the validity of the variables set included in the model (Kulkarni et al., 2010). AUC values range between 0.5 (low accuracy) and 1 (high accuracy).

Prediction performances (= probabilities of correct prediction: den-present or -absent) of the established models were also evaluated by the rates of concordance between predicted values by the models and observed values.

M4. Analysis 2: Analyses by traditional methods

The traditional methods (univariate analyses, not regression modeling) target only the "key factors" extraction, not the "key scale". The nine landscape feature categories (defined in *Step 1* and Table 1) and the control points (generated in *Step 3*) were shared with the spatial modeling protocol. The validity of these analytic methods is also discussed (see DISCUSSION: D2-2).

M4-1. Single point analysis

The first traditional analysis method regards the den site as just a "single point" habitat, not a complex of environmental features. This is the most primitive method of quantitative analysis of den site distribution patterns. This method is not capable of extracting detailed “key factors” of den site selection but is convenient for providing a brief overview of the tendencies of den sites distribution. The habitat of a den site was determined using only one major landscape feature: “wide road”, “narrow road”, “occupied building”, “vacant building”, “water place”, “riverbed”, “farmland”, “green covered area”, and “blank space” in a 10 m radius centered on the den point. An example of this determination of habitat is shown in Figure 6-B. The habitat of a control point (120 points in Obihiro and 730 points in Sapporo) was determined in the same way. The habitats of den sites and habitat availability were compared by 9 × 2 G-test of fitness (Sokal and Rohlf, 1994).

M4-2. Linear distance analysis

The second traditional analysis method evaluates the disturbing or attracting factors as “linear distance” from the den site. This popular method of quantitative analysis of relative usage of landscape can be used to extract “key factors” for den site selection. Nine variables for this analysis were set. The variables representing each den point were determined as the distances from each den to the nearest “wide road” (L-wroad), “narrow road” (L-nroad), “occupied building” (L-ocpbl), “vacant building” (L-vctbl), “water place” (L-water), “riverbed” (L-river), “farmland” (L-farm), “green covered area” (L-green), and “blank space”

(L-blank). An example of the measuring method of the values of each variable is shown in Figure 6-C. Detailed definitions of landscape feature categories and the corresponding variables and abbreviations are shown in Table 1. Values of the nine variables were calculated for den sites and control points (120 points in Obihiro and 730 points in Sapporo) and the values were compared by Mann-Whitney *U* test (Uraguchi and Takahashi, 1998).

RESULTS

In the Obihiro study area, a total of 35 fox dens were found (0.59 dens /2,793 people /km^2). All dens found were tunnels excavated in the ground. Most were dug in flat ground and a few dens were on a slope.

In the Sapporo study area, a total of 65 fox dens were found (0.18 dens /5,042 people /km^2). All dens reported in previous studies (21 dens) in 1997, 1998 (Tsukada et al., 2000) and 2003 (Oku et al., 2005) still existed exactly at the same location or in the close vicinity. The owners of these dens were considered to be the offspring of the previous owners, because red foxes tend to inherit the dens in which they were born and raised. The remaining 44 dens were newly found in the present study. Most dens were excavated in the ground, but eight found in the UPA were converted from artificial structures such as abandoned barns or stacks of scrap wood and building materials. For the dens dug in the ground, dens in riverbeds were on a slope but most were dug in flat ground.

R1. Established fox den site selection models

The best model consisting of the best combination of the “key factors” and “key scale” for den site selection by foxes was determined for each city. Higher ranked models for each study area are listed in Tables 2 and 3, and the confidence intervals of the regression coefficients included

Table 2. Selected variables in the best models for each concentric circle in Obihiro study area.
The numbers under the variables are partial regression coefficients of selected variables in each model. The partial regression coefficient indicates the contribution ratio of each variable. Ranks of models are given in order of AIC values. ΔAIC in this table indicates the difference in AIC value from the higher ranked model right above.

Rank of model	Radius of concentric circle (m)	AIC value	ΔAIC	Intercept	Variable								
					WROAD	NROAD	WATER	RIVER	OCPBL	VCTBL	FARM	GREEN	BLANK
1	500	46.2	0.0	1.749	-0.306	-0.709	-	-	-0.338	-	-	0.613	-
2	400	55.1	8.9	-0.005	-0.180	-0.489	-	-	-0.271	-	-	0.522	-
3	300	57.5	2.4	9.205	-0.133	-0.597	-	-	-0.407	-0.184	-	0.216	-
4	600	59.7	2.1	1.808	-0.186	-0.514	-	-	-0.201	-	-	0.275	-
5	200	73.1	13.4	5.616	-0.226	-0.616	-	-	-0.280	-0.190	-	0.047	-
6	100	75.7	2.6	3.456	-0.245	-0.290	-	-	-0.222	-0.131	-	0.766	-0.162
7	700	83.4	7.7	3.466	-0.192	-0.563	-	-	-0.159	-	-	0.041	-
8	800	105.0	21.6	1.501	-0.118	-0.302	-	-	-0.147	-	-	0.145	-
9	1000	126.2	21.2	-0.222	-0.160	-0.132	-	0.438	-0.054	-	-	0.203	-0.067
10	900	126.4	0.1	2.738	-0.196	-0.196	-	-	-0.049	-	-	0.141	-0.059

Table 3. Selected variables in the best models for each concentric circle in Sapporo study area.

The numbers under the variables are partial regression coefficients of selected variables in each model. The partial regression coefficient indicates the contribution ratio of each variable. Ranks of models are given in order of AIC values. ΔAIC in this table indicates the difference in AIC value from the higher ranked model right above.

Rank of model	Radius of concentric circle (m)	AIC value	ΔAIC	Intercept	Variable								
					WROAD	NROAD	WATER	RIVER	OCPBL	VCTBL	FARM	GREEN	BLANK
1	300	53.3	0.0	-10.167	-0.169	-	-	0.328	-0.128	-	-	0.575	-
2	400	56.5	3.2	-5.822	-0.266	-	-	0.192	-0.273	-1.022	-	0.590	-
3	200	64.2	7.7	-9.526	-0.186	-	-	0.344	-0.134	-	-	0.562	-
4	600	80.8	16.6	-8.018	-0.474	-	-	0.338	-0.235	-	-	0.422	-
5	500	91.1	10.3	-4.343	-0.314	-0.602	-	0.115	-0.093	-	-	0.476	-0.061
6	800	95.1	4.1	-4.326	-0.263	-0.353	-	0.147	-0.238	-	-	0.380	-
7	700	96.8	1.6	-2.783	-0.330	-	-	0.144	-0.300	-1.016	-	0.413	-
8	100	107.3	10.5	-2.265	-0.288	-0.724	-	0.141	-0.247	-	-	0.393	-
9	900	109.2	2.0	-8.850	-0.047	-	-	0.147	-0.259	-	-	0.645	-0.407
10	1000	120.0	10.7	-2.409	-0.268	-0.846	-	0.127	-0.270	-	-	0.419	-

in each model are shown in Tables 4 and 5. Changes in AIC values of the models depending on the sizes of concentric circles are shown in Figure 7. AUC values that indicate the model's accuracy were shown in Table 6. The rates of concordance between predicted results by the established models and observed values that indicate the prediction performance of the models were shown in Figure 8.

In the Obihiro study area, higher ranked models produced comparatively stable variables, as shown in Table 2. The lowest AIC value was given for the model with a 500 m radius concentric circle size (Figure 7) and the accuracy of this best model is sufficiently high (AUC= 0.987; Table 6). Extracted variables within the best size of concentric circle were WROAD, NROAD, OCPBL, and GREEN. The directions of effect of these variables were minus for WROAD, NROAD, and OCPBL, and plus for GREEN depending on partial regression coefficients. The prediction formula of the best model is shown below. "*p*" indicates the probability of fox denning at a targeted point.

$$p = \frac{1}{1 + \exp\{-(1.749 - 0.306\mathrm{WROAD} - 0.709\mathrm{NROAD} - 0.338\mathrm{OCPBL} + 0.613\mathrm{GREEN})\}}$$

This formula indicates the probability of denning by red foxes in the Obihiro urban area is high in areas that include low densities of wide roads, narrow roads, and occupied buildings, and a high density of green covered areas within a 500 m radius area. Probability of correct prediction by this Obihiro model was 92.3% (Figure 8-A).

Application example of this model is shown in Figure 9-A. If you

Table 4. Confidence intervals of the coefficients of the selected variables included in the models in each scale for Obihiro study area.

Variable	100m			200m			300m			400m			500m		
	Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI	
		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%
Intercept	3.456	0.583	6.861	5.616	3.213	8.776	9.205	3.864	15.670	-0.005	-2.813	2.700	1.749	-1.266	5.057
WROAD	-0.245	-0.436	-0.103	-0.226	-0.409	-0.079	-0.133	-0.273	-0.028	-0.180	-0.345	-0.059	-0.306	-0.571	-0.123
NROAD	-0.290	-0.529	-0.113	-0.616	-0.969	-0.356	-0.597	-1.123	-0.261	-0.489	-0.959	-0.180	-0.709	-1.282	-0.323
WATER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIVER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OCPBL	-0.222	-0.391	-0.101	-0.280	-0.518	-0.075	-0.407	-0.896	-0.023	-0.271	-0.491	-0.123	-0.338	-0.626	-0.146
VCTBL	-0.131	-0.248	-0.331	-0.190	-0.321	-0.083	-0.184	-0.339	-0.064	-	-	-	-	-	-
FARM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GREEN	0.766	0.432	1.250	0.047	-0.003	0.111	0.216	0.063	0.468	0.522	0.239	0.917	0.613	0.257	1.112
BLANK	-0.162	-0.317	-0.032	-	-	-	-	-	-	-	-	-	-	-	-

Variable	600m			700m			800m			900m			1000m		
	Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI	
		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%
Intercept	1.808	-0.976	4.584	3.466	1.711	5.617	1.501	0.005	3.113	2.738	1.238	4.421	-0.222	-1.923	1.486
WROAD	-0.186	-0.341	-0.079	-0.192	-0.348	-0.061	-0.118	-0.211	-0.039	-0.196	-0.302	-0.109	-0.160	-0.257	-0.077
NROAD	-0.514	-0.931	-0.230	-0.563	-0.885	-0.322	-0.302	-0.503	-0.152	-0.196	-0.323	-0.093	-0.132	-0.265	-0.020
WATER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIVER	-	-	-	-	-	-	-	-	-	-	-	-	0.438	0.209	0.719
OCPBL	-0.201	-0.348	-0.088	-0.159	-0.283	-0.052	-0.147	-0.252	-0.054	-0.049	-0.115	0.015	-0.054	-0.106	-0.012
VCTBL	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FARM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GREEN	0.275	0.115	0.534	0.041	-0.002	0.094	0.145	0.054	0.263	0.141	-0.041	0.346	0.203	0.058	0.363
BLANK	-	-	-	-	-	-	-	-	-	-0.059	-0.112	-0.011	-0.067	-0.126	-0.015

Table 5. Confidence intervals of the coefficients of the selected variables included in the models in each scale for Sapporo study area.

Variable	100m			200m			300m			400m			500m		
	Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI	
		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%
Intercept	-2.265	-4.295	-0.528	-9.526	-14.576	-6.195	-10.167	-16.125	-6.317	-5.822	-10.200	-2.870	-4.343	-7.322	-1.954
WROAD	-0.288	-0.434	-0.178	-0.186	-0.361	-0.063	-0.169	-0.386	-0.031	-0.266	-0.483	-0.124	-0.314	-0.513	-0.170
NROAD	-0.724	-1.132	-0.376	-	-	-	-	-	-	-	-	-	-0.602	-1.030	-0.245
WATER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIVER	0.141	0.083	0.207	0.344	0.206	0.564	0.328	0.175	0.573	0.192	0.113	0.299	0.115	0.061	0.178
OCPBL	-0.247	-0.391	-0.134	-0.134	-0.287	-0.022	-0.128	-0.331	0.022	-0.273	-0.487	-0.120	-0.093	-0.218	0.008
VCTBL	-	-	-	-	-	-	-	-	-	-1.022	-1.769	-0.472	-	-	-
FARM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GREEN	0.393	0.257	0.583	0.562	0.348	0.919	0.575	0.361	0.907	0.590	0.366	0.959	0.476	0.320	0.695
BLANK	-	-	-	-	-	-	-	-	-	-	-	-	-0.061	-0.129	0.000

Variable	600m			700m			800m			900m			1000m		
	Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI		Coefficient	95%CI	
		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%		2.5%	97.5%
Intercept	-8.018	-11.124	-5.725	-2.783	-4.959	-0.945	-4.326	-6.385	-2.680	-8.850	-11.851	-6.535	-2.409	-4.498	-0.595
WROAD	-0.474	-0.947	-0.084	-0.330	-0.547	-0.167	-0.263	-0.451	-0.138	-0.047	-0.099	0.001	-0.268	-0.424	-0.146
NROAD	-	-	-	-	-	-	-0.353	-0.725	-0.030	-	-	-	-0.846	-1.220	-0.522
WATER	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RIVER	0.338	0.227	0.486	0.144	0.089	0.211	0.147	0.089	0.216	0.147	0.096	0.207	0.127	0.075	0.184
OCPBL	-0.235	-0.393	-0.121	-0.300	-0.481	-0.156	-0.238	-0.394	-0.117	-0.259	-0.450	-0.090	-0.270	-0.420	-0.148
VCTBL	-	-	-	-1.016	-1.515	-0.619	-	-	-	-	-	-	-	-	-
FARM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GREEN	0.422	0.292	0.601	0.413	0.287	0.589	0.380	0.265	0.545	0.645	0.470	0.878	0.419	0.285	0.603
BLANK	-	-	-	-	-	-	-	-	-	-0.407	-0.774	-0.080	-	-	-

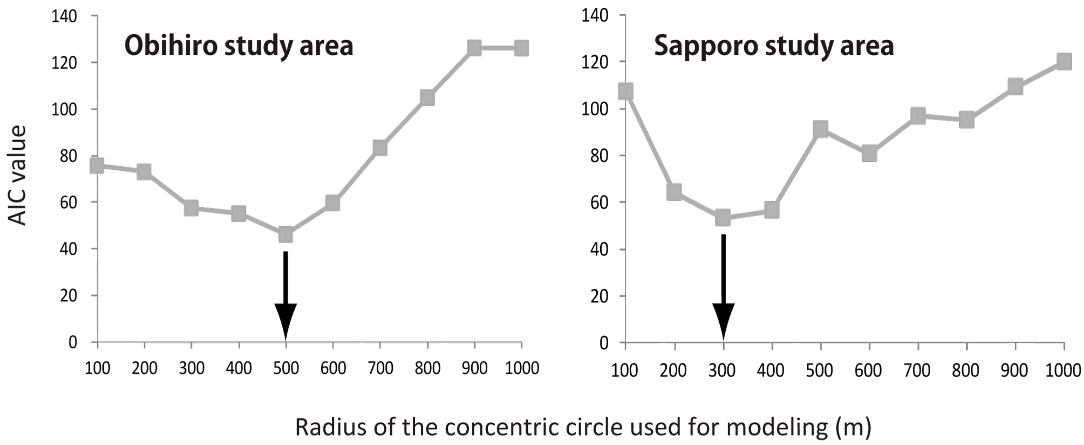


Figure 7. Changes in AIC values depending on the size of concentric circles in the two study areas.

AIC values of the best models of each of the ten sizes of concentric circles are shown. Arrows indicate the best radius of the concentric circles.

Table 6. Comparison of the model's accuracy among the variable types.

Type of variable	Obihiro			Sapporo		
	Selected variables	Model AUC	Model R^2	Selected variables	Model AUC	Model R^2
Percentages of landscape features*	WROAD NROAD OCPBL GREEN	0.987	0.781	WROAD RIVER OCPBL GREEN	0.995	0.904
Linear distance	L-river L-green	0.722	0.128	L-river L-ocpbl L-vctbl L-farm L-blank	0.881	0.298
Single point habitat	n/a**	-	-	n/a**	-	-

* The values are shown for the best model for each study area.

** Single point habitat is not applicable as the predictor variable for modeling because this variable is univariate.

A Obihiro Model		predicted		total
		den-absent	den-present	
observed	den-absent	113	7	120
	den-present	5	30	35
total		118	37	155

$$\text{Probability of correct prediction of the Obihiro model} = \frac{(113+30)}{155} = 0.923 = 92.3\ \%$$

B Sapporo Model		predicted		total
		den-absent	den-present	
observed	den-absent	729	1	730
	den-present	5	60	65
total		734	61	795

$$\text{Probability of correct prediction of the Sapporo model} = \frac{(729+60)}{795} = 0.992 = 99.2\ \%$$

Figure 8. The rates of concordance between predicted results by the established models and observed values for Obihiro (Box A) and Sapporo (Box B) models.
Pink cells indicate the case numbers that were correctly predicted whether dens should be present or absent. Prediction performance of each model was calculated as the probability of correct prediction.

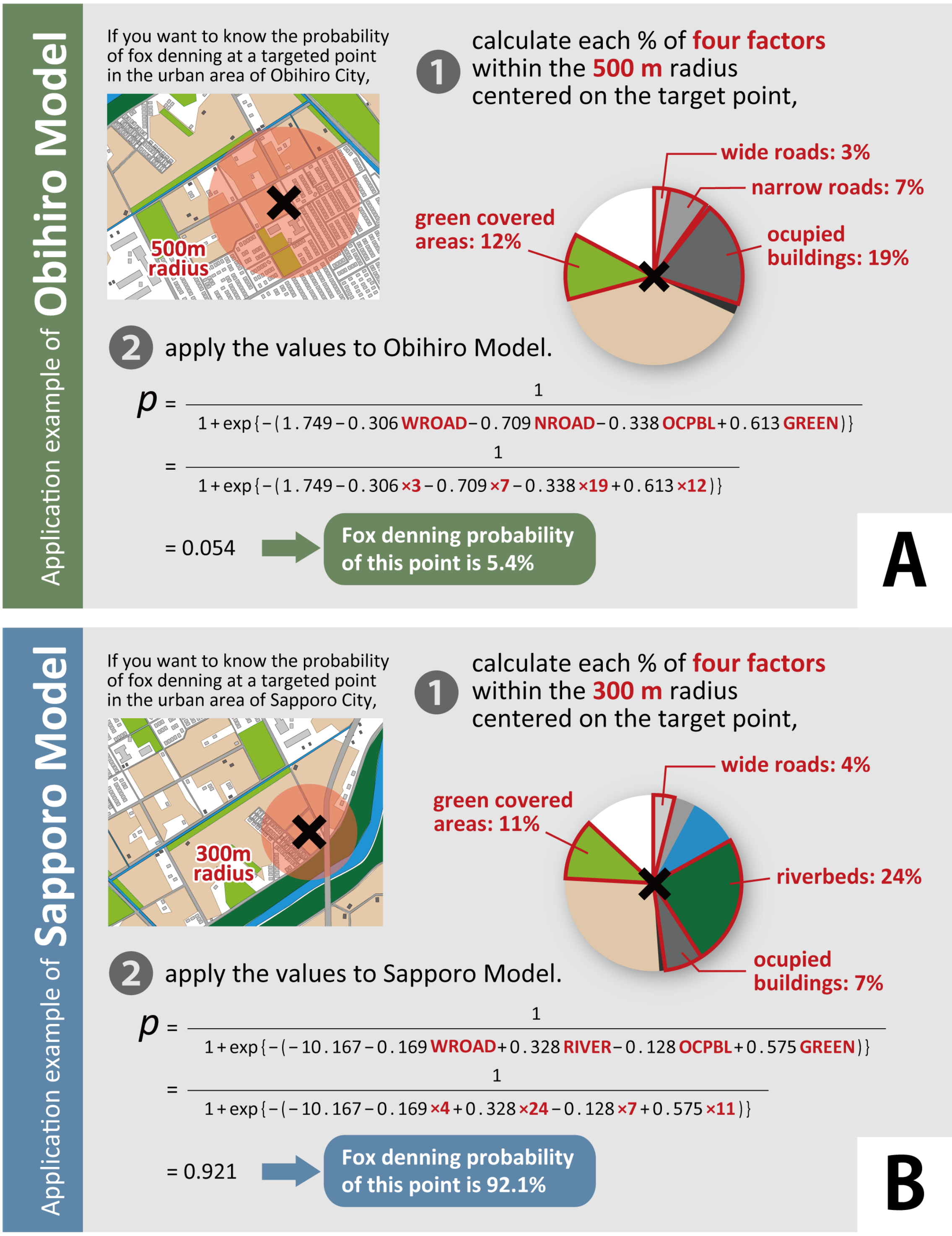


Figure 9. Application examples of the established models for the two cities.

want to know the probability of fox denning at a targeted point in the urban area of Obihiro City, 1) calculate each percentage of wide roads, narrow roads, occupied buildings, and green covered areas within the 500 m radius centered on the point, 2) apply the values to the model, and then, you can calculate the probability.

In the Sapporo study area, higher ranked models produced comparatively stable variables, as shown in Table 3. The lowest AIC value was given for the model with a 300 m radius concentric circle size (Figure 7) and the accuracy of this best model is sufficiently high (AUC= 0.995; Table 6). Extracted variables within the best size of concentric circle were WROAD, OCPBL, RIVER, and GREEN. The directions of effect of these variables were minus for WROAD and OCPBL, and plus for RIVER and GREEN depending on partial regression coefficients (Table 3). The prediction formula of the best model is shown below. "*p*" indicates the probability of fox denning at a targeted point.

$$p = \frac{1}{1 + \exp\{-(-10.167 - 0.169\mathrm{WROAD} + 0.328\mathrm{RIVER} - 0.128\mathrm{OCPBL} + 0.575\mathrm{GREEN})\}}$$

This formula indicates that the probability of denning by red foxes in the Sapporo urban area is high in areas that include low densities of wide roads and occupied buildings, and high densities of riverbeds and green covered areas within a 300 m radius area. Probability of correct prediction by this Sapporo model was 99.2% (Figure 8-B).

Application example of this model is shown in Figure 9-B. If you want to know the probability of fox denning at a targeted point in the urban area of Sapporo City, 1) calculate each percentage of wide roads, occupied buildings, riverbeds, and green covered areas within the 300 m radius centered on the point, 2) apply the values to the model, and then, you can calculate the probability.

R2. Results of traditional analyses

R2-1. Single point analysis

The tendency of den site distribution was examined by analysis using a single point habitat. Out of the 35 dens found in Obihiro study area, 16 (45.7%) were on "riverbed", 16 (45.7%) were in "green covered area", and the remaining 3 (8.6%) were in "farmland" (Table 7). Out of all 65 dens found in Sapporo study area, 37 (56.9%) were in "green covered area", 11 (16.9%) were in urban "farmland", 9 (13.8%) were on "riverbed", and the remaining 8 (12.3%) were in "vacant building" (Table 8).

R2-2. Linear distance analysis

The "key factors" for den site selection were determined from comparison of linear distance variables between den points and control points. Foxes in the Obihiro study area preferred places near "riverbed" (L-river) (p= 0.0037) and "green covered area" (L-green) (p= 0.0027) as den sites. No significant differences were found in the distance to "wide road" (L-wroad) (p= 0.9676), "narrow road" (L-nroad) (p= 0.9216), "water

Table 7. Distribution pattern of the red fox dens and control points per single point habitat in Obihiro study area.

Single point habitat	Number of den sites (%)		Number of control points (%)	
Wide road	0	(0.0)	-	-
Narrow road	0	(0.0)	-	-
Water place	0	(0.0)	-	-
Riverbed	16	(45.7)	13	(10.8)
Occupied building	0	(0.0)	-	-
Vacant building	0	(0.0)	19	(15.8)
Farmland	3	(8.6)	25	(20.8)
Green covered area	16	(45.7)	28	(23.3)
Blank space	0	(0.0)	35	(29.2)
Total	35	(100)	120	(100)

$G = 48.947$, $p < 0.0001$.

Table 8. Distribution pattern of the red fox dens and control points per single point habitat in Sapporo study area.

Single point habitat	Number of den sites (%)		Number of control points (%)	
Wide road	0	(0.0)	-	-
Narrow road	0	(0.0)	-	-
Water place	0	(0.0)	-	-
Riverbed	9	(13.8)	72	(9.9)
Occupied building	0	(0.0)	-	-
Vacant building	8	(12.3)	160	(21.9)
Farmland	11	(16.9)	122	(16.7)
Green covered area	37	(56.9)	175	(24.0)
Blank space	0	(0.0)	201	(27.5)
Total	65	(100)	730	(100)

$G = 57.005$, $p < 0.0001$.

place" (L-water) (p= 0.0990), "occupied building" (L-ocpbl) (p= 0.0719), "vacant building" (L-vctbl) (p= 0.9488), "farmland" (L-farm) (p= 0.8552), or "blank space" (L-blank) (p= 0.0673) from dens (Table 9). Foxes in the Sapporo study area preferred places near "riverbed" (L-river) (p <0.0001), "farmland" (L-farm) (p <0.0001), or "green covered area" (L-green) (p <0.0001) as den sites. No significant differences were found in the distance to "wide road" (L-wroad) (p= 0.3091), "narrow road" (L-nroad) (p= 0.5728), "water place" (L-water) (p= 0.7242), "occupied building" (L-ocpbl) (p= 0.3728), "vacant building" (L-vctbl) (p= 0.0941), or "blank space" (L-blank) (p= 0.3470) from dens (Table 10).

Table 9. Average distances (±SD) from the nearest landscape feature to the red fox dens and control points in Obihiro study area.

Linear distance parameter	Den site		Control point		p
	Average distance (m)	n	Average distance (m)	n	
L-wroad	173 (±132)	35	167 (±103)	120	0.9676
L-nroad	64 (±56)	35	61 (±51)	120	0.9216
L-water	141 (±185)	35	157 (±225)	120	0.0990
L-river	288 (±387)	35	722 (±1003)	120	0.0037 *
L-ocpbl	200 (±238)	35	195 (±108)	120	0.0719
L-vctbl	110 (±93)	35	109 (±86)	120	0.9488
L-farm	468 (±390)	35	531 (±480)	120	0.8552
L-green	115 (±176)	35	272 (±309)	120	0.0027 *
L-blank	246 (±168)	35	222 (±248)	120	0.0673

*$p < 0.05$

Table 10. Average distances (±SD) from the nearest landscape feature to the red fox dens and control points in Sapporo study area.

Linear distance parameter	Den site		Control point		*p*
	Average distance (m)	n	Average distance (m)	n	
L-wroad	306 (±364)	65	196 (±121)	730	0.3091
L-nroad	86 (±75)	65	77 (±42)	730	0.5728
L-water	370 (±514)	65	362 (±591)	730	0.7242
L-river	1024 (±996)	65	2446 (±1766)	730	< 0.0001 *
L-ocpbl	152 (±130)	65	143 (±84)	730	0.3728
L-vctbl	111 (±108)	65	79 (±57)	730	0.0941
L-farm	352 (±661)	65	1747 (±1364)	730	< 0.0001 *
L-green	155 (±425)	65	178 (±197)	730	< 0.0001 *
L-blank	106 (±89)	65	93 (±75)	730	0.3470

*p <0.05

DISCUSSION

In this study, a new spatial model established to specify the potential habitat of urban red fox dens with a view to preventing contamination by *E. multilocularis* eggs. This model detects the first priority of environmental requirements for den site selection by red foxes in urban areas to identify the suitable locations for delivering anthelmintic baits. The present study's approach focused on the den distribution of red foxes, the definitive host, which differs from previous studies that focused on observed cases of infection in humans or foxes. The new modeling protocol was developed by modifying a general modeling method commonly used for arthropods. A discussion is made below for the differences between the general modeling and the new protocol.

In addition to establishment of the new spatial model, two traditional habitat analyses were conducted to compare the tendencies of denning requirements between urban foxes in the present study and non-urban foxes from previous studies.

D1. Fox den site selection models

D1-1. Interpretation of the models

Obihiro City model suggested that red foxes heed the environment within a 500 m radius from their den sites, and prefer low densities of wide roads, narrow roads, and occupied buildings, and a high density of green covered areas within this range. For Sapporo City, their heeding range is 300 m radius and they prefer low densities of wide roads and occupied buildings, and high densities of rivers and green covered areas.

The difference in size of the heeding range for denning between the two cities may come from differences in sensitivity to the surroundings depending on the degree of urbanization, although this cannot be judged from the present study. Although the size of the ranges differed greatly between the two cities, foxes commonly focused on the densities of wide roads, occupied buildings and green covered areas for their den sites even if the degrees of urbanization were different (Tables 2 and 3, Figure 7).

In regard to the preference for sites with a high proportion of green covered areas, this was considered reasonable and appropriate because vegetated ground is easy to dig for denning (Roman, 1984), and the canopy will protect the den from direct sunlight and rain (Goszczynski, 1989; Uraguchi and Takahashi, 1998). Furthermore, a vegetated environment will have a high density of prey animals compared with artificial landscapes and thickets prevent easy access by humans. The avoidance of areas with a high density of wide roads and occupied buildings may arise from the low proportion of green covered areas in such areas. Alternatively, a high density of wide roads in their core living area may raise the risk of car accidents. In the present study, the categories “OCPBL” and “VCTBL” were purposely separated in order to clarify the ecological implication of building structures for red foxes, and the result of ignoring vacant buildings suggests that red foxes are nervous about the presence of occupants, not just building structures. In fact, some dens were observed in abandoned barns in Sapporo City. The tolerance to building structures could be developed in Sapporo population and vacant buildings may provide acceptable environment, which save effort of digging dens and can be even beneficial as a shelter from invaders, such as crows and raptores hunting cubs.

The avoidance of areas with a high density of narrow roads was confirmed only in Obihiro City. For narrow roads, the main users are not cars but pedestrians, bicycles, and dogs accompanied by owners. In the present study areas, foxes tended to avoid walking or cycling people but not cars as potential invaders. The presence of humans and dogs negatively affects denning activity (unpublished data). This result may be affected by varying degrees of tolerance by red foxes toward humans and dogs depending on the degree of urbanization of their territories, which was considered a prevailing reason why the heeding range for denning is larger in Obihiro City than in Sapporo although further research is needed on this topic.

The preference for riverbed areas was confirmed only in Sapporo City. Riverbeds have similar advantages to green covered areas for foxes. The study area in Sapporo City had a much lower proportion of green covered areas than that of Obihiro, hence, it was suspected that they select riverbed areas to compensate for the lack of the most suitable habitat.

D1-2. Improved points in the developed modeling protocol

The general modeling method required modifications as discussed in order to extract environmental factors for denning requirements for this mid-sized mammal in the micro-habitats of urban landscapes.

Point 1. Targeting "presence or absence" of dens, not "abundance" of individuals nor dens

Models of potential habitats of red foxes within the urban area need to be based on the "presence or absence" of the dens, not on the "abundance" of individuals. In arthropod modeling, it is recommended that the models need to be based on vector abundance rather than simply vector presence (Eisen and Eisen, 2008). However, this is not applicable to fox den-based modeling at a city level. The unit for red foxes is a family consisting of approximately 4-7 individuals and an exclusive territory maintained by the family members. Hence, the densities of fox individuals on a grid do not represent the suitability of habitat as is the case for arthropods, because fox territories do not overlap each other, and the density of individuals in a territory varies just depending on the family size. Moreover, the size of each territory is always larger than a standard grid on existing maps especially in the area having low fox densities, and the density of individual is too low to make a comparison. In contrast, the presence of dens represents the habitat suitability for foxes. Dens are the pivot of their territories, and suitable environments for making dens are fundamental to setting up a territory. I used the presence or absence of dens as the target of modeling. Neither the number nor density of dens makes any sense on this modeling because a fox family always owns and maintains multiple dens in a territory.

Point 2. Setting predictor variables appropriate for urban red foxes

New variables were set as predictor variables for the logistic regression analysis in this study, although the general modeling method conveniently uses landscape feature categories of existing thematic maps as predictor variables. My pre-observation study suggested that disturbance is the critical factor for the establishment of red foxes in urban landscape; however, few landscape categories in existing thematic maps were sufficient to evaluate these factors. Analysis with inappropriate variables will lead the extraction of exact environmental requirements into failure (Cecchi et al., 2008). Hence, more detailed categories focusing on the degree of disturbance and usage for red foxes are necessary to set appropriate variables to extract sufficient environmental requirements for foxes in urban landscapes. Nine new landscape features were set as variables for this purpose, and the analytical base map was newly rendered to fit these new variables.

Point 3. Modeling with a optimal resolution, "key scale"

The “key scale” was determined using multiple concentric circles (see METHODS: M3-2: *Step 4*), instead of using arbitrary sized grids (= resolutions) on the existing thematic maps. An arbitrary grid size has usually been used as a modeling unit in many previous studies; however, it was reported that modeling based on the proper scale for the target species is necessary to extract precise environmental factors (Cecchi et al., 2008; McPherson et al., 2004), or establishing a model based on an arbitrary grid size may lead to over- or under-estimates of potential as habitats (Austin, 2002; Gibson et al., 2004). Meanwhile, any grid or polygon on an existing thematic map is not always adoptable to extract the denning requirements of urban red foxes. The new method developed in this study solves the problem of the disagreement between arbitrary grid size and actual requisite scale of the target species by determining the scale for each study area in the process of modeling. My observations suggested that the size of the heeding range for denning can vary depending on their sensitivity to disturbance, for example, foxes in Sapporo City seem to be nervous about smaller range than foxes in Obihiro City. The new model determined the heeding ranges as circles of 500 m radius in Obihiro City (Table 2) and of 300 m in Sapporo City (Table 3), as “key scale”, i.e. modeling unit for each city.

D2. Traditional analyses

D2-1. Comparison with non-urban areas in previous reports

The results of analyses using two traditional methods in the present study and the results in previous papers showed similar tendencies of den site selection by red foxes; however, the new category of the riverbed environment revealed a more precise reason of the preference.

The result of the single point habitat analysis showed that foxes preferred riverbeds, farmlands, and green covered areas as den sites in both Obihiro and Sapporo City (Tables 7 and 8). Indicating preference to riverbeds and green covered areas was reasonable and agree with previous reports (Goszczynski, 1989; Roman, 1984; Uraguchi and Takahashi, 1998), as is described also in DISCUSSION: D1-1, and farmlands assumed to play a similar role in some cases. The preference of this kind of environment was frequently suggested in other landscapes (Krim et al., 1990; Meia and Weber, 1992; Nakazono and Ono, 1987; Roman, 1984; Scott and Selko, 1939; Sheldon, 1950; Uraguchi and Takahashi, 1998; Zhou et al., 1995).

Linear distance analysis in this study showed common tendencies in the two study areas, in that foxes preferred places near riverbeds and green covered areas as their den sites. On the other hand, they did not exhibit any interest in the distance to wide roads, narrow roads, occupied buildings, vacant buildings, water places, or blank spaces (Tables 9 and 10). The preference for vegetated environments was also reported in other non-urban areas, as mentioned above, and in particular their preference for sites in the vicinity of rivers is known (Takeuchi and Koganezawa, 1992; Uraguchi and Takahashi, 1998). In this study, preference for riverbeds was high in both cities regardless of the degree of urbanization, whereas a preference for water places was not confirmed (Tables 9 and 10), unlike in primitive forests and rural landscape (Roman, 1984; Uraguchi and Takahashi, 1998). In the present study, the categories "water place" and "riverbed" were purposely separated in order to extract the ecological implications of rivers for red foxes. The preference for riverbeds and the disregarding of water places suggests that they are attracted to rivers as a consequence of the river environment (sloping banks and dry sand that enable them to dig easily, few invaders, and many rodents as food, etc.), not just as a source of water.

Although green covered areas were preferred in both study areas, farmlands was preferred only in Sapporo City and disregarded in Obihiro City (Tables 9 and 10). Farmlands may compensate for the lack of green covered areas in Sapporo City. The different reaction to farmlands between foxes in Obihiro and Sapporo City may be caused by different levels of tolerance to disturbance by human activities. In fact, my direct observation of some dens made in farmlands in Sapporo City suggested the red foxes have some level of the tolerance to farming disturbance, because they came back and remade dens soon in exactly the same places even when the original dens were completely destroyed by farmers. Although these two categories of landscape, green covered area and farmland, could have huge difference in the degree of disturbance by human activities, it is not possible to judge the sensitivity or tolerance of red foxes to farming disturbance in the present study. Another variable that can express the degree of disturbance in farmland could be set to detect the sensitivity of the red foxes.

D2-2. Invalidity of traditional methods for urban foxes

Specification of key environmental factors for red fox den site selection should be conducted depending on the priorities of foxes among the environment variables tested. However, both the single point and linear distance analyses do not allow for determination of the rank order of each variable, although these methods provide a quick means to obtain an overview of the environmental tendencies. The unsuitability of these methods arises from the lack of suitability of variables in a heterogeneous urban landscape and the properties of the statistical tests (see METHODS: M4. Analysis 2).

Variables used for the single point and linear distance analyses are not appropriate to evaluate complex properties of landscape structure in an urban environment. The single point variables oversimplify the heterogeneous urban landscape with only one representative value for each unit to express the fox’s home range. Linear distance variables are also not appropriate for urban landscapes mainly consisting of artificial structures, such as roads and residences, at a high density. In the present study areas, the artificial structures were distributed densely and evenly across the areas; therefore, all points must be automatically located near to these. This is probably the reason why minimum linear distances from the artificial structures to actual den sites and to the random control points are not significantly different. In fact, the new modeling method extracted roads and occupied buildings as important avoiding factors for urban red foxes, whereas the linear distance analysis could not detect these artifacts variables (see RESULTS: R1 and R2-2, DISCUSSION: D1-1 and D2-1). Generating models were tried with the significant variables extracted in the linear distance analysis and found it was invalid (R^2= 0.128 for Obihiro, R^2= 0.298 for Sapporo; Table 6). The predictive abilities are also low compared with the best models established by use of the percentages of landscape features as predictor variables (AUC= 0.722 for Obihiro, AUC= 0.881 for Sapporo; Table 6).

Univariate analyses such as G-test and Mann-Whitney *U* test can only detect if the individual variables have significance or not. Because the mere detection of significant variables cannot judge the rank order of significance among them, multivariate analysis conducted in this study is necessary for the extracting the most affecting variables by detecting the weights (= contribution ratios) of individual variables. For example in non-urban landscapes, the landscape components of roads, houses, areas of vegetation, and rivers were listed as affecting environmental factors (Krim et al., 1990; Meia and Weber, 1992; Nakazono and Ono, 1987; Roman, 1984; Scott and Selko, 1939; Sheldon, 1950; Takeuchi and Koganezawa, 1992; Uraguchi and Takahashi, 1998; Zhou et al., 1995). However, the comparative ranks of these factors were unclear. The modeling approach can provide the contribution ratio and relative rank order of each variable. This approach can be adopted for all landscape types, including urban, suburban, rural, or primitive landscapes.

CONCLUSIONS

Deworming treatment by anthelmintic baiting needs to be conducted continuously at certain intervals to keep the local fox populations clean. So the baits must be delivered at appropriate sites which can perform maximum efficiency of deworming wild foxes. The den site selection models established in this study enable to specify the efficient sites for delivering baits. It will improve the cost-benefit performance of the baiting campaign.

In this section, I will make suggestions for *E. multilocularis* control strategy and summarize essentials and perspectives of red fox-based modeling, which plays a central role in the strategy, in accordance with the findings from a series of analytic procedures in the present study and the accumulated previous studies.

C1. Suggestions for anthelmintic baiting strategies

1. Aim to make the target area be occupied by an uninfected fox population.

Once the target area is occupied by fox families, the area will be protected as their territories, making it hard for the population in this area to be replaced by other, potentially infected, individuals from outside (Figure 2-B). The prevalence could decrease if the foxes are kept as a “clean population”.

2. Deliver the baits to the potential sites of fox inhabiting

The baiting sites must be determined on the basis of the denning probability that the place has, not just based on the current fox distribution. Current fox distribution certainly ensures high efficacy of deworming for the present, but this approach cannot adapt the prospective changes in fox distribution pattern. Specifying the potential sites of fox inhabiting would solve the problem fundamentally, and the models established in this study would be valuable for it.

3. Establish the model for every city and accumulate the model patterns

The variation of the models shown in this study suggests that the fox denning models may be classified into some patterns depending on the city type. If we could find the rules of the patterns, for example, the rule that red foxes change denning behavior depending on the degree of urbanization of their territories, we will be able to guess the suitable pattern of the model even for the city which fox distribution is unknown. It may allow us to quick perform a treatment of anthelmintic baiting with a better degree of precision without the laborious modeling process.

C2. Essentials of the spatial modeling protocol

The den site selection models of urban red foxes have successfully been established, and the new modeling protocol has also been developed in this study. The model has been designed to extract the key environmental factors and key spatial scale for den site selection simultaneously. Although it is generally considered that narrowing down of key factors for habitat selection in generalist species is difficult or impossible, the protocol developed in this study enabled it by use of the suitable variables for the target species. This modeling approach can be adopted for every type of habitat, including urban, suburban, rural, or primitive landscapes. The protocol includes some unique approaches, as listed below (see also DISCUSSION: D1-2).

1. Targeting "presence or absence" of dens, not "abundance" of individuals nor dens, especially in the area having low fox densities.
2. Setting predictor variables focusing on the degree of disturbance not only usability for red foxes.
3. Detecting the key spatial scale (= heeding range) for denning to clarify the appropriate modeling unit instead of applying arbitrary grid size or resolution.

C3. Future tasks and perspective

Modeling in this study targets the foxes' habitat use during breeding season. Expansion of the modeling season to non-breeding seasons will contribute to more efficient control of area contamination with *E. multilocularis* eggs. It is known that foxes change their behavior drastically depending on the season. They depart from their dens in autumn to winter and show different resource requirements from spring to summer, which is the middle of the breeding season. Models for breeding and non-breeding seasons are necessary to identify efficient sites for bating throughout the year.

Disease control tools must be universal and ubiquitous so that any person under any conditions can use and arrange them as the situation demands and at a low cost. However, a lack of thematic maps for the analysis of mid-sized generalist mammals in urban areas is the biggest problem at present. Quick modeling can be achieved if thematic maps including all variables which are proposed in this study were available. In this study, I used the free software and open-source analysis tools as much as possible, in order to minimize costs. Vector- or transmitter-based modeling can apply to the control of multiple zoonotic diseases from the same vectors or transmitters (Eisen and Eisen, 2008). Preparing a set of adequate thematic maps for the vectors and transmitters in urban areas is reasonable from this viewpoint as well.

ABSTRACT

Echinococcus multilocularis Leuckart, 1863 is a parasite which will cause the human alveolar echinococcosis (HAE), one of the most serious helminthic zoonoses. HAE is spreading widely in the northern hemisphere and the number of cases has been increasing in recent years. The main transmitter of the parasite to human is the red fox, *Vulpes vulpes* Linnaeus, 1758. Deworming wild red foxes by baiting with the anthelmintic praziquantel is being established as a preventive technique to control the parasite. Improvement of the cost-benefit performance of baiting treatment is required urgently to maintain the efficacy of deworming.

In the present study, the efficient sites to be delivered the anthelmintic baits in urban area were determined by habitat modeling of red fox den sites. Habitat modeling of the generalist (the species which does not have any critical requirements for environmental resources) such as red foxes is considered to be difficult by existent methods, so the new protocol suitable for urban red foxes was developed.

The study was conducted in urban regions of Obihiro (about 59.8 km^2) and Sapporo cities (about 367.9 km^2) in Hokkaido, Japan, in which red fox populations have been established. The two cities have different degrees of urbanization. Sampling of fox dens location was conducted by thorough field exploring on the basis of the information from

citizens. A total of 35 fox dens in Obihiro study area (from 2002 to 2004) and 65 dens in Sapporo (from 2004 to 2007) were found. As against the points with dens “present”, control points were dotted randomly on the analytical base map as “absence” data (120 points in Obihiro; 730 points in Sapporo). The base map was customized for analyzing red fox ecology inhabiting urban areas by modifying existent numerical information maps, residential maps, and aerial photographs, which consists of nine micro-habitat categories: “wide road”, “narrow road”, “occupied building”, “vacant building”, “water place”, “riverbed”, “farmland”, “green covered area”, and “blank space”. These nine categories were set based on the previous reports on red fox habitat and to express the urban landscape. Den site selection modeling was conducted by use of the materials above for the red fox population in each of Obihiro and Sapporo study areas. The modeling protocol was designed to detect the best combination of the key environmental factors and the key spatial scale that foxes pay attention to (named "heeding range") when they select den sites, although the existent method can only detect the key environmental factors. All possible models were generated using logistic regression analysis, with “presence” or “absence” of fox den as the objective variable, and the percentages of the nine micro-habitat categories as predictor variables to detect the key environmental factors. This procedure was conducted for each of ten sizes of concentric circles (100-1000 m) from dens and control points to detect the most affecting circle size, that is, the key spatial scale. Out of all models generated, the best model was selected using Akaike's information criterion (AIC) inspection. This procedure was done in the each of the two study areas.

Established models suggest that requirements for denning are low percentages of wide roads, narrow roads, and occupied buildings, but high percentages of green covered areas within the circle of 500 m radius in Obihiro fox population; low percentages of wide roads, occupied buildings, but high percentages of riverbeds and green covered areas within 300 m radius in Sapporo. The difference in size of the key spatial scale between the two cities populations may come from the differences in their sensitivities to the surrounding environments. Both populations focused on the densities of wide roads, occupied buildings and green covered areas in common for their den sites. Accuracy of these models were inspected by area under the curve (AUC) of receiver operating characteristic (ROC) curve, and the values showed that those models have sufficiently high accuracy (AUC= 0.987 for Obihiro model; 0.995 for Sapporo model). Besides, prediction performances were evaluated by calculating the rates of concordance between observed and predicted values, and the rates were also sufficiently high (92.3% for Obihiro model; 99.2% for Sapporo model).

In conclusion, the den site selection models of urban red foxes have successfully been established, and the new modeling protocol has also been developed. The established model could determine the efficient sites for delivering baits, and it will improve the cost-benefit performance of the deworming by anthelmintic baiting campaign. Although it is generally considered that habitat selection modeling for generalist species is difficult, but the protocol developed in this study enabled it by use of the suitable variables for the target species. This modeling approach can be adopted for every type of habitat, including urban, suburban, rural, or primitive landscapes. The variation of the models shown in this study suggests the necessity of accumulating models for various types of cities in order to reveal the patterns of the model. It will enable us to perform rapid and efficient deworming campaign.

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JAPANESE ABSTRACT

Echinococcus multilocularis Leuckart, 1863（多包条虫）は，人に重篤な疾患（多包虫症）を引き起こす人獣共通寄生虫であり，その患者数は近年，北半球で増加している．人への主な媒介者は *Vulpes vulpes* Linnaeus, 1758（アカギツネ）であり，野生のキツネ個体群を対象とした駆虫薬入りベイト散布実験が世界各地で行われてきた．このコントロール法は徐々に確立されつつあるが，地域個体群を常に非感染の状態に保つためには，定期的なベイト散布が必須であり，コストパフォーマンスの向上が望まれている．

本研究では，高効率な駆虫薬ベイト散布地点をしぼりこむために，アカギツネの営巣条件およびその確率予測モデルの構築を試みた．これまで，アカギツネのような，特定の環境に強く依存しないジェネラリスト種の生息地モデリングは難しいとされてきた．そこで，本研究では従来法を改良し，都市型アカギツネに適したモデリングプロトコルを開発した．

調査地は，アカギツネ個体群が定着しており，都市規模の異なる帯広市と札幌市の都市域（それぞれ約 59.8km^2 と約 367,9km^2）に設定した．地域住民からの情報をもとに調査地を限なく探索し，帯広で 35 ヶ所（2002～2004 年に探索），札幌で 65 ヶ所（2004～2007 年）の巣データを得た．これら，巣の”有”データに対して，”無”データとして対照点をランダムに生成し（帯広で 120 点，札幌で 730 点），解析用地図にプロットした．解析用地図は，既存の数値地図や主題図，航空写真などを改変して独自に作成したもので，9 つのカ

テゴリー（大道路，小道路，有人建築物，無人建築物，水場，河川敷，農地，緑地，およびその他）で構成される．これらのカテゴリーは，アカギツネの生息条件に関する過去の研究を参考に，さらに都市環境の特徴を反映するように独自に設定した．これらの材料をもちいて，帯広市と札幌市それぞれについてアカギツネの営巣地選択モデルを構築した．一般的なモデリング法は環境キーファクターのみを抽出する設計であるが，本研究では，環境キーファクターだけでなく，キースケール（営巣地としてキツネが周辺環境にこだわる半径範囲）も同時に抽出できるよう，以下のようにプロトコルを設計した．キースケール候補として，全ての巣と対照点について 10 種類の半径の同心円（半径 100～1000m）を設定し，その 10 サイズの同心円すべてについて仮モデルを作成（＝環境キーファクターのみを抽出）した．この仮モデルは，各サイズの同心円内に含まれる 9 つの環境カテゴリー（上述の解析用地図の構成要素）のそれぞれの面積割合を計算したものを予測変数，巣の有無を目的変数とした，総当りのロジスティック回帰分析により作成された．次に，全ての仮モデルの中から，赤池情報量規準（AIC）をもとに最適モデルを決定した．この工程を，帯広市と札幌市それぞれについて行なった．

こうして構築されたモデルにより，以下のことが明らかになった．帯広のアカギツネ個体群は，巣から半径 500m の環境にこだわりを示し，その半径内の大道路，小道路，および有人建築物の占める面積割合が低く，かつ，緑地面積割合の高い場所を営巣地として好む．一方，札幌個体群は，半径 300m 以内の大道路と有人建築物の占める面積割合が低く，かつ，河川敷と緑地の

面積割合が高い場所を営巣地として好むことが示唆された．この 2 都市間のキースケールの違いは，アカギツネの人工環境への耐性の違いに起因する可能性がある．一方，大道路，有人建築物，および緑地は両市に共通のキーファクターであった．モデルの精度を検定するために，受信者操作特性（ROC）曲線の曲線下面積（AUC）を算出したところ，帯広モデルで 0.987，札幌モデルで 0.995 と，十分に高かった．また，モデルの予測性能を測るために，観測値とモデルによる予測値との一致率を計算したところ，帯広モデルで 92.3%，札幌モデルで 99.2%と，十分に高かった．

以上のとおり，本研究では，予測性能の高い都市型アカギツネ営巣地選択モデルの構築およびモデリングプロトコルの開発に成功した．これにより，駆虫薬ベイト散布地点のしぼりこみが可能となった．また，対象種の生態にもとづいた予測変数を使うことで，これまで難しいとされてきたジェネラリスト種の生息地モデリングが可能となった．このプロトコルは，都市部に限らず，あらゆる環境に生息するアカギツネに対して応用が可能である．さらに，都市間でモデル構造に違いがみられたことから，アカギツネの営巣地モデルにはいくつかのパターンが存在することが予想される．効率的で迅速な駆虫施策を実現するために，今後，様々なタイプの都市モデルを蓄積する必要があるだろう．