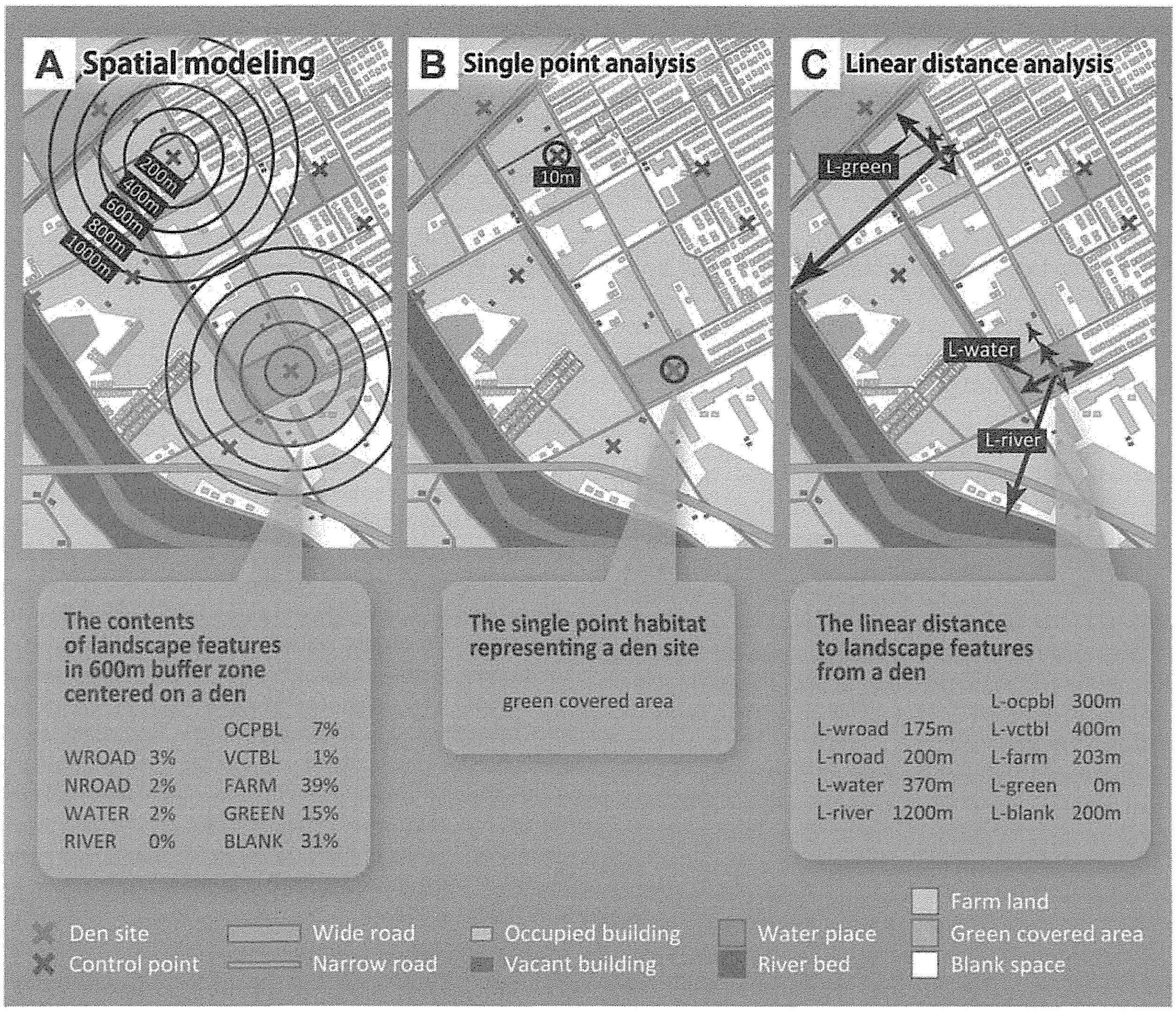

Figure 3 Example of customized analytical base map and calculation methods of three types of predictor variables. Panel **A** shows an example of the calculation of the values of nine variables for spatial modeling. Black open circles indicate ten sizes of concentric circle (100–1000 m in radius, at 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 dimensions of nine landscape feature categories included in the circle centered on a den site were calculated as shown in the pink call-out. Panel **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. Panel **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 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 3-A: pink balloon).

Step 6. Generating all possible models

All possible models (${}_9C_1 + {}_9C_2 + {}_9C_3 + \ldots + {}_9C_9 = 511$ 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, the higher the relative validity of the model. 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.

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 [63]. AUC values range between 0.5 (low accuracy) and 1 (high accuracy).

Supplemental 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: "Unsuitability of traditional methods for extraction of factors in urban landscapes").

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 pattern. 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 site 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 3-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 [64].

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 3-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 [41].

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 [9] and 2003 [12] 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.

Fox den site selection model

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 changes in AIC values of the models depending on the sizes of concentric circles are shown in Figure 4. AUC values that indicate the model validity (model's accuracy) are shown in Table 4.

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 4) and the accuracy of this best model is sufficiently high (AUC = 0.987; Table 4). 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.

Table 2 Selected variables in the best models for each concentric circle in Obihiro

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	0.00	1.749	−0.306	−0.709	-	-	−0.338	-	-	0.613	-
2	400	55.1	8.92	−0.005	−0.180	−0.489	-	-	−0.271	-	-	0.522	-
3	300	57.5	2.39	9.205	−0.133	−0.597	-	-	−0.407	−0.184	-	0.216	-
4	600	59.7	2.14	1.808	−0.186	−0.514	-	-	−0.201	-	-	0.275	-
5	200	73.1	13.41	5.616	−0.226	−0.616	-	-	−0.280	−0.190	-	0.047	-
6	100	75.7	2.63	3.456	−0.245	−0.290	-	-	−0.222	−0.131	-	0.766	−0.162
7	700	83.4	7.67	3.466	−0.192	−0.563	-	-	−0.159	-	-	0.041	-
8	800	105.0	21.62	1.501	−0.118	−0.302	-	-	−0.147	-	-	0.145	-
9	1000	126.2	21.24	−0.222	−0.160	−0.132	-	0.438	−0.054	-	-	0.203	−0.067
10	900	126.4	0.12	2.738	−0.196	−0.196	-	-	−0.049	-	-	0.141	−0.059

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.

$$p = \frac{1}{1 + \exp\left\{-\left(\begin{array}{r}1.749\text{–}0.306\mathrm{WROAD}\text{–}0.709\mathrm{NROAD}\\ -0.338\mathrm{OCPBL} + 0.613\mathrm{GREEN}\end{array}\right)\right\}}$$

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.

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 4) and the accuracy of this best model is sufficiently high (AUC = 0.995; Table 4). 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.

$$p = \frac{1}{1 + \exp\left\{-\left(\begin{array}{r}-10.167\text{–}0.169\mathrm{WROAD} + 0.328\mathrm{RIVER}\\ -0.128\mathrm{OCPBL} + 0.575\mathrm{GREEN}\end{array}\right)\right\}}$$

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.

Application examples of these two models are shown in Figure 5. The confidence intervals of the regression coefficients are shown in Additional file 1 and Additional file 2.

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

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	0.00	−10.167	−0.169	-	-	0.328	−0.128	-	-	0.575	-
2	400	56.5	3.25	−5.822	−0.266	-	-	0.192	−0.273	−1.022	-	0.590	-
3	200	64.2	7.69	−9.526	−0.186	-	-	0.344	−0.134	-	-	0.562	-
4	600	80.8	16.56	−8.018	−0.474	-	-	0.338	−0.235	-	-	0.422	-
5	500	91.1	10.27	−4.343	−0.314	−0.602	-	0.115	−0.093	-	-	0.476	−0.061
6	800	95.1	4.08	−4.326	−0.263	−0.353	-	0.147	−0.238	-	-	0.380	-
7	700	96.8	1.62	−2.783	−0.330	-	-	0.144	−0.300	−1.016	-	0.413	-
8	100	107.3	10.52	−2.265	−0.288	−0.724	-	0.141	−0.247	-	-	0.393	-
9	900	109.2	1.98	−8.850	−0.047	-	-	0.147	−0.259	-	-	0.645	−0.407
10	1000	120.0	10.74	−2.409	−0.268	−0.846	-	0.127	−0.270	-	-	0.419	-

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.

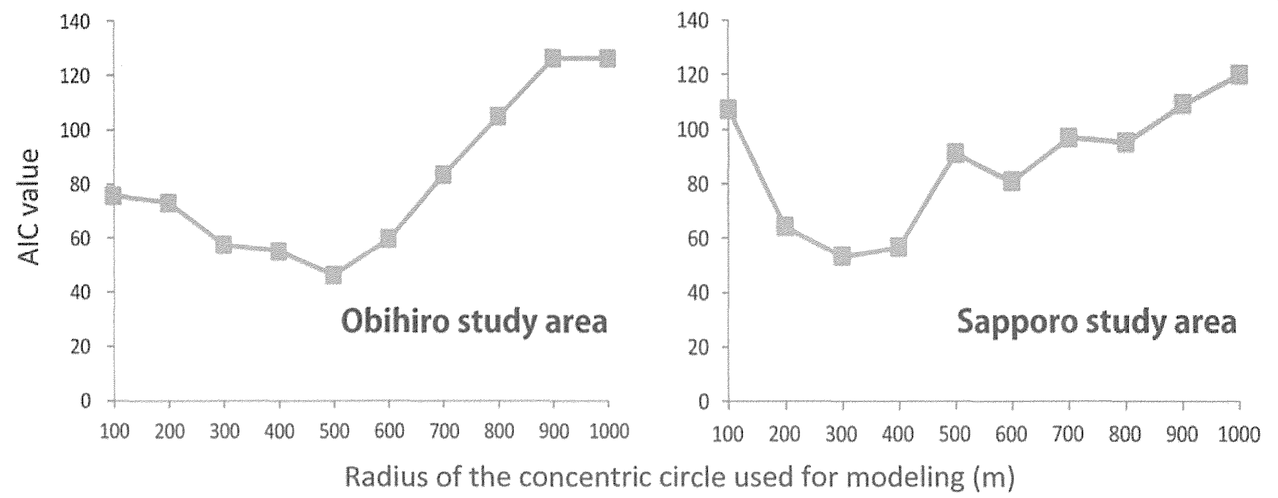

Figure 4 Changes in AIC depending on the size of concentric circles in the two study areas. Akaike's Information Criterion (AIC) values of the best models of each of the ten sizes of concentric circles are shown. The AIC value shows a minimum at 500 m in Obihiro (left) and at 300 m in Sapporo (right).

Traditional analyses

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, 16 (45.7%) were on "riverbed", 16 (45.7%) were in "green covered area", and the remaining 3 (8.6%) were in "farmland" (Table 5). Out of all 65 dens found in Sapporo, 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 6).

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 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 7). 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 8).

Table 4 Comparison of the models' discriminating abilities among the variable types

Type of modeling variable	Obihiro			Sapporo		
	Selected variables	Model AUC	Model R^2	Selected variables	Model AUC	Model R^2
Percentages of landscape features* (best model)	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 of each study area.
**Single point habitat is not applicable as the predictor variable for modeling because this variable is univariate.

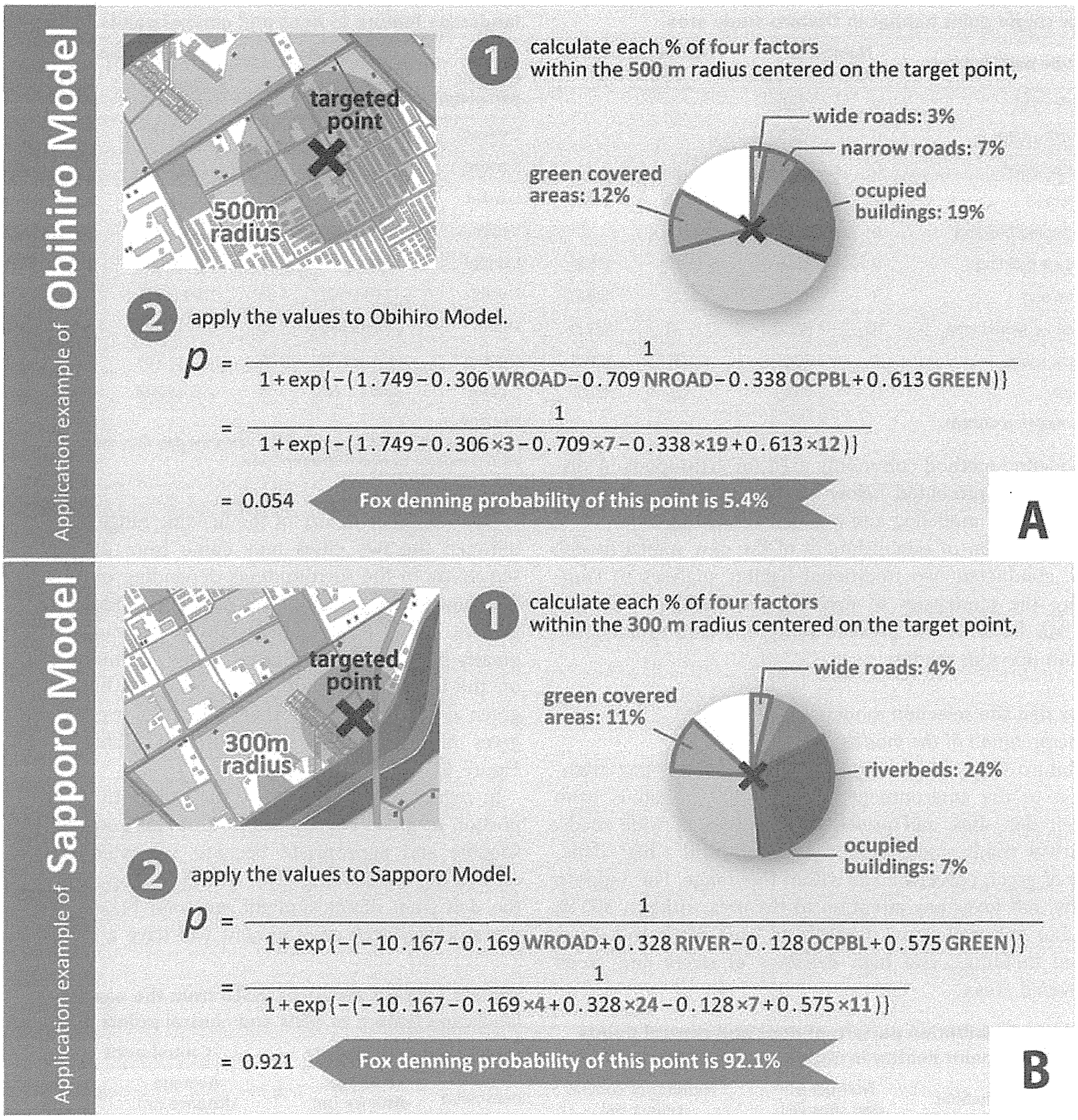

Figure 5 Application examples of the established models for the two cities. Panel **A** shows an application example of Obihiro model. If you want to know the probability of fox denning at a targeted point in the urban area of Obihiro City, 1) calculate each percentage of wide roads, narrow roads, occupied 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 get the answer of 5.4% of probability. Panel **B** shows an application example of Sapporo model. 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 get the answer of 92.1% of probability.

Discussion

In this study, we established a new spatial model to specify the potential habitat of urban red fox dens with a view to preventing contamination by *Echinococcus multilocularis* eggs. This model detects the first priority of environmental requirements for den site selection by red foxes in urban areas to identify the most efficient locations for delivering anthelmintic baits. Our 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. Spatial modeling was established by modifying a general

Table 5 Distribution pattern of 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, $p < 0.0001$.

modeling method commonly used for arthropods. A discussion is presented below for the differences between the general modeling and our new modeling.

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

Fox den site selection models

Interpretation of the models

Obihiro City model suggested that red foxes pay attention to 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, red foxes pay attention to the area within a 300 m radius and prefer low densities of wide roads and occupied buildings, and high densities of rivers and green covered areas.

Table 6 Distribution pattern of 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, $p < 0.0001$.

Table 7 Average distances (±SD) from the nearest landscape feature to dens and control points in Obihiro

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

*$p < 0.05$.
p indicates the significance probability when the den sites and control points were compared by Mann–Whitney *U* test.

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 (Table 2 and 3, Figure 4).

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 [38], and the canopy will protect the den from direct sunlight and rain [41,65]. Furthermore, a vegetated environment will have a high density

Table 8 Average distances (±SD) from the nearest landscape feature to dens and control points in Sapporo

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

*$p < 0.05$.
p indicates the significance probability when the den sites and control points were compared by Mann–Whitney *U* test.

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 the Sapporo population and vacant buildings may provide acceptable environments, 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 people walking or cycling 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 City, hence, it was suspected that they select riverbed areas to compensate for the lack of the most suitable habitat.

Modifications involved for the new modeling approach

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 [25]. 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 individuals 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. We 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

We set new variables used 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. Our pre-observation study suggested that disturbance is the critical factor for inhabiting 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 [31]. 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. We set nine new landscape features as variables for this purpose, and the analytical base map was newly rendered to fit these new variables.

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

The "key scale" was detected from multiple concentric circles (see Methods: 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 [31,66], or establishing a model based on an arbitrary grid size may lead to over- or under-estimates of potential as habitats [30,67]. Meanwhile, any grid or polygon on an existing thematic map is not always adoptable to extract the denning requirements of urban red foxes.

Our new method 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. Our 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 ranges than foxes in Obihiro City. Our 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.

Traditional analyses

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, our new category of the riverbed environment revealed a more precise reason for the preference.

The result of our single point habitat analysis showed that foxes preferred riverbeds, farmlands, and green covered areas as den sites in both Obihiro and Sapporo City (Tables 5 and 6). Indicating preference to riverbeds and green covered areas was reasonable and agree with previous reports [38,41,65], as described above, and farmlands assumed to play a similar role in some cases. The preference of this kind of environment was frequently suggested in other landscapes [36-43].

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 7 and 8). 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 [41,50]. In this study, preference for rivers was high in both cities regardless of the degree of urbanization, whereas a preference for water places was not confirmed (Tables 7 and 8), unlike in primitive forests and rural landscape [38,41]. 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, farmland was preferred only in Sapporo City and disregarded in Obihiro City (Tables 7 and 8). Farmland may compensate for the lack of green covered areas in Sapporo City. The different reaction to farmland between foxes in Obihiro and Sapporo City may be caused by different levels of tolerance to disturbance by human activities. In fact, our direct observation of some dens made in farmland in Sapporo City suggested the red foxes have some level of 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 differences 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.

Unsuitability of traditional methods for extraction of factors in urban landscapes

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: "Supplemental analyses by traditional methods").

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 our study areas, the artificial structures were distributed densely and evenly across the study 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: "Fox den site selection models" and "*Linear distance analysis*" and, Discussion: "*Interpretation of the models*" and "*Comparison with non-urban areas in previous reports*"). We tried generating models 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 4). The discriminating 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 4).

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 extracting the most contributing 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 most influential environmental factors [36-43,50]. However, the comparative ranks of these factors were unclear. Our new modeling method can calculate the contribution ratio and relative rank order of each variable. This modeling approach can be adopted for all landscape types, including urban, suburban, rural, or primitive landscapes.

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.

Accumulation of modeling trials in different cities may reveal variations in denning habits among the cities, and it may let us find some patterns shared among generated models. Recognition of the rules of the patterns, for example, the rule that red foxes change denning behavior depending on the degree of urbanization of their territories (see Discussion: "*Comparison with non-urban areas in previous reports*"), may allow us to quickly perform a mission of anthelmintic baiting with a better degree of precision without the laborious modeling process.

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 as we proposed in this study were available. In this study, we 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 [25]. Preparing a set of adequate thematic maps for the vectors and transmitters in urban areas is reasonable from this viewpoint as well.

Conclusions

Suggestions for anthelmintic baiting strategies for urban red foxes

Anthelmintic baiting needs to be conducted continuously to keep the local fox populations free from parasites. We suggest the effective strategy for it, as listed below.

1. Aim to make the target area be occupied by an uninfected fox population.
2. Deliver anthelmintic bait to the sites with a high probability of fox den presence based on the model by our protocol dedicated to urban fox ecology.
3. Establish the model for every city to adapt the variation of fox denning requirements and accumulate the model patterns.

Suggestions for the spatial modeling protocol of urban red fox ecology

Establishment of the model for red foxes inhabiting urban landscape requires some unique approaches, as listed below (see also Discussion: *"Modifications involved for the new modeling approach"*: Point 1–3).

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 for denning to clarify the appropriate modeling unit instead of applying arbitrary grid size (resolution).

Additional files

Additional file 1: Confidence intervals of the coefficients of selected variables included in the models in each scale for Obihiro.

Additional file 2: Confidence intervals of the coefficients of selected variables included in the models in each scale for Sapporo.

Competing interests
All authors declare they have no competing interest in this study.

Authors' contributions
TI carried out the study design, field data collection, image rendering for geographical analyses, statistical analyses, writing of the manuscript, and making tables and figures. MY contributed significantly to fundamental planning of the study design, discussing the analyses and study policy,

writing the manuscript, and making figures. KO supervised fundamental planning of the study design and discussing the analyses. YO and NN provided input on echinococcosis and its control methods that were necessary for planning the study, provided suitable field sites, arranged assistance for fieldwork, and discussed the study. KK supervised the study and provided research facilities, including financial support, as head of the research group. All authors read and approved the final version of the manuscript.

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