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Estimation of abundance and distribution of Japanese macaques using track-counts in snow

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ABSTRACT

We introduced a technique based on ground-based track counts in snow for simultaneously estimating the abundance and distribution of Japanese macaques *Macaca fuscata* (Blyth, 1875) and evaluated its efficiency by conducting a field trial in northern Japan. Within the 50 km^2 area, we selected 5 transects with consideration of the spatial distribution of vegetation, local climate, and geographical conditions contained in the entire area. Five trained researchers recorded the track counts three times in those geolocations that intersected with each transect. We estimated the macaque abundance by the line-intercept sampling (LIS) technique using the number of tracks and predicted its distribution by ecological-niche factor analysis (ENFA) using the tracks as a proof of macaques' presence. We confirmed that the LIS-based technique could yield reasonably accurate estimates of the number of individuals and troops, compared to the population estimates of macaques based on the home-range method. We successfully used ENFA in constructing a macaque distribution model that had a high predictive performance; this was verified by comparing the predicted macaque distribution with the actual use of habitat obtained by tracking radio-tagged troops in the study area.

Key-words: cost saving, ecological-niche factor analysis, line-intercept sampling, population density, primates

Introduction

Recently, conflict between humans and Japanese macaques *Macaca fuscata* (Blyth, 1875) has occurred in many part of Japan. A major reason for these conflicts is the damage caused by macaques to agriculture and private properties (Sprague 2002). There is a pressing need to establish a valid management plan for simultaneous damage control and animal conservation (Enari and Suzuki 2010). Generally, it is difficult to achieve such a plan without an appropriate status assessment of the subject species, such as understanding its population and distribution in the areas of concern (Caughley and Gunn 1996). We do not always require the accurate population statistics for the management of the species under consideration; that is, we have only to make a rough assessment with the adequate accuracy that meets a management goal in a subject area (Lancia *et al*. 1994, Morrison 2002). However, there are few efficient techniques for assessing the population of the species (including non-primate mammals) with low density inhabiting montane forests with rough and steep terrain, particularly in the range of a large-scaled heterogeneous landscape. Thus far, experts have estimated the population of Japanese macaques by using long-term observation studies (Takasaki 1981), home-range method based on radio tracking (Izumiyama *et al*. 2003), or a manpower-intensive approach in a limited area with high population density (Hanya *et al*. 2003). Thus, it is necessary to develop labor- and cost-saving techniques for the assessment of montane species with a fair amount of accuracy in a wide area.

Then, we devised a procedure for estimating the abundance and distribution of macaques in a montane region with cool-temperate deciduous forests, where the population density of macaques is approximately one-tenth of that in an area with temperate evergreen forests (Takasaki 1981). First, for estimating the abundance of macaques in a large area, we developed a ground-based track counting method by applying the line-intercept sampling (LIS) technique (Becker 1991, VanSickle and Lindzey 1991, Fattorini and Marcheselli 2002). The LIS technique is one of the probability sampling techniques used for estimating the abundance of a subject species by counting the animal tracks (ie, set of footprints) that intersect with line transects in a survey area. However, using the LIS technique, the species distribution inside the area cannot be measured. It is almost impossible to assume that macaques are uniformly distributed throughout the large area with a heterogeneous landscape. Thus, we attempted to predict the probability of macaque occurrence in the area by using species distribution models (Guisan and Zimmermann 2000). These models are used to estimate the probability of species occurrence in a study area by relating known species distributions to the spatial distribution of the relevant environmental variables. In our study, we have used the ecological-niche factor analysis (ENFA) (Hirzel *et al.* 2002) for predicting the macaque distribution by using animal tracks found in the area as the proof of macaques' presence.

In this paper, we introduced a combination technique, by using the methods adopted in population and landscape ecology, for simultaneously estimating the abundance and distribution of macaques. Then, we evaluated the efficiency of the combination technique by conducting a field trial in the northeastern part of Shirakami Mountains located in the northernmost mainland of Japan (Fig. 1). We confirmed the accuracy on the number of individuals and troops estimated using the LIS, compared to the population estimates based on the home-range method; in addition, the predictive performance of the distribution model computed by the ENFA was evaluated by comparing the predicted macaque distribution with actual distribution determined by tracking radio-tagged macaques in the study area.

Study Area

We set up a study area of 5 km × 10 km for counting macaque tracks in the northeastern part of the Shirakami Mountains, which is the transition zone from human settlements to inner montane areas (Fig. 1). The altitude of the study area ranges from 80 m to 600 m. The settlements are concentrated in narrow flatlands along rivers at an altitude below 200 m. Of the forested area, the primary forests, mainly consisting of *Fagus crenata*, were located in the inner montane area. The secondary forests consisting of deciduous broad-leaved trees and coniferous plantations of *Cryptomeria japonica* were located near the human settlements. The proportion of each type of land cover to the entire study area was 43.5% for broadleaf forests, 35.9% for conifer plantations, 15.1% for human settlements (including farmland), and 5.5% for grasslands. The area comes under the cool-temperate climatic zone. The mean air temperature in March 2008, the month in which our studies were conducted, was 3.4 ± 3.7 (SD) ° Centigrade (Shirakami Mountains World Heritage Conservation Center, unpubl.). The period of snowfall usually lasts from early December to late March. The maximum snow depth is 2 m in lowland areas and 3 m to 5 m in montane areas.

It was historically confirmed that the macaque population has been fully-distributed throughout the study area (Enari *et al*. 2006, Enari and Suzuki 2010). Human impacts on the natural distribution and habitat utilization of macaques could be small, because the declines in human population and their activities have advanced drastically across this district in recent years (Enari and Maruyama 2005). Furthermore, large-scaled population control has not been carried out in this district for the past several decades.

Material and Methods

Animals under study

Japanese macaques are gregarious forest mammals and usually move in troops on a daily basis within their territorial fixed-ranges. When male macaques grow up, they naturally tend to leave their natal troops; such solitary males and small male groups (ie, non-troop males) consequently move around the troops and, occasionally, join a non-natal troop (Sprague *et al*. 1998). Although the macaques are diurnal mammals, the time of their diurnal activity is typically short in winters (Wada and Tokida 1981, Nakayama 2002). The ranging behavior has been usually observed during 10:00-16:00 in the study area (H. Enari, unpubl.).

The distribution of macaques is primarily regulated by food resources and their refuge, which are defined by the conditions of vegetation, land use, climate, and topography (Iwamoto 1978, Iwano 1980, Mitani and Ikeguchi 1997, Hanya *et al*. 2004, Enari and Suzuki 2010). In particular, in snowy areas, the climate conditions and the amount of snow in the winter limits macaques' activities (Wada and Tokida 1981, Watanuki and Nakayama 1993). Therefore, the location of their refuge, such as forest slopes and evergreen conifers, which can protect them from snowstorms, could influence their habitat utilization.

Population estimation

The LIS technique entails the establishment of a baseline (projected x-axis) and several parallel transects extending perpendicular to the baseline (projected y-axis) (Becker 1991). Researchers follow these transects and count the tracks that were intersected by the subject animal. To evaluate the probability that the animal intersects these transects, it is necessary to measure the mean daily travel-distance of the animal in the projected x-axis direction, generally by using radio-tracking technique. Then, the population of the animal is estimated by multiplying the total number of counted tracks and the probability that the animal crosses transects. The details of the calculations based on equations by Becker (1991) are as follows:

First, we estimated the total projected *x*-axis distance traversed by all macaques inhabiting the study area ($\widehat{T}_x$) and its variance, as follows:

$$p_u = x_u q / D \tag{1}$$

$$\widehat{T}_{xi} = \sum_{u \in S_i} x_u / p_u \tag{2}$$

$$\widehat{T}_x = \sum_{i=1}^{r} \widehat{T}_{xi} / r \tag{3}$$

$$\mathrm{Var}(\widehat{T}_x) = \left[\sum_{i=1}^{r} (\widehat{T}_{xi} - \widehat{T}_x)^2 \right] / \left[r(r-1) \right] \tag{4}$$

where p_u is the probability that the *u*th macaque is contained in the sample; x_u is the projected *x*-axis distance traveled by the *u*th macaque; *q* is the number of transects; *D* is the length of the projected *x*-axis; *i* ($i = 1, 2, \cdots r$) indexes the repeated sample; and S_i is the set of the *i*th repeated sample. Equation (2) can hold true only if we ensure that $\max\{x_u\} \le D/q$ and that there is independence and randomness in the track-count sampling (Horvitz and Thompson 1952). Then, we calculated the estimate of the average projected *x*-axis distance traversed by a macaque inhabiting the study area ($\widehat{\mu}_x$) and its variance by tracking the radio-tagged animals:

$$\widehat{\mu}_x = \sum_{u \in S_R} x_u / n_R \tag{5}$$

$$\mathrm{Var}(\widehat{\mu}_x) = \left[\sum_{i=1}^{n_R} (x_u - \widehat{\mu}_x)^2 \right] / \left[n_R (n_R - 1) \right]. \tag{6}$$

where S_R is the sample of radio-tagged animals; and n_R is the number of times to measure the projected *x*-axis distance traversed by radio-tagged animals. We estimated the population total ($\widehat{T}_y$) and its approximation variance using the second-order Taylor-Series approximation:

$$\widehat{T}_y = \widehat{T}_x / \widehat{\mu}_x \quad (7)$$

$$\mathrm{Var}\left(\widehat{T}_y\right) \cong \left(\widehat{T}_x / \widehat{\mu}_x\right)^2 \left\{[\mathrm{Var}\left(\widehat{T}_x\right)/\left(\widehat{T}_x\right)^2] + [\mathrm{Var}\left(\widehat{\mu}_x\right)/\left(\widehat{\mu}_x\right)^2]\right\}. \quad (8)$$

In addition, we estimated 95% confidence interval for the population mean using non-parametric bootstrapping technique (Efron and Tibshirani 1986). We set the replication number at 10 000.

For estimating μ_x, we caught 3 adult-female macaques belonging to different troops (troops F, O, and S) in the study area by using box traps before the commencement of the research and attached radio collars (Advanced Telemetry Systems Inc., Isanti, MN) to each animal. The radio collar weighted 120 g, which was approximately 1% of the female's body mass and substantially less than the 5% of body mass recommended for maximum collar weight (American Society of Mammalogists 1998). We then recorded their radio fixes at 15-minute intervals during the daytime on sunny or cloudy days during March 2008. Consequently, we obtained the data on 20-day travel distance ($\max\{x_u\} = 1.84$), which comprised the tracking data on 8-day travel for troop F (mean ± SD, 1.0 ± 0.4 km), 5-day travel for troop O (mean ± SD, 0.9 ± 0.2 km), 7-day travel for troop S (mean ± SD, 1.1 ± 0.4 km). There was no significant difference in the travel distance among the 3 troops (Kruskal-Wallis test, df = 2, H = 0.9, P = 0.6). For simplifying the estimation procedure in this study, we assumed that the travel distance of troop and non-troop males was equal on the basis of a previous study (Muroyama *et al.* 2000).

The track counts are usually carried out by an airplane in the LIS (Becker 1991, VanSickle and Lindzey 1991). However, the air count generally involves high cost and technical difficulties in an area with a rough and steep terrain (such as our study area). We alternatively carried out the LIS-based estimation using ground-based track counts on foot or skis, which have an advantage of finding tracks regardless of landscape conditions. The LIS generally requires systematic sampling technique to count animal tracks (Becker 1991), ie, randomly selecting *r* points on the baseline (= the projected *x*-axis) and then setting up transects at each of the selected *r* positions. However, we adopted a simple repeated-sampling design to count tracks in the fixed transects (Fig. 1) in order to maintain uniformity in sampling efforts for every environmental condition in the study area as well as for saving workload. Although this simple repeated-sampling design violates the assumption of randomness in track counts, it would contribute to improve the accuracy of the result, considering the heterogeneous landscape in the present study area.

We first determined the interval between transects (D/q) at 2 km, based on the prerequisite of LIS ($\max\{x_u\} = 1.84 \le D/q$). Then, we set up these transects by the following 5 steps: (1) dividing the entire study area into 50 m × 50 m grid cells; (2) selecting several environmental factors that can potentially influence the probability of the macaque occurrence in a given area during winter (Table 1), according to previous studies (Iwamoto 1978, Iwano 1980, Wada and Tokida 1981, Hanya *et al*. 2004, Enari and Suzuki 2010, see also "Animal under Study"); (3) assigning the mean value of each environmental factor to each grid cell; (4) repeatedly generating possible layouts for parallel transects at 2-km intervals within the study area, ie, 2 km / 50m (grid cell size) = 40 layouts; and (5) selecting the one that had the environmental components most similar to those in the entire study area. We completed these operations by using ArcGIS 9.1 (ESRI, Redlands, CA). We performed a *Z*-test for comparing each environmental component in the entire study area and the transect set and found no significant differences in any environmental component between the entire study area and the transect set, except for the frequency of broadleaf forests ($P = 0.01$) and the grass frequency ($P = 0.01$). These 2 environmental factors especially displayed heterogeneous distribution within the study area.

On March 4, March 8, and March 12, 2008, we conducted the LIS-based survey every early morning before the macaques started their daily routine. Five researchers followed each transect and recorded the tracks that were marked only 1 day before the sampling. It was easy for them to distinguish clearly whether the tracks were a day old because of the high snowmelt rate in this month. The daily mean of the decreasing rate of snow depth in March 2008 was 4.2 ± 4.5 (SD) cm (Shirakami Mountains World Heritage Conservation Center, unpubl.). This study did not include the infant abundance estimation because infants are usually carried on their mothers' backs. In general, as snow depth increases, macaques shift to arboreal habitats (Watanuki and Nakayama 1993, Izumiyama 1999) or start walking in single-file lines in thin forest areas (Wada 1964). These behavioral characteristics of macaques cause overlapping transects that in turn cause potential difficulties in obtaining accurate counts. However, such difficulties can be avoided by conducting track counts in the late winter because in this period, macaques are usually found walking discretely on the ground because snow depth has decreased and the snow surface has relatively hard (Izumiyama 1999). In fact, when we preliminarily evaluated the accuracy of the present track-count method by following several troops with radio-collars, the mean count loss (ie, underestimate) on the number of tracks intersecting transects was 1.90 ± 1.92 (SD) individuals ($n = 11$) without infant abundance.

For reducing measurement errors, we carried out this survey after taking the following measures: (1) to follow the transects accurately, the researchers traveled by following a GPS device, which was preinstalled on the geolocation of each transect; (2) to maintain the intra- and inter-researcher reliability (Morrison 2002), we trained research novices (for at least 2 days) so that they would not overlook the tracks; and (3) to reduce the sampling biases (eg, in the daily travel distance of macaques and disappearance rate of tracks) caused by weather conditions, we counted tracks only when there was no snowfall.

In this study, we recorded respective tracks with separating those of the troops and non-troops for calculating each population estimate. To identify tracks marked by troop macaques or non-troop males, we initially measured the width of clusters of tracks on transects marked by the troops (being followed with radio-collars) in the area during the study period; as a result, every measured width was <120 m (*n* = 11). The minimum troop size observed in and around the study area was 13 individuals. It was unlikely that more than 1 troop crossed the same or a nearby segment of transects in the same direction and on the same day because the population density in the cool-temperate forests is quite low (<6 individuals/km^2) (Suzuki *et al*. 1975, Iwamoto 1978, Mito 2000) and the frequently occupied area of macaque troops in these forests does not overlap considerably (Imaki *et al*. 2000, Izumiyama *et al*. 2003, Enari *et al*. 2006). From these remarks, it was reasonable to suppose that the cluster with ≥13 tracks (oriented in the same direction) within a width of 120 m on transects was identified as the tracks that were marked by a troop.

According to this criterion to identify tracks marked by troops, it is also possible to calculate the number of troops in the area by using the abovementioned LIS technique. We then counted the number of the clusters of tracks meeting the criterion in the same samples, and estimated the abundance of troops using the same equations and variable value for $\hat{\mu}_x$.

Verification of population estimates

For the verification of the number of macaque individuals and troops estimated by the LIS, we conducted the population estimation by using the home-range method (eg, Brugiere and Fleury 2000). Details of this estimation method are given as follows. (1) From August 2003 to

February 2008, we intermittently set up a maximum of 20 box traps within the study area for each season and captured 25 adult female macaques in total. (2) We then attached radio collars to the captured macaques that belonged to different troops. (3) We followed them continuously to record their range and population size during February and March (late winter) 2008. In addition, we counted the adult females and males in each troop and roughly estimated the abundance of non-troop adult males, assuming the sum of the abundance of troop and non-troop adult males to be equivalent to that of adult females; in fact, the sex ratio of macaques is found to be approximately 1:1 (Takasaki and Masui 1984).

Prediction of macaque distribution

We predicted the winter macaque distribution, or the probability of macaque occurrence, using the tracks encountered during the LIS surveys as the proof of species presence. It was difficult for us to determine whether the area without any tracks implied that the habitat was unsuitable for macaques or whether it implied that our sampling intensity was inadequate. Then, we adopted the ENFA, which requires only the data of species presence to predict the species distribution. The ENFA builds on the ecological niche concept by assuming that the species are non-randomly distributed with respect to their eco-physiological preferences on various environmental conditions. A key feature of this method is that it summarizes the environmental variables into a few uncorrelated synthetic factors that can explain the species presence (similar to principle component analysis). These factors have 2 ecological meanings—marginality and specialization of the species niche. Marginality indicates the extent to which the mean of the species distribution differs from the mean of the overall distribution of available conditions in the entire reference area. Specialization indicates how specialized the species distribution is, as compared with the overall distribution of the environmental variables in the entire area. The first synthetic factor explains all marginality and partial specialization. The second and subsequent synthetic factors explain the remaining specialization. In addition, the ENFA yields general clues about the subject species' niche—ie, total marginality (*M*) and total specialization (*S*)—, by integrating all these species marginality and specialization factors. *M* ranges from 0 to 1. As the value of *M* increases, the species distribution becomes more biased with respect to the mean available environmental conditions in the reference area. Meanwhile, *S* ranges from 1 to ∞. As the value of *S* increases, the width of species niche decreases. For a detailed description of the ENFA, see Hirzel *et al*. (2002).

In our study, we prepared a macaques' presence map with raster-based grid cells (50 m × 50 m) using the presence data collected during the track counts. Because the present study focused on predicting the species-specific habitat in the geographic space, we used all the tracks as the macaques' presence data, without separating those of the troops and non-troops. The map contained 106 grid cells indicating macaques' presence. We then arranged the raster maps in the same format as the species map, for 10 environmental variables. We applied the same factors to these variables, which were used to determine the placement of transects (Table 1). For optimizing the normality of these variables, we transformed the distributions of each variable by using a Box-Cox transformation (Sokal and Rohlf 1981).

After summarizing these variables by the ENFA, we selected a few significant factors for further analysis, by using the broken-stick technique (Hirzel *et al*. 2002). For computing the species distribution, we used the distance geometric-mean algorithm, which is a common approach for maintaining a good generalization power of the model (Hirzel and Arlettaz 2003). The probability of macaque occurrence in each grid cell ranged from 0 (low) to 100 (high).

To evaluate the robustness and prediction power of our model, we adopted a *k*-fold cross-validation procedure (Fielding and Bell 1997) with $k = 10$, which is a commonly-used value while evaluating ENFA-based models. To improve the performance of our model, using an area-adjusted-frequency cross-validation technique (Boyce *et al*. 2002), we reclassified the probability of macaque occurrence into 4 classes (called bins) of equal size—very low (0–25), low (25–50), medium (50–75), and high probability (75–100) of macaque occurrence. Then, we computed the Boyce index on the basis of the calculation of Spearman's rank correlation (Boyce *et al*. 2002) as the measure of model accuracy.

We performed all these operations using the software BIOMAPPER 3.2 (Hirzel A. H., Hausser J., and Perrin N. University of Lausanne, Switzerland) and ArcGIS 9.1.

Validation of predicted macaque distribution

For further validation of the predictive performance of the macaque distribution model computed by the ENFA, we acquired geolocations as validation data from the above-mentioned 3 radio-tagged troops (troops F, O, and S), whose geolocations available were more abundant and accurate than those of the other troops. During February and March (late winter) 2008, we had followed these troops by identifying their radio signals and had recorded the geolocations of each troop at >5-hour intervals in daylight to restrain spatial autocorrelation among the locations of each troop in temporal succession. We used 36 geolocations of each troop, ie, 108 geolocations in total, as the validation data. Then, we counted the geolocations within areas with different probabilities for macaque occurrence, as predicted by the ENFA, and evaluated the actual habitat selection in each area by using Bonferroni z-statistics (Neu *et al*. 1974).

Results

Number of the individual macaques and troops

The total number of tracks on the transects marked by troop and non-troop macaques was 117, 160, and 112 in the first, second, and third samplings, respectively (Table 2). The unbiased estimate of μ_x ($=\overline{x_u}$) was 1.00 ± 0.37 (SD) km. Then, we calculated p_u at 0.5. The unbiased estimates of T_x for troop and non-troop macaques were 186.67 ± 26.44 (SD) km and 72.67 ± 10.35 (SD) km, respectively. Finally, we estimated the population total in the study area to be 185.92 individuals (95% CI, 138.32–205.92) for troop macaques and 72.38 individuals (95% CI, 53.83–80.15) for non-troop macaques.

The number of clusters of tracks on transects (identified as the tracks marked by troops) was 2, 5, and 4 in the 3 repeated samples. By using the same LIS-based equations, we estimated the number of troops to be 7.33 (95% CI, 7.21–7.68), ie, 0.15 troops/km^2.

On the basis of the home-range method, we totally observed 8 troops composed of 222 individuals, or 199 individuals when not considering infant abundance, in the study area during February and March (late winter) 2008. Among these troops, 74 adult female and 24 adult male macaques were noted; therefore, we roughly estimated the abundance of non-troop macaques to be 50 individuals in the study area.

Macaque distribution

To compute the probability of macaque occurrence, we retained 3 significant synthetic-factors (out of 10) by the broken-stick technique (Table 3). These 3 factors accounted for 64.3% of the total specialization of macaques' niche. Coefficients on the marginality axis (ie, factor 1), ranging from −1 to 1, had a positive coefficient value for the frequency of broadleaf forests and a negative value for the distance to settlements and average altitude. This indicated that the macaque occurrence was essentially associated with lowland broadleaf forests surrounding human settlements. Meanwhile, a negative value of average sunshine duration indicated that macaques tended to maintain a certain distance from areas without the cover (such as sunny areas that are natural flatlands and are mostly utilized as farmland). The second largest variance of the specialization (20.5%) attributed to the first factor indicated that macaques were fairly sensitive to a shift in their optimal conditions; that is, the breadth of optimal macaques' niche was restricted to lowland broadleaf forests in the environmental space. The other synthetic-factors accounted for other specializations, mostly related to the conifer frequency, average altitude, distance to settlements, and maximum snow depth (each absolute value was >0.4, as observed for factors 2 and 3 [Table 3]), indicating that the optimal niche breadth of macaques was narrow in those factors. Meanwhile, macaques were less sensitive to conditions such as average slope, grass frequency, frequency of the northern slope, and distance to the river or lake as their absolute values were <0.3. The total marginality (*M*) and specialization (*S*) were 0.30 and 1.64, respectively, suggesting that macaques' habitat did not drastically differ from the mean conditions in the entire area. However, their habitat was fairly restrictive on the range of conditions that it could withstand.

From these 3 synthetic factors, we computed a species distribution map for predicting macaques' occurrence in the entire area (Fig. 2). The area-adjusted frequency cross-validation procedure with 4 bins provided a mean Boyce index of 0.86 ± 0.19 (SD), indicating that our model was highly accurate. The map showed that 75.2% of the study area had considerably-low suitability for macaques' habitat, 15.6% was of low suitability, 5.6% was of medium suitability, and 3.6% was of high suitability. These results indicated that the macaque distribution was highly clumped.

Validating predicted macaque distribution

The validation data, obtained by radio-tracking, demonstrated that macaques intensively utilized the area with a high probability of species occurrence as predicted by the ENFA; whereas, the area with a very low probability was negatively occupied despite its high expected value (Bonferroni confidence interval; $P < 0.01$) (Table 4). This result indicates that the distribution model possesses sufficient predictive performance and robustness.

Discussion

Effects of the track-count method on the population estimation

The present results indicate that the abundance of non-troop macaques calculated by the LIS-based method was slightly overestimated. Considering that we verified this estimate value with reference not to the actual observed abundance but to theoretical value based on their sex ratio, further empirical research on the abundance of non-troop macaques would be required for carefully discussing its accuracy. Meanwhile, as for the abundance of troop macaques and the number of troops, our estimates from the LIS-based method were adequately validated, compared to each observed value from the home-range method. The population estimate of wild animals usually contains various sampling errors (Skalski 1991). These errors arise due to normal variations depending on the sample size as well as due to biases caused by inadequate research efforts and human error (Morrison 2002). The accuracy of the population estimate can be improved by reducing these biases. Because we conducted LIS on a heterogeneous landscape with a rough and steep terrain, the requirement of a normal LIS design in sampling, i.e., the randomness of spatial configuration of transects, was not fulfilled. Such violation of this requirement may need to be validated further in case of different landscape types; however, using the present procedure, we succeeded at least in maintaining a reasonable accuracy in the population assessment. This indicates that our sampling design, including sampling effort, can be considered of value if the following 3 points are addressed for reducing potential biases: (1) maintaining evenness in research efforts, ie, counting tracks in every environmental condition contained in the entire study area; (2) conducting the survey under similar climate conditions for regulating the disappearance ratio of tracks and reducing the variance of daily travel distance of macaques in the area (ie, for stabilizing the estimated value of μ_x); and finally (3) adequately trained researchers for minimizing simple human errors.

There is another advantageous ground-based track counting method for estimating the population of wild montane mammals with low density, termed intersection points counting method based on geometrical probability, or INTGEP (Hayashi *et al*. 1979). However, INTGEP requires more intensive research efforts than the LIS-based method, and therefore, the former method cannot be used for large-scale population estimation. In fact, the total length of the survey route required for estimating wild mammal populations per square kilometer is approximately 5 km for INTGEP (Hayashi 1997), whereas only 1.5 km was required for the LIS as demonstrated in this study. Thus, it is reasonable to consider that our LIS-based technique is one of the few practicable methods with reasonable accuracy for estimating macaque population in a wide area densely covered with montane forests where fresh snow of sufficient depth is available.

Effects of the track-count method on prediction of macaque distribution

Stockwell and Peterson (2002) have reported that the sample sizes of the presence points of a subject animal that are used to develop species distribution models generally affect the success rate of these models. In particular, it has been pointed out that these models cannot interpret the marginal niche condition of the species successfully when the sample size is extremely small (Pearson *et al*. 2007) As indicated in the mean Boyce index and from the comparative verification using the actual macaque distribution, the present sampling efforts, which were equivalent to those for the LIS, were undoubtedly sufficient for accurately predicting the macaque distribution. Recently, there have been several studies whose results support the validity of our sampling approach on the basis of the habitat requirements of subject animal; these studies have been successful in developing robust models for predicting a species distribution with less efforts for sampling (Hirzel and Guisan 2002, Zaniewski *et al*. 2002, Pearson *et al*. 2007).

In general, in niche-based distribution models (or those models that do not use the proof of animal absence), it has been generally considered that subject animals rarely occupy all the areas having suitable environments for them (Svenning and Skov 2004, Pearson *et al*. 2007). The same consideration holds true of macaques, because the additional factors that were not considered in the modeling (such as past catastrophes, eg, heavy snow; historical human influences, eg, overhunting; and geographic barriers, eg, high mountains) have historically limited the occupation of macaques in the geographical space (Iwano 1980, Koganezawa 1991, Mito 1992, Mitani and Ikeguchi 1997, Enari and Suzuki 2010). The researcher who refers this model must therefore carefully interpret the output of niche-based distribution models with due consideration of possible limiting factors of habitat occupation in a subject area (Pearson *et al*. 2007). We succeeded in predicting the species distribution probably because those limiting factors almost never existed in the study area (see Study area).

Practical application

As shown in the present results, the population density of macaques in the Shirakami Mountains appeared to be similar to that in the other cool-temperate forests (Suzuki *et al*. 1975, Iwamoto 1978, Mito 2000). On the other hand, the Shirakami macaques exhibited an extremely heterogeneous distribution, clumped in lowland forested areas around settlements, as indicated by the marginality axis from the ENFA. It is possible that the seasonal migration of the macaques resulted in this clumped distribution, considering that troops are usually entirely distributed in the area during all seasons except for winter (Enari *et al*. 2006). Several previous studies have already reported the similar winter migration to lower elevations in the mountainous regions caused by the spatial disposition of food resources and refuges to survive in harsh climate conditions (Koganezawa and Imaki 1998, Imaki *et al*. 2000, Izumiyama *et al*. 2003).

Such a heterogeneous species distribution logically implies that the population density is sensitive to the size and assignment of a survey area. This means that the estimate of the population density in a restricted range has a tendency to fluctuate widely even in neighboring geographical spaces. Hence, population assessment should not be implemented without understanding the multi-scaled structure of animal population. In this context, our labor- and cost-saving technique can be used to obtain reliable information on not only the abundance but also the ecological relationships between species occurrence and habitat quality by simply counting the tracks for a few days. In particular, our technique could be more valuable for continuous population monitoring in a fixed area because the estimate of μ_x by tracking the radio-tagged macaques, which is a labor-consuming work for LIS, is not always required in the following year or later, as long as LIS is conducted in the same area under similar weather conditions. Our method therefore can be a powerful tool for the population assessment of wild animals, including non-primate mammals inhabiting montane forests in snowy areas.

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Figure Legends

Fig.1. Map of study area, located in the northeastern Shirakami Mountains, the northernmost mainland of Japan. The length of transects for line-intercept sampling (L1–L5) was 5 km, and they were set parallel to each other at a 2-km interval.

Fig. 2. Probability of Japanese macaque occurrence during winter in the northeastern Shirakami Mountains, Japan, computed by the ecological-niche factor analysis.

Table 1. Environmental variables used in placing transects in order to count the track sets of Japanese macaques. These variables were also used in the ecological-niche factor analysis for predicting the habitat distribution. * Maps with these environmental variables were originally composed of a Boolean data set. We transformed these environmental maps into frequency maps by using the block statistics function in the geographic information system; that is, storing the dimensions of the nearest cells of each category within a square moving window of 500 m × 500 m.

Environmental variables	Source
Average altitude (m)	Digital elevation model; Geographical Survey Institute, Japan
Average slope (°)	Digital elevation model; Geographical Survey Institute, Japan
Frequency of northern slope	Digital elevation model; Geographical Survey Institute, Japan
Distance to river or lake (km)	Digital national land information; Ministry of Land, Infrastructure, Transport and Tourism, Japan
Maximum snow depth in March (m)	Climate mesh data (mean value of 1971-2000); Japan Meteorological Business Support Center
Average sunshine duration in March (hour)	Climate mesh data (mean value of 1971-2000); Japan Meteorological Business Support Center
Distance to settlements (km)	Digital national land information; Ministry of Land, Infrastructure, Transport and Tourism, Japan
Frequency of broadleaf forests*	National survey on the natural environment (5th survey, 1998); Biodiversity Center of Japan
Conifer frequency*	National survey on the natural environment (5th survey, 1998); Biodiversity Center of Japan
Grass frequency*	National survey on the natural environment (5th survey, 1998); Biodiversity Center of Japan

Table 2. Number of macaque tracks that intersected with each transect in the study area that was located in the Shirakami Mountains, Japan. These track counts were carried out 3 times in March 2008. T and NT mean the number of tracks marked by troop and non-troop macaques, respectively.

	Transects										Total	
	L1		L2		L3		L4		L5			
Repeated sampling	T	NT	T	NT	T	NT	T	NT	T	NT	T	NT
First	0	2	0	16	46	22	29	2	0	0	75	42
Second	35	5	0	4	18	7	39	0	27	25	119	41
Third	0	7	22	3	23	6	23	10	18	0	86	26

Table 3. Variance explained by the first 3 (out of 10) synthetic factors and coefficient values for each environmental variable, as computed by using the ecological-niche factor analysis for Japanese macaques in the study area that was located in the Shirakami Mountains, Japan. * The coefficient sign does not affect specialization.

Environmental variables	Factor 1 Marginality (100.0%) Specialization* (20.5%)	Factor 2 Specialization* (32.2%)	Factor 3 Specialization* (11.6%)
Frequency of broadleaf forests	0.47	−0.27	−0.30
Conifer frequency	−0.06	−0.55	0.14
Average altitude	−0.38	−0.49	0.14
Distance to settlements	−0.38	0.47	−0.61
Average slope	0.23	−0.02	−0.04
Grass frequency	0.11	−0.03	−0.04
Frequency of northern slope	−0.14	−0.07	−0.21
Distance to river or lake	−0.20	0.28	0.22
Maximum snow depth in March	0.26	−0.06	−0.58
Average sunshine duration in March	−0.54	−0.28	−0.28

Table 4. Actual number of Japanese macaques observed in areas with different probabilities of macaque occurrence that were predicted by the ecological-niche factor analysis.

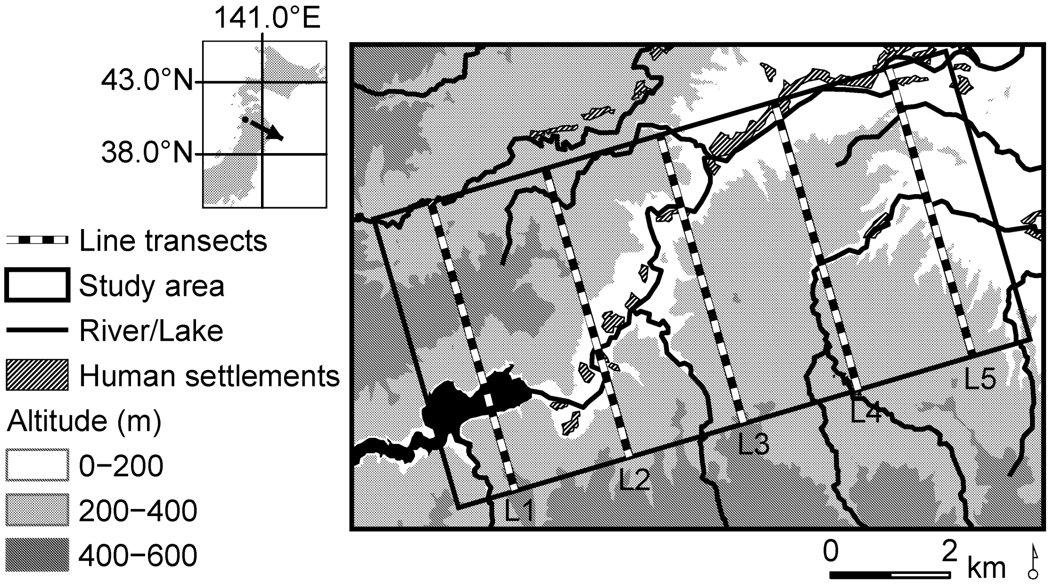
	Total area (km^2)	Proportion of total area (p_a)[a]	Number of macaques observed[b] N (%)	Expected number of macaques observed	99% confidence interval for proportion of macaque occurrence (p_m)[c]
Area with high probability	1.80	0.04	50 (46.30)	3.89	0.33–0.60
Area with medium probability	2.80	0.06	8 (7.41)	6.05	0.00–0.14
Area with low probability	7.80	0.16	17 (15.74)	16.85	0.06–0.26
Area with very low probability	37.60	0.75	33 (30.56)	81.22	0.18–0.43
Total	50.00	1.00	108 (100.00)	108.00	

[a] p_a represents "expected species-observation values," assuming that macaques occurred in each area in the exact proportion to availability.

[b] These were acquired using radio telemetry during February and March (late winter) 2008.

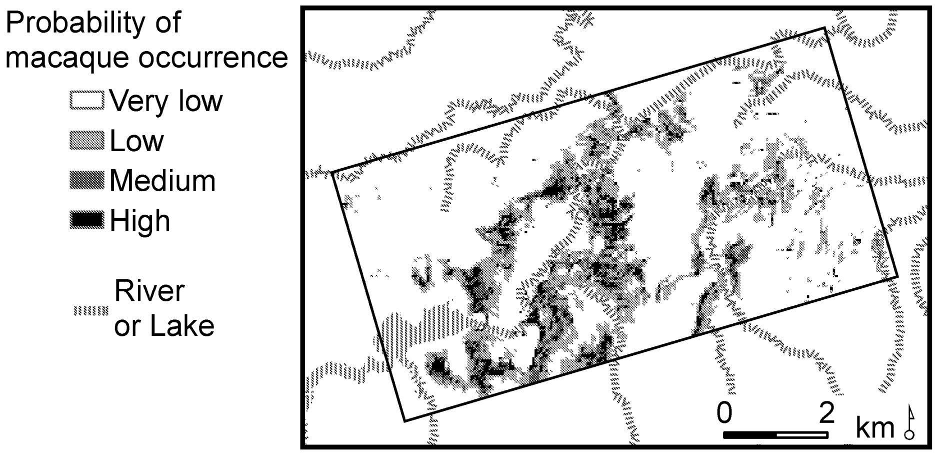
[c] p_m represents theoretical proportion of macaque occurrence and is compared to corresponding p_a to evaluate macaque habitat selectivity.

Fig. 1



141.0°E
43.0°N
38.0°N
Line transects
Study area
River/Lake
Human settlements
Altitude (m)
0−200
200−400
400−600
L1
L2
L3
L4
L5
0
2
km

Fig. 2


Probability of macaque occurrence
Very low
Low
Medium
High
River or Lake
0
2
km