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Research Article

Utilization of municipality records for the early-stage management of introduced raccoons in Japan

Emi Yamaguchi[1,2,3,*], Mutsuyo Kadohira[2], Kei Fujii[3,4], Kohei Kobayashi[5,6] and Mayura B. Takada[7]

[1]The United Graduate School of Agricultural Sciences, Iwate University, 3-18-8 Ueda, Morioka, Iwate 020-8550, Japan
[2]Obihiro University of Agriculture and Veterinary Medicine, 2-11 Inada, Obihiro, Hokkaido 080-8555, Japan
[3]Animal Research Center, Hokkaido Research Organization, Shintoku Nishi 5-39-1, Shintoku, Hokkaido 081-0038, Japan
[4]OAT Agrio Co., Ltd., 1-3-1 Kanda Ogawa-machi, Chiyoda-ku, Tokyo 101- 0052, Japan
[5]United Graduate School of Veterinary Sciences, Gifu University, Yanagido 1-1, Gifu, Gifu 501-1193, Japan
[6]EnVision Conservation Office, 5-2 Kita 9, Nishi 4, Kita-ku, Sapporo, Hokkaido 060-0809, Japan
[7]Faculty of Science and Engineering, Chuo University, Kasuga, Bunkyo-ku, Tokyo 112-8551, Japan

Author e-mails: *e.yamagti@gmail.com (EY), kadohira@clione.ne.jp (MK), fujii-k@camel.plala.or.jp (KF), k.kobayashi731@gmail.com (KK), mayura.203@g.chuo-u.ac.jp (MT)*

*Corresponding author

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Abstract

Rapid response is critical for management of invasive alien species (IAS). However, lack of ecological information at early stages of invasion is a challenge for development of management strategies. To facilitate development of an IAS management strategy, we investigated the stages of invasion and habitat preferences of raccoons (*Procyon lotor*) believed to be in the early stage of invasion at Tokachi, Hokkaido, Japan. We obtained raccoon records from local municipalities in Tokachi including trapping and individual biological data (2006–2014), necropsies conducted on 161 carcasses collected as roadkill or by traps (2009–2014), and track surveys (August–November, 2010). Female raccoon reproductive statuses indicated populations are established and actively breeding in Tokachi. Relative population densities (based on catch per unit effort) and annual changes in raccoon capture sites revealed raccoon expansions, which were likely localized to the western region, indicating district-level variation in invasion stages. The distribution of livestock farms may have positively influenced raccoon occurrence and body sizes. Half of sampled raccoons had recently eaten corn (*Zea maize*), presumably obtained from livestock feed. Therefore, livestock farms may represent preferred raccoon habitats and could facilitate raccoon establishment. In Tokachi, IAS management strategies (i.e., prevention, eradication, and impact mitigation) should be tailored to stage of invasion at the local level. In particular, increased monitoring and capture efforts in areas with many livestock farms might retard raccoon establishment. More broadly, at early stages of invasion, IAS data from local municipalities may facilitate development of management strategies.

Key words: early stage of invasion, landscape structure, livestock farm, Hokkaido, *Procyon lotor*

Introduction

Eradication of invasive alien species (IAS) can be achieved in a cost-effective manner with a high success rate when populations are small and localized, which limits removal efforts to relatively small areas (IUCN 2000; Simberloff 2003; Simberloff et al. 2005; Genovesi and Shine 2004; Ries

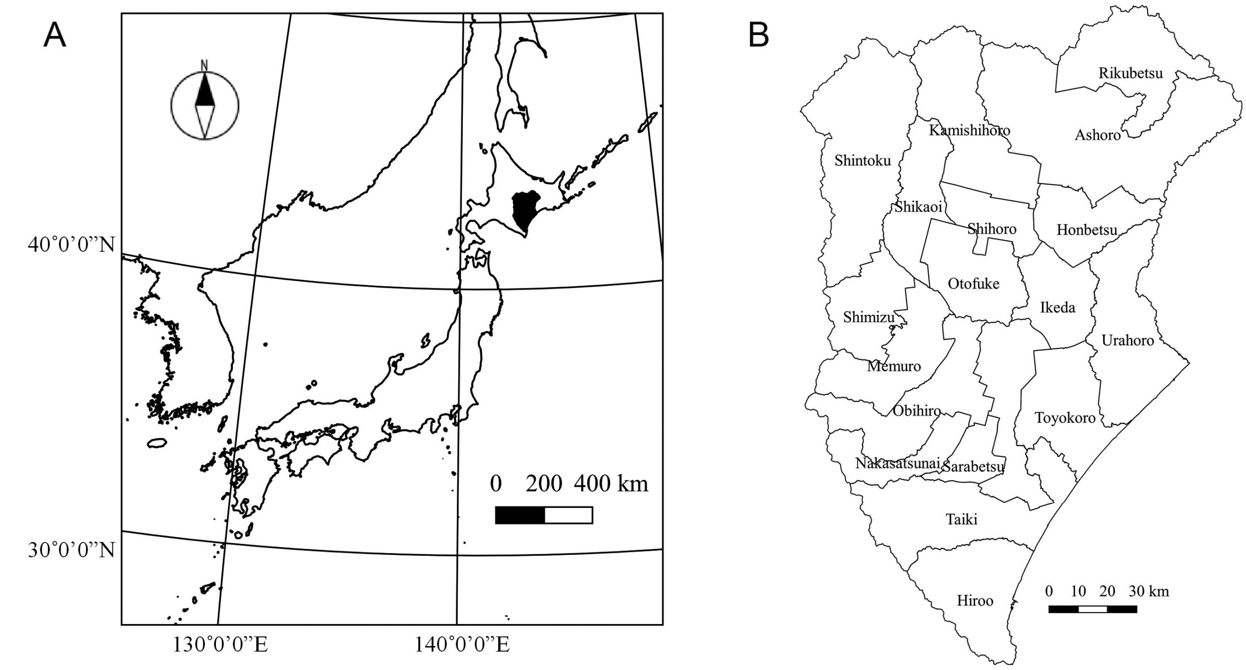

Figure 1. Map of Japan showing the location of Tokachi in black (A) and its municipalities (B).

et al. 2004). Additionally, assessing the social impact of IAS and public engagement in IAS management early can minimize social conflict and improve feasibility of management strategies (Crowley et al. 2017a, b). Management strategies should account for invasion stage (Mack et al. 2000; Kolar and Lodge 2001; Sakai et al. 2001; Genovesi and Shine 2004; Simberloff et al. 2005). These stages are categorized based on reproductive status and distribution trends as follows: (i) introduction stage (movement from a native habitat to a new one), (ii) establishment stage (successful reproduction and self-maintenance of populations in the wild), and (iii) expansion stage (population growth and spatial spread) (Sakai et al. 2001; Genovesi and Shine 2004). At introduction or establishment stages, development of management strategies is challenging because knowledge regarding the ecology of the IAS is limited (Epanchin-Niell and Hastings 2010). However, passively collected IAS data (i.e., capture and witness data) are occasionally recorded by local municipalities, even in the first two stages of invasion (early stages). These data may provide adequate ecological information for developing IAS management during early stages of invasion, even with limited resources.

Raccoons (*Procyon lotor* Linnaeus, 1758) are an IAS in Japan and negatively impacting native fauna and the agricultural industry (Ikeda et al. 2004). Raccoon distributions expanded to 17 prefectures by 2000, 42 prefectures by 2004, and all 47 prefectures by 2006 (Ikeda 2000; Ikeda et al. 2004; Kaneshiro and Yachimori 2007). This wide distribution can be attributed, in part, to irresponsible release and/or escape of imported pet raccoons (Agetsuma-Yanagihara 2004; Ikeda et al. 2004). Local municipalities implemented raccoon eradication programs, mainly focused on capture. The first raccoon was captured in Tokachi (Figure 1), a district in eastern

Hokkaido, Japan, in 2006, although a 1998 distributional survey of mammals did not reveal raccoons at this site (Biodiversity Center of Japan 2002). In addition, as of 2014, local municipalities reported agricultural damage attributed to raccoons was minimal (*unpublished municipalities' data*). Therefore, in Tokachi, raccoons are likely in the early stages of invasion. Predation on native species, consumption of agricultural crops, and invasion of human dwellings have been reported in some regions of Japan (Ikeda et al. 2004; Kaneda and Kato 2011; Hori et al. 2013; MAFF 2017) as well as Europe (Kauhala 1996; Bartoszewicz et al. 2008; Beltrán-Beck et al. 2012; García et al. 2012; Lassnig et al. 2020). Considering the rapid expansion of the introduced raccoon population (Lassnig et al. 2020), a management strategy for raccoons in Tokachi is urgently needed. Implementation of appropriate IAS management strategies at introduction or establishment stages could suppress further establishment of raccoon populations. However, raccoon capture data recorded by local municipalities in Tokachi have not been integrated for analyses of invasion status. In addition, practical capture methods based on raccoon ecology have not been developed.

We investigated invasion stages and habitat preferences of raccoons introduced into Tokachi from data obtained by local municipalities. To determine if raccoon invasion has reached the establishment stage, we examined the reproductive status of female raccoons from 2010 to 2014. In addition, we investigated if raccoon populations were growing and expanding spatially and in number based on three factors: 1) population densities estimated from the 2013–2014 raccoon capture data, 2) annual changes in numbers of captured raccoons, and 3) annual spatial changes in raccoon capture sites in Tokachi over 9 years (2006–2014). To identify habitat preferences, we investigated landscape factors influencing habitat use and body size. We hypothesized that livestock farms, forests, and rivers facilitate population establishment and focused on these three landscape features because (i) livestock farms and forests are key sites for raccoon feeding, kit delivery, and resting (Nixon et al. 2001; Zeveloff 2002; Gehrt 2003; Ikeda et al. 2004; Abe et al. 2006) and (ii) rivers are key feeding sites and movement corridors (Johnson 1970; Zeveloff 2002; Gehrt 2003). In addition, we surveyed diet composition to examine the hypothesis that livestock farms are important for raccoon populations (as determined by the detection of livestock feed in their stomachs). Finally, we propose high priority areas for raccoon management and recommend appropriate strategies based on invasion stage in Tokachi. We aimed to elucidate the feasibility of these processes by cooperation between researchers and municipalities as one approach to develop strategies for managing IAS at the early stages.

Materials and methods

Study area

The study area, Tokachi (42–43 °N, 142–144 °E), covers an area of 10,831 km^2 (Figure 1). The climate is boreal and characterized by a cold winter. Average temperatures were −6.9 °C in January and 19.4 °C in July, as measured between 2006 and 2015 in Obihiro, central Tokachi (Japan Meteorological Agency 2016). The landscape primarily consisted of forests in mountainous areas and agricultural plains divided into fields. Forests were dominated by Daimyo oak (*Quercus dentata* Thunb.), Manchurian ash (*Fraxinus mandshurica* Rupr.), Japanese elm (*Ulmus davidiana* var. *japonica* Rehder Nakai), and planted forests with species such as Japanese larch (*Larix kaempferi* Lam. Carrière). Primary agricultural crops included wheat (*Triticum aestivum* L.), potatoes (*Solanum tuberosum* L.), beet (*Beta vulgaris* ssp. *vulgaris* L.), and corn (*Zea maize* L.). In addition, dairy farming was a major economic activity in Tokachi, with more than 2,400 livestock farms, including 1,600 dairy farms (Statistics and Information Department, MAFF 2008). A 1998 survey of wild mammals in the region detected no raccoons (Biodiversity Center of Japan 2002), suggesting that they were likely introduced into Tokachi in the early 2000s. In western Tokachi, the relative raccoon population density estimated using camera trap data from one river was higher in open fields than in mountainous areas ($P < 0.001$; Supplementary material Appendix 1, Table S1, Figure S1), suggesting that open fields are the preferred habitats. Such habitats are where the source population appeared to be located and where our raccoon data were collected.

Data collection

Raccoon individual data

We obtained raccoon carcasses collected as roadkill or from box traps between 2009 and 2014. There were multiple opportunities to obtain carcasses of box-trapped individuals from both a municipality eradication program and our field survey. Some were obtained from a pest control project for red foxes (*Vulpes vulpes* Linnaeus, 1758). Permits for trapping were granted by the Tokachi General Subprefecture Bureau of the Hokkaido government (authorization no. Tokansei-1255 in 2013, Tokansei-349 in 2014). Based on postmortem examinations of the carcasses, we collected data on body weight, body length, sex, age (between 2009 and 2014), female reproductive status (between 2010 and 2014), and stomach contents (collected only in 2013 and 2014). Raccoon ages were determined based on body weight (Gehrt and Fritzell 1999; Asano et al. 2003a), size of the canine root apical foramen (Grau et al. 1970), and cranial suture obliteration (Junge and Hoffmeister 1980). Body sizes were used to calculate body mass index (BMI = Body weight [kg]/Body length^2 [m]) to determine nutritional condition (Kato et al. 2012). Female reproductive status and stomach contents were used to determine the success of establishment and diet composition of the raccoon population, respectively.

To determine the reproductive status of female raccoons, uteri were examined for fetuses or placental scars (Sanderson 1950). Numerous studies demonstrated that 1-year old female raccoons are not as sexually mature as

≥ 2-year old females (Junge and Sanderson 1982; Fiero and Verts 1986; Asano et al. 2003b; Kato et al. 2009). Consequently, the female raccoons were divided into the following three age groups: ≥ 2-years old, adults; 1-year old, yearlings; and < 1-year old, juveniles. The percentage of parous females was calculated as follows: number of raccoons with fetuses or scars/number of female raccoons examined. In addition, the average litter size was calculated. Since female raccoons are immature in their first year (Stuewer 1943), reproductive status in juveniles was not examined. Some raccoons without skulls were regarded as age unknown.

The stomach contents were washed with tap water over 1-mm mesh sieves, and the remains were categorized to determine diet composition. To minimize the effect of digestion, which depends on the food type, only the stomachs (upper digestive tracts) were used for analyses. Stomach contents were categorized by the naked eye. Some sample volumes were not adequate for quantitative evaluation, including the point-frame method (Chamrad and Box 1964; Hirasawa et al. 2006); therefore, the percentages of samples including each food category in the total examined stomach samples were calculated. Stomach samples without contents were excluded from the calculation.

Raccoon occurrence data

Reports of raccoon capture and roadkill between 2006 and 2014 were collected to assess annual changes in the number and spatial patterns of the raccoons. These occurrence data included road-killed and box-trapped individuals mentioned previously. The annual number of captures was organized by raccoon ages. Since some skulls were broken, which made it hard to identify cranial sutures, we classified raccoons either as < 1-year old or ≥ 1-year old based on body weight and apical foramen size. Capture reports without any individual data for age determination were regarded as age unknown. To collect occurrence data, we asked Tokachi General Subprefecture Bureau of the Hokkaido government to identify the reports including raccoons in all 19 municipalities in Tokachi district. The details of the reports were assessed through interviews with the municipalities with raccoon reports. Most raccoon occurrence data were obtained from box trapping activities in open fields. To describe the spatial patterns of raccoon capture sites, we divided the landscape into 5 km × 5 km square grid cells. We then determined the first year in which a raccoon was observed in each 25 km^2 landscape unit and grouped these records into three time periods: (i) 2006–2009, raccoon municipality eradication program implemented in the northwestern region; (ii) 2010–2011, raccoon municipality eradication program implemented in the central-west region; and (iii) 2012–2014, capture data increased between the northern and central-west regions. The relative population density was evaluated based on box trapping data between 2013 and 2014 that had a measure of catch per unit effort (CPUE =

Table 1. Trapping data used to estimate relative raccoon density in Tokachi, Hokkaido, Japan between 2013 and 2014.

Data source	Town	Year	Period	Trap nights
Eradication program	Shintoku	2013	Apr 1 to Dec 17	259
		2014	Apr 7 to Dec 5	242
	Memuro	2013	May 1 to Dec 2	126–215
		2014	Apr 18 to Dec 5	179–231
Authors' field survey	Shimizu	2013	Jul 6 to Oct 31	51–82
	Memuro, Obihiro	2014	Apr 26 to Sep 29	51–78

Number of captures/Number of nights traps were open), which was calculated using trapping data within 25 km^2 square grid cells. Trapping to determine CPUE was performed using box traps of the same size and shapes (Havahart Model 1089 or 1092; Woodstream, Litiz, PA, USA) with at least 50 trap nights per year between 2013 and 2014. The trapping was operated in western Tokachi by two municipalities, Shintoku and Memuro, and our own field survey (Table 1). Traps were placed along or near animal trails with previous raccoon sightings or raccoon tracks. Traps were set with bait, such as dog food and caramel-flavored snacks made from corn, and were checked every morning during trapping periods. All captured raccoons were sacrificed with CO_2 inhalation or gunshot according to the eradication program. Raccoons are inactive in cold weather below the freezing point (Zeveloff 2002); therefore, data obtained between November and March, when the average of minimum temperatures were below 0 °C in Obihiro, central Tokachi (Japan Meteorological Agency 2016), do not reflect the actual raccoon population density and were excluded from the calculation. The Experimental Animal Committee of Obihiro University of Agriculture and Veterinary Medicine approved the present studies (authorization nos. 25-145 and 26-116).

Track data

Track data, a typical sign of raccoon presence, were obtained to investigate habitat preference of raccoons. The survey was conducted in 26 areas (1–5 areas per municipality) suspected to be within the raccoon distribution area from a 2010 raccoon distribution survey report covering nine municipalities in Tokachi, a one-off project conducted by the Hokkaido government. Areas were roughly selected based on previous raccoon sightings or capture information obtained from the municipalities. In each area, 4–10 survey points were located on bare ground because tracks easily remain on the soil at riversides, which are important corridors for raccoons (Stuewer 1943; Zeveloff 2002; Gehrt 2003). Survey point were placed at least 200 m apart. In total, 186 points were surveyed. We searched for tracks on bare ground in circles with radii of about 10 m for 6 days at each point between August and November. These points were assessed based on whether a track was observed, even once. We excluded track data obtained at 60 points from four municipalities without raccoon data before the present survey. The remaining 126 points from six municipalities were located in western Tokachi.

Landscape data

The relationship between landscape composition and the presence or absence of raccoons or the BMI of adult male and female raccoons was analyzed to determine the characteristics of preferred habitats and nutritional conditions on a landscape level. Three landscape factors critical for raccoon behaviors (including traveling, foraging, and resting) were considered: rivers (km), percentage of forest area in buffer zone area (forest/buffer zone area), and livestock farm density (per km^2). Data were obtained from the National Land Numerical Information download service (MLIT 2016), reports of the 6th and 7th National Basic Survey on Natural Environment (Biodiversity Center of Japan 2006), and the 2005 World Census of Agriculture and Forestry (Statistics and Information Department, MAFF 2008). Vegetation in a rural area in Obihiro was updated with the vegetation data obtained from the 2011 Obihiro biodiversity conservation project (Obihiro City Citizen Environment Part Environment City Promotion Department 2012). Each factor was evaluated in buffer zones ranging from 400 m to 1100 m at 100-m intervals generated around each track survey or capture point using ArcGIS 10.0, Spatial Analyst extension (ESRI Japan, Tokyo) and Geospatial Modelling Environment (Beyer 2012). The circular areas consisted of minimum (r = 400 m, 50 ha) and maximum buffer zones (r = 1100 m, 380 ha), which reflected typical raccoon home ranges as determined in a suburban area in central Hokkaido by radio telemetry (81–184 ha; Kurashima and Niwase 1998).

Data analysis

Generalized linear mixed models (GLMMs) with binary responses and linear mixed models (LMMs) were used to explain two response variables: the presence of tracks or the BMI of adult male and female raccoons in relation to the peripheral landscape composition quantified at each point cluster partitioned as following. Track survey points or capture points < 900 m apart were regarded as a cluster sharing the same landscape structure and assigned the same cluster ID to minimize pseudoreplication. Each landscape variable was averaged for each cluster, and the models included the effect of each cluster as a random intercept. Some points were < 900 m apart but were continuously distributed across a large geographic space. In that case, assuming corridors and natural barriers (e.g., cliffs) hinder movement of the individuals, continuously distributed points were assigned cluster IDs based on these dividers. From the spring to summer, female raccoons lose substantial energy during kit delivery and lactation, which can challenge attempts to understand the effects of landscape composition. Consequently, BMI data for female raccoons between April and August were excluded from analysis. Raccoons in Hokkaido are also inactive in winter (Kurashima and Niwase 1998; Ikeda et al. 2001); therefore, no raccoons of either sex were captured between January and March. However, raccoons become active on mild day in winter (Zeveloff 2002), which cause some captures in November to December, when raccoons seem to be inactive because of low temperature. For model selection, Akaike's information criterion (AIC) was used for GLMMs and bias-corrected Akaike's information criterion (AICc) was used for LMMs including all potential combinations of explanatory variables. Lowest-AIC or lowest-AICc models were selected at each spatial scale. The optimal model was determined by comparing the AIC or AICc of the selected models at each spatial scale (Burnham and Anderson 2002). To assess the predictive strength, two types of variance (R^2) were derived (marginal variance explained by only fixed factors and conditional variance explained by both fixed and random factors) from the five lowest-AIC or lowest-AICc models (Nakagawa et al. 2017). The variance inflated factor (VIF) values among explanatory variables were calculated to check multicollinearity. All VIF values were less than ten, suggesting multicollinearity was within acceptable level (Quinn and Keough 2012). R for Windows 3.3.0 (R Core Team 2016) was used to conduct all statistical analyses.

Results

Descriptive data

In total, 161 raccoons were collected between 2009 and 2014. Juvenile raccoons were collected every year. In the case of the female raccoons, between 2010 and 2014, 31 of 34 uteri (91.2%) had fetuses or placental scars, which indicated successful establishment in Tokachi (Sakai et al. 2001; Genovesi and Shine 2004). The percentage of parous females based on age group were 90.0% (9/10) in yearlings, 93.8% (15/16) in adults and 87.5% (7/8) in age unknown individuals. The litter size in parous female raccoons ranged from 3 to 6 (mean ± standard deviation [SD], 4.47 ± 0.99; Figure 2), and the average was higher in the adult age group than in the yearling group (yearling: 3.86 ± 0.83; adult: 4.93 ± 0.85; Figure 2).

Since 2006, 196 capture and 4 roadkill data points have been collected from eleven local municipalities in Tokachi. Eight municipalities had no data for raccoons. Records have gradually increased, with a rapid increase in 2009 (Figure 3). In addition, the capture sites have expanded (Figure 4). Most capture and roadkill points were in western Tokachi, particularly along rivers and their tributaries. Initially, raccoons were caught in two areas roughly divided into the northwestern and central-western regions. However, since 2012, raccoons have been reported in the area between these two key regions. A few raccoons have also been reported in the northernmost and easternmost municipalities > 20 km from the western municipalities where the populations are established (Figure 4). The CPUE, the index of relative population density, was 0–2.69 per 25 km^2 square grid cell (average CPUE/grid cell = 0.52, Figure 5) between 2013 and 2014.

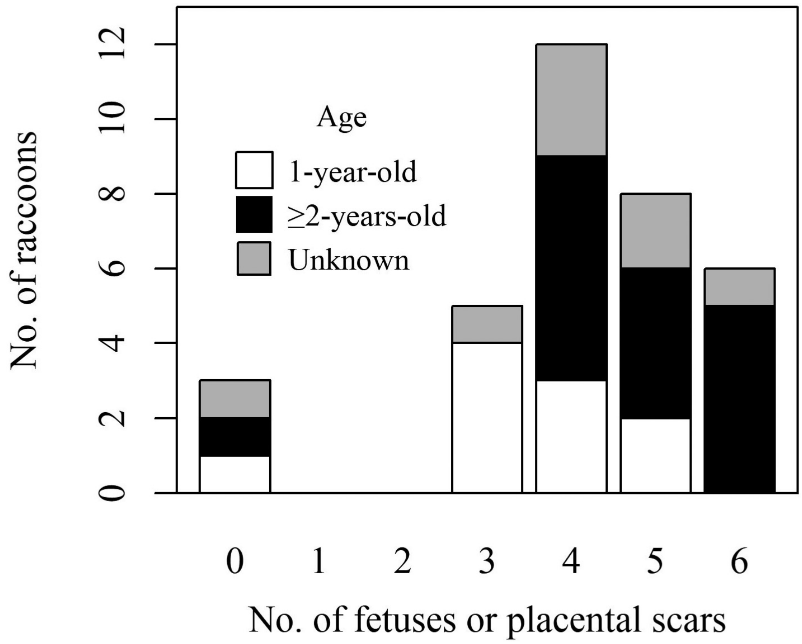

Figure 2. Distribution of raccoon litter size in Tokachi from 2010 to 2014, based on age group.

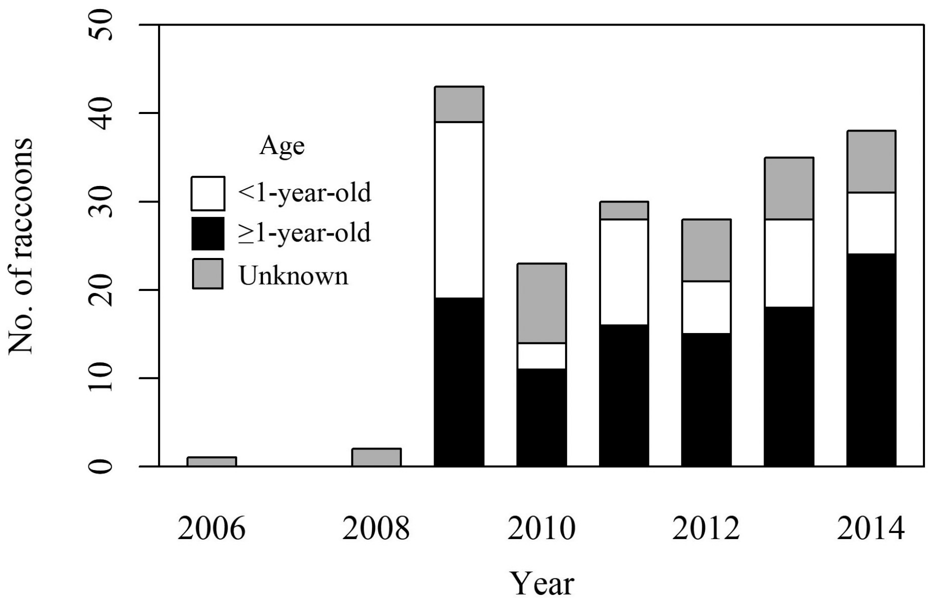

Figure 3. Annual changes in the number of raccoons collected in Tokachi from 2006 to 2014.

Diet composition contained various animal and vegetable materials (Table 2). Corn was most frequent (55%, 11/20 raccoons). Three raccoons consumed both corn and silage and concentrated feed pellets for cattle. Five of seven raccoons caught in the spring (March–May), which is not a corn-fruiting season, also had corn in their stomachs, suggesting that the animals obtained corn from livestock feed. Some raccoons had consumed riparian animals, including non-indigenous crustaceans, signal crayfish (*Pacifastacus leniusculus trowbridgii* Stimpson, 1857), and indigenous Ezo brown frogs (*Rana pirica* Matsui, 1991). Stomach contents of one raccoon included parts of another raccoon's paw (claws and phalanges).

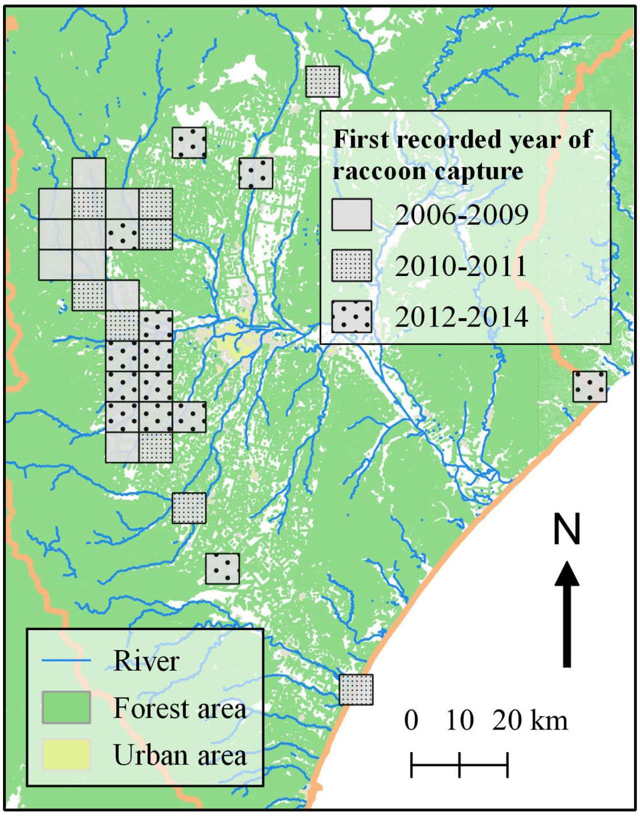

Figure 4. First recorded raccoon capture in each 5 km × 5 km grid cell in Tokachi from 2006 to 2014. Tokachi district is surrounded by an orange line.

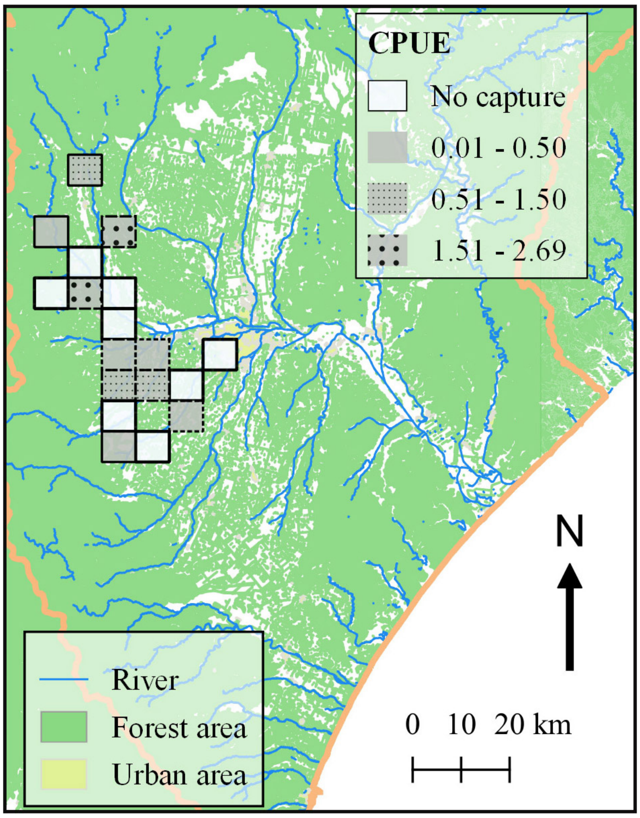

Figure 5. Relative densities of raccoons based on catch per unit effort (CPUE) in Tokachi between 2013 and 2014. Eradication program by municipalities, our own field survey, and both capture types are indicated by 5 km × 5 km grid cells with solid lines, sparse dashed lines, and dense dashed lines, respectively. Tokachi district is surrounded by an orange line.

Table 2. Food items found in raccoon stomachs in Tokachi, Hokkaido, Japan between 2013 and 2014.

$n = 20$		Occurrences
Plants		19
	Corn	11
	Concentrated feed pellets	3
	Fruits	2
	Leaves	19
Animals		13
	Mammals	1
	Birds	3
	Amphibians	2
	Fish	1
	Crustaceans	2
	Insects	7
	Unidentified vertebrates	4
Others	Plastics	1

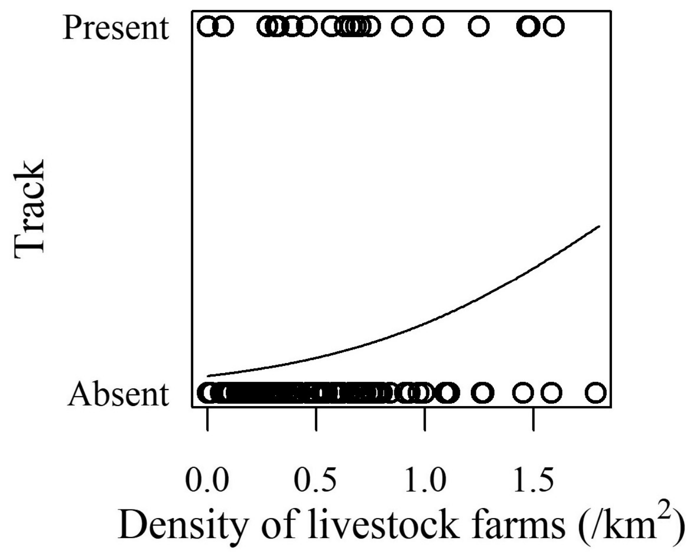

Figure 6. Relationship between the presence of raccoon tracks detected in a field survey in Tokachi in 2010 and the density of livestock farms within an 800-m radius of their capture sites. Actual values are marked with a circle; the predicted probability of presence based on the optimal model is indicated with a solid line (Table 2). In the calculation of the predicted value, the mean value was used for the total river length.

Modeling results

We detected raccoon tracks at 20 of 126 survey points in six municipalities in 2010. Appendix 2, Figure S2 shows the AIC values for GLMMs (number of clusters = 58), explaining the presence of tracks at each spatial scale. On average, each cluster included 2.17 points (SD = 1.72). The model with the lowest AIC had 800-m buffer zones. Livestock farm density was included in the models with the four lowest AIC values, although the parameter coefficients did not exceed twice the standard errors (Appendix 3, Table S2). Raccoon tracks were more frequent in areas with a high density of livestock farms within 800 m (Appendix 2, Figure 6; Appendix 3, Table S2). The marginal and conditional R^2 values for the model with the lowest AIC were 0.13 and 0.40, respectively. Both R^2 values were highest in the models with the four lowest AIC values (Appendix 3, Table S2).

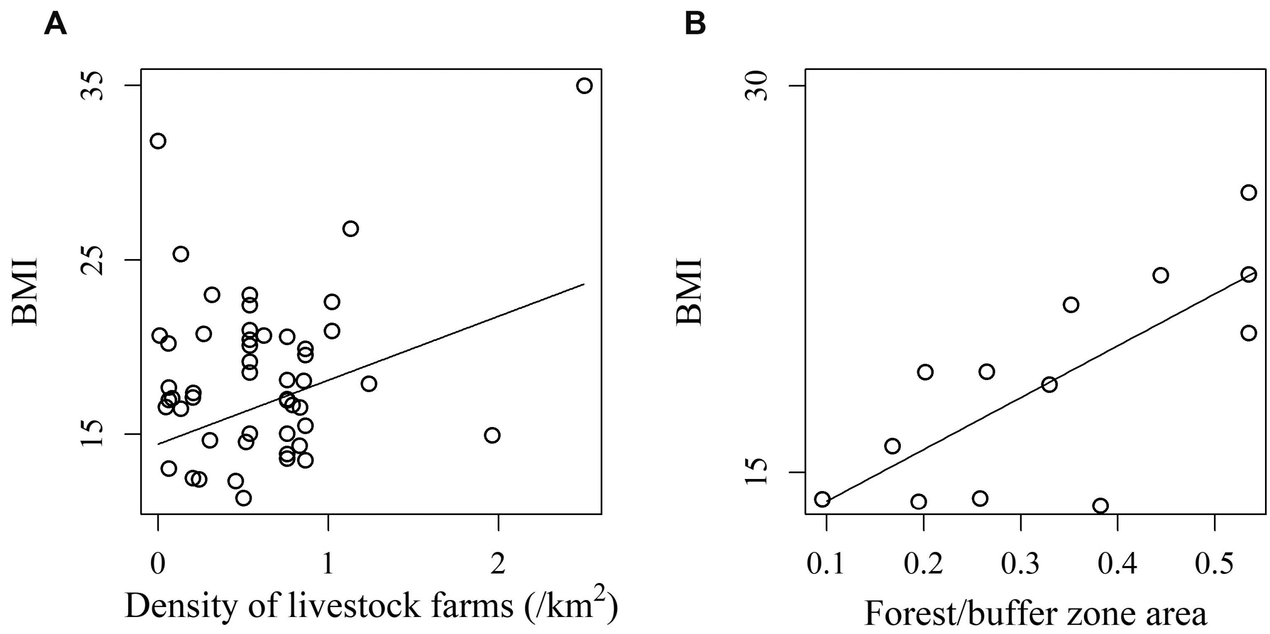

Figure 7. Relationship between raccoon body mass index (BMI) and key explanatory variables in each buffer, density of livestock farms within a 600-m radius for males (A) and forest/buffer zone area in a 700-m radius for females (B). Actual values are indicated by circles; the predicted BMI based on the best model is indicated with a solid line (Appendix 3, Table S2). In the calculation of the predicted value, the mean value was assigned to the other explanatory variables.

In LMM analyses of raccoon BMI, the scales of the model with the lowest AICc were 600 m for male raccoons (51 individuals, 25 clusters for capture points) and 700 m for female raccoons (13 individuals, 11 clusters for capture points) (Appendix 2, Figure S3). On average, each cluster included 2.04 (SD = 2.05) and 1.18 (SD = 0.57) points, respectively. The optimal model for male raccoons with 600-m buffer zones (ΔAICc > 2 compared with the second-best model) was a full model consisting of all explanatory variables (Appendix 3, Table S3A). In the model, the coefficient of livestock farm density was more than twice the standard error (Appendix 3, Table S3A). Livestock farm density was included in the models with the four lowest AICc values (Appendix 3, Table S3A). The marginal and conditional R^2 values for the model with the lowest AICc were 0.17 and 0.77, respectively. Both R^2 values were highest for the models with the five lowest AICc values (Appendix 3, Table S3A). Forest/buffer zone area was included in the models with the four lowest AICc values for female raccoons at 700-m buffer zones, and the coefficients were more than twice the standard errors (Appendix 3, Table S3B). Both marginal and conditional R^2 values for the model with the lowest AICc were 0.54; however, the model including the forest/buffer zone area and total river length had the highest predictive ability (Appendix 3, Table S3B; marginal R^2 = 0.63; conditional R^2 = 0.63). In the highest R^2 value model, only the coefficient of forest/buffer zone area was more than twice the standard errors. These results demonstrated that both male and female raccoons have higher BMI values in areas with dense livestock farms or abundant forests (Figure 7).

Discussion

Examining introduced raccoons in Tokachi, eastern Hokkaido, Japan, the raccoon population reached the establishment stage of invasion by 2010 based on reproductive success. However, the distribution was irregular across the district, therefore, the invasive stage seemed not to be even in this district. In addition, more and better-fed raccoons tended to inhabit areas with a high density of livestock farms, suggesting that livestock farms potentially facilitate population establishment, since a food supply was provided by these farms such as corn or pellets.

Parous female raccoons were captured every year since 2010. Juveniles were collected in 2009 (Figure 4) before the reproductive status of adult female raccoons was surveyed. These findings suggest that the establishment stage was reached by 2010 or earlier (Sakai et al. 2001; Genovesi and Shine 2004). Both the recent relative raccoon population densities and annual changes in raccoon capture sites over 9 years suggest that the raccoon population has expanded only in western Tokachi. The populations of invasive species grow through two phases impacted in general by Allee effects: a lag-phase characterized by slow spread and decreased likelihood of establishment, and an increase-phase characterized by rapid increase and spread following the former phase (Taylor and Hastings 2005). The CPUE based on raccoon capture data for western Tokachi in 2013 and 2014 indicated that these populations may currently be in the increase-phase (CPUE > 0.8; Asada 2013) in approximately one-fourth of the grid cells (22.2%, 4/18). Integrated raccoon occurrence data from local municipalities also indicated an increase in the number of captured raccoons, except in 2009 (the first year of the municipality eradication program) (Figure 4). Additionally, spatial trends showed that the capture sites only expanded in western Tokachi (Figure 5). In the eastern and northern regions, only two male raccoons were detected, and reproductive data for one individual in the south were not recorded. Young raccoons have been reported to travel long ranges (> 200 km, Priewert 1961; Lynch 1967), so raccoons in the eastern and northern regions may have traveled from the western region (i.e., populations may not be established outside of the western regions). These findings suggest that the raccoon population has only entered the establishment stage in western Tokachi. The number of captures changed with changes in capture effort, which were uneven across the district. Therefore, the survey results may not reflect the actual distribution of raccoons. However, some raccoons in the western region were caught by box traps set up for foxes, which are widely used in Tokachi and rarely in other areas. Considering all 19 municipalities in Tokachi have performed box trapping for foxes as a pest control project, the raccoon population in the western region is presumed to be larger than those in other areas.

The presence of tracks and male BMI were positively associated with landscapes characterized by large numbers of livestock farms (Appendix 3, Tables S2, S3; Figures 6, 7). Factors associated with livestock farms are presumably beneficial for raccoons and improve their nutritional conditions. This is supported by the frequent detection of corn in stomach contents (55%, 11/20; Table 2), potentially from livestock feed. Corn is a popular food source for raccoons in both native and non-native areas (Hamilton 1936; Giles 1940; Zeveloff 2002; Ikeda et al. 2004; MacGowan et al. 2006) and influences habitat use by the species. According to Beasley et al. (2007), the exploitation of crop fields by raccoons increases in the corn maturation season in Illinois, USA. Livestock farms with abundant corn feed are suitable foraging sites for raccoons throughout the year. Therefore, habitat use may be significantly associated with livestock farm density. Studies have demonstrated that supplemental foods, such as livestock feed, are not only palatable but also result in weight gain in various mammals (Boutin 1990). Our results from BMI and stomach contents analysis indicate nutritional conditions are probably improved in areas with high densities of livestock farms. Because these results are based on investigations at the landscape level, the direct relationship between livestock farms and raccoons (e.g., the dependency on livestock farms as nesting and feeding sites) should be assessed at a smaller scale in the future. In contrast, female raccoons inhabiting highly forested areas were relatively well-nourished in the autumn (Appendix 2, Figure 7; Appendix 3, Table S3). Feeding experiments and diet analyses have demonstrated that raccoons prefer fruits and acorns to corn (Hamilton 1936; Taulman and Williamson 1994; Zeveloff 2002). In autumn, caloric fruits and acorns are ripe and abundant in forests. In addition, in the present study, two raccoons with fruits in their stomachs were captured in the autumn (Table 2). Thus, raccoons potentially become well-nourished due to the availability of these caloric foods in this season. We did not analyze female raccoon nutritional conditions in the spring and summer when they lose substantial energy due to kit delivery and lactation. Determining the contribution to female population dynamics in the spring and summer requires assessment based on other features, such as reproductive status. Spatial scales of models explaining raccoon BMI (male: 600 m; female: 700 m) and track presence (800 m) reflect the radii of the home ranges (508–765 m) of suburban raccoons in Hokkaido, represented as circular areas (81–184 ha; Kurashima and Niwase 1998). The similarity suggests that the habitat resources of raccoons, including food and dens, influence habitat use and nutritional conditions, explaining the selection of models for both ecological characteristics based on landscape structure within the radii.

Based on our results and considering how invasion stage varied across Tokachi, a locally tailored strategy for the management of raccoon populations in Tokachi is required. Focus ought to be on capturing raccoons to suppress further population establishment in western Tokachi and monitoring raccoon introductions to prevent establishment in other areas. In particular, intensive capture operations and strengthening report-and-alert systems in areas with a high density of livestock farms are important strategies for the removal of well-nourished raccoons and for an enhanced understanding of raccoon distribution at the local level. This information will enable constructive decision-making by stakeholders, thereby improving the success of management strategies (Crowley et al. 2017b). Diet analyses of raccoons indicated that animals consumed native frogs and livestock feed (Table 2). This suggests that raccoons possibly affect populations of native species and the livestock industry in Tokachi, similar to other districts in Japan (Ikeda et al. 2004; Ikeda 2006; Kaneda and Kato 2011; Hori et al. 2013). Such information should inform the formulation of mitigation strategies. Fujii et al. (2012) also observed that raccoons in Tokachi carry the zoonotic pathogen *Salmonella* and therefore have the potential to influence pathogen transmission among livestock farms, particularly considering that raccoons frequent farms and consume livestock feed. These potential impacts should be assessed and appropriate management for this district should be implemented based on deliberation among interested parties, including environmental resource managers and livestock workers (Crowley et al. 2017a, b).

The relative raccoon population density was lower in Tokachi than in central Hokkaido, where the species has been established since the 1980s. In the present study, the average CPUE in Tokachi (0.52) was lower than the total average CPUE in central Hokkaido from 2009 to 2011 (3.63, Hokkaido government *unpublished data*). Based on percentage of parous females in yearlings and the average adult female litter size (Figure 2), raccoons are successfully reproducing in Tokachi. In addition, the percentage of parous females of yearlings in Tokachi (90.0%; Figure 2) was relatively high compared with those in other areas of the world (central Hokkaido, 66%; Kamakura, 64.9%; Iowa, 59%; Illinois, 66%; Missouri, 49%) (Fritzell et al. 1985; Clark et al. 1989; Ritke 1990; Asano et al. 2003b; Kato et al. 2009). Moreover, the average litter size of adult female raccoons (4.93; Figure 2) was high compared with those in other areas (central Hokkaido, 3.9; Kamakura, 4.0; North America, 2.0–4.8 [total data from yearlings and adults]). Unless appropriate IAS management strategies are implemented, the raccoon population might increase rapidly, with negative impacts in Tokachi.

We determined the stages of invasion and habitat preferences of raccoons in Tokachi using capture data from local municipalities to facilitate the appropriate management of this introduced species. Duscher et al. (2018) indicated that habitat preference in raccoons varied among invasive stages; therefore, management should be flexible, with continuous habitat assessment and evaluation through feedback systems. Because climate and geographical features influence the raccoon distribution in Europe and worldwide (Mori et al. 2015; Duscher et al. 2018; Louppe et al. 2019), further investigation considering these features might improve our understanding of habitat preferences. However, limited passively collected information is insufficient given the complexity of raccoon population ecology in the study area. In the future, ideally, all trapping data, not just successful cases, ought to be recorded. Detailed data related to population dynamics across an entire district would facilitate the estimation of population sizes using statistical approaches (Matsuda et al. 2002; Yamamura et al. 2008; Asada 2014). In Germany, population dynamics based on hunting bag records are utilized to evaluate raccoon population growth (Salgado 2018), which is applicable to evaluations of the effects of management in Tokachi. Detailed analyses of population dynamics would facilitate the estimation of the costs and effort required for the eradication of raccoons, based on simulation studies, as evidenced by the success of nutria (*Myocastor coypus* Molina, 1782) eradication in the United Kingdom (Gosling and Baker 1989). To address the lack of ecological information for IAS at the early stages, we propose strategic management programs based on specific invasion stages and habitat usage at a local level, supported by local municipality records, as an initial urgent response.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Comparison of relative population densities among four areas along the Shibusan River in western Tokachi, Hokkaido, Japan, based on camera trap data obtained in 2014.
Figure S1. Comparison of the frequency of raccoon photograph capture among four areas along a river in Tokachi, Hokkaido, Japan in 2014 (Table S1 for details).
Table S1. Frequency of photographs of raccoons for camera traps along a river in Tokachi, Hokkaido, Japan in 2014.
Appendix 2. Modeling results.
Figure S2. Akaike's information criterion (AIC) values for the best model explaining the presence of raccoon tracks based on landscape structure for each buffer.
Figure S3. Bias-corrected Akaike's information criterion (AICc) values for the optimal model explaining male (A) and female (B) raccoon body mass indexes (BMIs) based on landscape composition for each buffer size.
Appendix 3. Modeling results.
Table S2. Four models with the lowest Akaike's information criterion (AIC) values explaining the presence of raccoon tracks in Tokachi, Hokkaido, Japan in 2010 and coefficients of explanatory variables (standard error).
Table S3. Five models with the lowest bias-corrected Akaike's information criterion (AICc) explaining raccoon body mass index (BMI) in Tokachi, Hokkaido, Japan between 2009 and 2014 based on sex (male [A] and female [B]) and coefficients of their explanatory variables (standard error).

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