



Research Article

Assessing scale-dependent effects of resource availability on the habitat selection of Siberian roe deer (*Capreolus pygargus*) using a mixture model for the fecal pellet count

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Abstract

Resource selection is fundamental to understanding the ecology of a species because it is directly related to its survival and reproduction. The scale-dependent process for the habitat use of Siberian roe deer (*Capreolus pygargus*) was investigated in temperate forest to determine their resource priorities. Since imperfect detectability of fecal pellet count method can lead to false zeroes and overdispersion issues, we accounted for these issues using a zero-inflated model. The abundance of roe deer was constant between the deciduous forest and larch plantation. This might be due to the high productivity of temperate forest in the study area. However, the microhabitat use by roe deer differed between the forest types because of resource availability. Roe deer exhibit consistent pattern of microhabitat use in the larch plantations, while they exploited higher food quality in deciduous forests. Due to high resource availability, including food and covers, in larch plantation, habitat use of deer may not be limited by spatial variation on the resources. Moreover, we confirmed that weather, forest type, and ground conditions affected spatiotemporal variation in fecal pellet detection on a habitat and microhabitat scale. The zero-inflated model could make the fecal pellet count method more efficient and reliable without additional field surveys by correcting the detectability of fecal pellets. This simple statistical model can facilitate future research on ungulate and lagomorph populations.

Introduction

To survive and reproduce, species require a variety of resources, including food, cover, water, and space (Myserud et al., 1999; Tixier et al., 1997; Mátrai and Kabai, 1989). Spatial variation in these (and other) resources plays a significant role in driving the habitat selection process of individual species (Lee et al., 2022). Consequently, the relationship between resource availability and species abundance has been widely researched (Mancinelli et al., 2015; DePerno et al., 2003). Among these resources, food availability has been considered as a key factor in determining abundance (Morellet et al., 2013; Vospernik and Reimoser, 2008). Moreover, spatial variation in the resources affects not only the species abundance but also microhabitat use (Allen et al., 2014; van Beest et al., 2010). As ideal habitats that fulfill all the requirements for the proliferation and survival of a species are rare, the microhabitat use of a species is dependent on its prioritization of resources (Eom et al., 2020), which can differ between habitat types (Cimino and Lovari, 2003).

Siberian roe deer (*Capreolus pygargus*) is common, native ungulate species in South Korea, where the ungulate communities have become more complex due to restored populations of Amur goral (*Naemorhedus caudatus*) and introduced populations of alien species such as sika deer (*Cervus nippon*) and red deer (*Cervus elaphus*) (Banjade et al., 2023; Jang et al., 2020). Roe deer compete with the restored Amur goral (Eom et al., 2023), and the high density of roe deer population has led to increased human-wildlife conflicts, such as wildlife-vehicle collisions and crop damage (Baek and Lee, 2021; Bleier et al., 2012). However, scientific knowledge that could guide appropriate management actions to address these issues in South Korea remains

limited to few studies covering habitat selection by ungulate species (Eom et al., 2020; Son et al., 2017). Additionally, more efficient monitoring methods for ungulate populations are needed.

In present study, we employed fecal pellet counts to study the habitat use of roe deer. Fecal pellet counts have been widely used to analyze the spatial distribution of ungulates and lagomorphs (Alves et al., 2013; Prugh and Krebs, 2004) under the assumption of a linear relationship between the counts and abundance. However, this assumption can be violated due to variations in defecation rate among animals, decomposition rate of fecal pellets, and the ability of collectors. Spatiotemporal variation in the decomposition rate of fecal pellets can lead to discrepancies between the observed fecal pellet counts and the actual abundance of a target species (Popova et al., 2019; Brinkman et al., 2012; Forsyth et al., 2007). Several studies have attempted to address this issue by measuring the decomposition rate of fecal pellets in the field (Fiske and Chandler, 2011; Laing et al., 2003). However, this approach is costly, labor-intensive, and difficult to account for within-habitat variation in the detectability of a species based on fecal pellets.

Mixture models have recently been used to account for detectability in various field survey methods, including fecal pellet count, camera trapping, and direct observation (Burton et al., 2015; Ferreguetti et al., 2015; Goode et al., 2014; Royle, 2004). To improve the fecal pellet count method, we applied a mixture model in the present study. Specifically, the zero-inflated model comprises zero-inflated and count components, which account for the probabilities of both false zeroes and true zeroes in each component.

The aim of this study was to describe the habitat use of Siberian roe deer in natural deciduous forest and Japanese larch (*Larix kaempferi*) plantations. Resource availability for deer is dependent on vegetation type and structure (Eom et al., 2020), and we expected differences in habitat structure between the natural forest and artificial plantation (Lee

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et al., 2019, 2018). Therefore, we focused on examining the relationship between resource availability and habitat use for roe deer in the two forest types. Our first hypothesis was that the roe deer's habitat preferences would be based on the food availability within each forest type (H1). To determine these habitat preferences, we compared the roe deer abundance between the forest types. Moreover, we hypothesized that the microhabitat use pattern of roe deer would differ between the two forest types as mediated by resource availability (H2). We modeled the effects of resources availability on microhabitat use within each forest type. Finally, we tested whether the zero-inflated model could explain the spatiotemporal variation in the detectability of roe deer based on fecal pellet counts.

Material and methods

Study area

The study area was located in Mt. Gariwang, Pyeongchang, South Korea ($37^{\circ}27'38''-37^{\circ}30'35''$ N; $128^{\circ}28'30''-128^{\circ}33'56''$ E), which was 550 to 1,500 m above sea level (asl) with an area of 3,500 ha that consisted of temperate broadleaf mixed forest (Fig. 1). The annual mean temperature for the region was 11.3°C (range from -18.9 to 36.0°C), and the annual precipitation was 1,208.8 mm. Mt. Gariwang consisted of both natural forest and plantations (Fig. S1). The natural forest was primarily deciduous forest with an age of 40–50 years, dominated by Mongolian oak (*Quercus mongolica*; Korea Forest Service, 2022). In the plantations, even-aged Japanese larch was the most common species. The entire area of Mt. Gariwang was restricted to the public, with access limited to foresters and researchers. Thinning was conducted within some stands for habitat management, and unpaved forest roads for management was distributed across Mt. Gariwang. National Forest Office facilities, including an experimental plantation, lodge, and training field, were located within the area containing the plantations.

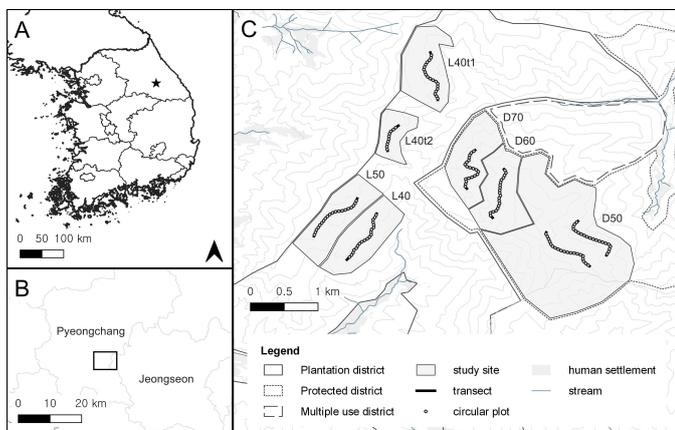


Figure 1 – Location of Pyeongchang (A; *) and study area (B; □), and sampling scheme (C) in the study of temperate forests, South Korea. Four study sites, including L40, L50, L40t1 and L40t2, were established at Japanese larch plantation district and three study sites, including D50, D60 and D70, were established at natural deciduous forest of protected district.

Two deer species, Siberian roe deer and water deer (*Hydropotes inermis*), inhabited in the study area (Son et al., 2017). The roe deer population was distributed across all of Mt. Gariwang, while the water deer population was smaller and mainly found along the low-altitude edge of the mountain, below 500–700 m asl. For this study, fecal data was collected exclusively for roe deer as the study sites for data collection were above 900 m asl and at least 1 km from the edge of the area.

Seven study sites were established in the deciduous forest and larch plantations. In the deciduous forest, we selected three stands: a 50-year-old (D50), a 60-year-old (D60), and a 70–80-year-old stand (D70). Two line transects (1 km long) were placed at the D50 site, while one line transect was established at each of the other sites. In the larch plantation, we selected four stands: a 40-year-old plantation (L40), a

50-year-old (L50) plantation, a 40-year-old plantation with 50 % thinning (L40t1), and a 40-year-old plantation with 75 % thinning (L40t2). At the L40t1 and L40t2 sites, thinning was conducted in November 2013. Each study site in the larch plantation had a single line transect, except for the L40t2 site. The L40t2 had a shorter line transect (500 m long) due to small size of the site. The line transects were divided into 10 or 20 sub-transects (50 m long), resulting in 80 sub-transects within the deciduous forest and 70 sub-transects within the larch plantations. Additionally, a circular plot (radius=5.64 m) was established at each sub-transect for the habitat survey.

Resource availability

We surveyed vegetation structure in each circular plot in August 2021 to assess the availability of food and cover for roe deer. The vegetation structure was classified into three vertical layers: ground (v_0 , <1 m in height), understory (v_1 , 1–2 m in height), and overstory (v_2 , >2 m in height) layers. Coverage for each layer was categorized into four categories: 0 (0 %), 1 (1–33 %), 2 (34–66 %), and 3 (67–100 %). The coverage of each layer was considered as an indicator of the quantity of food, concealment, and climatic cover. Moreover, we measured the coverage (%) of forbs, a high-quality food item for roe deer, to represent the food quality of the habitat (Adhikari et al., 2016).

To quantify the resource availability for each forest type, we modeled the effects of forest type on the vegetation structure. Linear regression was used to analyze the forbs, while interval regression was employed for vertical layers (v_0 , v_1 , and v_2). The goodness-of-fit for the models was evaluated using F and Chi-square tests. The modeling of resource availability was conducted using the survival package (ver. 3.2-13; Therneau, 2021) package in R 4.1.3 (R Core Team, 2022).

Fecal pellet count

Field sign surveys were conducted twice in May 2020 and 2021. The fecal pellet groups for roe deer were counted within each sub-transect. Only fecal pellet groups ($n=362$) containing more than four pellets were recorded to consider only fresh field signs. The survey was conducted at a speed of 1 km/h, and all investigators were well-trained. To account for the decomposition rate of the fecal pellets, habitat variables were surveyed within the circular plots, and this habitat data were associated with the fecal pellet counts for each sub-transect.

The weather, microclimate, and ground conditions were also recorded as they are crucial factors influencing the decomposition of fecal pellets (Murray et al., 2005; Prugh and Krebs, 2004). Temperature and relative humidity were recorded at 1-h intervals using three HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA). The average temperature ($temp$) for a week before the field sign survey was calculated. However, humidity variable was excluded from further analysis due to its high correlation with temperature. To describe the ground condition, percentage (%) of the following ground cover types was measured at each circular plot: vegetation, litter, rocky and bare ground. Then, principal component 1 (g_{PC1} ; explained variance=49.87 %) and principal component 2 (g_{PC2} ; 29.30 %) were calculated from the ground variables using principal component analysis in order to prevent multicollinearity issue in subsequent analyses (Fig. 2 and Tab. S2). To examine the effect of microclimate on the fecal pellet decomposition, we considered the characteristics of the forest stand (*forest type*, *age*, and *treatment*) and overstory layer (v_2).

The distribution of fecal pellet count exhibited zero inflation, with 57.84 % of the sample showing a zero count (Supplement S3). We used a zero-inflated Poisson (ZIP) model to account for the detectability of roe deer and their distribution. The ZIP model is a two-component mixture model that combines a probability mass function at zero with a Poisson distribution. We let denote the unobserved probability for fecal pellets and it was calculated using the point mass of the ZIP model. Thus, the ZIP model can be used to distinguish false zeroes from the detectability process and true zeroes from the count process. The ZIP

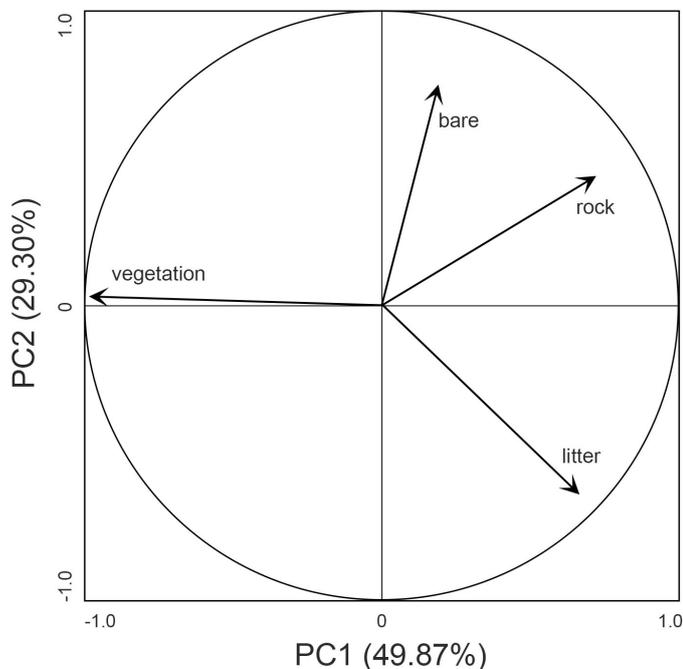


Figure 2 – Principal component analysis (PCA) biplot for ground variables.

model is given by the following equation (Zeileis et al., 2008):

$$P(Y_i = y_i) = \begin{cases} \pi_i + (1 - \pi_i)e^{-\mu_i} & \text{if } y_i = 0 \\ (1 - \pi_i) \frac{e^{-\mu_i} \mu_i^{y_i}}{y_i!} & \text{if } y_i > 0 \end{cases}$$

Null models were built using Poisson and ZIP distributions. Their performances were compared with expected number of zero counts and the corrected Akaike information criterion (AICc).

Roe deer abundance

We modeled the influence of forest type and year on roe deer abundance using the ZIP model. The global model for the abundance was formulated as follows: Count model [*year + forest type*] + zero-inflated model [*temp + g_{PC1} + g_{PC2} + v2 + forest type + forest type: g_{PC1}*]. Since *g_{PC1}* were dependent on forest type, the interaction term was included in the global model. We tested all possible combinations of the explanatory variables in the global model to explore the detection process of fecal pellets and test our hypotheses. The top model and candidate models ($\Delta AICc < 2$) were selected using the AICc. Residuals of top model were examined using Moran’s I and spline correlation to confirm the absence of any spatial correlation issues (Supplement. S4). The modeling of abundance was conducted using the *pscl* (ver. 1.5.5; Jackman, 2024), *MuMIn* (ver. 1.46.0; Barton, 2022) and *ncf* (ver. 1.3-2; Bjornstad, 2022) packages in R.

Roe deer habitat use patterns

To determine the habitat use strategies of roe deer in the two forest types, we conducted separate processes for each forest type. For the deciduous forest, candidate variables for the count part were *age*, *forb*, *v0*, *v1*, and *v2* and candidate variables for zero-inflated part were *age*, *g_{PC1}*, *g_{PC2}*, *v2* and *temp* for the zero-inflated part. As there were significant differences in *forb*, *v0* and *g_{PC1}* depending on *age*, their interaction terms were included as an explanatory variable in the next step of the modeling process. The global model for microhabitat use in the deciduous forest count part had the following equation: [*forb + v0+v1 + v2 + year + age + age:forb + age:v0*] + zero-inflated part [*g_{PC1} + g_{PC2} + v2 + temp + age + age:g_{PC1}*]. For the top model, post-hoc Tukey tests for *age* were conducted.

The candidate variables in the modeling for the larch plantations were *treatment*, *forb*, *v0*, *v1*, and *v2* for the count process and *treatment*,

g_{PC1}, *g_{PC2}*, *v2* and *temp* for the zero-inflated process. Due to a significant linear relationship between *v0* and *forb*, *v0* was excluded from the subsequent modeling process. As there were the spatial variation in *v1*, *forb* and *g_{PC1}* depending on *treatment*, their interaction terms were included in the global model for the larch plantations. Thus, the global model for microhabitat use in the larch plantations had the following equation: count part [*forb + v1 + v2 + year + treatment + treatment:forb + treatment:v1*] + zero-inflated part [*g_{PC1} + g_{PC2} + v2 + temp + treatment + treatment:g_{PC1}*]. Also, spatial autocorrelation in top models were examined using Moran’s I and spline correlation (Supplement S4). The modeling of habitat use was conducted using the *pscl* (ver. 1.5.5; Jackman, 2024), *MuMIn* (ver. 1.46.0; Barton, 2022), *emmeans* (ver. 1.7.5; Lenth, 2022) and *ncf* (ver. 1.3-2; Bjornstad, 2022) packages in R.

Results

Resource availability

We analyzed vegetation coverage in both forest types to determine the resource availability (Fig. 3). The coverage of forbs was estimated to be 5.05 % (CI 95 %: 1.60–8.50) and 21.57 % (17.89–25.26) in the deciduous forest and larch plantations, respectively (goodness-of-fit test, $F=41.21, p<0.001$). The coverage of ground layer was estimated to be 50.00 % (45.21–54.79) and 76.45 % (71.26–81.64) in the deciduous forest and larch plantations, respectively (deviance=46.51, $p<0.001$). The understory coverage was estimated to be 21.60 % (17.63–25.57) and 34.88 % (30.82–38.95) for the deciduous forest and larch plantations, respectively (deviance=19.68, $p<0.001$), while that of overstory layer was 76.67 % (73.10–80.24) and 75.68 % (71.84–79.52; deviance=0.14, $p=0.71$). The larch plantations thus provided more cover for concealment, while there was no difference in the climatic cover between forest types.

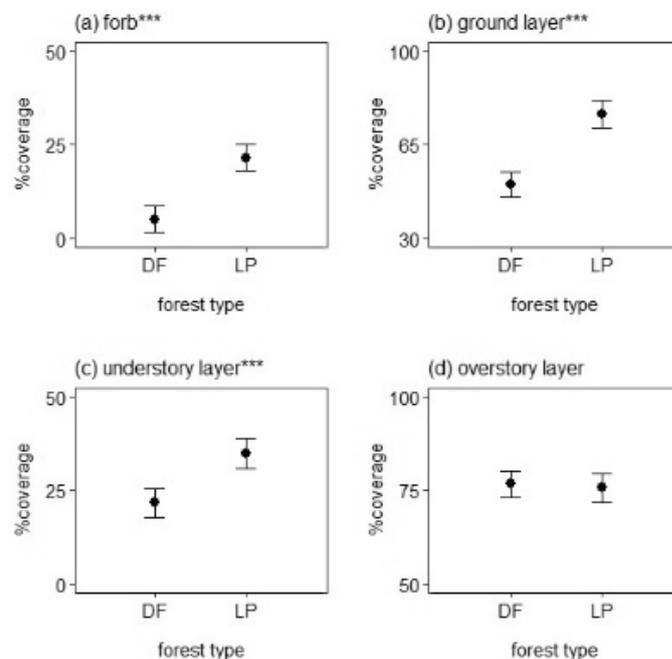


Figure 3 – Predicted average and CI 95% of resources in deciduous forest (DF) and larch plantations (LP) assessed using interval regression for the vegetation coverage and linear regression for the forbs. *** $p < 0.001$.

Roe deer abundance

Two null models were built with Poisson and ZIP distribution and their performances were compared (Supplement S3). While Poisson model predicted 100 zeros, ZIP model predicted 166 zeros which is same with the number of zeros in fecal pellet counts. The AICc value for the ZIP model was 821.53, indicating its better fit compared to the Poisson model (AICc for the Poisson model=974.23). The ZIP model was

Table 1 – Description of explanatory variables in the modeling process explaining the ecology of Siberian roe deer (*Capreolus pygargus*) in temperate forests of Mt. Gariwang.

Variable	Description	Mean	SD
<i>Abundance</i>			
year	year of survey; 2020 and 2021	-	-
forest type	forest type; deciduous forest (DF) and larch plantation (LP)	-	-
<i>Microhabitat</i>			
forb	Coverage [%]of forb, representing food quality of habitat	12.76	17.72
v0	Coverage [0, 1, 2, 3]of vegetation from the ground to 1 m height, representing food quantity of habitat	2.37	0.77
v1	Coverage [0, 1, 2, 3]of vegetation from 1 m to 2 m height, representing quantity of concealment cover	1.32	0.56
v2	Coverage [0, 1, 2, 3]of vegetation above 2 m height, representing quantity of climatic cover	2.82	0.43
forest age	age of deciduous forests; 50 yr (D50), 60 yr (D60) and 70 yr-old (D70)	-	-
treatment	treatment of larch plantations; 40 yr (L40), 50 yr (L50) and 40 yr-old plantations with 50% (L40t1) and 75% thinning (L40t2)	-	-
<i>Detectability</i>			
g _{PC1}	Principal component 1 (variance = 49.87%), representing coverage of vegetation on the ground	-	-
g _{PC2}	Principal component 2 (variance = 29.30%), representing coverage of bare ground	-	-
v2	Coverage [0, 1, 2, 3]of vegetation above 2 m height, representing quantity of climatic cover	2.82	0.43
temp	mean of temperature [°C]in study area for a week before survey	9.44	0.39

Table 2 – Candidate models ($\Delta AICc < 2$) with a zero-inflated Poisson (ZIP) distribution in the model explaining the abundance of Siberian roe deer (*Capreolus pygargus*) in deciduous forest and larch plantations.

Order	Model	df	logLik	AICc	Delta	Weight
1	Count[(Intercept)+year]+ Zero[(Intercept)+forest type]	4	-400.70	809.55	0.00	0.22
2	Count[(Intercept)+year]+ Zero[(Intercept)+temp+forest type]	5	-400.10	810.41	0.86	0.15
3	Count[(Intercept)+year+forest type]+ Zero[(Intercept)+forest type]	5	-400.28	810.77	1.22	0.12
4	Count[(Intercept)]+ Zero[(Intercept)+forest type]	3	-402.42	810.92	1.37	0.11
5	Count[(Intercept)+year+forest type]+ Zero[(Intercept)+g _{PC2} +forest type]	5	-400.41	811.04	1.49	0.11
6	Count[(Intercept)+year]+ Zero[(Intercept)+v2+forest type]	5	-400.49	811.19	1.64	0.01
7	Count[(Intercept)+year+forest type]+ Zero[(Intercept)+temp+forest type]	6	-399.47	811.24	1.69	0.01
8	Count[(Intercept)+year]+ Zero[(Intercept)+g _{PC1} +forest type]	6	-399.55	811.40	1.86	0.01

*Abbreviation: v2=coverage of overstory layer, g_{PC1}=principal component 1 for ground condition, g_{PC2}=principal component 2 for ground condition, temp=temperature

found to be more appropriate for our zero-inflated data, resulting from imperfect detectability.

To determine the habitat preferences of roe deer, we compared their abundance in the deciduous forest and larch plantations. The top model for the abundance included the year in the count part and forest type in the zero-inflated part (Table 2). The forest type was included in zero-inflated part of all candidate models. The top model revealed that the fecal pellet count in 2021 was 0.78 times that of 2020, and the detectability in the deciduous forest was 2.61 times higher than that in the larch plantation (goodness-of-fit test, $\chi^2 = 16.08$, $p < 0.001$, Table 3). Thus, roe deer abundance differed between the two years but showed no regional differences between the forest types. Despite the higher resource availability in the larch plantations, the abundance of roe deer in these plantations did not differ from that in the deciduous forests.

Roe deer habitat use patterns

The habitat use strategies of roe deer in both forest types were analyzed by examining the determining factors of microhabitat use. The top model for the deciduous forest included forbs and the ground layer in the count part, and g_{PC2} and temperature in zero-inflated part (Table 4). All candidate models included forb in count part, and included g_{PC2} and temperature in the zero-inflated part. The fecal pellet count in the deciduous forest increased with coverage of forbs and the effect of forbs was dependent on forest age ($\chi^2 = 44.46$, $p < 0.001$, Table 5). This suggests that microhabitat use of roe deer was dependent on food quality

Table 3 – Summary of the top model with a zero-inflated Poisson (ZIP) distribution in the model explaining the abundance of Siberian roe deer (*Capreolus pygargus*) in deciduous forest (DF) and larch plantations (LP).

Part	Variable	Beta (CI 95 %)	Z-value	p-value
Count	(Intercept)	0.92 (0.74~1.10)	10.12	<0.001
	year2021	-0.24 (-0.50~-0.01)	-1.85	0.06
Zero-inflated	(Intercept)	-0.39 (-0.79~0.01)	-1.92	0.06
	forest typeDF	0.96 (0.43~1.50)	3.53	<0.001

within habitat. In the contrast, the top model for larch plantation included only the year in the count part and, g_{PC1} and treatment in the zero-inflated part (Table 6). All candidate models for larch plantation included the variables found in the top model. In the larch plantation, fecal pellet count in 2021 was 0.49 times that of 2020 ($\chi^2 = 36.68$, $p < 0.001$, Table 7). The microhabitat use of roe deer in larch plantation was not influenced by resource availability.

Discussion

Scale-dependent habitat use by roe deer

We expected that the habitat preferences of roe deer would depend on the food availability within the deciduous forest and larch plantations.

Table 4 – Candidate models ($\Delta AICc < 2$) with a zero-inflated Poisson (ZIP) distribution in the model explaining the microhabitat use of Siberian roe deer (*Capreolus pygargus*) in deciduous forest.

Order	Model	df	logLik	AICc	Delta	Weight
1	Count[(Intercept)+forb+age+age:forb]+ Zero[(Intercept)+g _{PC2} +temp]	9	-157.39	331.80	0.00	0.20
2	Count[(Intercept)+forb+v0+age+age:forb]+ Zero[(Intercept)+g _{PC2} +temp]	10	-158.75	332.30	0.49	0.16
3	Count[(Intercept)+forb+age+age:forb]+ Zero[(Intercept)+g _{PC1} +g _{PC2} +temp]	10	-156.68	332.70	0.84	0.13
4	Count[(Intercept)+forb+v1+age+age:forb]+ Zero[(Intercept)+g _{PC2} +temp]	10	-156.70	332.70	0.89	0.13
5	Count[(Intercept)+forb]+ Zero[(Intercept)+g _{PC2} +temp+age]	7	-158.04	333.10	1.30	0.10
6	Count[(Intercept)+forb+v2+age+age:forb]+ Zero[(Intercept)+g _{PC2} +temp]	10	-159.18	333.20	1.35	0.10

*Abbreviation: age=forest age, v0=coverage of ground layer, v1=coverage of understory layer, v2=coverage of overstory layer, g_{PC1}=principal component 1 for ground condition, g_{PC2}=principal component 2 for ground condition, temp=temperature

Table 5 – Summary of the top model with a zero-inflated Poisson (ZIP) distribution in the model explaining the microhabitat use of Siberian roe deer (*Capreolus pygargus*) in deciduous forest.

Part	Variable	Beta (CI 95 %)	Z-value	p-value
Count	(Intercept)	0.60 (0.25~0.95)	3.38	<0.001
	forb	0.02 (0.00~0.03)	2.53	<0.01
	ageD60	-0.26 (-1.01~0.49)	-0.68	0.50
	ageD70	-0.23 (-1.11~0.65)	-0.51	0.61
	ageD60:forb	0.18 (-0.00~0.35)	1.95	0.05
	ageD70:forb	-1.03 (-2.23~0.16)	-1.69	0.09
Zero-inflated	(Intercept)	-6.77 (-10.31~-3.22)	-3.74	<0.001
	g _{PC2}	0.61 (0.07~1.15)	2.22	0.03
	temp	0.61 (0.07~1.00)	4.05	<0.001

*Abbreviation: age=forest age, g_{PC2} =principal component 2 for ground condition, temp=temperature

However, the abundance of this species did not differ between these two forest types. In many habitats, the quantity of food is generally the most limiting factor in determining the population size of a species (Saïd et al., 2009; Cimino and Lovari, 2003). Conversely, when food is sufficient across a landscape, the species does not need to consider it as a key factor in habitat selection (Gaudry et al., 2022). As such, roe deer populations in the study area were likely maintained at a consistent level due to sufficient food quantity of the temperate forests where ground vegetation was well developed.

Microhabitat selection by species often reflects their prioritization of resources and is determined by the resource availability within a habitat (Godvik et al., 2009). In the study, the food quality depending on forest types made the distinct pattern in microhabitat use of roe deer. The effect of food quality interacted with age of deciduous forests, as forb availability varied with the forest age. While the roe deer selected the sites with more high-quality forbs in deciduous forests, they did not exhibit a corresponding response to the food quality in larch plantations. This suggests that food quality did not limit the roe deer in larch plantation, where mean coverage of forb exceeded 20 % (Feuereisel, 2005). Contrary to the food resource, cover resources did not affect roe deer’s habitat use in the study area. Yellow-throated marten (*Martes flavigula*) is a predator of roe deer, but they opportunistically hunt them. Due to this low predation risk and high cover availability, roe deer may prioritize food rather than concealment cover when utilizing habitat (Rothley, 2002).

The habitat selection process generally occurs at four scales: overall species distribution, home ranges, resources, and specific sites (Decesare et al., 2012; Johnson et al., 2002). Thus, the effects of resources on species distributions can be scale-dependent (Morellet et al., 2011; Mysterud et al., 1999). For example, the quantity and quality of food can affect the habitat selection of roe deer at both the landscape and microhabitat scales (van Beest et al., 2010). In this study, the high food availability across the study area maintained consistent number of

roe deer, while the within-habitat variation in food quality affected this species’ microhabitat use in the deciduous forest. This suggests that habitat management should consider not only the resources themselves but also the spatial scale for their target species. The scale-dependent analysis of habitat selection strategy can aid in the understanding of the ecology of species.

Variation in the detectability of fecal pellets

Unaccounted variation in detectability of fecal pellets can lead to misleading results from fecal pellet counts method (Campbell et al., 2004; Laing et al., 2003). The decomposition of fecal pellets is determined by the decomposer community in the soil and is faster in warmer and wetter environments (Murray et al., 2005). As such the weather, including the temperature and humidity, play a crucial role in the detectability of fecal pellets (Sierra et al., 2017). Microclimate factors, such as solar radiation and soil humidity, can also contribute to spatial variation in pellet decomposition within a habitat (Crockatt and Bebbler, 2015; Prugh and Krebs, 2004). Moreover, we observed difference in detectability depending on the ground cover. The ground cover could prevent the contact between fecal pellets and decomposers on the ground.

Because of the spatiotemporal variation in fecal pellet decomposition, reliably estimating the decomposition rate of fecal pellets can be costly and labor-intensive, especially when estimating the decomposition rate in field. Instead, we employed a statistical approach to corrected for variation in detectability without measuring the decomposition rate in the field. Our models revealed that the detectability was affected by ground conditions, weather and habitat type. These effects differed between the forest types. In case of ground conditions, the detectability increased in deciduous forest as litter cover decreased. Organic matter, including litter, can stimulate the decomposition process by enhancing the decomposer communities (Ge et al., 2013). The decomposition process of pellets could be affected by ground condition at microhabitat scale. On the contrary, the detectability increased in larch plantation as vegetation cover decreased. The well-developed understory in larch plantation could obscure investigators’ vision, leading to increased detectability challenges. The effect of dense vegetation cover was interacted with treatment type of larch plantation. The vegetation coverage depending on the treatment type could mediate the effect of vegetation cover. Moreover, we observed that detectability was higher in deciduous forest than that of larch plantation. The difference of detectability between two forest types also could be due to the developed vegetation cover in larch plantation. This suggests that considering the spatial variation on investigators’ detection ability is crucial when applying fecal pellet counts.

Increased temperature generally facilitates the decomposition of pellets (Sierra et al., 2017; Murray et al., 2005). However, higher temperatures increased the detectability in the present study. This study was conducted in May under dry conditions. During this transitional season with a wide daily temperature range, low temperatures at night-time generates heavy dew on the ground. Such non-rainfall water source, including dew and fog, can affect the decomposition process under dry conditions (Grünzweig and Gliksmann, 2021). During the study period, the non-rainfall water source could be reduced as warmer, and it might

Table 6 – Candidate models ($\Delta AICc < 2$) with a zero-inflated Poisson (ZIP) distribution in the model explaining the microhabitat use of Siberian roe deer (*Capreolus pygargus*) in Japanese larch plantations..

Order	Model	df	logLik	AICc	Delta	Weight
1	Count[(Intercept)+year]+Zero[(Intercept)+g _{PC1} +treatment]	10	-180.03	381.88	0.00	0.45
2	Count[(Intercept)+year]+ Zero[(Intercept)+g _{PC1} +v2+treatment]	11	-179.60	383.40	1.52	0.21
3	Count[(Intercept)+forb+year]+ Zero[(Intercept)+g _{PC1} +temp+treatment]	11	-179.78	383.76	1.88	0.17
4	Count[(Intercept)+year]+ Zero[(Intercept)+g _{PC1} +g _{PC2} +treatment]	11	-179.78	383.76	1.88	0.17

*Abbreviation: treatment=treatment of plantation, v2=coverage of overstory layer, g_{PC1} =principal component 1 for ground condition

Table 7 – Summary of the top model with a zero-inflated Poisson (ZIP) distribution in the model explaining the microhabitat use of Siberian roe deer (*Capreolus pygargus*) in Japanese larch plantations.

Part	Variable	Beta (CI 95%)	Z-value	p-value
Count	(Intercept)	0.89 (0.68~1.10)	8.29	<0.001
	year	-0.71 (-1.09~-0.33)	-3.69	<0.001
Zero-inflated	(Intercept)	0.46 (-1.82~2.74)	0.40	0.69
	g _{PC1}	0.18 (-1.40~1.77)	0.23	0.82
	treatmentL50	-0.43 (-3.08~2.21)	-0.32	0.75
	treatmentL40t1	-5.02 (-9.92~-0.11)	-2.00	<0.05
	treatmentL40t2	-0.79 (-3.41~1.83)	-0.59	0.56
	treatmentL50:g _{PC1}	0.57 (-1.26~2.40)	0.60	0.05
	treatmentL40t1:g _{PC1}	-4.06 (-8.34~0.23)	-1.86	0.17
treatmentL40t2:g _{PC1}	-0.53 (-2.39~1.34)	-0.56	0.74	

*Abbreviation: treatment=treatment of plantation, g_{PC1} =principal component 1 for ground condition

mediate the positive effect of temperature on the detection. In deciduous forests, the non-rainfall water source could contribute to the temporal variation on detectability of fecal pellet counts.

In addition, we observed that the forest type affected the detectability of fecal pellets, and this was mediated by the microclimate. The habitat-dependent detectability can potentially lead to inaccurate results. This emphasizes the need to correct for detectability when employing fecal pellet count method. We confirmed the utility of zero-inflated models in accounting for the variability in detectability of fecal pellets. In this study, the ZIP models addressed the variation in detectability and the habitat use of roe deer separately without the need for additional field surveys. This approach has the potential to improve the ecological knowledge of species by making fecal pellet counts more efficient and reliable. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Figure S1 Representative photos of study area.

Table S2 Principal components analysis on ground variables.

Supplement S3 The zero inflated distribution of a response variable.

Supplement S4 Validation of top models in the modeling procedures.