이학석사 학위논문

Effects of hiking trails on the breeding performance of the Oriental tit (*Parus minor*)

등산로가 박새 번식에 미치는 영향에 대한 연구

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Abstract

The natural environment near urban agglomerations plays a crucial role in both conserving biodiversity and promoting human welfare. Human recreation activities in green areas within urban agglomerations may have both positive and negative effects on biodiversity and nature. However, research on anthropogenic impacts on wildlife in urban parks and forests within cities in Asia is poorly represented compared to other geographical areas, even though the Asian region is one of the most urbanized areas in the world. Therefore, it is necessary to determine how human activities affect wildlife in urban recreational parks and forests within Asian cities. Seoul is one of the largest Asian cities and contains within its borders many mountain parks heavily used by Seoul residents. Therefore, it represents an excellent environment to focus on anthropogenic effects on wildlife. The study evaluated the effects of hiking trails on the breeding of the Oriental tit (*Parus minor*) in nest boxes in forest habitats of the Gwanak Mountain – one of the heavily used recreational mountain areas within Seoul. I focused on breeding performance in a population of birds breeding in the provided 150-190 nest boxes during four breeding seasons. Distance between a hiking trail and a nest box was used as the primary variable for determining the effect of hiking on birds. Additionally, a comparison between two areas of the study sites differing in their use by humans also served as an indicator of the effect of human recreational activities on a bird: One area with smaller number of hikers, who used trails more exclusively and did not spread out from the trails into the forest, and the other area with larger number of hikers, who tend to spread out from the trails into the woods. Breeding performance of birds was measured by 11 variables that concerned nest box occupancy, clutch size, hatching success, brood size, as well as nestlings' growth and survival at early and late phases of breeding. The data analyses were performed in R using the linear mixed-effects models and generalized linear mixed-effects models. I have detected some positive and negative relationships between indicators of possible human impact (distance, area) and some breeding performance variables concerning the early stages of breeding (~ until day 5 of nestlings age). The variables concerning the later breeding stage did not show such associations. Proximity to hiking trails and the larger number of hikers that spread out from trails into the forest were related to negative impacts. Additionally, those effects appeared sometimes to be modified by the proportion of conifers through a possible effect of conifers providing visual coverage and diminishing the stress to birds from human presence. In addition to the adverse effects in the early breeding stage, two positive effects of proximity to hiking trails on breeding were detected at very initial stages of the breeding cycle: birds preferentially settled in boxes near the trails and females laid larger clutches in the nest boxes near the trails. However, the mechanisms responsible for these positive effects may not necessarily be related to human presence on trails. In general, the total breeding success was not affected by distance to hiking trails or by the number of hikers and how they use the area. These relatively weak effects of hikers on breeding performance by the Oriental tit (in comparison to published results from similar studies) suggest that the birds may adapt behaviorally to the constant presence of humans in their habitats. Also, we suspect that hikers in this study site may be relatively un-intrusive in their attitudes to birds nesting in nest boxes. This study is one of a few studies about the effects of human hiking and recreational activities on birds in urban parks and forests, and to my knowledge, it is the only one in Asia. The results point out that future research should be conducted to determine the detailed mechanisms responsible for the observed effects. Future research should also focus on combining observational and experimental approaches in various cities across Korea and Asia to be able to generalize the effects of humans on birds in Asian urban parks and forests.

Keyword: *Parus minor*, hiking trails, human disturbance, anthropogenic effects, nest boxes, breeding performance, nestling growth traits, nest preference

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Table of Contents

List of Figures

List of Tables

Introduction

According to the UN (2018), about 55% of the world's population lives in cities, and this proportion has been steadily increasing. Further studies have suggested that citizens have a desire to relieve stress from urban life, and they visit green areas such as parks or forests near urbanized areas (van den Berg, Hartig, and Staats 2007). Those natural environments, located within city boundaries or in their immediate vicinity, play a crucial role in conserving biodiversity while at the same time promoting human welfare with recreational activities (Bötsch et al. 2018; Smith-Castro and Rodewald 2010). The number of various studies and publications on human impacts in diverse natural ecosystems has been progressively increasing (Larson et al. 2016).

Larson et al. (2016) showed that the number of articles tackling these issues was limited before 2000, but since 2000 the number of articles has been increasing continuously. The anthropogenic impact was studied mostly in North America (37.7% studies), and Europe (26.6% studies). Only a handful of studies have been conducted in Asia (5.5%). However, most of all, the studies were conducted in the forest terrain rather than in urban agglomerations. Birds were the second most frequently studied taxonomic group, and Passeriformes were the most researched among birds. From among all analyzed papers, 60% reported negative effects of humans on birds. Positive effects and lack of apparent effects were reported (in similar proportions) in the remaining 40% of papers.

In Korea, there are only a handful of research reports published about anthropogenic impacts on wildlife (Choi, Nam, and Lee 2014; Seo and Thorne 2015). Therefore, my research is one of the few studies focusing on anthropogenic effects on birds in Korea. I chose birds from the family Paridae that often use nest boxes and became model subjects in the ecology of birds worldwide. There are 61 species of Family Paridae globally, and only six species are found in Korea. I focused on the Oriental tit (*Parus major minor*), which is a species with a wide geographical and ecological distribution in East Asia. It is distributed in a variety of habitats and is the most common species of Paridae in urbanized areas of Korea (Hong and Kwak 2011; Lee, Ku, and Park 2000; S. J. Park 2015). Indirect effects of human disturbance on the Oriental tit in Korea were explored in studies of the impacts of habitat fragmentation on the Oriental tit's distribution (Song and Kim 2016), and the effects of forest roads on the Oriental tit's breeding (Y.-S. Park, Lee, and Rhim 2005). In one study, the general reproductive biology of the Oriental tit was studied in urban forests in Korea by Jeong et al. (2012). However, none of the studies addressed the direct effects of human presence and recreational activities on breeding performance of tits in Korea. Therefore, I focused on the effects of hiking trails on the breeding performance of the Oriental tit.

The study aimed to evaluate the potential importance of human impact on the breeding of the Oriental tits in one of the mountainous, forested areas within Seoul city limits that is heavily used for hiking and recreation by city residents. This study is thought to form a solid basis for the future study of the human influence on birds in a typical recreational forested area within city borders. Based on the literature (Bötsch et al. 2018; Corsini et al. 2017; Hutfluss and Dingemanse 2019; J. R. Miller and Hobbs 2000; Remacha et al. 2016), I have considered several hypotheses relevant to the various stages of the breeding cycle that predict either negative or positive effects of proximity to hiking trails. First, I expected that the proximity to hiking trails could create a negative effect on **hatching success** and **nestlings' masses** because incubation and brooding were vital for eggs near hatching and very young nestlings. If humans on nearby hiking trails disturb incubation and brooding, then negative effects of proximity to a trail may be observed. Second, humans could also disrupt the natural feeding activity and pattern of parents. Therefore, I expected that the proximity to hiking trails would have a negative impact on **nestlings' mass** and **growth** because the food supply is essential for nestlings' development. Third, if predators avoid hunting near hiking trails, then I could observe a positive impact of proximity to trails on nests' and nestlings' survival. However, if predators are attracted to nesting sites when birds are vocally and visually responding to humans, then proximity to trails might decrease **survival of nestlings** by making it easier for predators to detect active nests. Finally, any effect of disturbance by humans through visually induced stress may be modified by the vegetation density because dense vegetation could provide more cover to birds, which may lead to lower the level of stress and higher breeding performance. Additionally, if the aforementioned hypothetical positive effects of the trail proximity on lowering predation existed, then I suspected that birds might prefer nesting near hiking trails to be protected. If such proximity to hiking trails is the preferred location, then birds winning the competition for preferred sites may be of different age or quality than those breeding far away from trails, which may result in the effect of trail proximity on the clutch size or parental care. I have considered all the above hypothetical mechanisms in the exploratory analysis of observational data of breeding performance in four breeding seasons.

Material and methods

Part 1. Data collection

1.1. Study site

The study was conducted in Gwanak mountain (37°25′44″N, 126°57′49″E), one of the heavily used mountains in Seoul metropolitan area, Korea. This site was composed of conifer, deciduous, and mixed forests surrounding Seoul National University campus (Korea Forest Service 2019). The study area includes the 'Protected ecosystem and scenery area (생태 · 경관보전지역).' There are regular and heavily used hiking trails (Figure 1a), as well as many small hiking paths used much less often.

1.2. Study species

The Oriental tit (*Parus minor*; previously *Parus major minor*) belongs to the family Paridae, which is often used in research on bird ecology world-wide. It may be viewed as a model species for representing small passerine birds breeding in secondary cavities near the urbanized area in East Asia. It is a common passerine bird species in our study site, and it frequently breeds in nest boxes.

1.3. Nest boxes

Breeding performance data were analyzed from 2014 to 2017 (Table 1). The first nest boxes were installed in 2011 and 2012, and Oriental tit regularly used them for breeding. During the study period, some old nest boxes were removed when they were damaged, so the number of nest boxes gradually decreased from 2014 to 2017.

1.4. GPS coordinates of nest box locations, hiking trails and areas used by visitors

I used the mobile GPS function to obtain GPS coordinates for each nest box and hiking trails in the study area and displayed them in a map using Google Earth software (Figure 1). As there were cases when the location of nest boxes changed between seasons, the GPS coordinates of the nest boxes were updated annually. All recorded hiking trail were categorized according to how heavily people used them. The hiking trails consisted of two types. The main hiking trails were used by a large number of people, including some wide trails paved with concrete. The secondary hiking paths were used much less heavily, and none of them were paved – they typically comprised narrow paths. I consider that my evaluation of how heavily a trail or path is reasonably accurate because it is based on assessments by several research team members who had spent 5-7 days per week over 3-4 months of each of the four breeding seasons.

1.5. Measuring the distances between hiking trails and nest boxes

We focused on determining the effect of proximity to the main hiking trails because they are the main source of human disturbance in the area. For each nest box, I estimated the distance to the nearest main hiking trail. The distances were measured using QGIS (QGIS Development Team 2019) for each year. To be able to measure these distances, the linear routes that mark the hiking trails were transformed into a set of evenly distributed points within the route. The results were checked manually, and any errors were corrected.

1.6. Nest box distribution by distance from the hiking trails

The distances between a nest box and the nearest hiking trail were not distributed evenly because nest boxes were hanged considering other methodological concerns and requirements needed to address the main questions of the long term ecological study, which does not focus on the effect of trail proximity on breeding. This research is only a small part of the long term research project. The number of nest boxes decreased as the distance to the trail increased (Figure 2). Accordingly, the distance was categorized into three classes with an approximately similar number of nest boxes in each category. The variable ***distance category*** had three levels indicating that a nest box was *near* (0 – 15 m; distance 1), *intermediate* (15 – 45 m; distance 2) or *far* (over 45 m; distance 3) away from the nearest main hiking trail (Figure 2).

1.7 The distinction between the two areas of the study site

The use of the area by the general public differs between the two parts of the study site. In part A (area A; Figure 3), the heavy human traffic was on trails, and people also tended to spread out to the surrounding forest, especially on weekends and holidays. In part BC (area BC; Figure 3), the human traffic was comparatively lower (however, the main trails are still quite crowded on weekends and holidays), and fewer people showed a tendency to leave the trails into the surrounding forest. All these evaluations are not based on actual counts of people, but on independent assessments by several team members from their repeated experiences in the field during several breeding seasons. Additionally, Human traffic on weekdays and weekends were counted from filming between sunrise and sunset at two locations (Figure 3; one movie per location per type of day of the week). The results showed that the number of people visiting area A was 2-3 times as high as in area BC. The data also revealed that the number of people was larger during weekends and holidays and that this was especially evident in area A. The maximum number of people for the weekend was 201 in area A and 81 in area BC. Likewise, the maximum number of people for the weekdays was 75 in area A and 67 in area BC.

1.8. Measuring the proportion of vegetation and the number of nest boxes around each active nest box

QGIS was used to calculate the proportion of conifers in all vegetation within a circle of 50 m radius around each nest box. Vegetation types and their distribution in Gwanak mountain were taken from the vegetation map from Korea Forest Service (Korea Forest Service 2019). Vegetation map had eight tree categories; 3 conifers (*Pinus rigida*, *Pinus densiflora*, other Conifers), 3 deciduous (*Quercus variabilis*, *Quercus acutissima*, other Quercus), *Robinia pseudoacacia*, and mixed forest type (conifer and deciduous). Finally, in order to account for the effect of the local density of available potential nest sites (nest boxes) on the nest box occupancy, I counted the number of all nest boxes within a 50 m radius around each nest using QGIS.

1.9. Breeding performance

Breeding performance of the Oriental tit was collected during consecutive four years (2014-2017), and I used only first breeding attempts. Regular monitoring was conducted from the first week of March to the end of the last breeding attempt (in July). At every visit to nest boxes, the presence of feces of birds, mosses, and feathers inside the nest box was noted as an indicator that nest box was being used. If the nest box was the empty or fecal matter and feathers were present, that nest box was visited once a week. The monitoring interval was determined by the composition of the materials in the nest box (Figure 4). If there were visible mosses on the floor of the nest box, then weekly monitoring was conducted. If mosses piled up, covered the floor thoroughly, and soft materials such as other animals' fur, human hair, or thread were present, it was assumed that the eggs would be laid within a few days. Therefore, the monitoring was conducted every five days. If eggs were present, researchers would visit the nest box at least four times during the laying and incubation period (approximately 24 days). From these visits, the researchers would determine the first egg-laying date, incubation start date, first nestling hatching date, clutch size.

To identify the exact hatching date, researchers visited the nest box daily for two days before the expected hatching date. After the eggs hatched, a nest was visited three times on day 3, 5, and 11 since the first hatching. We measured nestlings' body sizes on day 5 and day 11 since the first hatching (brood hatching date). Because nestlings grew approximately linearly between day 5 and day 11, this period is the best time to optimize the estimation of nestlings' growth rate. We did not measure the nestlings after day 11 to prevent the disturbance that may cause early fledging of nestlings.

Table 1. The number of nest boxes, clutches, eggs, and nestlings of the Oriental tits analyzed in this study during each of the study years.

Year	**2014**	**2015**	**2016**	**2017**	total
nest boxes	195	191	184	156	726
clutches	19	24	9	16	68
eggs	189	217	86	168	660
nestlings	172	179	62	151	564

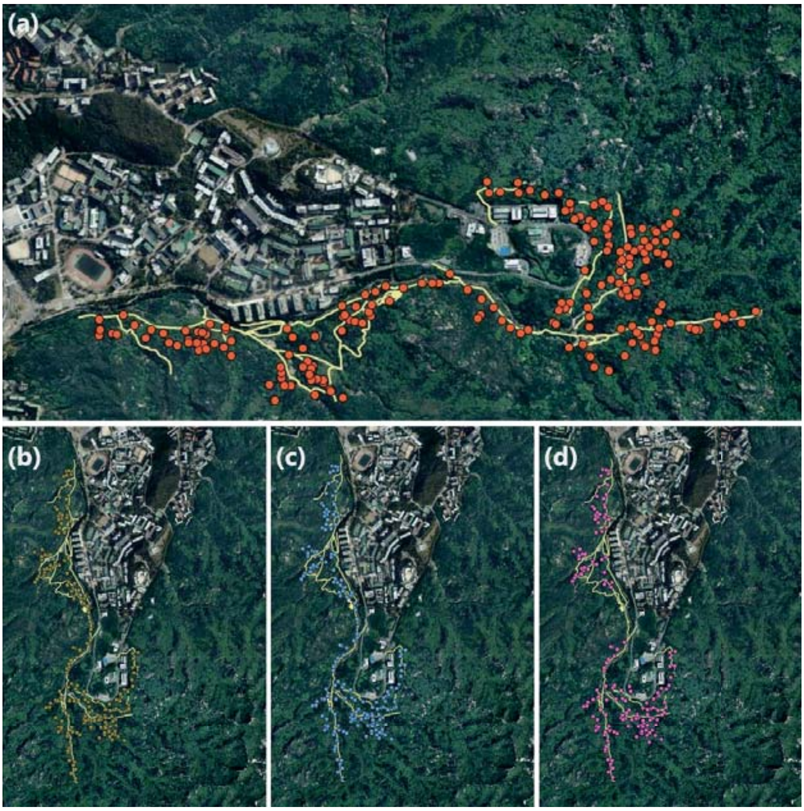

Figure 1. Distribution of nest boxes and hiking trails in the study site.

The number of nest boxes slightly varied between years: (a) 2014, (b) 2015, (c) 2016, (d) 2017. Hiking trails are marked as yellow lines.

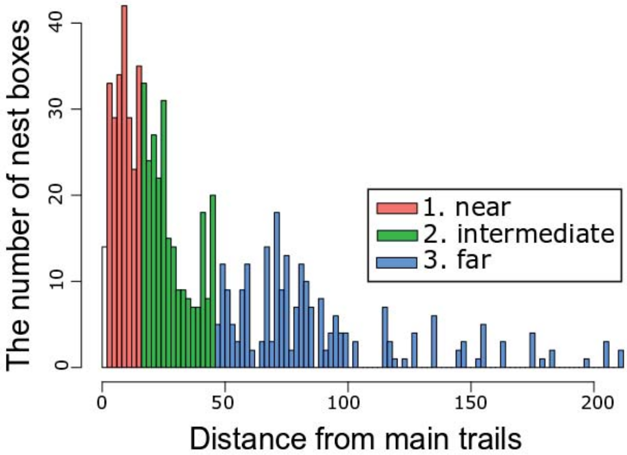

Figure 2. Distribution of distances to the nearest hiking trail (trails marked in yellow in Fig. 1) corrected for GPS location changes of some nest boxes from year to year.

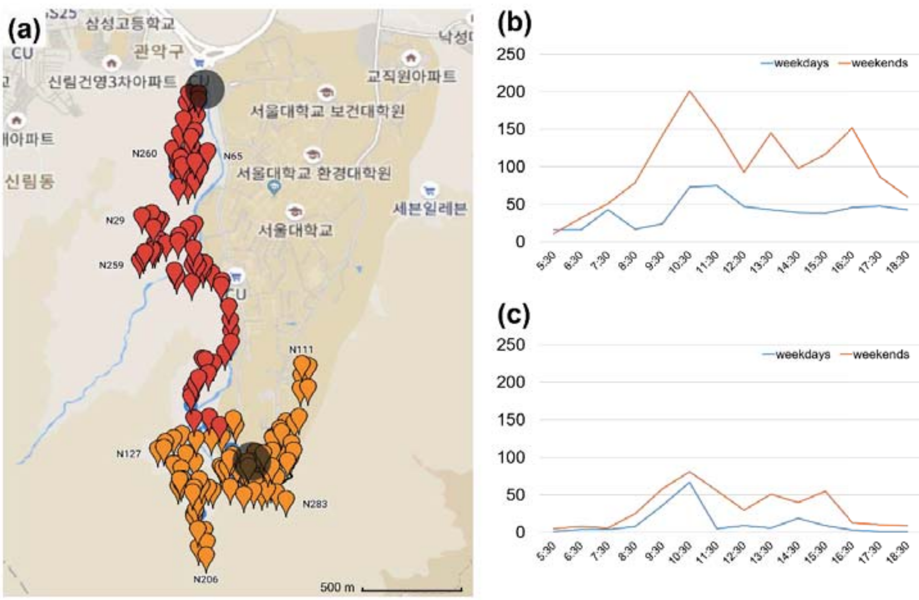

Figure 3. Division of study site into area A (red nest box locations in a) and BC (orange nest box locations in a), and comparison of the two areas for the number of hikers (b, c) on weekdays (blue line in b, c) and weekends (orange line in b, c) measured at locations marked with gray circle in (a).

Figure 4. Description of nest building stages.

(a) The first three early stages: birds bring mosses until the nest box bottom is covered with mosses. (b) The two later stages: Mosses continue to cover the floor completely, and soft nesting materials such as animals' fur, human hair, or thread were added to build internal layers of the nest cup.

Table 2. Summary of the monitoring protocol used by the field research team during breeding season

Stage of the Nest	Researchers' tasks	Monitoring Interval
Empty	Checking which nest boxes were used	Once a week
Only moss in the nest	Checking the amount of moss	Once every 5 or 7 days (depending on amount of moss)
Both moss and soft materials in the nest	Checking the amount of moss and soft materials such as animal fur, human hair, cotton and artificial thread	Once every 5 days
Eggs (laying and incubating)	Checking clutch size, eggs surface temperature, and measuring the size of eggs	At least 4 times during this period
Eggs were getting close to expected hatching date	Checking whether or not eggs hatched	Every day until eggs hatched
After hatching	Measuring nestlings' bodies	3 times for 11 days

The brood's hatching date was defined as the first day on which at least one nestling hatched, and it was referred to as day 1. When nestlings started receiving parental care, researchers visited on 3rd, 5th, and 11th days after hatching (day 3, day 5, and day 11). On day 3, each nestling was individually marked on the half of the nestlings' body skin using one of a dozen different color markers. Examination of the nestlings' skin confirmed that the marking did not cause any adverse effects. This individual marking allowed me to distinguish nestlings from each other. On day 5, the length of the right tarsus and the weight were measured using Dial calipers (ecotone, ±0.01mm) and an electronic scale (Smart weigh, ±0.001g). Additionally, the same process of taking measurements on day 5 was repeated on day 11.

Part 2. Data selection and analyses

2.1. Data selection

I decided to analyze the first breeding season to balance the environment and climate conditions. The first hatching date each year was set to 1 because the breeding season phenology was different from year to year.

2.2. Statistical analysis

Eleven response variables (Table 3) were analyzed using GLMM (generalized linear mixed-effects model) and LME (linear mixed-effects model) in the *lme4* package (ver. 1.1.21). Also, *glmmTMB* (generalized linear mixed-effects model using TMB (template model builder)) in the *glmmTMB* package (ver. 0.2.3) was used for the clutch size to confirm conclusions from the standard generalized linear mixed-effects model, but their results are not reported here. Response variables were divided into three groups. The first group of response variables contains two indicators of bird's general interest in a nest box as a breeding site: (1) nest building initiation and (2) nest box occupancy. Those were analyzed as binary variables (yes/no), and the details are shown Table 3. The second group of variables concerns characteristics of clutches and broods: (3) clutch size, (4) clutch hatching success, (5) hatching success rate, (6) brood survival, and (7) nestlings' survival rate. The last group of response variables describe nestlings' growth and survival: (8) nestlings' body mass on day 5, (9) individual nestling survival, (10) nestlings' body mass on day 11, and (11) nestlings' growth rate per day (details were in Table 3).

Model selection was performed using *dredge* function in *MuMIn* package in R (ver. 1.43.10) to determine the best model according to AICc (Akaike information criterion). All statistical analyses were conducted in R ver. 3.6.1 (R core team).

Table 3. Details about response variables

Interpretation	Variable name	Description
Indicators of using a nest box for a breeding site	Nest building initiation	Binary variable. If a nest box contained nest materials typical for the initial nest building phases like piled mosses or soft materials, then the nest box was classified as "occupied."
VERY EARLY PHASE	Nest box occupancy	Binary variable. If a nest box contained at least one oriental tit egg, it was defined as "occupied." If no egg was detected, then the nest box was classified as "unoccupied."
Characteristics of clutches and broods EARLY PHASE	Clutch size	Number of eggs laid in the nest box. Because it reflected a normal distribution, despite it was count data, the error is specified with a normal distribution. Additionally, it was analyzed with Conway-Maxwell-Poisson error distribution to check if both analyses yield consistent conclusions.
EARLY PHASE	Clutch Hatching Success	Binary variable. It was determined as "success" when at least one egg hatched, and "failure" if no egg hatched.
EARLY PHASE	Hatching success rate	Variable with Binomial error distribution. It was calculated as brood size divided by the clutch size and analyzed by using *cbind* function in R to create the variable for analysis.
GENERAL NESTLING PHASE	Brood survival	Binary variable. When at least one nestling survived in the nest until day 11, the brood was labeled "survived," otherwise "did not survive."
GENERAL NESTLING PHASE	Total nestlings' survival rate	It was defined as the number of nestlings on day 11 divided by the clutch size and was assumed to have binomial error distribution. It was analyzed by using *cbind* function in R to create the variable for analysis.
Nestlings growth and survival	Nestlings' body mass on day 5 (g)	The variable had a normal distribution.
EARLY PHASE LATE PHASE	Individual nestling survival	If each nestling in the nest survived from day 5 until day 11, i.e., during the period of intense growth, the variable has two levels: "survived" or "not survived." Because it was binary data, it used a binomial error distribution.
LATE PHASE	Nestlings' body mass on day11 (g)	It was analyzed with a normal distribution.
LATE PHASE	Nestlings' growth rate per day	It was calculated as (body mass on day 11 minus mass on day 5) divided by the number of days between those measurements. It had a normal distribution

2.3. Explanatory variables

Distance: Distance was categorized into three distances: distance 1, distance 2, and distance3. Details were shown in section 2.1.6. This variable was called as "distance" in the model.

Area: The study site was divided into two distinct areas (Figure 4a). Area A was an accessible place like an urban park because it had smooth, easy hiking trails and roads. Also, it was utilized as the central recreation place; for example, the streams in this area were crowded with children to swim. Area BC had two kinds of trails, either sloped and rocky paths or trails along the stream. This area was relatively more difficult to approach than area A, so it was less crowded.

Proportion of conifers: the proportion of surface area covered by conifers within surface area covered by vegetation in 50m radius circle around each nest box.

In the analyses of using the nest box for a breeding site, the number of nest boxes are included. Those reflected the density of potential nest sites for accounting possible conflict between the nest users. There were three variables associated with the analyses for using the nest box:

Available nest boxes: the number of all nest boxes around the focal nest box; this variable had five rank values (0, 1, 2, 3, 4); the maximum number of nest boxes is 9 in real, but I used five categories to account for small number of nest boxes surrounded by five or more nest boxes.

Used nest boxes: the number of nest boxes with at least signs of nest building or later stages of breeding in 50 radius circle around the focal nest box. The variable had five categories (0 ,1, 2, 3, 4).

Occupied nest boxes: the number of occupied nest boxes in a 50m circle around a focal nest box. The nest box was defined here as occupied if oriental tit laid at least one egg in a nest. This variable has two categories (0, 1).

In the analyses of nestlings' mass, growth, and survival, I included a variable indicating the size of brood (the number of nestlings that are being fed by parents) as a covariate for considering the competition among offspring for parental care. There were three variables related to this aspect of analyses:

Brood: mean brood size from day 5 to day 11 in each nest.

Brood5: brood size on day 5 in each nest.

Brood11: brood size on day 11 in each nest.

Hatching date: this was defined separately each year and the earliest time of hatching in that year as the hatching date = 1. It acted as a covariate to control for the effect of climate and environmental variation during a breeding season.

Year was included as a random factor in all analyses, and **Nest ID** was included as a random factor in analyses with multiple samples from one nest.

The models which had three-way interaction among area, distance and proportion of conifer had a serious limitation. Because each area could not cover all ranges of the proportion of conifers (Figure 5), a careful interpretation was required when the model contained three-way significant interactions. Since areas differed in the proportion of conifers, I faced a situation of co-linearity of explanatory variables. To handle this situation, I included models with only one of the variables (either area or proportion of conifers) and added those models to the set of models evaluated using the AIC criterion.

Additionally, Fig. 5c illustrates that the explanatory variable **proportion of conifers** had entirely different distribution in area A (right-skewed) than in area BC (left-skewed). This condition prevents any meaningful applications of proportion transformations before using the variable in analyses (proportions are, typically, often arcsine transformed). Therefore, the independent variable **proportion of conifers** in its un-transformed original form was used.

2.4. Visualizing the results

To describe the relationship between the explanatory and response variables, the plots were visualized in various packages in R. The relationship between the independent variables and dependent variables (**nest building initiation**, **nest box occupancy** and **clutch size**) were expressed with least square means in *lsmeans* package. Also, the relationship with the **hatching success rate**, **total nestlings' survival rate**, **nestlings' body mass on day 5** and **nestlings' growth rate per day** were illustrated with predicted values (marginal effects) in *sjPlot* package.

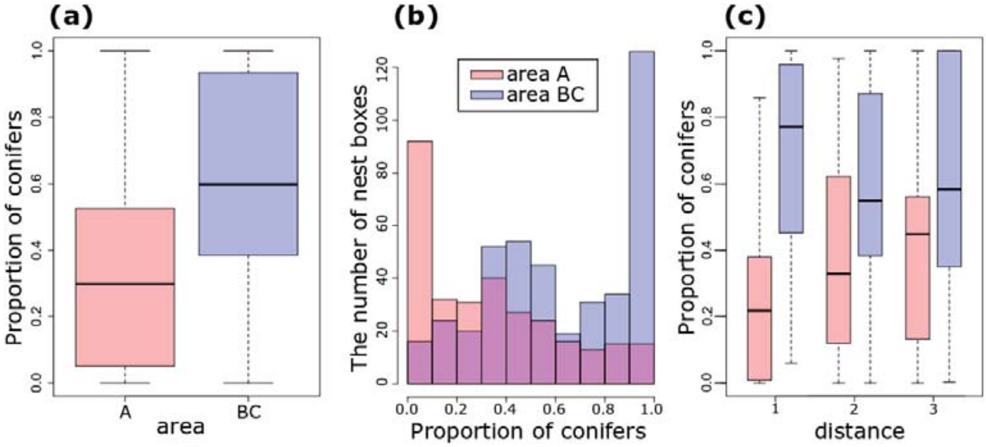

Figure 5. The difference between the two areas (area A and area BC) in the proportion of conifers. The pink and purple indicate area A and area BC, respectively. The difference is shown in (a) boxplot and (b) histogram. Also, the proportion of conifers at a distance to the nearest trail for each area is shown in (c).

Results

Part 1. Indicators of using a nest box for a breeding site

(1) Nest building initiation

To consider the density of nest sites, ***available nest boxes***, and ***used nest boxes*** were included in the initial models separately. After the two model evaluation procedures (either ***available nest boxes*** or ***used nest boxes***) were completed, I realized that models with ***available nest boxes*** gave the better fit to the data (based on AICc); the top 3 models are shown in Table 4. Additionally, I compared them with the best three models where ***used nest boxes*** were included (Table 4, bottom). There was no effect of the distance to the trail or the area on the **nest building initiation** in the best model (Table 4). The best model included ***proportion of conifers*** and ***available nest boxes*** (Table 5). In contrast, the second-best model additionally included ***area***, ***distance***, and interaction between ***area*** and ***distance*** and the same variables that were already present in the best model (Table 4 and Table 6). The probability of the **nest building initiation** increased with the ***proportion of conifers*** and decreased with the number of ***available nest boxes*** (Table 5, Figure 6). Although the interaction between ***area*** and ***distance*** in the second-best model was marginally non-significant, the interactions were visualized in Figure 7, which indicates a lack of consistent (across both areas) effect of distance to trail on the probability of birds initializing nest building.

Table 4. The comparison list of the six best models that explain variation in the nest building initiation. The total sample size is 726. ***Year*** was used as a random variable.

models	Intercept	proportion of conifers	area	distance	area :distance	available nest boxes	used nest boxes	df	logLik	AICc	delta	weight
m1	-0.54	0.52				-0.22		4	-447.09	902.2	0	0.54
m2	-0.49	0.59	+	+	+	-0.22		9	-442.81	903.9	1.65	0.24
m3	-0.54	0.53	+			-0.22		5	-447.08	904.3	2.03	0.20
m4	-1.22	0.72					0.22	4	-450.79	909.6	7.4	0.01
m5	-1.1	0.85	+	+	+		0.20	9	-446.41	911.1	8.85	0.00
m6	-1.2	0.80	+				0.22	5	-450.57	911.2	8.99	0.00

Table 5. The summary of the fixed effects in the best model for the nest building initiation (model m1 in table 4). The table concerns Figure 6. ***Year*** was used as a random factor.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0.544	0.284	-1.912	0.0558	.
proportion of conifers	0.521	0.249	2.089	0.0367	*
available nest boxes	-0.223	0.063	-3.528	0.0004	***

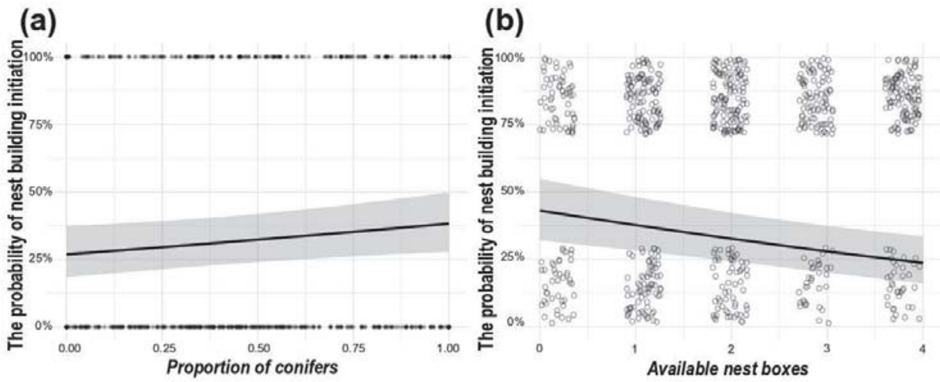

Figure 6. The effects of *proportion of conifers* (a) and *available nest boxes* (b) on the probability of the nest building initiation. Results of statistical analysis are in table 5. Unlike ***proportion of conifer*** as continuous data in (a), ***available nest box*** is count data, so it was expressed as "clouds". In (b), the lower "clouds" of circles indicate nest boxes that were not used (zero on the vertical axis) and the upper "clouds" of circles indicate nest boxes that were used (probability= 1).

Table 6. The summary of the fixed effects in the second-best model for the nest building initiation (model m2 in table 4). The table concerns Figure 7. ***Year*** was used as a random factor.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-0.486	0.316	-1.539	0.124	
distance2	-0.347	0.292	-1.189	0.234	
distance3	0.201	0.335	0.601	0.548	
area	-0.151	0.319	-0.473	0.637	
proportion of conifers	0.586	0.289	2.029	0.0425	*
Available nest boxes	-0.217	0.065	-3.338	8.45E-04	***
distance2:area	0.698	0.405	1.723	0.0849	.
distance3:area	-0.427	0.433	-0.988	0.323	

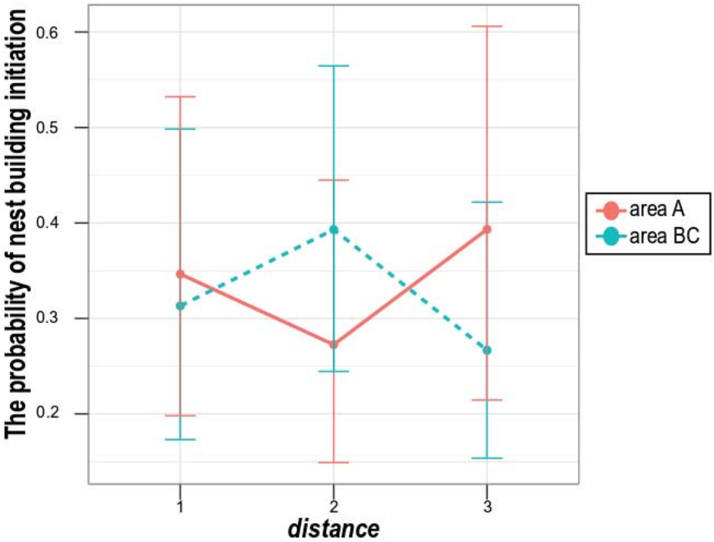

Figure 7. Relationship between *distance* and the nest building initiation in each area.

The solid pink line indicates the probability of the nest building initiation according to each distance in area A, and the dotted green line represents the probability of the nest building initiation according to each distance in area BC. Filled circles indicate the expected probability values and error bars indicate standard errors obtained from model m2 (Table 4). Statistical analysis is presented in Table 6. Statistical analysis is presented in Table 6.

(2) Nest box occupancy

Available nest boxes and ***used nest boxes*** were included in the initial models separately. After the two procedures of models' generation and evaluation (either with a***vailable nest boxes*** or ***used nest boxes***) were completed, I realized that models with ***available nest boxes*** gave the better fit to the data (based on AICc), and the top 3 best-fit models are shown in Table 7 (models m1, m2, m3). Additionally, I compared them with the best three models from analyses where ***used nest boxes*** were included (models m4, m5, m6 in Table 7). The effect of distance on the nest box occupancy in the best model (model m1 in Table 7) was different in area A than in area BC, as indicated by the significant ***area*** * ***distance*** interaction effect (Table 8, Figure 8). While there was no significant effect of ***distance*** on the nest box occupancy in area A, the probability of the nest box occupancy decreased with distance to trail in area BC (Table 9, Figure 8). This result led to a significant interaction between ***area*** and ***distance*** (Table 8, 9). As expected, the likelihood of the **nest box occupancy** decreased with the increase in the number of ***available nest boxes*** in the vicinity of a nest box (effect of ***available nest boxes*** in Table 8). This negative effect of the ***available nest boxes*** on the ***nest box occupancy*** is present in both areas, but only in area A, it was significant (Table 9; P=0.001), whereas it was marginally non-significant in area BC (Table 9; P=0.12).

Table 7. The list containing the three best models that explain variation in the nest box occupancy when *available nest boxes* were used in the full model, and the three best models where *occupied nest boxes* were used. The total sample size is 726. ***Year*** was used as a random variable.

models	Intercept	proportion of conifers	area	distance	area :distance	available nest boxes	occupied nest boxes	df	logLik	AICc	delta	weight
m1	-1.56		+	+	+	-0.36		8	-211.86	439.9	0	0.60
m2	-1.48	-0.24	+	+	+	-0.37		9	-211.73	441.7	1.79	0.25
m3	-1.35			+		-0.35		5	-216.37	442.8	2.91	0.14
m4	-2.11		+	+	+			7	-217.95	450.1	10.13	0.00
m5	-2.09		+	+	+		-0.34	8	-217.58	451.4	11.43	0.00
m6	-2.15	0.18	+	+	+			8	-217.87	451.9	12.02	0.00

Table 8. The summary of the fixed effects in the best model for the nest box occupancy (model m1 in table 7). The table concerns Figure 8. ***Year*** was used as a random factor.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-1.557	0.354	-4.403	1.07E-05	***
distance2	-0.805	0.515	-1.561	0.119	
distance3	0.641	0.452	1.417	0.157	
area	0.416	0.406	1.025	0.305	
available nest boxes	-0.355	0.105	-3.384	7.14E-04	***
distance2:area	0.182	0.658	0.276	0.783	
distance3:area	-1.639	0.622	-2.637	8.35E-03	**

Table 9. The summaries of the two sub-models from the best model in table 8. These are models run separately for each ***area*** in order to show the details of the ***area * distance*** interaction in the model m1 (Tables 7 and 8). The table concerns Figure 9. ***Year*** was used as a random factor.

	Effects	Estimate	Std. Error	z value	Pr(>|z|)	
area A	(Intercept)	-1.373	0.445	-3.087	2.02E-3	**
	Distance2	-0.785	0.521	-1.506	0.132	
	Distance3	0.752	0.468	1.606	0.108	
	available nest boxes	-0.559	0.171	-3.275	1.06E-3	**
area BC	(Intercept)	-1.324	0.345	-3.844	1.21E-4	***
	Distance2	-0.661	0.410	-1.613	0.107	
	Distance3	-1.044	0.430	-2.430	0.015	*
	available nest boxes	-0.211	0.137	-1.540	0.124	

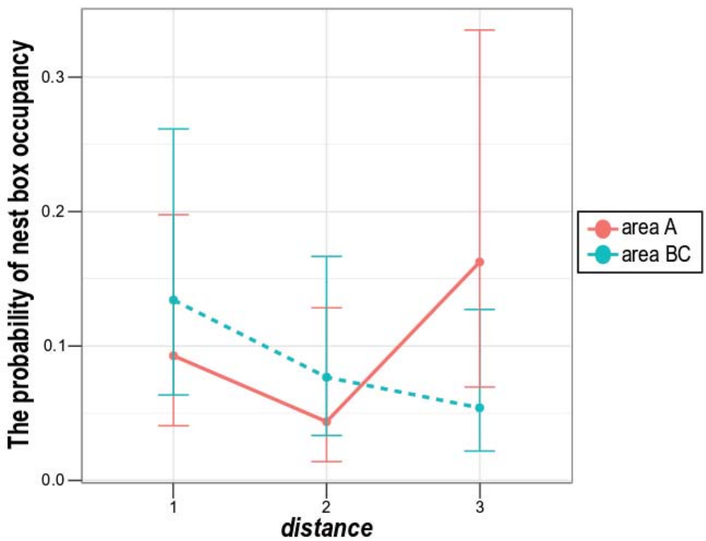

Figure 8. Relationship between *distance* and the nest box occupancy in each area.
The solid pink line indicates the probability of the **nest box occupancy** in area A, and the dotted green line represents area BC. Filled circles indicate the expected probability values and error bars indicate standard errors obtained from model m1 (Table 7). The results of statistical analyses are in Tables 8 and 9.

Part 2. Characteristics of clutches and broods

(1) Clutch size

As explained in the Methods, two different statistical methods were applied for the **clutch size**. First, I used the typical general mixed model approach assuming a normal distribution of error terms (Evans et al. 2009; Westneat et al. 2014). I also used the modern methods available in R that use the Conway-Maxwell-Poisson error distribution (details were shown in table 3). I compared the AICc of the three best models from the first analysis with the three best models from the second approach (Table 10). The results are not equivocal. The best model comes from the first approach and suggests that the effect of distance was different in each area (model m1; Tables 10 and 11). However, the next two models, one from the classical approach and one from the modern approach, show no effect of area or distance, and they differ from the best model by less than 0.5 of the AICc value (Table 10). It suggests that there might have been no effect of distance or area on the clutch size, but considering that there was such an effect then it was present only in area A (Tables 11 and 12): birds in area A laid larger clutches near the hiking trails (Table 12; Figure 9).

Table 10. The comparison list containing the three best models for the clutch size using classical general mixed model approach and the three best models from the analysis using glmmTMB package that assumes Conway-Maxwell-Poisson error distribution in the model. The total sample size is 67. ***Year*** was used as a random factor.

models	Intercept	area	distance	area:distance	proportion of conifers	family	df	logLik	AICc	delta	weight
m1	10.78	+	+	+		gaussian	8	-112.94	244.3	0	0.24
m2	10.24					gaussian	3	-119.14	244.6	0.33	0.20
m3	2.33					compois*	3	-119.18	244.7	0.42	0.19
m4	2.35	+				compois*	4	-118.34	245.3	1	0.14
m5	10.49	+				Gaussian	4	-118.44	245.5	1.2	0.13
m6	2.35				-0.042	compois*	4	-118.80	246.2	1.93	0.09

*compois: Conway-Maxwell-Poisson error distribution

Table 11. The summary of the best model for the clutch size (model m1 in table 10).
The table concerns Figure 9. ***Year*** was used as a random factor.

Effects	Estimate	Std. Error	df	t value	Pr(|t|)	
(Intercept)	10.784	0.523	7.952	2.06E+01	3.43E-08	***
distance2	0.277	0.636	59.489	0.435	0.665	
distance3	-0.952	0.524	59.136	-1.818	0.074	.
area	-1.282	0.492	60.077	-2.608	0.012	*
distance2:area	0.583	0.811	59.751	0.719	0.475	
distance3:area	1.925	0.755	60.228	2.549	0.013	*

Table 12. The summaries of the two sub-models from the best model in table 11. These are models run separately for each ***area*** in order to show the details of the ***area * distance*** interaction in the model m1 (Tables 10 and 11). ***Year*** was used as a random factor.

	Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
area A	(Intercept)	10.780	0.544	4.385	19.825	1.85E-05	***
	distance2	0.300	0.532	24.473	0.564	0.578	
	distance3	-0.961	0.434	24.103	-2.216	0.036	*
area BC	(Intercept)	9.652	0.456	7.013	21.168	1.29E-07	***
	distance2	0.665	0.573	34.521	1.161	0.253	
	distance3	0.828	0.623	34.834	1.329	0.192	

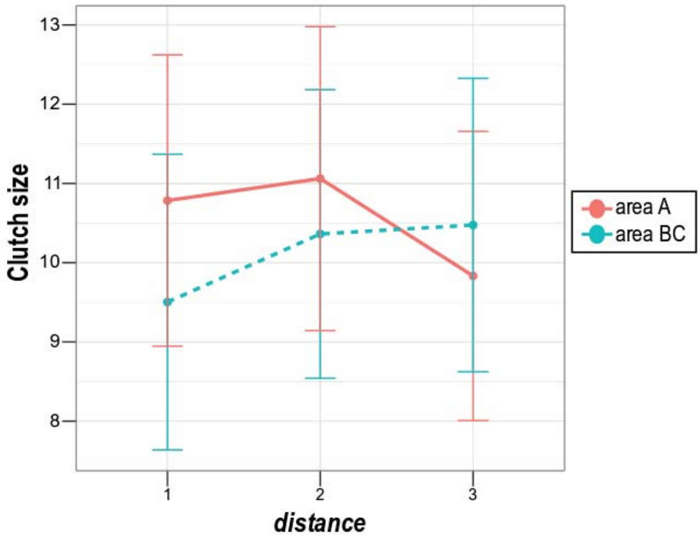

Figure 9. Relationship between *distance* and the clutch size in each area.

The solid pink line indicates the clutch size according to each distance in area A, and the dotted green line represents the clutch size according to each distance in area BC. Filled circles indicate the least square mean values and error bars indicate standard errors obtained from model m1 (Table 10). Results of statistical analyses are in Tables 11 and 12.

(2) Clutch hatching success

I ranked all models for the **clutch hatching success** by AICc and selected the top three models presented in Table 13. Neither ***distance*** nor ***area*** affected the likelihood that at least one egg hatched in a nest (***hatching success)***. The best model included only the random variable, ***year*** (Table 13, 14; Figure 10).

Table 13. The list of the top three models that explain variations in the clutch hatching success. The total sample size is 67. ***Year*** was used as a random variable.

models	Intercept	proportion of conifers	hatching date	df	logLik	AICc	delta	weight
m1	3.06			2	-12.25	28.7	0	0.43
m2	2.17	2.18		3	-11.55	29.5	0.79	0.29
m3	3.99		-0.09	3	-11.61	29.6	0.91	0.28

Table 14. The summary of the best model for the clutch hatching success (model m1 in table 13). The table concerns Figure 10. ***Year*** was used as a random factor.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	3.060	0.591	5.181	2.21E-07	***

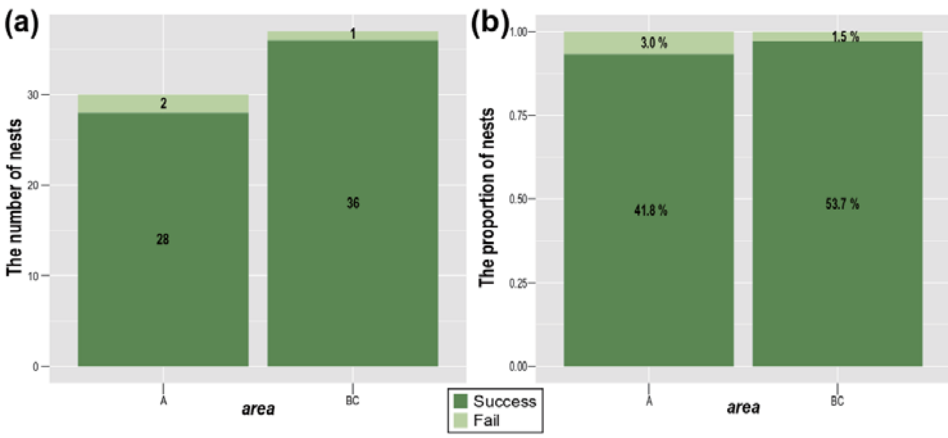

Figure 10. Clutch hatching success in in area A and BC presented as the number of nests (a) and as the proportion of nests (b). The dark green indicates nests in which at least one egg hatched (Clutch hatching success=1), and light green indicates nests where no hatching was observed (Clutch hatching success =0). Only two out of 30 nests failed to hatch in area A, and one out of 37 nests failed to hatch in area BC.

(3) Hatching success rate

I ranked all models for the **hatching success rate** by AICc and selected the top three models presented in Table 15. There was no effect of ***distance*** to trail on the **hatching success rate** in any of the three best models (Table 15). In general, the **hatching success rate** was higher in area BC than in area A (main effect of the ***area*** in table 16), but this effect was modified by the ***proportion of conifers*** (interaction between ***area*** and ***proportion of conifers*** in Table 16). In area A, the **hatching success rate** was the lowest in the forest with a low proportion of conifers, while in area BC, the opposite result was observed (Tables 16, 17; Figure 11). Additionally, the **hatching success rate** decreased with ***hatching date*** (marginally non-significant main effect at P=0.052; table 16; Figure 12), especially for area A but not BC (Table 17).

Table 15. The list of the top three models that explain variations in the hatching success rate. The total sample size is 67. ***Year*** was used as a random variable.

models	Intercept	proportion of conifers	hatching date	area	area :proportion of conifers	df	logLik	AICc	delta	weight
m1	1.23	1.90	-0.036	+	+	6	-161.39	336.2	0	0.61
m2	0.94	2.04		+	+	5	-163.25	337.5	1.3	0.32
m3	1.70	0.50	-0.054			4	-165.96	340.6	4.38	0.07

Table 16. The summary of the best model for the hatching success rate (model m1 in table 15). This table concerns Figure 11. ***Year*** was used as a random variable.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.227	0.330	3.724	1.96E-04	***
area	1.121	0.488	2.296	2.17E-02	*
proportion of conifers	1.898	0.633	2.999	2.71E-03	**
hatching date	-0.036	0.018	-1.944	0.0518	.
area:proportion of conifers	-2.550	0.866	-2.943	3.25E-03	**

Table 17. The summaries of the two sub-models from the best model in table 16. These are models run separately for each area in order to show the details of the *area * distance* interaction in the model m1 (Tables 15 and 16). This table concerns Figure 11. ***Year*** was used as a random variable.

	Effects	Estimate	Std. Error	z value	Pr(>|z|)	
area A	(Intercept)	2.118	0.662	3.2	1.37E-03	**
	proportion of conifers	1.875	0.724	2.591	9.58E-03	**
	hatching date	-0.157	0.042	-3.704	2.13E-04	***
area BC	(Intercept)	2.375	0.426	5.572	2.52E-08	***
	proportion of conifers	-1.074	0.546	-1.968	0.049	*
	hatching date	-0.004	0.020	-0.194	0.846	

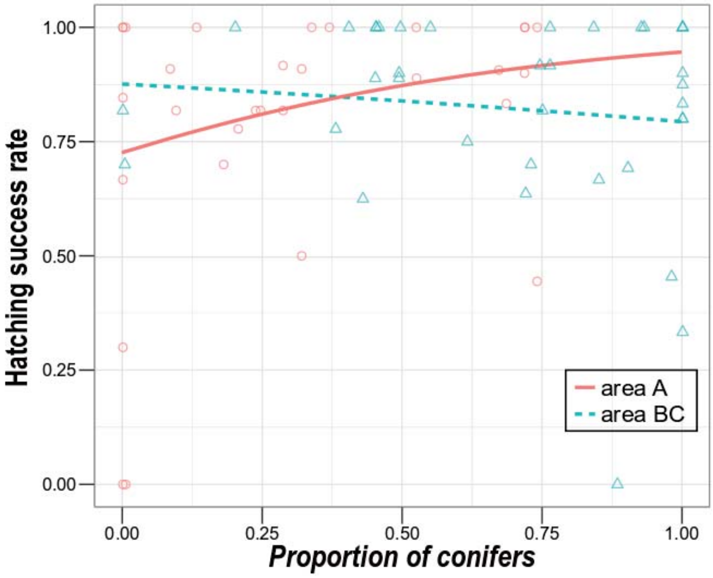

Figure 11. Relationship between *proportion of conifers* and the hatching success rate in each *area*. The raw data points of hatching success rate in area A (red circles) and B (green triangles), as well as the relationships predicted from the models in Table 17 are shown for area A (red solid line) and B (green broken line).

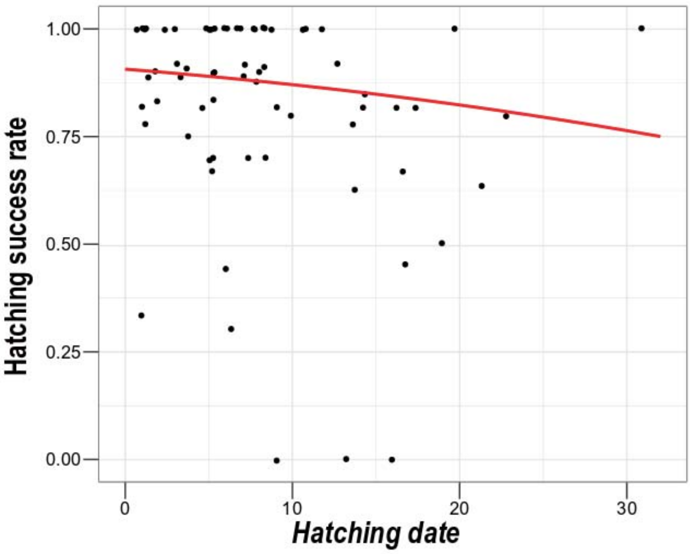

Figure 12. Relationship between the hatching success rate and *hatching date*. The red line indicates the predicted hatching success rate, and the black dots mark the raw data of the hatching success rate according to the hatching date. The hatching success rate is decreased over time.

(4) Brood survival

There was no significant effect of ***distance*** or ***area*** on the **brood survival** in any of the three best models (Tables 18 and 19; Figure 13). The best model included only random effects.

Table 18. The list of the three best models that explain variation in the brood survival. The total sample size is 64. ***Year*** was used as a random variable.

models	Intercept	proportion of conifers	area	df	logLik	AICc	delta	weight
m1	1.97			2	-24.10	52.4	0	0.42
m2	2.81	-1.47		3	-23.36	53.1	0.72	0.29
m3	2.61		+	3	-23.39	53.2	0.79	0.28

Table 19. The summary of the fixed effects in the best model for the brood survival (model m1 in table 18). The table concerns Figure 14. ***Year*** was used as a random variable.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.969	0.442	4.457	8.32E-06	***

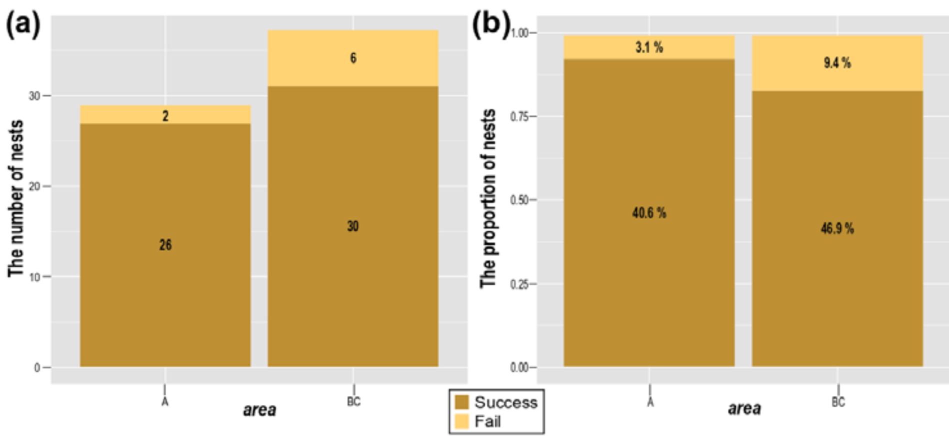

Figure 13. Brood survival in area A and BC presented as the number of nests (a) and as the proportion of nests (b). The dark yellow indicates nests in which at least one nestling survived (Brood survival = 1), and light yellow indicates nests where there was no nestling (Brood survival = 0). Only two out of 28 nests failed to survive until day 11 in area A, and six out of 36 nests failed to survive until day 11 in area BC.

(5) Total nestlings' survival rate

The best model (model m1 in Table 20) included every explanatory variable, including marginally non-significant three-way interaction between ***area***, ***distance***, and ***proportion of conifers*** (Table 21; three-way interaction P=0.056), which was shown in Figure 14. However, I believe that there were problems with this analysis. For example, the range of ***proportion of conifers*** values at ***distance 1*** in area A did not overlap at all with the range of ***proportion of conifers*** at ***distance 1*** in area BC (Figure 15a and b). Additionally, the effect of ***area*** might be confused with the effect of ***proportion of conifers*** because the majority of nest boxes in area A were located in areas with a low ***proportion of conifers***, and a majority of nest boxes in area BC were situated in areas with a high ***proportion of conifers*** (Figure 6). Therefore, it may be problematic to include both variables, especially in the model that seen to include all factors and their interactions. In order to address these issues, I decided to run models without considering ***area*** as a potential explanatory variable.

When the models were constructed without ***area***, then the effect of ***distance*** was modified by ***proportion of conifers*** (interaction in Table 22): if nest boxes were located in the forest with a low ***proportion of conifers***, then the survival rate was the smallest near hiking trails (at ***distance 1***). In locations with a large proportion of conifers, this was no longer true (Table 23; Figure 15).

Table 20. The list of the three best models that explain variation in the total nestlings' survival rate. The total sample size is 64. ***Year*** was used as a random variable. "a", "c", "d", and "h" means ***area***, ***proportion of conifers***, ***distance***, and ***hatching date***.

models	Intercept	h	c	a	d	a:c	a:d	c:d	a:c:d	df	logLik	AICc	delta	weight
m1	1.40	-0.11	3.70	+	+	+	+	+	+	14	-200.60	437.8	0	0.71
m2	1.61	-0.12	2.73	+	+	+	+	+		12	-205.49	441.1	3.32	0.14
m3	1.38	-0.11	3.92	+	+		+	+		11	-207.60	442.3	4.5	0.08

* a: ***area***, c: ***proportion of conifers***, d: ***distance***, h: ***hatching date***

Table 21. The summary of the fixed effects in the best model for the total nestlings' survival rate (model m1 in table 20). The table concerns Figure 15. ***Year*** was used as a random variable.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.398	0.334	4.190	2.80E-05	***
distance2	0.685	1.046	0.655	5.13E-01	
distance3	2.152	0.741	2.904	3.68E-03	**
proportion of conifers	3.699	1.515	2.441	1.47E-02	*
area	-2.571	0.773	-3.327	8.78E-04	***
hatching date	-0.106	0.021	-5.048	4.47E-07	***
proportion of conifers:distance2	-1.277	3.055	-0.418	6.76E-01	
proportion of conifers:distance3	-7.207	1.922	-3.750	1.77E-04	***
area:distance2	2.762	1.369	2.018	4.36E-02	*
area:distance3	0.729	1.169	0.624	5.33E-01	
proportion of conifers:area	0.202	1.731	0.117	9.07E-01	
proportion of conifers:area:distance2	-3.769	3.194	-1.180	2.38E-01	
proportion of conifers:area:distance3	4.197	2.191	1.916	5.54E-02	.

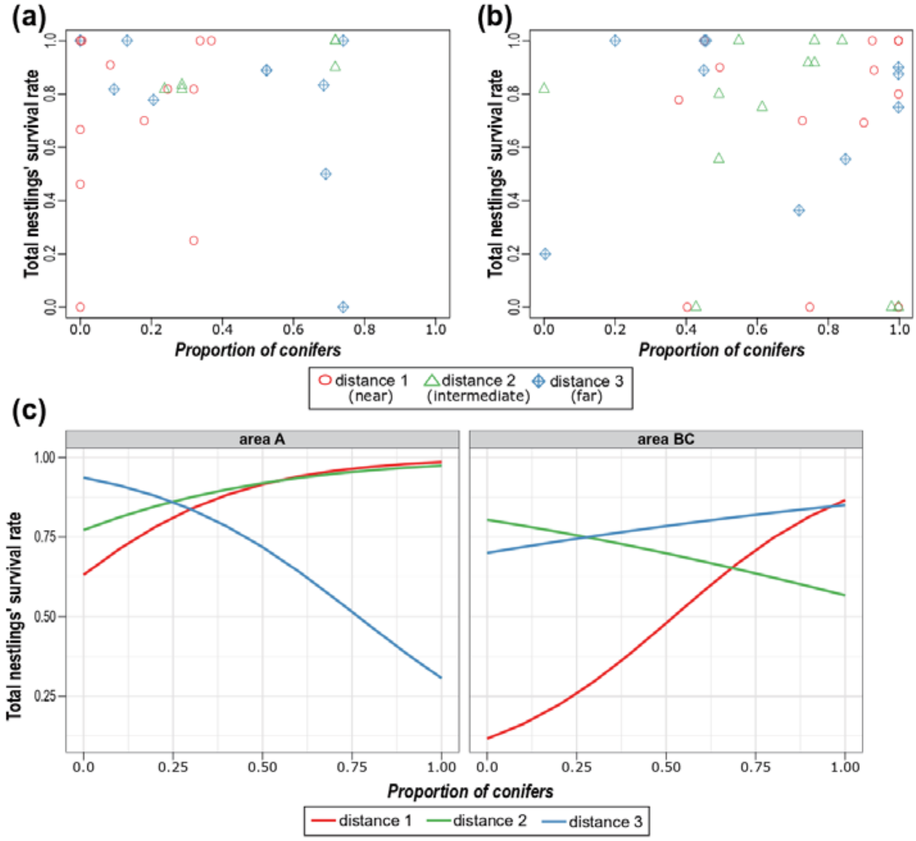

Figure 14. Relationship between *proportion of conifers* and the total nestlings' survival rate in each *area*. (a) and (b) shows the raw data points of the **total nestlings' survival rate** in area A and area BC. The red circles indicate ***distance 1***, the green triangles indicate ***distance 2***, and the blue diamond shapes indicate ***distance 3***. (c) describes the predicted **total nestlings' survival rate** in each area from model m1 (Table 20). The red line indicates ***distance 1***, the green line indicates ***distance 2***, and the blue line indicates ***distance 3***. Results of statistical analyses are in Table 21.

Table 22. The summary of the fixed effects in the best model for the total nestlings' survival rate excluding *area* variable. The table concerns Figure 16. ***Year*** was used as a random variable.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.207	0.290	4.167	3.09E-05	***
distance2	1.338	0.551	2.430	1.51E-02	*
distance3	0.790	0.425	1.860	6.29E-02	.
proportion of conifers	0.667	0.412	1.619	1.05E-01	
hatching date	-0.074	0.017	-4.309	1.64E-05	***
proportion of conifers:distance2	-2.085	0.871	-2.394	1.67E-02	*
proportion of conifers:distance3	-1.138	0.707	-1.611	1.07E-01	

Table 23. The summary of the three sub-models from the best model in Table 22. These are models run separately for each ***distance*** in order to show the details of the ***distance * proportion of conifer*** interaction in the best model excluding ***area*** (Tables 22). ***Year*** was used as a random variable.

	Effects	Estimate	Std. Error	z value	Pr(>|z|)	
distance1	(Intercept)	1.101	0.376	2.931	3.38E-03	**
	proportion of conifers	0.691	0.438	1.577	1.15E-01	
	hatching date	-0.060	0.022	-2.739	6.16E-03	**
distance2	(Intercept)	3.487	0.710	4.910	9.10E-07	***
	proportion of conifers	-2.120	0.870	-2.437	1.48E-02	*
	hatching date	-0.139	0.053	-2.644	8.18E-03	**
distance3	(Intercept)	1.620	0.650	2.494	1.26E-02	*
	proportion of conifers	0.031	0.670	0.046	9.63E-01	
	hatching date	-0.064	0.037	-1.744	8.11E-02	.

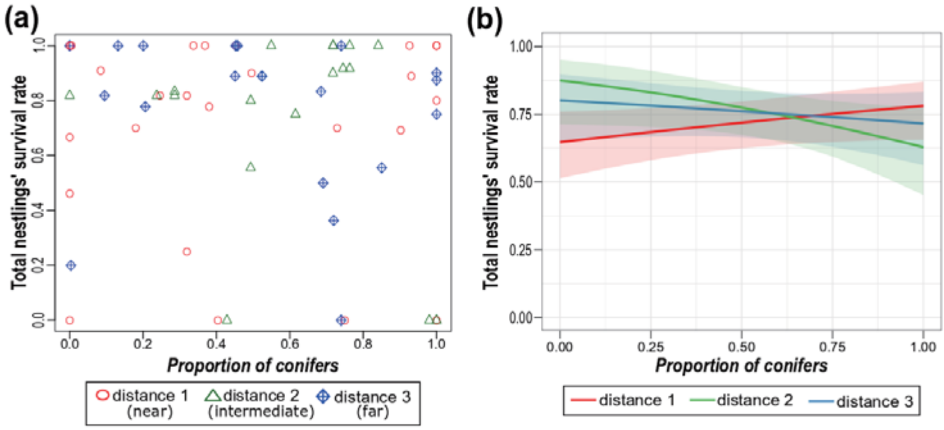

Figure 15. Relationship between *proportion of conifers* and the total nestlings' survival rate at different *distances*. (a) shows the raw data points of the **total nestlings' survival rate**. The red circles indicate ***distance 1***, the green triangles indicate ***distance 2***, and the blue diamond shapes indicate ***distance 3***. (c) describes the predicted **total nestlings' survival rate** in each ***distance*** from model m1 (Table 20). The red line indicates ***distance 1***, the green line indicates ***distance 2***, and the blue line indicates ***distance 3***. Also, the colored ranges around each line indicate the confidence interval. Results of statistical analyses are in Table 22 and 23.

Part 3. Individual nestlings mass, growth and survival

(1) Nestlings' body mass on day 5

Table 24 shows the top three models. The best model for nestlings' body mass on day 5 included the three-way interaction between ***area***, ***distance***, and ***proportion of conifers*** (Table 25; Figure 16). As already explained in the paragraph "**Total nestlings' survival rate**," I viewed such a model problematic and unreliable. Therefore, like before, I ran the model without considering ***area*** as a potential explanatory variable (Table 26; Figure 17).

When the models were constructed without ***area***, there was a positive effect of ***proportion of conifers*** on nestlings' body mass on day 5, as indicated by a significant main effect (Table 26). However, this effect was modified by ***distance*** (significant interaction in Table 26): the positive effect of ***proportion of conifers*** was visible for the nests located closer to hiking trails (***distance 1*** and ***distance 2***) while negative relationship was observed in nests located far away from hiking trails (***distance 3***; Figure 18). Although none of those effects of ***proportion of conifers*** for each distance was significant (Table 27), the significant ***distance*proportion of conifers*** interaction term in Table 26 suggested that the negative effect of ***proportion of conifers*** at ***distance 3*** was significantly different from the positive effect of ***proportion of conifers*** at ***distance 1***.

Table 24. The list of the top three models that explain variations in the nestlings' body mass on day 5. The total sample size is 532. ***Year*** and ***Nest ID*** were used as random variables. "a", "b", "c", "d", and "h" means ***area***, ***brood5***, ***proportion of conifers***, ***distance***, and ***hatching date***.

models	Intercept	h	b	c	a	d	a:c	a:d	c:d	a:c:d	df	logLik	AICc	delta	weight
m1	6.81	-0.25		13.72	+	+	+	+	+	+	16	-739.84	1512.7	0.00	0.93
m2	6.45	-0.23	0.05	12.02	+	+	+	+	+	+	17	-741.40	1518.0	5.27	0.07
m3	7.56	-0.25		8.345	+	+	+	+	+		14	-754.14	1535.0	22.26	0.00

* a: ***area***, b: ***brood5***, c: ***proportion of conifers***, d: ***distance***, h: ***hatching date***

Table 25. The summary of the fixed effects in the best model for the nestlings' body mass on day 5 (model m1 in table 24). The table concerns Figure 16. ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	6.809	1.098	9.702	6.199	1.16E-04	***
distance2	4.729	2.441	31.053	1.937	6.18E-02	.
distance3	2.783	1.422	38.120	1.957	5.77E-02	.
area	-1.738	1.809	45.642	-0.961	3.42E-01	
proportion of conifers	13.721	2.351	340.313	5.836	1.25E-08	***
hatching date	-0.252	0.026	313.235	-9.766	< 2E-16	***
area:distance2	-4.327	3.402	31.184	-1.272	2.13E-01	
area:distance3	0.233	2.631	37.017	0.089	9.30E-01	
proportion of conifers:distance2	-19.462	4.963	46.362	-3.921	2.89E-04	***
proportion of conifers:distance3	-18.763	3.452	105.092	-5.435	3.58E-07	***
area:proportion of conifers	-10.017	3.042	118.942	-3.293	1.31E-03	**
area:proportion of conifers:distance2	18.340	5.705	40.086	3.215	2.58E-03	**
area:proportion of conifers:distance3	15.185	4.497	55.713	3.376	1.35E-03	**

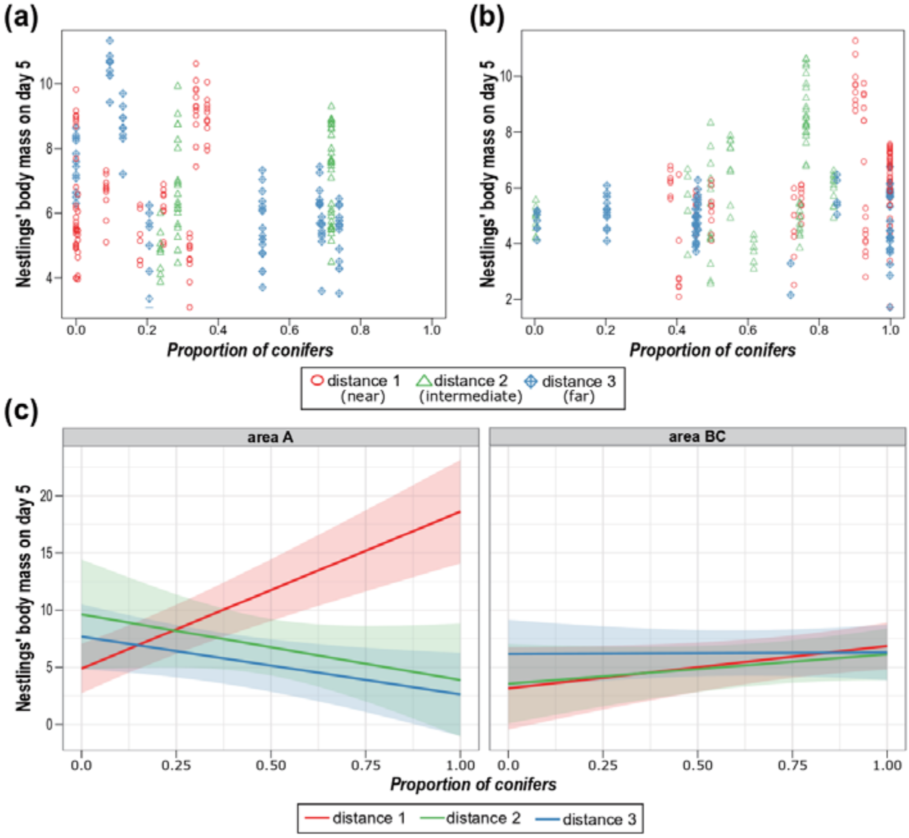

Figure 16. Relationship between *proportion of conifers* and the nestlings' body mass on day 5 in each *area*. (a) and (b) show the raw data points of the **nestlings' body mass on day 5** in area A and area BC. The red circles indicate ***distance 1***, the green triangles indicate ***distance 2***, and the blue diamond shapes indicate ***distance 3***. (c) describes the predicted **nestlings' body mass on day 5** in each area from model m1 (Table 24). The red line indicates ***distance 1***, the green line indicates ***distance 2***, and the blue line indicates ***distance 3***. Also, the colored ranges around each line indicate the confidence interval. Results of statistical analyses are in Table 25.

Table 26. The summary of the fixed effects in the best model for the nestlings' body mass on day 5 excluding *area* variable. The table concerns Figure 17. ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	6.259	1.094	7.388	5.720	5.93E-04	***
distance2	0.401	1.502	31.907	0.267	7.91E-01	
distance3	2.109	1.119	37.309	1.884	6.74E-02	.
proportion of conifers	2.632	1.022	54.254	2.575	1.28E-02	*
hatching date	-0.209	0.024	309.640	-8.601	4.02E-16	***
proportion of conifers:distance2	-0.981	1.963	38.689	-0.499	6.20E-01	
proportion of conifers:distance3	-3.915	1.701	44.342	-2.301	2.61E-02	*

Table 27. The summary of the three sub-models from the best model in Table 26. These are models run separately for each ***distance*** in order to show the details of the ***distance * proportion of conifer*** interaction in the best model excluding ***area*** (Tables 26). ***Year*** and ***Nest ID*** were used as random variables.

	Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
distance1	(Intercept)	6.647	1.304	7.600	5.098	1.09E-03	**
	proportion of conifers	1.942	1.300	16.982	1.494	1.54E-01	
	hatching date	-0.189	0.037	117.073	-5.067	1.52E-06	***
distance2	(Intercept)	3.409	1.504	11.730	2.267	4.31E-02	*
	proportion of conifers	2.307	1.625	9.373	1.419	1.88E-01	
	hatching date	0.183	0.090	23.243	2.020	5.51E-02	.
distance3	(Intercept)	10.123	1.126	16.620	8.987	8.72E-08	***
	proportion of conifers	-1.493	1.512	11.065	-0.988	3.44E-01	
	hatching date	-0.430	0.054	97.100	-7.982	2.91E-12	***

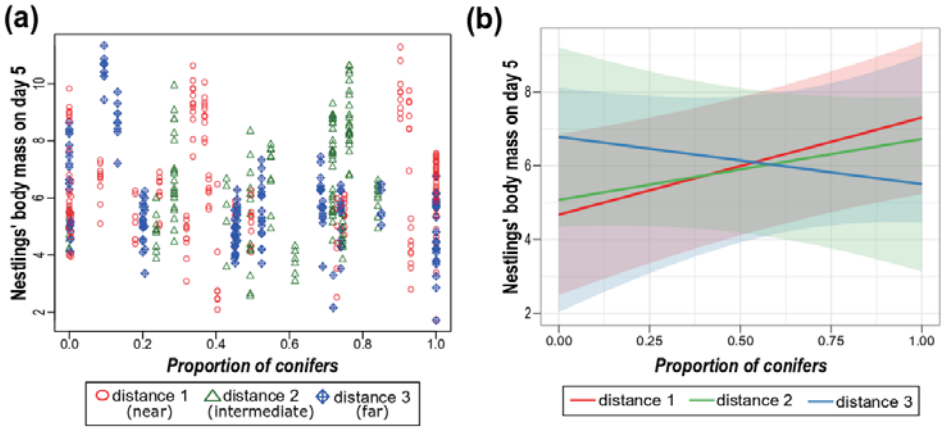

Figure 17. Relationship between *proportion of conifers* and the nestlings' body mass on day 5 at different *distance*. (a) shows the raw data points of the **nestlings' body mass on day 5**. The red circles indicate ***distance 1***, the green triangles indicate ***distance 2***, and the blue diamond shapes indicate ***distance 3***. (c) describes the predicted **nestlings' body mass on day 5** in each ***distance*** from model m1 (Table 26). The red line indicates ***distance 1***, the green line indicates ***distance 2***, and the blue line indicates ***distance 3***. Also, the colored ranges around each line indicate the confidence interval. Results of statistical analyses are in Table 26.

(2) Individual nestling survival

Distance and ***area*** did not affect the individual nestling survival in any of the three best models (Table 28). The only effect on the **individual nestling survival** was that of ***brood***, which was present in all three best models (Table 28 and 29). **Individual nestling survival** significantly increased as the brood size increased (Table 29, Figure 18).

Table 28. The list of the top three models that explain variation in the individual nestling survival. The total sample size is 486. ***Year*** and ***Nest ID*** were used as random variables.

models	Intercept	brood	hatching date	area	df	logLik	AICc	delta	weight
m1	-4.43	1.06			4.00	-62.85	133.80	0.00	0.58
m2	-4.62	1.06		0.01	5.00	-62.82	135.80	1.98	0.21
m3	-4.52	1.06	+		5.00	-62.84	135.80	2.02	0.21

Table 29. The summary of the fixed effects in the best model for the individual nestling survival (model m1 in table 28). The table concerns Figure 18. ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-4.431	1.065	-4.159	3.20E-05	***
brood	1.055	0.154	6.868	6.52E-12	***

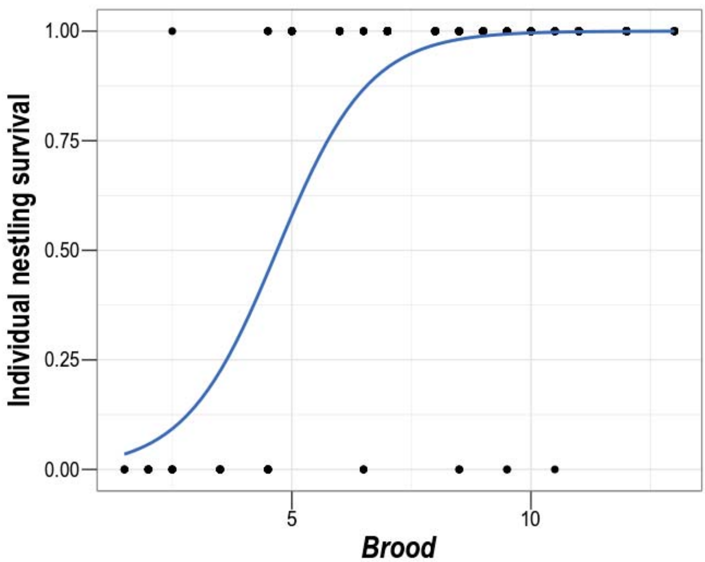

Figure 18. The relationship between *brood* and the individual nestling survival. The number of nestlings in the same nest has a positive effect on the survival of individual nestling. The result of statistical analysis is in Table 29.

(3) Nestlings' body mass on day 11

Unlike the other two models of the top three models in the top three models derived from the general nestlings' body mass on day 11 and ranked by AICc, the best model had all variables (Table 30). The three-way interaction between ***area, proportion of conifers,*** *and* ***distance*** were included in the best model without any statistical significance (Table 31). Additionally, in the best model, ***hatching date*** had a negative effect, and ***brood 11*** had a positive effect on the nestlings' body mass on day 11. As already explained in the paragraph "**Total nestlings' survival rate**," I viewed such a model problematic and unreliable and analyzed a model without ***area***.

When the model excluding ***area*** was constructed, no significant effects of ***distance***, ***conifers*** or interaction between them were observed (Table 32).

Table 30. The list of the top three models that explain variation in the nestlings' body mass on day 11. The total sample size is 486. ***Year*** and ***Nest ID*** were used as random variables. "a", "b", "c", "d", and "h" means ***area***, ***brood11***, ***proportion of conifers***, ***distance***, and ***hatching date***.

models	Intercept	h	b	c	a	d	a:c	a:d	c:d	a:c:d	df	logLik	AICc	delta	weight
m1	10.43	-0.15	0.38	-1.53	+	+	+	+	+	+	17	-748.36	1532.00	0.00	0.682
m2	10.28	-0.11	0.32								6	-762.30	1536.80	4.74	0.064
m3	10.66	-0.11	0.33	-1.35	+		+				9	-759.55	1537.50	5.46	0.044

* a: ***area***, b: ***brood11***, c: ***proportion of conifers***, d: ***distance***, h: ***hatching date***

Table 31. The summary of the fixed effects in the best model of the nestlings' body mass on day 11 (model m1 in table 30). ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	10.431	0.783	25.242	13.328	6.31E-13	***
distance2	1.648	1.855	29.027	0.889	3.81E-01	
distance3	-0.361	1.114	33.253	-0.324	7.48E-01	
area	-1.889	1.654	37.769	-1.142	2.61E-01	
proportion of conifers	-1.531	2.503	59.654	-0.612	5.43E-01	
hatching date	-0.147	0.031	17.399	-4.769	1.68E-04	***
brood11	0.380	0.062	16.145	6.122	1.41E-05	***
area:distance2	-0.501	2.726	29.690	-0.184	8.55E-01	
area:distance3	2.267	2.220	33.232	1.021	3.15E-01	
proportion of conifers:distance2	-2.704	4.196	36.956	-0.645	5.23E-01	
proportion of conifers:distance3	1.116	3.209	51.980	0.348	7.29E-01	
area:proportion of conifers	3.783	2.914	72.358	1.298	1.98E-01	
area:proportion of conifers:distance2	0.492	4.770	39.170	0.103	9.18E-01	
area:proportion of conifers:distance3	-3.733	3.851	48.157	-0.969	3.37E-01	

Table 32. The summary of the fixed effects in the best model for the nestlings' body mass on day 11 excluding *area* variable. ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	10.06512	0.67087	29.17145	15.003	2.99E-15	***
distance2	0.31431	1.08025	33.31991	0.291	7.73E-01	
distance3	0.1477	0.81389	35.72278	0.181	0.857	
proportion of conifers	0.27184	0.77867	38.5726	0.349	0.729	
hatching date	-0.13395	0.02538	20.95723	-5.279	3.13E-05	***
brood11	0.37086	0.05475	11.2536	6.773	2.73E-05	***
proportion of conifers:distance2	-1.14926	1.49259	43.78719	-0.77	0.445	
proportion of conifers:distance3	-0.56784	1.26208	38.96317	-0.45	0.655	

(4) Nestlings' growth rate per day (g/day)

The three best models were presented in Table 33. The top best model included almost all variables (except ***hatching date***), including the three-way interaction between ***area, proportion of conifers***, and ***distance*** (Table 34; Figure 19). However, as explained above (e.g., in "**Total nestlings' survival rate**" or "Nestlings' **body mass on day 5**"), this complex model includes serious issues related to the unbalanced data structure and small samples. Therefore, as before, I ran the model without considering ***area*** (Table 35), which resulted in no significant effect of ***distance*** or ***proportion of conifers*** or their interaction on the ***nestlings' growth rate per day***. The nestlings' growth rate was faster in larger broods. Also, the results of the models with the exception of ***area*** divided by ***distance*** are not displayed because the effects of ***brood*** for each distance had similar effects with Table 35.

Table 33. The list of the top three models that explain variation in the nestlings' growth rate per day. The total sample size is 486. ***Year*** and ***Nest ID*** were used as random variables.

models	Intercept	h	b	c	a	d	a:c	a:d	c:d	a:c:d	df	logLik	AICc	delta	weight
m1	0.86		0.07	-3.39	+	+	+	+	+	+	16	137.32	-241.50	0.00	0.98
m2	0.82	0.01	0.07	-3.86	+	+	+	+	+	+	17	134.29	-233.30	8.21	0.02
m3	1.12										4	114.68	-221.30	20.20	0.00

* a: ***area***, b: ***brood11***, c: ***proportion of conifers***, d: ***distance***, h: ***hatching date***

Table 34. The summary of the fixed effects in the best model of the nestlings' growth rate per day (model m1 in table 33). The table concerns Figure 19. ***Year*** and ***Nest ID*** were used as random variables.

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	0.856	0.195	27.892	4.385	1.50E-04	***
distance2	-0.490	0.454	17.040	-1.081	2.95E-01	
distance3	-0.827	0.268	22.118	-3.086	5.38E-03	**
area	-0.575	0.370	26.613	-1.555	1.32E-01	
proportion of conifers	-3.392	0.428	238.537	-7.922	8.90E-14	***
brood	0.071	0.013	277.414	5.631	4.39E-08	***
area:distance2	0.909	0.673	17.946	1.350	1.94E-01	
area:distance3	1.260	0.507	21.390	2.488	2.12E-02	*
proportion of conifers:distance2	3.458	0.901	24.086	3.838	7.89E-04	***
proportion of conifers:distance3	4.754	0.668	52.854	7.121	2.92E-09	***
area:proportion of conifers	3.752	0.602	62.524	6.235	4.32E-08	***
area:proportion of conifers:distance2	-4.338	1.104	22.398	-3.929	6.98E-04	***
area:proportion of conifers:distance3	-5.357	0.880	31.151	-6.086	9.43E-07	***

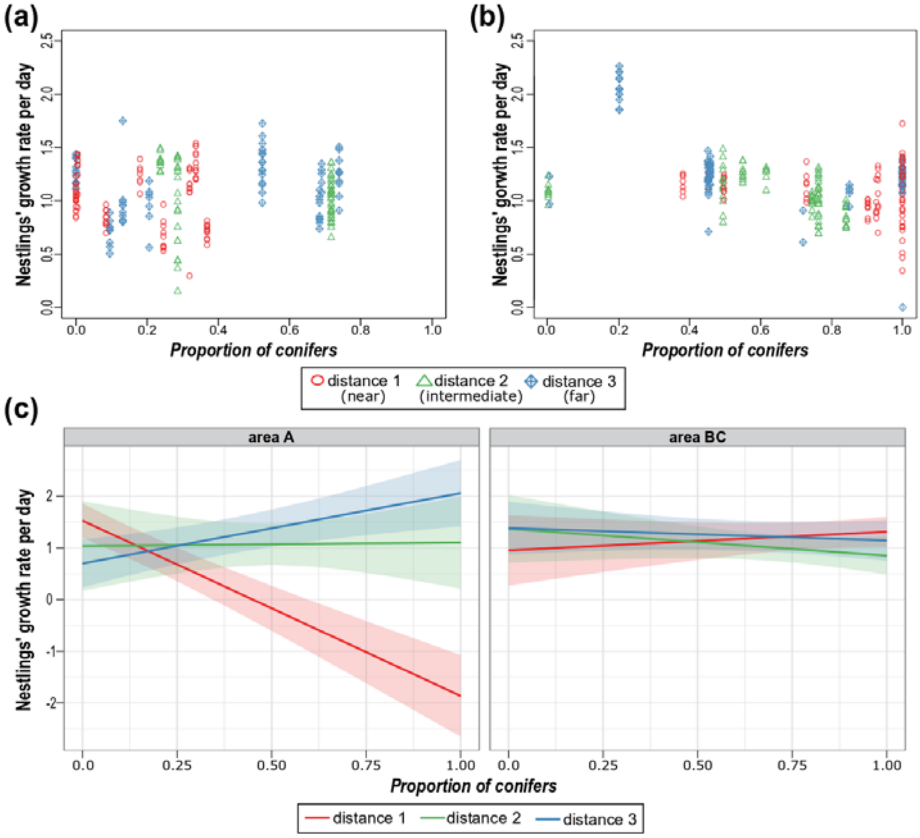

Figure 19. Relationship between *proportion of conifers* and the nestlings' growth rate per day in each *area*. (a) and (b) shows the raw data points of the **nestlings' growth rate per day** in area A and area BC. The red circles indicate ***distance 1***, the green triangles indicate ***distance 2***, and the blue diamond shape indicate ***distance 3***. (c) describes the predicted **nestlings' growth rate per day** in each area from model m1 (Table 33). Results of statistical analyses are in Table 34.

Table 35. The summary of the fixed effects in the best model for the nestlings' growth rate per day excluding *area* variable*.* *Year* and ***Nest ID*** were used as random variables**.**

Effects	Estimate	Std. Error	df	t value	Pr(>|t|)	
(Intercept)	0.875	0.154	26.673	5.672	5.26E-06	***
distance2	0.042	0.203	31.638	0.207	8.37E-01	
distance3	-0.037	0.152	34.922	-0.241	8.11E-01	
proportion of conifers	-0.156	0.134	45.087	-1.169	2.49E-01	
brood	0.038	0.011	226.331	3.306	1.10E-03	**
proportion of conifers:distance2	-0.251	0.270	40.322	-0.929	3.58E-01	
proportion of conifers:distance3	0.136	0.233	38.126	0.583	5.64E-01	

Discussion

I have observed the possible effects of human traffic only on the variables concerning the early stages of breeding. Three independent variables concerning early stages of breeding (**Nest box occupancy**, **Hatching success rate**, **Nestlings' body mass on day 5**), and one variable including a period of early breeding stage (**Total nestlings' survival rate**) indicated that humans might have had a negative effects on breeding of birds and that conifers might have protected birds from those effects. One variable related to the early breeding stage indicated a positive association with proximity to trails (**Nest box occupancy**) but only in the ***area*** with less heavy human traffic. Additionally, there is some evidence for larger **clutch size** in proximity to trails, but it is not conclusive. The remaining six variables (**Nest building initiation**, **Clutch hatching success**, **Brood survival**, **Nestlings' body mass on day11**, **Nestlings' growth rate per day**, **Individual nestling's survival**) did not show variation consistent with the effects of human traffic on breeding.

These suspected impacts by humans were either related to the proximity to hiking trails or to the general number of visitors and how humans behave in each area. The number of people was smaller in area BC than A, and people in area BC kept mostly on trails. In area A, a large number of people used the trails as well as they spread out into the forested zone more frequently than in the area BC. The results suggest that both of the impacts appeared to be modified by the protective role of a higher proportion of conifers that may provide coverage and diminish stress to birds from human presence. Below I discuss details of the detected relationships.

First, the **hatching success rate** was positively affected by an increase in the proportion of conifers in the area A where human traffic was heavy and spread out in the forest, but not in the area BC where fewer humans walked along hiking trails. It is consistent with the idea that the conifers provide protective cover from visually disturbing stimuli produced by people walking in the forest that may disturb incubation and brooding as well as the food provisioning by males to incubating females. Second, the **total nestlings' survival rate** was also the smallest near hiking trails but only for nests located in forests with a low proportion of conifers. It is also consistent with the hypothetical protective function of conifers. This variable combines hatching success with the survival of nestlings until day 11. As the variation of survival of older nestlings (5-11 days old) was not consistent with effects of humans, the effects detected for the total nestlings' survival rate are likely due to the effects at hatching stage (proved above) and at the early nestling phase (until day 5, not analyzed here). Third, the analysis of **nestlings' body mass on day 5** is also consistent with the protective role of conifers for the nests located not far from the hiking trails but not for the nests located far away from the trail where higher proportion of conifers was associated with higher nestling mass for reasons that we do not fully understand. These results are consistent with the idea that conifers might have given visual protection from disturbance by humans, which might have allowed parents to brood and feed young nestlings more efficiently, leading to larger body mass on day 5. Finally, the positive effect of conifers on the probability that **nest box occupancy** is also generally consistent with the protective role of conifers against the human disturbance of the process of **nest building initiation** even though no direct effect of ***distance*** or ***area*** was detected. However, no similar effects indicating human impact were detected in variables that concern older nestlings' daily growth rate and the subsequently produced body mass on day 11. These results suggest that the Oriental tit may be less susceptible to the adverse human effects at the later breeding phase (when nestlings are older than day 5).

I have also detected two possible positive effects of proximity to hiking trails on breeding variables concerning the very early stages of the breeding cycle. Although there was no consistent effect of the distance to trails on the ***nest box occupancy*** among the two areas, in the area with lower human presence and higher general proportion of conifers (area BC), the birds seemed to prefer nest boxes located near hiking trails, which is associated with higher proportion of conifers around the box (Figure6c). While the reasons for this apparent preference are not clear, it is consistent with the idea that birds prefer nest boxes in regions with more conifers. This preference is also compatible with the idea that birds may prefer locations near hiking trails only when this is not associated with higher exposure to predation, and dense conifers can hypothetically provide this protection. We cannot properly evaluate those hypotheses. The survival rate of nestlings is lower in the proximity of hiking trails only in regions with a lower proportion of conifers but not in areas with a large proportion of conifers. Survival is mostly shaped by predation in our population, mainly by snakes but also other animals (unpublished data). Hence, it is also theoretically possible that the Oriental tit can detect traces of predator scent, subsequently avoid areas where they sensed or encountered the predators(Ekner and Tryjanowski 2008) and seek areas near trails, where the predator presence might have been reduced by humans(Muhly et al. 2011). The second putative positive effect was indicated in the traditional generalized mixed model analyses of the ***clutch size***, but it was not confirmed by an analysis using *glmmTMB* (generalized linear mixed-effects model using TMB (template model builder). Even though this effect is not equivocal, it indicated that the Oriental tits laid larger clutches near hiking trails in the area more heavily used by people (area A), but not in the area less heavily used by visitors (area BC). It may indicate that females in better condition breed near hiking trails. These locations in area A are characterized with a small proportion of conifers (Figure 6c), and tits, in general, are known to used deciduous rather than coniferous trees as sources for food in breeding territories (Amininasab et al. 2016). If the territories with fewer conifers indeed provided more resources, it is possible that females in those territories have more resources for producing more eggs, or that the females in better condition compete and win territories near trails because they have more deciduous trees providing better resources. Both hypotheses are compatible with the previous study that deciduous forest provides better food resources for tits than coniferous forests (Amininasab et al. 2016). Similar positive effects were reported in some papers (Finney, Pearce-Higgins, and Yalden 2005), but not in others (Beale and Monaghan 2004; Bolduc and Guillemette 2003).

My results are similar in general terms to the previous studies, in which proximity to trails or recreation places had negative effects on birds' breeding activity or avian community (Arroyo and Razin 2006; Bötsch et al. 2018; Corsini et al. 2017; Hutfluss and Dingemanse 2019; Remacha et al. 2016) My study focused specifically on the effect of the proximity to hiking trails and the impact of a large number of people present on trails and within the forested area located in a large urban agglomeration. Previous studies about the anthropogenic effects on birds concerned a variety of issues. Some studies focused on the negative effects of anthropogenic habitat fragmentation or traffic noise (Satgé et al. 2019) or the harmful effects of urbanization at multiple spatial scales (Bueno-Enciso et al. 2016; Wiacek et al. 2015). Many studies that generally resemble my research detected the negative effects of humans on birds such as reduced clutch size, lower growth rate, breeding failure, and lower bird density and species richness (Arroyo and Razin 2006; Bötsch et al. 2018; Corsini et al. 2017; Glądalski et al. 2016; Mallord et al. 2007; Remacha et al. 2016; Smith-Castro and Rodewald 2010). Direct effects of human disturbance were usually measured and confirmed in areas located far away from urban habitats (Bolduc and Guillemette 2003; Lindsay, Craig, and Low 2008; McClung et al. 2004; Müllner, Eduard Linsenmair, and Wikelski 2004). On the other hand, little research on how human disturbance can affect birds has been conducted in urbanized parks and forests (Davis et al. 2010; S. G. Miller, Knight, and Miller 1998), none of which was conducted in

Asia. Therefore, my results will contribute to expanding the knowledge and to a deeper understanding of anthropogenic effects in recreational areas in large cities.

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국문 초록 (Abstract in Korean)

도시권 주위의 자연환경은 생물다양성을 보존하고 인간생활을 윤택하게 한다. 이러한 공간에서 사람들의 여가활동은 생물다양성과 자연에 양면적인 영향을 미친다. 아시아 지역은 세계에서 손꼽히게 도시화된 지역임에도 도시 숲 (도시 내 공원, 산림)에 사는 야생동물이 인간 활동으로부터 받는 영향에 대한 연구는 더디게 진행되었다. 따라서 아시아에 위치한 도시 숲에서 야생동물이 인간의 활동에 의해 어떤 영향을 받고 있는지 밝혀야 한다. 서울은 아시아에서 가장 큰 도시 중 하나이며, 주위 도시 숲은 시민들이 빈번히 이용하는 장소로 인간이 야생동물에게 끼치는 영향을 평가하는데 훌륭한 환경을 제공한다.

본 연구는 인간의 활동이 인공새집에 서식하는 박새(*Parus minor*)의 번식에 어떤 영향을 미치는지에 대해 평가한다. 이 조사는 서울 인근에서 가장 인기있는 산림 여가 활동 장소 중 한 곳인 관악산에서 이루어졌고, 2014년부터 2017년까지 4년 동안 190여 개의 인공새집에서 번식한 박새의 데이터를 수집하였다.

주요 변수는 등산로와 인공새집 사이의 거리로, 등산로가 박새 번식에 미치는 영향이다. 또 다른 변수는 조사지를 등산객 통행 횟수와 통행 방법(등산로 이용 방법 차이)에 따라 두 구역으로 구분한 것이다. 많은 사람들이 접근하기 쉬운 지형을 가지고 있는 등산로를 이용하는 사람과 나들이를 오가는 사람 등을 합해 통행 횟수가 많은 구역과 반면 산세가 가파르고 비교적 적은 수의 사람이 등산만을 목적으로 방문하는 구역은 번식 활동에 영향을 나타낸다.

분석은 인공새집 사용여부, 한배산란수, 부화율, 한배새끼수, 새끼성장율, 새끼 생존율 등 11개의 변수를 통해 R에서 선형혼합모형과 일반화된 선형혼합모형으로 이루어졌고, 부수적인 변수들은 통제되었다. 인간의 영향이 박새 번식 후반부에 영향을 미치지 않은 것과 달리 번식 초기 단계에서 등산로와 등산객의 수는 대체로 부정적인 영향을 미쳤다.

하지만 그 영향은 둥지 주위의 침엽수 비율에 따라 다른 방향으로 나타나기도 했다. 이는 침엽수가 사람들에게 새들의 모습을 제한적으로 보이게 하여 새가 스트레스를 상대적으로 적게 받게 하는 역할을 했을 것이기 때문이다. 부정적인 영향과는 반대로 번식 극초기의 단계에서는 등산로가 긍정적인 역할을 할 수 있다.

정확한 기제는 이 연구에서 밝혀지지 않았으나, 가까운 등산로에서 새들의 인공 새집 사용 빈도수와 한배산란수가 증가한 것으로 나타났다.

대체적으로 전체 박새의 번식 성공은 등산로와 인공 새집 간의 거리와 통행 횟수, 통행 방법에 따른 구역과의 연관성은 유의미하게 나타나지 않았다. 하지만 존재하는 일부 약한 관련성은 박새가 지속적으로 서식지에 출입하는 사람들과의 공존에 이미 적응했거나 이 서식지에 방문하는 사람들이 야생동물의 공간을 침입하지 않았을 것으로 추정된다.

후속 연구에서 본 연구의 결과에 대한 구체적인 기제를 탐구할 필요성이 있으며, 한국과 아시아의 여러 도시 산림에서 다양한 연구가 이루어져 인간이 야생동물에게 미치는 영향을 지속적으로 연구하여 일반화 해야한다.

주요어: 박새, 등산로, 인위적 영향, 인공 새집, 번식 능력, 새끼 생존 특성, 둥지 선호도

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