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Nest Predation Pressure Differs Between Urban Ground- and Hole-Nesting Birds: Evidence from a Multi-Year Artificial Nest Predation Experiment

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Simple Summary: Some bird species avoid to live in cities, whereas some other species can even thrive in urban settings. One important factor influencing on occurrence, abundance, and success of birds living in cities is nest predation. Urbanization changes nest predator communities, and thereby also nesting success of many species. Hole-nesters and open-cup nesters might differ in vulnerability of nest predation. Because finding of suitable number of nests for statistical analyses, we conducted a multi-year artificial ground nest and nestbox study to analyze effects of urbanization on nest predation pressure. We found that ground nest predation increased with urbanization. In the city, ground nest predation was greater than nestbox predation, whereas nestbox predation was greater than ground nest predation in forests. Ground nest predation decreased with tree cover and increased with the patch area. Our results indicated that ground nesters might avoid urban areas as nesting sites. The results suggest that nest predation is one important factor that could explain, why hole-nesting bird species outnumbered ground-nesting species in cities. The result give support for the hypothesis that nest predation pressure can modify urban bird assemblage structure.

Abstract: Urbanization changes the environment through physical constructions, disturbances, and altered resource availability. These modifications influence both prey and predator assemblages. Several studies have indicated that hole-nesting birds outnumber ground nesters in cities. Differential nest predation can be one reason behind this observation. We conducted a multi-year artificial nest predation experiment along an urban gradient by using artificial ground nests and nestboxes in Rovaniemi, Finland. Because visually searching avian predators dominate in cities, we predicted that nest predation of ground nests will increase with urbanization, whereas nests in holes will be better protected than ground nests. Ground nest predation increased with urbanization, being lowest in forest and rural areas, intermediate in suburban area and highest in urban area. However, there was no year-effects on artificial ground nest predation, suggesting that even a single-year results of artificial nest predation experiment can be reliable. In the city, ground nest predation was greater than nestbox predation. In forests, nestbox predation was greater than ground nest predation. Among ground nests, predation was greater in the city than in forests. Among nestboxes, predation was greater in forest than in urban or suburban habitats. Only the ground nest predation was greater in managed than in un-managed parks. Ground nest predation decreased with tree cover and increased with the patch area. No variables were entered in the models of the nestboxes. The results indicated that ground nesters might avoid urban areas as nesting sites. We assume that visually searching avian predators benefit from the lack of covering vegetation in city parks. However, because most avian nest predators, like corvids, are not effective nest predators of hole-nesting birds, urban areas are safe nesting areas for hole-nesters. The results suggest

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that nest predation is one important factor that could explain, why hole-nesting bird species outnumbered ground-nesting species in cities. The result give support for the hypothesis that nest predation pressure can modify urban bird assemblage structure.

Keywords: avian; predator-prey interaction; urban bird assemblages; traits; urbanization

1. Introduction

Urbanization changes environments in many ways, and animals, like predators, react to these changes correspondingly [1,2]. Several mechanisms like food supplementation, lack of natural areas and their fragmentation, decreased vegetation complexity, human-caused disturbances, pollution, noise, artificial light, interspecific competition, and availability of safe nesting sites have been indicated to be important drivers influencing urban bird assemblage composition and breeding success of urban birds [1,3–5]. According to the review of Chace and Walsh (2006) [1], urbanization decreases avian richness, increases avian biomass, prefers omnivorous, granivorous, and hole-nesting way of avian life. Moreover, avian survivorship in cities is influenced e.g., by novel resources (e.g., food and nest boxes), risk of collision with buildings, road-related mortality, changes in the predator composition, food availability, and diseases [1]. Nest predation is one important factor among others determining bird community structure and breeding success [6–8]. Many studies have indicated that urbanization causes important changes on nest predator communities, and thereby on structure of urban bird assemblages [7–9].

In general, nest predation rate in cities can decrease due to the lack of natural predators (like snakes). Some studies have suggested that urban environments are predator-free areas with a low predation pressure due to the low abundance of many natural predators (safe zone hypothesis; predation relaxation or safe habitat hypothesis [10–14]. Correspondingly, it has been assumed that due to low numbers of predators, some bird species, especially synanthropic species, are extremely abundant in cities [15].

Rodewald et al. (2011) [16] introduced the urban nest predation paradox hypothesis, which suggest that that resource subsidies in urban landscapes would decouple predator–prey relationships, as predators switch from natural to anthropogenic foods. If there are lot of alternative and easily accessible food resources for the nest predators, then these predators do not necessarily predate nests so effectively. The loss of important nest predators in urban habitats and prey switching of urban predators are assumed to explain this urban nest predator paradox [17].

According to the credit card hypothesis, a high food abundance and a low predation risk may be behind extremely high urban bird population densities in cities [16,18]. Availability of subsidized food for nest predators can depress rates of nest predation in cities [16]. Indeed, daily survival rate and predator activity can often be decoupled [16]. Even if the reproductive success in cities might be low, the highly predictable and continuous input of food resources in cities allows some urban species to live on their credit [18]. In the lack of predation, the losers among the fledglings may survive for a relatively long period, getting just enough energy to survive even if the reproductive success in cities might be low [18]. However, some studies have indicated that nest predation increases with urbanization or is not at least lower in urban than in non-urban areas (e.g., [17,19–21]).

In general, the results related to nest losses caused by predators in cities are heterogeneous and partly contradictory, the results of different studies favoring different hypotheses [22]. For example, according to a recent meta-analysis of Vincze et al. (2017) [23], results conducted by artificial nests (e.g., nests baited with real or fake eggs) indicate an

increase in predation with urbanization, whereas natural nests (e.g., nests in tree cavities) indicate a decrease in predation with urbanization. However, the discrepancy between the results of artificial and natural nest studies may be due to differences in experimental methodology. In general, hole nests have been more commonly studied than open cup nests in natural nest studies, whereas most artificial nest studies are mainly considered open cup ground nests [23]. It is also possible that some of the variety in the results of previous urban gradient studies might be due the fact that different habitats and different length of gradient are used in analyses. Also, abundance of nest predators and their roles in predation differs between habitats [8,24]. During the last few decades, some important avian nest predators, like corvids, have increased their numbers in cities [25,26]. Cities have also some specific features, like roads, fragmented green areas, lowered tree cover, and high human population density which may also change prey-predator interactions [27]. Partly due the heterogeneity of urban habitats in relation to their predator communities and alternative food resources, several hypotheses have been introduced to explain the observed nest predation patterns in cities [22].

The loss of key nest predators or the addition of new ones in cities could alter the structure of urban bird assemblages. It has been suggested that urbanization filter birds on the basis of their ecological traits [28]. Several studies have indicated that hole-nesting birds outnumber ground nesters in cities, and that ground-nesting bird species are most negatively influenced by urbanization [1,7,29,30]. However, the drivers behind this observation is not well known. In general, urbanization changes vegetation structure and nest predator communities, both of which will impact on nest predation rate. Therefore, differential nest predation towards ground and hole nests might cause differences also for urban bird assemblage composition.

Artificial nests baited with real or fake eggs offer a standardized method to study nest predation risk with large sample sizes, controlled study methods, and reasonable time resources [19]. Most of the earlier artificial nest predation studies in cities have been based on data of single-year and ground nests. To our best knowledge, neither long-term artificial nests studies nor studies using simultaneously both ground nests and nests in holes/nestboxes have been earlier conducted in urban environments. The main aim of this study is to explore nest predation of ground and hole nests along an urban gradient across multiple years, what factors influence nest losses in cities, and if the same factors explain nest losses of both nest types.

We hypothesized that predation will differ between urban and non-urban areas as well as between ground nests and nestboxes. Because of the lower vegetation cover in cities than in forests, we predicted that open-cup ground nests in cities will suffer from greater predation pressure compared to forests. Nest success depends upon the parent's ability to place a nest in a site from where predators will not find it. Nest predators might use either vision (visual predators; like avian nest predators, like crows) or odors (olfactory predators; like many mammal and snake predators) to locate nests. It is noteworthy, that sometimes nest sites can be concealed from visual predators but can be at the same time vulnerable for olfactory predators [31]. Because visually searching avian predators, mainly corvids, dominate in cities, we predicted that species with less conspicuous nests sites (nests in holes) will suffer lower nest predation pressure than species with more visible nests (open-cup ground nests). Because nest predator communities in forests contains also many mammalian nest predators that are also able to predate nests in holes, we predicted that predation rate in nest boxes would be greater in forests than in urban areas.

2. Materials and Methods

2.1. Study Area

The study was conducted in Rovaniemi area, northern Finland (66°32′ N, 24°12′ E; Figure 1a), where the landscape is dominated by coniferous Scots pine (*Pinus sylvestris*) forests which are intermixed by different types of mires (Rovaniemi municipality 2024, Wikipedia 2024). Rovaniemi is located in the Köppen-Geiger Dfc (cold, without dry season, and cold summer) climate type [32], and in middle boreal vegetation zone [33] in northern Finland. Rovaniemi municipality has at the beginning of this study (1993) a total of 56,054 inhabitants, and at end year of the study (2019) 63,042 inhabitants (Statistics Finland 2024). Because of its large area cover (8016.75 km^2) of the municipality, the area is sparsely populated (during the year 2003: 7.4 inhabitants/km^2 and during the year 2019: 8.3 inhabitants/km^2 [34–36]). However, most of the inhabitants (53,361) in Rovaniemi live in a 59 km^2 urban area with a human population density of 905 inhabitants/km^2 [34,36].

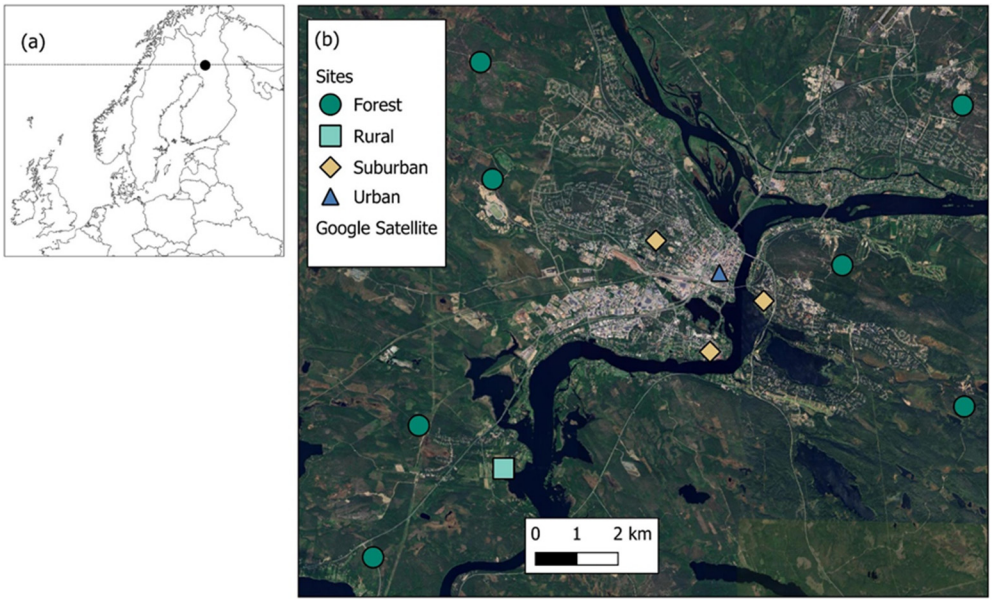


Figure 1. Location of the study city, Rovaniemi (black dot in the subfigure; a), and a satellite image of the study sites (**b**) (Map: Arto Vitikka, Arctic Centre. Satellite image by Google). Horizontal line in the subfigure (**a**) indicates the Arctic Circle.

Artificial nest predation experiments were conducted across an urban gradient (see defining of the urban gradient [37–39]) in urban and suburban areas of Rovaniemi as well as surrounding rural and forests areas of the city (Figure 1b). In this study, we used a classification and criteria proposed by Marzluff et al. (2001) [39] to separate urban, suburban, rural and forest (wild) areas when conducting an overall comparison in artificial ground nest predation in Rovaniemi study area. Human population density in urban site used in this study was 5717 inhabitants/km^2, and corresponding densities in suburban area was 1079, in rural area 120 and 0 in forest areas [40]. Based on a satellite map data (6 March 2024), built-up areas covered about 77% of the urban study site, whereas the corresponding values for the suburban, rural and forests areas were about 35%, 10%, and 0%. The size of the urban study area of the Rovaniemi is about 1.6 km^2, and it is dominated by high-rise buildings with 4–8 stories. The suburban study area is surrounding the urban area, and it is dominated by single-family house areas with their gardens. Parks in urban and suburban areas were mainly managed parks (92%; n = 25), whereas parks in suburban areas consists mainly unmanaged parks and woodlots (89%, n = 43). Managed parks have discontinuous tree and shrub cover, and they are continuously tended as regards lawn

mowing and shrub clipping by gardeners, whereas managed parks have more continuous tree cover, taller field layer vegetation [7]. Parks were surrounded by roads and buildings, and their range size was 0.25–11.5 ha. All parks are open for the public.

A special counting of nest box availability survey for the small-sized passerines, like the Blue Tit (*Cyanistes caeruleus*), the Great Tit (*Parus major*), the European Pied Flycatcher (*Ficedula hypoleuca*), and the Common Redstart (*Phoenicurus phoenicurus*) was conducted during the year 2023 during five-visit territory bird mapping project in urban and suburban study areas of Rovaniemi. The nest box density for the small-sized songbirds was about 30 boxes/km^2 in urban and 92 boxes/km^2 in suburban areas of Rovaniemi [41]. The rural study area is located about 7 km from the urban core area of Rovaniemi, and it consists of fields, separate houses and forests. The seven forest study sites are located between 2.6 and 11.2 km from the urban center of Rovaniemi, and are pine-dominated forests.

2.1.1. Ground- and Hole-Nesting Species

According to Jokimäki and Huhta (2002) [7], the abundance of ground nesting bird species is lower in urban than in suburban or forest areas, whereas no such habitat-related differences was found among hole nesting species in Rovaniemi area. In one study, only three ground nesting bird species (the Northern Wheatear [*Oenanthe oenanthe*], the Willow Warbler [*Phylloscopus trochilus*], and the Yellowhammer [*Emberiza citrinella*]) were detected to breed in urban and suburban parks in Rovaniemi [7]. In another study, Jokimäki et al. (2014) [42]) detected a total of 25 bird species, from which two were ground nesters (the Willow Warbler and the Yellowhammer) and five were hole-nesters (the Great Tit, the Blue Tit, the European Pied Flycatcher, the Great-spotted Woodpecker [*Dendrocopos major*], and the Tree Creeper [*Certhia familiaris*] in urban and suburban parks of Rovaniemi. According to the intensive forest bird surveys (161 point count stations surveyed yearly) conducted during the years 1990–1995 in Rovaniemi area, a total of 11 hole-nesting and 22 ground nesting bird species have been detected to breed in the surrounding forests of urban Rovaniemi (see methods and data [43]). A list of breeding ground- and hole-nesting species in Rovaniemi area, based on Jokimäki and Kaisanlahti-Jokimäki (2012) [44], is given in the Appendix A (Table A1). Only breeding land bird species (i.e., no gulls or duck species) in Rovaniemi area were included in this list. Information about species nesting sites (locations) were extracted from Chia et al. (2023) [45].

2.1.2. Nest Predators

The number of avian nest predator species varies between four and six in different habitats in Rovaniemi, whereas there are six common mammalian nest predators both in forest and rural habitats but only two in suburban and one in urban areas (Table 1). The Hooded Crow (*Corvus cornix*), the Eurasian Magpie (*Pica pica*), gulls (*Larus* spp.), the Great-spotted Woodpecker, and the red squirrel (*Sciurus vulgaris*) are the most important nest predators in urban and suburban areas of Rovaniemi [7,44]. Recently, also the Eurasian Jackdaw (*Corvus monedula*) has been included in the nest predator community in urban areas in Rovaniemi [45]. A large colony with 350 Black-headed Gull (*Larus ridibundus*) pairs and six Mew Gull (*Larus canus*) pairs breeds on a lake between the urban and suburban area of the Rovaniemi [44]. The red squirrel is the only important natural mammalian nest predator in urban areas of Rovaniemi. Leashed dogs accompanied by humans are quite common in parks of Rovaniemi, and practically no domestic cats (*Felis silvestris catus*) are roaming free in the wild in Rovaniemi area [7,45]. Only one snake species, adder (*Vipera berus*) distribution range reach Rovaniemi area, however it's abundance is very low.

Table 1. Potential natural nest predators in forest, rural, suburban and urban areas in Rovaniemi municipality. Information about the occurrence of potential nest predators in Rovaniemi study area were extracted from multiple sources: The Finnish Biodiversity Information Facility (all habitats; mammals & snakes [46]), Huhta et al., 1996 (forest habitats [24]), Jokimäki and Huhta 2000 (suburban and urban habitats [7]), Jokimäki et al., 2005 (urban and suburban habitats [8]) as well as author's unpublished data We also consulted some Finnish mammal and snake experts about the occurrence and abundance of potential mammalian [47] and snake nest predators [48] in Rovaniemi area. X = indicates that species occur commonly in the habitat; (X) = indicates that species can be sometimes detected in the habitat; - = indicates that species does not occur in the habitat. * = pairs/km^2 and ** = observations/km^2 based on author's own data from the year 2023 [41]).

Species	Forest	Rural	Suburban	Urban
Avian nest predators:				
Black-headed Gull *Larus ridibundus*	-	-	X	X
Black Woodpecker *Dryocopus major*	X	-	-	-
Eurasian Jackdaw *Corvus monedula*	-	-	2 *	17 *
Eurasian Jay *Garrulus glandarius*	X	X	-	-
Eurasian Magpie *Pica pica*	X	X	9 *	14 *
Eurasian Three-toed Woodpecker *Picoides tridactylus*	X	-	-	-
Great-spotted Woodpecker *Dendrocopos major*	X	X	2 *	<1 *
Hooded Crow *Corvus corone*	X	X	6 *	3 *
Mew Gull *Larus canus*	-	-	X	X
Raven *Corvus corax*	X	-	-	-
Siberian Jay *Perisoreus infaustus*	X	-	-	-
Mammalian nest predators:				
Pine marten *Martes martes*	X	X	-	-
Stoat *Mustella erminea*	X	X	(X)	-
Least weasel *Mustella nivalis*	X	X	(X)	-
Red fox *Vulpes vulpes*	X	X	-	-
Red squirrel *Sciurus vulgaris*	X	X	20 **	9 **
Brown rat *Rattus norvegicus*	-	-	(X)	-
Bank vole *Myodes glareolus*	X	X	X	-
Snake predators:				
Adder *Vipera berus*	X	X	(X)	-

2.2. Artificial Nest Predation Experiments

We used multiyear data collected during 1993 and 1996–1998 [7], 2001 [8], 2003 [49]), 2005 [50], 2009 [51], 2016 [52]; and and 2019 [53] (Table 2) to get a multiyear overview about the artificial ground nest predation. The use of older data from many different years helps to randomize the confounding effects of uncontrolled variables. Total numbers of artificial nests and their distributions in different habitats as well as overall predation rates are given in the Table 2.

The experimental study design and methods were basically similar during every study year. Artificial nests were established during the start of the main laying period of birds in Rovaniemi area, i.e., about during the second week of June, and nest fate was checked after two weeks of the establishment of nests. This two weeks' time period correspond for the incubation period of typical bird species in the study region. An artificial hole nest was a nestbox (Figure 2a; height 250 mm; wide 173 mm; entrance hole diameter 70 mm; without any predator-proofing). The 70 mm entrance hole enables red squirrels to entry into box, and sometimes squirrels also breed in these sizes of nest boxes (personal observations). An artificial ground nest placed under a tree or shrub was a hand- or foot-pushed small pit on the ground without any constructions (Figure 2b). Some grass or other vegetated material

was put both on the bottom of ground nest and on the nest box, and an egg was placed on nests. No special nest markings were used, instead a detailed description of the nest site was written down on the note book with GPS coordinates. A single egg (during 1993 two eggs) of the Japanese Quail (*Coturnix japonica*) was placed on each nest. Plasticine eggs were used during the years 1998 and 2003, whereas during the year 2019 either a plasticine and a quail eggs were used in specific nest. Only Quail eggs were used during the other study years. Plasticine eggs of Quail-sized were used to obtain information about predators responsible for predation.

Table 2. Artificial nest predation rates (%) with sample sizes (in parentheses) of ground and nest box nests during different study years in urban, center, suburban, rural and forest areas in Rovaniemi, Finland. * data from plasticine eggs, other data from Quail eggs.

Year	Urban	Suburban	Rural	Forest	Source *
(A) Ground nests					
1993	56 (16)	54 (19)		11 (18)	[7]
1996	84 (18)	6 (17)		4 (20)	[7]
1997	94 (17)	35 (7)			[7]
1998	79 (19) *	29 (24) *			[7]
2001	67 (25)	70 (30)			[8]
2003	92 (12) *	75 (16) *		20 (10) *	[49]
2005	90 (20)			5 (20)	[42,50]
2009	60 (10) *	40 (5) *	31 (16) *		[51]
2009	89 (9)	18 (6)	13 (16)	6 (32)	[51]
2016	80 (15)	17 (6)	7 (15)	6 (17)	[52]
2019	54 (13)	44 (27)		7 (15)	[53]
(B) Nest boxes					
2003	15 (13) *	46 (11) *		60 (10) *	[49]
2019	14 (7)	11 (19)		53 (15)	[53]

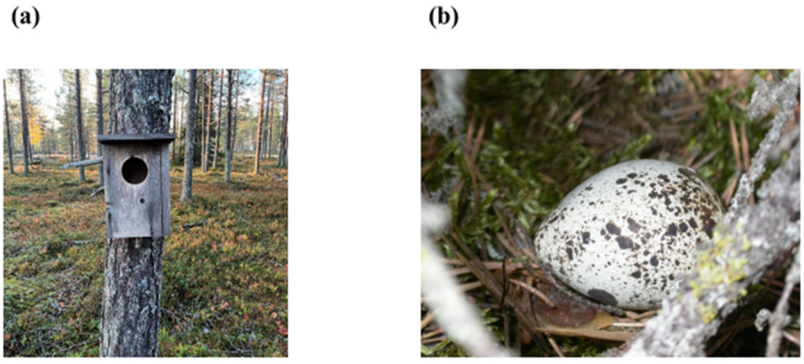


Figure 2. Examples of artificial nests: (**a**) nestbox in forest study site and (**b**) Quail egg in ground nest located in unmanaged urban park.

A nest with Quail egg was scored as predated if the egg disappeared or was broken. A nest with a plasticine egg was scored as predated if the egg was disappeared or if the egg has any marks of predators. If the plasticine egg had bill marks, the nest was scored as predated by avian predators, and if the egg had teeth marks, the nest was scored as predated by mammalian predators. Some nest loss events were scored as human-induced e.g., due to the grass-cutting or vandalism towards nestbox.

We used a paired study design where a ground and a nestbox nests were established in the same site (either urban and suburban park or forest) to compare artificial nest predation nests between urban or suburban and forest areas during the years 2003 and 2019. One ground nest and one nestbox was placed in a single urban or suburban park. In seven

forest study areas (Figure 1b), we correspondingly established an average 3.43 (range 1–8) ground nest and nestbox pairs per specific forest tract. The distance between nest pair in specific forest tract was at least 100 m.

In the paired study (with data of the years 2003 and 2019), a nest box was erected on the tree at the breast height, and a ground nest was established under the nearest shrub or small-sized tree (<5 m), normally about 10–15 m from the nest box. For the paired comparison of ground nests and nestboxes conducted during 2003 and 2019, we used human population density (people per 250 m × 250 m grid; Rovaniemi municipality 2023) around each nest as an estimate of urbanization level. Correspondingly, nest distance to the nearest road and trail, patch area (ha) and tree cover (within a 50 m radius circle around the nest) was measured by using satellite images. Number of dogs, cats, red squirrels, avian nest predators per species, and number of human visitors were estimated around each nest (<50 m) site by a single-visit five-minute survey conducted during the midday during the checking of the nest fate.

2.3. Statistical Methods

2.3.1. Long-Term Artificial Ground Nest Predation

To get a general overview about the influence of habitat type and study year on the ground nest predation across urban gradient, we run a Binary Logistic Regression by using ground nests with Quail eggs by using data of all study years. In this analysis by using a Forward (Wald) method, nest fate after 14 days exposure (0 = saved; 1 = predated) was set as dependent variable, and habitat type (0 = forest; 1 = rural; 2 = suburban or 3 = urban), study year as well as the interaction of habitat type x study year were set as predictors.

2.3.2. Data of Ground Nests and Nestboxes Collected During the Years 2003 and 2019

More detailed statistical tests were conducted by using a paired ground nest and nestbox data collected during the year 2003 (plasticine eggs used) and 2019 (quail eggs used). Because it possible that the paired ground nest and nestbox are not predated independently, we performed firstly the Durbin-Watson test to analyze if there is autocorrelation about predation rate. In this analysis, predation rate was a dependent variable and site ID (a paired ground nest and nestbox site) as independent variable. The Durbin-Watson test statistic will receive values between 0 and 4, and values between 1.5 and 2.5 will indicate that there is no serious autocorrelation. In our case, the test statistic value was 1.96, i.e., the paired ground and box nests in individual sites were predated independently from each other's. Thereafter we run we run a Binary Logistic Regression by using data of paired ground nests and boxnests collected during the years 2003 and 2019. In this analysis, nest fate after 14 days exposure (0 = saved; 1 = predated) was set as dependent variable, and nest type (0 = ground nest; 1 = nestbox), location (0 = forest; 1 = urban and suburban), egg type (0 = Quail egg [year 2019]; 1 = plasticine egg [year 2003]), number of visitors, dogs, squirrels and avian predators were set as predictors. In addition, all 2-way and 3-way interactions of nest type, location and egg type were included as predictors. Significance of variables was evaluated by using Wald's χ^2 statistic.

A forward stepwise logistic regression analysis and Wald χ^2 statistic were used to study the effects of human population density, patch area, distance to roads, distance to trails, tree cover, number of dogs, number of red squirrels, number of avian nest predators (all species pooled), and number of human visitors on predation rate in urban area (urban and suburban data pooled) on nest fate. In addition, Pearson χ^2 and Fisher's Exact tests were used in some comparisons, e.g., to analyze impacts of park management status on nest predation rate. All statistical analyses were conducted by using the IBM SPSS Statistical Programme (ver. 28.0.0.0 [54]).

3. Results

3.1. Influence of Habitat Type and Study Year on Ground Nest (With Quail Eggs) Predation Along an Urban Gradient

According to the Binary Logistic Regression analysis, habitat type influences on nest fate (β = 1.33, *SE* = 0.14, Wald χ^2 = 92.21, $p < 0.001$). Nest predation rate was higher in urban than in other three habitats, and higher in suburban than in rural and forest habitats (Figure 3). Neither the study year nor interaction between habitat x study year influences on nest predation.

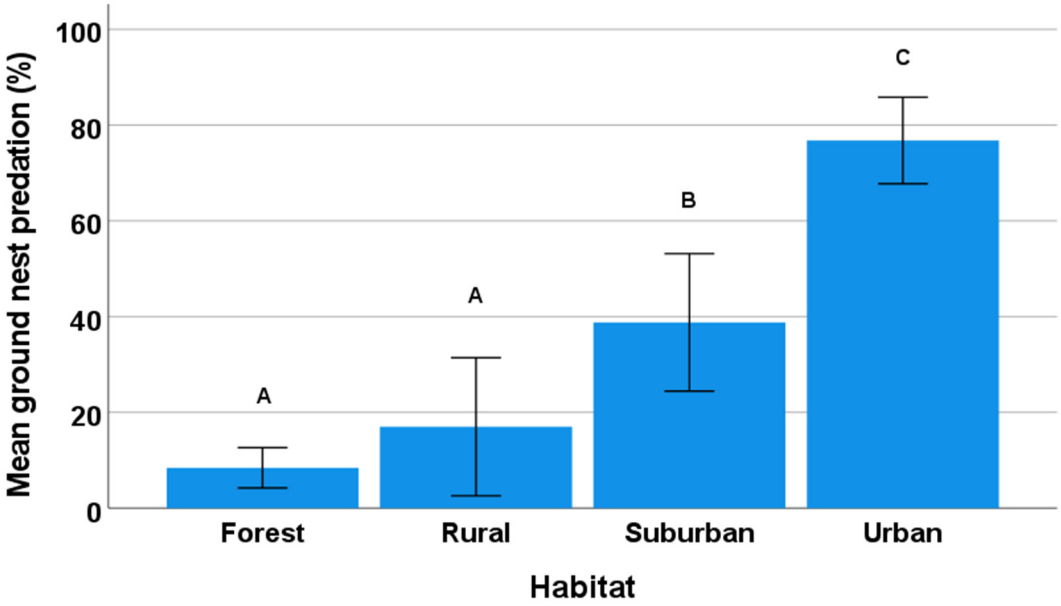


Figure 3. Artificial ground nest predation rate (Quail eggs; mean % ± 2*SE*) differences in forest (n = 122 nests; 7 study years), rural (n = 21 nests; 3 study years), suburban (n = 176 nests; 10 study years) and urban (n = 133 nests; 11 study years) habitats in Rovaniemi (χ^2 = 138.46, df = 3, $p < 0.001$). A Bonferroni adjustment was used for the post hoc pairwise comparisons, different letters indicate differences between groups at $p < 0.05$ level.

3.2. Nest Predation Rate Between Ground Nests and Nestboxes During 2003 and 2019

According to the Logistic Regression Analysis, nest predation rate differs between ground nests and nestboxes (β = 2.78, *SE* = 1.56, Wald χ^2 = 5.75, p = 0.017), being greater in ground nests (44.7%, n = 76) than in nestboxes (31.6%, n = 76). Also, the interaction term nest type x location was significant (β = −4.00, *SE* = 1.41, Wald χ^2 = 8.12, p = 0.004), indicating that location influences predation rates of ground nests and nestboxes differentially (Figure 4). In forest, predation rate in nestboxes (56.0%, n = 25) was higher than in ground nests (12.0%, n = 25), whereas in urban areas, predation in ground nests (60.8%, n = 51) was higher than in nestboxes (19.6%, n = 51). However, egg type (study year), and all variables related to predators and human visitors were insignificant.

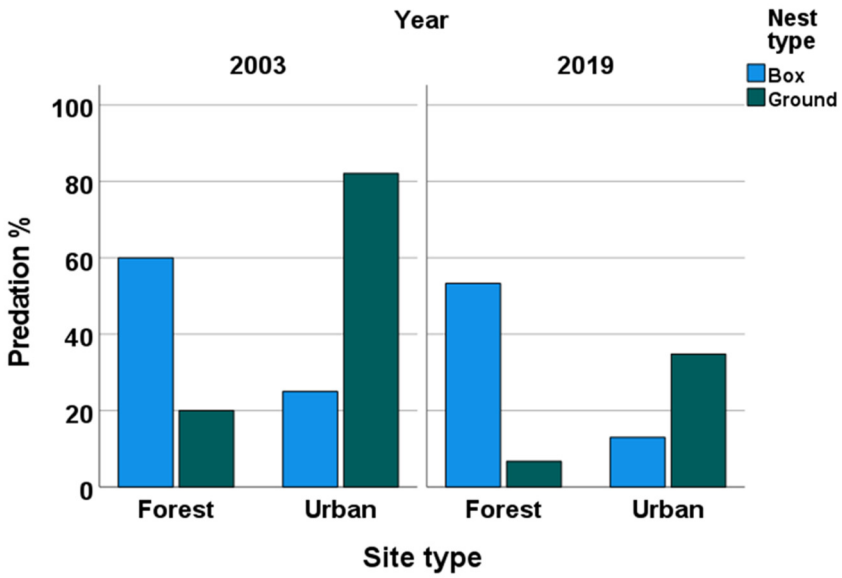


Figure 4. Nest predation rate (%) in nestboxes and ground nests during the year 2003 (plasticine eggs used; n = 10 in forests; n = 28 in urban areas; both in nestboxes and ground nests) and 2019 (Quail eggs used; n = 15 in forests; n = 23 in urban areas; both in nestboxes and ground nests) in Rovaniemi.

3.3. Factor Influencing on Nest Predation Rate in a Pooled Sample of Urban and Suburban Areas

3.3.1. Impacts of Park Management Status

Based on a pooled urban and suburban sample data from the years 2003 and 2019, ground nests located in managed parks suffered from greater nest predation rate (74.1%, n = 37) than nests located in non-managed parks (45.8%, n = 24, Pearson χ^2 = 4.25, p = 0.039). Correspondingly, park management status did not influence on nest predation rate in nestboxes (nest predation rate 25.9% in managed parks [n = 27], 12.5% in non-managed parks [n = 24]; Fisher's Exact test, p = 0.300).

3.3.2. Park-Specific Factors and Nest Predation

According to the Stepwise (forward) Logistic Regression Analysis by using a pooled urban and suburban sample data from the year 2003, ground nest predation decreased with tree cover (β = −8.339, SE = 3.217 Wald χ^2 = 6.72, p = 0.010). Correspondingly, according to the data from the year 2019, ground nest predation increased with the patch area (β = 0.231, SE = 0.152, Wald χ^2 = 2.31, p = 0.129). No variables were entered in the models of the nestboxes.

3.4. Causes of Nest Fates

Causes of nest fates of plasticine eggs (year 2003) were possible to identify from 27 nests in urban area (including suburban area), and only from seven nests in forest areas (Table 3). In general, avian nest predators dominated in both habitats and in both nest types, expect than nestboxes in forests were mammalian predator dominated. In urban area, four of the total nine avian predation events were caused by the Eurasian Magpie. The red squirrel was responsible predator for the one nest fate in nest boxes, both in urban and forest sites. No marks caused by rats, voles or mices were detected in any plasticine eggs. In urban area, humans destroyed 10% of artificial ground nests. A great amount of eggs (12) were also disappeared from the nests. However, small sample sizes hinder to do further statistical comparisons.

Table 3. Reasons of the artificial ground and nest box nest fates in urban and rural areas in Rovaniemi, Finland, based on the plasticine egg data from the year 2003.

	Avian	Mammal	Human	Disappeared	Total
Ground nests:					
Urban	9 (45.00 %)	1 (5.00 %)	2 (10.00 %)	8 (40.00 %)	20
Forests	1 (50.00 %)	0	0	1 (50.00 %)	2
Nest box nests:					
Urban	3 (42.86 %)	2 (28.57 %)	0	2 (28.57 %)	7
Forests	1 (20.00%)	3 (60.00%)	0	1 (20.00 %)	5

4. Discussion

The results indicated that ground nest predation increases with urbanization, predation being highest in urban area, intermediate in suburban area, and lowest in rural or forest areas. According to pooled urban and suburban data, ground nest predation rate was higher than nestbox predation, whereas in forests, nestbox predation rate was higher than ground nest predation. Among ground nests, predation rate was higher in combined urban and suburban data than in forest data, whereas opposite results were observed among nestboxes. Ground nests located in managed parks suffered from higher nest predation rate than nests located in non-managed parks, whereas management status did not influence nest predation rate in nestboxes. Depending on the study year, ground nest predation in urban and suburban areas either decreased with tree cover or increased with the patch area. No variables were entered in the models of the nestboxes. Most of the ground nests in urban area were predated by avian nest predators.

4.1. Artificial Ground Nest and Nestbox Predation: Role of Different Predators

The multi-year results of this study indicated that ground nest predation rate increased with urbanization, and therefore the results do not support the predation relaxation hypothesis [12–14]. Especially ground nests located in managed parks in Rovaniemi were vulnerable for predation. The results of this study indicated that predation of ground nests decreased with increasing tree cover, and most of the artificial ground nests were predated by avian predators. Many generalist avian nest predators, like corvids and gulls, have increased their numbers in many cities during the last few decades [25,55–57], and especially corvids have been reported to be important nest predators in human-dominated landscapes [7,58]. For example, Sorace and Gustin (2009) [59] have earlier reported the role of generalist predators (like the Eurasian Magpie) over specialist predators. A low vegetation cover in managed city parks may increase the searching efficiency of visually searching avian nest predators, like corvids, and thereby predation towards open cup ground nests [7].

According to the video-study by Rodewald and Kerns (2011) [60], mesopredators, like domestic cats, are important in urban landscapes, accounting for 35% of urban nest predation (see also [17]). However, there are no free-living cats in the city of Rovaniemi, partly because of the hard winter season conditions in the north make cats unable to survive across the winter. It is also noteworthy that there are many restrictions that hinders to keep cats free in Finland. Therefore, the role of cats as nest predator is very minimal, if any, in Rovaniemi area. Some studies have highlighted the important role of snakes as nest predators (e.g., [61]), even in urban areas [62]. However, only one snake species, the adder occurs in Rovaniemi area, and its' abundance in a study region is very low. and moreover, the species is practically absent from urban and suburban areas of Rovaniemi. We assume that due to the high road mortality (see e.g., [63]), ground dwelling mammalian or snake predators can seldom be important nest predators in cities. However, some

ground dwelling mammalian predators could be important in some urban areas. Foxes are numerous in some European cities and domesticated mammals, such as dogs and cats could be important predators in some urban areas. Malpass et al. (2018) [64] found similar rates of nest survival in the forest parks and residential neighborhoods Ohio metropolitan area (USA) for two passerine bird species, but interactions between predators and prey differed. In particular, domestic cats were over five times as likely to depredate cardinal nests in matrix habitats versus forest parks [65]. Also, in some other areas, small mammals, such as the rats, mices, and voles, have beeen involved in predation of bird nests especially in urbanized areas [66,67]. However, we did not detect any marks in plasticine eggs caused by rats, voles or mices, but two nestboxes were predated by the red squirrel.

According to Sorace and Gustin (2009) [59], different predator species respond differently to urbanization (e.g., the Eurasian Jackdaw prefers the most urbanized areas), and their responses might be dependent on the urbanization level of the individual city. In Rovaniemi, based on the abundance differences [41], the Eurasian Jackdaw and the Eurasian Magpie are the dominant nest predators in urban areas, the Hooded Crow is probably a more important predator in suburban area, whereas gulls can predate nest all over urban/suburban Rovaniemi. We assume that due to fragmentation of green areas and low vegetation cover in cities, visually searching avian nest predators can easily locate open-cup ground nests; i.e., their searching efficiency is greater in cities than in more natural areas (see also [2]).

Our results from one study year (2019) indicated that ground nest predation rate increased with the patch area in the city of Rovaniemi. This result differed from the results obtained from other types of habitats and areas, which have indicated that nest predation increases with fragmentation, and in greater in smaller than in larger patches as well as in edge than in interior areas (e.g., [24,67]), but partly correspond for the results obtained from urban areas. For example, Matthews et al. (1999) [68] indicated that nest predation was not related to patch size and distance edge in urban study conducted in Australia (see also [69]). We suppose that predators may direct their search in cities towards larger patches from where they can possible find more food, in our case nests. However, the response of nest predators to fragmentation is complex, taxon-specific, and context-dependent [70]. Indeed, nest predation rate in nest boxes was much lower than in ground nests in the city of Rovaniemi. Therefore, urbanization impacts differentially for species with different nest type.

Moreover, nest predation rate in nestboxes located in city was lower than in nestboxes located in surrounding forest areas. One obvious reason for this observation is that nest predator community able to predate nests in cavities/boxes are more diverse in forests than urban areas. For example, there are many woodpecker species in forest that do not occur at all, or at least are much rarer, in urban areas of Rovaniemi. Also, mammals have been reported to be important nestbox predators [71], and especially the pine marten, a species lacking from cities, can be very effective predator of nest boxes [72].

Therefore, unlike for the ground nests, urban areas can be safe nesting areas for the hole-nesting bird species. One obvious reason for this is that the main nest predators, corvids, are unable to predate the nests in nest boxes with small-sized nest entrance. Despite that we used quite a large entrance hole (70 mm) that able e.g., red squirrels (pers. observation), and probably also Eurasian Magpie, to get in boxes, nest predation rate was still low even these boxes in the city. This observation gives at least partly support for the urban nest predation paradox hypothesis [16]. These results suggested that urban nestboxes are safe from large-sized avian nest predators, like corvids. One potential nest predator group of nest boxes are woodpeckers, which are able to enlarge nest entrance hole, and have thereby also access in nest boxes with small entrance holes (e.g., [73,74]).

The only woodpecker species occurring in urban and suburban areas of Rovaniemi is the Great-spotted Woodpecker, which is still rare in the city (pers. observation). In addition, the use of predator-proofed nest boxes can decrease nest predation of nest boxes caused by woodpecker species [75]. Also, the mammalian nest predator assemblage able to predate nest boxes is very simple, consisting only the red squirrel, in Rovaniemi. Therefore, the nest predation losses in nest boxes is low in Rovaniemi. Based on our anecdotal field observations, we assume that human disturbance can be one important reason impacting on nest losses in the city parks. We have several observations about people inspecting nest boxes just of pure self-interest. Unfortunately, the data about the role of different predators were to scare for more detailed statistical analyses.

It is possible that there are differences in visibility of ground nests located in forest and urban study sites as well as nest located on the ground and nest boxes on tree trunks. If such differences exist, that will obviously influence predation efficiency of visually searching avian nest predators. Unfortunately, the current data do not enable to study this topic. However, we have found in our earlier studies that a high field layer of vegetation decreased the frequency of nest loss in urban areas, and experimentally covered nests were preyed upon less frequently than uncovered and control nests [7]. In general, managed parks were characterized by inadequate shrub and tree layers and a poorly-developed field layer. This in turn increased the visibility of open ground nests to visually-searching avian nest predators, and enhanced nest predation risk in managed parks relative to unmanaged park [7]. We have also indicated earlier in an urban gradient study that the risk of ground nest predation increased with the visibility in Finland, Italy and Spain [8].

In general, nest exposure for the predator is an import factor influencing on nest losses; the predator should obviously be able to spot nests from some vantage point. However, according to Ibáñez–Álamo et al. (2015) [76], there is only little knowledge of nest predator foraging habits and the mechanisms of locating nests. In practice, nest predators may use multiple variety of predator-specific strategies and cues, e.g., visibility, acoustic cues as well as olfaction to find nests. All of these factors may at least partly explain the differences in the ability to spot ground nests and holes. In addition, the conspicuousness of the nests itself or the colors of the eggs may also attract the attention of visually searching nest predators. Moreover, Grégoire et al. (2003) [77] have highlighted that nest characteristics might influence both on nest exposure and predation, and Cresswell (1997) [78] has indicated that nest vulnerability to predation depends on a combination of nest type and visibility. More research is needed to understand these mechanisms more detailed also in urban settings.

4.2. Urban Nest Predation and Bird Assemblages

We founded that ground nests suffered greater nest predation pressure than nestboxes in surburban and urban areas of Rovaniemi. We assume that this will impact also on the structure of the urban breeding bird assemblage. Earlier studies conducted in Rovaniemi area have indicated that urbanization benefits a hole-nesting behavior of birds over ground nesting (e.g., [7,42]). Based on these studies, only three ground nesting bird species, and no one of these species are very common or abundant. However, many hole-nesting species, are both common and abundant breeders in urban and suburban parks of Rovaniemi. All of these hole-nesting species are small in size, and prefer to use nest boxes with small entrance hole (28–32 mm), and thereby inaccessible for the large-sized avian nest predators. Also, predatory relaxation is obviously behind the worldwide success of the two urban exploiters, the House Sparrow (*Passer domesticus*) and the Rock Dove (*Columba livia*), both of which are hole-nesters using also holes in buildings [12]. However, during the last decades, the numbers of House Sparrow has declined heavily in many regions; one reason for the decline can be a decrease of suitable nesting sites [79].

Our results indicate open-cup ground nesting bird species might avoid urban habitants. Although Bonnington et al. (2015) [80] did not find clear support that the Eurasian Blackbird (*Turdus merula*) is sensitive to nest predation, they found some supports that nests located near the corvids and in areas with higher corvid activity had greater nest predation rate in Sheffield, UK. Based on the study conducted in Ohio, USA, Leston and Rodewald (2006) [81] even indicated that urban forests can act as an ecological trap for understory bird, the Northern Cardinal (*Cardinalis cardinalis*). Moreover, urban songbirds' response for the predators can be scale- and site-depended [82]. For example, Marzluff et al. (2007) [82] reported that at the smallest, patch-level scale, some bird species avoided areas with greater predator use, and failed nests were located of higher corvids occurrence than successful nests. We assume that nest predation pressure in any landscape depends on local predator assemblage (see e.g., [8,24]), and the relative impact impacts of predators on different nest types will vary correspondingly (see also [9]).

However, it is good to notice that it is possible that breeding season losses don't always influence overall population trends and therefore overall community composition [83,84]. Sometimes losses at other life history stages can be more likely to drive population trends. For example, it could be that increases in nest predation result in compensatory declines in other causes of mortality.

4.3. Study Limitations

We used artificial nests to study impacts of urbanization on nest losses. However, the results of artificial nests might differ from the natural nests [23,85]. For example, it is not sure if artificial nests are sufficient to evaluate natural nest predation rate, e.g., due to lack of parental care and nestling activity in artificial nests and the relatively large size of quail or hen eggs that are normally used in artificial nest experiments (e.g., [85]).

Also, studies have indicated that plasticine eggs can attract particular nest predators and that small mammals are more able to predate plasticine eggs than real eggs [86]. Indeed, we observed a greater predation pressure when we used plasticine eggs during the year 2003 than when we used Quail eggs during the year 2019, but we were not able to link the results for the mammalian predators due to the limited sample sizes.

Several studies have indicated that nest box nests have a lower predation risk than nests located in natural nest holes [73,87]; but see [88]), even in urban environments [85–89]. Because the nest predator assemblages differ between areas, e.g., there are no wild cats or snakes in urban Rovaniemi, the results of this study are not applicable e.g., for tropical areas with a more diverse nest predator assemblage. Also, the behaviour and strategies of the species using the two nest types differs, and this will not be necessarily evidenced in the artificial nest situation.

However, as compared for the natural nests, artificial nests can be used to collect data in a standard way, with fixed nest location types in different habitats [19]. According to the literature meta-analysis, results conducted by artificial nests (indicating increases in predation with urbanization) and natural nests (indicating decreases in predation with urbanization) might differ partly due to the differences in experimental design because hole nests have been more commonly used in natural nest studies than in artificial nest studies [23].

We used plasticine eggs to identify causes of nest predation events. However, camera traps or time-lapse video recording might give a more detailed information about predators of the nests [85,90] However, in urban environments, with lot of people and sparse vegetation cover, this option is practically non-reasonable because valuable cameras can be easily stolen or at least there can be vandalism towards cameras.

Our study was conducted in an urban area where mesocarnivores are practically absent. However, in some other areas, mesocarnivores (e.g., northern raccoons [*Procyon lotor*]) can be at least as important nest predators in cities as corvids (e.g., corvids; e.g., [60,91]. It is noteworthy, that two important nest predators, the red fox and the pine marten, have not yet urbanized in our study area despite that e.g., the red fox have been common in the Finnish periurban areas for a long time [92]. Therefore, our results are not fully applicable for all areas. However, many mesopredators have recently urbanized also in Finland. For example, the numbers of invasive raccoon dogs (*Nyctereutes procyonoides*) have increased heavily in Europe, and especially in Finland, during the last decades [93]. Because raccoon dogs are highly plastic both in their habitat and food use, racoon dog numbers will increase at least in suburban areas, and their predation towards urban birds' nests will correspondingly increase [93].

Our study was conducted only during a short (2 weeks) period during the main egg laying and hatching period. Therefore, the results underestimate the total nest predation rate because nests are predated also both during the nestling and fledgling periods. Also, other factors (e.g., poor weather conditions, lack of food) than nest predation influences on breeding success of birds [1,94], and nests are destroyed due the other reasons than only nest predation. For example, the main nest loss cause of the Common Redstart nesting in nest boxes in Rovaniemi forest areas was nest rejection (about 15.79% of the nest data from 2010–2019 [95]. Solonen (2001) [96] has indicated that the fledgling production of nest box nesting tits calculated per egg laid, per breeding attempt, or per successful nesting was lower in the urban populations than in the rural ones. These results highlighted the importance to study the whole nesting period instead of conducting the study only e.g., during the incubation period. According to review about avian productivity in urban landscapes, paucity of natural food in cities may lead to overall lower productivity per nesting attempt ([3], but see [92–95]). Solonen (2001) [96] has suggested that the poor quality of food before the breeding season in urban habitat's is at least partly responsible for the small clutch size of tits in cities.

The method used to assess predators near the nest (one five-minute survey per nest) could have influenced the predators observed. During midday, avian predators may be more likely to be active than some mammalian predators, and thereby our abundance estimates of mammals is an underestimation.

5. Conclusions

The results of this study indicated that nest predation pressure differentially influences urban ground- and hole-nesting birds, with ground nests suffering greater losses than nests in nestboxes. However, there are also other reasons than nest predation pressure why hole-nesters outnumber open-cup ground nesters in cities. For example, lack of green areas, inadequate tree cover and green area management are disadvantageous for ground nesting species. However, despite of lack of natural nesting sites in cities, large amount of nest boxes in private gardens and parks will benefit many secondary hole-nesters, and crevices in buildings are used by many kinds of hole-nesters [97]. However, human-provided nest sites will be beneficial mainly for secondary hole-nesters [94–97]. von Haartman (1968) [98] has indicated that there is severe competition for holes, and there is a high premium on choosing the nest-hole as early as possible. Therefore, it is not surprising that many urban bird species are resident hole-nesters [29,42,99].

To increase nesting facilities and success of ground nesting species in cities, preserving covering vegetation and reducing the intensity of management activities might be helpful. To increase nesting facilities and success hole-nesting species, erecting different types and sizes predation-proof nest boxes on trees will be a good management option [75]. To avoid human-caused disturbance, it would be good to erect nest boxes at sufficient height in

urban parks. However, saving large-sized old trees (snags) is detrimental to help nesting of primary hole-nesters.

In the future, it would be interesting to study, what happens for the avian bird assemblage structure, when new nest predator species colonize cities, and old nest predators increase their abundances in cities. We assume that due to the recent urbanization of the red fox [91] and the raccoon dog [93,100,101], nest predation rate of the ground nesters will increase also in urban areas in Finland. On the other hand, Jokimäki et al. (2017) [102] have indicated that red squirrel winter season abundance is approximately twice as high in urban habitats than in forests. Therefore, we assume that increase of squirrels in Finnish cities will also increase predation rate of birds nesting in holes.

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Appendix A

Table A1. A complete list of breeding ground- and hole-nesting species in forest, rural, suburban and urban areas in Rovaniemi area based on Jokimäki and Kaisanlahti-Jokimäki (2012) [44]. Notice that only breeding land bird species (i.e., no gull or duck species) in Rovaniemi areas were included in this list. Nest site locations are based on Chia et al. (2023) [45]. X = indicates common species; (X) = indicates occasional breeding species.

Species	Forest	Rural	Suburban	Urban
Ground nesters:				
Northern Hazel Grouse *Tetrastes bonasia*	X	-	-	-
Willow Grouse *Lagopus lagopus*	X	-	-	-
Eurasian Black Grouse *Lyrurus tetrix*	X	-	-	-
Western Capercaillie *Tetrao urogallus*	X	-	-	-
Common Pheasant *Phasianus colchicus*	-	X	X	-
Little Ringed Plover *Charadrius dubius*	-	X	X	-
Common Ringed Plover *Charadrius hiaticula*	-	X	-	-
Eurasian Golden Plover *Pluvialis apricaria*	-	X	-	-
Northern Lapwing *Vanellus vanellus*	-	X	-	-
Common Snipe *Gallinago gallinago*	-	X	-	-
Eurasian Woodcock *Scolopax rusticola*	X	X	X	-
Whimbrel *Numenius phaeopus*	-	X	-	-

Table A1. *Cont.*

Species	Forest	Rural	Suburban	Urban
Eurasian Curlew *Numenius arquata*	-	X	-	-
Common Redshank *Tringa totanus*	-	X	(X)	-
Common Greenshank *Tringa nebularia*	-	X	-	-
Green Sandpiper *Tringa ochropus*	X	X	-	-
Wood Sandpiper *Tringa glareola*	-	X	-	-
Common Sandpiper *Actitis hypoleucos*	-	X	(X)	(X)
Short-eared Owl *Asio flammeus*	-	X	-	-
Eurasian Sky Lark *Alauda arvensis*	-	X	-	-
Tree Pipit *Anthus trivialis*	X	-	-	-
Meadow Pipit *Anthus pratensis*	-	X	-	-
Yellow Wagtail *Motacilla flava*	-	X	-	-
White Wagtail *Motacilla alba*	-	X	X	X
Wood Warbler *Rhadina sibilatrix*	X	-	X	-
Common Chiffchaff *Phylloscopus collybita*	X	-	-	-
Yellowhammer *Emberiza citrInella*	X	X	X	-
Rustic Bunting *Schoeniclus rusticus*	X	-	-	-
Eurasian Reed Bunting *Schoeniclus schoeniclus*	-	X	X	-
Hole-nesters (including both primary and secondary hole-nesters):				
Common Kestrel *Falco tinnunculus*	X	X	-	-
Rock Dove *Columba livia*	-	-	X	X
Hawk-Owl *Surnia ulula*	X	(X)	-	-
Eurasian Pygmy Owl *Glaucidium passerinum*	X	(X)	-	-
Tengmalm's Owl *Aegolius funereus*	X	X	-	-
Common Swift *Apus apus*	X	-	-	X
Northern Wryneck *Jynx torquilla*	X	X	-	-
Black Woodpecker *Dryocopus martius*	X	-	-	-
Great Spotted Woodpecker *Dendrocopos major*	-	X	X	X
Eurasian Three-toed Woodpecker *Picoides tridactylus*	X	-	-	-
Common Redstart *Phoenicurus phoenicurus*	X	X	X	X
Spotted Flycatcher *Muscicapa striata*	X	X	X	X
European Pied Flycatcher *Ficedula hypoleuca*	X	X	X	X
Willow Tit *Poecile montanus*	X	X	X	-
Siberian Tit *Poecile cinctus*	X	-	-	-
Crested Tit *Lophophanes cristatus*	X	-	-	-
Coal Tit *Periparus ater*	X	-	-	-
Blue Tit *Cyanistes caeruleus*	(X)	X	X	X
Great Tit *Parus major*	X	X	X	X
Eurasian Treecreeper *Certhia familiaris*	X	-	-	-
Eurasian Jackdaw *Corvus monedula*	-	-	(X)	-
House Sparrow *Passer domesticus*	-	X	X	X
Eurasian Tree Sparrow *Passer montanus*	-	X	X	(X)

References

1. Chace, J.F.; Walsh, J.J. Urban effects on native avifauna: A review. *Landsc. Urban Plan.* **2006**, *74*, 46–69. [CrossRef]
2. Fleming, P.A.; Bateman, P.W. Novel predation opportunities in anthropogenic landscapes. *Anim. Behav.* **2018**, *138*, 145–155. [CrossRef]
3. Chamberlain, D.E.; Cannon, A.R.; Toms, M.P.; Leech, D.I.; Hatchwell, B.J.; Gaston, K.J. Avian productivity in urban landscapes: A review and meta-analysis. *Ibis* **2009**, *151*, 1–18. [CrossRef]
4. Reynolds, J.S.; Ibáñez-Álamo, J.D.; Sumasgutner, P.; Mainwaring, M.C. Urbanisation and nest building in birds: A review of threats and opportunities. *J. Ornithol.* **2019**, *160*, 841–860. [CrossRef]
5. Marzluff, J.M. Worldwide urbanization and its effects on birds. In *Avian Ecology and Conservation in an Urbanizing World*; Marzluff, J.M., Bowman, R., Donelly, R., Eds.; Kluwer Acadamic Publishers: Boston, MA, USA, 2001; pp. 19–47.

6. Osborne, P.; Osborne, L. The contribution of nest site characteristics to breeding-success among blackbirds Turdus merula. *Ibis* **1980**, *122*, 512–517. [CrossRef]
7. Jokimäki, J.; Huhta, E. Artificial nest predation and abundance of birds along an urban gradient. *Condor* **2000**, *102*, 838–847. [CrossRef]
8. Jokimäki, J.; Kaisanlahti-Jokimäki, M.L.; Sorace, A.; Fernández-Juricic, E.; Rodriguez-Prieto, I.; Jimenez, M.D. Evaluation of the "safe nesting zone" hypothesis across an urban gradient: A multi-scale study. *Ecography* **2005**, *28*, 59–70. [CrossRef]
9. Stracey, C.M.; Robinson, S.K. Does nest predation shape urban bird communities? In *Urban Bird Ecology and Conservation*; Lepczyk, C.A., Warren, P.S., Eds.; Studies in Avian Biology; University of California Press: Oakland, CA, USA, 2012; pp. 49–70.
10. Tomiałojc, L. The influence of predators on breeding Woodpigeons in London parks. *Bird Study* **1978**, *25*, 2–10. [CrossRef]
11. Tomiałojc, L. Synurbanization of birds and prey–predators relations. In *Animals in Urban Environments*; Luniak, M., Pisarski, B., Eds.; Ossolineum: Wrocław, Poland, 1982; pp. 131–137.
12. Gering, J.; Blair, R. Predation on artificial bird nests along an urban gradient: Predatory risk or relaxation in urban environments? *Ecography* **1999**, *22*, 532–541. [CrossRef]
13. Kosinski, Z. Effects of urbanization on nest site selection and nesting success of the greenfinch *Carduelis chloris* in Krotoszyn, Poland. *Ornis Fenn.* **2001**, *78*, 175–183.
14. Eötvös, C.B.; Magura, T.; Lövei, G.L. A meta–analysis indicates reduced predation pressure with increasing urbanization. *Landsc. Urban Plan.* **2018**, *180*, 54–59. [CrossRef]
15. Morozov, N.S. The Role of Predators in Shaping Urban Bird Populations: 1. Who Succeeds in Urban Landscapes? *Biol. Bull.* **2022**, *49*, 1057–1080. [CrossRef]
16. Rodewald, A.D.; Kearns, L.J.; Shustack, D.P. Anthropogenic resource subsidies decouple predator–prey relationships. *Ecol. Appl.* **2011**, *21*, 936–943. [CrossRef] [PubMed]
17. Stracey, C.M. Resolving the urban nest predator paradox: The role of alternative foods for nest predators. *Biol. Conserv.* **2011**, *144*, 1545–1552. [CrossRef]
18. Shochat, E. Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos* **2004**, *106*, 622–626. [CrossRef]
19. Wilcove, D.S. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **1985**, *66*, 1211–1214. [CrossRef]
20. Sasvari, L.; Csörgõ, T.; Hahn, I. Bird nest predation and breeding density in primordial and man–made habitats. *Folia Zool.* **1995**, *44*, 305–314.
21. Major, R.E.; Gowing, G.; Kendal, E. Nest predation in Australian urban environments and the role of the pied currawong Strepera graculina. *Aust. J. Ecol.* **1996**, *21*, 399–409. [CrossRef]
22. Morozov, N.S. The Role of Predators in Shaping Urban Bird Populations: 2. Is Predation Pressure Increased or Decreased in Urban Landscapes? *Biol. Bull.* **2022**, *49*, 1081–1104. [CrossRef]
23. Vincze, E.; Seress, G.; Lagisz, M.; Nakagawa, S.; Dingemanse, N.J.; Sprau, P. Does urbanization affect predation of bird nests? A meta–analysis. *Front. Ecol. Evol.* **2017**, *5*, 29. [CrossRef]
24. Huhta, E.; Mappes, T.; Jokimäki, J. Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. *Ecography* **1996**, *19*, 85–91. [CrossRef]
25. Gregory, R.D.; Marchant, J.H. Population trends of jays, magpies and carrion crows in the United Kingdom. *Bird Study* **1996**, *43*, 28–37. [CrossRef]
26. Benmazouz, I.; Jokimäki, J.; Lengyel, S.; Juhász, L.; Kaisanlahti-Jokimäki, M.L.; Kardos, G.; Paládi, P.; Kövér, L. Corvids in urban environments: A systematic global literature review. *Animals* **2021**, *11*, 3226. [CrossRef] [PubMed]
27. Francis, R.A.; Chadwick, M.A. *Urban Ecosystems: Understanding the Human Environment*; Routledge: London, UK, 2013.
28. Croci, S.; Butet, A.; Clergeau, P. Does urbanization filter birds on the basis of their biological traits. *Condor* **2008**, *110*, 223–240. [CrossRef]
29. Jokimäki, J.; Suhonen, J.; Jokimäki-Kaisanlahti, M.-L.; Carbó-Ramírez, P. Effects of urbanization on breeding birds in European towns: Impacts of species traits. *Urban Ecosyst.* **2016**, *19*, 1565–1577. [CrossRef]
30. Lakatos, T.; Chamberlain, D.E.; Garamszegi, L.Z.; Batary, P. No place for ground–dwellers in cities: A meta–analysis on bird functional traits. *Glob. Ecol. Conserv.* **2022**, *38*, e02217. [CrossRef]
31. Conover, M.R.; Borgo, J.S.; Dritz, R.E.; Dinkins, J.B.; Dahlgren, D.K. Greater sage-grouse select nest sites to avoid visual predators but not olfactory predators. *Condor* **2010**, *112*, 331–336. [CrossRef]
32. Peel, M.C.; Finlayson, B.L.; McMahon, T.A. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* **2007**, *11*, 1633–1644. [CrossRef]
33. Ahti, T.; Hämet-Ahti, L.; Jalas, J. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* **1968**, *5*, 169–211.
34. Rovaniemi Municipality. General Information. Available online: https://international.rovaniemi.fi/en/Services/About-Us/General-information (accessed on 3 September 2024).

35. Statistics Finland. *Population Structure/11 Ra—Key Figures on Population by Region, 1990–2023*; Statistics Finland's Free-of-Charge Statistical Databases: Helsinki, Finland. Available online: https://pxdata.stat.fi/PxWeb/pxweb/en/StatFin/StatFin__vaerak/statfin_vaerak_pxt_11ra.px/ (accessed on 7 September 2024).
36. Wikipedia. Rovaniemi. Available online: https://en.wikipedia.org/wiki/Rovaniemi (accessed on 6 March 2024).
37. Adams, C.E. *Urban Wildlife Management*, 3rd ed.; CRC Press: Boca Raton, FL, USA, 2016.
38. Blair, R.B. Land use and avian species diversity along an urban gradient. *Ecol. Appl.* **1996**, *6*, 506–519. [CrossRef]
39. Marzluff, J.M.; Bowman, R.; Donnelly, R. A historical perspective on urban bird research: Trends, terms, and approaches. In *Avian Ecology and Conservation in an Urbanizing World*; Marzluff, J.M., Bowman, R., Donelly, R., Eds.; Kluwer Acadamic Publishers: Boston, MA, USA, 2001; pp. 1–17.
40. Rovaniemi Municipality. *Grid-Based (250 m × 250 m) Data About Human Population Abundance in Rovaniemi Municipality*, Non-Publishable Data Provided by the Municipality of Rovaniemi; City of Rovaniemi, Rovaniemi, Finland, 2023. (Received on 23 February 2023).
41. Jokimäki, J. (University of Lapland, Rovaniemi, Finland). *Private unpublished data from the year* **2023**, 2025.
42. Jokimäki, J.; Kaisanlahti-Jokimäki, M.L.; Carbó–Ramírez, P. The importance of wooded urban green areas for breeding birds: A case study from Northern Finland. In *Avian Urban Ecology: Behavioural and Physical Adaptations*; Gil, D., Brumm, H., Eds.; Oxford University Press: Oxford, UK, 2014; pp. 201–213.
43. Jokimäki, J.; Huhta, E. Effects of landscape matrix and habitat structure on a bird community in northern Finland: A multi–scale approach. *Ornis Fenn.* **1996**, *73*, 97–113.
44. Jokimäki, J.; Kaisanlahti-Jokimäki, M.-L. (Eds.) *Rovaniemen Pesimälinnusto*; Arktisen Keskuksen Tiedotteita 57; Joutsen Median Painotalo oy: Oulu, Finland, 2012. Available online: https://lauda.ulapland.fi/handle/10024/59451 (accessed on 26 March 2024)(In Finnish with an English Summary).
45. Chia, S.Y.; Fang, Y.T.; Su, Y.T.; Tsai, P.Y.; Hsieh, C.; Tsao, S.H.; Juang, J.-Y.; Hung, C.-M.; Tuanmu, M.N. A global database of bird nest traits. *Sci. Data* **2023**, *10*, 923. [CrossRef]
46. The Finnish Biodiversity Information Facility. Suomen Lajitietokeskus. Available online: http://laji.fi (accessed on 5 April 2025).
47. Henttonen, H.; (Natural Resources Institute Finland, Helsinki, Finland). Professional Consultation, Small Mammals in Rovaniemi; Personal Written Communication, 26 March 2024.
48. Saarikivi, J.; (City of Helsinki, Helsinki, Finland). Professional Consultation, Snakes in Rovaniemi; Personal Written Communication, 26 March 2004.
49. Jokimäki, J.; (University of Lapland, Rovaniemi, Finland). Private unpublished data from the year 2003, 2025.
50. Kaisanlahti-Jokimäki, M.-L.; Jokimäki, J.; Huhta, E.; Siikamäki, P. Impacts of seasonal small–scale urbanization on nest predation and bird assemblages at tourist destinations. In *Urban Bird Ecology and Conservation*; Lepczyk, C.A., Warren, P.S., Eds.; Studies in Avian Biology; University of California Press: Berkeley, CA, USA, 2012; pp. 93–110.
51. Jokimäki, J.; (University of Lapland, Rovaniemi, Finland). Private unpublished data from the year 2009, 2025.
52. Jokimäki, J.; Suhonen, J.; Benedetti, Y.; Diaz, M.; Kaisanlahti-Jokimäki, M.-L.; Morelli, F.; Pérez-Contreras, T.; Rubio, E.; Sprau, P.; Tryjanowski, P.; et al. Land-sharing vs. land-sparing urban development modulate predator–prey interactions in Europe. *Ecol. Appl.* **2020**, *30*, e02049. [CrossRef]
53. Jokimäki, J. (University of Lapland, Rovaniemi, Finland). *Private unpublished data from the year* **2019**, 2025.
54. IBM Corp. *Released 2021. IBM SPSS Statistics for Windows, Version 28.0.0.0.*; IBM Corp.: Armonk, NY, USA, 2021.
55. Konstantinov, V.M.; Nowicki, W.; Pichurin, A.G. Recent changes in the avifauna of cities in European Russia and Eastern Poland–results of a questionnaire. *Acta Ornithol.* **1996**, *1*, 59–66.
56. Jerzak, L. Synurbanization of the magpie in the Palearctic. In *Avian Ecology and Conservation in an Urbanizing World*; Marzluff, J.M., Bowman, R., Donelly, R., Eds.; Kluwer Acadamic Publishers: Boston, MA, USA, 2001; pp. 403–425.
57. Marzluff, J.M.; McGowan, K.J.; Donnelly, R.; Knight, R.L. Causes and consequences of expanding American Crow populations. In *Avian Ecology and Conservation in an Urbanizing World*; Marzluff, J.M., Bowman, R., Donelly, R., Eds.; Kluwer Acadamic Publishers: Boston, MA, USA, 2001; pp. 331–363.
58. Marzluff, J.M.; Neatherlin, E. Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *Biol. Conserv.* **2006**, *130*, 301–314. [CrossRef]
59. Sorace, A.; Gustin, M. Distribution of generalist and specialist predators along urban gradients. *Landsc. Urban Plan.* **2009**, *90*, 111–118. [CrossRef]
60. Rodewald, A.D.; Kearns, L.J. Shifts in dominant nest predators along a rural–to–urban landscape gradient. *Condor* **2011**, *113*, 899–906. [CrossRef]
61. Weatherhead, P.J.; Blouin-Demers, G. Understanding avian nest predation: Why ornithologists should study snakes. *J. Avian Biol.* **2004**, *35*, 185–190. [CrossRef]
62. Reidy, J.L.; Stake, M.M.; Thompson, F.R., III. Golden–cheeked warbler nest mortality and predators in urban and rural landscapes. *Condor* **2008**, *110*, 458–466. [CrossRef]

63. Riley, S.P.; Brown, J.L.; Sikich, J.A.; Schoonmaker, C.M.; Boydston, E.E. Wildlife Friendly Roads: The Impacts of Roads on Wildlife in Urban Areas and Potential Remedies. In *Urban Wildlife Conservation*; McCleery, R., Moorman, C., Peterson, M., Eds.; Springer: New York, NY, USA, 2014. [CrossRef]
64. Malpass, J.S.; Rodewald, A.D.; Matthews, S.N.; Kearns, L.J. Nest predators, but not nest survival, differ between adjacent urban habitats. *Urban Ecosyst.* **2018**, *21*, 551–564. [CrossRef]
65. Smith, H.M.; Dickman, C.R.; Banks, P.B. Nest predation by commensal rodents in urban bushland remnants. *PLoS ONE* **2016**, *11*, e0156180. [CrossRef]
66. van Heezik, Y.; Ludwig, K.; Whitwell, S.; McLean, I.G. Nest survival of birds in an urban environment in New Zealand. *N. Z. J. Ecol.* **2008**, *32*, 155–165.
67. Keyser, A.J.; Hill, G.E.; Soehren, E.C. Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. *Conserv. Biol.* **1998**, *12*, 986–994. [CrossRef]
68. Matthews, A.; Dickman, C.R.; Major, R.E. The influence of fragment size and edge on nest predation in urban bushland. *Ecography* **1999**, *22*, 349–356. [CrossRef]
69. Thorington, K.K.; Bowman, R. Predation rate on artificial nests increases with human housing density in suburban habitats. *Ecography* **2003**, *26*, 188–196. [CrossRef]
70. Chalfoun, A.D.; Thompso, F.R., III; Ratnaswamy, M.J. Nest predators and fragmentation: A review and meta-analysis. *Conserv. Biol.* **2002**, *16*, 306–318. [CrossRef]
71. Dunn, E. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* **1977**, *46*, 633–652. [CrossRef]
72. Sorace, A.; Petrassi, F.; Consiglio, C. Long-distance relocation of nestboxes reduces nest predation by Pine Marten Martes martes. *Bird Study* **2004**, *51*, 119–124. [CrossRef]
73. Nilsson, S.G. The evolution of nest–site selection among hole–nesting birds: The importance of nest predation and competition. *Ornis Scand.* **1984**, *15*, 167–175. [CrossRef]
74. Skwarska, J.A.; Kalinski, A.; Wawrzyniak, J.; Banbura, J. Opportunity makes a predator: Great Spotted Woodpecker predation on Tit broods depends on nest box design. *Ornis Fenn.* **2009**, *86*, 109–112.
75. Marcus, J.M.; Hart, A.G.; Goodenough, A.E. Predator–Proofing Avian Nestboxes: A Review of Interventions, Opportunities, and Challenges. *Birds* **2023**, *5*, 1–23. [CrossRef]
76. Ibáñez–Álamo, J.D.; Magrath, R.D.; Oteyza, J.C.; Chalfoun, A.D.; Haff, T.M.; Schmidt, K.A.; Thomson, R.L.; Martin, T.E. Nest predation research: Recent findings and future perspectives. *J. Ornithol.* **2015**, *156*, 247–262. [CrossRef]
77. Grégoire, A.; Garnier, S.; Dréano, N.; Faivre, B. Nest predation in Blackbirds (*Turdus merula*) and the influence of nest characteristics. *Ornis Fenn.* **2003**, *80*, 1–10.
78. Cresswell, W. Nest predation: The relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* **1997**, *53*, 93–103. [CrossRef]
79. Jokimäki, J.; Suhonen, J.; Kaisanlahti-Jokimäki, M.-L. Differential long-term population responses of two closely related human-associated sparrow species with respect to urbanization. *Birds* **2021**, *2*, 230–249. [CrossRef]
80. Bonnington, C.; Gaston, K.J.; Evans, K.L. Ecological traps and behavioural adjustments of urban songbirds to fine-scale spatial variation in predator activity. *Anim Conserv.* **2015**, *18*, 529–538. [CrossRef]
81. Leston, L.F.; Rodewald, A.D. Are urban forests ecological traps for understory birds? An examination using Northern cardinals. *Biol. Conserv.* **2006**, *131*, 566–574. [CrossRef]
82. Marzluff, J.M.; Withey, J.C.; Whittaker, K.A.; David Oleyar, M.; Unfried, T.M.; Rullman, S.; DeLap, J. Consequences of habitat utilization by nest predators and breeding songbirds across multiple scales in an urbanizing landscape. *Condor* **2007**, *109*, 516–534. [CrossRef]
83. Baillie, S.R.; Peach, W.J. Population limitation in Palaearctic-African migrant passerines. *Ibis* **1992**, *134*, 120–132. [CrossRef]
84. Siriwardena, G.M.; Baillie, S.R.; Crick, H.Q.; Wilson, J.D. The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *J. Appl. Ecol.* **2000**, *37*, 128–148. [CrossRef]
85. Haskell, D.G. A reevaluation of the effects of forest fragmentation on rates of bird–nest predation. *Conserv. Biol.* **1995**, *9*, 1316–1318. [CrossRef]
86. Pärt, T.; Wretenberg, J. Do artificial nests reveal relative nest predation risk for real nests? *J. Avian Biol.* **2002**, *33*, 39–46. [CrossRef]
87. Mitrus, C. A comparison of the breeding ecology of collared flycatchers nesting in boxes and natural cavities. *J. Field Ornithol.* **2003**, *74*, 293–299. [CrossRef]
88. Czeszczewik, D. Breeding success and timing of the pied flycatcher *Ficedula hypoleuca* nesting in natural holes and nest–boxes in the Białowieza Forest, Poland. *Acta Ornithol.* **2004**, *39*, 15–20. [CrossRef]
89. Sudyka, J.; Di Lecce, I.; Wojas, L.; Rowiński, P.; Szulkin, M. Nest-boxes alter the reproductive ecology of urban cavity-nesters in a species-dependent way. *J. Avian Biol.* **2022**, *2022*, e03051. [CrossRef]

90. Krüger, H.; Väänänen, V.M.; Holopainen, S.; Nummi, P. The new faces of nest predation in agricultural landscapes—A wildlife camera survey with artificial nests. *Eur. J. Wildl. Res.* **2018**, *64*, 76. [CrossRef]
91. Haskell, D.G.; Knupp, A.M.; Schneider, M.C. Nest predator abundance and urbanization. In *Avian Ecology and Conservation in an Urbanizing World*; Marzluff, J.M., Bowman, R., Donelly, R., Eds.; Kluwer Acadamic Publishers: Norwell, MA, USA, 2001; pp. 243–258.
92. Vuorisalo, T.; Talvitie, K.; Kauhala, K.; Bläuer, A.; Lahtinen, R. Urban red foxes (*Vulpes vulpes* L.) in Finland: A historical perspective. *Landsc. Urban Plan.* **2014**, *124*, 109–117. [CrossRef]
93. Kauhala, K.; Kowalczyk, R. Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. *Curr. Zool.* **2011**, *57*, 584–598. [CrossRef] [PubMed]
94. Rodewald, A.D.; Kearns, L.J.; Shustack, D.P. Consequences of urbanizing landscapes to reproductive performance of birds in remnant forests. *Biol. Conserv.* **2013**, *160*, 32–39. [CrossRef]
95. Simula, J. Leppälinnun Phoenicurus phoenicurus pesimäbiologiasta Enontekiön Hetassa 2002–2018. *Kokko* **2019**, 18–22. (In Finnish)
96. Solonen, T. Breeding of the Great Tit and Blue Tit in urban and rural habitats in southern Finland. *Ornis Fenn.* **2001**, *78*, 49–60.
97. Tomasevic, J.A.; Marzluff, J.M. Cavity nesting birds along an urban–wildland gradient: Is human facilitation structuring the bird community? *Urban Ecosyst.* **2017**, *20*, 435–448. [CrossRef]
98. von Haartman, L.V. The evolution of resident versus migratory habit in birds. Some considerations. *Ornis Fenn.* **1968**, *45*, 1–7.
99. Paton, G.D.; Shoffner, A.V.; Wilson, A.M.; Gagné, S.A. The traits that predict the magnitude and spatial scale of forest bird responses to urbanization intensity. *PLoS ONE* **2019**, *14*, e0220120. [CrossRef]
100. Kauhala, K. Introduced carnivores in Europe with special reference to central and northern Europe. *Wildl. Biol.* **1996**, *2*, 197–204. [CrossRef]
101. Holopainen, S.; Väänänen, V.M.; Vehkaoja, M.; Fox, A.D. Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biol. Invasions* **2012**, *23*, 3795–3807. [CrossRef]
102. Jokimäki, J.; Selonen, V.; Lehikoinen, A.; Kaisanlahti-Jokimäki, M.-L. The role of urban habitats in the abundance of red squirrels (*Sciurus vulgaris*, L.) in Finland. *Urban For. Urban Green.* **2017**, *27*, 100–108. [CrossRef]

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